

First Record of *Palaelodus* (Aves: Phoenicopteriformes) from New Zealand

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ABSTRACT. The first record of the flamingo-like Palaelodidae (Phoenicopteriformes) is reported from the Early Miocene, St Bathans Fauna of Central Otago, New Zealand. Two distal tibiotarsi are described as a new *Palaelodus* species and a cranial fragment of a sternum is tentatively assigned to the same taxon. The new species is slightly smaller than *P. wilsoni* from the Late Oligocene–Early Miocene of Australia, and is distinguished from all congeners by a more robust shaft with a gradual expansion of width to the distal condyles.

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“... it is the ‘first’ that fixes the peg upon which he can hang all the subsequent and, we hope, oft-repeated contacts that eventually grow into a real understanding. The “first” has to come first in avian paleontology likewise and, sad to relate, that first may be restricted to a single bone or a mere fragment thereof.” (Loye Miller, 1950: 69).

Palaelodidae is an extinct family of long-legged aquatic birds presently considered to be the sister taxon of flamingos (Phoenicopteridae; Cheneval, 1983a; Heizmann & Hesse, 1995; Mlíkovský, 2002; Mayr, 2005). Known from Europe, Egypt, North and South America and Australia, they were first recognized when Milne-Edwards (1863) described

Palaelodus ambiguus, *P. crassipes* and *P. gracilipes* from St Gérard-le-Puy, of Aquitanian, European Mammal Neogene Reference Level MN 2a, or Early Miocene, age (Cheneval, 1983a). Later, Milne-Edwards (1867–1871) described two further species, *P. minutus* and *P. goliath*. Lambrecht (1933) synonymized *P. minutus* with *P. gracilipes*, a move not followed by Brodkorb (1963) or Švec (1981). However, Cheneval (1983a) accepted this synonymy when he revised the palaelodids from St Gérard-le-Puy, listing three species of *Palaelodus* in the Aquitanian deposits (*Palaelodus ambiguus*, *P. crassipes*, *P. gracilipes*) and transferring *Palaelodus goliath* to *Megapalaelodus* A.H. Miller, 1944.

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All four species were recognized by Heizmann & Hesse (1995), in the mid-Miocene fauna from Nördlinger Ries (MN 6) and just *P. crassipes* and *M. goliath* in the fauna from the Steinheimer Basin (MN 7) in Germany. Recently, Mayr & Smith (2002) described the new genus and species *Adelalopus hoogbutseliensis* for the largest and oldest (earliest Oligocene, MP 21), European palaelodid.

In a recent treatment of the European palaelodid fauna, Mlíkovský (2002) synonymized *Megapaloelodus* A.H. Miller with *Palaelodus* Milne-Edwards and *P. gracilipes* (including *P. minutus*) and *P. crassipes* with *P. ambiguus*, stating that "...the alleged morphological differences between *Palaelodus gracilipes*, *P. ambiguus*, and *P. crassipes* pointed out by Cheneval (1983a) and Heizmann & Hesse (1995) are clearly size dependent, and can be interpreted as intra-specific variability" (Mlíkovský, 2002: 106). The systematic and taxonomic treatment of many species adopted by Mlíkovský (2002) often differs from others and has attracted much criticism (e.g., Mourer-Chauviré, 2004). However, the large dataset presented by Cheneval (1983: fig. 1), provides a size distribution consistent with only two species of palaelodid in St Gérard-le-Puy, where *P. gracilipes* and *P. crassipes* are just small and large examples of *P. ambiguus*, and published differences do appear to be potentially of an allometric nature. In the absence of a comprehensive examination of the variation represented by these European palaelodids Mlíkovský's (2002) synonymies are premature, so four species of *Palaelodus* existed contemporaneously in Europe, although this total may ultimately be reduced to two.

Palaelodids range in age in Europe from the early Oligocene of Belgium (Mayr & Smith 2002), through the Late Oligocene to the Middle Miocene of France, Germany and Bohemia in the Czech Republic (Milne-Edwards, 1863, 1867–1871; Lambrecht, 1933; Švec, 1981; Cheneval, 1987; Heizmann & Hesse, 1995; Mlíkovský, 2002). Outside Europe, two undetermined species are reported from the early Oligocene of Egypt (Rasmussen *et al.*, 1987). The family is represented in North America by *Megapaloelodus connectens* A.H. Miller, 1944 from the Early Miocene of South Dakota (A.H. Miller, 1944; L. Miller, 1950, 1952) and *M. opsignus* Brodkorb, 1961, from the Pliocene of Oregon (Brodkorb, 1961). In South America, *Megapaloelodus* has been recorded from the Late Miocene of Argentina (Noriega, 1995) and *Palaelodus* cf. *P. ambiguus* from the late Oligocene—Early Miocene of Taubaté Basin in Brazil (Alvarenga 1990, *vide* Mayr, 2009).

Phoenicopteriforms are significant components of the Australian Oligo-Miocene to Pleistocene lacustrine faunas. Several taxa of true flamingos (A.H. Miller, 1963; Rich *et al.*, 1987, 1991; Vickers-Rich, 1991) and two species of palaelodids, a smaller *Palaelodus pledgei* Baird & Vickers-Rich, 1998 and a larger *P. wilsoni* Baird & Vickers-Rich, 1998, are relatively abundant (Baird & Vickers-Rich, 1998; Boles, 2006). Both palaelodids are found in the Oligo-Miocene Etadunna and Namba Formations of South Australia. A single specimen from Pleistocene deposits in Cooper Creek, South Australia, was attributed to *P. wilsoni*, making it the youngest record for the family (Baird & Vickers-Rich, 1998). This specimen was recently re-evaluated, and while confirmed as a palaelodid, it is doubtful whether it is conspecific with *P. wilsoni* (Worthy, 2008).

In both Northern and Southern Hemispheres, palaelodids usually derive from lacustrine deposits and are known from

abundant material in some localities (Cheneval, 1983a; Heizmann & Hesse, 1995; Mlíkovský, 2002; Mayr, 2005). Nevertheless, their biology and ecology are poorly known. They have long tarsometatarsi (though not so long as in flamingos), which are laterally compressed and associated with other modifications of the leg that Cheneval (1983a) and Cheneval & Escuillié (1992) interpreted as adaptations for diving. However, no diving birds have elongate legs, and the stated modifications of the leg, laterally compressed shaft of the tarsometatarsus and enlarged cnemial crest of the tibiotarsus, would equally facilitate pushing a leg through deep water while wading. A laterally compressed tarsometatarsus would be unique in waders and alternatively could be explained by a shared ancestry with grebes (Podicipedidae), because these birds also have compressed tarsometatarsi (e.g., Mayr, 2004). Flamingos, to which palaelodids are most closely related, are now known to be the sister taxon to grebes based on robust genetic data and morphological traits (van Tuinen *et al.*, 2001; Mayr, 2004; Hackett *et al.*, 2008). The cranium of *Palaelodus* has been described by Cheneval & Escuillié (1992). It confirms the phylogenetic affinity of *Palaelodus* and flamingos, but shows palaelodids had a superficially crane-like premaxilla markedly different from flamingos. But unlike cranes, *Palaelodus ambiguus* had a deep mandible, interpreted by Cheneval & Escuillié (1992) to mean it had a filter-feeding apparatus as is well known in flamingos. Also, *Palaelodus* had well-developed salt glands indicating an ability, shared with flamingos, to feed in saline waters. These observations suggest that *Palaelodus* was a wading bird capable of obtaining food from saline waters. The coexistence of a diversity of flamingos and palaelodids in Australia for most of the Neogene is doubtless related to the widespread availability of extensive shallow saline lakes throughout this period (Pledge & Tedford, 1990; Woodburne *et al.*, 1994; Alley, 1998).

The St Bathans Fauna was recently named and described from the upper Early Miocene (19–16 Ma) Bannockburn Formation, Manuherikia Group in Central Otago, New Zealand (Worthy *et al.*, 2007). The source beds are lacustrine in nature and their extent and nature indicates a paleolake some 5600 km² in area with deltaic river facies entering it (Douglas, 1986; Pole *et al.*, 2003). The avifauna of the St Bathans Fauna is dominated by anseriforms, with a minimum of eight taxa in five genera (Worthy *et al.*, 2007, 2008). The avifauna also comprises such diverse taxa as tubenoses (Procellariiformes), birds of prey (Accipitriformes), rails (Rallidae) and another as yet unidentified representative of Gruiformes, gulls (Laridae) and Charadriiformes with features of typical waders, a heron (Ardeidae), pigeons (Columbidae), parrots (Psittaciformes), swiftlets (Apodidae), owl-nightjars (Aegothelidae) and passerine birds (Passeriformes). Fish, frogs, reptiles and mammals are also represented. This lake provided suitable habitat for wading birds, so given the temporal relativity and geographic proximity with Australian Oligo-Miocene faunas, phoenicopteriforms might also be expected. The purpose of this contribution is to describe such a discovery, the first record of a palaelodid from New Zealand, which is significant for the ecological reconstruction of paleo-Lake Manuherikia and the New Zealand avifauna in general.

The St Bathans Fauna provides the first insight into the terrestrial fauna resident on that part of Zealandia that is now New Zealand for the entire Tertiary. Zealandia is the India-sized area of continental crust that encompasses New

Caledonia, Chatham Islands, New Zealand and Macquarie Island (Campbell & Hutching, 2007; Goldberg *et al.*, 2008). New Zealand has long been thought to have a vicariant component to its fauna (Fleming, 1979; Stevens, 1980; Gibbs, 2006), but recently the controversial suggestion that Zealandia was entirely submerged during the Late Oligocene 25–22 Ma, requiring the entire terrestrial biota to have been derived by colonization following long-distance over-water dispersal, has been vigorously debated (Pole, 1994; Gibbs, 2006; Heads, 2006; Waters & Craw, 2006; Campbell & Hutching, 2007; Knapp *et al.*, 2007; Ladiges & Cantrill, 2007; Trewick *et al.*, 2007; Goldberg *et al.*, 2008; Landis *et al.*, 2008; McDowall, 2008). The St Bathans Fauna provides direct evidence of the composition of the terrestrial biota just 3–4 million years after the maximal submergence of Zealandia, so the endemicity and relatedness of that biota to those of Australia, the presumed major source of dispersed taxa, is crucial to understanding the history of Zealandia's biota.

Methods

Abbreviations: *LF*, Local Fauna; *L*, left; *Ma*, million years ago; *R*, right. Institutions: *CM*, Canterbury Museum, Christchurch, New Zealand; *MV*, Museum Victoria, Melbourne, Victoria, Australia; *NMNZ*, Museum of New Zealand Te Papa Tongarewa, Wellington (formerly National Museum of New Zealand, Dominion Museum, and Colonial Museum), New Zealand; *SAM*, South Australian Museum, Adelaide, South Australia, Australia; *UCMP*, University of California, Museum of Paleontology, Berkeley, California, USA.

Names for specific bone landmarks follow the anatomical nomenclature of Baumel & Witmer (1993) with English translations thereafter, or Howard (1929).

Comparative material

Below we specify only the phoenicopteriform material of immediate relevance to our comparisons. For the Australian fossils, we give age, local fauna and locality details to allow interpretation of their temporal range.

Palaelodidae

Palaelodus wilsoni Baird & Vickers-Rich, 1998, Oligo-Miocene: SAM P.22706, distal R tibiotarsus (+imperfect L tarsometatarsus), Croc Pot Point (Minkina LF), Lake Palankarina (Baird & Vickers-Rich, 1998) (informally also known as Tortoise Hole Locality, pers. comm. Neville Pledge 11 July 2008); SAM P.27973, distal L tibiotarsus, Mammalon Hill (Ngama LF), Lake Palankarina; SAM P.41250, distal R tibiotarsus, SAM North (Ditjimanka LF), Lake Palankarina. MV P. 187012, distal R tibiotarsus, Lake Palankarina; MV P. 187018, distal L tibiotarsus, Neville's Nirvana, Lake Palankarina.

Palaelodus ?wilsoni, Pleistocene: SAM P.25151, distal R tibiotarsus, Cooper Creek, South Australia (Worthy, 2008).

Palaelodus pledgei Baird & Vickers-Rich, 1998, Oligo-Miocene: SAM P.27997, proximal R tarsometatarsus, paratype, Croc Pot Point, UCMP Site 3 (V5762) (Minkina LF), Lake Palankarina (Baird & Vickers-Rich, 1998); SAM P.42002, distal R tibiotarsus, SAM North Quarry, Lake Palankarina, Lake Eyre Subbasin, South Australia.

Palaelodus ambiguus Milne-Edwards, 1863, Oligo-Miocene: CM Av11394, L tibiotarsus; CM Av11396, R tibiotarsus, St Gérard-le-Puy, France.

Phoenicopteridae

Phoenicopterus chilensis Molina, 1782, modern: SAM B.25448, South America.

Phoenicopterus ruber Linnaeus, 1758, modern in Africa, Europe, Asia, Caribbean, South America; extinct Australia, Pliocene (A.H. Miller, 1963): SAM B.11552.

The following Australian fossil flamingos (A.H. Miller, 1963; Rich *et al.*, 1987) were examined to more completely assess distribution of characters diagnostic of palaelodids.

Phoenicopterus novaehollandiae A.H. Miller, 1963, Oligo-Miocene: SAM P.39231, R tibiotarsus, Mammalon Hill, Lake Palankarina, Etadunna Formation, South Australia.

Ocyplanus proeses de Vis, 1905, Pliocene: SAM P.35225, cast of referred distal R tibiotarsus, originally described as *Phoeniconaias gracilis* A.H. Miller, 1963, collected Stirton Quarry, = Site 1, UCMP V-5772, Lake Kanunka, Lake Eyre Subbasin, South Australia.

Xenorhynchopsis tibialis de Vis, 1905, Pleistocene: SAM P.35226, cast of lectotype distal R tibiotarsus, Cooper Creek.

Xenorhynchopsis minor de Vis, 1905, Pleistocene: SAM P.35227, cast of holotype, distal R tibiotarsus, collected at Unduwumpa (a Gregory Site), Cooper Creek.

Results

Systematic Paleontology

Order Phoenicopteriformes Sharpe, 1891

Family Palaelodidae (Stejneger, 1885)

Genus *Palaelodus* Milne-Edwards, 1863

The new species described here for NMNZ S.51258 is referred to Palaelodidae because of the following unique combination of characters derived from Lydekker (1891), L. Miller (1950), Švec (1981), and Baird & Vickers-Rich (1998) (Figs 1, 2): (1) the lateral tuberosity for the attachment of the *retinaculum extensorium tibiotarsi* is approximately circular and prominent, located laterally to the *pons supratendineus* (supratendinal bridge) and separated from the lateral margin of the bone and from the proximal margin of the *incisura intercondylaris*; (2) the intercondylar incision is deep, broadens proximally and extends into proximo-medial face of medial condyle; (3) the *sulcus extensorius* is located centrally on the shaft, is narrow (a third of shaft width) and deep; (4) the proximal end of the supratendinal bridge is widely separated from the medial margin of the shaft by a robust rounded ridge; (5) the supratendinal bridge is not elongate; (6) the *condyli lateralis et medialis* have deep tendinal pits just caudad of their cranial projections; (7) the distal margins of the lateral and medial condyles are distinctly notched; (8) the distal cranial part of the medial condyle is markedly inflated medially; (9) the *trochlea cartilaginis tibialis* has a prominent medial ridge; (10) the medial edge of the supratendinal bridge is excavated in a furrow separating it from the medial margin; (11) the intercondylar incision lacks a prominent distally directed articular facet for the *eminentia intercotylaris* of the tarsometatarsus, i.e. the “anterior intercotylar tubercle” of Švec (1981).

We note the following additional tibiotarsal characters that further define this family: (12) the medial attachment for the *retinaculum extensorium tibiotarsi* forms a low

rounded zone on the medial side of the *sulcus extensorius* just proximal to the tendinal bridge; (13) the lateral and medial condyles lack significant projection caudad of the shaft; (14) in cranial view, the cranial part of the medial condyle is displaced medially such that it is entirely mesad of the supratendinal bridge resulting in a relatively wide notch between the condyles.

Of these characters, we consider character 1 an autapomorphy of the Palaelodidae: in no other birds is the lateral attachment of the *retinaculum extensorium tibiotarsi* a prominent, near circular, tuberosity: it is usually elongate and located near the margin of the extensor sulcus. Baird & Vickers-Rich (1998) used three of these characters to distinguish flamingos from palaelodids as follows (character number above to which these relate): intercondylar incision, shallower, not so deeply extending into proximo-medial face of medial condyle (2); distal tendinal pits shallower (6); notches in distal margins of lateral and medial condyles shallower (7). However, we found the expression of these characters variable intra- and/or interspecifically, and so treat them as synapomorphies of Phoenicopteridae and Palaelodidae, rather than as autapomorphies of Palaelodidae. Further, while Baird & Vickers-Rich (1998) stated that the distal opening of the extensor canal is rounded and narrow in *Palaelodus* but rounded and broad in flamingos, we find this difference to be inconsistent. While the combination of characters 1–14 is unique to palaelodids, apart from character 1, individually, all the other characters are either present convergently in some other families or are plesiomorphic in palaelodids.

Flamingos differ from palaelodids including the new species described below as follows: the lateral attachment of the *retinaculum extensorium tibiotarsi* is an elongate crest, linked to, or closely approaching, an elevated, distally directed articular facet for the intercotylar eminence of the tarsometatarsus; the medial attachment for the extensor retinaculum is a prominent crest on the ridge medially of the extensor sulcus; the extensor sulcus is wider and more laterally located; the medial bounding ridge is narrower; the supratendinal bridge is more elongate; the lateral and medial condyles project significantly caudad of the shaft; the distal anterior part of the medial condyle is not inflated medially; the medial condyle is not so far offset medially, so it lies distad and in line with the tendinal bridge, resulting in a narrower anterior notch between the condyles; the *trochlea cartilaginosa tibialis* lacks a prominent medial ridge.

In other large birds with some similarity to palaelodids, the lateral attachment for the extensor retinaculum, if present, is not circular (e.g., ardeids, pelecanids, threskiornithids, and ciconiids), but more elongate, and in those birds with elongate tibiotarsi (e.g., species of *Grus*, *Ciconia*, *Ardeotis*), the lateral attachment for the extensor retinaculum is always associated with an intercondylar tubercle, an elevated distally directed prominent facet for articulation with the intercotylar

eminence of the tarsometatarsus, see character 101 of Mayr & Clarke (2003), which is presumed to act as a locking mechanism in the tibial-tarsal joint.

The fossil is referred to *Palaelodus* as it does not differ from members of this genus to any significant degree (Cheneval, 1983a; L. Miller, 1950; Baird & Vickers-Rich, 1998). *Megapalaelodus connectens* A.H. Miller, 1944 is a much larger species and was distinguished by deeper distal notches in the medial condyle (L. Miller 1950). The European species *P. goliath* was referred to *Megapalaelodus* solely on size, and if Mlíkovský's (2002) synonymy of *Megapalaelodus* with *Palaelodus* is accepted, then the family had only one globally-distributed genus during the Miocene.

Palaelodus aotearoa n.sp.

Figs 1–3

Holotype. NMNZ S.51799, a distal right tibiotarsus, collected 10 February 2009 by the University of New South Wales, NSW, Australia/Canterbury Museum, Christchurch, NZ/ Museum of New Zealand Te Papa Tongarewa, Wellington, NZ expedition.

Diagnosis. A *Palaelodus* species within the size range of *P. wilsoni* and *P. ambiguus* (Tables 1, 2) but tibiotarsus with a relatively broader shaft for its distal width, a less concave medial margin above the medial condyle, and a broader extensor sulcus that is more widely separated from the medial margin.

Etymology. For Aotearoa, a Maori name for New Zealand.

Measurements of holotype. Distal width 13.9 mm, craniocaudal depth of lateral condyle 13.7 mm, craniocaudal depth of medial condyle 14.8 mm, shaft width proximal side tendinal bridge 10.2 mm, minimum shaft width 7.5 mm, preserved length 81.6 mm.

Paratype (Figs 2, 3). NMNZ S.51258, a distal right tibiotarsus, collected 12 January 2008 by the University of New South Wales, NSW, Australia/University of Adelaide, South Australia/Canterbury Museum, Christchurch, NZ/ Museum of New Zealand Te Papa Tongarewa, Wellington, NZ expedition.

Measurements of paratype. Distal width 13.7 mm, craniocaudal depth of lateral condyle 13.9 mm, craniocaudal depth of medial condyle 15.0 mm, shaft width proximal side tendinal bridge 9.7 mm, minimum shaft width preserved 9.1 mm, preserved length 25.0 mm.

Holotype locality. Bed HH1b, 9.5–9.58 m above base of the Bannockburn Formation, Trench Excavation, foot of hill 50 m across terrace from river bank at 44.90780° S; 169.85844° E, Manuherikia River, Home Hills Station, Otago, New Zealand; ca. 10–15 cm thick sand & cobble layer; Fossil Record Number in the archival Fossil Record File of the Geological Society of New Zealand H41/f0103.

Table 1. Distal and shaft widths (mm) of tibiotarsi for *Palaelodus* species, European taxa after Cheneval (1983a).

species	distal width mean (range) s.d., n	shaft width mean (range) s.d., n	SW/DW
<i>Palaelodus gracilipes</i>	11.1 (9.7–12.2) 0.19, 77	5.8 (5.0–6.7) 0.17, 41	52.2%
<i>Palaelodus ambiguus</i>	12.5 (10.6–20.0) 0.68, 316	6.6 (4.8–9.1) 0.27, 200	52.8%
<i>Palaelodus crassipes</i>	14.9 (14.0–16.2) 0.49, 8	7.9 (7.3–8.3) 0.13, 5	53.0%
<i>Megapalaelodus goliath</i>	18.1 (16.7–20.4) 1.06, 17	8.2 (7.6–9.0) 0.24, 6	45.3%
<i>Palaelodus aotearoa</i> S.51799	13.9	7.5	53.9%

Table 2. Measurements (mm) of tibiotarsi of *Palaelodus aotearoa* compared to selected *Palaelodus* species. Depth of the lateral and medial condyles is in craniocaudal plane. SW1 and SD1 were measured at a point twice the distance the proximal side of the supratendinal bridge was from the distal end. SW2 is taken level with the proximal margin of the supratendinal bridge. Abbreviations: DW is distal width, MC is medial condyle, LC is lateral condyle, SW is shaft width.

specimens	DW	LC depth	MC depth	SW min	SW1	SD1	SW2	MC/DW depth	SW1/DW	SW2/DW
<i>Palaelodus wilsoni</i>										
SAM P.22706	16.5	15.9	17.7	7.4	7.6	6.1	—	107.3	46.1	—
SAM P.27973	14.6	13.3	15.4	—	—	—	8.4	105.5	—	57.5
SAM P.41250	—	—	—	7.3	7.6	6.0	10.0	—	—	—
MV P.187018	ca. 17.2	—	18.7	7.7	7.7	6.3	11.2	108.7	44.8	65.1
MV P.187012	—	—	—	—	7.1	6.1	10.6	—	—	—
? <i>Palaelodus wilsoni</i>										
SAM P.25151	16.4	16.8	18.8	—	9.5	7.1	10.2	114.6	56.7	62.2
<i>Palaelodus ambiguus</i>										
CM Av11396	12.9	12.0	13.2	6.6	6.9	4.9	8.1	102.3	53.5	62.8
CM Av11394	14.0	13.5	14.8	6.8	7.0	4.7	8.1	105.7	50.0	57.7
<i>Palaelodus aotearoa</i>										
NMNZ S.51799	13.9	13.7	14.8	7.5	7.9	5.6	10.2	106.5	56.8	73.4
NMNZ S.51258	13.7	13.9	15.0	—	—	—	9.7	109.3	—	70.7

Paratype locality. Bed HH1a, 6.88–7.0 m above base of Bannockburn Formation, main quarry at 44.907944° S, 169.858222° E, Manuherikia River, Otago, New Zealand; Fossil Record Number in the archival Fossil Record File of the Geological Society of New Zealand H41/f88.

Stratigraphy/Age/Fauna. Bannockburn Formation, Manuherikia Group, Early Miocene (Altonian); 19–16 Ma; St Bathans Fauna.

Description and comparisons. Both NMNZ S.51799 and NMNZ S.51258 are stained black and have slightly worn edges to the condyles (Figs 1, 2), consistent with the transported and disarticulated nature of specimens in both deposits and are inferred to have been accumulated in the sublittoral zone. Their distal widths are within the size range for the Australian *P. wilsoni* and the European *P. ambiguus*, indicating a medium-sized palaelodid (Table 1). To capture the observation that in *P. aotearoa* the shaft expands in width more gradually towards the condyles and is relatively wider than in other taxa, three different width measurements were taken (Table 2). A standard least shaft width measurement, only ascertainable for NMNZ S.51799, was 53.9% of distal width in *P. aotearoa*, a ratio higher than the ratio of the means for the European palaelodid species, and higher than values for *P. ambiguus* (CM specimens), or for *P. wilsoni* individuals. Secondly, we measured width and depth values (SW1 and SD1) of the shaft where the distance to the proximal side of the supratendinal bridge was half that to the distal end (Table 2). Thirdly, we measured shaft width at the proximal end of the supratendinal bridge (SW2; Table 2). Values for SW2 relative to distal width (SW2/DW) of 57.7 and 62.8% in specimens of *P. ambiguus* (Table 2) are about 7–9% greater than SW1/DW. Equivalent ratios for *P. wilsoni* (57–65%) are similar to those for *P. ambiguus* but less than the values of 70.7 and 73.4% for *P. aotearoa*. In summary, the tibiotarsal shaft of *P. aotearoa* is both relatively stouter than that of the European and Australian *Palaelodus* species and widens much more gradually towards the distal end, rather than abruptly to create a step in anterior view. *Palaelodus aotearoa* is substantially larger than *P. pledgei*, as revealed by the condylar width of the paratype tarsometatarsus SAM P. 27997 and a here referred distal tibiotarsus SAM P.42002.

Tentatively referred specimen. An additional probable phoenicopteriform specimen was found in 2008 in bed HH1a. NMNZ S.51257 is a fragment of the cranial part of a sternum (Fig. 4), 23.2 mm wide and preserving the base of the carina, about 14 mm of the left and 11 mm of the right *sulcus articularis coracoidei*, and dorsally the medial part of the *pila coracoidea*. On this fragment the left coracoidal sulcus overlaps above the right sulcus medially, the coracoidal sulci are roughly in the same plane as the adjacent *labrum internum*, a *spina externa* is inferred by the presence of a preserved base, the ventral margin of the coracoidal sulci slope caudally rather than being near right angles to mid-line, the anterior margin of the *pila coracoidea* lacks a *spina interna* and has a broad central notch, and the carina has a broad base. The caudal margin of the *pila coracoidea* drops abruptly down onto the *pars cardiaca*, but little of this facies is preserved. Compared with other large carinate birds found to-date in the St Bathans Fauna, accipitrid sterna have a similar general form to the preserved fragment but differ with the anterior margin of the *labrum internum* forming a face at an abrupt angle to the adjacent coracoidal articular facet. Anseriforms and gruiforms, with the exception of *Balearica* (Mayr & Clarke, 2003), which differs markedly in shape from the fossil, differ markedly in having non-overlapping coracoidal sulci. Other large birds that might be expected in the New Zealand faunas all differ markedly. Some phalacrocoracids are similar with overlapping coracoidal sulci, but differ trenchantly by much thinner dorsoventral depth and that the labrum internum is developed as a prominent cranially directed facet to receive an opposing facet on the coracoid. In pelecaniids, large procellariiforms, such as *Macronectes*, *Thalassarche*, and *Diomedea*, and in most ciconiids, the coracoidal sulci do not overlap and, in all these taxa, the labrum internum forms a large facet as seen in phalacrocoracids. The fragment is very similar in shape to the only published image of a palaelodid sternum that we are aware of, a cranial sternal fragment attributed to *Palaelodus* [= *Megapalaelodus*] *goliath* by Milne-Edwards (1867–1871: plate 87). It appears to be of appropriate size for *Palaelodus aotearoa*, based on relative sizes of *Phoenicopterus* distal tibia and sterna, so we tentatively refer it to the new taxon.

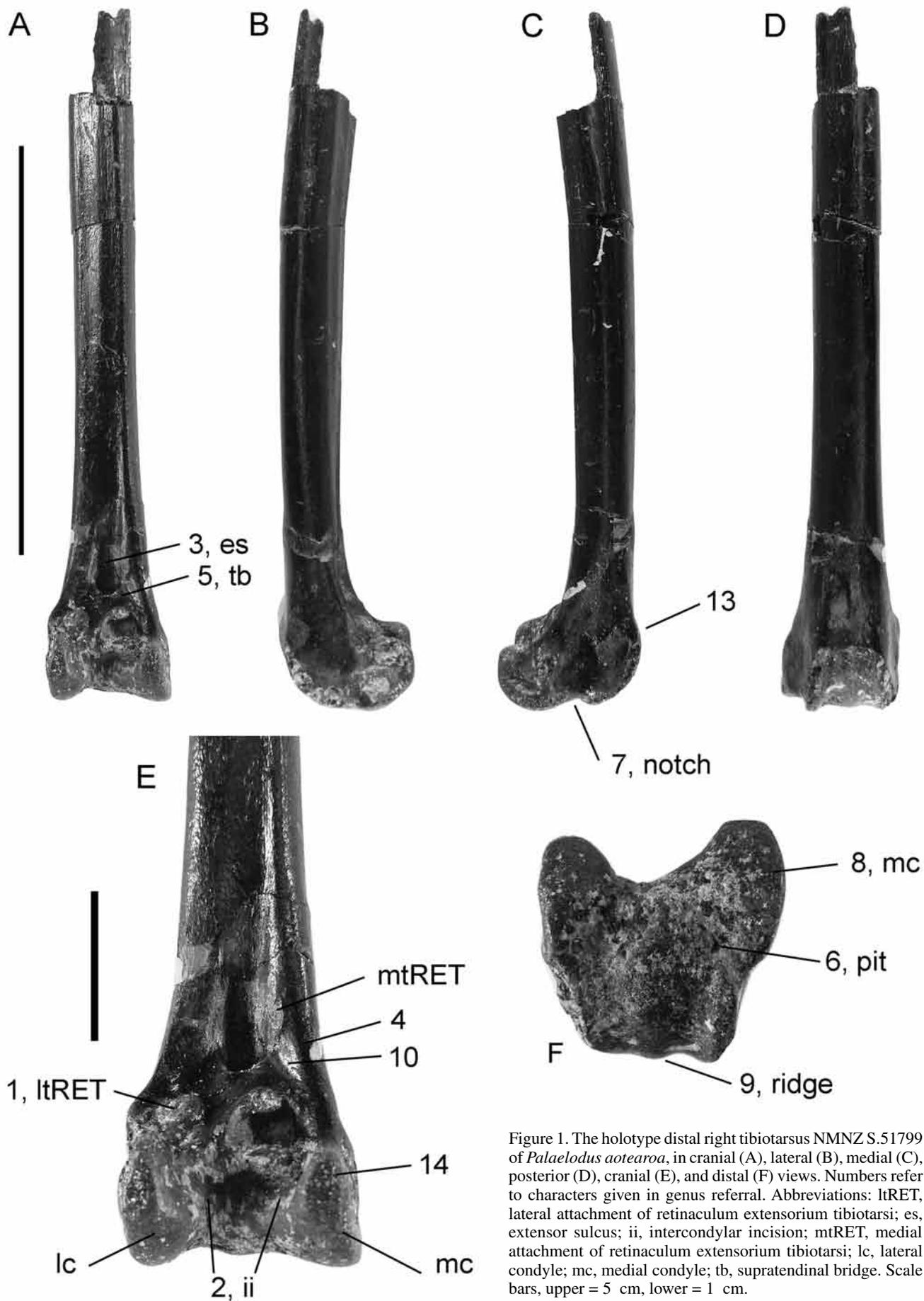


Figure 1. The holotype distal right tibiotarsus NMNZ.S.51799 of *Palaelodus aotearoa*, in cranial (A), lateral (B), medial (C), posterior (D), cranial (E), and distal (F) views. Numbers refer to characters given in genus referral. Abbreviations: ltRET, lateral attachment of retinaculum extensorium tibiotarsi; es, extensor sulcus; ii, intercondylar incision; mtRET, medial attachment of retinaculum extensorium tibiotarsi; lc, lateral condyle; mc, medial condyle; tb, supratendinal bridge. Scale bars, upper = 5 cm, lower = 1 cm.

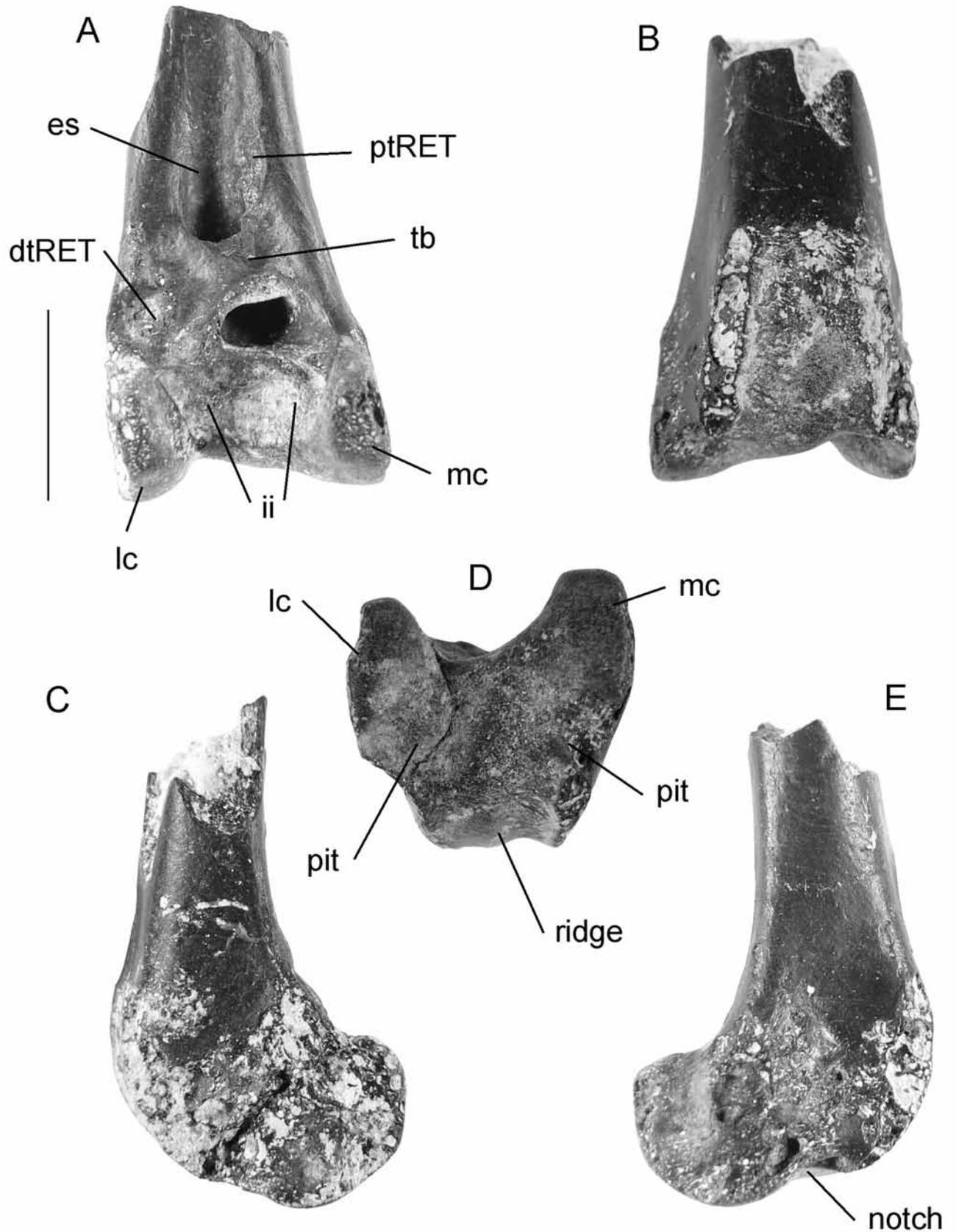


Figure 2. The paratype distal right tibiotarsus NMNZ S.51258 of *Palaelodus aotearoa*, in anterior (A), posterior (B), distal (C), lateral (D), and medial (E) views. Abbreviations as in Fig. 1. Scale bar = 1 cm.

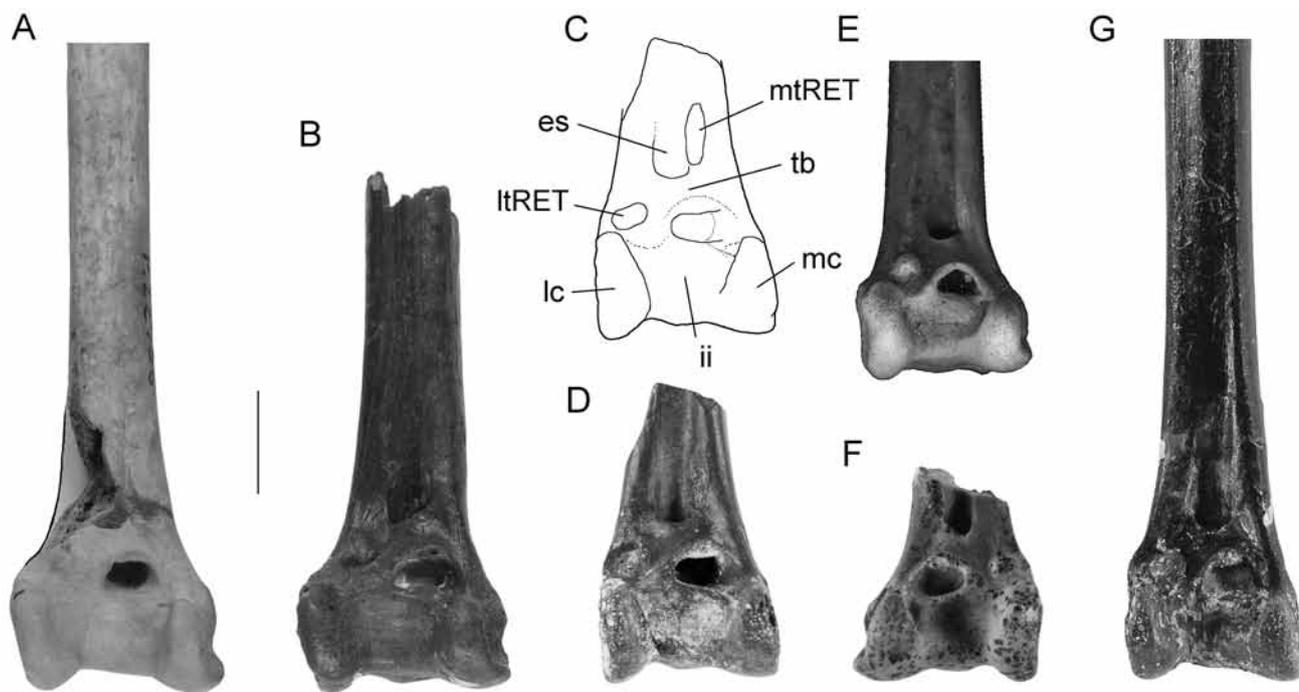


Figure 3. Distal tibiotarsi of *Palaelodus* species compared in cranial views: A, *P. wilsoni* SAM P.22706; B, *Palaelodus* sp. indet. SAM P.25151; C, D, *P. aotearoa* NMNZ S.51258; E, *P. ambiguus*, CM Av11396; F, *P. wilsoni*, SAM P.27973; and G, *P. aotearoa* NMNZ S.51799. A and F illustrate size range in *P. wilsoni*. Scale bar = 1 cm. Abbreviations as in Fig. 1.

Discussion

We report here the first fossil phoenicopteriform from New Zealand, based on two, or possibly three, fossil bones. The tibiotarsi fragments represent a species that can unambiguously be referred to the family Palaelodidae. They are described here as a new species *Palaelodus aotearoa*. Palaelodids had a global distribution in the Oligo-Miocene, with species in Australia (Baird & Vickers-Rich, 1998), Europe (Milne-Edwards, 1863, 1867–1871; Lambrecht, 1933; Švec, 1981; Cheneval, 1987; Heizmann & Hesse, 1995; Mayr & Smith, 2002; Mlíkovský, 2002), Egypt (Rasmussen *et al.*, 1987), North America (A.H. Miller, 1944; L. Miller, 1950, 1952; Brodkorb, 1961), and South America (Noriega, 1995). In Australia, *Palaelodus* is known from inland Oligo-Miocene (26–24 Ma) lacustrine deposits in the Etadunna and Namba Formations of South Australia by the two species *P. wilsoni* and *P. pledgei* (Baird & Vickers-Rich, 1998; Boles, 2006). The first of these is also recorded from Pleistocene deposits in Cooper Creek, South Australia (Baird & Vickers-Rich, 1998), and while the specific identity is questioned (Worthy, 2008), the generic referral is not doubted, making it the youngest record for the family. The New Zealand *Palaelodus aotearoa*, at 19–16 Ma in age, thus bridges this temporal gap for palaelodids in Australasia and provides evidence of a distinct lineage of palaelodids in New Zealand in the Early Miocene. The available material does not warrant a phylogenetic assessment of its relationships, but with its stouter shaft, it differs more from the Australian taxa than they do from the European ones. It is hoped that future discoveries will make such an assessment possible.

There is uncertainty about how many species of *Palaelodus* should be recognized in Europe. Apart from *Palaelodus goliath*, three species (*Palaelodus ambiguus*, *P. crassipes*, and *P. gracilipes*) are recognized (e.g., Cheneval,

1987; Heizmann & Hesse, 1995), although these were reduced to just one (*P. ambiguus*) by Mlíkovský (2002). Research to address the specific diversity of European palaelodids appears warranted, as acknowledged by Mayr (2009), as the data presented by Cheneval (1983a, fig. 1) shows variation across these three taxa that could be consistent with a single species. Moreover, for these three essentially identical “taxa” to have existed sympatrically and contemporaneously for about 12 million years from the Late Oligocene to the Middle Miocene (Heizmann & Hesse, 1995; Mlíkovský, 2002; Mayr, 2005) without divergence is less parsimonious than that they be considered a single taxon. Modern examples where congeneric taxa are nearly identical in skeletal morphology and differ by size are probably the result of very recent speciation events, for example the Australasian teal (Joseph *et al.*, 2009). If Mlíkovský’s (2002) synonymy is supported by further research, only two palaelodids, *P. ambiguus* and *P. goliath* lived in sympatry in Europe, having been found together in many sites. In Australia, the two *Palaelodus* species had a similar size disparity, with *P. pledgei* smaller than European *P. gracilipes*, and *P. wilsoni* in the size range of European *P. ambiguus*–*P. crassipes*. *Palaelodus aotearoa* is much smaller than *P. goliath* or the *Megapalaelodus* spp., in the size range for *P. ambiguus* and at the small end of the range for *P. wilsoni*, indicating it is a medium-sized palaelodid.

The addition of *Palaelodus aotearoa* to the St Bathans Fauna significantly affects perception of the avian diversity (particularly of waterbirds) in Miocene New Zealand. Paleolake Manuherikia (ca. 5600 km²) supported a diverse community of waterbirds with waterfowl, wading charadriiforms, a heron (Ardeidae) and a palaelodid now known.

More than 3000 avian fossils have been prepared from the St Bathans Fauna and, as yet, true flamingos (Phoenicopteridae), cormorants (Phalacrocoracidae), darters

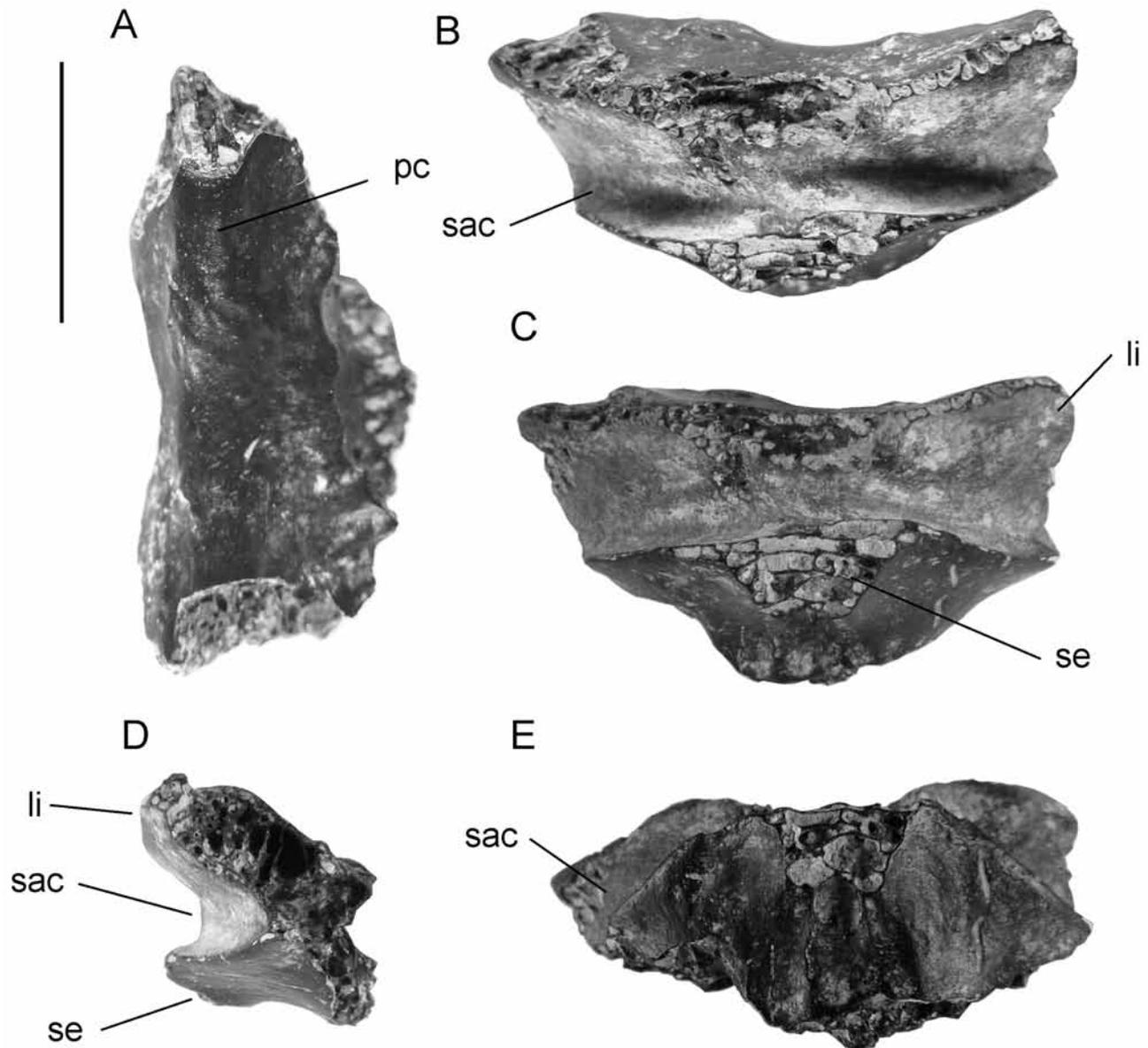


Figure 4. Views of NMNZ S.51257 in dorsal (A), cranial (B, C), left lateral (D), and ventral (E) views. Abbreviations: pc, pila coracoidea; sac, sulcus articularis coracoideus; li, labrum internum; se, base of spina externa. Scale bar = 1 cm.

(Anhingidae) and pelicans (Pelecanidae) are unknown from the fauna, despite their presence in the Oligo-Miocene of Australia (e.g., Boles, 2006). It is possible that these families may truly be absent from the St Bathans Fauna, but the recent discovery of *Palaelodus*, reported here, indicates that such a conclusion might well be premature. Instead, taphonomic limitations of the site may be a source of potential constraint on species representation and their numerical abundance. The St Bathans Fauna is derived from lacustrine fossil deposits that were laid down in shallow water in sandy—silty layers between layers of clay. Ripples in the sand layers reveal some wave action or water flow. Fossils are often concentrated on the down-flow side of shallow humps on the original lake bed and are also often found in the lee of larger objects like oncolites, adding further support to there having been a significant flow or current during the deposition of the beds. Further, there is complete disarticulation of all skeletons and most bones show variable wear consistent with erosion due to the tumbling action in the wave zone. Lastly, the fossil

assemblage has higher proportions of elements that present least resistance to flow, e.g., carpometacarpi and coracoids. There are no entire pelves or sterna known and no fossil longer than 15 cm, even though fragments derive from some much larger bones. To summarize, these taphonomic biases result in all truly terrestrial taxa being very rare and bones larger than 15 cm absent, creating a marked bias against the discovery of identifiable fragments of all taxa larger than shelducks.

Waterfowl dominate the St Bathans assemblage and is explicable because ducks of the present day often aggregate in large flocks and so would be expected to dominate fossil deposits. *Palaelodids* can be very abundant in some deposits, with thousands of bones from St Gérard-le-Puy (Cheneval & Escuillié, 1992), suggesting that they too lived in flocks, but in South Australian deposits they occur as isolated specimens and are relatively rare with only one or two specimens per quarry or locality (Baird & Vickers-Rich, 1998; THW pers. obs., paleontology catalogue South Australian Museum).

Thus, the two, possibly three, specimens reported here from New Zealand of a medium-sized species of palaeodid suggest that it too probably lived in small numbers in paleo-Lake Manuherikia, not in the vast flocks flamingos can form. While we might expect truly terrestrial taxa, e.g., pigeons, owl-nightjars to be rare in a lacustrine deposit (Worthy *et al.*, 2007), the fact that some waterbirds, e.g., a heron (Scofield *et al.*, 2010), is about as rare as the palaeodid, suggests that despite several thousand fossils documenting the avifauna, the current absence of the waterbirds listed above does not mean they were actually absent from the Miocene biota of Lake Manuherikia.

Despite these limitations, the developing St Bathans Fauna already reveals an avifauna with similarities to that of present day New Zealand and little in common with Oligo-Miocene Australia. There are no shared species, and as yet no casuariids, dromaiids, megapodiids, dromornithids, podicipedids, anhingids, phalacrocoracids, phoenicopterids, burhinids or cactuoids in the St Bathans Fauna, all of which have an Oligo-Miocene record in Australia (Boles, 2006; THW pers. obs.). The New Zealand waterfowl assemblage was dominated by oxyurines, as were waterfowl faunas in Australia and globally, and a tadornine was present as in Australian faunas, but all taxa differ at the generic level (Worthy *et al.*, 2007; Worthy & Lee, 2008; Worthy, 2009). Given the globally widespread distribution of *Palaeodius*, generic distinction of the New Zealand palaeodid would not be expected, but its specific distinction from Australian taxa is consistent with the endemism of other New Zealand taxa.

The distinctiveness of the St Bathans Fauna can inform the debate on whether New Zealand was completely drowned during the Late Oligocene–Early Miocene 25–22 Ma (Pole, 1994; Gibbs, 2006; Heads, 2006; Waters & Craw, 2006; Campbell & Hutching, 2007; Treweek *et al.*, 2007; Landis *et al.*, 2008). While genetic studies of extant taxa are providing a growing body of data indicating that some diverged from sister taxa elsewhere long before the Oligocene highstand, for example hyriid molluscs (Graf & Foighil, 2000), freshwater crayfish (Apte *et al.*, 2007), anostostomatid orthopterans (Pratt *et al.*, 2008), geckoes (Chambers *et al.*, 2001), wattlebirds and stitchbirds (Driskell *et al.*, 2007; Shepherd & Lambert, 2007), kakapo and kaka (Tavares *et al.*, 2006), and kauri (Knapp *et al.*, 2007), only a fossil record can reveal what was actually present. The St Bathans Fauna has already revealed a number of taxa for which a vicariant origin is most likely, e.g., sphenodontids, leiopelmatid frogs, large flightless moa (Aves: Dinornithiformes), acanthisittid wrens, and an archaic stem terrestrial mammal (Worthy *et al.*, 2006, 2007, 2010; Jones *et al.*, 2009; Tennyson *et al.*, 2010). Some other taxa indicate a longevity in New Zealand of modern lineages since at least the Early Miocene, for example, anserines similar to *Cereopsis*, columbids of the *Hemiphaga* lineage, *Aegothales*, *Pelecanoides* and diplodactyline geckoes, (Lee *et al.*, 2009; Worthy *et al.*, 2007, 2008, 2009). In addition, parrots, accipitrids, herons, shelducks and other waterfowl, rails and passerines including honeyeaters, while not known to be closely related to modern taxa, convey a distinctly New Zealand character to the fauna as a whole (Worthy *et al.*, 2007; Scofield *et al.*, 2010). Of those so far reported, only the swiftlet (*Collocalia*), cracticid songbirds and a crocodylian (Molnar & Pole, 1997; Worthy *et al.*, 2007) are representative of families no longer found in the New Zealand fauna, but Pleistocene and present cooler temperatures probably explain their absence. In short, all archetypical “New Zealand” endemic vertebrate

taxa known from New Zealand in the Recent fauna are now known to have been present in the Early Miocene at a time perhaps no more than 3–4 Ma after maximal drowning of New Zealand. If New Zealand was completely submerged as Landis *et al.* (2008) contend, then all such taxa would need to have dispersed to New Zealand in this short period and no such taxa would have arrived in the subsequent 16 million years. Moreover, in some cases, e.g., leiopelmatids, sphenodontids, the recently discovered archaic mammal, and birds such as dinornithiforms, acanthisittids and aptornithids, there are no known source populations from which such dispersals could have emanated.

Our observations of the St Bathans Fauna, minimally some 3–4 million years after the maximal submergence, reveals a diverse fauna with little or no close relationship to the nearest up-wind land mass—Australia. Rather we see a mix, even then, of ancient endemics of Gondwanan origin and global influences such as members of the radiations of oxyurine anatids and palaeodids. In summary, the imperfect St Bathans Fauna already provides significant evidence of the persistence of taxa on Zealandia through the highstand, and minimally reveals a fauna whose general endemism indicates that it had been evolving in isolation for millions of years. Given the limited depositional settings so far sampled and the brevity of investigations to date, compared to faunas such as those from Saint-Gérard-le-Puy and Sansan in France (Milne-Edwards, 1867–1871; Cheneval, 1983b, 1984), there will be many more first records yet for the St Bathans Fauna. Because this is the only fauna documenting the terrestrial vertebrate biota of New Zealand during the Tertiary, many first records representing novel lineages can be expected as increasingly more of New Zealand’s Tertiary biota is documented for the first time.

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