

A new fossil from the mid-Paleocene of New Zealand reveals an unexpected diversity of world's oldest penguins

Gerald Mayr¹  · Vanesa L. De Pietri² · R. Paul Scofield²

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Abstract We describe leg bones of a giant penguin from the mid-Paleocene Waipara Greensand of New Zealand. The specimens were found at the type locality of *Waimanu manneringi* and together with this species they constitute the oldest penguin fossils known to date. Tarsometatarsus dimensions indicate a species that reached the size of *Anthropornis nordenskjöldi*, one of the largest known penguin species. Stem group penguins therefore attained a giant size very early in their evolution, with this gigantism existing for more than 30 million years. The new fossils are from a species that is phylogenetically more derived than *Waimanu*, and the unexpected coexistence of *Waimanu* with more derived stem group Sphenisciformes documents a previously unknown diversity amongst the world's oldest penguins. The characteristic tarsometatarsus shape of penguins evolved early on, and the significant morphological disparity between *Waimanu* and the new fossil conflicts with recent Paleocene divergence

estimates for penguins, suggesting an older, Late Cretaceous, origin.

Keywords Fossil birds · Sphenisciformes · Waipara Greensand · *Waimanu* · *Crossvallia*

Introduction

The Paleogene fossil record of penguins (Sphenisciformes) has been intensively studied in recent years, with numerous new taxa having been described (Tambussi et al. 2005; Slack et al. 2006; Clarke et al. 2010; Ksepka and Ando 2011; Fordyce and Thomas 2011; Ksepka et al. 2012; Jadwiszczak et al. 2013; Mayr 2016; Acosta Hospitaleche and Olivero 2016). Knowledge of the earliest period of penguin evolution, however, is still very patchy, and few penguin remains have been reported from Paleocene localities.

The oldest published fossils are two species of the taxon *Waimanu* from the Paleocene Waipara Greensand in New Zealand (Slack et al. 2006). *Waimanu manneringi* stems from strata that are 60.5–61.6 million years old, whereas the age of the smaller *W. tuatahi* was estimated at 58–60 million years (Slack et al. 2006). *Waimanu* is congruently recovered as the phylogenetically most basal penguin taxon in all phylogenetic analyses and shows many plesiomorphic features that distinguish it from other Sphenisciformes (Clarke et al. 2007; Clarke et al. 2010; Ksepka et al. 2012; Chávez Hoffmeister 2014).

The next-oldest penguin is *Crossvallia unienwillia* from the late Paleocene (59.2–56 million years ago [mya]) of Antarctica (Tambussi et al. 2005; Jadwiszczak et al. 2013). Due to the fragmentary preservation of the partial holotype skeleton, the phylogenetic affinities of *Crossvallia* are ill-constrained, and the single analysis in which the taxon is

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✉ Gerald Mayr
Gerald.Mayr@senckenberg.de

Vanesa L. De Pietri
VDePietri@canterburymuseum.com

R. Paul Scofield
pscofield@canterburymuseum.com

¹ Ornithological Section, Senckenberg Research Institute and Natural History Museum Frankfurt, Senckenberganlage 25, 60325 Frankfurt am Main, Germany

² Canterbury Museum, Rolleston Avenue, Christchurch 8050, New Zealand

included recovered it in an unresolved polytomy at the base of a clade including all other penguin taxa except *Waimanu* (Chávez Hoffmeister 2014).

A remarkable feature of penguin evolution is the rapid occurrence of large body size in the early Cenozoic. Even the two *Waimanu* species had a body size comparable to that of the Emperor Penguin (*Aptenodytes forsteri*), which is the largest extant penguin, and *C. unienwillia* was distinctly larger than *A. forsteri* (Jadwiszczak et al. 2013). Truly giant penguins, with a body length above 1.3 m, occur in Eocene and Oligocene strata and belong to the taxa *Anthropornis*, *Palaeudyptes*, *Kairuku*, *Pachydyptes*, *Inkayacu*, and *Icadyptes* (Clarke et al. 2007, 2010; Ksepka et al. 2012), with the Eocene *Anthropornis nordenskjöldi* and *Palaeudyptes klekowskii* being widely regarded as the largest penguin species (Jadwiszczak 2001; Acosta Hospitaleche 2014).

Here, we report a partial left tarsometatarsus with four associated pedal phalanges of a giant penguin from the mid-Paleocene of New Zealand. The specimens were found in situ at the type locality of *W. manneringi* in the Waipara Greensand at Waipara River, Canterbury Province (43° 03' 26" S, 172° 35' 47" E). They come from strata about 11 m above those yielding the *W. manneringi* holotype and two meters below a stratigraphic horizon that contained undescribed remains of *Waimanu*. A sediment sample taken from this latter horizon includes a dinoflagellate species, which was named *Apteodinium "trifolliculum"* by Browne et al. (2016: 404) and is only known from the early late Teurian stage (about 61 mya; Chris Clowes, pers. comm.).

Material and methods

The fossil specimens are in the collection of Canterbury Museum, Christchurch, New Zealand (CM). To assess their phylogenetic affinities, we scored 27 tarsometatarsal characters in a comprehensive data matrix of 75 humeral and tarsometatarsal characters (Chávez Hoffmeister 2014). We added 35 tarsometatarsal scorings for *W. manneringi*, which was not included in the original data set, and newly scored or corrected 16 tarsometatarsal characters for *W. tuatahi* (see [Electronic Supplementary Material](#) for the nexus file). The following characters were scored for the new fossil (CM 2016.158.1): 41:2, 42:0, 43:1, 44–49:0, 50:1, 51:0, 52:0, 53:1, 54:3, 55:0, 56:1, 57:1, 58:1, 59:0, 60:1, 61:0, 62–64:0, 65:2, 66:0. Character scorings for *W. manneringi* are: 41:1, 42:0, 43:1, 44–49:0, 50:1, 51:0, 52:0, 53:1, 54:3, 55:0, 56:0, 57:1, 58:1, 59:0, 60:1, 61:0, 62:1, 63:0, 64:0, 65:2, 66:0, 67:0, 68:2, 69:1, 70–74:0, 75:1. The following characters, which were scored as unknown for *Waimanu tuatahi* by Chávez Hoffmeister (2014), were newly coded: 42:0, 43:1, 45:0, 46:0, 49:0, 50:1, 52:0, 53:1, 54:3, 56:0, 63:0, 64:0, 74:0. In addition, two of Chávez Hoffmeister's (2014) character

scorings for *Waimanu tuatahi* were corrected (original state in brackets): 58:1 [58:0], 61:0 [61:1], one further character state was modified: 33:? [33:–]. The analysis was run with the heuristic search modus of NONA 2.0 (Goloboff 1993) through the WINCLADA 1.00.08 interface (Nixon 2002), using the commands hold 10000, mult*1000, hold/10, and max*. Bootstrap support values were calculated with 1000 replicates, ten searches holding ten trees per replicate, and TBR branch swapping without max*. Trees were rooted with Gaviiformes.

Results

With a length of 81.6 mm, the tarsometatarsus of new fossil (CM 2016.158.1) is one of the largest penguin tarsometatarsi reported so far (Table 1). The bone exhibits a distinctive morphology that is very different from *Waimanu* (Fig. 1), and with regard to its stouter proportions and morphological details, it corresponds with the tarsometatarsi of more derived Sphenisciformes.

The elongation index—that is, the ratio of tarsometatarsus length to the width of the proximal end of the bone—is 2.0 for the new fossil from the Waipara Greensand, whereas it is about 3.0 in *Waimanu tuatahi* and 2.6 in *W. manneringi*. In proximal view, the tarsometatarsus of CM 2016.158.1 most closely resembles the late Eocene Antarctic taxa *Marambiornis* and *Anthropornis* in the configuration of the hypotarsus (Chávez Hoffmeister 2014; Jadwiszczak 2015). The sulcus for the tendon of the flexor digitorum longus (FDL) muscle is centrally positioned and deep, and lateral of it, there is a shallow sulcus for the tendon of the flexor hallucis longus (FHL) muscle (Fig. 1d). Of the two crests bordering the FDL sulcus, the medial one is well-developed, whereas the crest lateral of this sulcus is plantarly prominent but proximodistally short; a third hypotarsal crest of similar length to the medial one, but with little plantar prominence, laterally borders the sulcus for the tendon of FHL. The hypotarsus of the new fossil is clearly distinguished from that of *Waimanu*, in which the intermediate hypotarsal crest is much longer but plantarly less prominent and the main sulcus, for the tendon of FDL, is narrower and opens lateroplantarly instead of plantarly (Fig. 1h).

As in *Waimanu*, there are two equally sized proximal vascular foramina (Fig. 1a); in *Inkayacu*, *Kairuku*, and *Palaeudyptes*, by contrast, the medial proximal vascular foramen is reduced, whereas it is the lateral foramen that is reduced in *Anthropornis* (the tarsometatarsus of *Pachydyptes* and *Icadyptes* is unknown). An unusual feature of CM 2016.158.1 is the presence of two widely separated plantar openings for the medial proximal vascular foramen (Fig. 1b), which are not found in other stem group Sphenisciformes. As in *Waimanu*, there is only a weakly

Table 1 Dimensions of the new tarsometatarsus from the Waipara Greensand (CM 2016.158.1) in comparison with other very large penguin species. The proximal width of the tarsometatarsus of *Crossvallia unienwillia* was estimated from the width of the distal tibiotarsus

	Tarsometatarsus, length	Tarsometatarsus, proximal width
CM 2016.158.1	81.6	>40.5
<i>Crossvallia unienwillia</i>	—	[~36–37]
<i>Anthropornis nordenskjöldi</i>	81.4–88.1 ^a	>34.4–39.1 ^a
<i>Anthropornis grandis</i>	74.7–78.7 ^a	>36.6 ^a
<i>Palaeudyptes klekowskii</i>	66.6–91.3 ^{a, b}	27.3–> 40.1 ^a
<i>Palaeudyptes gunnari</i>	59.0–64.5 ^a	>30.0–33.4 ^a
<i>Kairuku grebneffi</i>	67.6 ^c	>41.0 ^c
<i>Kairuku waitaki</i>	63.6 ^c	41.2 ^c
<i>Inkayacu paracasensis</i>	76.3 ^d	45.9 ^d
<i>Waimanu manneringi</i>	78.0	31.1
<i>Waimanu tuatahi</i>	65 ^e	—

^a After Myrcha et al. (2002)

^b After Acosta Hospitaleche (2014)

^c After Ksepka et al. (2012)

^d After Clarke et al. (2010)

^e After Slack et al. (2006)

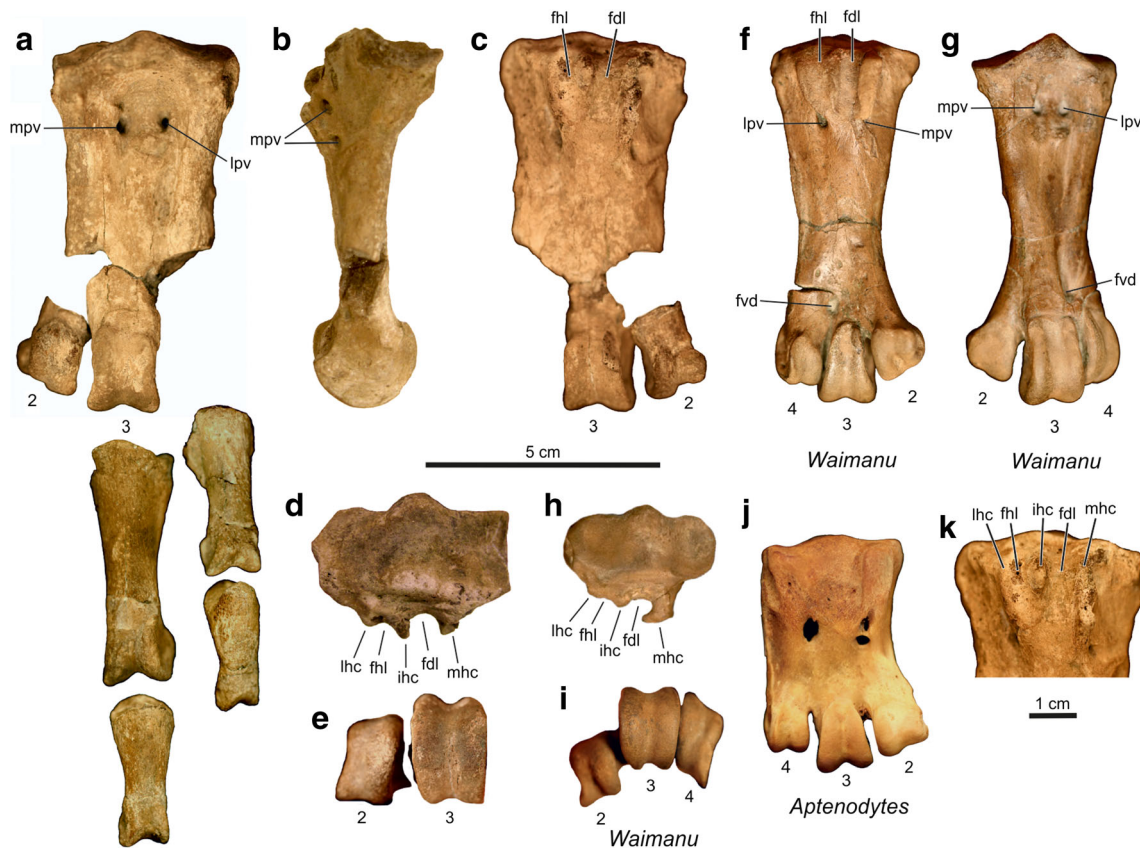


Fig. 1 **a–e** Penguin foot bones from the Paleocene Waipara Greensand in New Zealand (CM 2016.158.1), with tarsometatarsus in **a** dorsal, **b** medial, **c** plantar, **d** proximal, and **e** distal view. The broken trochlea metatarsi II is brought in its approximate position in **a** and **c**. **f–i** Right tarsometatarsus of the holotype of *Waimanu manneringi* from the Waipara Greensand (CM zfa35, mirrored to ease comparisons). **j** Left tarsometatarsus of the extant Emperor Penguin, *Aptenodytes forsteri*, in plantar view. **k** Detail of proximal end of tarsometatarsus of CM

2016.158.1 in plantar view, with hypotarsal crests and sulci labeled. *Fdl* sulcus for tendon of flexor digitorum longus muscle, *fhl* sulcus for tendon of flexor hallucis longus muscle, *fvd* distal vascular foramen, *ihc* intermediate hypotarsal crest, *lhc* lateral hypotarsal crest, *lpv* opening of lateral proximal vascular foramen, *mhc* medial hypotarsal crest, *mpv* opening(s) of medial proximal vascular foramen. Tarsometatarsal trochleae are numbered. Same scale bar for **a–j**

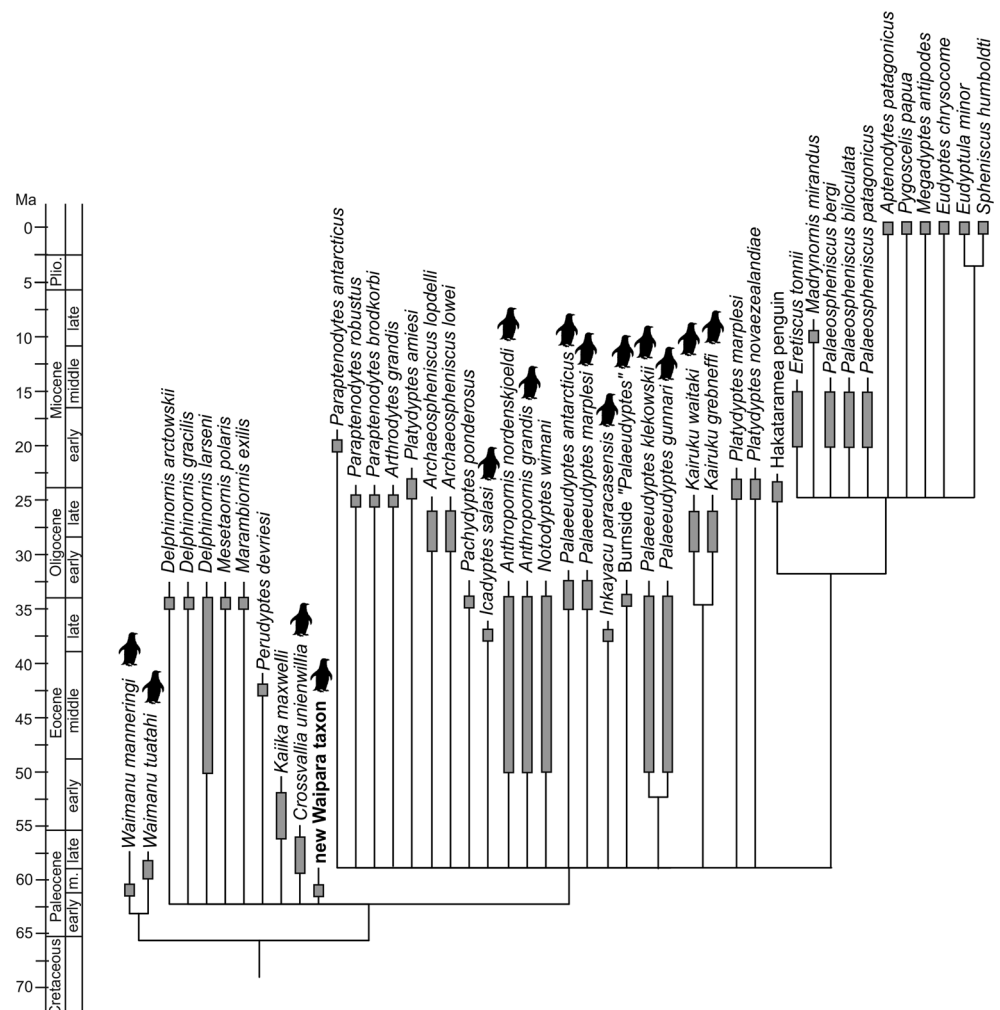
developed sulcus between the (fused) third and fourth metatarsals on the dorsal surface of the bone. The shaft lacks the pronounced convexity on its medial margin, which characterizes the tarsometatarsus of *Anthropornis* (Myrcha et al. 2002). Unlike in *Waimanu*, the dorsal and plantar articular surfaces of the trochlea metatarsi III are proximodistally short and the plantar surface does not taper proximally. The trochlea metatarsi II resembles that of *Anthropornis* in its proportions.

The presence of a distal vascular foramen cannot be definitely assessed, because the corresponding area is broken. Although the remaining portion preserves a structure that we tentatively interpret as the medial border of the foramen, the feature was scored as unknown in the phylogenetic analysis. A distal vascular foramen is plesiomorphically present in *Waimanu*, *Delphinornis*, *Mesetaornis*, and *Marambiornis*, which are recovered as the phylogenetically most basal stem group Sphenisciformes in current phylogenies (Clarke et al. 2007, 2010; Ksepka et al. 2012). The pedal phalanges are identified as the two proximal phalanges of the third and fourth toes.

The phylogenetic analysis resulted in a poorly resolved consensus trees, which supports placement of the new fossil from the Waipara Greensand in a clade comprising all sphenisciform taxa to the exclusion of *Waimanu*. Within that latter clade, it was recovered in a polytomy together with *Crossvallia* and the Eocene taxa *Kaiika*, *Perudyptes*, *Delphinornis*, *Mesetaornis*, and *Marambiornis* (Fig. 2). None of the nodes was retained in the bootstrap analysis, which is not unexpected in light of the fact that of some critical taxa either the humerus or the tarsometatarsus are unknown. Derived features, in which the new Waipara penguin differs from *Waimanu* and agrees with more crownward fossil penguins, include the lower elongation index of the tarsometatarsus and the shape of the hypotarsus, with the FDL sulcus opening plantarly and being laterally bordered by a well-developed crest.

In size, the new tarsometatarsus corresponds well with the equally large *C. unienwillia*. In this latter species, the distal end of the tibiotarsus has a width of 35.7 mm (Jadwiszczak et al. 2013). Because the width of the distal tibiotarsus

Fig. 2 Placement of the new fossils in the consensus tree of the phylogenetic analysis (length = 304, CI = 0.41, RI = 0.74); none of the nodes were retained in the bootstrap support analysis. Gray bars indicate stratigraphic occurrences (after Ksepka and Ando 2011); divergence dates are hypothetical. Penguin icons denote giant species



corresponds with that of the proximal tarsometatarsus, the unknown tarsometatarsus of the *C. unienwillia* holotype must have had about 90% the proximal width of CM 2016.158.1. We therefore cannot exclude the possibility that the new fossils belong to *Crossvallia*, but an assignment to this taxon would be entirely conjectural in the absence of any overlapping skeletal elements.

Discussion

Together with the fossils of *W. manneringi*, the specimens described in the present study are the earliest published penguin remains. However, the flattened and wide tarsometatarsus of the new taxon from the Waipara Greensand exhibits a much more derived morphology than the tarsometatarsus of *Waimanu* and clearly stems from a taxon that is situated more crownward than *Waimanu* in the phylogenetic tree of penguins.

This coexistence of *Waimanu* with more derived stem group Sphenisciformes during the mid-Paleocene is unexpected and documents that early penguin diversity was greater than what was suggested by the previously known fossil record. In particular, the new fossil shows that the characteristic tarsometatarsus shape of penguins evolved much earlier than previously hypothesized. *Waimanu* and the new species from the Waipara Greensand must have been distinguished in locomotory characteristics and likely occupied different ecological niches, which enabled their coexistence in the mid-Paleocene of New Zealand. The feet of *Waimanu* may have played a greater role in underwater propulsion than they do in extant penguins, where the forelimbs assist in diving and the feet only function as steering devices (e.g., Kato et al. 2006). It is furthermore likely that the flattened and widened tarsometatarsi of more derived penguins—that is, taxa other than *Waimanu*—are functionally correlated with the unique upright posture and waddling gait of penguins, so that *Waimanu* and the new Waipara Greensand taxon may have also differed in aspects of their terrestrial locomotion.

In size and proportions, the new tarsometatarsus corresponds with that of small individuals of *Anthropornis nordenskjöldi* (compare Fig. 1a, c with Myrcha et al. 2002: Figs. 5 and 6), for which a total body length of about 165 cm was estimated (Jadwiszczak 2001). Although the new tarsometatarsus is only slightly longer than that of *W. manneringi*, its much stouter proportions suggest a heavier and larger bird (see Simpson 1946 for allometric correlations of tarsometatarsus proportions of penguins). Stem group penguins therefore reached a giant size very early in their evolution, and size increase appears to have commenced soon after flightlessness released penguins from aerodynamic constraints, with giant species existing over a period of at least 30 million years, from the mid-Paleocene to the late

Oligocene. Why giant species disappeared towards the Neogene remains elusive, but the evolution of odontocete whales was considered as a factor that contributed to their demise (Ando and Fordyce 2014).

The new fossils described here also bear on divergence estimates of penguins, which are controversially resolved in calibrated molecular analyses. Whereas some authors (Baker et al. 2006) located the split of penguins from their sister taxon in the Late Cretaceous, about 71 mya, more recent genomic analyses supported a mid-Paleocene divergence of penguins, about 62 mya (Jarvis et al. 2014; Prum et al. 2015; see also Mitchell et al. 2015). However, the existence of stem group Sphenisciformes by that time, which are phylogenetically more derived than *Waimanu*, suggests that these mid-Paleocene divergence estimates are too young. A divergence of Sphenisciformes in the mid-Paleocene would require the evolution of the penguin body plan and a substantial diversification of stem group taxa within an extremely short period of time, and we consider Late Cretaceous divergence estimates to be in better accordance with the fossil record.

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