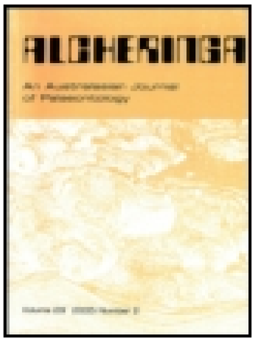


Taylor & Francis
Taylor & Francis Group

Alcheringa: An Australasian Journal of Palaeontology

ISSN: 0311-5518 (Print) 1752-0754 (Online) Journal homepage: https://www.tandfonline.com/loi/talc20

Leg bones of a new penguin species from the Waipara Greensand add to the diversity of very large-sized Sphenisciformes in the Paleocene of New Zealand

Gerald Mayr, Vanesa L. De Pietri, Leigh Love, Al Mannering & R. Paul Scofield

To cite this article: Gerald Mayr, Vanesa L. De Pietri, Leigh Love, Al Mannering & R. Paul Scofield (2019): Leg bones of a new penguin species from the Waipara Greensand add to the diversity of very large-sized Sphenisciformes in the Paleocene of New Zealand, Alcheringa: An Australasian Journal of Palaeontology, DOI: 10.1080/03115518.2019.1641619

To link to this article: https://doi.org/10.1080/03115518.2019.1641619

Leg bones of a new penguin species from the Waipara Greensand add to the diversity of very large-sized Sphenisciformes in the Paleocene of New Zealand

GERALD MAYR, VANESA L. DE PIETRI, LEIGH LOVE, AL MANNERING and
R. PAUL SCOFIELD

MAYR, G., DE PIETRI, V.L., LOVE, L., MANNERING, A. & SCOFIELD, R.P., 9 August 2019. Leg bones of a new penguin species from the Waipara Greensand add to the diversity of very large-sized Sphenisciformes in the Paleocene of New Zealand. *Alcheringa XX*, xxx–xxx. ISSN 0311-5518

We describe a new large-sized species of the Sphenisciformes (penguins) from Paleocene strata of the Waipara Greensand in New Zealand. ?*Crossvallia waiparensis*, sp. nov. is represented by leg bones of a single individual as well as two tentatively referred proximal humeri and resembles *Crossvallia unienwillia* from the late Paleocene of Antarctica in size and morphology. The new species is the fifth published species of stem group Sphenisciformes from the Waipara Greensand and the fourth one, which has been formally named. It is distinguished from a recently reported tarsometatarsus of an unnamed large-sized penguin species from the Waipara Greensand and is the oldest well-represented giant penguin. ?*C. waiparensis* approaches the size of the Eocene taxa *Anthropornis* and *Palaeeudyptes* and provides further evidence that penguins attained a very large size early in their evolutionary history.

Gerald Mayr [gerald.mayr@senckenberg.de], Senckenberg Research Institute and Natural History Museum Frankfurt, Ornithological Section, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany; Vanesa L. De Pietri [vdepietri@canterburymuseum.com], Al Mannering [alman@slingshot.co.nz], R. Paul Scofield [pscofield@canterburymuseum.com], Canterbury Museum, Rolleston Avenue, Christchurch 8050, New Zealand; Leigh Love [lvlove@xtra.co.nz], PO Box 49, Waipara 7483, New Zealand. *Received 24.4.2019; revised 10.6.2019; accepted 5.7.2019.*

Key words: Aves, birds, evolution, fossil birds, morphology, systematics, taxonomy.

THE WAIPARA GREENSAND in Canterbury, New Zealand, is arguably the most significant locality for Paleocene penguin fossils. The first specimens from these Teurian (about 62–58 million years ago [Ma]) marine deposits were collected more than three decades ago (Fordyce & Jones 1986) and were described by Slack *et al.* (2006). The latter authors distinguished two species, which they classified in the taxon *Waimanu*. The type species is *Waimanu manneringi*, whereas the second species assigned to *Waimanu* was recently classified into to the new taxon *Muriwaimanu* and is now known as *Muriwaimanu tuatahi* (Mayr *et al.* 2017a).

In the past years, a number of new penguin fossils were described from the Waipara Greensand and other Paleocene localities in New Zealand. One of the most completely preserved of these is the holotype of *Sequiwaimanu rosieae* from the Waipara Greensand, which is represented by a partial skeleton including the skull and most limb bones except for the tarsometatarsus (Mayr *et al.* 2017a). *W. manneringi*, *M. tuatahi*, and *S. rosieae* were already large stem group representatives of the Sphenisciformes, which reached or even surpassed the size of the largest extant penguin species, the Emperor penguin (*Aptenodytes forsteri*).

However, there were even larger penguins in the Paleocene of New Zealand, which had body sizes comparable with those of the long-known (e.g., Simpson 1971) giant Eocene and Oligocene penguins. One of these is an unnamed species, which is only represented by an incomplete tarsometatarsus from the Waipara Greensand and was described by Mayr *et al.* (2017b). Another very large species from coeval strata is *Kumimanu biceae* from late Paleocene (55.5 –59.5 Ma) exposures at Hampden Beach in New Zealand, which is known from a partial skeleton and is among the largest fossil penguins (Mayr *et al.* 2017c).

All of the above fossils represent very archaic stem group Sphenisciformes, which are outside a clade including the post-Paleocene species (Ksepka & Ando 2011, Chávez Hoffmeister 2014, Mayr 2017, Mayr *et al.* 2017a,c). Here we describe a new large-sized penguin from the Waipara Greensand, which is represented by leg bones of a single individual and two tentatively referred proximal ends of the humerus. This species is the best preserved giant Paleocene penguin known to date and shows the greatest similarity to *Crossvallia unienwillia*, the only Paleocene stem group

https://doi.org/10.1080/03115518.2019.1641619

Fig. 1. ?*Crossvallia waiparensis*, sp. nov. from the Waipara Greensand in New Zealand. **A–L**, overview of the leg bones preserved in the holotype (CM 2018.23.9) and **M–O**, tentatively referred proximal end of a left humerus (CM 2016.158.3). **A–C**, Left tibiotarsus in cranial (**A**), caudal (**B**) and lateral (**C**) view. **D–F**, Right tibiotarsus in cranial (**D**), caudal (**E**) and lateral (**F**) view. **G**, **H**, Distal end of left femur in cranial (**G**) and caudal (**H**) view. **I–K**, Right tarsometatarsus in cranial (**I**), plantar (**J**) and distal (**K**) view. **L**, Pedal phalanx. **M–O**, Tentatively referred proximal end of left humerus in caudal (**M**), ventral (**N**) and cranial (**O**) view. Abbreviations: cms, crista musculi supracoracoidei; fvd, foramen vasculare distale; fvp, foramen vasculare proximale; pst, pons supratendineus; stv, sulcus transversus. Scale bar = 50 mm. [Colour online].

representative of the Sphenisciformes from outside New Zealand, which is based on a poorly preserved partial skeleton from the Thanetian (59.2–56 Ma) of Antarctica (Tambussi *et al.* 2005, Jadwiszczak *et al.* 2013).

Material and methods

The fossils are housed in the collection of Canterbury Museum, Christchurch, New Zealand (CM); Museo de La Plata, La Plata, Argentina (MLP); and Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ). Osteological terminology follows Baumel & Witmer (1993).

Systematic palaeontology

AVES Linnaeus, 1758
SPHENISCIFORMES Sharpe, 1891

cf. *Crossvallia* Tambussi *et al.*, 2005

?Crossvallia waiparensis, sp. nov.

Holotype. CM 2018.23.9: associated leg bones of a single individual, including the distal end of the left femur, both tibiotarsi, the right tarsometatarsus, and a pedal phalanx (Fig. 1A–L).

Etymology. The species epithet refers to the type locality.

Differential diagnosis. The new species is distinguished from:

- *Waimanu manneringi* in: larger size (width of distal tibiotarsus 33.8 mm versus 29.5 mm in *W. manneringi*; Mayr *et al.* 2017a), tarsometatarsus stouter, with medial portion of proximal end tapering into a narrow projection, dorsal openings of foramina vascularia proximalia more widely spaced and hypotarsus proportionally shorter.

- *Muriwaimanu tuatahi* in: much larger size (tarsometatarsus length 81.1 mm versus 65 mm in *M. tuatahi*; Slack *et al.* 2006), tarsometatarsus stouter, with medial portion of proximal end tapering into a narrow projection, dorsal openings of foramina vascularia proximalia more widely spaced and hypotarsus proportionally shorter.
- *Sequiwaimanu rosieae* in: larger size (width of distal tibiotarsus 33.8 mm versus 24.9 mm in *S. rosieae*; Mayr *et al.* 2017a), distal end of femur with semicondyli fibularis et tibiofibularis more laterally directed.
- *Kumimanu biceae* in: smaller size (width of distal tibiotarsus 33.8 mm versus ∼48 mm in *K. biceae*; Mayr *et al.* 2017c), condylus medialis of distal tibiotarsus distinctly smaller than condylus lateralis (of equal size in *K. biceae*); distal end of femur with sulcus between semicondyli fibularis et tibiofibularis (sulcus fibularis) narrower and deeper.
- *Crossvallia unienwillia* in: distal end of tibiotarsus mediolaterally narrower than distal end of femur (of equal width or even wider in *Crossvallia unienwillia*, with the actual dimensions of femur and tibiotarsus being 38.2/33.8 mm versus 35.7/>35.7 mm in *C. unienwillia*; Jadwiszczak *et al.* 2013).
- all post-Paleocene Sphenisciformes of which leg bones are known in: tibiotarsus with sulcus extensorius more medially situated and condylus medialis more medially protruding; tarsometatarsus with proximal end tapering into a medial projection and trochlea metatarsi IV more laterally projected.

Type locality and horizon. Waipara Greensand, Waipara River, Canterbury, New Zealand; from site S2 of Mayr *et al.* (2017a), the holotype was found *in situ* 4 metres above the debris at the base of the cliff at 43°03′28.2″S, 172°35′44.4″E; collected in 2011 by Leigh Love.

Tentatively referred specimens. CM 2016.158.3: proximal end of left humerus (Fig. 1M–O), from the Waipara Greensand, Waipara River, Canterbury, New Zealand; collected in 2014 by Leigh Love just upstream from White Gorge at the exposure of the Mt. Ellen Member at 43°03′08.0″S, 172°36′38.0″E; the collection was on the surface of this exposure.

CM 2016.158.2: fragmentary and worn proximal end of left humerus, from the Waipara Greensand, Waipara River, Canterbury, New Zealand, found loose about 10 metres stratigraphically above the locality of an undescribed pelagornithid bird (Mayr in press); collected in 2014 by Leigh Love at site S3 of Mayr *et al.* (2017a).

Measurements (in millimetres). Femur, distal width, 38.2. Left tibiotarsus, length, 237; proximal end, maximum craniocaudal depth, 51.6; proximal end, mediolateral width across cotylae, 25.6; distal end, mediolateral width across condyles, 21.4. Right tibiotarsus, length, 229; proximal end, maximum craniocaudal depth, 49.0; proximal end, mediolateral width across cotylae, 29.0; distal end, mediolateral width across condyles, 33.8. Right tarsometatarsus, length 81.1; maximum proximal width as preserved, 36.3; distal width 38.8; width of trochlea metatarsi III, 13.4. Phalanx, length, 41.1; distal width, 10.4. Tentatively referred proximal end of left humerus CM 2016.158.3, proximal width, 48.5.

Description and comparisons. The distal end of the femur (Figs 1G, H and 2A–C) exhibits a deep and sharply delimited sulcus patellaris. The condylus medialis has an essentially flat caudal surface. The sulcus fibularis, between the semicondyli fibularis et tibiofibularis (terminology after Elzanowski 2008), is well defined. Unlike in *Muriwaimanu tuatahi*, the semicondylus fibularis forms a lateral convexity, which is set off from the remainder of the condylus lateralis. The fossa poplitea is moderately deep. The distal end of the femur resembles that of *Sequiwaimanu rosieae* (Fig. 2E–J), but in distal view the semicondyli fibularis et tibiofibularis are somewhat more laterally directed. The semicondylus tibiofibularis of *Crossvallia unienwillia* (Fig. 3G, H) appears to be broader than that of ?*C. waiparensis*, which we attribute to the fact that the femur of the holotype of *C. unienwillia* is poorly preserved and the distal end of the bone badly abraded.

Both tibiotarsi are preserved in the holotype (Fig. 1A–F). Owing to diagenetic deformation, the bones differ in length and morphology, with the left tibiotarsus being longer than the right one. The crista cnemialis cranialis has a straight cranial margin, and in cranial view the medial portion of the crista patellaris forms a proximally directed, pointed tip. The long crista fibularis reaches distally almost to the middle of the tibiotarsus. The distal ends of the left and right tibiotarsus exhibit markedly different morphologies, which we attribute to diagenetic distortion of the left tibiotarsus. The distal end of the right tibiotarsus resembles the distal tibiotarsus of *Sequiwaimanu rosieae* and *Waimanu manneringi* in its shape (Fig. 2). As in the latter species but unlike in post-Paleocene Sphenisciformes, the sulcus extensorius is medially located. Furthermore, unlike in geologically younger penguins, the condyles are widely separated and the condylus medialis is medially protruding and much smaller than the condylus lateralis. As preserved, the pons supratendineus of the right tibiotarsus is very narrow in its midsection, but we can not exclude the possibility that this is a preservational artefact. In both bones, the caudal surface of the distal end is too damaged to assess the shape of the trochlea cartilaginis tibialis. Compared with the distal end of the femur, the tibiotarsus of ?*C. waiparensis* is proportionally smaller than that of *C. unienwillia*, but meaningful

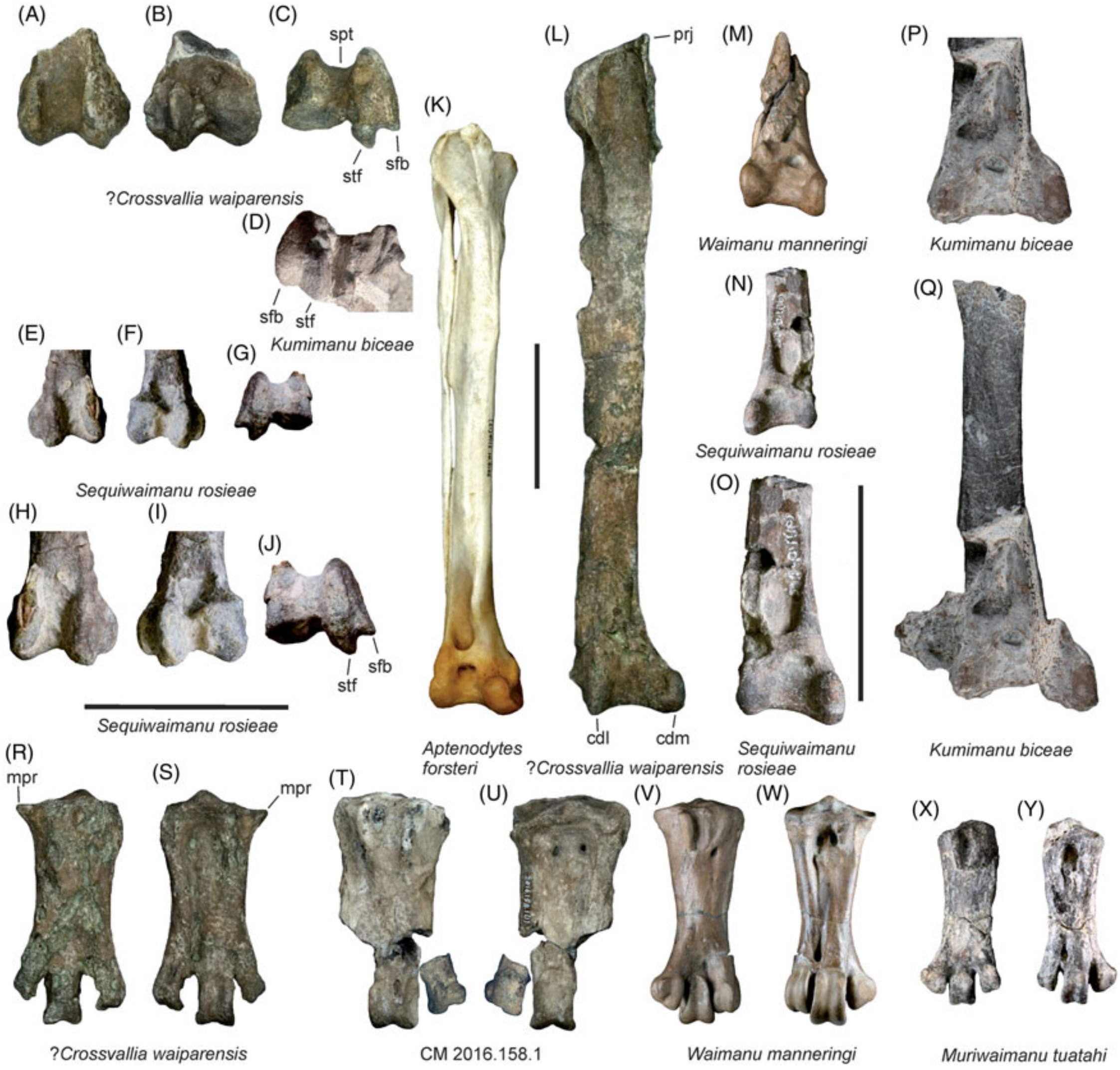
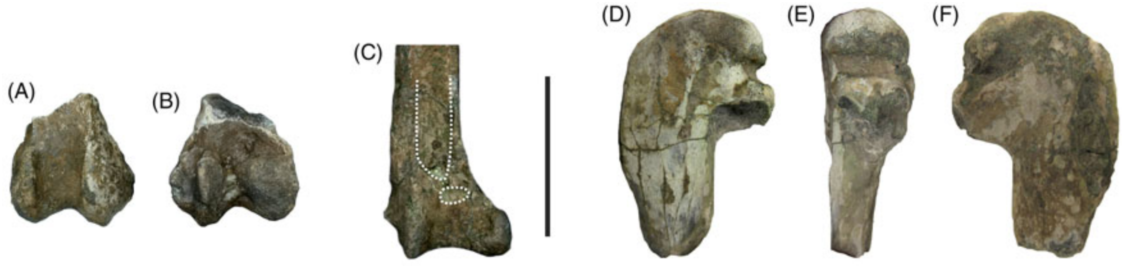


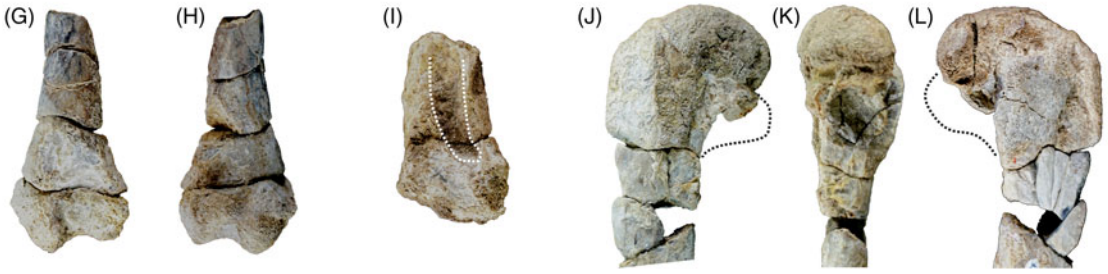
Fig. 2. ?*Crossvallia waiparensis*, sp. nov. from the Waipara Greensand, bones of the holotype (CM 2018.23.9) in comparison with the extant Emperor penguin (*Aptenodytes forsteri*) and other penguins from the Paleocene of New Zealand. **A–C**, ?*C. waiparensis* (holotype), distal end of left femur in cranial (**A**), caudal (**B**), and distal (**C**) view. **D**, *Kumimanu biceae* (holotype, NMNZ S.45877), distal end of right femur in distal view (some surrounding matrix digitally removed). **E–J**, *Sequiwaimanu rosieae* (holotype, CM 2016.6.1), distal end of right femur in cranial (**E**, **H**), caudal (**F**, **I**) and distal (**G**, **J**) view; in **H–J**, the bones are mirrored and brought to the same size as the ?*C. waiparensis* femur. **K**, Tibiotarsus of *Aptenodytes forsteri* in cranial view (left side, mirrored). **L**, ?*C. waiparensis* (holotype), right tibiotarsus in cranial view. **M**, Distal end of right tibiotarsus of *Waimanu manneringi* (holotype, CM zfa 35) in cranial view. **N**, **O**, Distal end of left tibiotarsus of *S. rosieae* (holotype, CM 2016.6.1) in cranial view; in **O**, the bone is mirrored and brought to the same size as the ?*C. waiparensis* tibiotarsus. **P**, **Q**, Partial right tibiotarsus of *K. biceae* (holotype, NMNZ S.45877) in cranial view; in **P**, the condylus medialis was digitally brought in its presumed original position and adhering bone fragments and matrix were digitally removed. **R**, **S**, ?*C. waiparensis* (holotype), right tarsometatarsus in plantar (**R**) and dorsal (**S**) view. **T**, **U**, Partial left tarsometatarsus of an unnamed very large penguin from the Waipara Greensand (CM 2016.158.1) in plantar (**T**) and dorsal (**U**) view. **V**, **W**, Right tarsometatarsus of *W. manneringi* (holotype, CM zfa 35) in plantar (**V**) and dorsal (**W**) view. **X**, **Y**, Right tarsometatarsus of *Muriwaimanu tuatahi* (CM zfa 34) in plantar (**X**) and dorsal (**Y**) view. Abbreviations: cdl, condylus lateralis; cdm, condylus medialis; mpr, medial projection of proximal tarsometatarsus; prj, proximal projection of crista patellaris; sfb, semicondylus fibularis; spt, sulcus patellaris; stf, semicondylus tibiofibularis. Scale bars = 50 mm; same scale for all figure panels except **H–J** and **O**. [Colour online].

morphological comparisons are not possible owing to the very poor preservation of the bone in the *C. unienwillia* holotype (Fig. 3G, H).

The tarsometatarsus (Fig. 1I–K) has a proportionally wider shaft than the tarsometatarsi of *Waimanu manneringi* and *Muriwaimanu tuatahi* (tarsometatarsi of *Sequiwaimanu rosieae*, *Kumimanu biceae* and *Crossvallia unienwillia* are unknown). Of giant Eocene stem group Sphenisciformes, only few associated limb bones of single individuals are known, and compared with *Anthropornis* and *Palaeeudyptes* (Jadwiszczak 2012), ?*C. waiparensis* has a proportionally longer tarsometatarsus. The proximal end of the bone is characterized by a distinct medial projection formed by the cotyla medialis, which corresponds to the medially projected condylus medialis of the tibiotarsus. The hypotarsus is badly damaged, but it can still be seen that it is proximodistally longer than in *Waimanu manneringi* and *Muriwaimanu tuatahi*. The foramina vascularia proximalia are of equal size. Owing to the fact



?Crossvallia waiparensis



Crossvallia unienwillia

Fig. 3. **A–C**, Holotype (CM 2018.23.9) and **D–F**, tentatively referred proximal humerus (CM 2016.158.3) of ?*Crossvallia waiparensis*, sp. nov. from the Waipara Greensand in New Zealand, in comparison with **G–L**, the holotype of *Crossvallia unienwillia* (MLP 00-I-10-1) from the Thanetian of Antarctica. **A**, **B**, Distal end of left femur in cranial (**A**) and caudal (**B**) view. **C**, Distal end of right tibiotarsus in cranial view; the dotted line indicates the sulcus extensorius. **D–F**, Proximal end of tentatively referred left humerus in caudal (**D**), ventral (**E**) and cranial (**F**) view. **G**, **H**, Distal end of right femur in cranial (**G**) and caudal (**H**) view. **I**, Distal end of right tibiotarsus in cranial view; the dotted line indicates the sulcus extensorius. **J–L**, Proximal end of left humerus in caudal (**J**), ventral (**K**) and cranial (**L**) view; the dotted lines indicate the broken portion of the bone. Scale bar = 50 mm. [Colour online].

that the medial hypotarsal crest is broken, it can not be discerned whether there was a single plantar openings for the medial proximal vascular foramen, as in most Sphenisciformes, or whether this foramen opened into two plantar foramina, which is the case in the tarsometatarsus of the large, unnamed sphenisciform from the Waipara Greensand described by Mayr *et al.* (2017b). A foramen vasculare distale is present, and there is also a canalis interosseus distalis. The trochleae are damaged and the incisurae intertrochleares therefore appear wider than they were originally. The trochlea metatarsi II seems unusually small, but this impression is in part caused by the fact that the plantar portion of the trochlea is broken and missing. In distal view, the trochlea metatarsi III is about as deep in dorsoplantar direction as it is wide mediolaterally. As in *Waimanu* and *Muriwaimanu*, the trochlea metatarsi IV is more laterally projected than in post-Paleocene Sphenisciformes.

The single pedal phalanx preserved in the holotype (Fig. 1L) has an asymmetric proximal end. Judging from the latter feature and the length of the bone, it presumably represents the first phalanx of the second toe.

The leg bones of the holotype exhibit some damage, which we attribute to the activity of marine scavengers. Possible boring holes of invertebrates are found on the plantar surface of tarsometatarsus and the caudal surfaces of the right and left tibiotarsi. Similar structures are also known from other avian remains from Paleogene deep sea strata (e.g., Ksepka *et al.* 2012, fig. 4; Mayr *et al.* 2015).

The proximal humeri CM 2016.158.3 and CM 2016.158.2 are tentatively referred to ?*C. waiparensis* based on their matching size. Because CM 2016.158.2 is fragmentary and poorly preserved, the following description refers to the well-preserved specimen CM 2016.158.3 (Fig. 1M–O). In size and morphology, this fossil resembles the poorly preserved proximal humerus of *Crossvallia unienwillia* (Fig. 3J–L) from which it differs in a somewhat smaller caput humeri and a somewhat less marked fossa at the insertion site of musculus coracobrachialis cranialis (Jadwiszczak *et al.* 2013). In concordance with other Sphenisciformes, the insertion scar of musculus supracoracoideus (crista musculi supracoracoidei; Fig. 1M), on the caudal surface of the bone, is markedly elongated. As in *Sequiwaimanu*, *Kumimanu*, *Muriwaimanu* and *Kaiika*, this scar is raised, whereas it is flat in other stem group Sphenisciformes. As in other Paleocene stem group Sphenisciformes, the crista musculi supracoracoidei reaches distally only to the level of the midsection of the fossa pneumotricipitalis and it is therefore not as long as in other stem group Sphenisciformes, such as the early Eocene *Kaiika* (Fordyce & Thomas 2011) and the middle Eocene *Perudyptes* (Ksepka & Clarke 2010). CM 2016.158.3 differs from the humerus of *Sequiwaimanu* in that the caput humeri does not exhibit a distally protruding projection and in that the crista bicipitalis is shorter and runs more perpendicular to the longitudinal axis of the bones. It is distinguished from the larger humerus of *Kumimanu biceae* in the proximodistally longer ventral section of the proximal end.

CM 2016.158.3 differs from the much smaller humerus of *Muriwaimanu tuatahi* in that there is no marked notch between the crista bicipitalis and the tuberculum ventrale, the crista bicipitalis does not form a marked convexity, the sulcus transversus is narrower, the proximodorsal margin of the humerus has a convex profile (more angled in *M. tuatahi*), and the crista musculi supracoracoidei is not strongly projected. As in *C. unienwillia* and *Kaiika*, the proximodorsal margin of the bone, i.e., the section from the crista deltopectoralis to the caput humeri, has a convex profile, whereas it is more angled, with a more proximally situated and more prominent crista musculi supracoracoidei, in many geologically younger stem group Sphenisciformes (e.g., *Inkayacu*, *Kairuku*; Clarke *et al.* 2010, Ksepka *et al.* 2012). CM 2016.158.3 is, however, distinguished from the proximal humerus of *Kaiika* in that the crista bicipitalis does not form a marked convexity. In agreement with other very large stem group Sphenisciformes, there is no distinct second fossa pneumotricipitalis. On the cranial surface of the bone, the fossa for the insertion of musculus deltopectoralis is not as deep and sharply delimited as in many post-Eocene stem group Sphenisciformes. Unlike in *Inkayacu*, *Platydyptes* and *Palaeeudyptes*, a well-developed sulcus for the coracobrachialis nerve is absent (Chávez Hoffmeister 2014, character 24). The shaft of the bone is dorsoventrally narrower than in many other stem group Sphenisciformes (the humerus is particularly stout in the very large-sized taxa *Anthropornis* and *Pachydyptes*; Jadwiszczak 2006, Mayr *et al.* 2017b).

Discussion

With a length of 81.1 mm, the tarsometatarsus of ?*Crossvallia waiparensis*, sp. nov. corresponds in size with the tarsometatarsi of *Anthropornis nordenskjoeldi* and *Palaeeudyptes klekowskii*, which are among the largest Eocene stem group Sphenisciformes (Table 1). It is difficult to differentiate ?*C. waiparensis* from the similar-sized *Crossvallia unienwillia* from the Thanetian of Antarctica, owing to the very poor preservation of the holotype and only known specimen of the latter species. In the present study, we pursue a conservative approach and tentatively assign the new species to the taxon *Crossvallia*, even though the distal end of the tibiotarsus of *C. unienwillia* is proportionally narrower relative to the distal end of the femur than that of ?*C. waiparensis*. This classification is only based on overall similarity and the very large size of the new fossil and *C. unienwillia*, but we consider a cautious taxonomic approach more appropriate than the erection of an ill-diagnosed new genus-level taxon.

As detailed in the differential diagnosis, ?*C. waiparensis* is clearly distinguished in size and morphology from other named stem group Sphenisciformes from the Waipara Greensand, that is, *Waimanu manneringi*, *Muriwaimanu tuatahi*, and *Sequiwaimanu rosieae* (the holotype of ?*C. waiparensis* mainly differs from *S. rosieae* in its much larger size, but as noted above, the tentatively referred proximal humeri can be differentiated from the humerus of *S. rosieae* in osteological features).

The new species is the second formally named penguin species from the Paleocene of New Zealand that distinctly exceeds the Emperor penguin (*Aptenodytes forsteri*) in size. The other species, *Kumimanu biceae*, stems from Hampden Beach (Mayr *et al.* 2017c) and represents an even larger species with stouter limb bones. Another very large-sized stem group sphenisciform from the Waipara Greensand is based on a partial tarsometatarsus (CM 2016.158.1) and has not yet been identified to species (Mayr *et al.* 2017b). The tarsometatarsus of ?*Crossvallia waiparensis* differs from this unnamed tarsometatarsus in that the bone is less stout and the medial side of the proximal end forms a distinct projection, and in that the trochlea metatarsi III is less deep in dorsoplantar direction (compare Fig. 1K with Mayr *et al.* 2017b, fig. 1e). The tarsometatarsus of the unnamed, large sphenisciform from the Waipara Greensand described by Mayr *et al.* (2017b) may indicate the presence of another taxon of giant penguins in the Paleocene of New Zealand, but currently it is not possible to differentiate it from *Kumimanu biceae*, of which the tarsometatarsus is unknown. Even though we can not definitely exclude the possibility that the proximal humeri CM 2016.158.3 and CM 2016.158.2 are from the same species as the tarsometatarsus CM 2016.158.1, we consider it more likely that they belong to ?*C. waiparensis*, which has a more slender tarsometatarsus indicating a less robustly built bird.

?*C. waiparensis* and the unidentified species to which the just mentioned partial tarsometatarsus from the Waipara Greensand (CM 2016.158.1) belongs are the oldest of the giant early Cenozoic penguins known to date. Like all other penguins from the Waipara Greensand, ?*C. waiparensis* is a very archaic stem group representative of the Sphenisciformes, which is distinguished from geologically younger species in a number of plesiomorphic features. This is particularly true for the distal end of the tibiotarsus, which has more widely separated condyli, a more medially protruding condylus medialis and a more medially situated sulcus extensorius than the distal tibiotarsus of post-Paleocene Sphenisciformes. The tarsometatarsus likewise differs from the corresponding bone of geologically younger Sphenisciformes in the shape of the trochlea metatarsi IV, which is more laterally directed. We consider it possible that these differences indicate disparate locomotory characteristics, and the feet of Paleocene stem group Sphenisciformes may have either played a greater role in subaquatic locomotion, or these

Table 1. Measurements (in millimetres) of selected bones of ?*Crossvallia waiparensis*, sp. nov. in comparison with other giant penguins and the largest extant species, the Emperor penguin (*Aptenodytes forsteri*). The humerus is only tentatively referred to ?C. *waiparensis*, sp. nov.

	Humerus, proximal width	Femur, distal width	Tibiotarsus, length	Tibiotarsus, distal width	Tarsometatarsus, length
?*Crossvallia waiparensis*, sp. nov.	48.5	38.2	237/229	21.4/33.8	81.1
Crossvallia unienwillia	∼53[a]	35.7[a]	–	35.7[a]	–
unnamed giant Waipara penguin (CM 2016.158.1)	–	–	–	–	81.6[b]
Kumimanu biceae	75.0[c]	–	>151.3[c]	∼48[c] [reconstr.]	–
Palaeeudyptes klekowskii	44.7[d]	–	235[e]	34.7[e]	66.6–91.3[f,g]
Palaeeudyptes gunnari	42.6[d]	–	224[e]	28.8–30.0[e]	59.0–64.5[f]
Palaeeudyptes marplesi	–	–	–	–	
Kairuku grebneffi (holotype)	55.5[h]	42.3[h]	244.0[h]	∼40.6[h]	67.6[h]
Kairuku waitaki (holotype)	∼48.1[h]	42.4[h]	–	∼42.8[h]	63.6[h]
Pachydyptes ponderosus	68.2[d]	–	–	–	–
Inkayacu paracasensis	–	47.3[i]	244.0[i]	–	76.3[i]
Icadyptes salasi	61.7[j]	–	–	–	–
Anthropornis nordenskjoeldi	∼57[d]	46.6[e]	–	44.7[e]	81.4–88.1[f]
Anthropornis grandis	–	–	–	–	74.7–78.7[f]
Archaeospheniscus wimani	–	27.7[e]	211[e]	–	45.5–>52.6[f]
Aptenodytes forsteri	39.2–40.0[k]	31.6–32.0[k]	28.0–29.7[k]	28.0–29.7[k]	43.7–46.0[k]

[a] After Jadwiszczak *et al.* (2013).
[b] After Mayr *et al.* (2017b).
[c] After Mayr *et al.* (2017c); note that the proximal humerus width in table 1 of the latter reference is erroneous, the correct measurement was given in the text.
[d] After Mayr *et al.* (2017c: table 1).
[e] After Jadwiszczak (2006).
[f] After Myrcha *et al.* (2002).
[g] After Acosta Hospitaleche (2014).
[h] After Ksepka *et al.* (2012).
[i] After Clarke *et al.* (2010).
[j] After Ksepka *et al.* (2008).
[k] After Stephan (1979).

archaic stem group representatives were not yet adapted to an upright stance in a similar manner to geologically younger penguins (Mayr *et al.* 2017a, b).

Altogether, five species of differently sized stem group Sphenisciformes have now been reported from the Waipara Greensand, with a few more still awaiting their description. The species-level diversity of penguins in the Paleocene of New Zealand therefore probably approached that of the stem group Sphenisciformes from the Eocene of Seymour Island (Antarctica), from where ten species are currently known (Mayr 2009, Ksepka & Ando 2011). Accordingly, there seems to have been a radiation of penguins in the earliest Cenozoic, which resulted in high numbers of species that coexisted in geographically restricted areas. The formation of different size classes may have been fostered by niche segregation, and competition at breeding sites may have played an important role.

The fossils from the Waipara Greensand and Hampden Beach document that penguins attained a giant size very early in their evolution. A very large size evolved independently several times within stem group Sphenisciformes (Mayr *et al.* 2017c) and is likely to have been due to inter- and intraspecific competition for breeding sites and food resources on land and in the sea. Whereas competition with other penguins certainly played a major role in the attainment of a giant size, the extinction of very large-sized penguins was probably due to competition with marine mammals (Simpson 1975, Ando & Fordyce 2014, Mayr *et al.* 2017c).

Acknowledgements

VDP and RPS thank Carolina Acosta Hospitaleche, Martin de los Reyes and Nadia Haidr for providing access to the *Crossvallia unienwillia* holotype in the Museo de La Plata. Comments from two anonymous reviewers improved the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

The study was partly supported by a grant to VDP, RPS and, and GM from the Marsden Fund Council from Government funding, managed by Royal Society Te Apārangi.

ORCID

Gerald Mayr http://orcid.org/0000-0001-9808-748X
Vanesa L. De Pietri http://orcid.org/0000-0002-3786-9741
R. Paul Scofield http://orcid.org/0000-0002-7510-6980

References

Acosta Hospitaleche, C., 2014. New giant penguin bones from Antarctica: systematic and paleobiological significance. *Comptes Rendus Palevol 13*, 555–560.

Ando, T. & Fordyce, R.E., 2014. Evolutionary drivers for flightless, wing-propelled divers in the Northern and Southern Hemispheres. *Palaeogeography, Palaeoclimatology, Palaeoecology 400*, 50–61.

Baumel, J.J. & Witmer, L.M., 1993. Osteologia. In *Handbook of Avian Anatomy: Nomina Anatomica Avium*, 2nd edition. Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E. & Vanden Berge, J.C., eds, Publications of the Nuttall Ornithological Club, Cambridge, Massachusetts, 23, 45–132.

Chávez Hoffmeister, M., 2014. Phylogenetic characters in the humerus and tarsometatarsus of penguins. *Polish Polar Research 35*, 469–496.

Clarke, J.A., Ksepka, D.T., Salas-Gismondi, R., Altamirano, A.J., Shawkey, M.D., D'Alba, L., Vinther, J., DeVries, T.J. & Baby, P., 2010. Fossil evidence for evolution of the shape and color of penguin feathers. *Science 330*, 954–957.

Elzanowski, A., 2008. The avian femur: morphology and terminology of the lateral condyle. *Oryctos 7*, 1–5.

Fordyce, R.E. & Jones, C.M., 1986. The world's oldest penguin? *Geological Society of New Zealand Newsletter 74*, 56–57.

Fordyce, R.E. & Thomas, D.B., 2011. *Kaiika maxwelli*, a new Early Eocene archaic penguin (Sphenisciformes, Aves) from Waihao Valley, South Canterbury, New Zealand. *New Zealand Journal of Geology and Geophysics 54*, 43–51.

Jadwiszczak, P., 2006. Eocene penguins of Seymour Island, Antarctica: taxonomy. *Polish Polar Research 27*, 3–62.

Jadwiszczak, P., 2012. Partial limb skeleton of a 'giant penguin' *Anthropornis* from the Eocene of Antarctic Peninsula. *Polish Polar Research 33*, 259–274.

Jadwiszczak, P., Acosta Hospitaleche, C. & Reguero, M., 2013. Redescription of *Crossvallia unienwillia*: the only Paleocene Antarctic penguin. *Ameghiniana 50*, 545–553.

Ksepka, D.T. & Ando, T., 2011. Penguins past, present, and future: Trends in the evolution of the Sphenisciformes. In *Living Dinosaurs. The Evolutionary History of Modern Birds*. Dyke, G. & Kaiser, G., eds, John Wiley and Sons, Chichester, 155–186.

Ksepka, D.T. & Clarke, J.A., 2010. The basal penguin (Aves: Sphenisciformes) *Perudyptes devriesi* and a phylogenetic evaluation of the penguin fossil record. *Bulletin of the American Museum of Natural History 337*, 1–77.

Ksepka, D.T., Clarke, J.A., DeVries, T.J. & Urbina, M., 2008. Osteology of *Icadyptes salasi*, a giant penguin from the Eocene of Peru. *Journal of Anatomy 213*, 131–147.

Ksepka, D.T., Fordyce, R.E., Ando, T. & Jones, C.M., 2012. New fossil penguins (Aves, Sphenisciformes) from the Oligocene of New Zealand reveal the skeletal plan of stem penguins. *Journal of Vertebrate Paleontology 32*, 235–254.

Mayr, G., 2009. *Paleogene Fossil Birds*. Springer, Heidelberg, 262 pp.

Mayr, G., 2017. *Avian Evolution: The Fossil Record of Birds and Its Paleobiological Significance*. Wiley-Blackwell, Chichester, 293 pp.

Mayr, G., Goedert, J.L. & Vogel, O., 2015. Oligocene plotopterid skulls from western North America and their bearing on the phylogenetic affinities of these penguin-like seabirds. *Journal of Vertebrate Paleontology 35*, e943764.

Mayr, G., De Pietri, V.L., Love, L., Mannering, A.A. & Scofield, R.P., 2017a. A well-preserved new mid-Paleocene penguin (Aves, Sphenisciformes) from the Waipara Greensand in New Zealand. *Journal of Vertebrate Paleontology 37*, e139816915.

Mayr, G., De Pietri, V.L. & Scofield, R.P., 2017b. A new fossil from the mid-Paleocene of New Zealand reveals an unexpected diversity of world's oldest penguins. *The Science of Nature 104*, 9.

Mayr, G., Scofield, R.P., De Pietri, V.L. & Tennyson, A.J.D., 2017c. A Paleocene penguin from New Zealand substantiates multiple origins of gigantism in fossil Sphenisciformes. *Nature Communications 8*, 1927.

Mayr, G., De Pietri, V.L., Love, L., Mannering, A.A. & Scofield, R.P., in press. Oldest, smallest, and phylogenetically most basal pelagornithid, from the early Paleocene of New Zealand, sheds light on the evolutionary history of the largest flying birds. *Papers in Palaeontology*.

Myrcha, A., Jadwiszczak, P., Tambussi, C.P., Noriega, J.I., Gazdzicki, A., Tatur, A. & Del Valle, R., 2002. Taxonomic revision of Eocene Antarctic penguins based on tarsometatarsal morphology. *Polish Polar Research 23*, 5–46.

Simpson, G.G., 1971. Review of fossil penguins from Seymour Island. *Proceedings of the Royal Society of London, Series B, Biological Sciences 178*, 357–387.

Simpson, G.G., 1975. *Fossil penguins*. In *The Biology of Penguins*. Stonehouse, B., ed., The Macmillan Press, London, 19–41.

Slack, K.E., Jones, C.M., Ando, T., Harrison, G.L., Fordyce, R.E., Arnason, U. & Penny, D., 2006. Early penguin fossils, plus mitochondrial genomes, calibrate avian evolution. *Molecular Biology and Evolution 23*, 1144–1155.

Stephan, B., 1979. Vergleichende Osteologie der Pinguine. *Mitteilungen des Zoologischen Museums in Berlin 55, Supplement Annalen für Ornithologie 3*, 3–98.

Tambussi, C.P., Reguero, M.A., Marenssi, S.A. & Santillana, S.N., 2005. *Crossvallia unienwillia*, a new Spheniscidae (Sphenisciformes, Aves) from the late Paleocene of Antarctica. *Geobios 38*, 667–675.