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### New fossil penguins (Aves, Sphenisciformes) from the Oligocene of New Zealand reveal the skeletal plan of stem penguins

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## NEW FOSSIL PENGUINS (AVES, SPHENISCIFORMES) FROM THE OLIGOCENE OF NEW ZEALAND REVEAL THE SKELETAL PLAN OF STEM PENGUINS

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**ABSTRACT**—Three skeletons collected from the late Oligocene Kokoamu Greensand of New Zealand are among the most complete Paleogene penguins known. These specimens, described here as *Kairuku waitaki*, gen. et sp. nov., and *Kairuku grebneffi*, sp. nov., reveal new details of key elements of the stem penguin skeleton associated with underwater flight, including the sternum, flipper, and pygostyle. Relative proportions of the trunk, flippers, and hind limbs can now be determined from a single individual for the first time, offering insight into the body plan of stem penguins and improved constraints on size estimates for ‘giant’ taxa. *Kairuku* is characterized by an elongate, narrow sternum, a short and flared coracoid, an elongate narrow flipper, and a robust hind limb. The pygostyle of *Kairuku* lacks the derived triangular cross-section seen in extant penguins, suggesting that the rectrices attached in a more typical avian pattern and the tail may have lacked the propping function utilized by living penguins. New materials described here, along with re-study of previously described specimens, resolve several long-standing phylogenetic, biogeographic, and taxonomic issues stemming from the inadequate comparative material of several of the first-named fossil penguin species. An array of partial associated skeletons from the Eocene–Oligocene of New Zealand historically referred to *Palaeudyptes antarcticus* or *Palaeudyptes* sp. are recognized as at least five distinct species: *Palaeudyptes antarcticus*, *Palaeudyptes marplesii*, *Kairuku waitaki*, *Kairuku grebneffi*, and an unnamed Burnside Formation species.

### INTRODUCTION

Fossil penguins have long been of interest to paleontologists and the general public for their unique morphology, Austral distribution, and the ‘giant’ size attained by many species (Simpson, 1976; Fordyce and Jones, 1990; Jadwiszczak, 2009; Ksepka and Ando, 2011). Despite the discovery of thousands of individual fossils of these flightless marine birds, there has long been little direct evidence of the overall body plan of Paleogene penguins due to a scarcity of complete remains. This situation has improved with recent descriptions of associated skulls and postcranial material (Slack et al., 2006; Clarke et al., 2007, 2010; Ksepka et al., 2008; Ksepka and Clarke, 2010). Still, no Paleogene specimen preserving the trunk, hind limb, and forelimb of a single individual has previously been reported, and some parts of the skeleton have remained completely unknown. Thus standing height, proportions, and wingspan in stem Sphenisciformes have remained poorly constrained, hampering understanding of functional complexes and lifestyles. Here, we describe three associated skeletons from two new species that offer the first data on many key areas of skeletal anatomy.

New Zealand has the highest diversity of living penguins, and the continually expanding fossil record indicates a high level of penguin diversity throughout most, if not all, of the Cenozoic, with 19 formally named species (including those described here) and at least two distinct undescribed species reported to date (Fordyce and Thomas, 2011; Ksepka and Ando, 2011). Of note are the first-named fossil penguin, *Palaeudyptes antarcticus*

Huxley, 1859, and the oldest named penguin, *Waimanu manneringi* Jones, Ando, and Fordyce, in Slack et al., 2006. New Zealand fossil penguin records now span all Cenozoic epochs, and substantial subfossil material is also known (e.g., Worthy, 1997).

Huxley (1859:675) first reported a fossil penguin more than 150 years ago, based on an incomplete tarsometatarsus (Fig. 7Q–R) from North Otago, New Zealand, that was “found by a native in the limestone of Kakaunui [sic], and was brought to Mr. Mantell imbedded to some extent in a matrix which was readily recognizable as that particular limestone.” The single bone became the holotype for Huxley’s species *Palaeudyptes antarcticus*. This early report had profound and perhaps unintended consequences on the later study of fossil penguins. Largely due to historical priority, and often with little justification, many fossils were later referred to *Palaeudyptes antarcticus*. Furthermore, because a tarsometatarsus was the first penguin fossil to be described, this element was ascribed privileged status both in terms of frequent designation of isolated tarsometatarsi as holotypes for new species, and in estimating relationships between fossil taxa (until recently, in a non-cladistic framework). Basic information on the holotype of *Palaeudyptes antarcticus* has long remained lacking—it has not previously been scored as a single terminal in a published phylogenetic analysis, and the identity of the “particular limestone” of Huxley (1859:675) has been uncertain (Simpson, 1946, 1971). Based on visits to candidate localities, we now have little doubt as to the age and horizon of the holotype. The only limestone at or near Kakanui whence a penguin fossil might be recovered in a matrix sufficiently soft to separate cleanly from the bone is the Ototara Limestone (sensu Edwards, 1991). This unit at Kakanui spans latest Eocene (Runangan Stage) to earliest Oligocene (Whaingaroan Stage) beds, of which soft

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TABLE 1. Revised status of New Zealand specimens previously assigned to *Palaeudyptes antarcticus*.

Specimen	Material	Formation	Locality	Age	Marples (1952)	Simpson (1971)	Present study
NHMUK A1048	Tarsometatarsus	Ototara Limestone	Kakanui	earliest Oligocene	<i>Palaeudyptes antarcticus</i> (holotype)	<i>Palaeudyptes antarcticus</i> (holotype)	<i>Palaeudyptes antarcticus</i> (holotype)
OM GL430 (C47:17)	Tarsometatarsus (1)	Burnside Formation	Burnside Quarry	late Eocene	cf. <i>Palaeudyptes antarcticus</i>	<i>Palaeudyptes</i> sp.	<i>Palaeudyptes antarcticus</i>
OM GL429 (C50:25–47)	Vertebrae, hind limb elements	Burnside Formation	Burnside Quarry	late Eocene	<i>Palaeudyptes antarcticus</i>	<i>Palaeudyptes marplei</i> (holotype)	<i>Palaeudyptes marplei</i> (holotype)
OM GL435 (C48:73–81)	Partial forelimb and hind limb	Burnside Formation	Burnside Quarry	late Eocene	<i>Palaeudyptes antarcticus</i>	<i>Palaeudyptes</i> sp.	Unnamed species (Burnside Formation taxon)
OU 12652	Partial skeleton	Kokoamu Greensand	Waihao River	late Oligocene	—	—	<i>Kairuku waitaki</i> (holotype)
OU 22094	Partial skeleton	Kokoamu Greensand	Duntroon	late Oligocene	—	—	<i>Kairuku grebneffi</i> (holotype)
OU 22065	Partial skeleton	Kokoamu Greensand	Waihao River	late Oligocene	—	—	<i>Kairuku grebneffi</i>
OM GL1593 (C47:22) (D.P.3)	Partial skeleton	Kokoamu Greensand	Duntroon	late Oligocene	<i>Palaeudyptes antarcticus</i>	<i>Palaeudyptes</i> sp.	<i>Kairuku</i> sp.
OM GL427 (OM C47:23) (D.P.4)	Partial skeleton	Kokoamu Greensand	Duntroon	late Oligocene	<i>Palaeudyptes antarcticus</i>	<i>Palaeudyptes</i> sp.	<i>Kairuku</i> sp.
OM GL 432 (C47:25) (D.P.6)	Vertebra and pectoral elements	Kokoamu Greensand	Duntroon	late Oligocene	<i>Palaeudyptes antarcticus</i>	<i>Palaeudyptes</i> sp.	<i>Kairuku</i> sp.
OU 22168	Humerus, distal ulna	Kokoamu Greensand	Kokoamu Cliffs	late Oligocene	—	—	<i>Kairuku</i> sp.
OU 22353	Partial skull and skeleton	Kokoamu Greensand	Awamoko Stream	late Oligocene	—	—	<i>Kairuku</i> sp. (juvenile)
OM GL1680 (C47:24) (D.P.5)	Partial wing, fragmentary coracoid (2)	Kokoamu Greensand	Duntroon	late Oligocene	<i>Palaeudyptes antarcticus</i>	<i>Palaeudyptes</i> sp.	cf. <i>Kairuku</i>
OM GL1601 (OM C:47:34) (G.47.1)	Coracoid	Kokoamu Greensand	Duntroon	late Oligocene	<i>Palaeudyptes antarcticus</i>	<i>Palaeudyptes</i> sp.	cf. <i>Kairuku</i>
MNZS 1449	Partial skeleton	Uncertain	Seal Rock, Nelson	late Oligocene	<i>Palaeudyptes antarcticus</i>	<i>Palaeudyptes</i> sp.	Sphenisciformes indet.
OM GL431 (OM C47:18)	Partial tarsometatarsus	Burnside Formation (3)	Burnside Quarry	late Eocene	<i>Palaeudyptes antarcticus</i>	<i>Palaeudyptes</i> sp.	Sphenisciformes indet.

OM specimens have been recently renumbered and original “D.P.” and “G” field numbers used by Marples (1952) and “C” museum numbers used by Marples (1952) and Simpson (1971) are also provided to facilitate comparison.

Notes: (1) This partial tarsometatarsus was collected along with several elements including a partial humerus and femur. Simpson (1971) observed that these materials probably do not represent a single taxon and we refer only the tarsometatarsus to cf. *P. antarcticus*, considering other elements Sphenisciformes indet. (2) These specimens could not be located in the OM collections and may be lost (see Jones, 1995). We relied on descriptions and figures of Marples (1952) for evaluation. (3) These specimens were collected from the Concord Greensand but are probably reworked from the underlying Burnside Marlstone (Marples, 1952; Simpson, 1971).

bioclastic bryozoan calcarenite from the upper (Whaingaroan) section seems the most probable source. No datable amounts of matrix remain on the holotype, precluding further refinement of age.

Long after the work of Huxley (1859) and Hector (1872a), field work and study by B. J. Marples resulted in the first synthesis of fossil penguins from New Zealand. Marples' (1952) treatise provided one of the most detailed comparative treatments of penguin anatomy. Marples considered 38 Eocene and Oligocene specimens, including several revisited here. Marples (1952, 1953, 1960) first detailed many aspects of archaic penguin morphology, which remain at the core of recent morphological data matrices for penguin phylogeny. Yet, a complete picture of the skeleton in early penguins has remained elusive, and many aspects of the evolutionary relationships and taxonomy of the New Zealand taxa have remained unresolved.

Marples (1952) used taxonomic names conservatively; he assigned 11 specimens spanning ~10 Ma, and a wide range of size and morphological variation, to *Palaeudyptes antarcticus*

(Table 1). Brodkorb (1963) later referred two of Marples' specimens from the Eocene Burnside Formation to a new species, *Palaeudyptes marplei* Brodkorb, 1963, but retained Marples' other specimens in *P. antarcticus*. Simpson (1971), however, identified only the holotypes of *Palaeudyptes antarcticus* and *Palaeudyptes marplei* to the species level. Noting morphological differences, problems of non-overlapping sets of elements, and what he considered an unrealistic stratigraphic range for a single species, Simpson (1971) referred all remaining specimens to *Palaeudyptes* sp.

Later research has shown that the New Zealand “*Palaeudyptes*” specimens do not belong to monophyletic group (Jones, 1995; Clarke et al., 2007; Ksepka and Clarke, 2010), and that taxonomic revision is needed. However, the fragmentary nature of the holotype of *Palaeudyptes antarcticus* and the fact that many of Marples' most complete specimens lack a tarsometatarsus has until now hindered attempts at such work. New discoveries, below, allow many of these issues to finally be resolved.

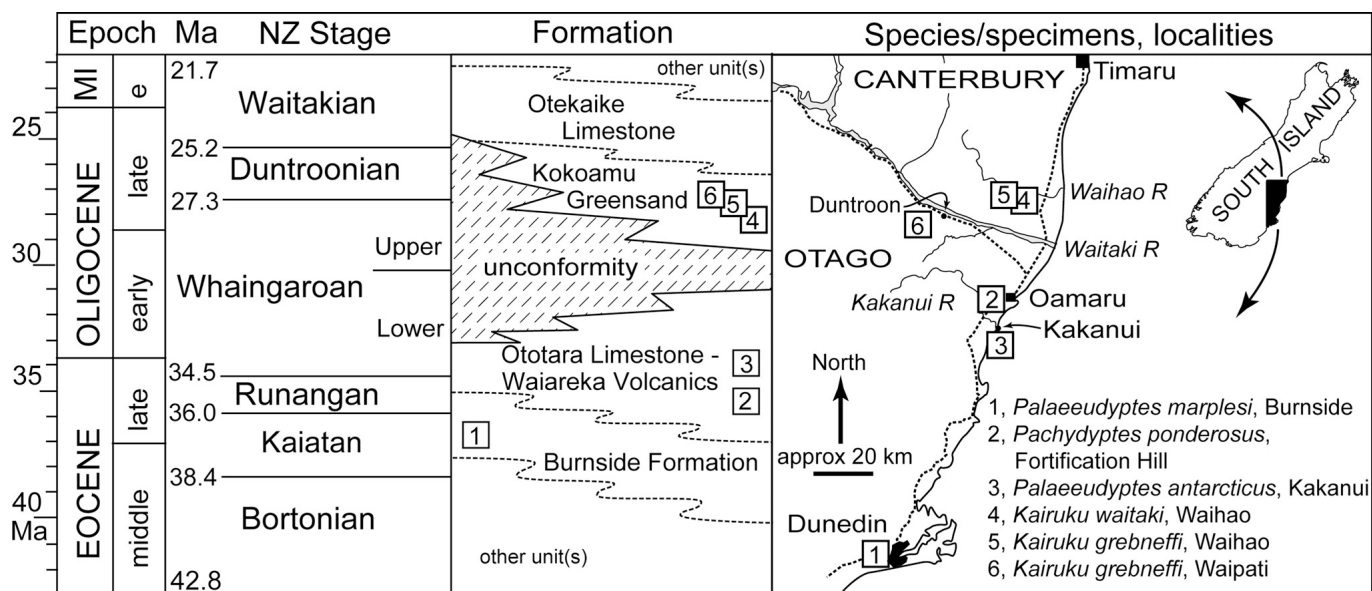


FIGURE 1. Stratigraphy and localities for New Zealand fossil penguins. Chronostratigraphy based on Hornibrook et al. (1989), Cooper (2004), and Hollis et al. (2010).

## GEOLOGICAL CONTEXT

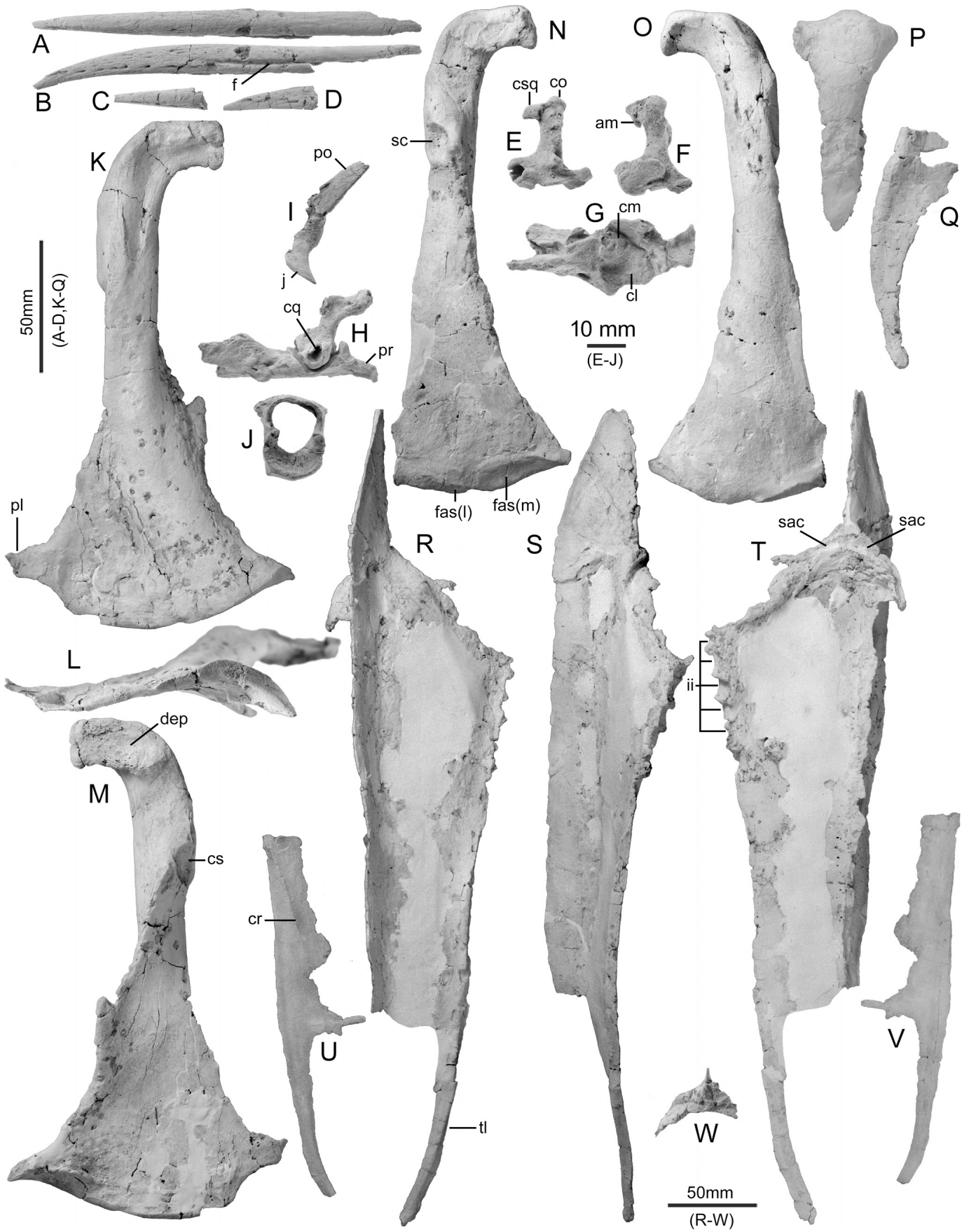
The specimens described here were collected from the late Oligocene Kokoamu Greensand of North Otago and South Canterbury, South Island, New Zealand. We also reference specimens from the Burnside Formation and Ootara Limestone; all units are from the southern Canterbury Basin of eastern South Island (Fig. 1). Formations and localities are reviewed below. Correlations are based on New Zealand stages, as summarized by Cooper (2004). Each fossil has a unique New Zealand Fossil Record Number (e.g., J40/f190), to identify the exact locality and horizon; details are held by the Geosciences Society of New Zealand.

The Burnside Formation (Burnside Mudstone or Burnside Marl of some early workers), at its type locality of Burnside Quarry, is a massive, grey, slightly cemented calcareous mudstone that produces rich foraminiferal microfaunas, occasional macroinvertebrates, and rare vertebrates (Wood, 1968). The formation spans the local upper Bortonian to Runangan Stages (late Eocene) (Wood, 1968). An outer shelf to upper bathyal depositional environment is likely. Rare penguin fossils include a skull (Fordyce, 2003) and a few sets of associated postcranial elements (Marples, 1952; Ando, 2007), including the holotype of *Palaeudyptes marplesi*. One associated specimen (OM GL429) has been referred to (e.g., Ksepka and Clarke, 2010) as the Burnside "*Palaeudyptes*" taxon in anticipation of formal designation of a new species (Ando, 2007). All reported penguin remains from the Burnside Formation (Table 1) are from the Kaiatan (early late Eocene) part of the sequence. In the Dunedin district, the upper contact of the Burnside Formation is unconformable with the Concord Greensand. Penguin fossils are known from the basal Concord Greensand. Some specimens may be reworked from the Burnside Formation (Marples, 1952; Simpson, 1971), but others are probably autochthonous.

In North Otago, the Ootara Limestone overlies the Burnside Formation. The Ootara Limestone comprises soft to cemented, massive to decimeter-bedded (locally centimeter- to millimeter-bedded), bryozoan-dominated bioclastic limestone (packstone to grainstone) with localized brachiopod coquina and oncolite horizons, grading both laterally and vertically into massive to bed-

ded tuffaceous muddy limestone (wackestone) (Edwards, 1991). These deposits represent warm water shoal settings close to small volcanoes, but distant from the coast, adjacent to open water. Most outcrops are at and near the modern North Otago coast. The bryozoan-bioclastic facies has yielded the holotypes of *Palaeudyptes antarcticus* and *Pachydyptes ponderosus* Oliver, 1930, as well as large benthic foraminifera (*Amphistegina*, *Asterigerina*) indicative of shallow warm waters (Finlay, in Marples, 1952). The Ootara Limestone is variably overlain, draping, or intruded by the Eocene/Oligocene submarine (Surtseyan) basaltic Deborah-Waiareka Volcanics (Gage, 1957; Cas et al., 1988; Edwards, 1991). The upper contact is widely unconformable. At Kakanui, the upper Ootara Limestone at Campbell Beach and the Kakanui River mouth is early Oligocene (lower Whaingaroan Stage, *Subbotina angiporoides* zone, 30.1–34.5 Ma) (Hollis et al., 2010). Here, soft bryozoan-bioclastic limestone 3–5 m below the cemented upper contact of the unit separates cleanly from macrofossils, and we consider it the likely source for the *P. antarcticus* holotype. A tuffaceous muddy facies lower in the Ootara Limestone (local Runangan Stage, latest Eocene) located several hundred meters upstream from the Kakanui River mouth is a less likely type horizon due to differences in sedimentary adherence to fossil bone.

All new specimens described here were collected by R.E.F. and assistants from the Kokoamu Greensand (Gage, 1957; Maerewhenua Greensand of Marples, 1952), which overlies and truncates the Ootara Limestone and lateral equivalents. The Kokoamu Greensand is calcareous throughout. At the base, the unit is massive, bioturbated, and muddy, whereas the upper part has a greater component of very fine quartz sand and more calcareous bioclastic sand and is massive to dm- to cm-bedded. Brachiopods and pectinids predominate, along with occasional vertebrate remains, in the upper greensand. In the Duntroon district, the upper greensand (horizon for OU 22094) can be diffusely cm- to dm-bedded, but the occurrence and preservation of fossils is consistent with generally quiet conditions mostly below storm wave base. In the Waihao district, the greensand has a higher component of very fine quartz sand than near Duntroon, and is thicker (15+ m); the lower part is massive and bioturbated (horizon for OU 12652), whereas the upper half



has repeated diffuse dm-bedding with less evident bioturbation (horizon for OU 22065). The scarcity of planktic foraminiferal bioevents in the mid-Oligocene and discontinuous sequences of macroinvertebrates hampers biostratigraphic subdivision of the Kokoamu Greensand; variation in thickness and lack of distinctive marker beds also hamper correlation between outcrops. Nevertheless, the age of the Kokoamu Greensand is well constrained to the local upper Whaingaroan to middle Duntroonian Stages (late Oligocene, 29–30 to 26 Ma; Cooper, 2004) on the basis of planktic and benthic foraminifera (Hornibrook et al., 1989), ostracods (Ayress, 1993), and strontium isotope dates (Graham et al., 2000).

The inferred quiet depositional setting is consistent with the preservation of the new specimens detailed here. For each, all elements were closely associated on a single bedding plane. Size, color, preservation, left-right distribution, lack of duplicated bones, and lack of other penguin fossils nearby indicate that each is a single individual. Some bones show slight burial deformation and evidence of bioerosion. Aside from the new material, the Kokoamu Greensand has yielded the penguins *Archaeospheniscus lowei* Marples, 1952, *Archaeospheniscus lopdelli* Marples, 1952, *Duntroonornis parvus* Marples, 1952, and *Platydyptes novaesealandiae* Oliver, 1930.

**Institutional Abbreviations**—**AMNH**, Department of Ornithology, American Museum of Natural History, New York, U.S.A.; **IB/P/B**, Prof. A. Myrcha University Museum of Nature, University of Bialystok, Bialystok, Poland; **MNZS**, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; **MUSM**, Museum of San Marcos University, Lima, Peru; **NHMUK**, Natural History Museum, London, U.K.; **OM**, Otago Museum, Dunedin, New Zealand; **OU**, Geology Museum, University of Otago, Dunedin, New Zealand; **UCMP**, University of California Paleontology Museum, Berkeley, California, U.S.A.; **UCZ**, Department of Zoology, University of Canterbury, Christchurch, New Zealand.

#### SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758

SPHENISCIFORMES Sharpe, 1891 (sensu Clarke et al., 2003)

*KAIRUKU*, gen. nov.

(Figs. 2–7)

**Diagnosis**—Three apomorphies diagnose *Kairuku*: absence of the crista medialis hypotarsi (present in all other sphenisciforms), medial border of the tibiotarsus strongly convex in distal view, and stout femoral proportions (midshaft width >15% total length). The long, narrow sternum, and flattened, plate-like pygostyle are unique among described species of Sphenisciformes. However, because these elements are unknown in most Paleogene sphenisciforms, the aforementioned features are potentially plesiomorphic and their diagnostic nature remains unverified.

**Age and Range**—Late Whaingaroan and/or early Duntroonian stage—late Oligocene, New Zealand.

**Etymology**—*Kairuku*, diver, with the connotation of returning with food; from the Maori kai (food) plus ruku (dive).

**Type Species**—*Kairuku waitaki*, sp. nov.

**Included Species**—*Kairuku waitaki*, sp. nov., *K. grebneffi*, sp. nov.

**Comment**—Sphenisciformes is used in the sense of Clarke et al. (2003). Spheniscidae is here restricted to crown penguins—the clade formed by the common ancestor of all extant penguins and all of its descendants, following Clarke et al. (2003). *Kairuku*, a stem penguin, is therefore included in Sphenisciformes but excluded from Spheniscidae.

*KAIRUKU WAITAKI*, sp. nov.  
(Figs. 2, 4–7; Table 2)

**Diagnosis**—Wide separation between the processus transversus of the first and second synsacral vertebrae is an autapomorphy of the species. *Kairuku waitaki* further differs from *K. grebneffi* by the downturned tip of the upper beak, patella with more squared femoral articular surface, tarsometatarsus with mediolaterally wider and less dorsoplantarly deep hypotarsus, and more strongly developed medially oriented flange projecting from plantar-medial corner of trochlea metatarsi II.

**Etymology**—*Waitaki*, name of the large river bounding Canterbury and Otago; the northern Maori equivalent is waitangi. Translation: wai, water; tangi or taki, tears.

**Holotype**—OU 12652: Rostral tip of beak (Fig. 2A–B), partial right lacrimal (Fig. 2I), left and right quadrates (Fig. 2E–H), articular portion of mandible (Fig. 2H), atlas (Fig. 2J) and five other cervical vertebrae, four thoracic vertebrae (Fig. 6Q), six ribs and two isolated uncinate processes, nearly complete synsacrum (Fig. 6A–C), five free caudal vertebrae, nearly complete left and right coracoids (Fig. 2N–O), omal portions of left and right scapulae, two fragments of sternum (Fig. 2U–W), proximal two-thirds of left humerus (Fig. 4F–I), sesamoid of m. scapulothoracicus, left radius, badly eroded left ulna, left and right radiales, left ulnare, complete left and proximal right carpometacarpus, complete left and partial right phalanx II-1 (all distal wing elements in Fig. 5I–J), partial left and right ilia (Fig. 6A–C), complete left and right femora (Fig. 6G–H), nearly complete left and proximal end of right tibiotarsi (Fig. 7A), proximal left fibula, left patella (Fig. 6I–J), complete right tarsometatarsus (Fig. 7H–L), and 14 pedal phalanges (Fig. 7H). Collected by R.E.F. in 1977 and R.E.F. and M. A. Fordyce in 1982.

**Locality and Horizon**—Bank of the Waihao River, South Canterbury; near latitude 44°47'S, longitude 170°57'E; New Zealand Fossil Record Number J40/f190. Massive bioturbated beds of lower Kokoamu Greensand, late Whaingaroan or early Duntroonian stage (late Oligocene).

**Measurements**—See Table 2.

**Description**—A few fragments of the cranium are preserved. The beak (Fig. 2A–B) is long and narrow, as in most other stem penguins. The rostral tip resembles that of extant *Aptenodytes* in the moderate ventral deflection and pronounced development of neurovascular foramina. The midline suture between the premaxillae along the internarial bar is obliterated. A narrow lateral furrow, continuous with the nares, fades away before reaching the rostral tip. A similar furrow is present in *Acadlyptes*

← FIGURE 2. *Kairuku* cranial and pectoral elements. *Kairuku waitaki*, gen. et sp. nov., holotype (OU 12652): Tip of beak in **A**, dorsal and **B**, lateral views; **E**, right quadrate in cranial view; **F**, left quadrate in caudal view; articular portion of mandible in **G**, dorsal view and in **H**, lateral view with quadrate in articulation; **I**, right lacrimal in lateral view; **J**, atlas in cranial view; left coracoid in **N**, dorsal and **O**, ventral views; sternal trabecula in **U**, ventral and **V**, dorsal views; **W**, sternal fragment in cranial view. *K. grebneffi*, sp. nov., referred specimen (OU 22065): Tip of beak in **C**, dorsal and **D**, lateral views; right coracoid in **K**, ventral **L**, proximal, and **M**, dorsal views; **P**, omal portion of the scapula; **Q**, omal portion of the furcula; sternum in **R**, ventral, **S**, lateral, and **T**, dorsal views. All specimens coated with sublimed ammonium chloride. **Abbreviations**: **am**, tubercle for m. adductor mandibulae externus pars profunda; **cl**, cotyla lateralis; **cm**, cotyla medialis; **co**, capitulum oticum; **cq**, cotyla quadratojugal; **cr**, crest on sternum; **cs**, cotyla scapularis; **csq**, capitulum squamosum; **dep**, depression on processus acrocoracoideus; **f**, furrow; **fas(l/m)**, facies articularis sternalis (lateral and medial); **j**, articular facet for jugal; **il**, incisurae costalis; **pl**, processus lateralis; **po**, processus orbitalis; **pr**, processus retroarticularis; **sac**, sulcus articularis coracoideus; **tl**, trabecula lateralis.

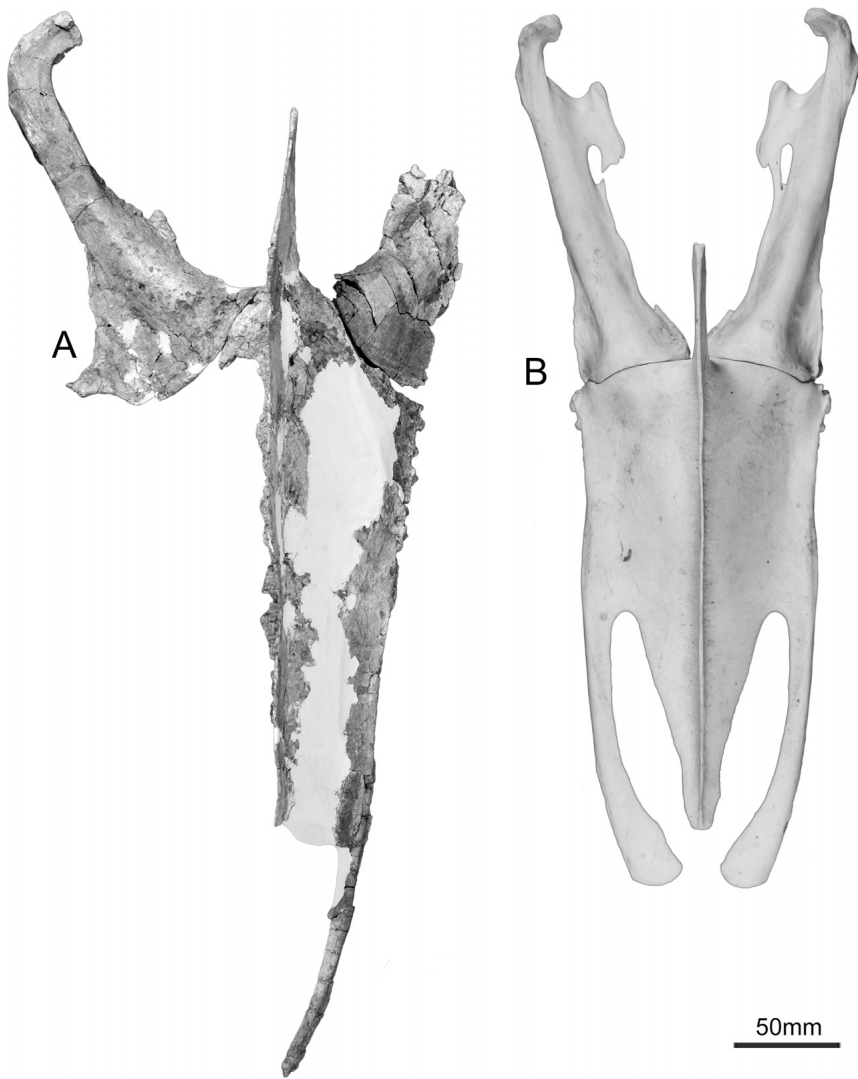


FIGURE 3. Comparison of the sternum and coracoids of **A**, *Kairuku grebneffi*, sp. nov. (OU 22065), and **B**, extant *Aptenodytes forsteri* (UCZ 1054).

*salasi* Clarke et al., 2007, and also occurs in some species of Procellariiformes and ‘Pelecaniformes’ (Clarke et al., 2007; Ksepka et al., 2008). The partial lacrimal (Fig. 2I) preserves a flat, plate-like articular facet for the jugal and the lateral margin of the processus orbitalis. A small roughed surface represents the contact with the frontal, indicating that the lacrimal maintained an open contact with the frontal, as in extant penguins. The degree of projection of the lacrimal lateral to the orbit remains uncertain and whether the descending process was perforated is also uncertain as the medial margin is lacking. The quadrate (Fig. 2E–F) is notably stockier than that of extant penguins; the capitulae, shaft, and condyles are all markedly broader relative to the height of the processus oticus. On the left quadrate, a hook-like process for attachment of the *m. adductor mandibulae pars profunda* projects ventrally from the capitulum squamosum as in other stem penguins (Bertelli et al., 2006), but unlike extant penguins in which the variably developed ridge or tubercle for this insertion remains separate from the capitula. The processus orbitalis of the quadrate is lost.

A fragment of the mandible includes the left articular region (Fig. 2G–H). The orientation and morphology of the mandibular cotylae are similar to those in extant penguins, although the cotyla lateralis is more deeply concave. A well-developed pro-

cessus retroarticularis is present, but its precise shape and also the presence or absence of a processus medialis cannot be verified. A foramen pierces the mandible just anterior to the condylus lateralis, as in other stem penguins but not in extant penguins (Ksepka and Bertelli, 2006). A deep fossa aditus canalis mandibulae is present. Based on intact edges, a moderate-sized fenestra caudalis mandibulae perforated the mandible within this fossa.

Four incomplete thoracic vertebrae are preserved. Judging from extant penguins, these elements include the third and fourth, a vertebra of uncertain position, and the caudal-most thoracic vertebra. The corpus of the presumed third thoracic vertebra shows a transitional articular morphology, with a subheterocoelous facies articularis cranialis and a weakly concave facies articularis caudalis. A cranially placed processus ventralis was originally present, but is broken off at its base. Thoracic vertebra four (Fig. 6Q–S) is weakly opisthocoelous and possesses an unusually wide processus transversus with a squared lateral edge, a squared processus spinosus with a thickened dorsal margin, and a processus ventralis, of which only the broken base remains. The third, fourth, and unlocalized thoracic vertebrae differ from those of crown penguins in that the corpus is more strongly mediolaterally compressed, and the fovea costalis is placed both closer to the base of the processus transversus and further caudally. The

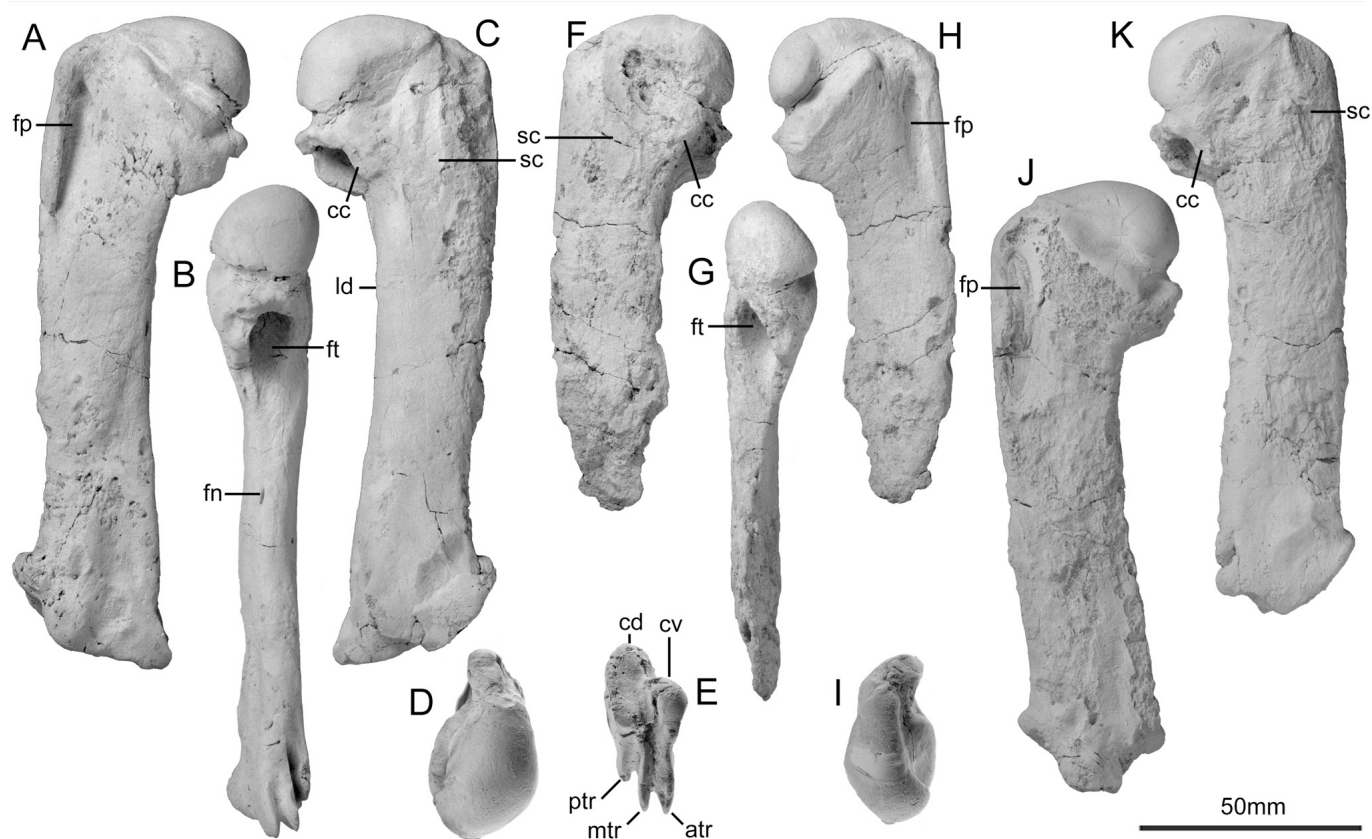


FIGURE 4. Humeri of *Kairuku* species. Humerus of *K. grebneffi*, sp. nov., referred specimen OU 22065 in **A**, cranial, **B**, ventral, **C**, caudal, **D**, proximal, and **E**, distal views. *K. waitaki*, gen. et sp. nov., holotype (OU 12652) in **F**, cranial, **G**, ventral, **H**, caudal, and **I**, proximal views. *K. grebneffi*, sp. nov., holotype (OU 22094) in **J**, cranial and **K**, caudal views. All specimens coated with sublimed ammonium chloride. **Abbreviations:** atr, anterior trochlear ridge; cc, m. coracobrachialis caudalis insertion scar; cd, condylus dorsalis; cv, condylus ventralis; ld, m. longissimus dorsi insertion scar; mtr, medial trochlear ridge; fn, foramen nutricum; fp, fossa for m. pectoralis insertion; ft, fossa tricipitalis; ptr, posterior trochlear ridge; sc, m. supracoracoideus insertion scar.

presumed caudal-most thoracic vertebra lacks a processus ventralis and is deeply opisthocelous. The processus transversus is narrower than in the more anterior vertebrae and tapers to a subtriangular tip. The fovea costalis is located at the cranial margin of the lateral face of the corpus, but is placed closer to the base of the processus transversus than in extant penguins. These morphologies are also present in the presumed caudal-most thoracic vertebra of *Palaeudyptes marplesii* (OM GL429), although the corpus is dorsoventrally taller and craniocaudally shorter in that taxon (possibly due in part to deformation).

Six partial ribs are present and do not differ notably from extant penguin ribs. Two free uncinat processes show strong caudal expansion as in extant penguins.

A nearly complete synsacrum (Fig. 6A–C) has nine discernable incorporated vertebrae; the missing caudal portion would have included several more elements. Although somewhat eroded, the cranial surface of the first synsacral vertebra remains convex. A shallow fovea costalis is developed caudal to the level of the processus transversus. In extant penguins and *Archaeospheniscus lopedelli*, the fovea occurs cranial to this level. Projection of the zygapophysis cranialis of the cranial-most synsacral vertebra is also markedly greater than in extant penguins. Craniocaudal separation between the processus transversus of the first and second synsacral vertebrae is uniquely wide (autapomorphic) compared to other penguins, including *Kairuku grebneffi*, sp. nov. Contacts for the ilium indicate that the synsacrum and ilium remained un-

fused as in all other penguins except for extant *Pygoscelis* (see Clarke et al., 2003). Over the preserved length, the synsacrum is straight, in contrast to extant penguins where the synsacrum is subtly flexed so that the ventral margin is concave. Some degree of flexion may, however, have occurred at the caudal end, which is not preserved. At the cranial end of the synsacrum, the ventral surface is smoothly rounded, again in contrast to extant penguins where the ventral margins of the first few elements form a sharp crest. Caudally, the sulcus ventralis synsacri is slightly deeper than in extant penguins. Few other stem penguin synsacri are known, but an isolated sacrum attributed to *Anthropornis nordenskjoeldii* Wiman, 1905, also lacks a ventral keel (Jadwiszczak and Mörs, 2011), which we interpret as a plesiomorphic feature, and exhibits a pronounced swelling near the cranial tip, which is lacking in *Kairuku*.

Five free caudal vertebrae are preserved and are not in sequence. Thus, directional change in proportions is uncertain. The apex of the processus spinosus is bilobed in intact specimens. The size of the neural canal and processus spinosus vary among the elements, with the canal occupying one-third to one-half of the total height of the arcus vertebrae. Zygapophyses cranialis are reduced, but based on manual articulation probably contacted the adjacent vertebrae. In extant penguins, the zygapophyses cranialis are too widely separated from the adjacent vertebrae to form an articulation. The dorsal surface of each processus transversus is deeply excavated.



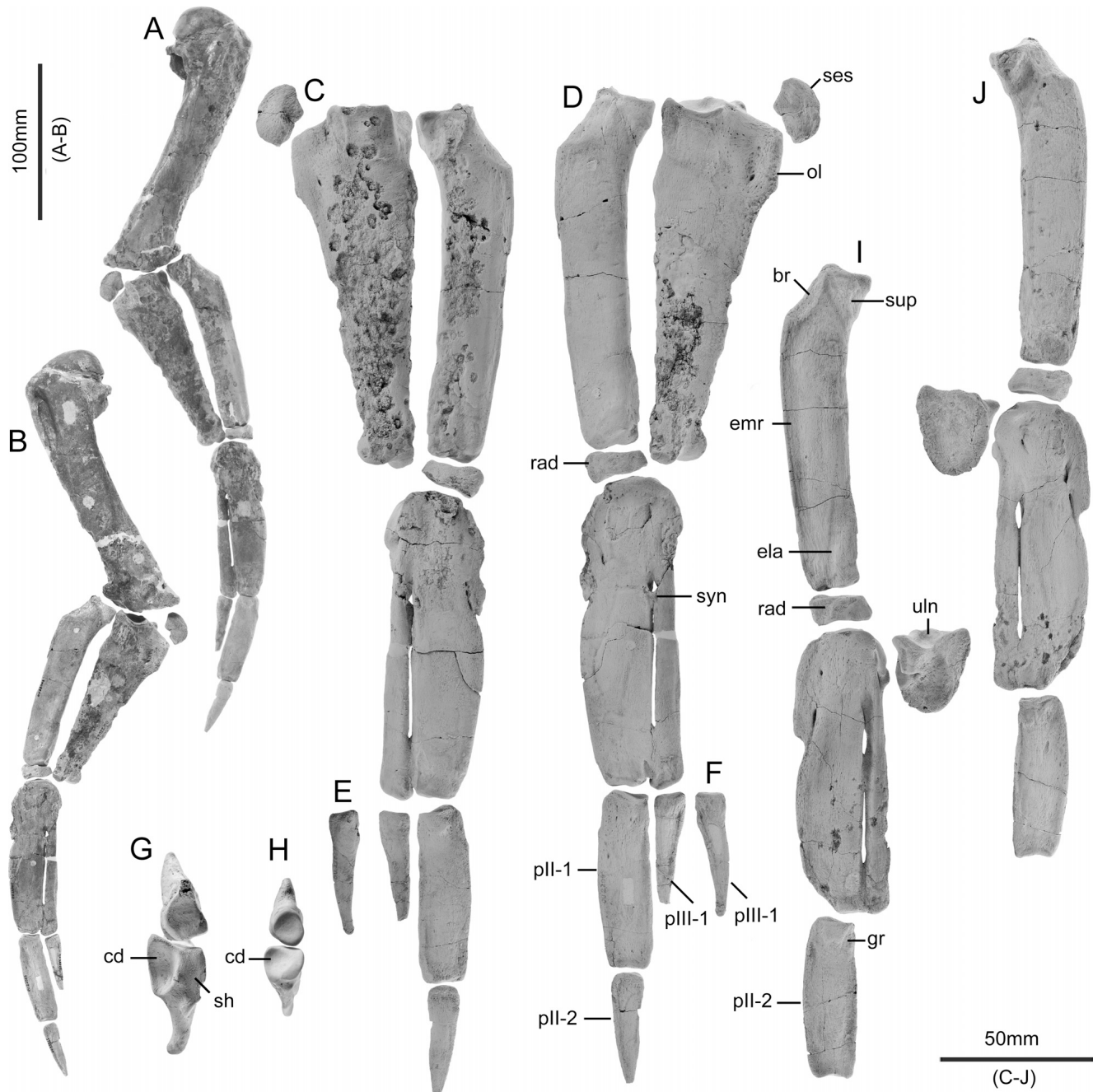


FIGURE 5. Wing elements of *Kairuku* species. *K. grebneffi*, sp. nov., referred specimen (OU 22065): articulated left wing in **A**, caudodorsal and **B**, cranioventral views; distal wing in **C**, dorsal and **D**, ventral views; and right phalanx III-1 in **E**, dorsal and **F**, ventral views. Proximal view of the radius and ulna of **G**, *K. grebneffi*, sp. nov. (OU 22065), with extant **G**, *Aptenodytes forsteri* (UCZ 1054) for comparison. *K. waitaki*, gen. et sp. nov., holotype (OU 12652): radius, radiale, ulnare, carpometacarpus, and phalanx II-1 in **I**, dorsal and **J**, ventral views. Specimens coated with sublimed ammonium chloride, except **A**, **B**, and **H**. **Abbreviations**: **br**, insertion of m. brachialis; **cd**, cotyla dorsalis; **ela**, groove for tendon of extensor longus alulae; **emr**, impression for tendon of m. extensor metacarpi radialis; **gr**, groove for the tendons of m. flexor digitorum superficialis and m. flexor digitorum profundus; **ol**, olecranon; **pII-1**, phalanx II-1; **pII-2**, phalanx II-2; **pIII-1**, phalanx III-1; **rad**, radiale; **ses**, sesamoid of m. scapulotriceps tendon; **sh**, shelf adjacent to cotyla dorsalis; **sup**, insertion of m. supinator; **syn**, synchrondrosis; **uln**, ulnare

The coracoid (Fig. 2N–O) is relatively shorter, thinner in dorsoventral shaft cross-section, and more flared proximally than in extant penguins. Total length is within the range of extant *Aptenodytes forsteri* (Emperor Penguin) despite the significantly larger size of other skeletal elements. The processus acrocoracoideus bears a pronounced dorsal depression with a raised ster-

nal rim, in contrast to the convex surface in extant penguins. The deep, circular cotyla scapularis is continuous with the flat facies articularis humeralis. Intact portions of the medial margin suggest that a completely enclosed coracoidal fenestra (sensu Zusi, 1975) was present, though the processus procoracoideus has been lost. The distinct, triangular processus lateralis contrasts

with the obsolete process of extant penguins; this feature remains poorly known in other fossil penguins due to its delicate nature. Most interestingly, the facies articularis sternalis is separated into two distinct sections: a large, dorsoventrally deep, concave facet bounded omally by a thin raised lip of bone lies medial of the long axis midline of the bone, and a smaller, narrower convex facet lies lateral to the midline (Fig. 2L). Both facets extend partially onto the ventral face of the coracoid.

A small omal portion of the left scapula has a subcircular facies articularis humeralis, similar to that of *Icadyptes salasi*, rather than ovoid as in extant penguins. The ventrolateral tip, however, is more pointed. The tuberculum coracoideum is small and sub-hemispherical. The acromion and all but the most proximal portion of the corpus are lost. The corpus in the bioeroded right scapula is strongly flattened.

A sternal fragment, including the left sulcus articularis coracoideus and part of the carina (Fig. 2W), appears more strongly curved ('U'-shaped) in cranial view than in extant penguins, though less so than in *Platydyptes* (see Fordyce and Jones, 1990; Ando, 2007). The intact sulcus articularis coracoideus is separated at the midline by a short distance from its counterpart. Only a slight labrum externum serves to support the coracoid, whereas the labrum internum is strongly projected, and articulates with the medial articular facet of the coracoid. As in extant penguins, the trabecula lateralis (Fig. 2U–V) is thin, elongate, and has a convex cranial face. A low but well-demarcated crest runs caudomedially across the main body of the sternum, fading to a nearly imperceptible ridge as it meets the border of the incisura lateralis.

On the proximal end of the left humerus (Fig. 4F–I), the contiguous sulcus ligamentum transversus and incisura capitis form a deep sulcus. Orientation of the intumescencia humeri is similar to that in stem penguins such as *Archaeospheniscus lowei* and *Pachydyptes ponderosus*. The tuberculum ventrale is damaged, but the shaft carries intact insertion scars for the m. supracoracoideus and m. latissimus dorsi. The former is elongate and angled; the latter is small and ovoid. The fossa tricipitalis is relatively small and is undivided. The intact proportions of the shaft suggest that it maintained its width or tapered distally, rather than expanding distally.

A free sesamoid found with the specimen is, based on comparisons with extant penguins, probably the sesamoid of the m. scapulotriceps tendon. No element matching the smaller sesamoid for the tendon of m. humerotriceps was recovered. This element was also not recovered with the articulated wing in the holotype of *Icadyptes salasi* (see Ksepka et al., 2008), raising the possibility that the tendon of the m. humerotriceps did not form a sesamoid in basal stem penguins. Alternatively, this small ossification may have been present but lost post-mortem.

On the left radius (Fig. 5I–J), the cotyla humeralis is less circular than in extant penguins, the dorsal face being nearly flat. There is an abrupt deflection between the proximal end of the radius and the shaft. A very shallow concavity along the cranial border of the proximal radius is marked by the insertion of the m. brachialis, which is more strongly concave and proximodistally shorter in extant penguins. On the dorsal surface of the proximal end, the subtriangular insertion scar for the m. supinator resembles that of extant penguins. The presumed left ulna is too eroded to provide anatomical details.

As in extant penguins, the ulnare is subtriangular and fan-shaped, bearing little resemblance to the ulnare of volant birds. It is similar to that of *Icadyptes salasi* in its rounded cranial angle, which is more pointed in extant penguins. A scar on the ventral surface presumably represents the insertion of the m. flexor carpi ulnaris (fide Watson, 1883). This muscle is completely tendinous and has a longer insertion scar in extant penguins (Schreiweis, 1982). The radiale is similar to that in extant penguins.

On the caudoventral margin of the carpometacarpus, a small ovoid facet is placed adjacent to, but not continuous with, the trochlea carpalis. This feature has not previously been noted in penguins and is absent in extant penguins. The homologous surface in *Pachydyptes ponderosus* and Burnside "*Palaeedyptes*" is continuous with the trochlea carpalis. The function of this facet is uncertain, because the ulnare does not bear a corresponding articular surface, and does not appear to contact this portion of the carpometacarpus when the bones are articulated. Metacarpal III has suffered the loss of the distal tip; thus the relative lengths of the metacarpals remain uncertain.

In dorsal view, the distal margin of the manual phalanx II-1 is concave, giving the element a less perfectly rectangular profile than in extant penguins. A deep dorsal groove along the proximal half of the caudal margin of the phalanx most likely represents the course of the fused tendons of the m. flexor digitorum superficialis and m. flexor digitorum profundus (see Schreiweis, 1982).

A fragment of the ala preacetabularis ilii and the cranial half of the rim of the acetabulum are preserved, and do not differ noticeably from those of extant penguins.

The complete right femur (Fig. 6G–H) is markedly more robust than is typical for penguins, even accounting for allometric effects (Table 3). The crista trochanteris projects well proximal of the head. A raised, irregular surface on the lateral face of the crista trochanteris represents the attachment surface for insertions of the m. iliofemoralis externus, m. iliotrochantericus caudalis, m. iliotrochantericus cranialis, and m. iliotrochantericus medialis, the last two of which are fused in penguins (Schreiweis, 1982). Compared to extant penguins, the scars marking these insertions extend farther distally along the shaft. In this regard, the femur of *K. waitaki* resembles that of *Palaeedyptes marplesii* and differs from most other fossil penguins. The linea intermuscularis cranialis extends about two-thirds of the length of the shaft before dividing. On the caudal face of the shaft, a flat scar representing the common insertion of the m. obturatorius medialis and m. obturatorius lateralis is placed just medial of the iliotrochantericus insertions. In extant penguins, this insertion is typically depressed. The distal end of the femur is wide, with unusually weak caudal projection of the condylus lateralis. As in other penguins, a small pit on the distal face of the condylus lateralis marks the origin of the m. tibialis cranialis.

A large, block-like patella (Fig. 6I–J) has deep groove for the tendon of the m. ambiens, but whether it was enclosed or open is not discernable due to damage.

The tibiotarsus (Fig. 7A) shows strong craniocaudal compression of the shaft toward the distal end (some compression at midshaft is from crushing). A small intact portion of the cnemial crest indicates a degree of proximal projection similar to extant penguins and weaker than in procellariiforms. The wide, deep sulcus extensorius is placed near the midline of the shaft. A thick convex tubercle is present on the distal margin of the pons supratendineus. Dense osteosclerotic bone exposed by breakage reveals that the compacta accounts for about 60% of the shaft cross-section. The proximal end of the right fibula is intact but preserves no significant morphological features.

The well-preserved right tarsometatarsus (Fig. 7H–L) is substantially wider than the holotype tarsometatarsus of *Palaeedyptes antarcticus* (Fig. 7Q–R), which is nearly equal in length. As in *Palaeedyptes* (*P. antarcticus*, *P. klekowskii* Myrcha, Tatur, and del Valle, 1990, *P. gunnari* [Wiman, 1905], and *P. marplesii*), *Inkayacu*, *Palaeospheniscus*, and *Eretiscus*, the foramen vasculare proximale laterale is large and ovoid, and the foramen vasculare proximale mediale is reduced to a minute perforation. Most notably, the tarsometatarsus differs from all other penguins in lacking a crista hypotarsi medialis. A large, roughened tuberositas m. tibialis cranialis arises about midway along

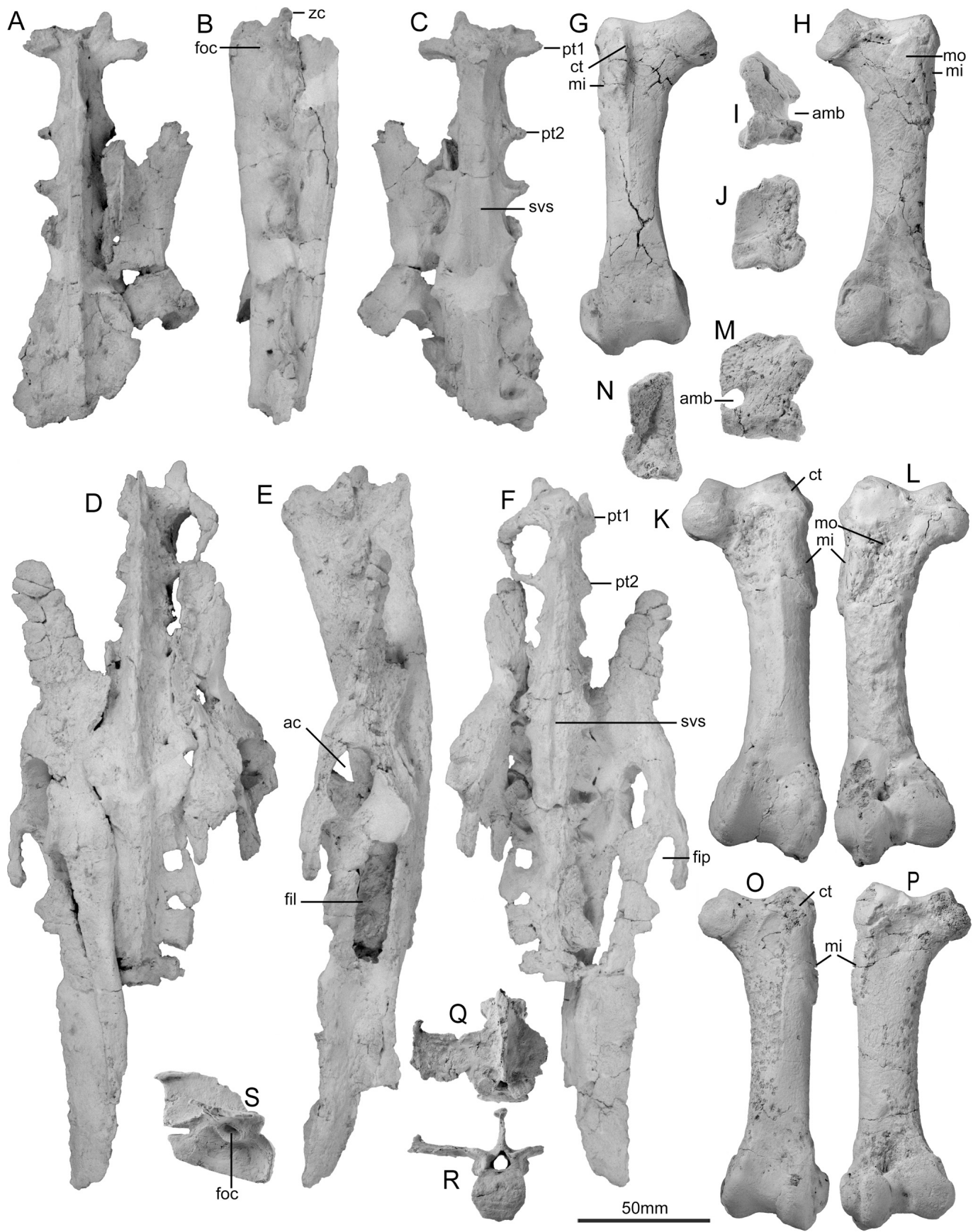


TABLE 2. Measurements of *Kairuku* specimens in millimeters.

		<i>Kairuku waitaki</i> OU 12652	<i>Kairuku grebneffi</i> OU 22065	<i>Kairuku grebneffi</i> OU 22094	<i>Kairuku</i> sp. OU 22353	<i>Kairuku</i> sp. OM GL427	<i>Kairuku</i> sp. OM GL 432
Sternum	Maximum length	—	460+	—	—	—	—
Coracoid	Maximum length	187.1	191.5 (r)	—	—	—	—
Humerus	Maximum length	—	176.6 (r)	—	—	—	162.9
	Length (head to condylus ventralis)	—	173.4 (r)	163.8 (r)	—	164.9	161.6
	Midshaft width	—	30.5 (r)	—	—	32.1	31.9
	Midshaft depth	—	15.8 (r)	—	—	12.6	12.3
	Length	—	117.8 (r)	—	113.8 (l)	114.8	110.4
Ulna	Length	107.0	116.8 (r)	—	—	115.7	—
Radius	Length	93.5	99.9 (r)	—	97.6 (r)	98.7	94.4
Carpometacarpus	Length	52.8	58.5 (r)	—	—	—	—
Phalanx II-1	Length	—	40.5 (r)	—	—	—	—
Phalanx II-2	Length	—	37.2 + (r)	—	—	—	—
Phalanx III-1	Length	—	—	—	—	—	—
Femur	Maximum length	127.3	143.9 (l)	132.9 (l)	135.0 (r)	—	—
	Proximal width	46.8	48.3 (l)	—	—	—	—
	Midshaft width	20.0	21.8 (l)	—	—	—	—
	Midshaft depth	19.6	20.9 (l)	—	—	—	—
	Distal width	42.4	42.7 (l)	42.3 (l)	—	—	—
Tibiotarsus	Maximum length	—	243.0 / 244.0	244.0 (l)	~ 242 (r)	—	—
	Length excluding cnemial crest	—	234.0 / 233.0	231.0 (l)	~ 235 (l)	—	—
Tarsometatarsus	Maximum length	63.6	—	67.6 / 67.6	61.2 (r)	—	—
	Length to distal groove in MT III	62.6	—	66.0 / 66.3	60.9 (r)	—	—
	Proximal width	41.2	—	41.0+ / 41.0+	—	—	—
	Width at narrowest point	34.0	—	35.5 (r)	33.5 (r)	—	—
	Distal width	50.6	—	50.0 + (r)	—	—	—
	Width of trochlea metatarsi III	16.2	—	16.1 / 15.7	—	—	—

the shaft of metatarsal III. The sulcus longitudinalis dorsalis lateralis is very deep, but the sulcus longitudinalis dorsalis medialis is barely perceptible. A short, wide, and low ridge represents the coalesced crista lateralis hypotarsi and crista intermedialis hypotarsi (separate in *P. antarcticus*). Trochlea metatarsi II projects nearly to the level of trochlea metatarsi III, but trochlea metatarsi IV is more proximally retracted. The plantar-medial corner of trochlea metatarsi II projects markedly laterally. This projection is pronounced in *Waimanu tuatahi* Ando, Jones, and Fordyce (in Slack et al., 2006) and is moderately developed in *Waimanu manneringi*. Given the weak projection in *K. grebneffi* and other fossil penguins, development of the flange in *Waimanu* and *K. waitaki* may be convergent. A foramen vasculare distalis is absent.

Fourteen pedal phalanges were recovered (Fig. 7H). The proximal articular facet of phalanx II-1 is markedly asymmetrical, with strong projection of the plantar-lateral corner presumably corresponding to the asymmetry of trochlea metatarsi II. The phalanges otherwise closely resemble those of extant penguins. All three toes exceed the tarsometatarsus in length. The unguals are more similar to the claw-shaped unguals of *Eudyptes* or *Spheniscus* than the more dorsoventrally flattened unguals of *Aptenodytes forsteri*. However, in life the shape including the keratinous sheath may vary significantly between taxa with similar bony unguals (D.T.K., pers. observ.).

*KAIRUKU GREBNEFFI*, sp. nov.  
(Figs. 2–7)

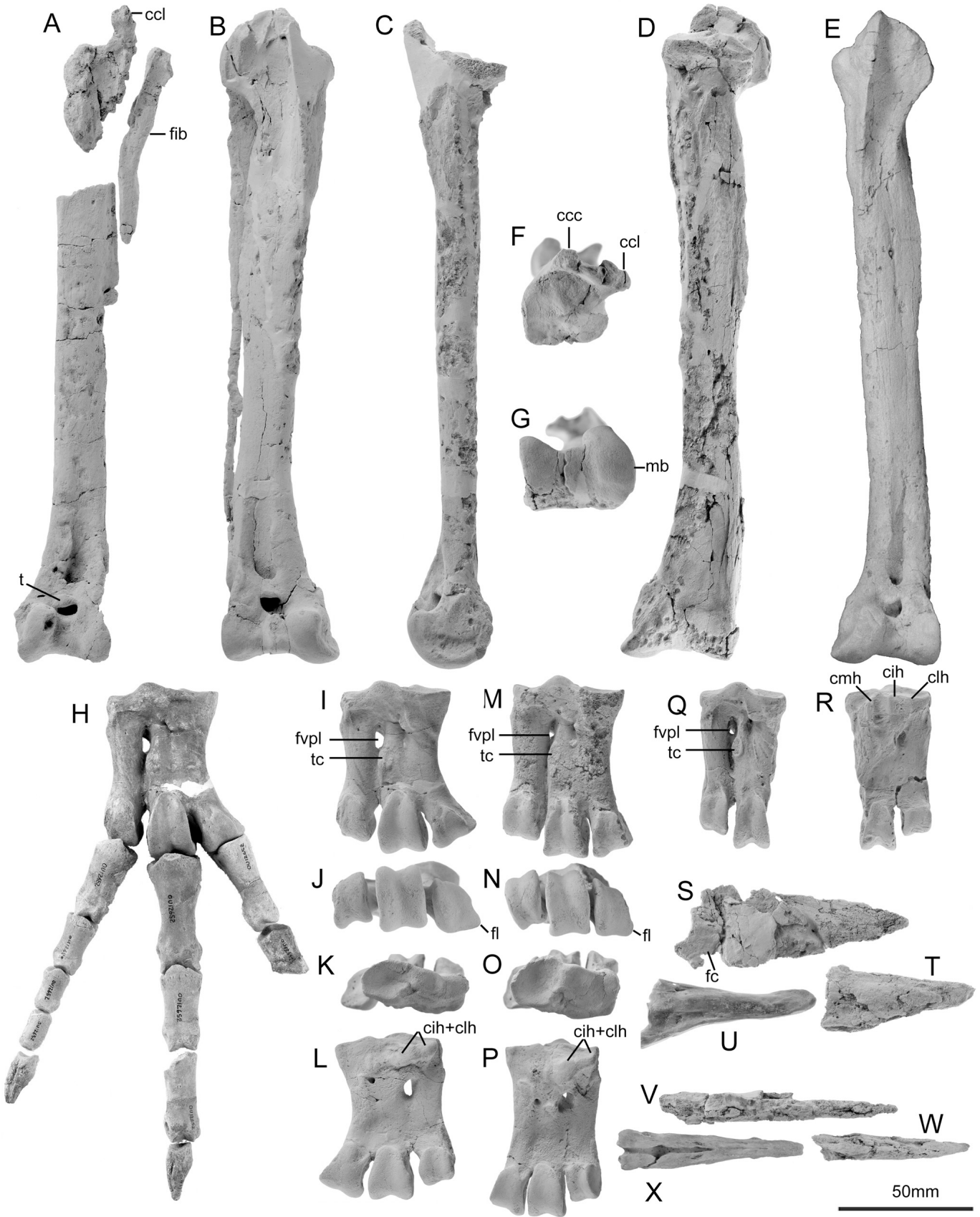
**Diagnosis**—*Kairuku grebneffi* differs from *K. waitaki* by the straight tip of the upper beak, patella with more proximodistally elongate articular surface for femur, dorsoplantarly deeper hypotarsus, and less concave medial margin of the tarsometatarsus. All specimens are larger than the *K. waitaki* holotype, but given limited sample size and the range of intraspecific size variation in penguins, this difference may not be diagnostic.

**Etymology**—Named after Andrew Grebneff, skilled field paleontologist and preparator, who worked in the Department of Geology, University of Otago, from 1985 until his sudden death in 2010.

**Holotype**—OU 22094: cervical vertebra, thoracic vertebra, synsacrum (Fig. 6D–F), partial pygostyle, rib fragments, right and left coracoids, omal portions of right and left scapula, right humerus (Fig. 4J–K), radius and ulna, partial left and right os coxae (Fig. 6D–F), left and right femora (Fig. 6O–P), patella, complete left and distal right tibiotarsus (Fig. 7E), both tarsometatarsi (Fig. 7M–P), and six pedal phalanges. Collected by R.E.F., A. Grebneff, and C.M.J., January 1991.

**Referred Specimen**—OU 22065: rostral tip of beak (Fig. 2C–D), atlas, partial synsacrum, five free caudal vertebrae and pygostyle (Fig. 7T–W), four partial ribs, partial sternum (Figs. 2R–T, 3A), omal portion of furcula (Fig. 2Q), nearly complete right and proximal left coracoid (Fig. 2K–M), omal portion of right scapula (Fig. 2P), right forelimb (lacking only ulnare and sesamoid for tendon of m. humerotriceps) (Fig. 5A–G), left phalanges II-1 and III-1, partial left and right os coxae, nearly

← FIGURE 6. Pelvic elements of *Kairuku waitaki*, gen. et sp. nov., holotype (OU 12652): pelvis in **A**, dorsal, **B**, lateral, and **C**, ventral views; right femur in **G**, cranial and **H**, caudal views; left patella in **I**, medial and **J**, articular views; thoracic vertebra 4 in **Q**, dorsal, **R**, cranial, and **S**, lateral views. *K. grebneffi*, sp. nov., holotype (OU 22094): pelvis in **D**, dorsal, **E**, lateral, and **F**, ventral views; right femur in **O**, cranial and **P**, caudal views. *K. grebneffi*, sp. nov., referred specimen (OU 22065): right femur in **K**, cranial and **L**, caudal views; left patella in **M**, lateral and **N** articular views. All specimens coated with sublimed ammonium chloride. **Abbreviations:** **ac**, acetabulum; **amb**, canal for tendon of m. ambiens; **ct**, crista trochanteris; **fil**, foramen ilioischadicum; **fp**, fenestra ischiopubica; **fo**, fovea costalis; **mi**, coalesced insertion scars for m. iliofemoralis externus, m. iliotrochantericus caudalis, m. iliotrochantericus cranialis, and m. iliotrochantericus medialis; **mo**, insertion of m. obturatorius medialis and m. obturatorius lateralis; **pt1**, first processus transversus; **pt2**, second processus transversus; **svs**, sulcus ventralis synsacri; **zc**, zygapophysis cranialis.



complete left and right hind limbs lacking left fibula and left patella (tarsometatarsi badly damaged), and six pedal phalanges (Figs. 6K–N, 7B–D, F–G). Collected by R.E.F., A. Grebneff, C.M.J., and S. Munro, in September 1989.

**Locality and Horizon**—The holotype OU 22094 is from Waipati catchment (Waipati stream is a small tributary of the Maerewhenua River), near the town of Dunroon, North Otago (near latitude 44°51'S, longitude 170°37'E); New Zealand Fossil Record Number I40/f334. It was found in a heavily bioturbated, massive, weathered green-brown, richly glauconitic, calcareous greensand with sparse macroinvertebrates in the upper Kokoamu Greensand about 1.5 m below the lowest concretionary Otekaikai Limestone; Dunroonian stage (late Oligocene). The referred specimen OU 22065 is from the bank of the Waihao River, South Canterbury (near latitude 44°48'S, longitude 170°57'E); New Zealand Fossil Record Number J40/f191. It was in a dm-bedded calcareous quartzose greensand with sparse macroinvertebrates in the middle Kokoamu Greensand, about 14 m below a prominent unconformity which marks the base of the overlying cross-bedded and nodular Otekaikai Limestone; Dunroonian stage (late Oligocene). OU 22065 was collected stratigraphically higher from the same sequence as the holotype of *K. waitaki*. Biostratigraphic resolution is insufficient to ascertain which of the two specimens of *K. grebneffi* might be younger.

**Measurements**—See Table 2.

**Description**—A small fragment of the beak in OU 22065 (Fig. 2C–D) is similar to that of *Kairuku waitaki* in cross-section, slenderness, and texturing, but shows no ventral deflection at the tip. The beak fragment thus resembles the straight distal tip in *Icadyptes salasi*. This may reflect differences in foraging strategy between *K. waitaki* and *K. grebneffi*. Given the preservation of other elements in OU 22065, it seems unlikely that deformation has flattened the beak tip.

The atlas of OU 22065 (Fig. 2J) is nearly complete and closely resembles that of extant penguins, though the incisura fossae is proportionally deeper and the fossa condyloidea more strongly concave. The region of the processus ventralis is missing. In OU 22094, the corpus of a complete posterior cervical vertebra is strongly dorsoventrally compressed, with heterocoelous articular facets. A rough excavation occurs on the ventral surface of the corpus just caudal to the articular facet, and the base of the strong processus ventralis is preserved caudal to this excavation. Both the arcus vertebrae as a whole and the processus spinosus are very low. A large foramen transversarium is present. The articular facets of the zygapophyses cranialis are more elongate than those of the zygapophyses caudalis and are craniocaudally expanded relative to the condition in extant penguins.

A nearly complete, but flattened, middle or caudal thoracic vertebra from the holotype is deeply opisthocelous, bears a wide, deep fovea costalis, and preserves the base of a cranially placed processus ventralis.

The complete synsacrum of OU 22094 (Fig. 6D–F) incorporates at least 12 vertebrae; the last element could represent a 13th synsacral vertebra or the proximal-most free caudal crushed against the synsacrum. The articular surface on the cranial-most synsacral vertebra is strongly convex. The ventral margin of the

TABLE 3. Proportions of the femur in fossil penguins.

Taxon	Specimen	Femur length	Midshaft width × 10 / Length
<i>Kairuku waitaki</i>	OU 12652	128.7	1.55
<i>Kairuku grebneffi</i>	OU 22065 (left)	143.1	1.54
<i>Kairuku grebneffi</i>	OU 22094 (left)	133.5*	1.72*
Sphenisciformes indet. (Seal Rock specimen)	MNZS 1449	122+**	~ 1.50
<i>Archaeospheniscus lopdelli</i>	OM GL 428	~128	~ 1.40
<i>Archaeospheniscus lowei</i>	OM GL 407	115.3	1.30
<i>Inkayacu paracasensis</i>	MUSM 1444	145.9	1.40
<i>Palaeudyptes marplei</i>	OM GL 429	142.9	1.34
Antarctic femur***	IB/P/B 0230	145.5	1.24
cf. <i>Palaeudyptes gunnari</i>	IB/P/B 0103	123.6	1.32

\*The hindlimb shows signs of pathology (see text) so this value is considered unreliable.

\*\*This specimen is abraded and so would have been slightly longer when complete.

\*\*\*This is the largest specimen sufficiently intact to take the relevant measurements from the Seymour Island (Eocene, Antarctica) specimens reported by Jadwiszczak (2006b) who considered it to represent *Anthropornis*, *Palaeudyptes klekowskii*, or *Palaeudyptes gunnari*.

cranial end of the synsacrum in OU 22094 appears more compressed than in *Kairuku waitaki*, but this may reflect post-mortem deformation. *Waimanu manneringi* has only 11–12 synsacral elements, a synsacrum assigned to *Palaeospheniscus bergi* Moreno and Mercerat, 1891, has 12 (Simpson, 1946), and most extant penguins have 13 (Ksepka and Clarke, 2010). This implies a lower number of synsacral vertebrae is plesiomorphic in penguins (Ksepka and Clarke, 2010). However, because 14 vertebrae are present in a synsacrum assigned to the giant stem penguin *Anthropornis nordenskjoeldii*, this feature may be more homoplastic (Jadwiszczak and Mörs, 2011).

Five free caudal vertebrae in OU 22065 differ from those in extant penguins in being less proximodistally elongate and bearing a taller processus spinosus with a more strongly bilobate apex. The terminal free caudal possesses a shelf-like caudal projection from the ventral margin of the corpus that would partially underlie the preceding vertebra in articulation. The processus transversus is more strongly laterally projected and narrower than in extant penguins.

The pygostyle is partial in OU 22094 (Fig. 7T, W) and complete but abraded in OU 22065 (Fig. 7S, V). This element is elongate and subtriangular in lateral profile, and is mediolaterally compressed with an ovoid cross-section. In contrast, the pygostyle of extant penguins has a triangular cross-section with a flat, widened ventral base (Fig. 7U, X). A caudal projection from the ventral margin of the corpus arises at the midline and appears to be single in *K. grebneffi*, unlike the two separate, laterally placed projections in extant penguins.

The right scapula clavicularae of the furcula in OU 22065 (Fig. 2P) has a thin sharp caudal margin, whereas the cranial margin is thickened and rounded. The furcula appears less strongly curved

← FIGURE 7. Lower leg bones of *Kairuku*. *Kairuku waitaki*, gen. et sp. nov., holotype (OU 12652): **A**, left tibiotarsus in cranial view; **H**, articulated left foot in dorsal view; left tarsometatarsus in **I**, dorsal, **J**, distal, **K**, proximal, and **L**, plantar views. *K. grebneffi*, sp. nov., holotype (OU 22094): **E**, left tibiotarsus in cranial view; left tarsometatarsus in **M**, dorsal, **N**, distal, **O**, proximal, and **P**, plantar views; pygostyle in **T**, lateral and **W**, ventral views. *K. grebneffi*, sp. nov., referred specimen (OU 22065): right tibiotarsus in **B**, cranial, **C**, medial, **D**, caudal, **F**, proximal, and **G**, distal views; pygostyle in **S**, lateral and **V**, ventral views. Tarsometatarsus of *Palaeudyptes antarcticus* (OU 22167, cast of NHMUK A1048) shown for comparison in **Q**, dorsal and **R**, plantar views. Pygostyle of *Aptenodytes forsteri* (UCZ 1054) shown for comparison in **U**, lateral and **X**, ventral views. Specimens coated with sublimed ammonium chloride except for **U** and **X**. **Abbreviations:** **ccc**, crista cnemialis cranialis; **ccl**, crista cnemialis lateralis; **ch**, crista intermedialis hypotarsi; **chl**, crista lateralis hypotarsi; **cml**, crista medialis hypotarsi; **fc**, free caudal vertebra; **fib**, fibula (incomplete); **fvpl**, foramen vasculare proximale laterale, **mb**, medial border of distal end of tibiotarsus; **t**, tubercle on pons supratendineus, **tc**, tuberositas m. tibialis cranialis.

than in extant penguins, though a complete element is necessary to confirm overall shape.

A nearly complete, slightly deformed sternum (OU 22065; Figs. 2R–T, 3) provides the best example to date of this element from a stem penguin. The sternum is elongate and narrow compared to that of extant penguins. A small space separates the left and right sulcus articularis coracoideus. These sulci are more deeply bounded at the margins corresponding to the medial and lateral articular facets of the coracoid. Cranial projection of the apex carina is marked, and the apex is directed nearly parallel to the long axis of the sternum. Keel shape closely resembles the condition in *Aptenodytes*. The carina is low and probably extended the entire length of the sternum, though the caudal margin is missing. At least five incisurae intercostale are present. They are craniocaudally elongate and mediolaterally compressed compared to those of extant penguins. The trabecula lateralis is elongate and narrow, with a strongly convex ventral face and a flat dorsal face.

The coracoids (Figs. 2 K–M, 3) resemble those of *K. waitaki*. Although the processus acroracoideus is relatively longer in *K. grebneffi*, this difference falls within the range of intraspecific variation for extant penguins. A faint depression traverses the shaft of the coracoid, running caudolaterally from the level of the processus procoracoideus to near the center of the shaft before fading. This groove, which represents the course of the tendon of the m. supracoracoideus, is much better developed in *Pachydyptes ponderosus* and *Platydyptes marplei* (see Ando, 2007). Because of bone loss, it is uncertain whether the coracoidal fenestra was closed.

The wings in OU 22065 and OU 22094 are nearly identical, although the former is larger. Relative proportions of the wing elements (Fig. 5A–B) are very close to those observed in *Icadyptes salasi*, the only other stem penguin preserving a complete wing. In both taxa, the most noticeable proportional difference from extant penguins is that the carpometacarpus is relatively longer and the phalanges are relatively shorter (Table 4). These differences are more pronounced in *Kairuku*. Proportional differences in the wing do not appear to be due to simple allometry, given that the smallest extant species, *Eudyptula minor*, shows proportions more similar to *Kairuku* than does the largest extant species, *Aptenodytes forsteri*.

Overall proportions of the humerus are most similar to those of *Palaeudyptes klekowskii*, particularly in terms of the narrow and weakly flattened shaft. Muscle insertions are well preserved in OU 22065 (Fig. 4A–E). On the cranial face, the m. pectoralis insertion forms a deep, oblong fossa as in extant penguins. On the caudal face, the insertion scar for the m. supracoracoideus is elongate, slightly depressed, and shifted towards the ventral border of the shaft. It is well separated from the small, ovoid m. latissimus dorsi scar. The undivided tricipital fossa appears comparable in volume to that of OU 12652. A wide scar for the

insertion of the m. coracobrachialis caudalis partially bounds the tricipital fossa, extending to the proximal border of the tuberculum ventrale. In extent and orientation of this scar, OU 22065 resembles *Pachydyptes ponderosus* and differs from the Burnside Formation "*Palaeudyptes*," though orientation is variable in extant penguins. The tuberculum ventrale is deeply indented. On the cranial face of the shaft, a distinct humeral arterial sulcus is present. This structure is an osteological correlate for the humerus arterial plexus, a vascular counter current heat exchanger (Thomas et al., 2011). Distally, pronounced depressions indicate strong development of the entepicondylar and ectepicondylar ligaments, which serve to stiffen the articulations between the humerus, radius, and ulna. Three trochlear ridges are fully developed bounding deep grooves for the tendons of the m. scapulotricipitalis and m. humerotricipitalis (Fig. 4E). The condylus ventralis is prominent, hemispherical, and bordered by a wide shelf.

OU 22065 preserves the longest humerus reported for a penguin, measuring 173.4 mm from the proximal end to the distal tip of the condylus ventralis, or 176.6 mm if the distal trochlear ridges (often broken in fossils) are included. The humerus of the holotype of *Pachydyptes ponderosus* measures 172.5 mm (175.8 mm including the trochlear ridges), but is much stouter.

The radius (Fig. 5C–D, G) is similar to that of *K. waitaki*. A very shallow concavity along the cranial border of the proximal radius is marked by the insertion of the m. brachialis. This insertion site is more strongly concave and proximodistally shorter in extant penguins. A groove marking the path of the tendon of the m. extensor metacarpi radialis incises the dorsal surface of the radius near the cranial margin.

On the right ulna (Fig. 5 C–D), a deep cotyla dorsalis is developed at the articular surface and a wide adjacent shelf of bone forms an articulation for the counterpart surface of the humerus. As noted by Ando (2007), the articular surface for the radius is concave in proximal view (Fig. 5G), so that the ulna contacts the proximal radius at both its caudal and ventral surfaces as in outgroup taxa, but unlike extant penguins. The proximal process developed in *Platydyptes novaeseelandiae* and *Platydyptes marplei* Simpson, 1971, is absent. The olecranon is tab-like with a squared posterior border, differing from the more rounded border in the Burnside Formation "*Palaeudyptes*" and *Icadyptes salasi*. A small foramen perforates the olecranon. The morphology of the distal condyles is similar to that in extant penguins.

The carpometacarpus (Fig. 5C–D) lacks a processus extensorius. The processus pisiformis is obsolete. Whereas it is difficult to determine with certainty whether metacarpal I bore a distal facet in *K. waitaki*, the distal margin of metacarpal I tapers to a pointed tip in *K. grebneffi* and a facet is clearly absent. A short ossified synchondrosis connects metacarpals II and III near the proximal end of the spatium intermetacarpale, dividing it into a

TABLE 4. Proportions of flipper elements in *Kairuku* and other penguins.

	Indices of humerus shape				Percentage of total wing length			
	Length (mm)	Width index	Thickness index	Flatness index	Humerus	Ulna	Carpometacarpus	Phalanges
<i>Kairuku grebneffi</i> (OU 22065)	173.4	0.18	0.09	1.93	34.0%	23.2%	23.0%	19.5%
Burnside Formation taxon (OM GL435)	152.1	0.20	0.09	2.21	—	—	—	—
<i>Icadyptes salasi</i> (MUSM 899)	167.0	0.22	0.10	2.14	34.5%	24.1%	20.5%	20.8%
<i>Aptenodytes forsteri</i> (n = 12)	125.1 ± 4.1	0.20	0.08	2.39	34.2%	24.1%	18.9%	22.7%
<i>Eudyptes chrysolophus</i> (n = 3)	63.3 ± 2.3	0.22	0.09	2.45	31.5%	25.4%	19.8%	23.3%
<i>Eudyptula minor</i> (n = 3)	44.4 ± 1.2	0.17	0.07	2.30	33.9%	25.4%	19.5%	21.2%
<i>Pygoscelis adeliae</i> (n = 5)	68.0 ± 2.4	0.21	0.08	2.59	34.9%	24.0%	18.9%	22.2%
<i>Spheniscus magellanicus</i> (n = 6)	69.2 ± 3.8	0.18	0.08	2.40	32.8%	24.4%	19.6%	23.1%

short, rounded proximal opening and a long slit-like distal opening. Metacarpal III extends farther distally than metacarpal II.

Phalanx II-1 differs from that in *K. waitaki* (OU 12652) in that the distal articular face is flat rather than concave in dorsal view, and the groove for the tendons of the m. flexor digitorum superficialis and m. flexor digitorum profundus is shallower. Phalanx II-2 is narrower than in extant penguins. The total length of digit II is subequal to that of the carpometacarpus, as in *Icadyptes salasi*. The length of digit II significantly exceeds that of the carpometacarpus in extant penguins. Phalanx III-1 retains primitive proportions, being shorter than phalanx II-1, and also lacks the proximally directed process that is present in extant penguins.

Parts of the pelvis in OU 22094 (Fig. 6D–F) and OU 22065 show complete fusion between the ilium, ischium, and pubis, but unbroken edges indicate the ilium was not fused to the synsacrum. The crista dorsolateralis ilii is strongly laterally projected, contributing to a deep depression caudal of the foramen ilioischadicum. The foramen is craniocaudally elongate ovoid, much longer than the acetabulum. The smaller, ovoid fenestra ischiopubica appears to have been nearly closed caudally by contact, if not fusion, between the pubis and ischium.

The femora in OU 22094 are markedly asymmetrical; the right element is considered to be pathological. In OU 20065, a massive, raised, and largely smooth scar on the lateral face of the crista trochanteris marks the insertions of the m. ilirotrochantericus cranialis and m. ilirotrochantericus medialis; the insertions are more strongly developed than in OU 22094 or *K. waitaki*. Placement of muscle scars and proportions of the femur are otherwise similar to those in *K. waitaki*.

The patella is more proximodistally elongate and mediolaterally compressed than in *K. waitaki* in both specimens. Proportions resemble those in *Palaeodyptes marplei*. The pathway for the ambiens tendon is completely enclosed in OU 22065 (Fig. 6M), and was possibly enclosed in OU 22094, though the margins are damaged.

The tibiotarsus (Fig. 7B–G) differs from that in extant penguins in the stronger craniocaudal compression of the shaft (particularly at the proximal and distal ends) and the greater mediolateral expansion of the distal end. In distal view, the medial margin is strongly convex (Fig. 7G), whereas it is straight in extant penguins, *Waimanu manneringi*, and *Paraptenodytes antarcticus* Moreno and Mercerat, 1891.

Aside from features noted in the diagnosis and the slightly more proximodistally elongate tubercle for m. tibialis cranialis, the tarsometatarsus of OU 22094 (Fig. 7M–P) agrees with that of *K. waitaki*, sharing the reduced size of the foramen vasculare proximale mediale, lack of a crista medialis hypotarsi, and coalescence of the crista lateralis hypotarsi and crista intermedialis hypotarsi.

#### KAIRUKU sp.

**Referred Material**—OM GL427 (listed as OM C47.23, or Marples' Field No. D.P. 4 in older literature): associated beak, vertebrae, coracoids, and a nearly complete wing. OM GL432 (formerly OM C47.25 or Marples' Field No. D.P. 6): associated cervical vertebra, coracoid, ulna, and carpometacarpus. OU 22353: associated rostral half of beak, several vertebrae including partially unfused synsacrum, fragments of scapula and coracoid, distal right humerus, left ulna and radius, left and right carpometacarpus, left manual phalanx III-1, left ilium, pubis, and ischium, left and right femora, tibiotarsi, and tarsometatarsi, and one pedal phalanx.

**Locality and Horizon**—Kokoamu Greensand (Maerewhenua Greensand of Marples, 1952) near Duntroon (Otago), for OM specimens, as detailed by Marples (1952). OU 22353 is from the massive bioturbated Kokoamu Greensand in an overhang, 2+ m below the cemented base of the Otekaike Limestone, at the base of cliffs on the south bank of Awamoko Stream, North Otago;

near latitude 44°55'S, longitude 170°43'E; New Zealand Fossil Record Number I41/f0182.

**Comments**—Several previously described specimens, as well as new material in the OU collections, can be assigned to *Kairuku* but cannot be placed to the species level because we have not identified distinguishing apomorphies on the represented elements. We review these specimens briefly below; OM specimens were described by Marples (1952) and Simpson (1971).

Specimen OU 22353 is a partially articulated skeleton that represents a sub-adult bird based on numerous indicators of skeletal immaturity, including bone texture, indistinct boundaries of muscle insertions, and the incompletely fusion of the synsacrum, os coxae, and metacarpals. Comparable elements are intermediate in size between the holotype individuals of *K. waitaki* and *K. grebneffi* except for the tarsometatarsus, which is smaller, potentially due to incomplete development. Long bones of the extant Emperor Penguins reach adult proportions well before co-ossification of tarsal elements is complete (D.T.K., pers. observ.), so it is likely the animal had already approached full standing height.

Specimens OM GL427 and GL432 were assigned to *Palaeodyptes antarcticus* by Marples (1952) and *Palaeodyptes* sp. by Simpson (1971), and are here referred instead to *Kairuku*. Significant differences between these specimens and other materials referred to *Palaeodyptes* have already been noted (Fordyce and Jones, 1990) and these specimens were included in phylogenetic analyses both at the specimen level (Clarke et al., 2007) and together as Duntroon "*Palaeodyptes*" (Ksepka and Clarke, 2010). Those studies recovered OM GL427 and GL432 as more closely related to the crown clade Spheniscidae than the Burnside Formation "*Palaeodyptes*." Both specimens preserve an ulna with the distinct tab-like, squared olecranon as present in *K. grebneffi* (ulna incomplete in *K. waitaki*), and OM GL432 preserves the small facet on the caudoventral margin of the carpometacarpus. The size of both specimens is closest to *K. grebneffi*, but the material is too incomplete to rule out a large individual of *K. waitaki*. Some slight proportional differences are noted, particularly the wider and flatter humerus. This may be attributable to crushing in the OM specimens, which are more poorly preserved than the OU specimens. Given the data at hand, we assign both specimens to *Kairuku* but not to a particular species.

OM GL427 includes a portion of the beak comprising the processus frontalis and processus maxillaris of the premaxillae but lacking the rostral tip. Morphology is similar to that of *Kairuku waitaki* for overlapping regions and shows additionally that the premaxillae remain fused along the caudal part of the internarial bar.

## PHYLOGENETIC ANALYSIS

### Data Set

New anatomical data from the *Kairuku* specimens form the basis for 17 new phylogenetically informative characters. The total morphological data set includes 245 characters from the osteology, myology, integument, and reproductive biology of penguins drawn from previous phylogenetic and comparative work (Zusi, 1975; Schreiweis, 1982; O'Hara, 1989; Giannini and Bertelli, 2004; Bertelli and Giannini, 2005; Ksepka et al., 2006; Acosta Hospitaleche et al., 2007; Ando, 2007; Clarke et al., 2007, 2010; Ksepka and Clarke, 2010; Ksepka and Thomas, 2012). Complete character descriptions are provided in Supplementary Information (available online at [www.tandfonline.com/UJVP](http://www.tandfonline.com/UJVP); see also Ksepka and Clarke, 2010).

Sequence data from the genes RAG-1, 12S, 16S, COI, and cytochrome b were combined with the morphological data to complete the combined matrix. Sequence were aligned for each individual gene using Clustal X (Thompson et al., 1997) and



manually inspected and adjusted. GenBank accession numbers are provided in Supplementary Information.

A total of 58 penguin taxa representing all living species and all reasonably well-known fossil species were included. Outgroup representation includes 13 species from the extant sister taxon of Sphenisciformes, Procellariiformes (e.g., Hackett et al., 2008). Two species from Gaviiformes were included to provide a more distal outgroup. Trees were rooted to Gaviiformes.

A nexus file of the combined phylogenetic data set is available with the Supplementary Information and from Dryad ([dx.doi.org/10.5061/dryad.93j174jd](https://doi.org/10.5061/dryad.93j174jd)).

### Search Strategy

Phylogenetic analyses were conducted using PAUP\*4.0b10 (Swofford, 2003) with a heuristic search strategy (1000 replicates of random taxon addition saving 10 trees per replicate, with TBR branch swapping). All characters were equally weighted, multistate codings were used only to represent polymorphism, and branches with a minimum length of zero were collapsed.

### Results

Analysis of the combined data set resulted in 684 most parsimonious trees (MPTs) of 5410 steps. Analysis of the morpho-

logical data set resulted in 5470 MPTs of 650 steps. Topologies of the combined (Fig. 8A) and morphology-only strict consensus trees (Fig. 8B) are identical for all included stem penguin taxa. In the morphology-only tree, resolution is poorer within the penguin crown clade and different species pairings are supported within *Eudyptes*, *Pygoscelis*, and Procellariiformes. These differences, however, do not affect the position of *Kairuku*.

## DISCUSSION

### Phylogenetic Position of *Kairuku*

*Kairuku* is a monophyletic taxon placed within the stem portion of Sphenisciformes. Our placement of *Kairuku* agrees with previous analyses that considered less complete exemplars of *Kairuku* sp. (OM GL 427 + 432) (Clarke et al., 2007; Ksepka and Clarke, 2010). *Kairuku* occupies a position one node basal to the contemporary taxa *Archaeospheniscus* and *Duntronornis*. A crownward position for *Kairuku* relative to *Palaeudyptes*, *Pachydyptes*, *Icadyptes*, and the Burnside Formation "*Palaeudyptes*" is supported by several derived features, including absence of a distal facet on metacarpal I for the alular phalanx, metacarpal III extending distal to metacarpal II, and lack of a distinct groove between the intermediate hypotarsal crests of the tarsometatarsus. *Kairuku* can be excluded from

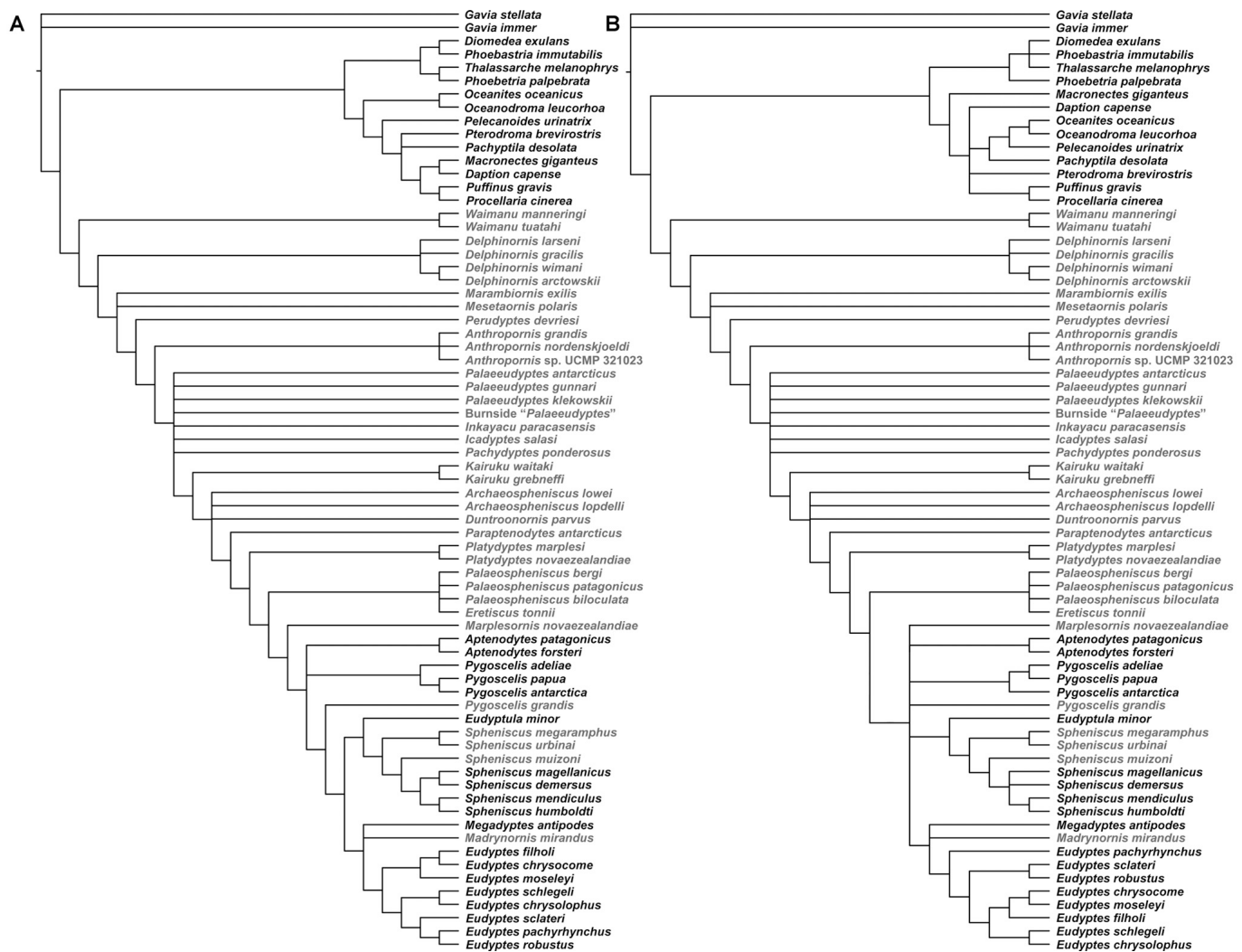


FIGURE 8. **A**, Strict consensus tree of 684 MPTs (tree length [TL] = 5410 steps, rescaled consistency index [RC] = 0.377, retention index [RI] = 0.698) from combined analysis. **B**, Strict consensus of 5470 MPTs (TL = 650 steps, RC = 0.554, RI = 0.901) from morphological analysis. Fossil taxa indicated in grey font.

the clade uniting *Archaeospheniscus*, *Dunroonornis*, and more crownward penguins by retention of the following primitive character states: wider separation between the insertion scars for the m. supracoracoideus and m. latissimus dorsi, humeral shaft thin or maintains width distally, highly angled distal condyles of the humerus (angle between main axis of shaft and tangent of condylus dorsalis and condylus ventralis less than 45°), and presence of a wider shelf adjacent to condylus ventralis.

#### Emptying the *Palaeudyptes antarcticus* 'Taxonomic Wastebasket'

*Kairuku waitaki* and *K. grebneffi* are excluded from the genus *Palaeudyptes*, because both species are placed closer to the crown clade than to the type species *Palaeudyptes antarcticus*. Thus, another piece of the obstinate taxonomic puzzle involving *Palaeudyptes* is resolved. Unfortunately, there is not yet a strong phylogenetic basis for restricting *Palaeudyptes* to a monophyletic group of species, due to the incomplete nature of the holotype of *Palaeudyptes antarcticus*, which behaves as a labile 'wildcard' taxon resulting in a large number of equally parsimonious trees. However, we can recognize several features that are known to occur in combination only in *Palaeudyptes antarcticus* and a set of putative close relatives, for example, distinct projection of the crista hypotarsi medialis, reduction of the foramen vasculare proximale laterale, and an arrangement of the metatarsal trochleae where trochlea metatarsi II extends nearly to the level of trochlea metatarsi III and trochlea metatarsi IV is proximally retracted. All of these features are either confirmed or unobservable due to incompleteness in *Palaeudyptes antarcticus*, *P. marplei*, *P. klekowskii*, *P. gunnari*, and the Burnside Formation "*Palaeudyptes*." Although this observation is insufficient to prove the monophyly of these five taxa, we prefer to retain these species within the genus *Palaeudyptes* rather than erect a set of new genera that face a high likelihood of future synonymy. Ultimate resolution of this issue must await more complete material for at least *Palaeudyptes antarcticus*. Given recent discoveries, the prospects for this are reasonable.

Our results remove the large set of specimens referable to the genus *Kairuku* from the taxonomic wastebasket involving *Palaeudyptes antarcticus*. Perhaps the most serious implications of previous concepts of *Palaeudyptes antarcticus* (as a catch-all for large mid-Cenozoic penguin fossils) have been the obfuscatory effects on penguin paleobiogeography. Some fragmentary remains from outside of New Zealand have been assigned either directly or tentatively to *Palaeudyptes antarcticus*, but these assignments have since been shown to be unsubstantiated. Simpson (1957) described a humerus and tibiotarsus from the late Eocene of Australia as *Palaeudyptes* cf. *antarcticus*, but the humerus appears to represent a more crownward species than *P. antarcticus*, whereas the tibiotarsus is phylogenetically uninformative beyond placing the fossil within Sphenisciformes (Ksepka and Clarke, 2010). More recently, Tambussi et al. (2006) referred a humerus from the late Eocene of Antarctica directly to *Palaeudyptes antarcticus*. As observed by Jadwiszczak (2006a), the basis for this referral is not readily apparent, because no humerus can be referred to *Palaeudyptes antarcticus* through association. We stress that verifiable records of *Palaeudyptes antarcticus* are limited to just two specimens from the late Eocene/early Oligocene of New Zealand (Table 1). An Eocene penguin species with a cosmopolitan distribution would have important implications for the paleobiology and biogeography of stem Sphenisciformes, but there is no solid evidence for any fossil species displaying a wide or circumpolar distribution.

#### The Skeletal Plan of Giant Stem Penguins

*Kairuku* reveals for the first time the overall postcranial morphology of a stem penguin. Proportions are quite different from

any extant penguin species. In particular, the hind limbs are distinctly shorter and stouter, and the trunk and flippers are more elongated. Longer flippers are predicted based on observed allometric patterns in Spheniscidae (Livezey, 1989), although the shape and length of the sternum are surprising. Along with the slender elongate beak, these proportions indicate a graceful but powerful form that would contrast strongly with the typically small, squat, short-beaked penguins of the present day.

In extant penguins, the coracoids are greatly elongated, pillar-like, and aligned nearly parallel to the long axis of the sternum. Fordyce and Jones (1990) noted that the shape of the coracoids in *Kairuku* suggested a more divergent orientation for these elements, though the sternum was unknown at that time. The pronounced 'U'-shaped arrangement of the sulci articularis coracoidei would also serve to rotate the coracoids so as to place the triosseal canal more nearly on the lateral-most point of the torso than it would be placed were the sulci arranged as in extant penguins (Fig. 3). It has been hypothesized that an increase in the length of the coracoids in penguins functions to provide more space to accommodate the hypertrophied m. supracoracoideus (Jenkins, 1974). This muscle is instrumental in powering the upstroke, which generates thrust in wing-propelled diving birds (Bannasch, 1994). Elongation of the coracoids is present in all penguins. Notably, the coracoids are longer than the humerus in all species except the basal taxon *Waimanu tuatahi*, in which the coracoid is still greatly elongated. This adaptation could probably only have evolved after the loss of aerial flight, because a wing position too far forward of the center of gravity would likely cause imbalance in flight. In *Kairuku*, the coracoids are less elongate proportional to other parts of the skeleton compared to extant penguins. However, the sternum is greatly elongated, providing a larger area of origin for the m. supracoracoideus. Overall muscle mass of the m. pectoralis and m. supracoracoideus nonetheless were probably not substantially greater (relative to body size) than in extant penguins because the sternal keel was quite low. A narrow, elongate sternum is also present in undescribed specimens of the more crownward taxon *Platydyptes* (see Fordyce and Jones, 1990; Jones, 1995; Ando, 2007), suggesting that this shape may have characterized a long interval of penguin evolution.

Also of interest is the pygostyle morphology. The pygostyle in *Kairuku* more closely resembles the mediolaterally compressed element seen in most procellariiforms than the pygostyle in crown penguins, which is stout and subtriangular in cross-section with a flat ventral surface. The only other record of a stem penguin pygostyle is an Eocene Antarctic specimen from an immature individual reported by Jadwiszczak (2006b). That specimen also appears to lack the flat ventral margin that contributes to the subtriangular in cross-section in extant penguins, but because the distal end is missing, the overall shape remains unknown.

Pygostyle morphology in extant penguins reflects a shift in the use of the tail. The rectrices of extant penguins are not arrayed to form the spreadable 'fan' that is used as a rudder during flight by volant birds. Instead, the loosely arranged rectrices form a short, stiff, wedge-shaped tail (Giannini and Bertelli, 2004). Particularly in the long-tailed *Pygoscelis*, these feathers are often employed to help prop the bird upright when standing. Osteological correlates of feather morphology have not been identified in the pygostyle of penguins. Thus, the shape of the rectrices in *Kairuku* remains uncertain. At the least, it can be noted that the shape of the pygostyle in *Kairuku* is less resistant to bending and suggests that tail-propping may not have been employed by early penguins.

*Kairuku* had a proportionally shorter femur and longer tibiotarsus than extant penguins. Amongst extant penguins, the tibiotarsus accounts for a comparable portion of total hind limb length in *Aptenodytes*, though proportions in that genus reflect reduction of tarsometatarsus length. The shaft is significantly more slender in the femora of other stem penguins comparable in size to *Kairuku waitaki* (Table 3). Some specimens from the New

Zealand Paleogene of similar size and stoutness may belong to close relatives of *Kairuku*, for example, the early Oligocene ‘Glen Murray penguin,’ based on the measurements provided by Grant-Mackie and Simpson (1973). Unfortunately, the poor preservation of the remaining elements (tibiotarsus and tarsometatarsus) of the Glen Murray penguin precludes further comparisons.

The size of ‘giant’ penguins—a term typically applied to those taxa clearly larger than the living Emperor Penguin—has been much discussed. Huxley (1859:675) estimated that *Palaeudyptes antarcticus* “might have stood between four and five feet” (1.2–1.5 m) high. Shortly afterward, Hector (1872b) grossly overestimated the height of the larger *Pachydyptes ponderosus* at “six to seven feet” (1.8–2.1 m). Oliver (1930) later gave the height of *Pachydyptes ponderosus* as 150 to 180 cm (about 5–6 feet). Nonetheless, Hector’s overestimate remained pervasive in popular accounts for some time (see Simpson, 1946, 1976). Marples (1952:29), working with an array of specimens here referred to *Kairuku* sp., *Palaeudyptes marplei*, and the Burnside Formation “*Palaeudyptes*,” estimated the standing height as “approximately five feet” (1.5 m). Because all of the above-mentioned taxa were then known from just a few limb bones, the accuracy of these size estimates remained questionable. Simpson (1946) showed that reconstructed heights for fossil taxa varied greatly depending on which limb bone was used to generate the value and also which extant species’ proportions were used in ‘scaling up.’

More recently, Livezey (1989) and Jadwiszczak (2001) provided regression-based estimates of size in fossil penguins. Livezey (1989) did not reconstruct height but estimated that the largest fossil penguins reached up to 81 kg. Jadwiszczak (2001) estimated mass and body length, and standing height based on scaling body length down by 5–10%. These estimates were primarily based on the dorsoventral breadth of the tarsometatarsus. Results suggested that the largest sampled taxon, *Anthropornis* sp., reached heights of 1.54–1.62 m and a mass of 89.9 kg. These regressions provided an estimate of penguin size in the absence of relatively complete skeletons for large stem taxa. However, Jadwiszczak (2001:153) considered the resultant values “nothing more than rough predictions” due to the incomplete nature of the material at hand.

*Kairuku* demonstrates that limb bones cannot be scaled reliably to determine body size, because of the different proportions of skeletal elements between stem and living penguins. Forelimb elements are particularly likely to yield overestimates due to allometric scaling. The length of the flipper skeleton is less than the length of the hind limb skeleton (excluding the digits) in small to moderate-sized extant penguins, but greater than that of the hind limb skeleton in the largest extant genus *Aptenodytes*. In *Kairuku*, the flipper is even longer proportional to the hind limb. Further, it is important to note that the femur is held nearly horizontally in life in most birds including penguins and thus contributes very little to standing height. Thus, it is the lower hind limb (along with the trunk, neck, and head) that is of relevance.

We estimated standing height for *Kairuku grebneffi* from OU 22065, the most complete specimen for the relevant bones. Our estimates apply to an animal in standing posture, with the body leaning slightly forward and the neck in a gently curved posture. In this pose, hind limb length is equivalent to the tibiotarsus + tarsometatarsus length. The slight difference between the absolute length of the bones and the combined height in standing stance is compensated for by the underlying fatty footpad and synovial cartilages in life. Trunk length is equivalent to 90% sternum + coracoid length, accounting for the more angled orientation of the coracoid in the fossil and slight overlap of the caudal portion of the sternum with the hind limb in standing pose. Because only the atlas and a few fragments of skull are preserved in

OU 22065, the height of the neck and head was extrapolated by assuming that the neck accounts for the same proportion of total height as in extant penguins.

We estimate that OU 22065, the largest specimen of *Kairuku grebneffi* reported here, stood about 1.28 m tall. Although impressive, this represents a significantly lower value than previous estimates for the giant penguins. As noted by Simpson (1975), standing height is of the most interest to the public but length is perhaps a more relevant measurement given the large proportion of time penguins spend in the water. In underwater flight posture, *Kairuku* would have approached 1.5 m in length by virtue of the elongate projecting beak and trailing toes.

As *Kairuku* is one of the largest known penguins, we question published standing heights of >1.5 m for other penguins based on bones clearly smaller than those of *Kairuku*. The overestimates probably do not account for different proportions of extant and stem penguins, and also scale up overly generous sizes for the extant Emperor Penguin. Reported heights for Emperor Penguins in the popular literature vary greatly, typically ranging from 1.0 to 1.5 m. These secondary accounts typically lack specimen voucher numbers (some appear erroneously high) and the values are not clearly stated as standing heights versus lengths (namely, beak to tail or claw tips with the bird in swimming position). Standing height is rarely provided in scientific reports and most measurements are of length from beak tip to claws. Prévost (1961) recorded measurements from 86 wild individuals of *A. forsteri* and reported a maximum standing height of 1.08 m. Friedman (1945) measured 22 wild individuals and found a range of 0.83–0.97 m. Stonehouse (1975) summarized field, museum, and literature values for length of *A. forsteri* and calculated an average of 1.15 m, indicating a standing height close to 1 m. These values agree with our own observations of standing heights of 0.81–0.94 m obtained from 11 complete *A. forsteri* skins in the AMNH collections.

In summary, we interpret reported measurements above 1.0 m for Emperor Penguins as lengths rather than standing heights. Discrepancies between older fossil penguin size estimates and the dimensions indicated for *Kairuku* reflect lack of knowledge of body proportions in penguins, and the use of single fossil bones to extrapolate proportions from those of the Emperor Penguin skeleton. The largest fossil penguin species would have towered over living Emperor Penguins, but probably never reached typical human standing heights. Note that a large degree of error remains even when working with relatively complete skeletons. In *Kairuku*, the length of the neck is extrapolated from extant penguins. However, proportionally elongate cervical vertebrae have been noted in stem penguins (Jenkins, 1974; Jadwiszczak, 2006b) and future discoveries of more complete vertebral columns may support revising this estimate upwards. Of course, penguins assume a variety of postures in life and full extension of the neck (as in the ‘ecstatic display’ of mating pairs) or flexion of the neck (as in a huddled animal) can significantly increase or decrease height compared to the ‘neutral’ posture used to estimate height here.

One question that still remains open is the maximum size reached by penguins. *Pachydyptes ponderosus* is widely regarded as the largest penguin reported, but is known from only a coracoid, humerus, and carpometacarpus. These elements are extremely close in length to the corresponding elements of the largest *Kairuku* specimen, but are more robust. Direct scaling from the coracoid would suggest that *Pachydyptes ponderosus* was 115% the size of *Kairuku grebneffi*, whereas the humerus and carpometacarpus would instead suggest a slightly smaller animal. As shown in this study, there is little basis for accurate size estimation from single bones. Given the uniquely elongate trunk and slender flipper of *Kairuku*, it is quite plausible this taxon was taller than *Pachydyptes ponderosus* but also less massive.

## CONCLUSIONS

The pace of discovery and description of fossil penguins has accelerated dramatically in the past few years. Yet, few species are known from skeletons approaching the completeness of *Kairuku waitaki* and *K. grebneffi*. Whether the body plan of these taxa represents a general archetype for 'giant' penguin or specialization in a particular clade remains to be seen, though the stout hind-limb proportions at least seem to be restricted to *Kairuku* and a few other taxa. Isolated beak fragments suggest a variety of morphologies in localities such as Seymour Island (Jadwiszczak, 2006a; D.T.K., pers. observ. UCMP specimens); perhaps stem penguins had diverse feeding ecologies. *Kairuku waitaki* and *K. grebneffi* also add to the diversity of New Zealand's late Oligocene penguin fauna, which now includes 10 species (5 from the Kokoamu Greensand alone). Given the short span of the late Oligocene and the potential presence of undiscovered species, high diversity along the shores of the South Island is unquestioned. These levels are comparable to the species-rich Seymour Island penguin fauna in the late Eocene (Wiman, 1905; Myrcha et al., 1990; Jadwiszczak, 2006b, 2009) and add to growing evidence that penguins were significantly more abundant and diverse in the Paleogene than they are today.

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