

New penguin remains from the Pliocene of Northern Chile

STIG A. WALSH¹ & MARIO E. SUÁREZ²

¹Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK, and ²Museo Paleontológico de Caldera, Avenue Wheelwright 001, Caldera, Chile

Abstract

Until recently, all described fossil penguin species from South America were recovered from the Atlantic coast. The description of three fossil species of *Spheniscus* from Peru and Chile now allows a clearer estimate of the historical diversity on the Pacific coast. Here we describe a further new species from a Pliocene level of the Bahía Inglesa Formation, northern Chile. This taxon, the first to be described from this sequence, is based on a partial skeleton lacking a skull. These remains are clearly referable to the living genus *Pygoscelis*, and share a mosaic of characters with extant species of the genus. *Pygoscelis grandis* sp. nov. was around the size of a King Penguin, and therefore much larger than any extant *Pygoscelis* species. Our cladistic analysis places *P. grandis* within the *Pygoscelis* clade as the sister taxon of living representatives. Living species of *Pygoscelis* have a sub-Antarctic distribution, and the presence of this species slightly south of the Tropics during the Pliocene may relate to end Neogene global cooling.

Keywords: *Spheniscidae*, *Pliocene*, *South America*, *Bahía Inglesa Formation*

Introduction

The spheniscid fossil record of South America is particularly diverse, due in large part to the pioneering work of Ameghino (e.g. 1891, 1895) and Simpson (e.g. 1946, 1972). Around 12 fossil penguin species are currently recognised from Tertiary deposits of South America, making the continent second only to New Zealand in terms of fossil diversity. However, although fossil remains have long been expected on the South American Pacific coast, until the 1980s all spheniscid material was restricted to marine sequences of Patagonia (Fordyce and Jones 1990). The first penguin specimens to be recorded from the Pacific coast came from the mid-Miocene to late Pliocene Pisco Formation of Peru (Muizon and DeVries 1985). These remains were considered osteologically close to *Spheniscus* (Cheneval 1993), but despite the recovery of abundant specimens

including several complete and associated/articulated skeletons, none of these species were described until the present century (Walsh and Hume 2001; Stucchi 2002; Emslie and Correa 2003; Stucchi et al. 2003).

The first occurrence of fossil Spheniscidae from Chile was recorded by Walsh and Hume (2001). These abundant but isolated remains came from a bonebed horizon of the Bahía Inglesa Formation of northern Chile (Figure 1A,B) that was initially thought to be late Miocene to early Pliocene in age, but has since been dated as Late Miocene based on radiometric techniques (see below). The authors also regarded these Chilean remains as close to *Spheniscus*, but noted that they were around 25% larger than those of extant *Spheniscus humboldti*. No new species was erected because of their disarticulated state and the possibility that the remains might be referable to the more complete material from the Pisco Formation of Peru. Acosta Hospitaleche et al. (2002) later

Correspondence: S. A. Walsh, Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK.
E-mail: s.walsh@nhm.ac.uk

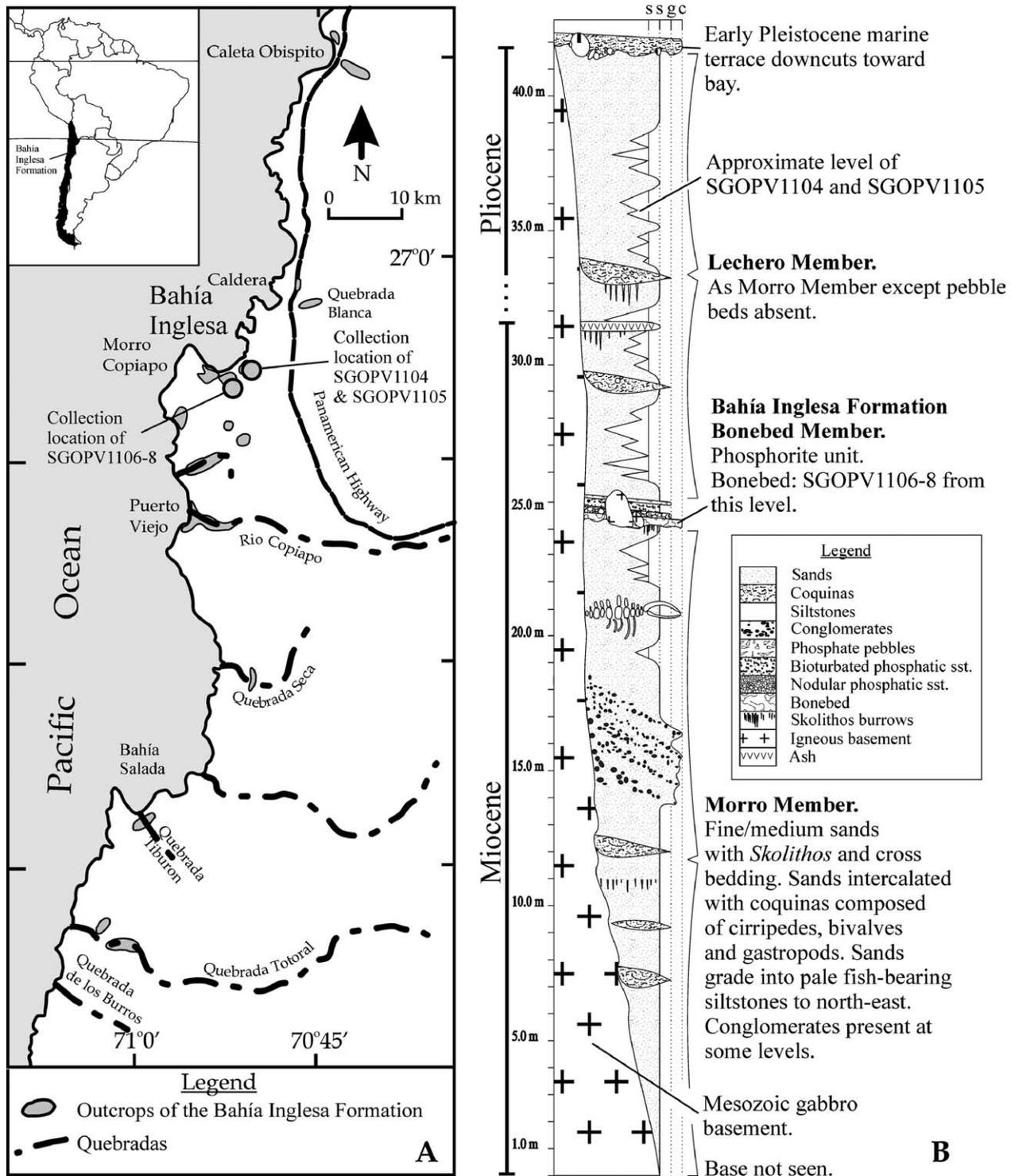


Figure 1. (A) Collection locality showing other outcrops of the Bahía Inglesa Formation on the northern Chile coast (after Marquardt et al. 2000). (B) Stratigraphy and age of the Bahía Inglesa Formation, with collection horizons for the material described here.

reviewed new material from the Bahía Inglesa site and listed the presence of at least five species, including *Palaeospheniscus* sp., *Paraptenydytes robustus*, *Paraptenydytes antarctica* and a new species of *Pygoscelis* (Acosta Hospitaleche pers. com., 2004). Although we have neither examined the material of Acosta

Hospitaleche et al. (2002) nor encountered specimens definitely referable to these species in the Bahía Inglesa Formation, we accept the possibility that they may be present in the sequence.

The recent description of *Spheniscus urbinai* (Stucchi 2002) and *Spheniscus megaramphus* (Stucchi

et al. 2003) from the Miocene of the Pisco Formation of Peru has allowed us to recognise that most material referred to cf. *Spheniscus* by Walsh and Hume (2001) probably belongs in *S. urbinai*. However, at least one recently recovered specimen, an incomplete rostrum (UOP/01/89), lacks the pronounced dorsal convexity seen in lateral view that is a distinguishing characteristic of *S. urbinai*, and is likely to be referable to *S. megaramphus*. Confirmation of the presence of this species must await recovery of more diagnostic material, but it is highly likely that the range of at least one of the Miocene Pisco Formation spheniscids extended 1600 km south, from Peru to Chile.

The first fossil species from the Pliocene of Chile, *Spheniscus chilensis*, was recently described by Emslie and Correa (2003). This material was recovered from the Pliocene of the Mejillones Formation, 550 km north of the Bahía Inglesa Formation. Around the size of living species, *S. chilensis* is clearly unlike the spheniscid remains previously recorded from the Bahía Inglesa site, although a humerus recently collected by one of us (SW) from a newly recognised Pliocene vertebrate-bearing horizon in the Bahía Inglesa Formation is very close to that described for *S. chilensis*. The possibility exists that this species is also present at the site, probably bringing the diversity for the formation to nine species.

Here, we provide a description of a new species from the formation. This material consists of an associated partial skeleton that was recovered by SW in 1999 from the same new horizon from which the putative *S. chilensis* humerus came, and is the first fossil penguin to be named from the formation. This new taxon is clearly referable to *Pygoscelis*, but was around the size of the extant King Penguin (*Aptenodytes patagonicus*) and, therefore, much larger than any living species of the genus. Since the *Pygoscelis* species mentioned by Acosta Hospitaleche et al. (2002) falls within the size range of living taxa (Acosta Hospitaleche, pers. comm., 2004), two species of *Pygoscelis* appear to have been present at the site.

All specimens described here are accessioned to the collections of the Museo Nacional de Historia Natural, Santiago, Chile. Specimen repository abbreviations are as follows: BMNH = British Museum of Natural History, London, UK; SGOPV = Museo nacional de historia natural, Santiago, Chile; UOP = University of Portsmouth, England.

Stratigraphy

The marine Bahía Inglesa Formation (Figure 1A) consists of over 42 m of siltstones, fine sands, shelly coquinas, pebble beds and phosphatites, and represents a shallow marine setting deposited within 10 km of the shore (Marquardt et al. 2000; Walsh 2002; Walsh and Naish 2002). In the type area 1 km

inland of Bahía Inglesa bay on the coast of north-central Chile (Figure 1A), these sediments were deposited into a series of grabens formed in the Mesozoic igneous basement (Godoy et al. 2003), today visible as a series of roughly NE–SW trending inliers. Three lithostratigraphic members are recognizable in this region; the coarse conglomeratic basal Morro Member (Unit 1 of Walsh and Hume 2001); the phosphorite Bahía Inglesa Formation Bonebed Member (Unit 2 of Walsh and Hume 2001), and the fine sand and siltstone Lechero Member (Unit 3 of Walsh and Hume 2001) from which SGOPV-1104 and SGOPV-1105 were recovered. A phosphatite bonebed with a lateral extent of at least 4.0 km² occurs at the base of the Bahía Inglesa Formation Bonebed Member. Three specimens referred to the species described here (SGOPV-1106–8) came from this horizon.

Based on microfossil biostratigraphy the Lechero Member is 4.5–2.6 Ma (Tsuchi et al. 1988; Ibaraki 1995). The shark assemblage of this member is characterized by the abundance of *Carcharodon carcharias* (Long 1993), and the additional presence of *Prionace glauca* provides good evidence supporting a Pliocene age for SGOPV-1104 and SGOPV-1105. However, an ash layer occurs within the Lechero Member, approximately seven meters above the top of the Bahía Inglesa Formation Bonebed Member. This provides a K–Ar age of 7.6 ± 1.3 Ma (Marquardt et al. 2000; Godoy et al. 2003), indicating that the lower part of the Lechero Member is late Miocene in age, and thus the bonebed and SGOPV-1106–8 are no younger than Tortonian. Although it is not possible to assign a precise age to SGOPV-1104 and SGOPV-1105, their provenance from several metres above the ash layer suggests an early Pliocene age for these specimens.

Systematic palaeontology

Sphenisciformes Sharpe, 1891

Spheniscidae Bonaparte, 1831

Pygoscelis Wagler, 1832

Type species: Pygoscelis papua (Forster, 1781)

New species: Pygoscelis grandis sp. nov. (Figures 2–5).

Derivation of name: grandis, Latin, “large”, in recognition of the strikingly large size of this species compared with extant species.

Holotype: A partial associated skeleton (SGOPV-1104) (Figure 2).

Topotype: Left tarsometatarsus (SGOPV-1105; Figure 2) missing the trochlea for digit IV, recovered from within one metre of SGOPV-1104 and believed to be from the same horizon.

Type horizon and locality: Lechero Member of the Bahía Inglesa Formation, ?early Pliocene, Bahía Inglesa (S27° 08' 37.8", W070° 50' 27.1"), Chile.

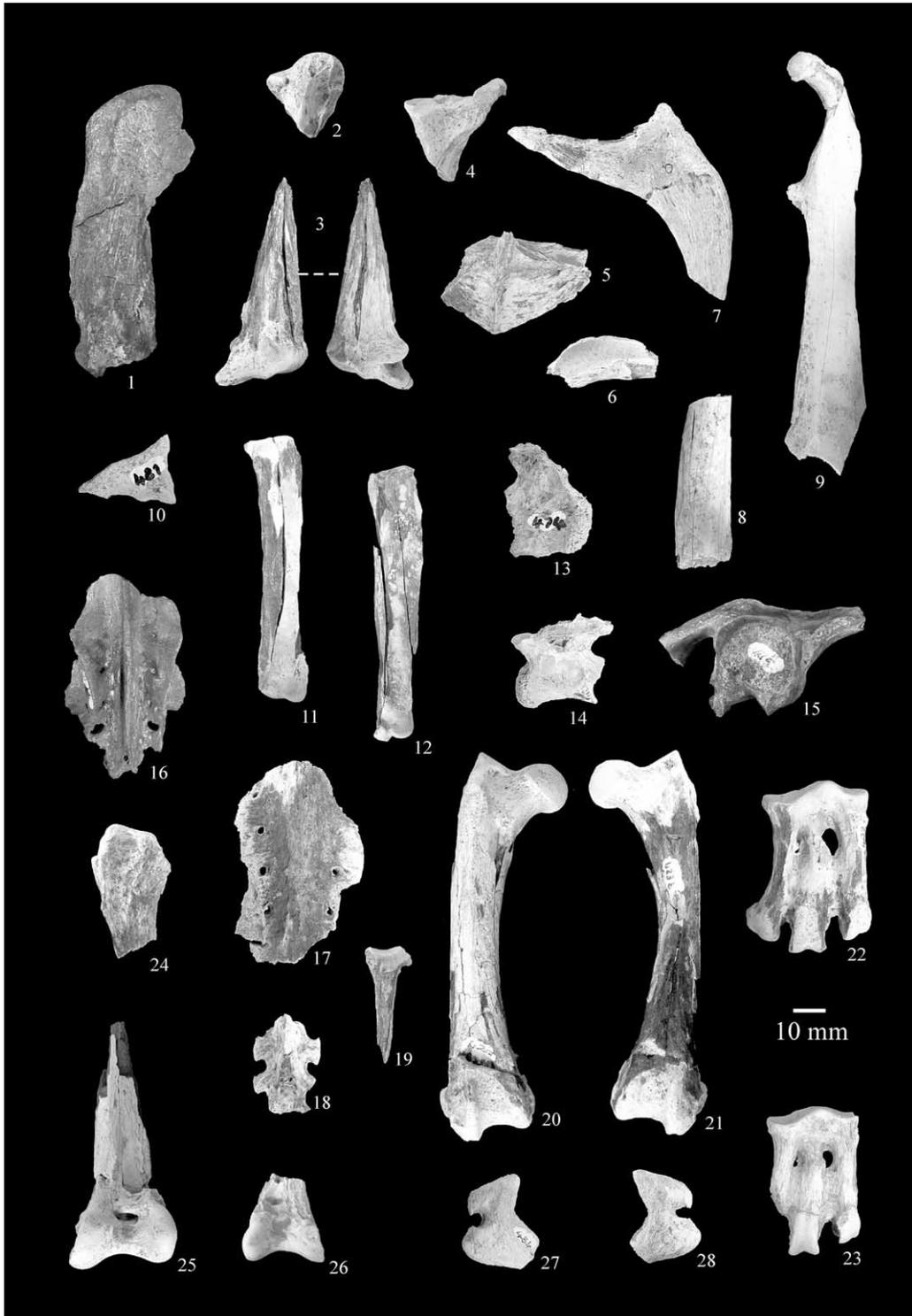


Figure 2. Selection of holotype and referred material of *Pygoscelis grandis* sp. nov. (2–14 and 17–28 are from SGOPV-1104; 1, SGOPV-1106; 15, SGOPV-1108; 16, SGOPV-1107 and 23, SGOPV-1105). 1, left humerus in caudal view; 2, caput fragment of right humerus in ventral view, showing development of tricipital fossa partition; 3, caudal and cranial view of distal portion of left humerus; 4, cranial portion of left scapular; 5–6, fragments of sternum; 7, lateral view of left cranial fragment of furculum; 8, mid portion of right coracoid and 9, left coracoid both in ventral view; 10, right ulnare; 11, left radius; 12, left ulna; 13–14, thoracic vertebrae in lateral view; 15, right pelvis in lateral view; 16–18, synsacral fragments in dorsal view; 19, proximal right fibula; 20, right and 21, left femora in cranial view; 22–23, left tarsometatarsi in dorsal view; 24, proximal and 25, distal left tibiotarsus fragments in cranial view; 26, distal right tibiotarsus fragment in cranial view; 27–28 left and right patellae.

Material: SGOPV-1104 comprises three fragments of sternum, left coracoid, mid portion of right coracoid, distal portion of left humerus, caput fragment of right humerus, right ulnare, left ulna, left radius, fragment of left furculum, proximal portion of left scapula, five thoracic vertebrae, pygostyle vertebra, synsacrum in four fragments, 13 ribs, left and right femora, left and right patellae, proximal and distal regions of left and right tibiotarsi, proximal right fibula, left tarsometatarsus, indet. phalange and 224 unidentified fragments.

Referred material: Left humerus missing distal extremity (SGOPV-1106) caudal portion of synsacrum (SGOPV-1107) and incomplete right pelvis (SGOPV-1108). All specimens were recovered from the bonebed and are hence late Miocene in age.

Preservation: Both SGOPV-1104 and SGOPV-1105 are heavily weathered and fragmentary as a result of extended exposure. Except for SGOPV-1106, which has lost much of its cortical bone, specimens recovered from the Bahía Inglesa Bonebed Member (SGOPV-1106–8) are well preserved.

Diagnosis: Distinguishable from other species of the genus by its large size and the following autapomorphies: craniocaudal compression of tibiotarsus not marked; extensor canal broad relative to diaphyseal width and situated on lateral margin of diaphysis; lateral proximal vascular foramen of tarsometatarsus larger than medialis, and by the following character complex: greatest diaphysial width of humerus >24%; tricripital fossa weakly bipartite; fusion of ilium and synsacrum absent; ilioischiatric foramen larger than diameter of acetabulum; femur curved in anterior view; tuberculae for the retinaculi m. fibularis well developed; medial condyle of tibiotarsus extends further than lateral condyle.

Description

Forelimb skeleton

The dorsal and ventral margins of both the radius and ulna (Figure 2(11,12)) are damaged, precluding determination of the shape of these elements. However, with a length of 81 and 87 mm respectively, they were clearly large and rather robust. The preserved regions nevertheless do not appear to have been particularly wide (as is seen in *Spheniscus*) and conform well to the overall morphology of *Pygoscelis*. A right ulnare (Figure 2(10)) is preserved, which is sharply triangular and most similar in shape to that of *P. papua*.

The humerus (Figure 2(2,3)) is fragmentary in the holotype, being represented by a portion of the head and distal extremity (right side) and by a fragment of the distal epiphysis (left side). However, a more complete *Pygoscelis*-type humerus (SGOPV-1106; Figure 2(1)) was collected from the bonebed and is

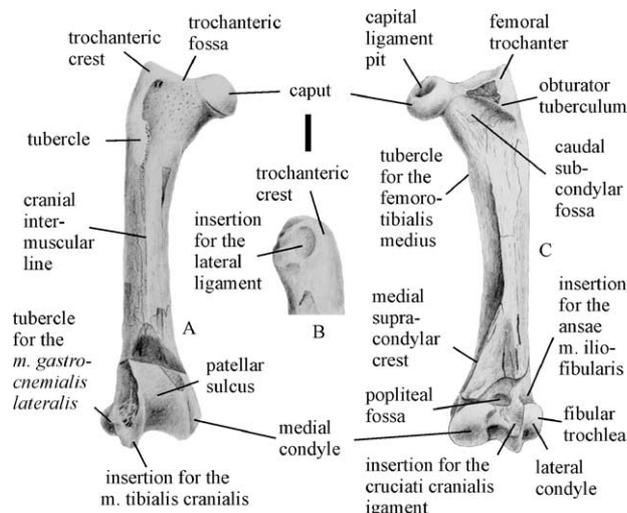


Figure 3. Right femur (SGOPV-1104) in A, cranial; B, lateral; and C, caudal views. Scale bar represents 10 mm.

referred to *P. grandis* as it is within the same size range as SGOPV-1104. At 95 mm long (reconstructed length approximately 105 mm) and 28 mm at its widest point, this specimen is comparatively short and extremely robust, with an estimated total length/maximum diaphysial width ratio of 0.26, as in *Aptenodytes* and *P. papua*. The shaft is arcuate as in all extant spheniscids (except *Eudyptula minor*) with a well-developed bicripital crest. The tricripital fossa is covered in matrix in SGOPV-1106, but is weakly bipartite in SGOPV-1104 (Figure 2(2)), as in other species of *Pygoscelis* (except *P. antarctica*, which is strongly bipartite), *Eudyptula minor* and *Spheniscus*. The medial crest is ventrally directed. In SGOPV-1104 the ventral tubercle for the humerus-ulna articular ligament is well developed, but the dorsal tubercle and dorsal condyle are not preserved in any of the specimens, preventing measurement of the shaft-trochlea angle. As in all extant *Pygoscelis*, the proximal trochlear process (Figure 2(3)) extends beyond the ventral margin of the shaft (Bertelli and Giannini, 2005).

One coracoid missing small areas of its medial, lateral and proximal margins is preserved (Figure 2(9)). The shaft (134 mm long) is straight, with a strongly ventrally-directed acrocoracoid (almost 90 degrees). In *Pygoscelis tyreei*, the only other fossil *Pygoscelis* species known, the procoracoid forms a fenestra (Simpson 1972), unlike extant *Pygoscelis*. The condition in SGOPV-1104 is not possible to determine due to damage in this region.

A left cranial fragment of furculum (Figure 2(7)) was preserved. This strongly arcuate element is flat on the medial side, but bears a marked concavity on the lateral side, with a ridge extending along the dorsal margin of the lateral surface. In *Aptenodytes patagonicus* the concavity is present on both sides of the furculum, while *A. forsteri* lacks the cavity altogether;

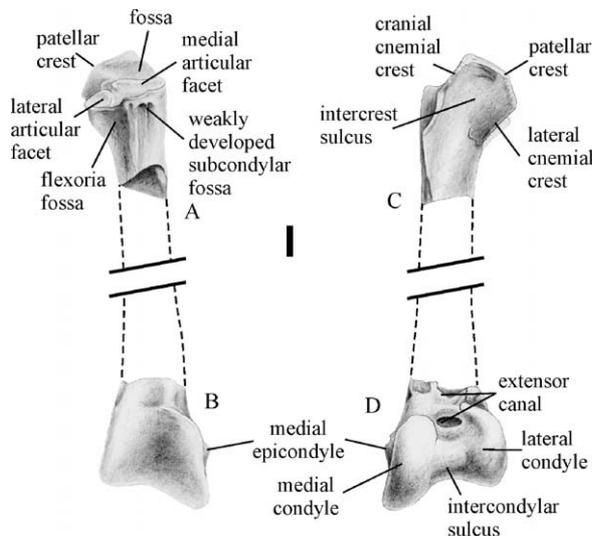


Figure 4. Left tibiotarsus fragments (SGOPV-1104). A and B, caudal view; C and D, cranial view. Scale bar represents 10 mm.

in *Pygoscelis* the concavity is found in *P. papua*. In all Spheniscidae examined, this region of the furculum is markedly more medially concave than in SGOPV-1104. A cranial fragment of left scapular (Figure 2(4)) including the humeral facet also was recovered, but is too fragmentary for useful description.

Appendicular skeleton

The synsacrum is known only from fragments of the posterior region (Figure 2(16–18)). The dorsal crest is well developed but rather narrow and, unlike in *Spheniscus*, does not rise higher than the dorsal margin of the rectimarginate iliosynsacral suture. The ventral surface is flat with a moderately well-developed ventral sulcus, as in *P. papua*. It is possible to unite SGOPV-1107 and SGOPV-1108 (pelvis), indicating that they came from an individual of the same size, and potentially even the same individual.

The vertebrae recovered with SGOPV-1104 (Figure 2(13,14)) are all poorly preserved, but are otherwise unremarkable within the Spheniscidae.

Hindlimb skeleton

A well-preserved right pelvis (SGOPV-1108; Figure 2(15)) missing the cranial portion of the ilium, the caudal portion of the ischium, and all of the pubis was recovered from the Bahía Inglesa Formation Bonebed, but this element is not preserved in SGOPV-1104. The acetabular foramen is larger than the ilioischial foramen (as in *P. antarctica* and *Spheniscus humboldti*), and noticeably flared. The preacetabular tubercle is poorly developed. The pelvis and synsacrum were not fused in either SGOPV-1104

or referred specimens. Unlike other extant genera, fusion is common, although not universal in species of *Pygoscelis*; no fusion was observed by us in any specimens of *Pygoscelis adelaie* examined.

The femur (Figures 2(20,21) and 3(a–c)) lies within the size range of *Aptenodytes forsteri*. The diaphysis is curved such that the medial margin is concave as in *P. papua*, *Eudyptula minor* and *Eudyptes crestatus*. The ligament pit of the head is large, and occupies some 25% of the articular surface of the head. The trochanteric crest is well-defined and prominent, is rounded in lateral view, and bears a well-developed distal tubercle. The femoral trochanter and obturator tuberculae form a short equilateral triangle, shorter than in *Spheniscus*. Both the cranial and caudal intramuscular lines are prominent and well-defined. The lateral epicondyle is not well developed, and the tubercles for the attachment of the ansa iliofibularis are flat and weak.

Both tibiotarsi are represented only by their proximal and distal epiphyses (Figures 2(24–26) and 4(a–d)). The sub-condylar fossa (for example seen in *Spheniscus*) on the caudal proximal epiphysis is shallow and weakly bipartite. Like *Aptenodytes*, *Spheniscus* and *Eudyptula* the proximal region is not strongly craniocaudally compressed; in living *Pygoscelis* and all *Eudyptes* examined compression is strong. In SGOPV-1104 the fibular crest is too damaged to determine its shape. Unlike extant *Pygoscelis* the extensor canal is broad and situated on the lateral margin of the cranial surface. The medial condyle extends further than the lateral condyle, as in *P. papua* and *P. adeliae*, but not in *P. antarctica*.

The tarsometatarsus (Figures 2(22,23) and 5(a,b)) is very similar in overall morphology to that of *P. antarctica*, but around the size of the same element in *Aptenodytes patagonicus*. The mean elongation index is 1.85. The intercotylar prominence is pronounced and remains the same height from its dorsal margin to where it meets the hypotarsus. The tuberosities for the extensor ligaments are prominent, elongate and well

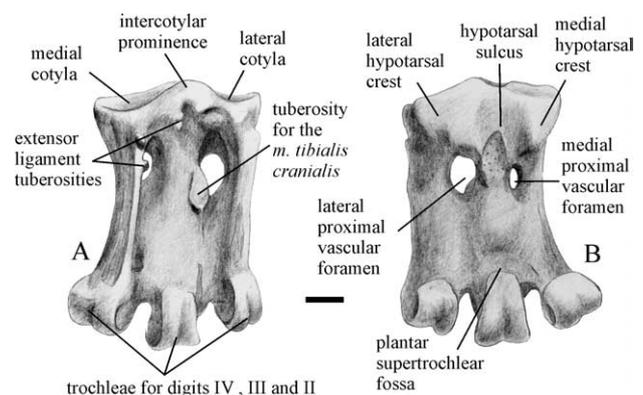


Figure 5. Left tarsometatarsus (SGOPV-1104) in A, dorsal and B, plantar views. Scale bar represents 10 mm.

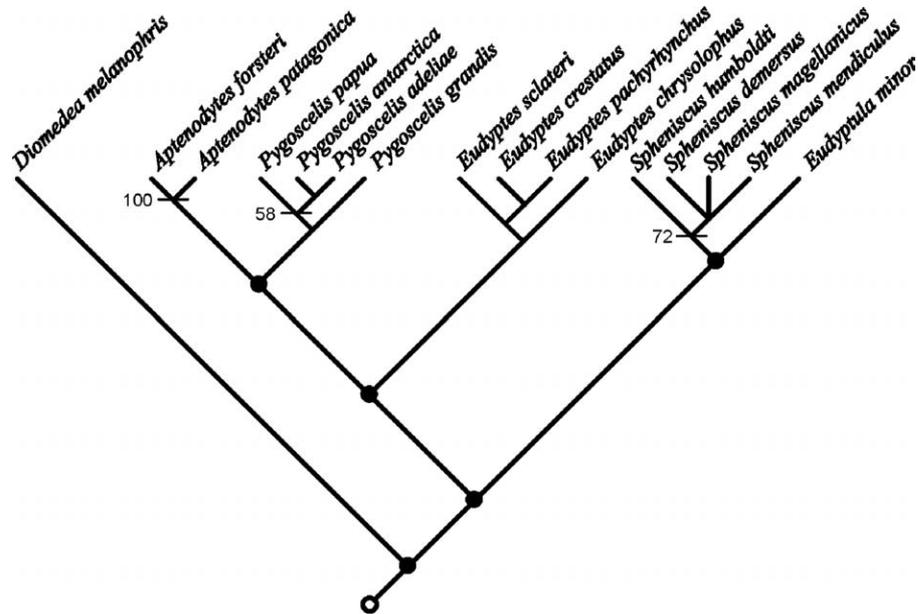


Figure 6. Strict consensus of nine most parsimonious trees of length 85 steps. See text for discussion.

defined. The tuberosity for the *m. tibialis cranialis* is well defined and raised but flat, and situated on metatarsal III. Two well-developed calcaneal ridges are discernable. As in *Aptomodytes* and living *Pygoscelis*, the plantar exit of the medial proximal foramen is below the medial calcaneal ridge but, unlike these taxa, the lateral proximal vascular foramen is larger than the medial.

Phylogenetic analysis

In this analysis, 37 osteological characters (13 of which were multi-state) of the skull and postcrania were coded for *Pygoscelis grandis*, 14 extant penguin taxa and the outgroup, *Diomedea melanophris* (Appendix 1). A list of comparative material is given in Appendix 2. Of the 17 recognised extant penguin species, *Eudyptes robustus*, *E. chrysolophus* and *Megadyptes antipodes* were excluded due to insufficient comparative material. *Eudyptula minor albosignata* was coded as *Eu. minor*. The data matrix (Appendix 2) was analysed using PAUP* 4.0 b10 (Swofford 2002), with all characters run unordered and with equal weighting, with *D. melanophris* defined as the outgroup.

We note from our comparative studies that intraspecific variability of osteological characters is not only common in living Spheniscidae, but is often rather pronounced (particularly in *Spheniscus*). Although the tendency toward more than one character state within the same taxon can be phylogenetically informative, polymorphic characters arguably lack utility for species diagnosis in fossil forms, where well-defined character states are necessary for identification of isolated material.

Since most fossil penguin species have been and continue to be erected on the basis of such isolated material (Fordyce and Jones 1990), we chose to exclude from the analysis characters we had observed to be polymorphic.

A branch-and-bound search found nine trees of equal length 85, with a consistency index of 0.5647, retention index of 0.6574 and a rescaled consistency index of 0.3712. In all nine trees *P. grandis* occupies the same position (*P. grandis* (*P. papua* (*P. adeliae* + *P. antarctica*))), strongly supporting inclusion of SGOPV-1104 in *Pygoscelis*. However, bootstrap analysis (2000 replicates) returned a support value of only 58% (Bremer support = 1) for *Pygoscelis* excluding *P. grandis*. *Eudyptes* is unresolved, with five of the nine trees finding *E. chrysolophus* outside the clade and, in three of those, as sister taxon to *Aptomodytes* + *Pygoscelis*. An *Aptomodytes* clade is well supported (bootstrap = 100%, Bremer support = 3). *Eu. minor* and *Spheniscus* are sister groups in all trees, although the topology within *Spheniscus* is variable. Although *Spheniscus* received relatively good support values (bootstrap = 72%, Bremer support = 1), *Eudyptes* was not supported. A strict consensus tree was calculated from the nine recovered trees (Figure 6).

Discussion

The exclusion of two extant penguin taxa from this data set is likely to alter the rooting and topology of any recovered trees, as would the inclusion of other outgroup taxa. However, the intention of our phylogenetic analysis was to provide support for

inclusion of *P. grandis* sp. nov. in *Pygoscelis* rather than a detailed analysis of relationships within extant Spheniscidae (for a comprehensive analysis of extant spheniscid relationships using combined data sets see Bertelli and Giannini 2005). Our phylogenetic results are at least consistent with comparisons of osteological specimens, where *P. grandis* shares some features with *P. adeliae* and *P. antarctica*, but overall is more similar to *P. papua*.

Nevertheless, placement of the new species as sister to *P. papua* (*P. antarctica* + *P. adeliae*) is inconsistent with Bertelli and Giannini's (2005) analysis of mitochondrial sequence data. Although these authors failed to recover a *Pygoscelis* clade, *P. papua* and *P. antarctica* also formed a group in their strict consensus cladogram (Davis and Renner 2003). Bertelli and Giannini (2005) also conducted an analysis of 159 morphological, integumentary, mycological and behavioural characters that did recover *Pygoscelis*, albeit with weak support. In this an alternative arrangement of *P. antarctica* (*P. papua* + *P. adeliae*) was recovered, although the strict consensus of an analysis that used these characters combined with the molecular data produced an arrangement similar to that of the molecular analysis, but with better support.

Although Bertelli and Giannini's (2005) analyses included a wide range of data, we suspect that our results would in any case have differed because our data matrix includes only nine cranial characters, whereas those authors used 35. The postcrania of modern penguins is relatively conservative (Fordyce and Jones 1990) and the skull is likely to be comparatively more informative. However, because SGOPV-1104 lacks a skull it was necessary for the present analysis to concentrate on postcrania. If skull material of *P. grandis* is ever recovered the position of this species within *Pygoscelis* is likely to change, but considering our analysis is based only on postcranial material, inclusion of this new species in *Pygoscelis* is unlikely to be affected. Relatively weak support for a *Pygoscelis* clade appears to be consistent in previous morphological analyses, and the poorer support for inclusion of *P. grandis* in the clade should not in itself be a cause for concern.

The topology of our strict consensus tree diverges to give two inclusive clades: (*Eudyptes* (*Pygoscelis* + *Aptenodytes*)) and (*Spheniscus* + *Eudyptula*). This arrangement is almost identical to the consensus tree generated from osteological data given by O'Hara (1989), although that study included *Megadyptes*, and *Aptenodytes* was found basal to *Pygoscelis*. The arrangement is also similar to the phylogeny based on integument and behaviour presented by Giannini and Bertelli (2004), and on a variety of character types (excluding molecular) in Bertelli and Giannini (2005). Because we were unable to include *Megadyptes* our results are not

directly comparable with those authors, but consensus appears to be emerging with regard to the existence of a *Spheniscus* + *Eudyptula* clade.

Bertelli and Giannini's (2005) biogeographic hypothesis indicates that *Spheniscus* was a relatively recent radiation that occurred after the ancestor ("Clade A", p. 217) reached South America following the eastward-flowing cold currents. The dominance of fossil *Spheniscus* species in Miocene sequences along the Pacific coast of South America is certainly consistent with this radiation route, and provides some evidence of the minimum age of this vicariance event. The observed variability of character states in species of *Spheniscus* is also supportive of a relatively recent radiation event, and we suspect that better resolution of the arrangement of species in our cladistic analysis would have been possible had we included polymorphic characters, as they may relate to transitional morphological states.

Contrary to Zusi's (1975) argument based on morphology alone, Bertelli and Giannini (2005) were only able to find weak support for a *Pygoscelis* + *Aptenodytes* clade, and did not recover this relationship in their combined analysis. The results of our study are more consistent with older morphological analyses, but we nevertheless regard the outcome of the combined approach of Bertelli and Giannini (2005) as the best current estimate of spheniscid relationships, at least for extant taxa.

Livezey (1989) found *Pygoscelis* to exhibit the strongest degree of sexual dimorphism of all extant species. We estimate that *Pygoscelis grandis* was around the size of the living King Penguin (*Aptenodytes patagonicus*), and therefore, significantly larger than any living representative of the genus. This extant to fossil species size difference is greater than that observed between male and female individuals in specimens of any living species we have examined, and we are confident that the material of Acosta Hospitaleche et al. (2002) is referable to a second, smaller, species of *Pygoscelis*, rather than to a female *P. grandis*. Furthermore, we have examined tibiotarsi from the Bahía Inglesa Bonebed Member that display the characteristic cranio-caudal compression of the proximal diaphysis evident in species of *Pygoscelis*, and are very close to the same element in *P. antarctica*. These specimens are within the size range expected from the size of the cranial material of Acosta Hospitaleche et al. (2002), and exhibit a far greater degree of proximal region cranio-caudal compression than in *P. grandis*. Because *P. grandis* is also represented in the Late Miocene bonebed fauna, it seems likely that there were at least two species of *Pygoscelis* in the Bahía Inglesa region at the end of the Miocene.

Although species of *Pygoscelis* today have a characteristically sub-Antarctic distribution, vagrants of *P. papua* have been reported from as far north as

43°S on the Atlantic coast of South America, and also reach New Zealand and Australia (Davis and Renner 2003). It is, however, surprising that less than five million years ago the genus was present on the Pacific coast at a present day latitude of 27°S. One possibility is that these specimens represent the chance preservation of individuals that were vagrants at extreme range. However, although by no means abundant at the site, the presence of at least three individuals (two from the Lechero Member and at least one represented by non-replicated elements from the Bahía Inglesa Bonebed Member) suggests that this is unlikely. Moreover, the smaller *Pygoscelis* species reported by Acosta Hospitaleche et al. (2002) is represented by at least three skulls (Acosta Hospitaleche pers. com., 2004) from the Bahía Inglesa Bonebed Member, lending support to the idea that both species were comparatively frequent visitors to the region. The condensed nature of the Bahía Inglesa Bonebed Member precludes determination of whether the two species were coeval inhabitants of the area, but as the smaller species has so far not been recovered from Pliocene levels, its presence in the region after the Miocene cannot presently be confirmed.

A second possibility is that the trend toward global cooling at the end of the Neogene resulted in cold enough temperatures and suitable feeding conditions for colonies of these penguins to be established in southern Chile. If so, *Pygoscelis grandis* may have been a seasonal visitor to the region. As noted by Simpson (1972) for *P. tyreei*, we cannot assume that the thermal requirements and behaviour of this extinct species would have equated those of living representatives. For now the significance of two species of a genus of penguin that is today restricted to sub-Antarctic waters must remain speculative.

Fossil penguins are a particularly important component of the Bahía Inglesa Formation avifauna, and fossil seabirds also are likely to be present at other outcrops of the formation along the Chilean coast (Figure 1A). Continued collection from these, and other poorly prospected localities will likely increase our knowledge of spheniscid diversity in the eastern Pacific.

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Appendix 1. List of characters.

Skull		
1. Jugal bar	Straight	(0)
	Slightly curved	(1)
	Strongly curved	(2)
2. Mandible	Ramus deepened close to mid point	(0)
	Close to even depth along ramus	(1)
3. Mandible thickening	< 10% of total length	(0)
	10–18% of total length	(1)
	> 18% of total length	(2)
4. Temporal fossae	Separated at midline by raised area	(0)
	Meet or almost meet at midline	(1)
5. Temporal crest	Weakly developed	(0)
	Strongly developed	(1)
6. Transverse nuchal crest	Poorly developed or absent	(0)
	Well developed	(1)
7. Lateral edge of supraorbital fossae	Constant width	(0)
	Narrows rostrally	(1)
	Thickening absent	(2)
8. Width of the posterior process of the articular in dorsal view	Broad, roughly the size of the articular surface	(0)
	Narrow, smaller than articular surface	(1)
9. Length of the posterior process of the articular in dorsal view	Short, roughly the length of the articular surface	(0)
	Equal to, and with partial shelf to internal process	(1)
	Longer than internal process and medially concave	(2)
Coracoid		
10. Coracoid fenestra on medial margin	Present or partially formed	(0)
	Absent	(1)
Humerus		
11. Greatest diaphysial width relative to the total length	≤ 20%	(0)
	21–23%	(1)
	≥ 24%	(2)
12. Diaphysial shape	Diaphysis approximately uniform width	(0)
	Widest in middle	(1)
	Widest distally	(2)
13. Curvature of diaphysis	Straight	(0)
	Slightly arcuate	(1)
14. Tricipital fossa	Not bipartite	(0)
	Weakly bipartite	(1)
	Strongly bipartite	(2)
15. Angle between diaphysis and trochleae	< 45°	(0)
	45–55°	(1)
	56–65°	(2)
Ilium		
16. Fusion with synsacrum	Complete or tendency to fuse	(0)
	Absent	(1)
17. Preacetabular iliac blade expansion	Anterior portion expanded	(0)
	Expanded region more proximal	(1)
18. Ilioschiatic foramen size relative to acetabulum	Larger	(0)
	Approximately equal	(1)
	Smaller	(2)
19. Ilioschiatic foramen occluded dorsally by synsacrum	Yes	(0)
	No	(1)

Appendix 1: continued

Femur		
20. Diaphysis in anterior view	Straight	(0)
	Curved	(1)
21. Posterior intermuscular scar	Weak	(0)
	Strong	(1)
Patella		
22. Cranial margin	With shallow or no groove	(0)
	With deep semi-angular groove	(1)
	With round enclosed or almost enclosed foramen	(2)
Tibiotarsus		
23. Length relative to femur	> 2 × femoral length	(0)
	< 2 × femoral length	(1)
24. Craniocaudal compression of proximal region	Not marked	(0)
	Marked	(1)
25. Extensor groove width relative to width of distal diaphysis	Broad	(0)
	Narrow	(1)
26. Position of extensor groove: on distal diaphysis	Lateral margin	(0)
	Central	(1)
27. Fossa flexoria	Absent	(0)
	Present	(1)
28. Fibular crest	Rounded	(0)
	Angular	(1)
29. Retinaculi m. fibularis	Poorly developed	(0)
	Well developed	(1)
30. Distal extension of condyles	Lateral extends further than medial condyle	(0)
	Equal extension	(1)
	Medial extends further than lateral condyle	(2)
Tarsometatarsus		
31. Fusion of metatarsals	Complete (only one visible)	(0)
	Shallow intertarsal grooves	(1)
	Deep intertarsal grooves	(2)
32. Mean elongation index	≥ 2.5	(0)
	≤ 2.4	(1)
33. Tubercle of the tibialis anticus	Flat	(0)
	Raised	(1)
34. Medial proximal foramen exit on plantar surface	Medial to inner calcaneal ridge	(0)
	Below inner calcaneal ridge	(1)
35. Proximal foramina in dorsal view	Lateral larger than medial	(0)
	Equal in size	(1)
36. Number of well-developed hypotarsal crests	Four	(0)
	Three	(1)
	Two	(2)
37. Hypotarsal channel	Present	(0)
	Absent	(1)

Appendix 2: Comparative material

All comparative material held within the collections of the Natural History Museum, Tring. All specimens are full or partial skeletons unless stated.

Diomedea melanophris. 1884.2.29.23; S/1963.28.2; skull—1914.11.25.2. *Aptenodytes patagonicus*. 1846.4.15.33; 1846.4.15.31; 1846.4.15.32; S/1972.1.24; S/2000-12.1; S/1952.1.28; S/1952.1.29. *Aptenodytes forsteri*. 1846.4.15.26; 1846.4.15.27; 1846.4.15.28; 1850.9.7.2; 1905.12.30.419; 1998.55.2; S/1972.1.25. *Pygoscelis papua*. 1860.12.19.5; 1884.3.26.1; 1895.7.4.1; 1900.8.17.1; S/2001.45.2; S/1952.3.135; 1846.4.15.29; 1895.7.4.1; 1898.7.12; skulls—1898.7.1.1; S/1952.1.30; S/1973.66.5. *Pygos-*

celis adeliae. 1849.10.2.2; 1910.11.5.1; 1846.4.15.34; 1850.9.7.1; S/1952.1.31; S/1952.1.32; S/1952.1.33; S/1952.1.34; S/1952.1.35; S/1952.1.36; S/1965.10.1; 1966.4.2; skull—S/1952.1.37. *Pygoscelis antarctica*. S/1973.66.6; S/1966.4.1; skull—1844.1.18.87. *Eudyptes crestatus*. 1898.7.1.12; 1898.7.1.13; 1898.7.1.14; 1898.7.1.15; 1852.1.17.92; 1869.2.24.6; S/1956.14.1; S/1956.14.2; S/1952.1.39; S/1952.1.136; 1998.12.6; S/1964.14.2; S/1964.14.1; S/1852.3.136; skulls—S/1973.30.1; S/1973.30.2. *Eudyptes sclateri*. S/1952.1.26; S/1952.1.38. *Eudyptes pachyrhynchus*. S/1972.1.26. *Eudyptes chrysolophus*. S/1952.1.40; skulls—S/1952.3.137–140; S/1984.94.1; S/2001.36.1; S/2001.36.2;

S/2001.36.3. *Eudyptes schlegeli*. S/1952.3.142. *Eudyptula minor*. S/2002.2.1; S/1966.51.1; 1896.2.16.38; S/1952.1.41. *Eudyptula albosignata*. S/1881.1.17.105; skull-S/1952.3.143. *Spheniscus demersus*. S/1998.23.2; 1905.7.23.1; 1898.7.1.8; 1898.7.1.9; S/1952.3.144; S/1998.48.24. *Spheniscus humboldti*. S/1998.12.8; S/2000.7.1;

S/1961.15.1; S/1952.1.42; S/1998.12.1; skull-S/2001.50.16. *Spheniscus magellanicus*. 1891.7.20.133; S/1952.1.43; S/2001.45.1; S/1972.1.27; 1869.2.27.7; *Spheniscus mendiculus*. skulls-S/1973.1.3; S/1973.1.1; S/1973.1.2. *Megadyptes antipodes*. Skull-1852.1.17.11; sternum with coracoids-1880.10.25.3.

Appendix 3: Data matrix.

A forsteri	11000	10001	22121	11200	11100	01112	11011	21
A patag	11000	10001	22121	11200	01100	01012	11011	21
P papua	20000	00001	21111	00211	02111	11112	21111	21
P antar	20100	01000	11121	00010	02111	11101	21111	21
P adeli	20100	01001	11111	10210	02111	11112	21111	21
Eu mino	10100	12100	02010	101?1	02101	11012	21100	11
E crest	20200	10??0	12120	102?1	11110	01112	21100	21
E chrys	20200	10??0	02121	?????	?????	?????	??0?	??
E pachy	20200	10??0	12121	102?0	1?110	11111	2?100	21
E sclat	20200	10???	1212?	102?0	01110	01102	2?10?	21
S demer	10111	12120	12110	10210	11101	11102	21100	21
S magel	10111	11120	12111	10110	11100	11112	21100	21
S humbo	10111	12120	12110	10010	01100	11112	21100	21
S mendi	10111	12120	?21??	10110	11100	111?2	21100	21
P grand	?????	?????	2111?	1?011	02100	01?12	21110	21
D melan	01100	00??0	00000	000?0	00000	00100	00000	00