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New Series, Vol. 8, No. 4

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**A NEW SPECIES OF PENGUIN  
FROM THE LATE MIOCENE OF CHILE,  
with Comments on the Stratigraphic Range of *Palaeospheniscus***

by  
**Richard D. Benson**  
Research Associate  
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**A New Species of Penguin from the Late Miocene of Chile,  
with Comments on the Stratigraphic Range of *Palaeospheniscus***

by Richard D. Benson

*Abstract.* A late Miocene penguin skull from Chile, labelled “species undetermined” by a commercial fossil dealer and obtained by the Science Museum of Minnesota, is a new species provisionally referred to *Spheniscus*. An unknown number of like skulls belonging to this same new species have been placed on the commercial fossil market, sometimes with the identification “*Palaeospheniscus* sp.” The named species of *Palaeospheniscus* are all early Miocene in age and are not contemporary with this new species, but several unnamed species of *Palaeospheniscus*, known from fragmentary remains, appear in the middle, and perhaps also late, Miocene.

**Introduction**

Specimen P2001.10.2, a fossil penguin skull lacking its beak (Fig. 1), was purchased at the 2001 Tucson Gem and Mineral Show and donated to the Science Museum of Minnesota. The specimen’s label gave its formation and age as “Huarra Formation, Antofagasto [*sic*], Chile” and “Early Pliocene”. The specimen from Antofagasta is actually of late Miocene age.

**Geological Setting**

The Huarra Formation, as it is often called in English-language websites, is called the Bahía Inglesa Formation in paleontological literature (e.g. Rojo 1985, Walsh and Hume 2001, Acosta Hospitaleche and Canto 2005). The three members of the Bahía Inglesa Formation are (1) the Morro Member, dated to middle-to-late Miocene on the basis of its shark fauna, (2) the Bonebed Member, 7 m beneath an ash layer dated  $7.6 \pm 1.3$  Ma, and dated by its shark fauna as late Miocene, and (3) the late Miocene-to-Pliocene Lechero Member, which contains the 7.6 Ma ash layer, but the upper part of the member is dated 4.5-2.6 Ma on the basis of its foraminifers (Walsh and Suárez 2006). The Morro and Lechero members both consist of cross-bedded fine-to-medium sands, and the intervening Bonebed Member of phosphatic arkose (Walsh and Suárez 2006). Cavities within specimen P2001.10.2 contain the fine-grained, slightly effervescent, yellowish brown phosphatic arkose (S. Evanoff, personal communication, 2015),

DORSAL

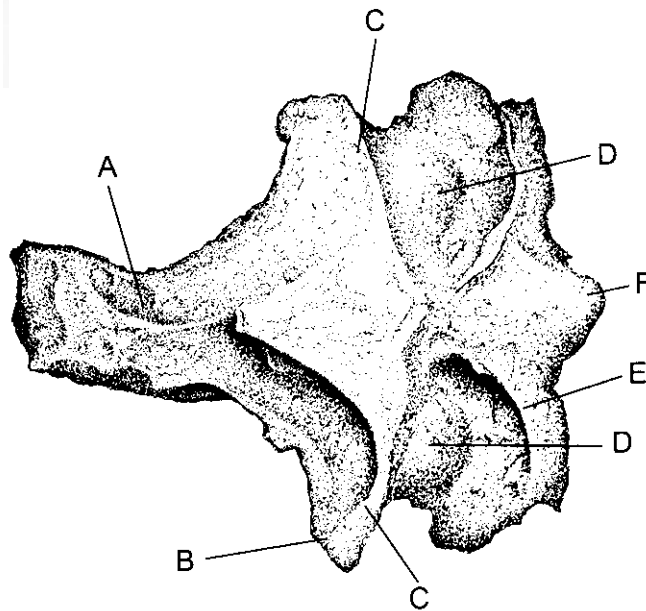


Figure 1. Skull of *Spheniscus anglicus*, sp. nov., P2001.10.2, natural size. **a** and **b**, dorsal view; **c** and **d**, posterior view. A, nasal fossa; B, postorbital process; C, temporal crest; D, temporal fossa; E, nuchal crest; F, cerebellar prominence; G, foramen magnum.



POSTERIOR

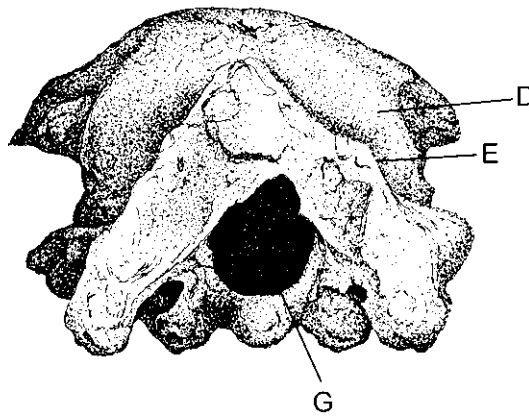


Figure 1. Skull of *Spheniscus anglicus*, sp. nov., P2001.10.2, natural size. **a** and **b**, dorsal view; **c** and **d**, posterior view. A, nasal fossa; B, postorbital process; C, temporal crest; D, temporal fossa; E, nuchal crest; F, cerebellar prominence; G, foramen magnum.

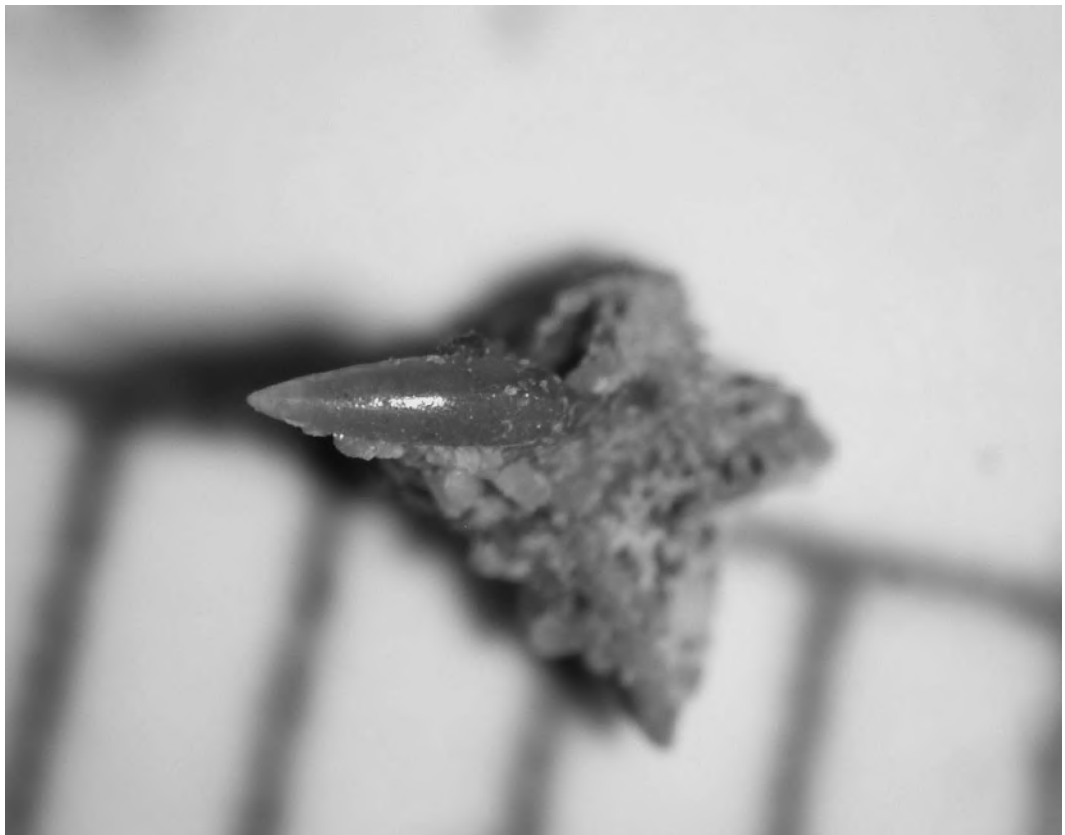


Figure 2. Shark dermal denticle recovered from braincase of P2001.10.2. The specimen is reclining on a scale in millimeters.

typical of the Bonebed Member. Among the samples of matrix taken from the foramen magnum of the skull was a shark dermal denticle (L. Hallgren, personal communication, 2015), also yellowish brown in color (Fig. 2). Other penguin material, but not including a skull, has been collected from the Lechero Member and assigned to *Pygoscelis* sp. (Walsh and Suárez 2006).

Systematic Paleontology

Class Aves

Order Sphenisciformes

Family Spheniscidae

*Spheniscus anglicus*, sp. nov.

*Description.* P2001.10.2 represents a fairly large penguin, smaller than *Aptenodytes forsteri* (Emperor Penguin) and *A. patagonicus* (King Penguin), but larger than any of the modern species of any of the other modern genera. P2001.10.2 is a cranium without a rostrum. The fossil's color is the Moderate yellowish brown of Goddard et al. (1963). Only the top and back of the cranium are at all well-preserved, the ventral parts of the skull being also lost. The temporal fossae are very wide, and are much deeper posteriorly than anteriorly, so as to display a bulbous cranium; roughly triangular in shape, they narrow medially as blunt points at the cranial midline. The temporal crests are very slightly concave (almost straight-lined) at the temporal fossae; the lateral ends of the crests are slightly anterior to the medial ends. The nuchal crests are strongly concave at the temporal fossae. The nasal fossae are well-developed and almost meet at the midline but are smaller than the temporal fossae. The postorbital process is stubby and projects laterally. The cerebellar prominence is rounded but narrower than in the early Miocene *Paraptenodytes antarcticus* and in modern penguins. The foramen magnum is subcircular, slightly wider than high. The occipital condyle is oval, wider than high, as is typical for penguins. For measurements, see Table 1.

*Etymology.* Although the Anglican clerical biretta in top view, with its triangular, opposite, underfolded parts meeting at the midline beneath the opposite overfolded parts, vaguely resembles the skull of *S. anglicus* in dorsal aspect, with its triangular temporal fossae beneath the anterior and posterior portions of the skull table, the species is named for the Bahía Inglesa Formation (Latin *anglicus*, *anglica* = Spanish *ingleso*, *inglesa*). The name would also appear to be in the format of other penguin species epithets such as *antarcticus*, *magellanicus*, and

*patagonicus*.

*Type locality, horizon, age.* Chile, Antofagasta; Bahía Inglesa Formation, Bonebed Member; late Miocene, Early Hemphillian equivalent, absolute age ~8 Ma.

Table 1. Skull measurements in millimeters of *Spheniscus anglicus*, sp. nov., and other penguins (from Stucchi 2002, Stucchi et al. 2003, Acosta Hospitaleche and Gasparini 2006).

	<b>A</b>	<b>B</b>	<b>C</b>	<b>D</b>	<b>E</b>	<b>F</b>	<b>G</b>
<i>Spheniscus anglicus</i>	77	65	18	13	14	8	6
<i>Spheniscus humboldti</i>	59	48	13	11	11	7	4
<i>Spheniscus magellanicus</i>	61	51	12	11	11	7	4
<i>Spheniscus mendiculus</i>	51	41	11	9	10	5	3
<i>Spheniscus megaramphus</i>	78	74	21	14	14	9	7
<i>Spheniscus urbinai</i>	76	73	20	15	15	-	-
<i>Aptenodytes forsteri</i>	87	67	17	15	15	9	6
<i>Pygoscelis adeliae</i>	63	52	18	11	11	5	4
<i>Pygoscelis papua</i>	65	53	17	11	11	6	4

**A**, length from nasofrontal hinge to cerebellar prominence.

**B**, postorbital width.

**C**, interorbital width.

**D**, foramen magnum height.

**E**, foramen magnum width.

**F**, occipital condyle width.

**G**, occipital condyle height.

### The Temporal Fossa as a Taxonomic Character

Although fossil penguin skulls are rare in comparison with fossil penguin postcranial bones (Simpson 1946, Marples and Finlay 1952, Acosta Hospitaleche 2013), most of the known fossil skulls possess well-developed temporal fossae, which indicate a piscivorous diet (Zusi 1975, Ksepka and Bertelli 2006, Acosta Hospitaleche 2013). Among modern penguins only the predominantly fish-eating genus *Spheniscus* also has large temporal fossae (Zusi 1975), although the closely-related small-bodied penguin genus *Eudyptula* has short but fairly wide, large temporal fossae for its size (personal observation).

*Terminologies.* The temporal fossa, which houses the jaw-closing temporal muscle (M. adductor mandibulae externus), is bounded anteriorly and posteriorly by what may be called, respectively, the temporal crest and the nuchal crest, although some authors (e.g. Acosta Hospitaleche 2013:399) call these crests by the unnecessarily longer terms “temporal nuchal crest” and “transverse nuchal crest”. Although Acosta Hospitaleche (2013) cites Baumel and Witmer (1993) for the use of these terms, Baumel and Witmer (1993:118) call the temporal crest the temporal crest, not the temporal nuchal crest. If the left and right temporal fossae are long enough to extend almost to the dorsal midline of the skull, a third kind of “crest” can also be formed, which some authors (e.g. Simpson 1946:11, Marples 1960:186, Stucchi 2002:19, Clarke et al. 2007:11546, Ksepka et al. 2008:136) call a “sagittal crest”, and which Acosta Hospitaleche (2013:405) calls by the longer name “sagittal nuchal crest”. This sort of “sagittal crest”, however, is not homologous with the elevated sagittal crest of some mammals, but, not at all elevated above the skull table, is merely an artifact of long temporal fossae leaving only a narrow space between them. If this structure must have a name, we might call it, with Bertelli et al. (2006:4), a “longitudinal crest”, but with the understanding that the presence of such a “longitudinal crest” is only a special case of the temporal fossae being neither too short (so that a wide space of skull occurs between them), nor too long (so that *no* skull space occurs between them, crest-like or otherwise). Of course, such a “longitudinal crest” is not necessarily homologous in the taxa in which it appears.

*Ontogeny.* The temporal fossa grows ontogenetically, probably in at least

two dimensions: dorsally in length, and presumably anteriorly in width. The dorsad length-growth of temporal muscle and the temporal fossa is observable in ontogenetic series of *Spheniscus* penguins (in other modern penguin genera the temporal fossa is poorly developed). Little has been published on this subject, but Ksepka and Bertelli (2006) report that in skulls of *Spheniscus* spp. the left and right temporal fossae of juveniles are more widely separated from the midline than is seen in adult skulls. We also seem to have a partial ontogenetic series of *Spheniscus anglicus* skulls. Other skulls from Antofagasta and assignable to *S. anglicus* are on the commercial fossil market. One such skull, displaying the yellowish brown coloration of the phosphatic arkose of the Bonebed Member, and advertised by Mr. Bob Reis, a fossil dealer based in Raleigh, North Carolina, is of particular interest for being apparently the skull of a juvenile when compared with the adult individual P2001.10.2. The Raleigh skull agrees in all particulars with P2001.10.2 except that the medial ends of its temporal fossae are somewhat further apart than in P2001.10.2, in which they touch at the midline.

Herring and Teng (2000) have documented the temporal muscle's anterior and ventral pulls which contribute to the width-growth and length-growth of the temporal fossa in the developing skull of pigs (*Sus scrofa*). They illustrate, with strain-gauge graphs, the tension of the ventral pull of the muscle, which increases the temporal fossa transversely (dorsally), and the anterior compression jamming the parietal into the frontal, thus widening the temporal fossa and creating a sharp temporal crest.

*Taxonomy.* Such developmental processes driven by the functioning of the M. adductor mandibulae externus have produced the various configurations of the penguin temporal fossa, which are quite diverse and taxon-specific. Acosta Hospitaleche (2013), for example, distinguished two (unnamed) species of late Eocene penguins in the Submeseta fauna of Seymour Island on the basis of their differently-formed temporal fossa, among other anatomical characters.

*Spheniscus anglicus* seems to have a temporal fossa of the *Spheniscus* type. In this type the temporal fossa is much deeper posteriorly than anteriorly, and develops more ventrally than dorsally so that dorsally it comes to a point, unlike the temporal fossae of other (fossil) taxa which are dorsally more square-ended. The fossae of modern *Spheniscus* are less developed than are those of

fossil *Spheniscus* with known skulls, but there are some differences in this respect among the modern species. The temporal fossa of adult *Spheniscus demersus* (Jackass Penguin), which has the greatest gape of all modern penguins (Zusi 1975), is somewhat longer than that of adult *S. humboldti* (Humboldt Penguin). In the large-bodied fossil species *Spheniscus megaramphus* Stucchi et al. 2003 and *S. urbinai* Stucchi 2002 the fossae are much longer before coming to their points. Acosta Hospitaleche and Canto (2007) reasonably say that the temporal fossae of these larger penguins are enhanced by allometry. In *S. anglicus* the fossa is similar to those of these larger species, but is relatively longer and relatively wider ventrally. (Skulls are unknown for the late Miocene *Spheniscus muizoni* Göhlich 2007 and the Pliocene *S. chilensis* Emslie & Guerra Correa 2003.)

With the loss of the ventral parts of the skull of *S. anglicus* and its generally poor-quality surface detail in which cranial-nerve and other foramina are unclear, the assignment to *Spheniscus* is provisional, based on the skull's *Spheniscus*-like temporal fossa and its relatively young age (late Miocene).

### Comparisons

*Spheniscus anglicus* is best compared with other penguins of similar, or near-similar, age, ranging from middle Miocene through Pliocene. The known skulls of Paleogene penguins, such as that of the middle Eocene *Perudyptes devriesi* Clarke et al. 2007, the late Eocene *Icadyptes salasi* Clarke et al. 2007, and the late Eocene *Inkayacu paracasensis* Clarke et al. 2010, differ greatly from those of the more upclade Miocene penguins (Clarke et al. 2007, Ksepka et al. 2008, Acosta Hospitaleche et al. 2013). Besides *S. anglicus*, as many as four other penguin taxa, all with known skulls, may occur in the Bonebed Member of the Bahía Inglesa Formation.

*Pygoscelis calderensis* Acosta Hospitaleche, Chávez-Hoffmeister & Fritis 2006, based entirely on cranial material from the Bonebed Member, is smaller-bodied than *Spheniscus anglicus*. Like the modern species of the mostly krill-eating genus *Pygoscelis*, *P. calderensis* lacks a well-developed temporal fossa. Also, the *calderensis* cerebellar prominence is much more rounded than that of *S. anglicus*, and its postorbital process is thin and directed ventrally (stubby and directed laterally in *S. anglicus*).

*Spheniscus urbinai* has been reported from a variety of late Miocene and early Pliocene horizons of the Pisco Formation in Peru (Stucchi 2007). This species also occurs in Chile in the Bonebed Member according to Walsh and Suárez (2006) and Chávez-Hoffmeister (2007a,b), although this is denied by Acosta Hospitaleche and Tambussi (2008). Slightly larger than *Spheniscus anglicus*, *S. urbinai* has a temporal fossa that differs from that of *S. anglicus* as stated above.

*Spheniscus megaramphus*, the largest named species of *Spheniscus*, occurs in the Pisco Formation at its Montemar Norte horizon dated about 10 Ma (Stucchi 2007), but is also said to occur in the Bonebed Member by Walsh and Suárez (2006) and Chávez-Hoffmeister (2007a,b), but not by Acosta Hospitaleche and Tambussi (2008). Whether or not *S. megaramphus* and/or *S. urbinai* occur in the Bonebed Member, these two species of *Spheniscus* are both larger than *Spheniscus anglicus* and are distinct from it anatomically.

Another species of *Spheniscus* may occur in the Bahía Inglesa Formation, although not in the Bonebed Member. Emslie and Guerra Correa (2003) named a Pliocene species, *S. chilensis*, based on numerous bones (but no skull) from the Caleta Herradura de Mejillones Formation in Chile. This species, which is smaller than *S. anglicus*, is contemporary with the Bahía Inglesa Formation's upper level of the Lechero Member, in which it may occur (Walsh and Suárez 2006). The late Miocene *Spheniscus muizoni* (of Clarendonian-equivalent age) is not known to be contemporary with the geologically younger *S. anglicus* (Early Hemphillian equivalent). Also, *S. muizoni*, about the size of *S. chilensis* and *S. demersus*, is smaller than *S. anglicus*.

Five Bonebed skulls assigned to *Palaeospheniscus* sp. by Acosta Hospitaleche and Canto (2005, 2007) are smaller than *S. anglicus* by about 12%. Their temporal fossa is almost square-ended, as in *Parapternodytes antarcticus* (see Simpson 1946), and the fossae end well short of the midline, unlike *S. anglicus*, in which the fossae meet at the midline as blunt points. *Palaeospheniscus* will be further discussed below.

The middle Miocene *Madrynornis mirandus* Acosta Hospitaleche et al. 2007, known by an articulated skeleton from the Puerto Madryn Formation in Argentina, is about the size of *Pygoscelis adeliae* (Adelie Penguin), therefore



smaller than *Spheniscus anglicus*. Although once thought to be early late Miocene (Acosta Hospitaleche et al. 2007), the Puerto Madryn Formation is now regarded as late middle Miocene (Acosta Hospitaleche and Cione 2012, Chávez-Hoffmeister 2014), about 3 My older than previously believed. *M. mirandus* differs from *S. anglicus* in having a much lesser dorsal extent of the temporal fossa. In dorsal view each temporal fossa of the *Madrynornis* skull accounts for about one quarter of skull width, leaving about one half of skull width between the fossae, and in this middle half of the skull the temporal and nuchal crests merge into one crest. The *Madrynornis* temporal fossa is considerably smaller than the *Madrynornis* nasal fossa; in *S. anglicus* the reverse is the case. The systematic position of *Madrynornis* is controversial (see below in the paragraph on *Marplesornis*). A cladistic analysis performed by the original describers of *Madrynornis* was flawed by a local rooting anomaly by which most of the in-group (including *Palaeospheniscus*) was turned inside-out and caused, among other errors, *Palaeospheniscus* to be nested within the clade of modern penguins (as the sister-group to *Aptenodytes*).

*Marplesornis novaezealandiae* (Marples 1960) from the Pliocene of New Zealand is a large penguin the size of *Aptenodytes patagonicus*, therefore larger than *S. anglicus*. The *Marplesornis* skull, humerus, ulna and radius are the same size as those of *A. patagonicus*, although the coracoid is smaller than that of the King Penguin (Marples 1960). The temporal fossa of *M. novaezealandiae* superficially resembles that of *Paraptenodytes* in general shape and size (Marples 1960), even perhaps with a *Paraptenodytes*-like backward-pointing chevron-shaped temporal crest (although this is badly eroded), and so is quite unlike that of *S. anglicus*. Marples (1960:194) originally assigned his new species to *Palaeospheniscus* because the “specimen, as far as can be compared, appears to be palaeospheniscine”, although “a different genus . . . if a tarsometatarsus is discovered . . . may be necessary.” Simpson (1972) assigned the *novaezealandiae* species to the new genus *Marplesornis* not because an un-*Palaeospheniscus* tarsometatarsus was ever discovered, but on the basis of its unique coracoid, and that in general this Pliocene species resembles modern penguins more than it does any known Miocene or earlier penguin. In the cladistic analysis of Clarke et al. (2007) *Marplesornis* was found to be the sister-group to all modern penguins.

Subsequent cladistic analyses have broadly similar results. Ksepka et al. (2012) find *Marplesornis* in the same position but with the addition that *Madrynornis* is part of the modern *Eudyptes-Megadyptes* clade. Chávez-Hoffmeister et al. (2014) find *Marplesornis* to be the sister-group to a *Madrynornis mirandus* + (the Pliocene African) *Inguza predemersus* clade plus the clade of all modern penguins.

### **Why is *Palaeospheniscus* Claimed to Occur in the Bonebed?**

At present there are two entirely distinct groups of crania from the Bonebed which are both assigned to “*Palaeospheniscus* sp.”: (1) the five skulls published by Acosta Hospitaleche and Canto (2005, 2007), and (2) some skulls on the commercial fossil market which are identified by their dealers also as “*Palaeospheniscus* sp.”, but which are assignable to *S. anglicus*. It would seem inadvisable to assign either of these two late Miocene groups to the early Miocene genus *Palaeospheniscus* (which lacks any known cranial material). Of all the genera of penguins reported from the Bonebed, however, Acosta Hospitaleche and Canto (2005, 2007) decided that the South American Miocene *Palaeospheniscus* seemed, provisionally, to be the best candidate for their Bonebed skulls, since these skulls are distinct from that of *Paraptenodytes*, and since they were also identifying humeri and tarsometatarsi from the Bonebed as *Palaeospheniscus*.

In the revision summarized by Acosta Hospitaleche and Tambussi (2008), the three currently accepted species of *Palaeospheniscus*, all from the early Miocene Gaiman Formation in Argentina, are, in order of increasing size, *P. bergi* (Moreno & Mercerat 1891), *P. patagonicus* Moreno & Mercerat 1891, and *P. biloculata* (Simpson 1970). Acosta Hospitaleche and Canto (2007) assigned 5 Bonebed postcranial bones to *Palaeospheniscus biloculata* and 11 more to *P. cf. P. biloculata*. The skulls were assigned to *Palaeospheniscus* sp., presumably on the basis of size, to an unspecified species of *Palaeospheniscus* rather than to the larger-bodied *P. biloculata*.

There is basic agreement in three studies regarding the systematic position of *Palaeospheniscus*. Cladistic analyses by Clarke et al. (2007) and Ksepka et al. (2012) find that actual early Miocene *Palaeospheniscus* spp. form a clade with the early Miocene small-bodied genus *Eretiscus* outside the clade of all modern penguins; Chávez-Hoffmeister et al. (2014) find that *Palaeospheniscus* and

*Eretiscus* are either closely related or else paraphyletic neighbors (in a polytomy downclade from the modern genera). Taxa of a *Palaeospheniscus* clade (or of a *Palaeospheniscus-Eretiscus* clade) younger than the early Miocene are yet to be named.

Acosta Hospitaleche, Canto and Tambussi (2006) reported a humerus from the middle Miocene Coquimbo Formation in Chile. They assigned this bone, which displays characters shared by *Palaeospheniscus* and *Eretiscus* and is the size of *P. bergi*, to cf. *Palaeospheniscus*. Chávez-Hoffmeister (2014) has noted that among the penguin skeletal elements most commonly preserved as fossils, the humerus is the least taxonomically diagnostic and most easily confusable for generic assignment. He did, however, identify 10 discriminating characters of the humerus by which *Spheniscus* and *Palaeospheniscus* can usually be distinguished. By the use of these characters, Chávez-Hoffmeister (2014) finds that the Coquimbo Formation “cf. *Palaeospheniscus*” humerus, which most closely resembles the geologically younger *Spheniscus chilensis* and modern species of *Spheniscus* in size and shape, is most likely *Spheniscus*. Two middle Miocene records of *Palaeospheniscus*, however, are accepted by all parties. A tarsometatarsus from the middle Miocene Chilcatay Formation in Peru assigned by Acosta Hospitaleche and Stucchi (2005) to *Palaeospheniscus* sp. is valid, and a humerus from the Puerto Madryn Formation assigned to *Palaeospheniscus bergi* by Acosta Hospitaleche and Cione (2012) is valid for some species of *Palaeospheniscus* in the middle Miocene (Chávez-Hoffmeister 2014).

Because of the fragmentary nature of most of the penguin fossil record, occurrences of *Palaeospheniscus* younger than the early Miocene have not yet been named as new species of that genus. Instead, the stratigraphic ranges of the three (early Miocene) species of that genus have simply been extended upward. Clarke et al. (2007), for example, chart *Palaeospheniscus patagonicus*, the medium-sized species, as persisting from the earliest Miocene to about 15 Ma in the middle Miocene, a species duration of about 9 My. Acosta Hospitaleche and Cione (2012), as noted above, identified a humerus from the middle Miocene Puerto Madryn Formation as—not *Palaeospheniscus* sp., nor *P. cf. P. bergi*, nor *P. size P. bergi*—but literally as *Palaeospheniscus bergi*, although Acosta Hospitaleche and Cione (2012) stated that their *bergi* assignment was based on

size alone. This identification would give *P. bergi* a species duration of about 11 My. Another humerus from the Cerro Plataforma Beds in western Argentina was reported by Acosta Hospitaleche et al. (2013) more certainly as *P. bergi*, as the identification was based not only on size but also on morphogeometric analysis. The age of the Cerro Plataforma has been uncertain; publications of its age have ranged from late Eocene to Miocene (Acosta Hospitaleche et al. 2013). The occurrence of *P. bergi* here would seem to indicate that this unit is early Miocene. Most remarkably, Acosta Hospitaleche and Canto (2007) referred humeri and tarsometatarsi from the late Miocene Bonebed Member to *Palaeospheniscus biloculata*, as noted above. This identification would give *P. biloculata* a longevity of about 16 My, close to the entire length of the Miocene. Chávez-Hoffmeister (2014) has revised these specimens as *Spheniscus* sp., cf. *Spheniscus*, and Spheniscidae indet.

A long species duration for any one of these three taxa is of course possible. If, however, such extraordinary longevity is claimed for all three of them, credulity is more strained. Accordingly, a theoretical paper by Acosta Hospitaleche (2006) explained the taxonomic longevity of all the species of *Palaeospheniscus* (and of *Parapternodytes*) as the result of slow rates of morphological change permitting very lengthy stages of ecological generalism for these penguins and therefore longer species durations. Perhaps new discoveries over time will tell whether these species were actually long-lived or whether the species of *Palaeospheniscus* were being used as body-size categories rather than as natural species.

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