

South American fossil penguins: a systematic update

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ABSTRACT - During the last few years, we have worked on the systematics and paleobiology of the South American and Antarctic fossil penguins. As a result, we have obtained new data about their past biodiversity. Concerning South American fossil penguins, particularly the Tertiary ones, we can point out that, based on phylogenetic and morphometric analyses practiced on skulls and appendicular skeleton, we recognised three non taxonomic groups, partially in agreement partially with the systematic scheme proposed by Simpson: “Paraptenodytinae”, “Palaeospheniscinae” and “Spheniscinae”. These species are recorded exclusively from South America and morphologically have more resemblance with the living species than the fossil penguins from others regions of the Southern Hemisphere. This suggests that the evolutionary and biogeographical history of the penguin fauna of Argentina, Chile and Peru followed different routes from those of Antarctica, New Zealand and Australia.

Key words - *Spheniscidae, fossil penguins, systematics, South America.*

Les manchots fossiles sud-américains: une mise au point systématique - Ces dernières années, nous avons travaillé sur la systématique et la paléobiologie des manchots fossiles d’Amérique du Sud et de l’Antarctique, ce qui a abouti à des résultats au sujet de leur biodiversité dans le passé. En ce qui concerne les manchots fossiles sud-américains et en particulier ceux du Tertiaire, nous pouvons relever le fait que, sur la base d’analyses phylogénétiques et morphogénétiques pratiquées sur des crânes et squelettes, nous avons identifié trois groupes taxonomiques en accord avec le schéma proposé par Simpson : “Paraptenodytinae”, “Palaeo”Spheniscinae” and “Spheniscinae”. Ces espèces sont observées exclusivement en Amérique du Sud et s’apparentent morphologiquement davantage aux espèces vivantes qu’aux manchots fossiles d’autres régions de l’hémisphère sud. Cela suggère de prime abord que l’histoire évolutive et biogéographique des manchots d’Argentine, du Chili et du Pérou aurait suivi des routes différentes de celles des formes l’Antarctique, de la Nouvelle Zélande et de l’Australie.

Mots clés - *Spheniscidae, manchots fossiles, systématique, Amérique du Sud.*

INTRODUCTION

Several authors have considered different systematic arrangements for penguin taxa and have proposed a wide spectrum of specific combinations. Simpson (1946, 1970, 1971, 1972, 1973, 1975, 1976, 1981) was the palaeontologist who studied these birds in greatest detail. In his well-known systematic scheme (Simpson, 1946), the result of an extensive revision, he classified all the penguin species in five subfamilies: Paleospheniscinae, Paraptenodytinae, Palaeodyptinae, Anthropornithinae and Spheniscinae. Later (Simpson, 1972), he recognized only nine species and four genera among the Patagonian fossil species: *Palaeospheniscus gracilis* Ameghino, 1899; *Palaeospheniscus bergi* Moreno & Mercerat, 1891, *Palaeospheniscus patagonicus* Moreno & Mercerat, 1891, *Palaeospheniscus wimani*

Ameghino, 1905, and *Chubutodyptes biloculata* Simpson, 1970 (included in the Subfamily “Paleospheniscinae” Simpson, 1946); *Paraptenodyptes antarcticus* Moreno & Mercerat, 1891, *Paraptenodyptes robustus* (Ameghino, 1895), and *Paraptenodyptes brodkorbi* Simpson, 1972 (included in the “Paraptenodytinae” Simpson, 1946); and *Arthrodyptes grandis* Ameghino, 1901 (within the Anthropornithinae Simpson, 1946) (Simpson, 1972). Soon thereafter, he added the new species *Eretiscus tonni* (Simpson, 1981).

In his catalogue, Brodkorb (1963) listed fifteen species and recognized only a part of the subfamilies proposed by Simpson (1946). He moved *Arthrodyptes* Ameghino, 1905 with its single species *Arthrodyptes grandis* (Ameghino, 1905) (= *Paraptenodyptes grandis* Ameghino, 1901) from the Anthropornithinae to the Palaeodyptinae Simpson, 1946. On the other hand, Brodkorb (1963) kept a similar arrangement

Species	Stratigraphy and age	Locality
<i>Eretiscus tonni</i>	Gaiman Formation. Early Miocene.	Gaiman, Argentina
<i>Palaeospheniscus bergi</i>	Gaiman Formation. Early Miocene.	Gaiman, Argentina
<i>Palaeospheniscus patagonicus</i>	Gaiman Formation. Early Miocene.	Gaiman, Argentina
<i>Palaeospheniscus biloculata</i>	Gaiman Formation. Early Miocene. Bahía Inglesa Formation. Late Miocene- Early Pliocene.	Gaiman, Argentina Caldera, Chile
<i>Paraptenodytes robustus</i>	San Julián Formation. Late Eocene- Early Oligocene. Bahía Inglesa Formation. Late Miocene- Early Pliocene.	Gran Bajo de San Julián, Argentina. Caldera, Chile
<i>Paraptenodytes antarctica</i>	Monte León Formation. Early Miocene. Puerto Madryn Formation. Early Late Miocene. Bahía Inglesa Formation. Late Miocene- Early Pliocene.	Gaiman, Argentina. Co. Avanzado, Argentina. Caldera, Chile
<i>Arthrodytes andrewsi</i>	San Julián Formation. Late Eocene- Early Oligocene.	Gran Bajo de San Julián, Argentina
<i>Spheniscus megaramphus</i>	Pisco Formation. Late Miocene- Early Pliocene	Montemar level, Peru.
<i>Spheniscus urbinai</i>	Pisco Formation. Late Miocene- Early Pliocene	Sacaco Sur, Montemar and Aguada de Lomas levels, Perú
<i>Spheniscus chilensis</i>	Caleta Herradura de Mejillones Formation. Late Pliocene	Tiburón Fósil, Península de Mejillones, Chile
<i>Spheniscus muizoni</i>	Pisco Formation, latest middle or earliest Late Miocene.	Cerro La Bruja, Perú.
<i>Pygoscelis calderensis</i>	Bahía Inglesa Formation, Middle Miocene – Middle Pliocene.	Mina La Fosforita, Bahía Inglesa, Chile.
<i>Pygoscelis grandis</i>	Lechero Member of the Bahía Inglesa Formation (Late Miocene- ?early Pliocene).	Bahía Inglesa, Chile.
<i>Madrynornis mirandus</i>	Puerto Madryn Formation. Early Late Miocene.	Playa Villarino, Argentina.
<i>Icadyptes salasi</i>	Otuma Formation, late-Middle to Late Eocene.	Ullujaya Valley of the Rio Ica, Department of Ica, Perú.
<i>Perudyptes devriesi</i>	Paracas Formation, Middle- Late Eocene.	Quebrada Perdida. Department of Ica, Perú.

Table 1 - Fossil record of South American fossil penguins (data compiled and updated from Acosta Hospitaleche, 2007; Acosta Hospitaleche et al., 2007 and Clarke et al., 2007).

of species within the other subfamilies. In the “Paleospheniscinae” Simpson, 1946, he included *Palaeospheniscus gracilis* Ameghino, 1899 (= *P. medianus* Ameghino, 1905 and *Apterydytes ictus* Ameghino, 1901); *P. patagonicus* Moreno & Mercerat, 1891; *P. menzbieri* Moreno & Mercerat, 1891 (= *P. interruptus* Ameghino, 1905 and *P. planus* Ameghino, 1905); *P. rothi* Ameghino, 1905 (= *P. intermedius* Ameghino 1905 and *P. affinis* Ameghino, 1905); *Perispheniscus robustus* (Ameghino, 1895) (= *Palaeospheniscus robustus* Ameghino, 1895 and *Treleudytes crassa* Ameghino, 1905); *Paraspheniscus bergi* (Moreno & Mercerat, 1891) and *P. nereius* (Ameghino, 1901). In the “Paraptenodytinae”, Brodkorb included *Paraptenodytes antarcticus* (Moreno & Mercerat, 1891); *P. andrewsi* Ameghino, 1901 (= *Arthrodytes andrewsi* Ameghino, 1905); *P. curtus* Ameghino, 1901 (= *Metancyornis curtus* Ameghino, 1905); *Isotremornis nordenskjöldi* Ameghino, 1905; *Pseudospheniscus interplanus* Ameghino,

1905 (= *P. planus* Ameghino, 1905); *Pseudospheniscus concavus* Ameghino, 1905 (= *P. convexus* Ameghino, 1905) and *Neculus rothi* Ameghino, 1905.

Nevertheless, the suprageneric panorama of penguin taxonomy grew more complicated. Simpson’s scheme (1946) was questioned by Marples (1952), who proposed several options in order to emend his systematic arrangement. Warned by the critics, Simpson (1971) suddenly abandoned his own ideas and never used them again in his following works. Only recently have these subfamilial units been reevaluated in their meaning and extent. Jadwiszczak (2006) and Acosta Hospitaleche et al. (2008) support a restrictive and non systematic use.

In addition, an attempt to base a systematic classification on osteological characters was carried out by Zusi (1975). He recognized two different lineages in the modern Spheniscidae on the basis of the morphology of the skull: one

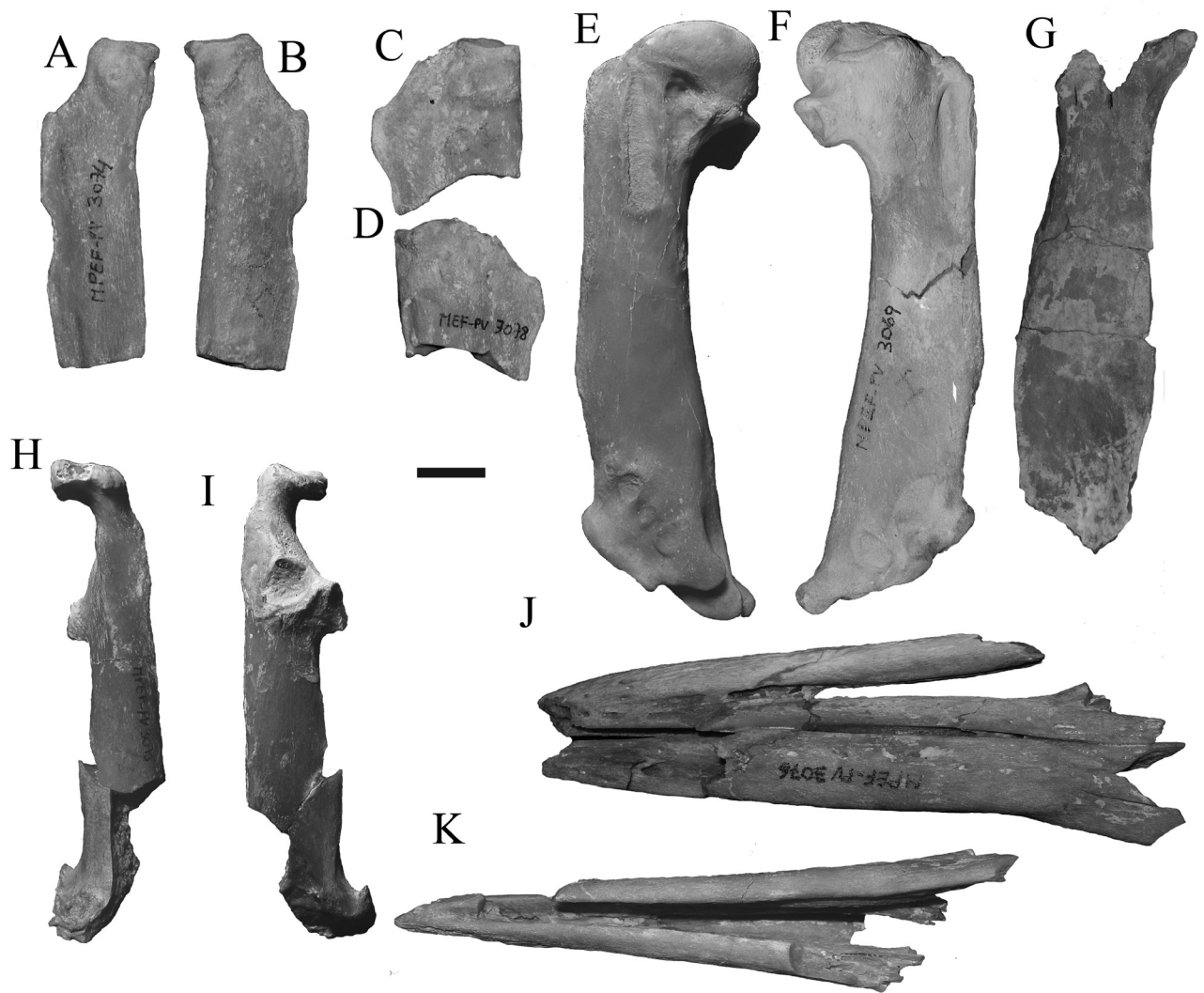


Figure 1 - *Palaeospheniscus patagonicus* Moreno & Mercerat, 1891 from the Gaiman Formation (Early Miocene) at Rawson, Chubut Province, Argentina. A- Left radius with the distal end lacking (MPEF-PV 3074) in anterior view, B- Left radius with the distal end lacking (MPEF-PV 3074) in posterior view, C- Proximal end of left ulna (MPEF-PV 3078) in posterior view, D- Proximal end of left ulna (MPEF-PV 3078) in anterior view, E- Left humerus (MPEF-PV 3069) in posterior view, F- Left humerus (MPEF-PV 3069) in anterior view, G- Fragmentary left scapula (MPEF-PV 3077) in anterior view, H- Right coracoid with the distal end lacking (MPEF-PV 3073) in anterior view, I- Right coracoid with the distal end lacking (MPEF-PV 3073) in posterior view, J- Rostrum (MPEF-PV 3076) in lateral view, K- Rostrum (MPEF-PV 3076) in palatal view. (Modified from Acosta Hospitaleche et al., 2008). Scale bar: 10 mm.

characterized by having the processus retroarticularis similar in size to the fossa articularis quadratica and the rostrum over the plane of the lamina parasphenoidalis that is subparallel to the crista tomialis; this group includes the *Pygoscelis* and *Aptenodytes* species. Moreover, some postcranial characters can be mentioned e.g. the presence of a coracoid without a fenestra and a foramen vasculare proximale mediale of the tarsometatarsus opened proximally to the crests of the hipotarsus. The second lineage is characterized by the presence of the processus retroarticularis smaller than the fossa articularis quadratica and the rostrum at the same level as the lamina parasphenoidalis that is in an oblique plane respect to the crista tomialis; here are included *Spheniscus*,

Eudyptula, *Eudyptes* and *Megadyptes* species. Some other features are the presence of a fenestra on the medial side of the coracoid and the tarsometatarsus with foramen vasculare proximale mediale open internally to the hypotarsal crests (Zusi, 1975).

After that, Livezey (1989) made a statistical analysis using living and some fossil taxa. However, his results were not used for any systematic purpose.

A very different classification is that obtained from the molecular analysis done by Sibley et al. (1988) and, later, by Sibley & Monroe (1990), which suggested that Spheniscidae are a monophyletic group included in the Order Ciconiiformes (Suborder Ciconii, Parvorder Ciconiida, Superfamily

Procellaroidea), recognizing 17 living species.

Based on integumentary characters, Giannini & Bertelli (2004) conducted a phylogenetic analysis, agreeing with the monophyly of the Spheniscidae and every living genus proposed by O'Hara (1989) and confirmed by Acosta Hospitaleche (2004), and later by Bertelli & Giannini (2005) and Acosta Hospitaleche et al. (2007) on the basis of osteological analyses.

When Simpson did his work on Patagonian fossil species (Simpson, 1946), he only knew one articulated fossil specimen for his anatomical comparisons, belonging to *Parapterodytes antarcticus*, from the Gaiman Formation (Early Miocene). Now, we can also include three other articulated or associated skeletons from Argentina, assigned to *Palaeospheniscus biloculata* (Acosta Hospitaleche, 2007) and *Palaeospheniscus patagonicus* (Acosta Hospitaleche et al., 2008) from the same unit, and the third one belonging to *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato & Cozzuol, 2007 from the Puerto Madryn Formation, early Late Miocene (Acosta Hospitaleche et al., 2007). Additionally, *Icadyptes salasi* Clarke, Ksepka, Stucchi, Urbina, Giannini, Bertelli, Narváez & Boyd, 2007 from the Otuma Formation, late Middle - Late Eocene, *Perudyptes devriesi* Clarke, Ksepka, Stucchi, Urbina, Giannini, Bertelli, Narváez & Boyd, 2007 from the Paracas Formation, late-Middle to Late Eocene, and *Spheniscus muizoni* from de Pisco Formation, latest Middle - earliest Late Miocene were described.

The main scope of the present work is to compile the scattered information about South American fossil penguins, updating the published data and including our personal observations.

BACKGROUND

It is necessary to make some brief commentaries about the history of each taxon in order to better understand the systematic arrangement of these birds.

One of the first genera to be described was *Palaeospheniscus* Moreno & Mercerat, 1891, including the following species: *P. antarcticus* Moreno & Mercerat, 1891; *P. patagonicus* Moreno & Mercerat, 1891; *P. menzbieri* Moreno & Mercerat, 1891, and *P. bergi* Moreno & Mercerat, 1891. Thereafter, the species *P. interruptus* Ameghino, 1905; *P. robustus* Ameghino, 1894; *P. nereius* Ameghino, 1901; *P. medianus* Ameghino, 1905; *P. planus* Ameghino, 1905; *P. rothi* Ameghino, 1905; *P. gracilis* Ameghino, 1898; *P. intermedius* Ameghino, 1905, *P. wimani* (Ameghino, 1905) and *P. affinis* Ameghino, 1905, were included.

In 1891, the genus *Apterodytes* Ameghino, 1891 was erected and some years later *Apterodytes ictus* Ameghino, 1905 was designated as the type species. Later, the genus was replaced by *Palaeoapterodytes* because the name was already occupied by another taxon, an arthropod named *Apterodyta* Sop, 1786 (Ameghino, 1905). However, Simpson (1946) mentioned it as *Apterodytes* Ameghino, 1891, considering that *A. ictus* Ameghino, 1905 constitutes a *nomen*

vanum. The complexity of the situation increased still more when Simpson (1972) cited it as *Palaeoapterodytes ictus* (Ameghino, 1891), commenting that this species would be a Spheniscidae of doubtful affinities.

As a part of his extensive work published in 1905, Florentino Ameghino removed the species *P. nereius* Ameghino, 1901 and *P. bergi* Moreno & Mercerat, 1891 from the genus *Palaeospheniscus* and using the same material, he erected the new genus *Paraspheniscus* Ameghino, 1905, which was considered synonymous of *Palaeospheniscus* by Simpson (1946).

On the other hand, *Perispheniscus* Ameghino, 1905, with its single species *P. wimani* Ameghino, 1905, was diagnosed from its supposed differences with *Paraspheniscus* and *Palaeospheniscus*, but some years later it was considered a synonym of *Palaeospheniscus* (Simpson, 1972).

Three species belonging to the same genus, *Pseudospheniscus interplanus* Ameghino, 1905, *P. concavus* Ameghino, 1905 and *P. convexus* Ameghino, 1905 were considered as synonyms of *Palaeospheniscus* by Simpson (1972).

On the other hand, *Argyrodyptes microtarsus* Ameghino, 1905, described from a fragment of a tibiatarus and a femur, as well as *Neculus rothi* Ameghino, 1905 described from a broken tarsometatarsus, were removed from the Spheniscidae and considered as taxa of doubtful affinities (Simpson, 1972).

The only species referred to *Isotremornis* Ameghino, 1905, *I. nordenskjöldi* Ameghino, 1905, was removed and assigned to *Parapterodytes* (Simpson, 1972).

The genus *Parapterodytes* Ameghino, 1891 consists of the following species: *P. antarcticus* (Moreno & Mercerat, 1891), founded on material previously referred to *Palaeospheniscus antarctica* Moreno & Mercerat, 1891 (Ameghino, 1905); *Parapterodytes curtus* Ameghino 1901, described on the basis of a tarsometatarsus that years later was considered as belonging to a new taxon, *Metancylornis* Ameghino, 1905; *Parapterodytes grandis* Ameghino, 1901, later removed to the new genus *Arthrodytes* Ameghino, 1905; *Parapterodytes andrewsi* Ameghino, 1901, whose preliminary assignment was modified to also include it in the genus *Arthrodytes* Ameghino, 1905 (Ameghino, 1905); *Parapterodytes robustus* (Ameghino, 1895), that was amended by Simpson (1972) because it had originally be designated as *Palaeospheniscus robustus* Ameghino, 1895; and finally *Parapterodytes brodkorbi* Simpson, 1972, that was described on the basis of the same material as *Isotremornis nordenskjöldi* Ameghino, 1905. Nevertheless, this last reassignment is somewhat confusing since, in the same work published by Simpson (1972), the same material (originally referred to *I. nordenskjöldi*) is considered in different ways: as a synonym of *Parapterodytes antarcticus* (Moreno & Mercerat, 1891), and, on the other hand, as the holotype of *P. brodkorbi*.

Treleudytes crassa Ameghino, 1905 (type species of *Treleudytes* Ameghino, 1905) was later amended by

Simpson (1946) as *T. crassus* Ameghino 1905.

As previously mentioned, *Arthrodytes* Ameghino, 1905, was named from material assigned to *Paraptenodytes*, including *A. grandis* Ameghino, 1905 and *A. andrewsi* Ameghino, 1905.

One of the remains that had been considered as an indeterminate species of *Palaeospheniscus* (Simpson, 1946), had become the holotype of *Chubutodyptes bilocolata* Simpson, 1970, constituting the only report of the genus. Recently, this species was placed in *Palaeospheniscus* (Acosta Hospitaleche, 2004, 2007)

The tiniest material known from South America was the basis for the erection of *Mycrodytes tonni* Simpson, 1981. The species was amended as *Eretiscus tonni* (Simpson, 1981) when Olson (1986) realized that the name *Mycrodyta* had already been applied to an arthropod.

In addition, as previously mentioned, the Patagonian species *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato & Cozzuol, 2007 was recently recognized, based on a very complete skeleton (Acosta Hospitaleche et al., 2007).

All the holotypes of the species described above were discovered in Argentina and later some of them were found in Chile and Perú.

During the last five years, a large number of penguin remains have been studied. Five different species from Peru, and three new ones from Chile were described. Four new species belonging to the modern genus *Spheniscus* were erected. *S. urbinai* Stucchi, 2002 and *S. megaramphus* Stucchi, Urbina & Giraldo, 2003 come from the Middle Miocene, *S. muizoni* Göhlich, 2007 from the latest Middle - earliest Late Miocene of Peru, and *S. chilensis* Emslie & Guerra Correa, 2003 from the Late Pliocene of Chile. The other two species are older in age, and belong to new genera. They are *Perudyptes devriesi* Clarke, Ksepka, Stucchi, Urbina, Gianini, Bertelli, Narváez & Boyd, 2007 from the late Eocene, and *Icadyptes salasi* Clarke, Ksepka, Stucchi, Urbina, Gianini, Bertelli, Narváez & Boyd, 2007 from the late Middle - Late Eocene.

Complementing the South American penguin record, two fossil species belonging to the living genus *Pygoscelis* were described from Chile: *P. calderensis* Acosta Hospitaleche, Chávez & Fritis, 2006 from the Middle Miocene - Pliocene and *P. grandis* Walsh & Suárez, 2006 coming from the Early Pliocene.

Other skulls from Chile have been studied and were preliminarily assigned to "Paleospheniscinae", pending a more comprehensive analysis when additional material becomes available (Acosta Hospitaleche & Canto, 2005, but see Chávez, 2007 and Acosta Hospitaleche & Canto, 2007).

SYSTEMATIC PROPOSAL

Fossil and modern material belonging to the following institutions was examined: Museo de La Plata (MLP), Museo Argentino de Ciencias Naturales Bernardino Rivada-

via (MACN), Museo Paleontológico Egidio Feruglio (MEF-PV), Argentina; Museo de Historia Natural de la Universidad de San Marcos (MUSM), Lima, Perú; American Museum of Natural History (AMNH), University of Florida (UF), United States; Museo Geológico Prof. Humerto Fuenzalida V., Universidad Católica del Norte (UCN), Antofagasta, Museo Nacional de Historia Natural (SGO-PV), Santiago, Chile; and Muséum National d'Histoire Naturelle (MNHN), Paris, France.

Osteological terminology follows Baumel & Witmer (1993) and, when necessary, Simpson (1946) and O'Hara (1989). We use the classification proposed by Simpson (1946, 1971). Measurements were taken with Vernier calipers with 0.01 mm increments and included in Table 1.

Order Sphenisciformes Sharpe, 1891

Family Spheniscidae Bonaparte, 1831

““Paleospheniscinae” type”

Characterization. Tarsometatarsus. Elongation index (maximum length /proximal width) greater than 2 (in the “Paraptenodytinae” and “Spheniscinae” it is smaller than or equal to 2). Shallow *sulcus longitudinalis dorsalis lateralis* and *medialis*, particularly the *medialis*, which occupies less than half of the *facies cranialis*. Metatarsal II more depressed craniocaudally than in the “Paraptenodytinae” and “Spheniscinae”. The *incisura intertrochlearis lateralis* reaches a more proximal level than the *incisura medialis*. Foramen *vasculare proximale laterale* always present and unlike the condition in “Paraptenodytinae”, where the foramen *vasculare proximale mediale* is quite reduced and never opens on the *facies caudalis*. *Fossa infracotylaris dorsalis medialis* triangular. *Crista lateralis hypotarsi* less developed than the *medialis*, and divided into two by a small longitudinal furrow. Weak *crista intermediae hypotarsi*.

Humerus. *Fossa tricipitalis* divided into two unequal cavities by a *crus dorsale fossae* more developed than in some fossil “Spheniscinae”, unlike the “Paraptenodytinae” where the fossa is single. The fossa over the *tuberculum ventrale* is oriented laterocranially, different from the “Paraptenodytinae”, where it is lateral as in *Madrynornis mirandus*. *Sulcus ligamentosus transversus* separated into two parts as in the new species already mentioned, with the most internal part deeper than the other and separated from the *incisura capitis*

Including two genera: *Eretiscus* and *Palaeospheniscus*.

Eretiscus Olson, 1986

Type species: *Mycrodytes tonni* Simpson, 1981.

Mycrodytes Simpson, 1981

Eretiscus Olson, 1986

Emended diagnosis. The original diagnosis is based only on a tarsometatarsus (Simpson, 1981), but it was extended and some characters of the humerus have been added.

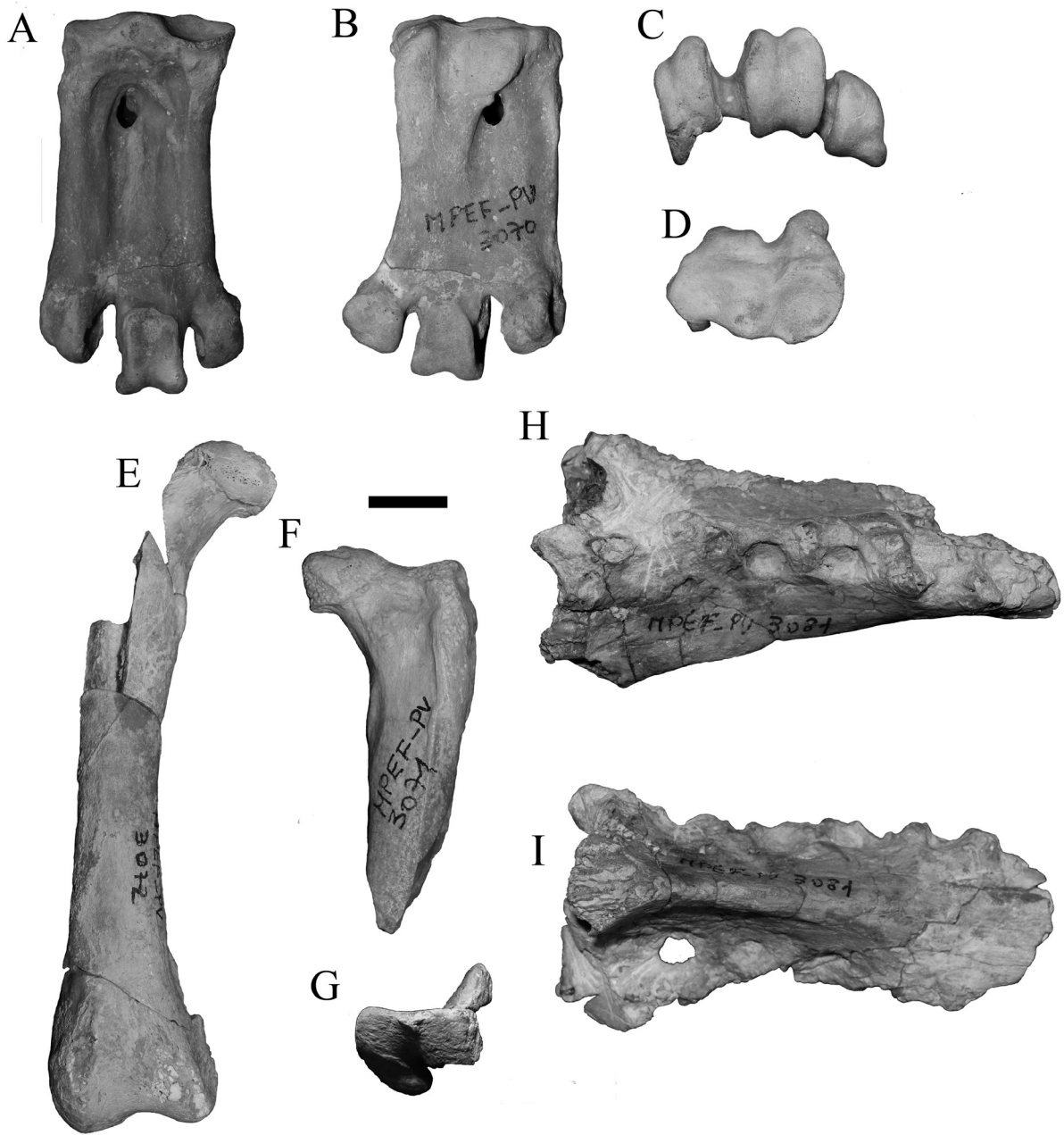


Figure 2 - *Palaeospheniscus patagonicus* Moreno & Mercerat, 1891 from the Gaiman Formation (Early Miocene) at Rawson, Chubut Province, Argentina. A- Right tarsometatarsus (MPEF-PV 3070) in anterior view, B- Right tarsometatarsus (MPEF-PV 3070) in distal view, C- Right tarsometatarsus (MPEF-PV 3070) in posterior view, D- Right tarsometatarsus (MPEF-PV 3070) in proximal view, E- Proximal end of left femur (MPEF-PV 3071) in anterior view, F- Right femur (MPEF-PV 3071) in anterior view, G- Synsacrum in lateral view, H- Synsacrum in dorsal view. (Modified from Acosta Hospitaleche et al., in press). Scale bar: 10 mm.

Tarsometatarsus. The *tuberositas musculi tibialis cranialis* is rounded and prominent, greater than in other species of this subfamily. The elongation index is about 2.66, larger than in *Palaeospheniscus*. Hypotarsus with two developed crests and without a *foramen vasculare proximale mediale*, whereas it is open in the *facies caudalis* of *Palaeospheniscus*. *Foramen vasculare proximale laterale* small

and lateral to the *crista lateralis hypotarsi*.

Humerus. Slender and small in size. Diaphysis smoothly curved (characters indicated by Simpson, 1981).

Eretiscus tonni (Simpson, 1981)
(Simpson, 1981: figs. 1, 2)

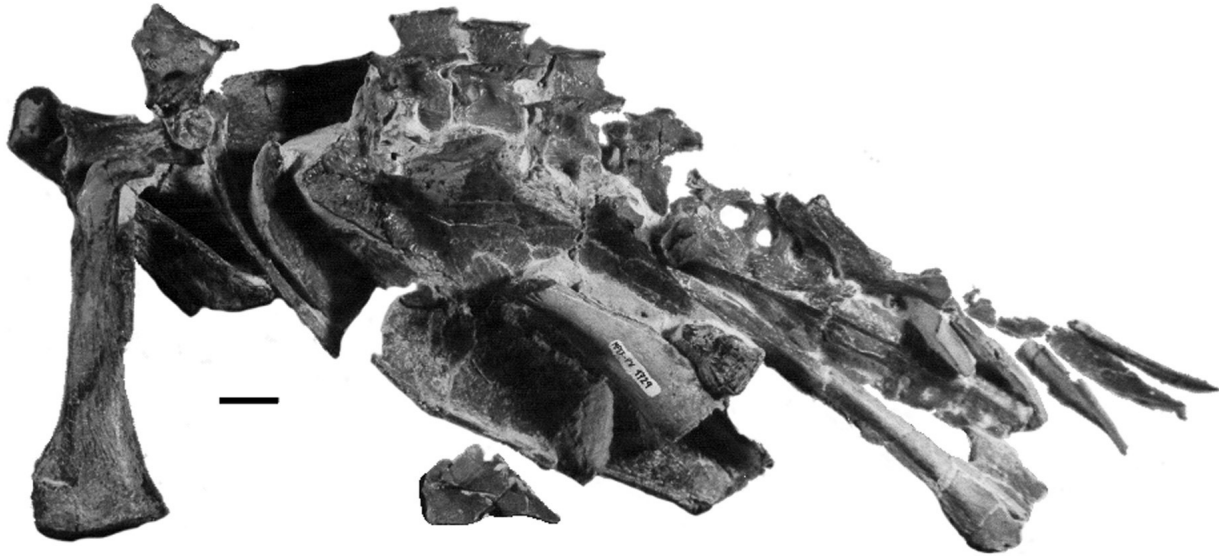


Figure 3 - *Palaeospheniscus biloculata* (Simpson, 1970). MEF-PV 1729 from the Puerto Madryn Formation (early Late Miocene) at Puerto Madryn, Chubut Province, Argentina. Articulated skeleton (Modified from Acosta Hospitaleche, 2007). Scale bar: 20 mm.

Microdytes tonni Simpson, 1981
Eretiscus tonni Olson, 1986

Holotype: MLP 81-VI-26-1, tarsometatarsus

Assigned material: MLP 69-III-29-25 (proximal end of left humerus), MEF-PV 507 (left humerus), MEF-PV 508 (right humerus).

Provenience: Bryn Gwyn, Gaiman. Chubut Province. Gaiman Formation. Early Miocene.

Diagnosis: As for the genus.

Palaeospheniscus Moreno & Mercerat, 1891

Type species *Palaeospheniscus patagonicus*

Moreno & Mercerat, 1891

Paraspheniscus Ameghino, 1905

Perispheniscus Ameghino, 1905 (only the tarsometatarsus which constitutes the holotype of the genus, not the humerus mentioned by Ameghino, 1905)

Treleudytes Ameghino, 1905

Chubutodyptes Simpson, 1970

Diagnosis: Larger than *Eretiscus*.

Tarsometatarsus. *Fossa supratrochlearis plantaris* considerably expanded. *Foramen vasculare proximale mediale* present only in the *facies caudalis*, unlike *Eretiscus*, where it is absent in both *facies*, and *foramen vasculare proximale laterale* opened laterally to the strong crests of the hypotarsus. External lateral face showing a lamina sharply projected towards the *facie caudalis* that is absent in *Eretiscus*. Total length between 28 and 40 mm with an elongation index between 2.03 and 2.35.

Humerus. Conspicuous *angulus preaxialis*, with the diaphysis just a bit wider distally to this angle. The fossa

over the *tuberculum ventrale* is oriented laterocranially. *Sulcus ligamentosus transversus* divided into two parts, with the inner portion deeper than the other one and separated from the *incisura capitis*. Small *facies musculi pectoralis* and a deep and oblique *facies musculi supracoracoideus*.

Femur. Rounded *crista tibiofibularis*. Deep *fossa poplitea*. The fossa located proximally to the *sulcus patellaris* is absent.

Tibiotarsus. Wide and oblique *pons supratendineus*, with a well developed tubercle. *Canalis extensorius* oval in section. There are no tubercles on the internal margin of the *sulcus extensorius*. Double *epicondylus medialis*.

Palaeospheniscus bergi Moreno & Mercerat, 1891 (Moreno & Mercerat, 1891: figs.I: 2, 4, 18, 19, 20, 25, 26; II: 7)

P. medianus Ameghino, 1905

P. affinis Ameghino, 1905

P. rothi Ameghino, 1905

P. bergi Moreno y Mercerat, 1891

P. gracilis Ameghino, 1898

P. interruptus Ameghino, 1905

P. nereius Ameghino, 1901

P. planus Ameghino, 1905

Paraspheniscus bergi (Moreno & Mercerat, 1891)

P. nereius (Ameghino, 1901)

Holotype: MLP 20-81 (tarsometatarsus)

Referred material: MLP 20-234 (tarsometatarsus), MLP 240 (tarsometatarsus), MLP 241 (tarsometatarsus), MLP 414 (tarsometatarsus), MLP 20-491 (humerus), MLP 20-519 (humerus), MLP 97-VI-1-11 (tarsometatarsus), MLP 97-VI-1-12 (tarsometatarsus), MLP 97-VI-1-13 (tar-

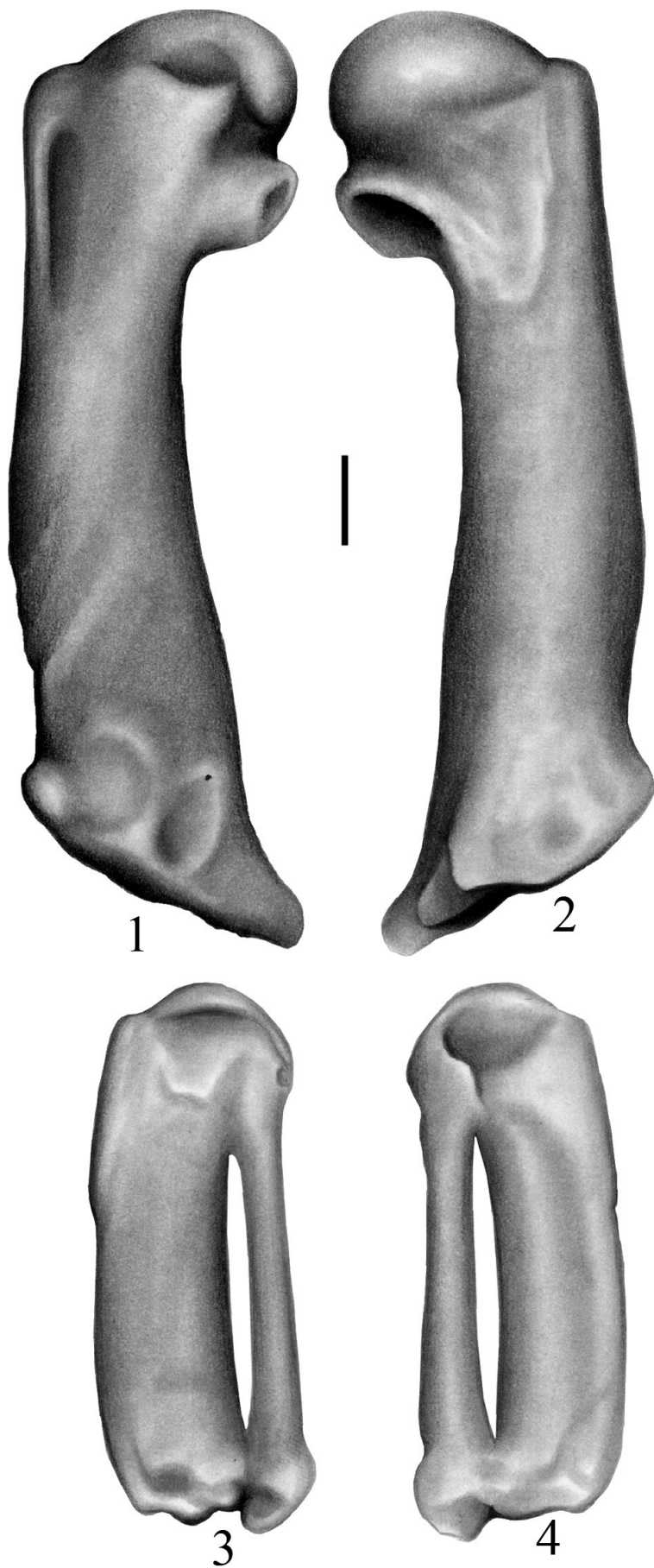


Figure 4 - *Palaeospheniscus biloculata* (Simpson, 1970). MEF-PV 1729 from the Puerto Madryn Formation (early Late Miocene) at Puerto Madryn, Chubut Province, Argentina. A- humerus in anterior view, B- humerus in posterior view, C- carpometacarpus in anterior view, D- carpometacarpus in posterior view. (Modified from Acosta Hospitaleche, 2007). Scale bar: 10 mm.

sometatarsus), MACN A-11035 (tarsometatarsus), MACN A-11036 (tarsometatarsus), MACN 11047 (two humeri), MACN 11206 (tarsometatarsus), MACN 12926 (tarsometatarsus), MEF- PV 1366 (humerus), MEF- PV 1369 (three tarsometatarsi).

Provenance: Bryn Gwyn, Gaiman, Chubut Province. Gaiman Formation. Early Miocene.

Diagnosis: Tarsometatarsus. Slender, in accordance with the smaller size of the genus, total length between 28 and 36 mm and an elongation index between 2.06 and 2.16.

Humerus. Total length between 68 and 70 mm, smaller than *P. patagonicus* and *P. biloculata*.

Palaeospheniscus patagonicus Moreno & Mercerat, 1891

(Moreno & Mercerat, 1891: figs. I: 7, 8, 9, 12, 13, 15, 16, 21, 25, 27; II: 5)

Figures 1 and 2

P. menzbieri Moreno & Mercerat, 1891

P. patagonicus Moreno & Mercerat, 1891

P. robustus Ameghino, 1894

P. intermedius Ameghino, 1905

Treleudytes crassa Ameghino, 1905 (only the tarsometatarsus that constitutes the holotype, not the humerus mentioned by Ameghino, 1905).

Holotype: MLP 20-34 (tarsometatarsus)

Referred material: MLP 20-14 (humerus), MLP 20-44 (humerus), MLP 20-50 (humerus), MLP 20-62 (tarsometatarsus), MLP 20-68 (humerus), MLP 20-69 (humerus), MLP 20-235 (tarsometatarsus), MLP 20-237 (tarsometatarsus), MLP 20-528 (humerus), MLP 20-530 (humerus), MLP 20-541 (humerus), MLP 20-549 (humerus), MLP 20-550 (humerus), MLP 20-560 (humerus), MLP 71-II-10-1 (humerus), MLP 97-VI-I-9 (tarsometatarsus), MACN 11044 (tarsometatarsus), MEF-PV 1366 (two humeri), MEF-PV 1369 (two tarsometatarsi).

Provenance: Bryn Gwyn, Gaiman, Chubut Province. Gaiman Formation. Early Miocene.

Diagnosis.

Tarsometatarsus. Intermediate in robustness and size between *P. bergi* and *P. biloculata*, with a total length between 38 and 40 mm. Development of the hypotarsus just larger than in *P. bergi*.

Humerus. Total length between 72 and 82 mm.

Palaeospheniscus biloculata (Simpson, 1970)

(Simpson, 1970: figs. 4: 1-4)

Figures 3 and 4

Chubutodyptes biloculata Simpson, 1970

Perispheniscus wimani Ameghino, 1905 (only the tarsometatarsus that constitutes the holotype, not the humerus mentioned by Ameghino, 1905)

Holotype: AMNH 3346 (proximal end and diaphysis of a right humerus)

Referred material: MLP 20-236 (tarsometatarsus), MLP 20-565 (humerus), MLP 77-XII-22-1 (humerus), MLP 97-VI-1-10 (tarsometatarsus), MACN 11206 (tarsometatarsus), MEF-PV 1729 (right humerus, right scapula, right coracoid and distal end of the left one, sternum, ribs, five thoracic vertebrae, synsacrum, pygostyle, pelvic girdle and right carpometacarpus), AMNH 3341 (humerus).

Provenance: Bryn Gwyn, Gaiman, Chubut Province. Gaiman Formation. Early Miocene. The MEF-PV 1729 comes from the same formation, in the El Indio Locality, Puerto Madryn, Chubut Province.

Diagnosis: Larger than *P. patagonicus*.

Tarsometatarsus. Total length more than 43 mm, being the largest species of the genus. Lateral divergence of the trochlea for digit II greater than in *P. bergi* and *P. biloculata*. *Crista lateralis hypotarsi* more developed than in the other species of the genus, reaching the *fossa supratrochlearis plantaris*. Absence of a *crista intermediate hypotarsi*.

Humerus. Total length between 88 and 94 mm, bigger than *Eretiscus*, *P. bergi* and *P. patagonicus*.

Commentaries. Simpson (1970) named the new genus *Chubutodyptes* on the basis of a fragmentary humerus that had been considered previously as probably belonging to *Eretiscus* sp. (Simpson, 1946). Fortunately, the study of a new nearly complete skeleton (MEF-PV 1729) belonging to the same taxon, has allowed to recognize that *Chubutodyptes* is in fact a junior synonym of *Palaeospheniscus*. We could also amend the diagnosis of *Palaeospheniscus biloculata* by assigning in an accurate way other elements different from the humerus.

““Paraptenodytinae” type”

Characterization: Tarsometatarsus. Relatively short, with an elongation index smaller than 2, as in the “Spheniscinae”, whereas in the “Paleospheniscinae” it is always greater than 2. Trochlea II strongly divergent in comparison with the “Paleospheniscinae” and the “Spheniscinae” and metatarsal II a little depressed. *Foramen vasculare proximale laterale* always present and opened on the *facies caudalis*. *Foramen vasculare proximale mediale* smaller than or equal in size to the previous one, and, unlike the condition in the “Paleospheniscinae”, reaching both facies.

Humerus. *Fossa tricipitalis* without internal partitions, without *crus dorsale*; it is small in the fossil species of “Spheniscinae” and larger in the “Paleospheniscinae”. Straight diaphysis and variable *angulus preaxialis*. The fossa located on the *tuberculum ventrale* is oriented laterally as in the “Spheniscinae”, whereas it is laterocranial in the “Paleospheniscinae”. *Sulcus ligamentosus transversus* non-bipartite and joined to the *incisura capitis*, unlike the “Paleospheniscinae” where it is separated into two parts.

Three species are included in two genera (*Paraptenodytes robustus*, *P. antarcticus* and *Arthrodytes andrewsi*).

Paraptenodytes Ameghino, 1891

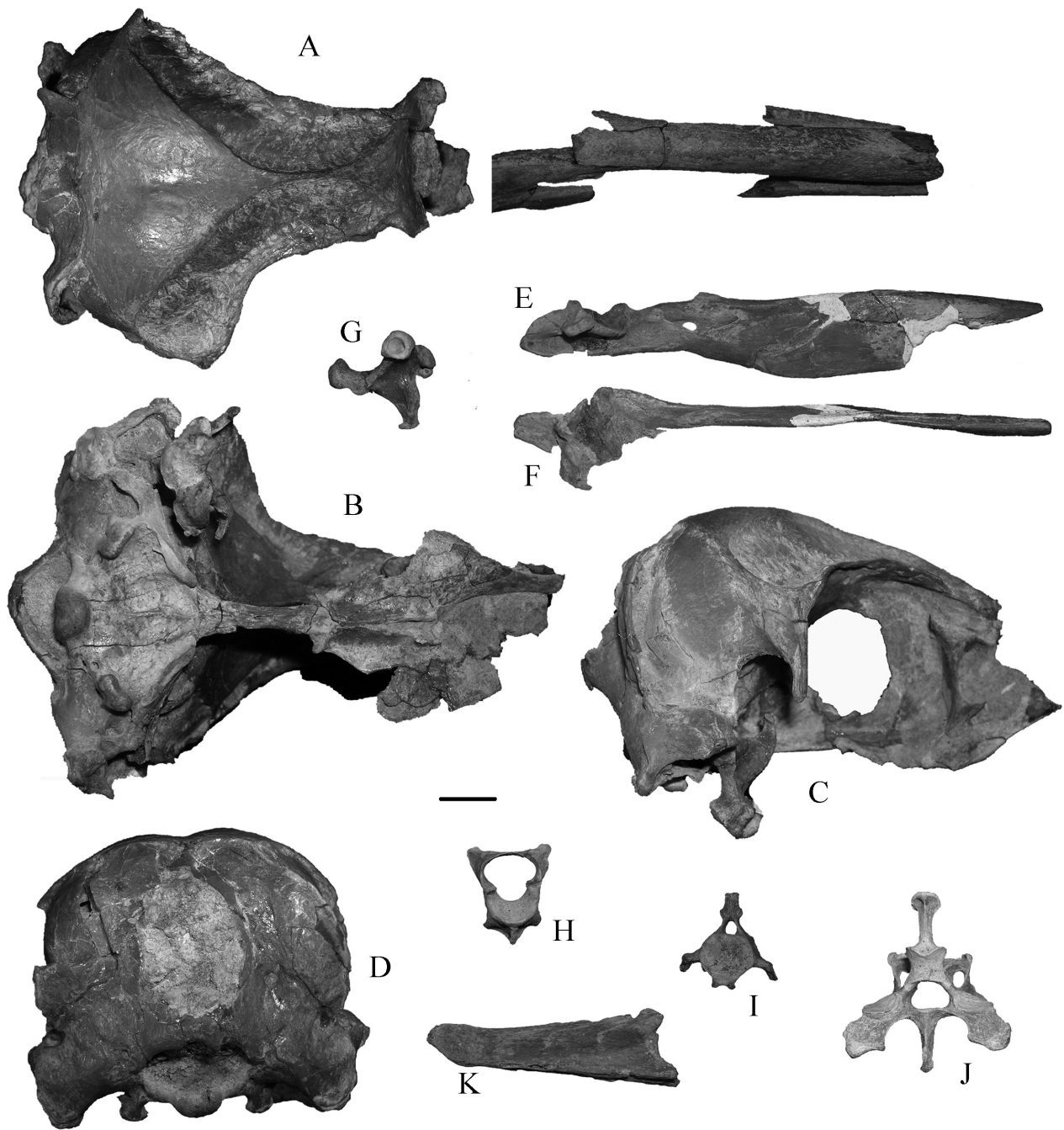


Figure 5 - *Madrynornis mirandus* (MEF-PV 100), from the Puerto Madryn Formation (early Late Miocene) at Playa Villarino, Península Valdés, Chubut Province, Argentina. A- skull in dorsal view, B- skull in palatal view, C- skull in lateral view, D- skull in occipital view, E- mandible in internal view, F- mandible in dorsal view, G- quadrate, H- atlas, I- caudal vertebra, J- cervical vertebra, K- pygostyle. Scale bar 1cm. (Modified from Acosta Hospitaleche et al., 2007).

Type species. *Palaeospheniscus antarcticus* Moreno & Mercerat, 1891
Metancylornis Ameghino, 1905
Isotremornis Ameghino, 1905

Diagnosis.

Tarsometatarsus. Metatarsals distally inclined towards the medial side. Both *foramina vascularia proximalia* open at the same level. *Tuberositas musculi tibialis cranialis* extended and rounded. *Sulci longitudinalis dorsalis* shallow and subequal in size. Absence of *fossae infracotylaris dorsalis medialis* and *lateralis*. Lateral surface with a rib weakly

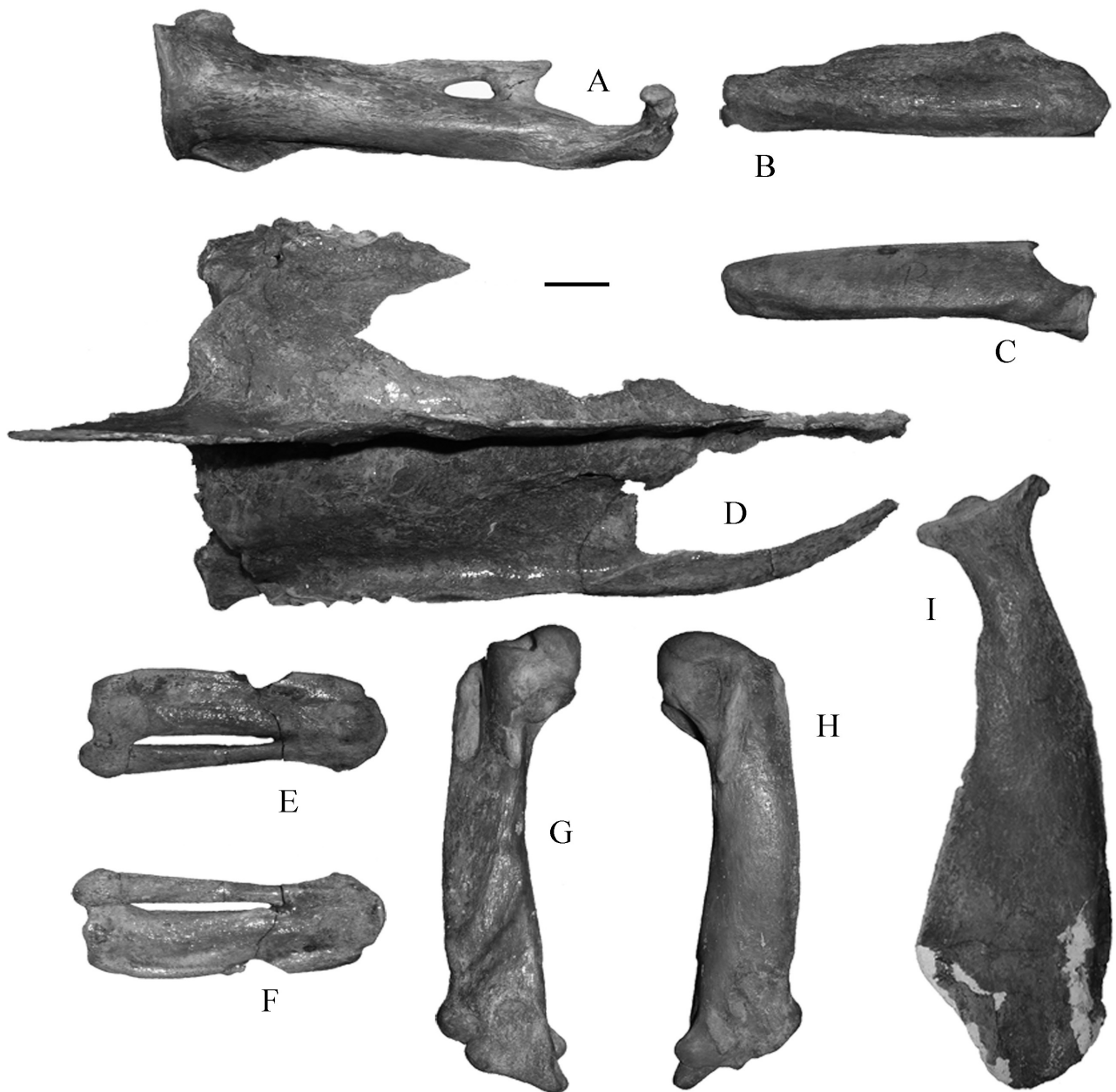


Figure 6 - *Madrynornis mirandus* (MEF-PV 100), from the Puerto Madryn Formation (early Late Miocene) at Playa Villarino, Península Valdés, Chubut Province, Argentina. A- coracoids in anterior view, B- cubitus in anterior view, C- radius in anterior view, D- sternum in anterior view, E- carpometacarpus in anterior view, F- carpometacarpus in posterior view, G- humerus in anterior view, H- humerus in posterior view, I- scapula in anterior view. Scale bar 1cm. (Modified from Acosta Hospitaleche et al., 2007).

marked towards the *facies caudalis*. Robust trochleas, with a strong trochlear divergence. The cranial extension of the trochlea IV is larger than those of digits II and III. Trochlea III triangular in shape, with strong and divergent margins. Hypotarsus with two parallel *cristae intermediae*, one *cristae medialis* developed proximally to the *foramen vasculare*

proximale mediale (oblique to the *cristae intermediae*), and one weakly developed *crista lateralis hypotarsi*, proximal and lateral to the *foramen vasculare proximale laterale*.

Humerus. Straight diaphysis, with an *angulus preaxialis* very small or absent, whereas it is large in *Arthrodytes*. Rounded *condylus ventralis* and *dorsalis*, unlike those

of *Arthrodytes* that are elongated. Total length between 90 and 150 mm.

Including two species: *P. antarcticus* and *P. robustus*.

Paraptendytes antarcticus (Moreno & Mercerat, 1891)

(Moreno & Mercerat, 1891: figs. II: 1, 2, 4)

Palaeospheniscus antarcticus Moreno & Mercerat, 1891.

Holotype: MLP 20-2, complete right femur; MLP 20-4, incomplete right tibiotarsus; MLP 20-6, incomplete right tarsometatarsus.

Referred material: AMNH 3338 (near complete skeleton including skull, coracoid, scapulae, humerus, femur, tibiotarsus, tarsometatarsus, cervical and dorsal vertebrae and a fragmentary sternum), MEF-PV 1369 (tarsometatarsus).

Provenance: Monte León Formation, Leonense. Early Miocene.

Diagnosis:

Skull. *Prominentia cerebellaris* smaller than in the “Spheniscinae”. *Processus paroccipitalis* ventrocranially projected, whereas in the “Spheniscinae” they are ventrally directed. *Crista nuchalis temporalis* oblique towards the strong *crista sagittalis*, and the straight *crista transversa*. Deep *fossa temporalis*, as in MEF-PV 100. Thin *processus postorbitalis*. *Fossa glandulae nasale* without a supraorbital edge. Sigmoid and not flattened pterygoids as in others Spheniscidae.

Tarsometatarsus. Total length about 42 mm. Well developed hypotarsus. Both *cristae intermediae hypotarsi* internally extended to the *foramina vascularia proximalia*. *Crista medialis hypotarsi* proximal and externally developed to the *foramen vasculare proximale mediale*, and *crista lateralis hypotarsi* a little proximally differentiated.

Humerus. Slender, but larger and less robust than in *P. robustus*. Diaphysis narrower distally. Proximal epiphysis less robust than in *P. robustus*. *Fossa tricripitalis* a little smaller than in *P. robustus*.

Tibiotarsus. Narrow and oblique *pons supratendineus*, without any tubercle. *Canalis extensorius* sub-rounded in section. On the internal edge of the *sulcus extensorius* appears a well developed tubercle. Single and rounded *epicondylus medialis*.

Femur. *Impressiones iliotrochantericae* limiting a fossa on the *facies cranialis*. Rounded *crista tibiofibularis*. Wide and shallow *fossa poplitea*, divided by a small longitudinal crest. Big development of the fossa located proximally to the *sulcus patellaris*. *Capitis* and *trochanter femoris* at the same level.

Commentaries. According to Moreno & Mercerat (1891), the MLP 20-2, MLP 20-4 and MLP 20-6 belong to the same skeleton. In addition to them, the specimen AMNH 3338 has allowed to extend the diagnosis and description of this species.

Paraptendytes robustus (Ameghino, 1895) (Ameghino, 1985: fig. 36)

Arthrodytes grandis Ameghino, 1905

Isotremornis nordenskjöldi Ameghino, 1905

Paraptendytes grandis Ameghino, 1901

P. robustus (Ameghino, 1895)

P. brodkorbi Simpson, 1972

P. curtus Ameghino 1901

Metancylornis curtus Ameghino 1905

Holotype: BM(NH) A/591 (humerus).

Referred material: MLP 89-XII-25-1, humerus, MACN 11041, distal end of left femur and proximal end of a right one (= MLP M-609 y MLP M-610 respectively), MACN 11032 (MLP M-600), incomplete left tarsometatarsus; MACN 11032 (MLP M-601), distal end of left femur; MACN 11032 (MLP M-602), right humerus; MACN 11032 (MLP M-603), distal fragment of left humerus, MLP M-615, right tarsometatarsus; MLP M-616, proximal end of right humerus.

Provenance: San Julián, Santa Cruz Province, San Julián Formation, Juliense. Late Eocene- Early Oligocene.

Diagnosis: The preservation state of the material does not allow to base a diagnosis on the tarsometatarsus. Nevertheless, the size of its humerus makes possible to differentiate it from *P. antarcticus*.

Humerus. Robust but small, whereas it is slender and more elongate in *P. antarcticus*. The diaphysis is wide and the proximal epiphysis is proportionally larger than in *P. antarcticus*. The *fossa tricripitalis* is a little larger than in *P. antarcticus*.

Commentaries: Simpson (1972) considered that *Isotremornis nordenskjöldi* constitutes a synonym of *Paraptendytes antarcticus* (Simpson, 1972: p. 19), but in the same work he founded the species *Paraptendytes brodkorbi* on the same material (Simpson, 1972: p. 24-25). We concluded from the present study that there is no basis for such a conclusion.

Arthrodytes Ameghino, 1905

Type species: *Paraptendytes grandis* Ameghino, 1901

Diagnosis: Considerably larger than any other South American species.

Humerus. Straight diaphysis and *angulus preaxialis* larger than in *Paraptendytes*. Elongate *condylus ventralis* and *dorsalis*, whereas they are rounded in *Paraptendytes*. Total length of 142 mm.

Femur. Large in size and diaphysis rounded in section but depressed distally. Deep and well defined *fossa poplitea*. Absence of *linea intermuscularis*.

Commentaries: It was erected by Ameghino (1905) to include two of the specimens described by himself in 1901: *Paraptendytes grandis* and *Paraptendytes andrewsi*. His main reason for this change was the large size of

the remains. In the same way, Simpson (1946) considered it as a valid genus and recognized that the two species were of uncertain affinities. Nevertheless, this same author also discussed a possible transfer of *A. grandis* to *Anthropornis* (belonging to the Anthropornithinae group), and the assignment of *A. andrewsi* (that would be more closely related to *Paraptenodytes*) to a new genus (Simpson, 1946). But according to the original diagnosis of the subfamilies (Simpson, 1946), only the material coming from Antarctica, Australia and New Zealand should be included in the Anthropornithinae. *Arthrodytes* does not display the main defining characters of this subfamily. We conclude that *A. andrewsi* is the only valid species of the genus, considering *A. grandis* as a synonym of *P. robustus*.

Arthrodytes andrewsi (Ameghino, 1901)

(Ameghino, 1905: figs. 7: 37; 8: 38-39)

Paraptenodytes andrewsi Ameghino, 1901, p.81.

Holotype (casts): MLP M-606, complete right humerus; MLP M-607, incomplete coracoid; MLP M-608, proximal end of a right scapula.

Assigned material: Only the holotype.

Provenance. Bajo de San Julián, Santa Cruz Province. Juliense. Late Eocene – Early Oligocene.

Diagnosis. As for the genus.

“Spheniscinae” type

Being the group which includes all living taxa, its original diagnosis was based principally on integumentary features (Williams, 1995) among other characters. In this paper, we extend the characterization to incorporate osteological characters, in order to make comparison possible with the other subfamilies.

Characterization: *processus retroarticularis* smaller than the fossa articularis quadratica, proximal end of the femur corresponding to the caput femoris. Large rounded and bipartite *fossa tricipitalis* with the ventral part smaller and deeper than the dorsal portion. Tibiotarsus with *sulcus intercondylaris* deeper and wider than in “Paraptenodytinae”; *sulcus intercnemialis* reaching the proximal end with uniform depth along its length; *pons supratendineus* oblique and broad; *fossa flexoria* shallow; *epicondylus medialis* single and rounded, with the presence of a *fossa flexoria*. *Crista fibularis* with sharp edges as in *Paraptenodytes*. Elongation index (total length/proximal width) of tarsometatarsus less than 2 (smaller than in “Paleospheniscinae” and similar to “Paraptenodytinae”). *Foramina vascularia proximalia medialis* smaller than *lateralis*; only the *foramen vasculare proximale laterale* opens directly on plantar side. Presence of *tuberositas popliteus*.

Spheniscus megaramphus Stucchi, Urbina & Giraldo, 2003

(Stucchi et al., 2003: figs. 2-8)

Type species. *Spheniscus demersus* (Linnaeus, 1758).

Holotype: MUSM 175 (fragmentary skull and incomplete mandible).

Referred materials. MUSM 362 (fragments of skull and mandible), MUSM 363 (fragments of skull and rostrum), MUSM 364 (two fragmentary mandibles) and MUSM 365 (fragments of skull and mandibles).

Provenance: Pisco Formation. Montemar level (Late Miocene). Peru.

Diagnosis: 30 % larger than the living species. Rostrum 60 % longer than in the modern species of *Spheniscus* and proportionally narrower. Straight mandible with a short *fossa articularis quadratica* that is more robust than in the living species of the genus (Stucchi et al., 2003).

Spheniscus urbinai Stucchi, 2002

(Stucchi, 2002: figs. 2-7)

Holotype: MUSM 401 (nearly complete skeleton including a fragmentary skull, incomplete mandible, humerus, coracoids, left radius, right femur, right tibiotarsus, synsacrum, pelvic girdle, sternum, 16 cervical and thoracic vertebrae, tarsometatarsus and phalanges).

Referred material: MUSM 402 (right tibiotarsus, right femur, patella, right humerus, right coracoid, scapulae, sternum, ulna, radius, left carpometacarpus), MUSM 403 (fragmentary skull and an incomplete rostrum), MUSM 269 (fragmentary skull and mandible), MUSM 404 (rostrum) and MUSM 405 (rostrum).

Provenance: Pisco Formation. The specimens MUSM 401, 402, 403 and 269 come from the Sacaco Sur level (Early Pliocene), whereas MUSM 404 comes from the Montemar level and MUSM 405 from the Aguada de Lomas level (Late Miocene).

Diagnosis: 25% larger than the living species of the genus and similar in size to *S. megaramphus*. Compared to *S. megaramphus*, the rostrum is shorter and its base is wider, higher and more curved (Stucchi, 2002).

Spheniscus chilensis Emslie & Correa Guerra, 2003

(Emslie & Correa Guerra, 2003: fig. 2)

Holotype: UCN-1-130697 (complete left humerus).

Referred material (paratypes): UF 144101 (two left mandibles missing ends), UF 144102 (cervical vertebra), UF 143296- UF 143297 (two right scapulae), UF 144154 (right coracoid), UF 144124- UF 144125- UF 144155- UF 144156 (four right coracoids missing sternal ends), UF 144104- UF 144105 (two left humeri), UF 144106- UF 144126- UF 144157- UF 144159- UF 144171 (six left humeri missing proximal ends), UF 143295- UF 144107- UF 144109- UF 144124 (four right humeri), UF 143295- UF 144127- UF 144128- UF 144160 (three right humeri missing proximal ends), UF 144129 (left radius), UF 143299, UF 144110, UF 144130, UF 144133, (six right radii), UF

144134- UF 144161- UF 144162 (three left ulnae), UF 144163 (right ulna), UF 143298- UF 144111- UF 144135 (three left carpometacarpi), UF 144112- UF 144136- UF 144138- UF 144164 (five right carpometacarpi), UF 144139 (wing phalanx), UF 144113 (synsacrum), UF 144147 (proximal end of synsacrum), UF 144165 (left femur with ends damaged), UF 144114 (proximal left femur), UF 144140 (left femur missing proximal end), UF 144115- UF 144141- UF 144148 (three distal halves of left femora), UF 144166 (distal end of left femur), UF 144117- UF 144149 (two right femora missing proximal ends), UF 144167 (distal end of right femur), UF 144142 (shaft of right femur), UF 144150- UF 144168 (two distal left tibiotarsi), UF 144169 (proximal end of right tibiotarsus), UF 144143 (distal shaft of right tibiotarsus), UF 144170 (shaft of right tibiotarsus), UF 144144 (right fibula), UF 1443293- UF 143294- UF 144120 (three left tarsometatarsi with damaged proximal ends).

Provenance: Tiburón Fósil Locality, Península de Mejillones, Chile. Caleta Herradura de Mejillones Formation (Late Pliocene).

Diagnosis: Humerus with deep fossa at proximal anconal surface below head (fossa is shallow in *Spheniscus humboldti*, *S. demersus* and *S. mendiculus*, shallow to moderately deep in *S. magellanicus*), relatively smaller and narrower entepicondylar process (broad and rounded in all living *Spheniscus*), relatively slender shaft similar to *S. magellanicus* and *S. demersus* (more robust in *S. humboldti*), and distal end with or without pneumatic fossa in distal view (no fossa present in all living *Spheniscus*). Tibiotarsus with relatively larger distal foramina and broader distal external shaft than in all living *Spheniscus*. Tarsometatarsus with shallow anterior grooves below proximal foramina (grooves deep in all Recent *Spheniscus*). The ulna, radius, carpometacarpus and femur of the fossil species show minor differences with the living species (Emslie & Correa, 2003).

Spheniscus muizoni Göhlich, 2007

(Göhlich, 2007: figs. 2, 3, 4A, C, E, G, I, 5A).

Holotype: MNHN PPI 147 (partial postcranial skeleton including: incomplete left and right coracoid (MNHN PPI 147a), cranial end of left and incomplete right scapula (MNHN PPI 147b), incomplete left and right humerus (MNHN PPI 147c), left ulna (MNHN PPI 147d), proximal and distal end of right femur (MNHN PPI 147e), right and proximal end of left tibiotarsus (MNHN PPI 147f), proximal end of left fibula (147g), right complete tarsometatarsus (MNHN PPI 147h), cranial portion of sternum with articular sulcus for coracoid and fragment of the craniolateral process (MNHN PPI 147i), two fragmentary thoracic vertebrae (MNHN PPI 147j), seven caudal vertebrae (MNHN PPI 147k), fragmentary synsacrum (MNHN PPI 147l).

Referred material (paratypes): MNHN PPI 148 (fragmentary distal half of left coracoid), MNHN PPI 155 (incomplete right coracoid), MNHN PPI 149 (left ulna), MNHN PPI 150 (left radius), MNHN PPI 154 (right carpometacarpus), MNHN PPI 151 (distal end of right femur),

MNHN PPI 152 (cranial end of pygostyle), MNHN PPI 153 (rib fragment without ends).

Provenance: Cerro La Bruja, Peru. Pisco Formation, latest Middle or earliest Late Miocene.

Diagnosis: Smaller than any other modern genus, similar in size to *Spheniscus magellanicus*.

Carpometacarpus. Distinct step between the proximal carpal trochlea and the extensor process of the alular metacarpal, almost complete fusion of proximal alular digit with the major metacarpal (less advanced in *S. chilensis*), and an open spatium without ossified synchondroses (unlike *S. chilensis*).

Humerus. Head barely swollen proximally, outline without proximal notch between *tuberculum dorsale* and the head, but proximal outline less steep (in caudal view) than in all compared extant species of *Spheniscus*. Proximal border of *fossa tricripitalis* not ventrocaudally projected, as in *S. urbinai* and *S. chilensis*, but unlike in extant *Spheniscus* and *Pygoscelis*. Proximal border of *fossa tricripitalis* in ventral view straight and almost horizontal, as in extant *Spheniscus* species. Distinct concave indentation of crista bicipitalis between *tuberculum ventrale* and shaft. *Angulus preaxialis* more proximal than in other penguins. Caudalmost tip of the ventral epicondylus proximovertrally oriented, and cranialmost tip of ventral epicondylus ventrodistally projected, somewhat longer and oriented slightly more distally than in *S. chilensis*.

Femur. Head and trochanter at the same level, *condylus medialis* cranially very low and hardly projected (unlike any other penguin), *condylus lateralis* prominent and reaching further proximally than medial one.

Tibiotarsus. Straight and relatively narrow, deep medial impression of the medial collateral ligament situated mediocaudally on proximal end.

Tarsometatarsus. Quite elongate and slender (elongation index of 2.07, higher than in *S. urbinai*, but smaller than in *Palaeospheniscus*), long and deep *sulci valvulae extensorius*, extremely deep *fossa dorsalis infracotylaris*; *foramina proximalia vascularia* on different level (as in *Palaeospheniscus*), *foramen vasculare proximale mediale* situated very proximomedially; *crista hypotarsalis medialis* oriented mediodistally, bent medially and divided into two parts (a lateral thin and shorter crest, and a blunt and low one). Trochlea II and IV of about same length distally (unlike in *Palaeospheniscus*); *condylus laterale* of trochlea III (in distal view) at same level dorsally as trochlea IV (distally recessed in extant *Spheniscus* and *S. chilensis*), trochlea III dorsally at about same level, trochlea II oriented somewhat obliquely; trochlea IV (in distal view) distally tapering (Göhlich, 2007).

Pygoscelis calderensis Acosta Hospitaleche, Chávez & Fritis, 2006

(Acosta Hospitaleche et al., 2006: Fig. 3)

Type species: *Pygoscelis papua* (Forster, 1781)

Holotype: SGO-PV 790 (skull with rostral portion missing).

Referred material: SGO-PV 791 (incomplete skull) and SGO-PV 792 (basicranial fragment).

Provenance: “Los Dedos” locality, Mina La Fosforita, Bahía Inglesa, Chile. Bahía Inglesa Formation, Middle Miocene – Middle Pliocene.

Diagnosis: Deep fossa glandulae nasale limited by a supraorbital edge constant in width (about 20 mm) and narrower than in any living *Pygoscelis*. Frontals stick-like, 1 mm wide at the interorbital region, narrower than in *P. antarctica* and *P. papua*. Shallow fossa temporalis of 10 mm width. Slender processus postorbitalis in comparison to *P. papua* and *P. antarctica*, ventrolaterally projected, as in *P. papua* (in *P. adeliae* and *P. antarctica* they are parallel to the sagittal plane). Processus paroccipitalis more ventrally directed and prominentia cerebellaris rounded, whereas it is acute in all living *Pygoscelis* species (Acosta Hospitaleche et al., 2006).

Pygoscelis grandis Walsh & Suárez, 2006
(Walsh & Suárez, 2006: figs. 2-5)

Holotype: SGOPV-1104 (partial associated skeleton which 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, 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: SGOPV-1106 (left humerus missing distal end), SGOPV-1107 (caudal portion of synsacrum) and SGOPV-1108 (incomplete right pelvis).

Provenance: Bahía Inglesa, Chile. Lechero Member of the Bahía Inglesa Formation (Late Miocene- ?early Pliocene).

Diagnosis. Larger than any other species of the genus. Craniocaudal compression of tibiotarsus not marked; sulcus extensorius broad relative to diaphyseal width and situated on lateral margin of diaphysis; foramen vasculare proximale laterale larger than the medialis, greatest diaphyseal width of humerus 24%; fossa tricipitalis weakly bipartite; without fusion of ilium and synsacrum, ilioischiatric foramen larger than the acetabular; femur curved in anterior view; tubercle for the retinaculi m. fibularis well developed; condylus mediale of tibiotarsus extends further than the laterale (Walsh & Suárez, 2006).

Madrynornis mirandus Acosta Hospitaleche, Tambussi, Donato & Cozzuol, 2007
Figs. 5, 6 and 7

Type species *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato & Cozzuol, 2007.

Holotype: MEF- PV 100 (a nearly complete and articulated skeleton including: skull with partially preserved rostrum, mandible missing distal portion, 27 vertebrae, pygostyle, pelvis, left and right femora, right patella, left and right tibiotarsi and fibulae, left and right tarsometatarsi, 16 pedal phalanges (2 and ungual of second digit, 1, 2, and 3 of third digit, 1, 3, and 4 of fourth digit of the left side; 1 of second digit, 1, 2, 3, and ungual of third digit, and 2, 3, and 4 of fourth digit of the right side), sternum, 13 ribs, right scapula, left and right coracoids, furcula, left and right humeri, right ulna, right radius, right carpometacarpus).

Provenance: Playa Villarino, Península Valdés, Chubut Province. Puerto Madryn Formation. Early Late Miocene.

Diagnosis: Crista occipitalis transversa expanded into posterolaterally directed wings (not developed in *Pygoscelis*), fossa temporalis more triangular and deeper than in *Paraptendytes*, processus postorbitalis slender and longer than in *Spheniscus*, arcus jugalis slightly curved compared to that in *Eudyptes* and *Pygoscelis*, interorbital region narrower than in *Spheniscus* and *Eudyptes*. Sulcus glandulae nasalis without an external edge as in *Spheniscus* and *Paraptendytes* (edge present in *Pygoscelis*); lamina parasphenoidalis broader than in all living species. Ramus mandibularis straight with the fossa retroarticularis longer than in *Paraptendytes* and *Spheniscus*, and extending beyond the fossa articularis quadratica.

Humerus. Straight (slightly curved in *Palaeospheniscus* and *Spheniscus*), proximal and distal ends subequal and angulus preaxialis smaller than in *Spheniscus* and *Pygoscelis*. Shaft trochlear angle (ca. 38) smaller than in *Paraptendytes* and *Palaeospheniscus*. Large rounded and bipartite fossa tricipitalis with ventral part smaller and deeper than the dorsal portion (undivided in *Paraptendytes*). Foramen ilioischadicum smaller than the foramen acetabulare (unlike *Eudyptula* and *Palaeospheniscus*).

Femur. Trochanter femoris much higher than the head, unlike the living species, crista trochanteris broad but poorly developed compared with extant species. Sulcus intercondylaris deeper and wider than in *Paraptendytes*; sulcus intercnemialis uniform in depth along its length (irregular depth in *Pygoscelis*); supratendinosus bridge oblique and broader than in *Paraptendytes*, *Pygoscelis*, and *Spheniscus*. Fossa flexoria shallower than in *Pygoscelis* and *Spheniscus*. Epicondylus medialis single (double in *Spheniscus*) and rounded (elongate in *Pygoscelis*). Crista fibularis with sharp edges as in *Paraptendytes*, *Spheniscus*, and *Pygoscelis adeliae* (rounded in the remaining species).

Tarsometatarsus. Elongation index of 1.79 (smaller than in *Palaeospheniscus*). Foramen vasculare proximale mediale smaller than the laterale (subequal in *Pygoscelis*, *Eudyptes*, *Eudyptula*, and *Paraptendytes*); only the Foramen vasculare proximale laterale opens directly on the

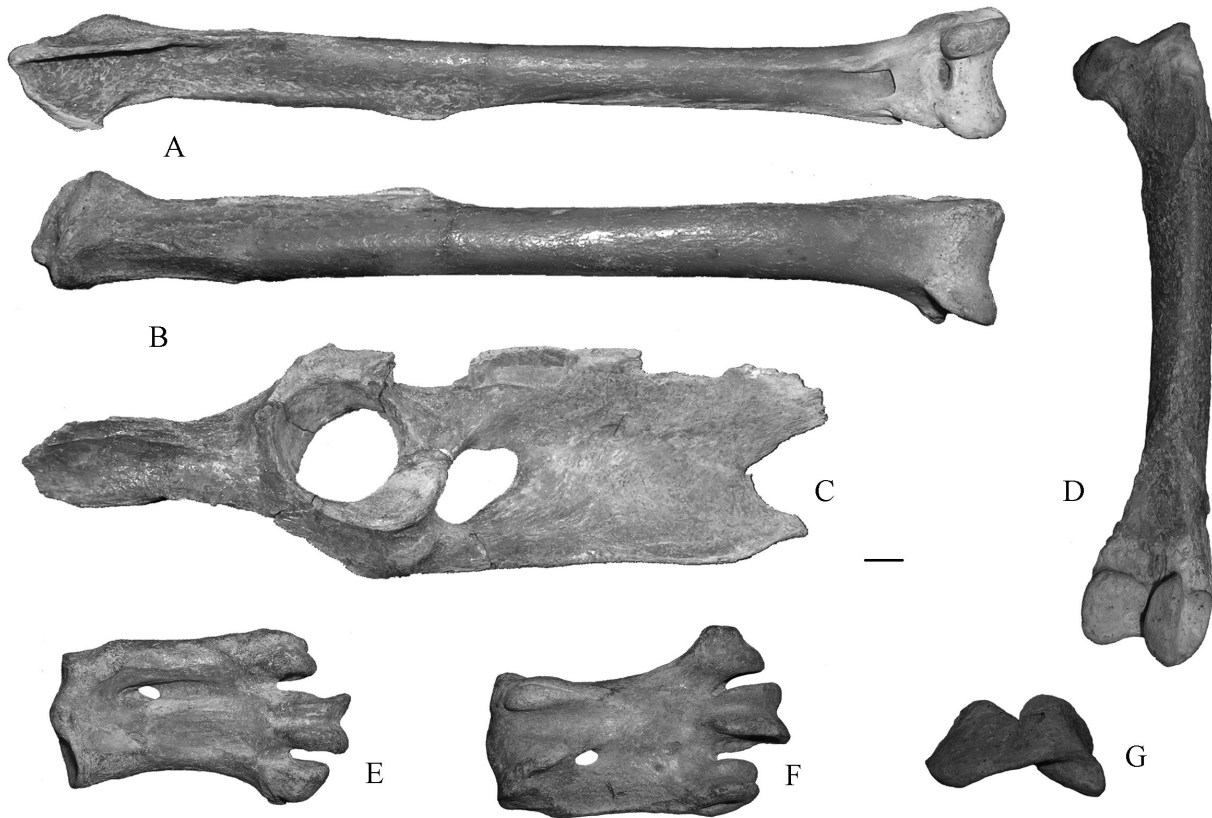


Figure 7 - *Madrynornis mirandus* (MEF-PV 100), from the Puerto Madryn Formation (early Late Miocene) at Playa Villarino, Península Valdés, Chubut Province, Argentina. A- tibiotarsus in anterior view, B- tibiotarsus in posterior view, C- pelvic girdle, D- femur, E- tarsometatarsus in cranial view, F- tarsometatarsus in caudal view, G- patella. Scale bar 1 cm. (Modified from Acosta Hospitaleche et al., 2007).

plantar side (both of them open on the plantar surface in *Pygoscelis* and *Parapterodactylus*). Trochlear edges sturdier than in *Spheniscus* (Acosta Hospitaleche et al., 2007).

Icadyptes salasi Clarke, Ksepka, Stucchi, Urbina, Giannini, Bertelli, Narváez & Boyd, 2007

Holotype: MUSM 897 (skull, axis, and eight additional cervical vertebrae, partial right and left coracoids, cranial end of the left scapula, left humerus, radius, ulna, proximal carpals, carpometacarpus, and phalanges)

Provenance: Ullujaya Valley of the Rio Ica, Department of Ica, Peru. Otuma Formation, late-Middle to Late Eocene.

Diagnosis: Beak forming more than two-thirds of the skull length, fusion of the premaxillae and palatines, axis with an elongate hypophysis terminating in a greatly mediolaterally expanded disk-like plate, a deep ovoid fossa on the lateral surface of the acrocoracoid process, humerus straight and broad, metacarpal I with a flat carpal trochlea, and metacarpals II and III subequal in distal extent (Clarke et al., 2007).

Perudyptes devriesi Clarke, Ksepka, Stucchi, Urbina, Giannini, Bertelli, Narváez & Boyd, 2007

Holotype: MUSM 889 (skull, mandible, cervical vertebrae and ribs, humeri, left carpometacarpus, synsacrum, femora, right tibiotarsus, and left tarsometatarsus)

Provenance: Quebrada Perdida. Department of Ica, Peru, basal portion of the Paracas Formation, Middle-Late Eocene.

Diagnosis: *Processus postorbitalis* anteroventrally directed, marked anterior expansion of the *rostrum parasphenoidalis*; posterior ridge forming the *sulcus scapulotricipitalis* of the humerus distally projected to the middle ridge, femur with a convex articular surface for the antitrochanter (Clarke et al., 2007).

CONCLUSIONS

We distinguished four different forms of humeri. (1) Humerus with a bipartite *fossa tricripitalis*, high *crus dorsale fossae*, a laterocranial fossa over the *tuberculum ventrale* and a *sulcus ligamentaris transversus* divided into two parts. *Eretiscus tonni* (Simpson, 1981), *Palaeospheniscus*

bergi Moreno & Mercerat, 1891, *P. patagonicus* Moreno & Mercerat, 1891, and *P. biloculata* (Simpson, 1970) have this type. (2) Straight humerus with a single *fossa tricipitalis* (lack of *crus dorsale fossae*), a lateral fossa over the *tuberculum ventrale* and a non-divided *sulcus ligamentaris transversus*, recognized in *Paraptenodytes robustus* (Ameghino, 1895), *Paraptenodytes antarcticus* (Moreno y Mercerat, 1981) and *Arthrodytes andrewsi* (Ameghino, 1901). (3) Humerus with a bipartite *fossa tricipitalis* like in living genera. (4) Straight humerus, a lateral fossa over the *tuberculum ventrale*, a bipartite *fossa tricipitalis*, a low *crus dorsale fossae* and a *sulcus ligamentaris transversus* divided into two parts. *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato & Cozzuol, 2007 displays this type.

Concerning the tarsometatarsi, we recognized four different morphologies. (1) Tarsometatarsus with an elongation index larger than two, a flattened metatarsal II, and a *foramen vasculare proximale medialis* open only in cranial side. This type is found in *Eretiscus tonni* (Simpson, 1981), *Palaeospheniscus bergi* Moreno & Mercerat, 1891, *P. patagonicus* Moreno & Mercerat, 1891, and *P. biloculata* (Simpson, 1970). (2) Tarsometatarsus with an elongation index smaller than two, a *foramen vasculare proximale lateralis* larger than the *foramen medialis* and a strongly divergent trochlea II. *Paraptenodytes robustus* (Ameghino, 1895), *Paraptenodytes antarcticus* (Moreno y Mercerat, 1981) and *Arthrodytes andrewsi* (Ameghino, 1901) display this type. (3) Tarsometatarsus with elongation index less than 2. *Foramina vascularia proximalia medialis* smaller than *lateralis*; only the *foramen vasculare proximale laterale* opens directly on plantar side. Presence of *tuberositas popliteus*. We found it in the species assigned to modern genera. (4) Tarsometatarsus with an elongation index about 1.79, an extremely small *foramen vasculare proximale mediale* and a strongly divergent trochlea II. *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato & Cozzuol, 2007 shows this morphology.

As far as we know, one particular humeral form could be related to a tarsometatarsus type. *Madrynornis mirandus* and *Palaeospheniscus patagonicus* are undoubted examples of this.

The supposed overestimated taxonomic diversity (see for example Simpson 1976) appears to be a consequence of the erection of numerous taxa without a suitable diagnosis.

As a result of our studies and following the rules of the International Code of Zoological Nomenclature, *Paraspheniscus* Ameghino, 1905, *Chubutodyptes* Simpson, 1970, *Perispheniscus* Ameghino, 1905 and *Treleudytes* Ameghino, 1905 are considered *junior synonyms* of *Palaeospheniscus*. In the same way, *Palaeospheniscus medianus* Ameghino, 1905, *P. affinis* Ameghino, 1905, *P. rothi* Ameghino, 1905, *P. gracilis* Ameghino, 1898, *P. interruptus* Ameghino, 1905, *P. nereius* Ameghino, 1905, *P. planus* Ameghino, 1905, *Paraspheniscus bergi* (Moreno & Mercerat, 1891) and *P. nereius* (Ameghino, 1901) are considered *junior synonyms* of *Palae-*

ospheniscus bergi. *Palaeospheniscus patagonicus* is treated here as a *senior synonym* of *Palaeospheniscus menzbieri* Moreno & Mercerat, 1891, *P. robustus* Ameghino, 1894, *P. intermedius* Ameghino, 1905 and *Treleudytes crassa* Ameghino, 1905. The latter is also the *nomen correctum* of *Treleudytes crassus*. We also consider as *synonymous junior* of *Palaeospheniscus biloculata* nov. comb. the taxa *Chubutodyptes biloculata* Simpson, 1970 and *Perispheniscus wimani* Ameghino, 1905.

The genera *Isotremornis* Ameghino, 1905 and *Metancylornis* Ameghino, 1905 are *junior synonyms* of *Paraptenodytes*. The species *Paraptenodytes antarcticus* is the *senior synonym* of *Palaeospheniscus antarcticus* Moreno & Mercerat, 1891; while *Arthrodytes grandis* Ameghino, 1905, *Isotremornis nordensjkoeldi* Ameghino, 1905, *Paraptenodytes brodkorbi* Simpson, 1972, *P. curtus* Ameghino, 1901, *P. grandis* Ameghino, 1901 and *Metancylornis curtus* Ameghino, 1905 are *junior synonyms* of *Paraptenodytes robustus*.

Arthrodytes constitutes a monotypic genus and *Arthrodytes andrewsi* is considered as the *senior synonym* of *Paraptenodytes andrewsi* Ameghino, 1901.

Besides, *Apterodytes ictus* Ameghino (1905), *Neculus rothi* Ameghino, 1905, *Pseudospheniscus interplanus* Ameghino, 1905 and *Palaeospheniscus wimani* Ameghino, 1905 are considered *nomina nulla*. On the other hand, we consider *Palaeospheniscus concavus* Ameghino, 1905, *Palaeospheniscus convexus* Ameghino, 1905, *Pseudospheniscus concavus* Ameghino, 1905 and *Pseudospheniscus convexus* Ameghino, 1905 as *nomina nuda*.

Consequently, the only Patagonian *nomina inviolata* are *Palaeospheniscus bergi* Moreno & Mercerat, 1891 and *Palaeospheniscus patagonicus* Moreno & Mercerat, 1891.

From more than 30 species historically described, only nine are currently recognized as valid. Nevertheless, fossil penguin diversity has increased with the nine species erected during the last decade: *Spheniscus urbinai*, *S. megaramphus*, *Spheniscus chilensis*, *Spheniscus muizoni*, *Perudyptes devriesi*, *Icadyptes salasi*, *Pygoscelis calderensis*, *Pygoscelis grandis* and *Madrynornis mirandus*.

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ADDENDUM

The aims and extent of this work correspond to our ambitions of the year 2004, but after this paper was written, many contributions on fossil penguins began to appear. As the state of the knowledge has changed since then, we have updated some points in this manuscript, including data

published between 2004 and 2007 (Bertelli and Giannini, 2005; Acosta Hospitaleche, 2005, 2006, 2007; Acosta Hospitaleche et al., 2007, 2008; Clarke et al., 2007; Walsh and Suárez, 2006).

REFERENCES

- Acosta Hospitaleche, C. 2004. Los pingüinos (Aves, Sphenisciformes) fósiles de Patagonia. Sistemática, biogeografía y evolución. Ph.D Thesis, Facultad de Ciencias Naturales y Museo, UNLP, La Plata, 321 pp.
- Acosta Hospitaleche, C. 2005. Systematic revision of *Arthrodytes* Ameghino, 1905 (Aves, Spheniscidae) and its assignment to the Paraptenodytinae. *Neues Jahrbuch für Geologie und Paläontologie*, 7:404-414.
- Acosta Hospitaleche, C. 2006. Taxonomic longevity in penguins (Aves, Spheniscidae). *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, 241: 383-403.
- Acosta Hospitaleche, C. 2007. Revisión sistemática del género y especie *Palaeospheniscus biloculata* nov. comb. (Aves, Spheniscidae) de la Formación Gaiman. *Ameghiniana*, 44: 417-426
- Acosta Hospitaleche, C. & Canto, J. 2005. Primer registro de cráneos de *Palaeospheniscus* (Aves, Spheniscidae), procedentes de la Formación Bahía Inglesa (Mioceno Medio-Tardío), Chile. *Revista Chilena de Historia Natural*, 78: 489-495.
- Acosta Hospitaleche, C. & Canto, J. 2007. Comentarios acerca de "Observaciones sobre la presencia de *Paraptenodytes* y *Palaeospheniscus* (Aves: Sphenisciformes) en la Formación Bahía Inglesa, Chile". *Revista Chilena de Historia Natural*, 80: 261-264.
- Acosta Hospitaleche, C., Fritis, O., Tambussi, C. P. & Quinzio, A. L. 2002. Nuevos restos de pingüinos (Aves Spheniscidae) en la Formación Bahía Inglesa (Mioceno superior- Plioceno inferior) de Chile. *Actas del I Congreso Latinoamericano de Paleontología*, 16. Santiago de Chile.
- Acosta Hospitaleche, C. & Gasparini, G. 2004. Análisis multivariado de caracteres cuantitativos craneanos en Spheniscidae (Aves, Sphenisciformes). *Comunicaciones de la Asociación Paleontológica Argentina*. Diamante, 29 de noviembre- 1° de diciembre de 2004. Resúmenes, 3.
- Acosta Hospitaleche, C., C. Tambussi, M. Donato & M. Cozzuol. (2007). *Madrynornis mirandus*, a new early Late Miocene penguin (Aves, Spheniscidae) from Patagonia. *Acta Paleontologica Polonica*, 52: 299-314.
- Acosta Hospitaleche C., Castro, L. N., Scasso, R., Tambussi, C. & Castro, L. (2008). *Palaeospheniscus patagonicus* (Aves, Spheniscidae): new discoveries from the Early Miocene of Argentina. *Journal of Palaeontology*, 82: 565-575.
- Ameghino, F. 1891. Enumeración de las aves fósiles de la República Argentina. *Revista Argentina de Historia Natural. Buenos Aires*, 1: 441-453.
- Ameghino, F. 1895. Sur les oiseaux fossiles de Patagonie. *Boletín del Instituto Geográfico de Argentina*, 15: 501-602.
- Ameghino, F. 1901. L'âge des formations sédimentaires de Patagonie. *Anales de la Sociedad Científica Argentina*, 51: 20-39, 65-91.
- Baumel, J. & Witmer, L. M. 1993. Osteologia. In: Baumel, J., King, A., Breazile, J., Evans, H., Vanden Berge, J. (Ed), *Handbook of avian anatomy: Nomina Anatomica Avium*, Publications of the Nuttall Ornithological Club, Massachusetts.
- Bertelli, S. & Giannini, N. 2005. A phylogeny of extant penguins (Aves: Sphenisciformes) combining morphology and mitochondrial sequences. *Cladistics*, 21:209-239.
- Brodkorb, P. 1963. Catalogue of fossil birds. 1 (Archaeopterygiformes through Ardeiformes). *Bulletin of the Florida State Museum, (Biological Sciences)*, 7 (4): 177-293. Gainesville.
- Chávez, M. 2007. Sobre la presencia de *Paraptenodytes* y *Palaeospheniscus* (Aves: Sphenisciformes) en la Formación Bahía Inglesa, Chile. *Revista Chilena de Historia Natural*, 80: 255-259.
- Clarke, J., Ksepka, D., Stucchi, M., Urbina, M., Giannini, N., Bertelli, S., Narváez, Y., Boyd, C. 2007. Paleogene equatorial penguins challenge the proposed relationship between biogeography, diversity, and Cenozoic climate change. *Proceedings of the National Academy of Sciences of United States of America*, 28: 11545-11550.
- Cozzuol, M. A., Tambussi, C. P. & Noriega, J. I. 1993. Un pingüino (Aves: Spheniscidae) de la Formación Puerto Madryn (Mioceno Medio) en Península Valdés, Chubut, Argentina, con importantes implicancias filogenéticas. *Ameghiniana*, 30: 327-328.
- Emslie S. D & C. Guerra Correa. 2003. A new species of penguin (Spheniscidae: *Spheniscus*) and other birds from the late Pliocene of Chile. *Proceedings of the Biological Society of Washington*, 116: 308-316.
- Giannini, N. P. & S. Bertelli. 2004. Phylogeny of extant penguins based on integumentary and breeding characters. *The Auk*, 121: 421-434.
- Göhlich, U. 2007. The oldest fossil record of the extant penguin genus *Spheniscus*—a new species from the Miocene of Peru. *Acta Paleontologica Polonica*, 52: 285-298.
- Grant, W. S., Duffy, D. C. & Leslie, R. W. 1994. Allozyme Phylogeny of *Spheniscus* Penguins. *The Auk*, 111: 716-720.
- International Commission on Zoological Nomenclature, 2000. International Code of Zoological Nomenclature, International Trust for Zoological Nomenclature. London.
- Jadwiszczak P. 2006. Eocene penguins of Seymour Island,

- Antarctica: the earliest record . taxonomic problems and some evolutionary considerations. *Polish Polar Research*, 27: 287-302.
- Livezey, B. C. 1989. Morphometric patterns in Recent and fossil penguins (Aves, Sphenisciformes). *Journal of the Linnean Society*, London, 219: 269-307.
- Marples, B. J. 1952. Early Tertiary penguins of New Zealand. *Geological Survey Palaeontological Bulletin*, 20: 1-66.
- Moreno, F. & Mercerat, A. 1891. Catálogo de los pájaros fósiles de la República Argentina conservados en el Museo de La Plata. *Anales del Museo de La Plata (Paleontología Argentina)*, 1: 7-71 pp.
- O' Hara, R. 1989. *Systematics and the study of Natural History, with an estimate of the phylogeny of the living penguins (Aves: Spheniscidae)*, Harvard University, Cambridge, 171 pp.
- O' Hara, R. 1991. An estimate of the phylogeny of the living penguins (Aves: Spheniscidae). *American Zoology*, 29:11A
- Olson, S. L. 1986. A replacement name for the fossil penguin *Microdytes* Simpson (Aves: Spheniscidae). *Journal of Paleontology*, 60: 785-785.
- Sibley, C. G., Hlquist, J. E. & Monroe, B. L. 1988. A classification of the living birds of the world based on DNA- DNA hybridization studies. *Auk*, 105: 409-423.
- Sibley, C. G. & Monroe, B. 1990. *Distribution and Taxonomy of Birds of the World*. Yale University Press., New Haven & London., 1-1111. pp.
- Simpson, G.G. 1946. Fossil penguins. *Bulletin of the American Museum of Natural History*, 87 (1): 1-100, figs. 1-33. New York.
- Simpson, G.G. 1970. Miocene penguins from Victoria, Australia, and Chubut, Argentina. *Memoirs of the Natural History Museum*. Victoria, 31: 17-24.
- Simpson, G. G. 1971. A review of the pre-Pleistocene penguins of New Zealand. *Bulletin of the American Museum of Natural History*, 144: 319-378.
- Simpson, G.G. 1972. Conspectus of Patagonian Fossil Penguins. *American Museum Novitates*, 2488: 1-37.
- Simpson, G. G. 1973. Tertiary penguins from the North Island of New Zealand. *Journal of the Royal Society of New Zealand*, 3 (3): 441-452, 5 figs.
- Simpson, G. G. 1975. Notes on variation in penguins and on fossil penguins from the Pliocene of Langebaanweg, Cape Province. South Africa. *Annals of the South African Museum*, 69: 59-72.
- Simpson, G. G. 1976. *Penguins. Past and present, here and there*. Yale University press New Haven. London.
- Simpson, G.G. 1981. Notes on some fossil penguins, including a new genus from Patagonia. *Ameghiniana*, 18 (3-4): 266-272, lám 1. Buenos Aires.
- Stucchi, M. 2002. Una nueva especie de *Spheniscus* (Aves: Spheniscidae) de la Formación Pisco, Perú. *Boletín de la Sociedad Geológica del Perú*, 94: 19-26.
- Stucchi, M., Urbina, M. & Giraldo, A. 2003. Una nueva especie de Spheniscidae del Mioceno tardío de la Formación Pisco, Perú. *Bulletin Institut Français d'Etudes Andines*, 32: 361-375.
- Tambussi, C., Reguero, M., Marensi, S. & Santillana, S. 2005. *Crossvallia unienwillia*, a new Spheniscidae (Sphenisciformes, Aves) from the Late Paleocene of Antarctica. *Geobios*, 38: 667-675.
- Williams, T. D. 1995. *The penguins. Spheniscidae*. Birds families of the world. Oxford University Press: 295pp.
- Walsh, S. & Suárez, M. 2006. New penguin remains from the Pliocene of Northern Chile. *Historical Biology*, 18: 115-126
- Zusi, R. L. 1975. An interpretation of skull structure in penguins. pp. 59-84 In: Stonehouse, B. (Ed), *The biology of penguins.*, Macmillan Press, London & Basingstoke.