A new Miocene penguin from Patagonia and its phylogenetic relationships

CAROLINA ACOSTA HOSPITALECHE, CLAUDIA TAMBUSSI, MARIANO DONATO, and MARIO COZZUOL

We describe a new medium-sized penguin, *Madrynornis mirandus* gen. et sp. nov., from the early late Miocene Puerto Madryn Formation, Chubut Province, Argentina. Although it is evident that extant and fossil penguins form a remarkably homogeneous family of birds, Spheniscidae, their within-group phylogenetic relationships are less obvious. In order to identify the phylogenetic position of the new taxon, we conducted a phylogenetic analysis using 44 osteological characters sampled from 14 representative species of all living genera and five fossil species of Spheniscidae. The family is clearly monophyletic and *Madrynornis mirandus* is closely related to living taxa. Our phylogenetic interpretation is congruent with biostratigraphic data, with *Paraptenodytes* from the early Miocene (about 20 Ma) located at the base of the Spheniscidae. Classically, two basic tarsometatarsal types were recognized (one for pre-Miocene and the other for the post-Miocene penguins) based on the pattern of the proximal foramina and the hypotarsus. *Madrynornis mirandus* exhibits an arrangement of the proximal foramina and a degree of metatarsals fusion similar to that in the living forms, although its elongation index (total length/proximal width) is reminiscent of the extinct *Paraptenodytes* (a penguin historically recognized as a pre-Miocene form, coming from the early Miocene of Argentina). *Madrynornis* reveals that the two basic tarsometatarsal types co-existed among Miocene penguins.

Key words: Aves, Spheniscidae, penguins, Miocene, Puerto Madryn Formation, Chubut Province, Argentina.

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Introduction

Penguins are obligate marine wing-propelled diving birds with an exclusively austral history that extends back 55 million years (Tambussi et al. 2005). The group displays a mosaic of ancient and derived characters making it a very interesting subject from a phylogenetic viewpoint. Various authors have studied the extant penguin species, but there is no consensus about their phylogenetic relationships (e.g., Zusi 1975; O'Hara 1989; Sibley and Monroe 1990; Grant et al. 1994) and these hypotheses have not been properly confronted with those obtained from fossil data.

There are several localities from which spheniscids have been recovered. All of them are restricted to Cenozoic sites in the Southern Hemisphere, including Antarctica (Myrcha et al. 2002; Tambussi et al. 2006), Africa (Simpson 1971), Australia and New Zealand (Fordyce and Jones 1990 and literature cited therein), and South America. Particularly, in the last area there are at least four Miocene to Pliocene penguin species known form Peru (Stucchi 2002; Stucchi et al. 2003;

Acosta Hospitaleche and Stucchi 2005; Göhlich 2007; see also Muizon and DeVries 1985), at least five recovered from Miocene to Pliocene sediments in Chile (Walsh and Hume 2001; Acosta Hospitaleche et al. 2002; Emslie and Correa 2003), and finally many species from the Paleogene and Neogene of Patagonia (Simpson 1946, 1972, 1981; Clarke et al. 2003). The Patagonian fossil penguins include a wide array of taxa erected mainly on the basis of differences in limb morphology (Simpson 1946, 1972, 1981). These penguins are late middle Eocene–late Miocene in age (Tonni 1980; Cione and Tonni 1981; Clarke et al. 2003) and therefore some of them are contemporary with the Chilean and Peruvian species.

The rich collections of other Argentinean fossil penguins are almost completely restricted to the latest Oligocene–early Miocene Leonian Marine Stage and consist mainly of various isolated bones, with the single exception of *Paraptenodytes antarcticus* (Moreno and Mercerat, 1891).

Here we report on a complete skeleton of a new Patagonian species of penguin from the lower part of the upper

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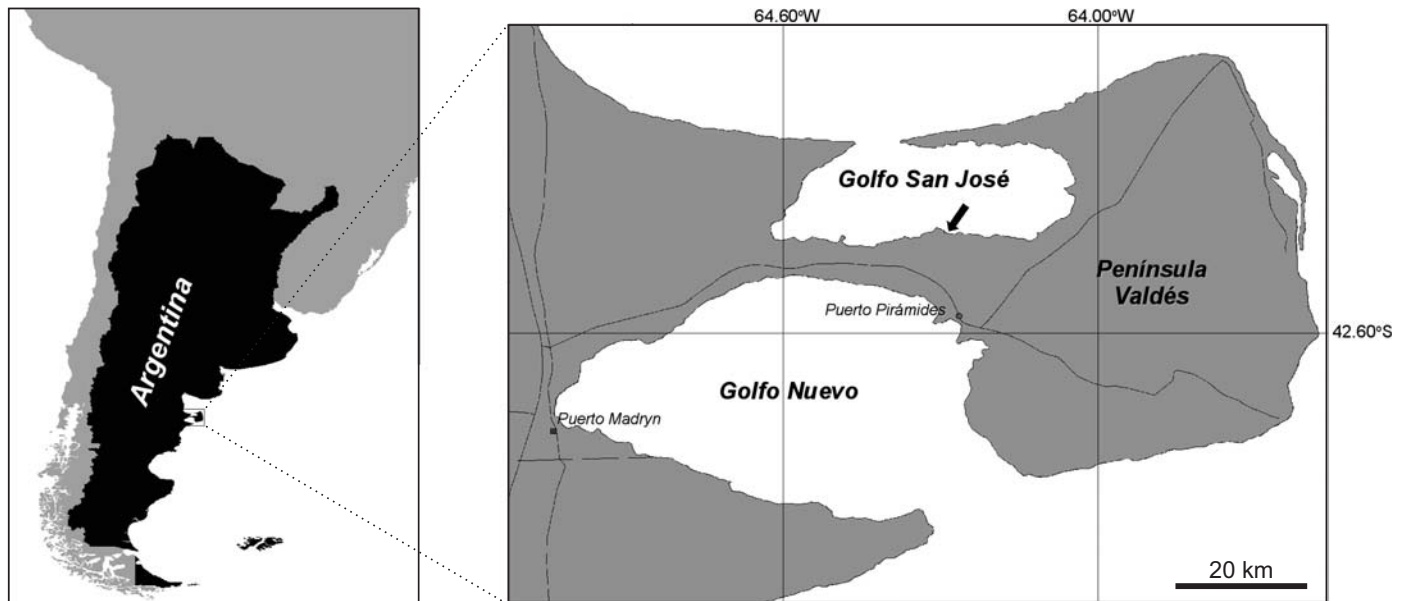http://app.pan.pl/acta52/app52-299.pdf

Fig. 1. Map of Península Valdés, Chubut Province (Argentina) indicating Playa Villarino, Puerto Madryn Formation, early late Miocene, the locality from which the holotype of *Madrynornis mirandus* gen. et sp. nov., MEF-PV 100, was collected. The penguin locality is indicated by an arrow.

Miocene Puerto Madryn Formation, Chubut Province, Argentina. These remains were previously mentioned by Cozzuol et al. (1993). We provide a thorough description of the skull and postcranial remains in order to diagnose a new genus and species, and to discuss its phylogenetic position and taxonomic status.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; IAA, Instituto Antártico Argentino, Ciudad Autónoma de Buenos Aires, Argentina; MEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MLP, Museo de La Plata, Ciudad de La Plata, Argentina.

Material and methods

Comparative materials used in this study are listed in Appendix 1. A phylogenetic analysis was conducted including 22 species (14 representative species of all living genera and five fossil species of Spheniscidae, as well as three outgroups) using 44 morphological characters (Appendix 2) to determine the phylogenetic position of the new taxon. The sources for the morphological characters used here were O'Hara (1989), Acosta Hospitaleche (2004), and Bertelli and Giannini (2005); we modified these characters as needed (Appendix 2). Outgroup comparison was used for the determination of character polarity and rooting (Nixon and Carpenter 1993). The selected outgroups were *Diomedea exulans* Linnaeus, 1758, *Fregata magnificens* Mathews, 1914, and *Gavia immer* (Brunnich, 1764), according to phylogenetic hypotheses proposed by various authors (e.g., Van Tuinen et al. 2001; Mayr 2004). *G. immer* was used as root.

Phylogenetic analysis of our data matrix (Appendix 3) was done using TNT v.1.0 (Goloboff et al. 2003) and Winclada version 1.00.08 (Nixon 2002). The characters were considered equally weighted and coded as non-additive. Heuristic searches were performed, with 10,000 replications. Consistency and retention indices were obtained from Winclada, which was also used to manipulate the tree, prepare figures, and analyze character distribution.

Osteological terminology with English equivalents of the Latin names follows Baumel and Witmer (1993) and, where necessary, Simpson (1946), O'Hara (1989), and Kanfeder (1994). Description style is according to Pycraft (1898). We follow the systematics proposed by Martínez (1992) for the modern species, and by Simpson (1946, 1972) and Acosta Hospitaleche (2004) for the fossil penguins. Measurements were taken with Vernier calipers with 0.01 mm increments.

Geologic setting

The specimen was found in an outcrop on the southern coast of Golfo San José, Península Valdés, Chubut Province, Argentina, close to Punta Tehuelche (Fig. 1). In addition to the specimen described here (Fig. 2), remains of mollusks, complete and articulated remains of crabs, sharks, bony fishes, seals, and baleen whales were found.

The outcrop is a small cliff that reaches about two meters above sea level and forms a platform around the base of the main cliff. It is part of the lower levels of the Puerto Madryn Formation (Haller 1978), known informally as "Entrerriense" because it is considered to be a correlate of marine beds cropping out in the Entre Ríos Province, northeastern Argentina (Frenguelli 1926; Scasso and del Río 1987; Scasso et al.

Fig. 2. Miocene penguin *Madrynornis mirandus* gen. et sp. nov., MEF-PV 100 (holotype), Puerto Madryn Formation, early late Miocene, Playa Villarino, Península Valdés, Chubut Province, Argentina. Photo of the articulated skeleton before preparation.

2001). The age of the Puerto Madryn Formation is early late Miocene based on radiometric data (9.4 Ma, Zinsmeister et al. 1981; 10.0 ± 0.3 Ma, Scasso et al. 2001).

The base of the Tortonian is characterized worldwide by a sea level drop of about 100 m below the present level (Haq et al. 1987). Since the Puerto Madryn Formation environment is of relative shallow waters, close to the coast, changing to a terrestrial environment at the top (Scasso and del Río 1987; Dozo et al. 2002), it seems reasonable to infer that the base of this unit may be late Serravalian in age, when episodes of moderate sea level rise occurred. High sea levels above the present one are observed again at the base of the Messinian, which is, however, in disagreement with the age indicated by the faunal association.

The extraordinary preservation of vertebrates and invertebrates (Cozzuol 1993, 2001; Riva Rossi et al. 2000; del Río et al. 2001) may in part be due to rapid burial after a storm, which deposited a large volume of sediment in a short time. Articulated vertebrate remains, complete crabs and mollusk aggregation in life position indicates a rapid burial event with very little or no exposure after the event. A series of storm deposits along the sequence was described by Scasso and del Río (1987), Scasso et al. (2001), and del Río et al. (2001). The best preserved specimens are normally found at the top of massive layers of fine, silty sandstones of a less than a meter thick. No evidence of post-burial predation or scavenging was observed.

Systematic paleontology

Order Spheniscformes Sharpe, 1891
Family Spheniscidae Bonaparte, 1831
Genus *Madrynornis* nov.

Type species: *Madrynornis mirandus* sp. nov., monotypic.
Derivation of the name: From Madryn, for its stratigraphic provenance,

the Puerto Madryn Formation, and *ornis*, Greek, referring to a "bird of Madryn". Gender is masculine.

Diagnosis.—Differs from all other known spheniscids by the following combination of characters: transverse occipital crest expanded into posterolaterally directed wings (not developed in *Pygoscelis* Wagler, 1832); temporal fossa more triangular and deeper than in *Paraptenodytes* Ameghino, 1891; post-orbital process slender and longer than in *Spheniscus* Brisson, 1760; jugal arch only slightly curved compared to that in *Eudyptes* Vieillot, 1816 and *Pygoscelis*; interorbital narrower than in *Spheniscus* and *Eudyptes*; nasal fossa without an external edge as in *Spheniscus* and *Paraptenodytes* (edge present in *Pygoscelis*); parasphenoidal plate broader than in all living species. Mandibular ramus straight with the retroarticular process longer than in *Paraptenodytes* and *Spheniscus*, and extending beyond the articular fossa. Humeral diaphysis straight (slightly curved in *Palaeospheniscus* Moreno and Mercerat, 1891 and *Spheniscus*); proximal and distal subequal and preaxial angle smaller than in *Spheniscus* and *Pygoscelis*; shaft-trochlear angle (ca. 38°) smaller than in *Aptenodytes* Miller, 1778 and *Palaeospheniscus*. Large rounded and bipartite tricipital fossa with ventral part smaller and deeper than the dorsal portion (undivided in *Paraptenodytes*). Foramen ilioischiadicum smaller than the foramen acetabular (unlike *Eudyptula* Bonaparte, 1856 and *Palaeospheniscus*). Femur with trochanter much higher than the head, unlike the living species; trochanter crest broad but poorly developed compared with extant species; intercondylar groove deeper and wider than in *Paraptenodytes*; intercnemial groove reaches proximal end with uniform depth along its length (irregular depth in *Pygoscelis*); supratendinosus bridge oblique and broader than in *Paraptenodytes*, *Pygoscelis*, and *Spheniscus*; fossa flexoria shallower than in *Pygoscelis* and *Spheniscus*; medial epicondyle single (double in *Spheniscus*) and rounded (elongate in *Pygoscelis*). Fibular crest with sharp edges as in *Paraptenodytes*, *Spheniscus*, and *Pygoscelis adeliae* (rounded in the remaining species). Elongation index (total length/proxi-

mal width) of tarsometatarsus 1.79 (smaller than in *Palaeosphensicus*). Medial proximal vascular foramen smaller than the lateral (subequal in *Pygoscelis*, *Eudyptes*, *Eudyptula*, and *Paraptenodytes*); only the lateral proximal vascular foramen opens directly on plantar side (both of them open on the plantar surface in *Pygoscelis* and *Paraptenodytes*); trochlear edges sturdier than in *Spheniscus*.

Temporal and geographic distribution.—Early late Miocene, Puerto Madryn Formation, Argentina. Playa Villarino (S 42° 25', W 64°16'), Golfo San José, Chubut Province (Fig. 1).

Comments.—Simpson (1946) established five subfamilies of Spheniscidae based on characters of the humerus and tarsometatarsus: Palaeospheniscinae, Paraptenodytinae, Anthropornithinae, Palaeeudyptinae, and Spheniscinae (including all living forms).

Following the criticism of Marples (1952), Simpson (1971) abandoned his subfamilial division of the Spheniscidae after examining the fossil penguins from New Zealand.

Although we do not have enough evidence to propose the adoption of a suprageneric arrangement, our current studies on the penguin faunas from Antarctica and South America allow us (CAH and CT) to identify groups that are partially equivalent to those of Simpson's classification (Acosta Hospitaleche 2003, 2004; Tambussi et al. 2006; but see Ksepka et al. 2006).

Madrynornis differs from the *Palaeospheniscus* species and *Eretiscus tonnii* in having a shorter tarsometatarsus, smaller shaft-trochlear angle, and both proximal vascular foramina well developed. A bipartite tricipital fossa and a smaller shaft-trochlear angle differentiate *Madrynornis* from *Paraptenodytes* sp. and *Arthrodytes andrewsi*, the largest Patagonian penguin even discovered. *Madrynornis* is distinguished from *Anthropornis grandis* and *A. nordenskjoeldi* by having a shorter tarsometatarsus, a weakly curved rather than sigmoid humerus, and a larger and bipartite tricipital fossa. It differs from *Palaeeudyptes* species by the presence of both proximal vascular foramina and a larger and bipartite tricipital fossa. Finally, although the metatarsal fusion is stronger than in living species, a bipartite tricipital fossa, short tarsometatarsus, small shaft-trochlear angle and similar development of the proximal vascular foramina are shared with these forms.

Madrynornis mirandus sp. nov.
Figs. 2–7.

Holotype: *Madrynornis mirandus*, a nearly complete and articulated skeleton, MEF- PV 100, collected by one of the authors (MC). It includes: 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.

Derivation of the name: From Latin, *mirandus*, wonderful. From the excellent preservation of the skeleton.

Measurements.—Skull: total length, ca.145 mm; postorbital width, 51 mm; mandible length, ca. 111 mm; posterior height of mandible, 9.7 mm; height at level of mandibular angle, 15.5 mm. Sternum: total length, 136 mm; width at posterior most costal facet, 66 mm. Coracoid: length, 8.48 mm; distal width, 31 mm. Scapula: length, 114.2 mm; width of articular end, 23.9 mm. Humerus: length, 79.1 mm; distal width, 20.5 mm. Ulna: length, 59.1 mm. Radius: length, 57.8 mm. Carpometacarpus: length, 48.6 mm; proximal width, 15.8 mm. Pelvis: length among midline, 99 mm. Femur: length, 85.9 mm. Tibiotarsus: maximum length, 134.6 mm; distal width, 16.9 mm. Tarsometatarsus: length, 36.5 mm; proximal width, 18.1 mm; distal width, 19.1 mm. Pygostyle: length, 44 mm. Left phalanges (length) of the second digit: 2 (19.4 mm) and ungual (15.6 mm); of the third digit: 1 (25.4 mm), 2 (20.7 mm), and 3 (20.2 mm); and of the fourth digit: 1 (20.2 mm), 3 (14.4 mm), and 4 (14.8 mm). Right phalanges (length) of the second digit: 1 (22.7 mm); of the third digit: 2 (25.6 mm), 2 (21.7 mm), 3 (19 mm), and ungual (18.1 mm); and of the fourth digit: 2 (15.5 mm), 3 (14.4 mm), and 4 (14.8 mm).

Diagnosis.—As for the genus.

Description and comparisons.—Skull: Similar in size to the Adelie Penguin, *Pygoscelis adeliae* (Hombron and Jacquinot, 1841). The cerebellar protuberance projects more distally than the paroccipital process (Figs. 3A, 6A), while in *Pygoscelis antarctica* (Forster, 1781) they project slightly further posteriorly. The paroccipital processes are ventrally directed as in the living species, whereas in *Paraptenodytes* they are bifid and caudally projected. The transverse occipital crest is expanded posterolaterally and wing-like, similar to *Spheniscus*, *Eudyptes*, and *Paraptenodytes*. The sagital crest (apparent in *Paraptenodytes*) is absent in *Madrynornis*. The occipital region is trapezoidal in shape, but is subcircular in *Paraptenodytes* and quadrangular in *Eudyptes*, *Eudyptula*, and *Spheniscus*. The temporal fossa is deep and triangular with its dorsal tip not reaching the position of the sagittal crest. The postorbital processes are thin, long (Figs. 3A, 6A), and project ventrally, whereas in *Paraptenodytes* they are directed posteriorly. The frontals form a medial crest much narrower than in the living species, and which is absent in *Paraptenodytes*. The entire jugal arch is gently curved, a characteristic shared with *Spheniscus*. Extreme curvature of the anterior portion of the arch is a feature of *Eudyptes*, *Pygoscelis adeliae*, and *P. antarctica*, and to a lesser degree of *P. papua* Forster, 1781, *Megadyptes* Milne-Edwards, 1880, and *Aptenodytes* (Zusi 1975). The basitemporal plate is broader than in all the compared species. The pterygoid (narrow and rod-like in *Paraptenodytes*) is expanded to form a thin, horizontal plate similar to that seen in extant species. The tomial crest is above the level of the parasphenoidal plate, as in *Aptenodytes* and *Pygoscelis*, but is not parallel as in *Aptenodytes forsteri* Gray, 1844.

The mandible is straight. The medial process, larger than in *Paraptenodytes,* bears a medially directed hook-like projection. The caudal fenestra is oval and the rostral fenestra is absent. On the medial surface of the mandible, extending
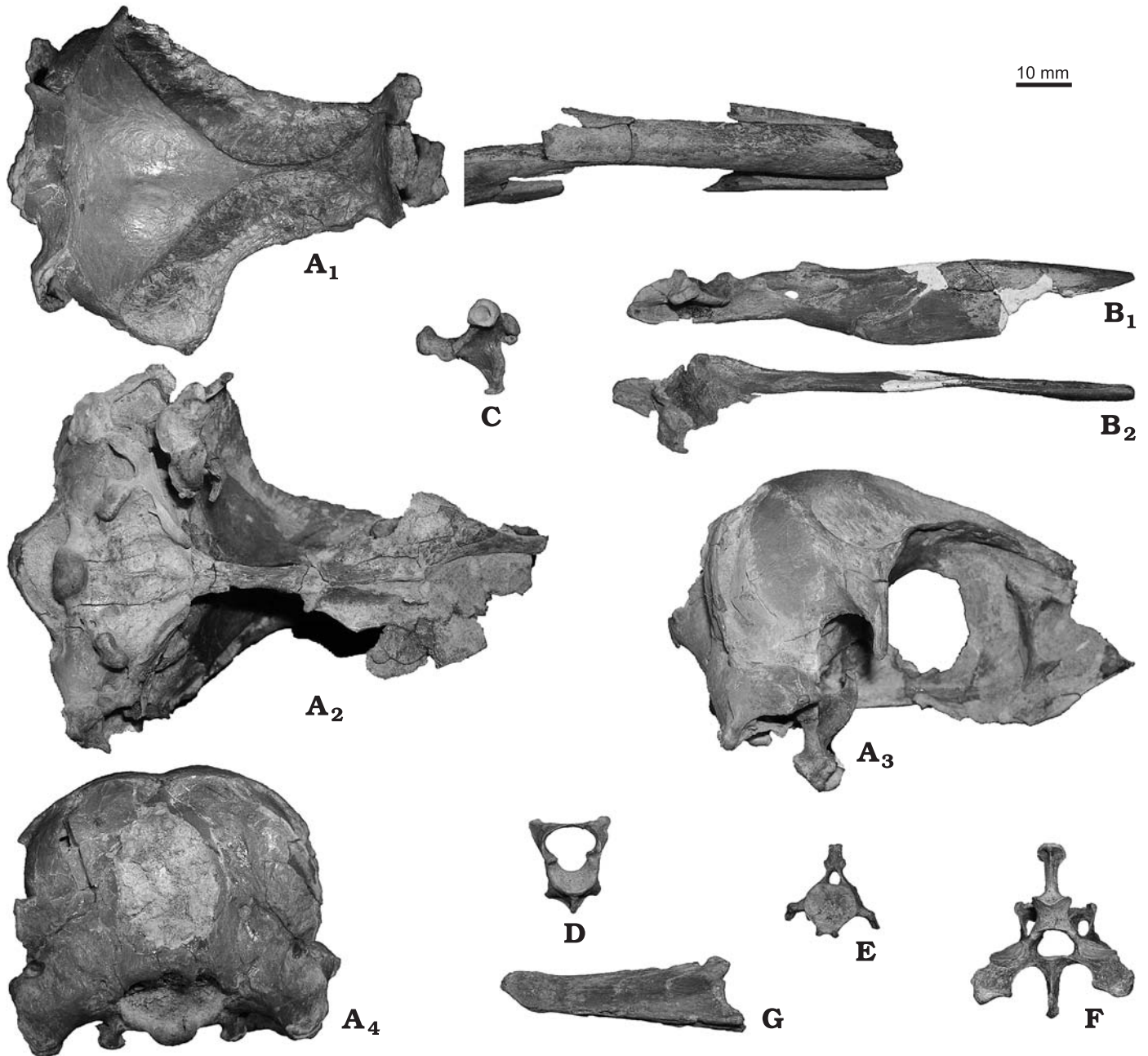
Fig. 3. Miocene penguin *Madrynornis mirandus* gen. et sp. nov., MEF-PV 100 (holotype), Puerto Madryn Formation, early late Miocene, Playa Villarino, Península Valdés, Chubut Province, Argentina. **A**. Skull, dorsal (A_1), palatal (A_2), lateral (A_3), and occipital (A_4) views. **B**. Mandible, internal (B_1) and dorsal (B_2) views. **C**. Quadrate, lateral view of the left quadrate. **D**. Atlas, cranial view. **E**. Caudal vertebra, cranial view. **F**. Cervical vertebra, cranial view. **G**. Pygostyle, lateral view.

from the medial mandibular fossa to the retroarticular process, appears a deep groove (shallow in *Paraptenodytes*).

Vertebrae: An atlas (Fig. 3D), 12 cervical, 7 dorsal, and 7 caudal vertebrae are preserved. The centra of the cervical vertebrae are strongly heterocoelous (Fig. 3F), and have laterally compressed hypapophyses that widen distally. The spinous processes are poorly developed, as in *Paraptenodytes*. The centra of the dorsal vertebrae are opistocoelous; the caudal vertebrae are platyan (Fig. 3E). The pygostyle (Fig. 3G) is triangular in caudal view and notably larger than in extant species.

Sternum: The costal margin is short, with six deep impressions for the rib insertions. The lateral trabeculae reach the caudal margin, unlike in *Spheniscus* where the processes extend farther caudally. The sternal rostrum (Fig. 4D) is preserved and shows a closer similarity to *Spheniscus* than to *Pygoscelis*.

Furcula: This element is broadly U-shaped, with unflattened clavicles similar to those of *Spheniscus*. A deep depression (less evident in *Pygoscelis*) extends along the dorsal edge.
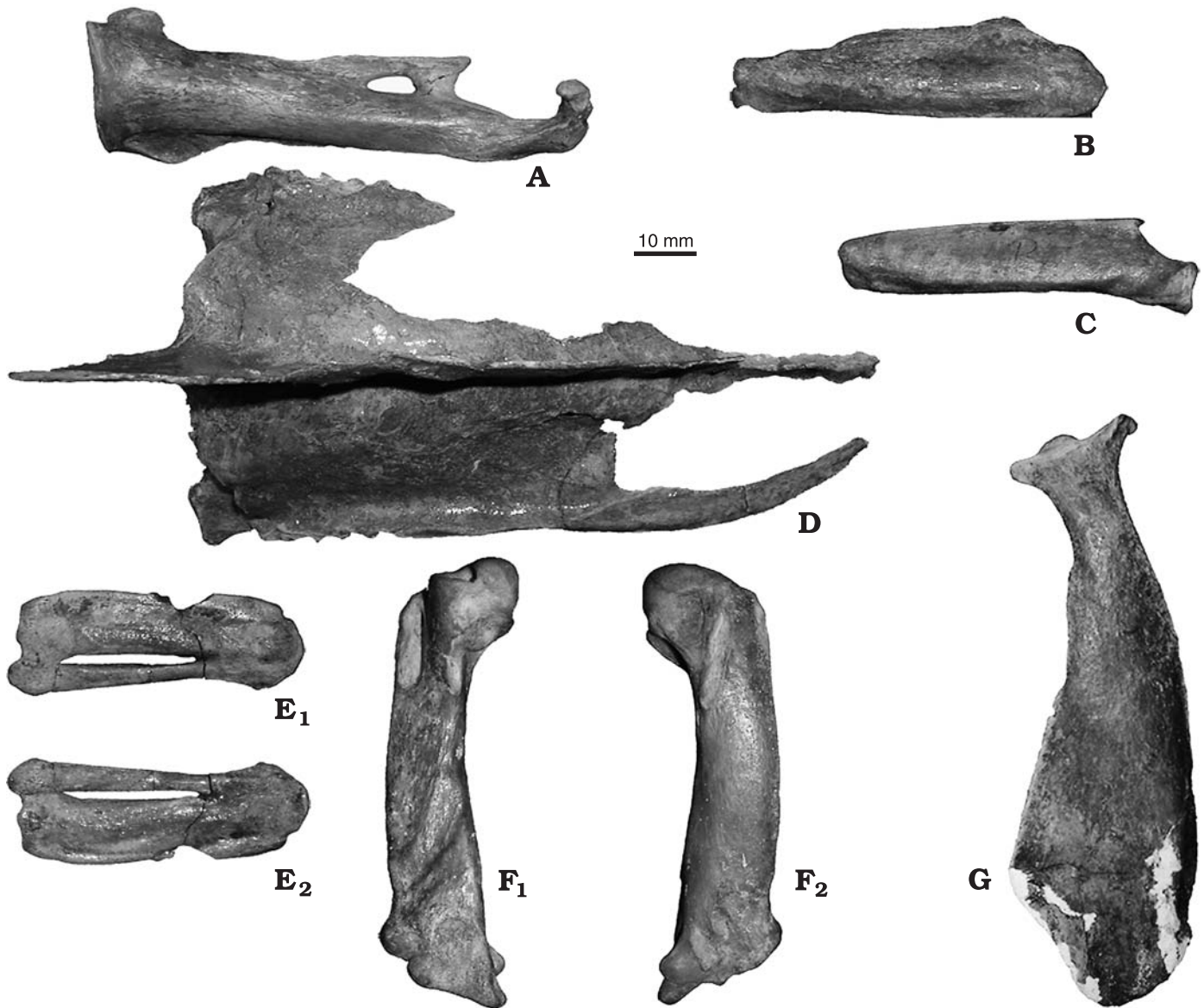
Fig. 4. Miocene penguin *Madrynornis mirandus* gen. et sp. nov., MEF-PV 100 (holotype), Puerto Madryn Formation, early late Miocene, Playa Villarino, Península Valdés, Chubut Province, Argentina. **A**. Left coracoid, anterior view. **B**. Right cubit, anterior view. **C**. Right radius, anterior view. **D**. Sternum, anterior view. **E**. Right carpometacarpus, anterior (E$_1$) and posterior (E$_2$) views. **F**. Right humerus, anterior (F$_1$) and posterior (F$_2$) views. **G**. Right scapula, anterior view.

Scapula: This element is thin (Fig. 4G), broad and more curved than in the living species.

Coracoid: The coracoid foramen is oval as in *Aptenodytes forsteri*, *Eudyptula*, and *Spheniscus*, and is completely closed (Fig. 4A).

Humerus: Intermediate in size between *Spheniscus* and *Pygoscelis*, but more slender than in *Pygoscelis* (Figs. 4F, 7A). The degree of torsion between the axis of the head and the flattened plane of the diaphysis (Simpson 1946) is large in *Madrynornis* as in *Paraptenodytes* and the living penguins, and unlike the very small angle seen in other fossil species. The transverse groove is divided in two by a protuberance, as in *Paraptenodytes*. This tubercle is smaller than in *Pygoscelis* and narrower than in *Spheniscus*. The ventral tubercle is very prominent, but smaller than in the fossil species compared. There is a laterally situated fossa on the tubercle as in *Pygoscelis adeliae* and *Spheniscus*, whereas in *Pygoscelis antarctica* it is situated more cranially and is intermediate in *Eudyptes* (this fossa has not been named to the best of our knowledge). Both ends of the impression of the coracobrachialis cranialis muscle are elliptical, but are rounded in the compared Recent species. The impression decreases in thickness distally, unlike in *Spheniscus* where it remains the same width throughout its length. The configuration of the trochlear processes (Figs. 4E, 7A) is the non-*Spheniscus* type (O'Hara 1989, 1991): the proximal trochlear process extends beyond the humeral shaft.

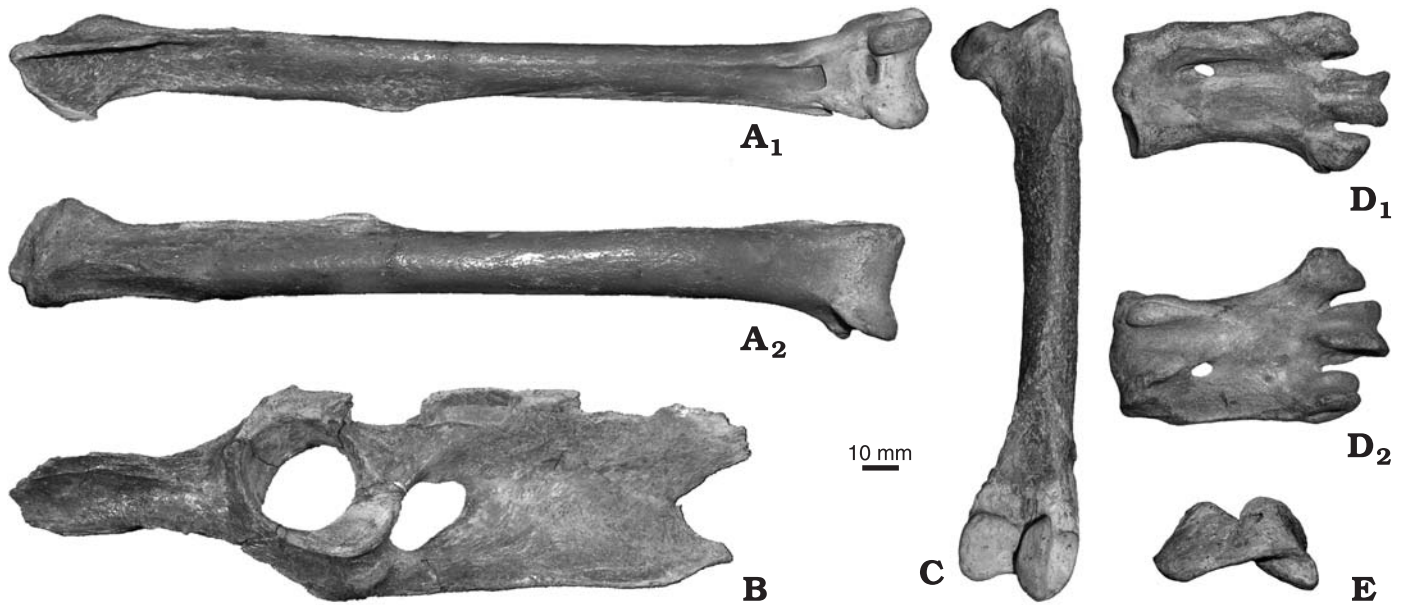The shaft-trochlear angle (between the condyle and the

Fig. 5. Miocene penguin *Madrynornis mirandus* gen. et sp. nov., MEF-PV 100 (holotype), Puerto Madryn Formation, early late Miocene, Playa Villarino, Península Valdés, Chubut Province, Argentina. **A**. Right tibiotarsus, anterior (A$_1$) and posterior (A$_2$) views. **B**. Pelvic girdle, right side, lateral view. **C**. Right femur, caudal view. **D**. Left tarsometatarsus, cranial (D$_1$) and caudal (D$_2$) views. **E**. Right patella, lateral view.

axis of the diaphysis, *sensu* Simpson 1946) is small (ca. 38°), but bigger than in *Pygoscelis*. The impression of the supracoracoideus muscle is oblique to the axis, as in *Paraptenodytes*, *Spheniscus*, *Eudyptes*, and *Aptenodytes*, although this scar is shorter in the Recent species.

Ulna: This element is similar in size to *Pygoscelis*. The ventral edge is curved, being straight in *Spheniscus*.

Radius: The bicipital tubercle is well developed, forming a sharp anteriorly directed projection (Fig. 4C).

Carpometacarpus: The distal end is widest as in *Spheniscus*, but narrower than in *Pygoscelis* (Fig. 4E). The dorsal edge is concave as in *Eudyptula*. In *Madrynornis*, *Spheniscus*, and *Pygoscelis*, the metacarpal major bone is more distally extended than the minor, whereas they are extended equally in *Aptenodytes*. Both metacarpal bones are more strongly fused and the intermetacarpal distance is much narrower in *Eudyptes*.

Pelvis: The acetabular foramen is rounded and larger than the oval ilioischiadic foramen (Fig. 5B), as in *Eudyptes* and *Megadyptes*. The antitrochanter projects dorsally between them.

Femur: The shaft is straight, as in *Spheniscus*. The fossa located on the head is moderately deep, similar to *Eudyptes* and *Spheniscus*, but shallower than in *Paraptenodytes*. In caudal view, the trochanter projects almost transversally to the shaft, such as in *Pygoscelis*. This prominence forms a continuous edge on the caudal surface, that constitutes the antitrochanteric articular facet (Fig. 5C), a feature only present in *Pygoscelis adeliae*. The trochanter crest extends proximally less than in other extinct species. In external lateral view, the iliotrochanteric impressions are developed over an irregular surface, in contrast to *Spheniscus*. The cranial intermuscular line extends

from those impressions along the cranial surface, as in *Paraptenodytes*. The obturator impressions are located on a small flattened area, whereas in the extant species, they occupy a well-defined depression. The caudal intermuscular line is less apparent than in *Paraptenodytes*. The patellar groove is deeper than in the compared species. The strong condylar edges form a deep intercondylar groove, wider than in *Paraptenodytes*. The medial supracondylar crest is more medial and pronounced than in the compared fossil species. The scar for the insertion of the tendon of the muscle tibialis cranialis muscle is sharp, resembling that of *Spheniscus*, and is better developed than in *Paraptenodytes*.

Tibiotarsus: This element is similar in size to that of *Pygoscelis papua.* The intercnemial groove (Fig. 5A) retains equal depth along its length, as in *Spheniscus*. The cnemial crest is poorly developed, more so than in *Paraptenodytes*, and shows a moderate lateral deflection. The flexor fossa is shallow, as in *Eudyptula* and all the fossils compared. The fibular crest (Fig. 5A) extends over a proportionally greater area than that of *Spheniscus* and *Eudyptes*, and is rounded; in *Paraptenodytes* it is quadrangular. The extensor groove is positioned centrally as in *Spheniscus*, whereas it is lateral in *Aptenodytes*. The tubercle where the retinaculi musculi fibularis attaches is barely developed. The condyles are approximately equal in their distal extension, as in *Spheniscus* and *Eudyptula*, whereas the medial condyle extends further in *Paraptenodytes* and the remaining living species. The lateral condyle is elongate and the medial condyle is more or less rounded. Both condyles lack grooves on their margins. An acute edge on the lateral condyle is absent, as in *Paraptenodytes*. The medial condyle possesses a prominent edge, similar to *Pygoscelis* and *Spheniscus*. The lateral epicondylar
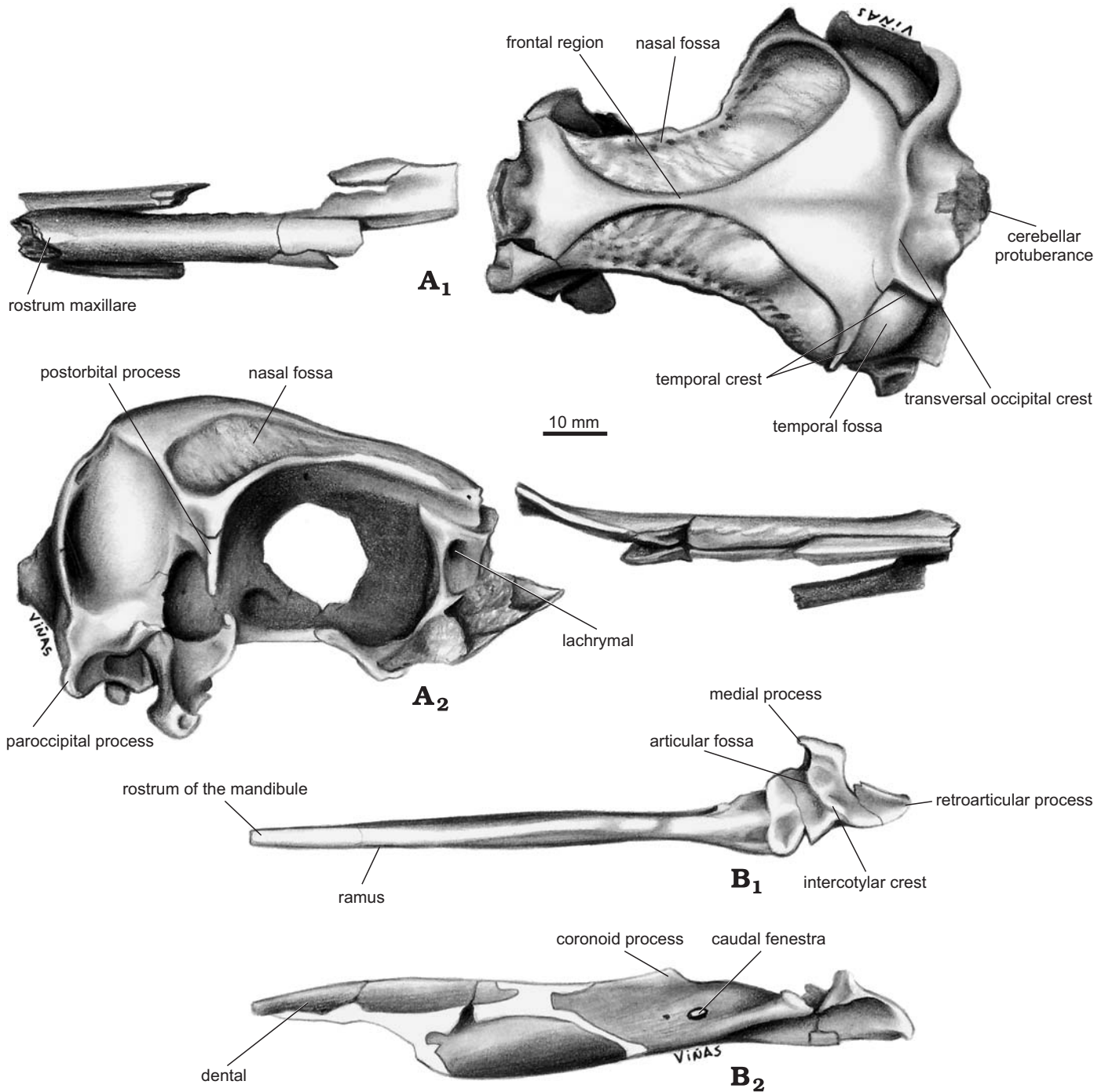
Fig. 6. Miocene penguin *Madrynornis mirandus* gen. et sp. nov., MEF-PV 100 (holotype), Puerto Madryn Formation, early late Miocene, Playa Villarino, Península Valdés, Chubut Province, Argentina. **A**. Skull, dorsal (A_1) and lateral (A_2) views. **B**. Mandible, dorsal (B_1) and lateral (B_2) views. All reconstructions.

depression is poorly developed, as in *Paraptenodytes*. The medial epicondyle is rounded as in *Eudyptula*.

Fibula: The distal end seems to have been unfused suggesting that the tibiotarsus and fibula were linked synostotically.

Tarsometatarsus: This element is similar in size to that of *Pygoscelis papua*, although *Madrynornis* has a larger elongation index. The intercotylar prominence (Fig. 5D) is low and well-rounded. The subcotylar fossa is well developed

and triangular, as in *Spheniscus* and unlike in *Paraptenodytes*. The medial hypotarsal crest is barely divided (well divided in *Paraptenodytes*); there are two intermediate crests (single in *Paraptenodytes*) and one lateral crest, as in *Paraptenodytes* (Fig. 5D). The tuberosity for insertion of the tibialis cranialis muscle are laterally positioned (more central in *Paraptenodytes*). The shallow and small medial longitudinal groove is shorter than in *Paraptenodytes* and does not
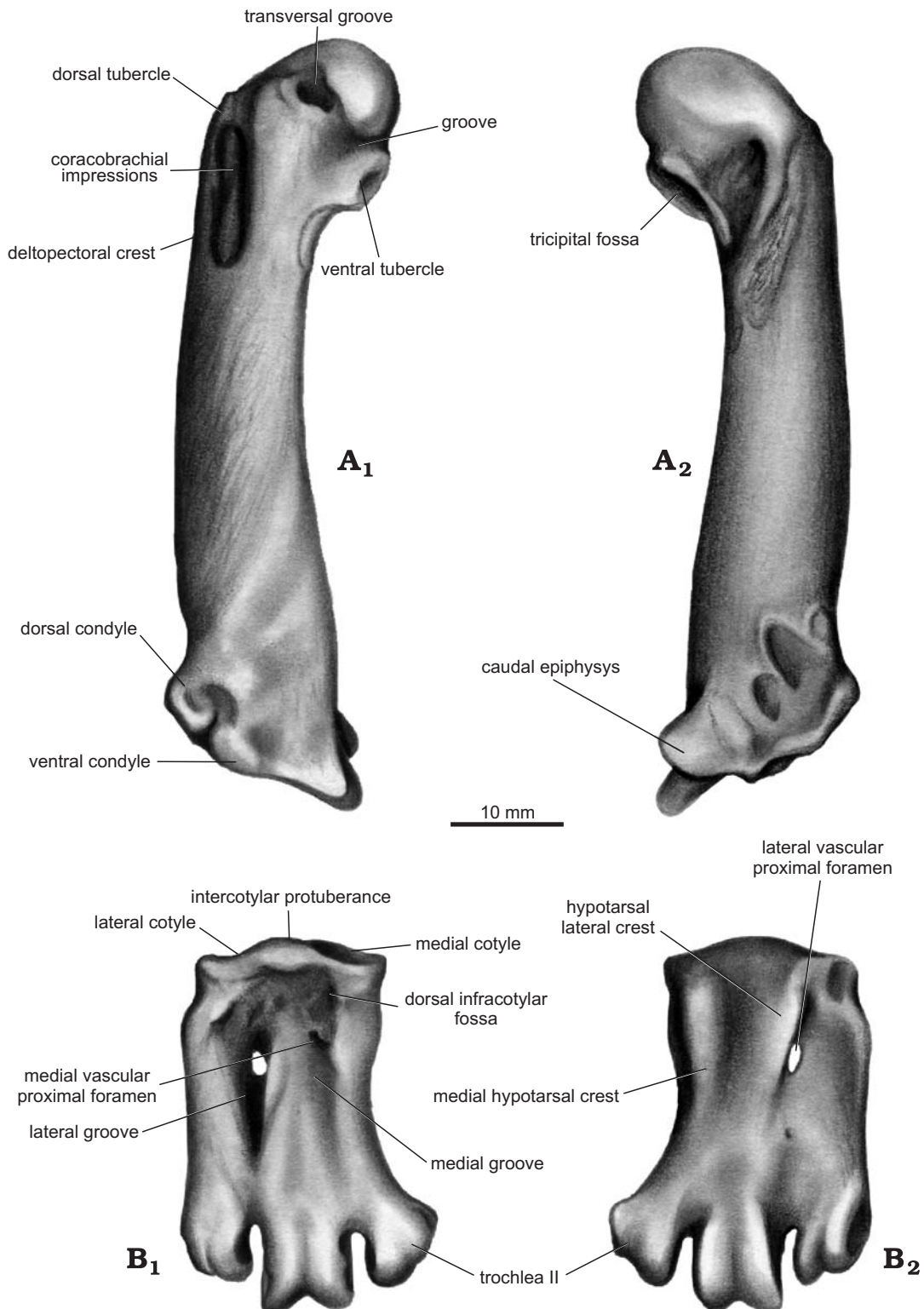
Fig. 7. Miocene penguin *Madrynornis mirandus*, gen. et sp. nov., MEF-PV 100 (holotype), Puerto Madryn Formation, early late Miocene, Playa Villarino, Península Valdés, Chubut Province, Argentina. **A**. Right humerus, cranial (A_1) and caudal (A_2) views. **B**. Right tarsometatarsus, cranial (B_1) and caudal (B_2) views. All reconstructions.

reach the intertrochlear incisure. The lateral longitudinal groove is deeper than in *Paraptenodytes*, although as in that species neither groove extends as far as the proximal limit of the inscisure. The medial and lateral proximal vascular fo-ramina are unequal in size: the lateral foramen is larger than the medial and exits on the plantar surface (in *Parapteno-dytes* the sub-equally sized foramina both exit plantarly). As in *Paraptenodytes*, metatarsal fusion is stronger than in Re-
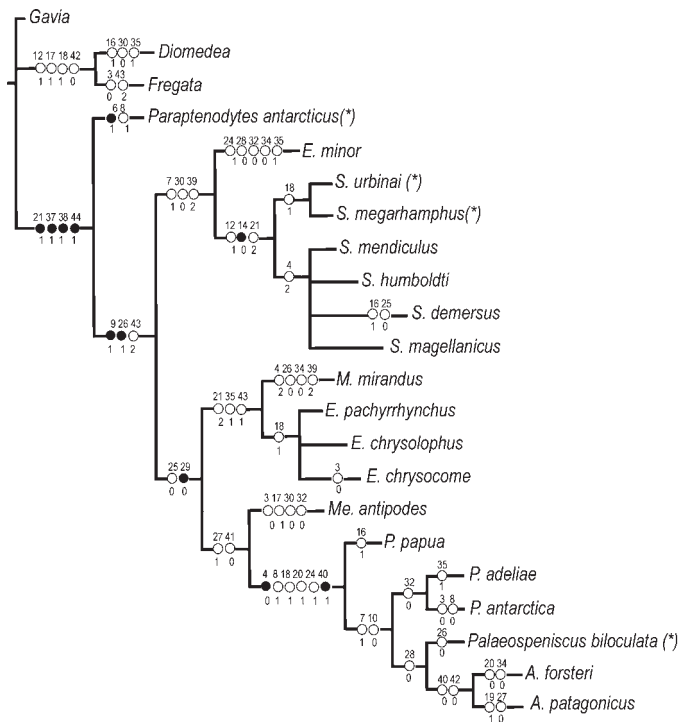
Fig. 8. Single most parsimonious tree of the Spheniscidae resulting from analysis of the character matrix in Appendix 3. Filled circles are unambiguous synapormorphies, open circles are homoplasious characters (both at state level), numbers above and below circles are character number and state numbers respectively. Asterisks indicate fossil species. Abbreviations: *E.*, *Eudyptula*; *S.*, *Spheniscus*; *M.*, *Madrynornis*; *Me.*, *Megadyptes*; *P.*, *Pygoscelis*; *A.*, *Aptenodytes*.

cent species; *Eudyptula* has the extreme condition with the metatarsals separated by deep furrows. The trochlea of metatarsal II exhibits stronger lateral divergence than in *Pygoscelis*, *Eudyptes*, and *Spheniscus*; the trochlea of metatarsal III possesses strong, distally divergent trochlear edges, and the trochlea of metatarsal IV is approximately straight and has less distal elongation than *Spheniscus*.

Phalanges: There are no fossil phalanges available for comparison with *Madrynornis*. The 16 phalanges of *Madrynornis* are similar in shape to those of the living species; they are more robust than those of *Spheniscus magellanicus*.

Phylogenetic results

The main goal of the analysis was to determine the position of *Madrynornis mirandus* in the context of penguin phylogeny. Since we are restricted to skeletal characters, we do not intend to test previous results based on more complete data sets (Bertelli and Giannini 2005).

However, this gave us the opportunity to asses the impact that relatively well known fossil species may have in the phylogenetic hypothesis based only on Recent taxa. Besides *Madrynornis*, four other fossil species were included: *Paraptenodytes antarcticus* (upper Oligocene–lower Miocene Gai-

man Formation, Patagonia; Simpson 1946), *Spheniscus urbinai*, *S. megarhamphus* (upper Miocene of Pisco Formation, Peru; Stucchi 2002; Stucchi et al. 2003), and *Palaeospheniscus biloculata* comb. nov. (lower Miocene Gaiman Formation of Patagonia; Acosta Hospitaleche 2004).

A single tree (length 118 steps, CI = 44, RI = 67) resulting from analysis of the character matrix in Appendix 3 was obtained (Fig. 8). The topology contains the clades A (*Eudyptula* + *Spheniscus*), B (*Aptenodytes*+*Pygocelis* + *Megadytes* + *Eudyptes*), and C (*Aptenodytes* + *Pygocelis*) of the morphological consensus tree of Bertelli and Giannini (2005: 214, fig. 2).

Two main differences are apparent. First, *Megadytes antipodes* groups with *Pygocelis* + *P. biloculata* + *Aptenodytes*, not with *Eudyptes*, as in Bertelli and Giannini (2005). The clade *Megadytes* + *Eudyptes* has relatively low support, especially on skeletal traits (only one unambiguous character), and hence the stability of the group is precarious.

We also failed to recover a monophyletic *Pygocelis*, which appears as paraphyletic in our tree. Bertelli and Giannini (2005; Fig. 6) reported only one skeletal character supporting the *Pygocelis* clade, but five more, from soft anatomy and breeding behavior. As we only used skeletal characters it is not surprising that the clade could not be recovered.

With the single exception of *P. antarcticus* (for which 62.8% of the characters were scored), all fossil penguins group inside modern clades. This species appears as the sister group to remaining penguins, both fossil and living. The genus *Paraptenodytes* is known from the lower Miocene Monte León Formation of Patagonia (Simpson 1946) and recently was reported from the upper middle–lower upper Miocene Puerto Madryn Formation, the same level from which *M. mirandus* was recovered (Acosta Hospitaleche 2003). *P. antarcticus* exhibits a suite of primitive features compared to modern species, along with some clear penguin synapomorphies. In our dataset, four unambiguous synapomorphies define Spheniscidae, including *Paraptenodytes*.

The position of *Palaeospheniscus biloculata*, grouping here with *Aptenodytes*, should be taken with caution because the only associated specimen available is quite incomplete (only 25.6 % of the characters can be scored). However, it is interesting to note that this early Miocene species is nested among modern penguins, not separated from them as suggested earlier (Simpson 1946, 1972).

Not surprisingly, *Spheniscus urbinai* (44.2% of the characters scored) and *S. megarhamphus* (32.5% scored) groups with the living *Spheniscus* species. Interspecific relationships within this genus cannot be confidently assessed with our data since species of *Spheniscus* are distinguished primarily on the basis of soft anatomy (Bertelli and Giannini 2005).

Finally, *Madrynornis mirandus*, for which almost the entire skeleton is known (97.6% of our characters can be scored), appears in the tree as the sister group of *Eudyptes*. This position is supported by three non exclusive derived characters (21, 35, 43). Character 21 (state 2) is shared with all the *Eudyptes* species included, but also by five of the six species of *Spheniscus* (except *S. megarhamphus*, for which

the condition is unknown). Character 35 (state 1) is shared with *Eudyptes chrysocome* (unknown in the other two *Eudyptes* species) but also with *Eudyptes minor* and *Pygoscelis adeliae*. Finally, character 43, in its state 1, is shared with *E. chrysocome* (unknown in the other two *Eudyptes* species) and with *P. biloculata*.

Discussion and conclusions

Simpson (1946) provided the first suprageneric systematics of the Spheniscidae, and his study has remained the basis for all other analyses of penguin relationships. Giannini and Bertelli (2004) made a phylogenetic arrangement of the living species based on integumentary characters. Subsequently, Bertelli and Giannini (2005) tested their proposal using a morphological and molecular data set. Our analysis is the first to employ cladistic methods to a data matrix 179–183.

Since the referral of isolated elements to a given species is always problematic we have preferred to base our phylogenetic analysis on articulated or associated specimens wherever possible. In essence, we used the near complete skeleton of *Paraptenodytes antarcticus*, the unpublished associated material of *Palaeospheniscus biloculata* comb. nov. (Acosta Hospitaleche 2004) and skeletons of all the modern genera (including two fossil species of *Spheniscus*) as a basis for establishing the phylogenetic relationships of *Madrynornis*.

Although it is evident from observations and comparisons that extant and fossil penguins constitute a remarkably homogeneous family of birds, their within-group phylogenetic relationships are less obvious. In our analysis, Spheniscidae is easily recognized as a monophyletic group based on osteological characters alone (characters 21[1], 37[1], 38[1], 44[1]), in agreement with Mayr (2004) and Bertelli and Giannini (2005). *Madrynornis mirandus* sp. nov. is the first species described from Argentinean rocks that is closely related to the living forms.

According to this analysis, *Palaeospheniscus biloculata* is the sister taxon of *Aptenodytes*, but we regard its location as questionable and suggest that its placement may be a consequence of the large amount of missing data.

Simpson (1946) stated that pre-Miocene penguins have a more elongate tarsometatarsus with more completely fused metatarsals than the Recent forms. Zusi (1975) recognized two variable tarsometatarsal types in extant species based on the pattern of the proximal foramina in relationship to the hypotarsus. *Madrynornis* resembles the Recent species in the degree of fusion of the metatarsals and the location of the proximal foramina, but the elongation index is similar to the pre-Miocene forms.

As one might expect, *Paraptenodytes* from the early Miocene (about 20 Ma) is located at the base of the Spheniscidae. This outcome further supports the possibility that modern forms would have appeared in the Miocene.

Aknowledgements

Addendum

Some phylogenetic studies were published shortly after the preparation of this manuscript, however, they could not be incorporated into this project. See for example: Slack et al. (2006) and Ksepka et al. (2006).

References

Acosta Hospitaleche, C. 2003. *Paraptenodytes antarcticus* (Aves: Sphenisciformes) en la Formación Puerto Madryn (Mioceno tardío temprano), provincia de Chubut, Argentina. *Revista Española de Paleontología* 18: 179–183.

Acosta Hospitaleche, C. 2004. *Los pingüinos (Aves, Sphenisciformes) fósiles de Argentina. Sistemática, biogeografía y evolución*. Unpublished Ph.D. thesis. 321 pp. Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Ciudad de La Plata.

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. and Stucchi, M. 2005. Nuevos restos terciarios de Spheniscidae (Aves, Sphenisciformes) procedentes de la costa del Perú. *Revista de la Sociedad Española de Paleontología* 20: 1–5.

Acosta Hospitaleche, C., Fritis, O., Tambussi, C., and Quinzio, A. 2002. Nuevos restos de pingüinos (Aves: Spheniscidae) en la Formación Bahía Inglesa (Mioceno superior–Plioceno inferior) de Chile. *Actas del Primer Congreso Latinoamericano de Paleontología de Vertebrados*, 16. Santiago de Chile.

Ameghino, F. 1891. Enumeración de las aves fósiles de la República Argentina. *Revista Argentina de Historia Natural* 1: 441–453.

Baumel, J. and Witmer, L.M. 1993. Osteologia. *In*: J.J. Baumel, A.S. King, A.M. Lucas, J.E. Breazile, and H.E. Evans (eds.), *Handbook of Avian Anatomy: Nomina Anatomica Avium*, 45–132. Publications of the Nuttall Ornithological Club, Cambridge, Massachusetts.

Bertelli, S. and Giannini, N. 2005. A phylogeny of extant penguins (Aves: Sphenisciformes) combining morphology and mitochondrial sequences. *Cladistics* 21: 209–239.

Bonaparte, C.L. 1831. Saggio di una distribuzione metodica degli animali vertebrati. *Giornale Arcadico di Scienze Lettere ed Arti* 52: 155–189.

Bonaparte, C.L. 1856. Espéces nouvelles d'oiseaux d'Asie et d'Amérique et tableaux para lléliques des Pélagiens ou Gavae. *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences* 42: 764–776.

Brisson, M. 1760. *Ornithologie ou méthode contenant la division des oiseaux en ordres, sections, genres, espèces et leurs varietes*. 632 pp. Bauche, Paris

Brünnich, M.T. 1764. *Ornithologia borealis, sistens collectionem, avium ex*

omnibus, imperio Danico subjectis, provinciis insulisque borealibus Hafni? factam, cum descriptionibus novarum, nominibus incolarum, locis natalium et icone. 80 pp. Kall & Godiche, Kopenhagen.

Cione, A.L. and Tonni, E.P. 1981. Un pingüino de la Formación Puerto Madryn (Mioceno tardío) de Chubut, Argentina. Comentarios acerca del origen, la paleoecología y zoogeografía de los Spheniscidae. *Anales del Congreso Latinoamericano de Paleontología* 2: 591–604.

Clarke, J.A., Olivero, E.B., and Puerta, P. 2003. Description of the earliest fossil penguin from South America and first Palaeogene vertebrate locality of Tierra del Fuego, Argentina. *American Museum Novitates* 3423: 1–18.

Cozzuol, M.A. 1993. *Mamíferos acuáticos del Mioceno medio y tardío de Argentina. Sistemática, Evolución y Biogeografía.* Unpublished Ph.D. thesis. 148 pp. Facultad de Ciencias Naturales y Museo de La Plata.

Cozzuol, M.A. 2001. A fossil "northern" seal, from Argentina. Implications for phylogeny and biogeography. *Journal of Vertebrate Paleontology* 21: 415–421.

Cozzuol, M.A., Tambussi, C.P., and 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.

del Río, C.J., Martínez, S., and Scasso, R.A. 2001. Nature and origin of spectacular marine Miocene beds of northeastern Patagonia (Argentina): paleoecological and bathymetric significance. *Palaios* 16: 135–159.

Dozo, M.T., Monti, A., Bouza, P., Vucetich, M.G., Cione, A., Tonni, E., and Scillato-Yané, G. 2002. Geología y vertebrados continentales en cercanías de Punta Delgada (Neógeno de Península Valdés, Chubut, Argentina). *Actas XV Congreso Geológico Argentino* 1: 536–541.

Emslie S.D. and Correa, C.G. 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.

Fordyce R.E. and Jones, C.M. 1990. Penguin history and new fossil material from New Zealand. *In*: L.S. Davis and J.T. Darby (eds.), *Penguin Biology*, 419–446. Academic Press, San Diego.

Forster, J.R. 1781. Historia Aptenodytae. Generis avivm orbi avstrali proprii. *Commentationes Societatis Regiae Scientiarum Gottingensis* 3: 121–148.

Frenguelli, J. 1926. El Entrerriense del golfo Nuevo en el Chubut. *Boletín de la Academia Nacional de Ciencias de Córdoba* 29: 191–270.

Giannini, N.P. and Bertelli, S. 2004. Phylogeny of extant penguins based on integumentary and breeding characters. *Auk* 121: 421–434.

Göhlich, U.B. 2007. The oldest fossil record of the extant penguin genus *Spheniscus*—a new species from the Miocene of Peru. *Acta Palaeontologica Polonica* 52: 285–298.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M., and Szumik, C.A. 2003. Improvements to resampling measures of group support. *Cladistics* 19: 324–332.

Grant, W.S., Duffy, D.C., and Leslie, R.W. 1994. Allozyme phylogeny of *Spheniscus* penguins. *Auk* 111: 716–720.

Gray, G.R. 1844. *The Zoology of the Voyage of H.M.S. Erebus and Terror, During the Years 1839–43.* 17 pp. E.W. Janson, London.

Haller, M. 1978. Estratigrafía de la región al poniente de Puerto Madryn, Chubut, Argentina. *Actas VII Congreso Geológico Argentino* 1: 285–297.

Haq, B.U., Hardenbol, J., and Vail, P. 1987. Chronology of fluctuating sea levels since the Triassic. *Science* 235: 1156–1167.

Hombron, J.B. and Jacquinot, H. 1841. Description de plusieurs oiseaux nouveaux ou peu connus, provenant de l'expédition autour du monde faite sur les corvettes l'Astrolabe et la Zélée. *Annales Des Sciences Naturelles, Zoologie* 16: 312–320.

Kanfeder, K.M. 1994. *Różnorodność fauny pingwinów kopalnych antarktycznej Wyspy Seymour w oparciu o analizę humeri z kolekcji Instytutu Biologii Filii Uniwersytetu Warszawskiego w Białymstoku.* Unpublished Ph.D. thesis. 124 pp. Instytut Biologii, Uniwersytet Warszawski, Białystok.

Ksepka, D., Bertelli, S., and Giannini, N. 2006. The phylogeny of the living and fossil Sphenisciformes (penguins). *Cladistics* 22: 412–441.

Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.* 824 pp. Laurentius Salvius, Stockholm.

Lowe, P. 1933. On the primitive characters of the penguins and their bearing on the phylogeny of the ostrich and its allies. *Proceedings of the Zoological Society of London* 1: 185–247.

Marples, B.J. 1952. Early Tertiary penguins of New Zeland. *Geological Survey Palaeontological Bulletin* 20: 1–66.

Martínez, I. 1992. Order Sphenisciformes. *In*: J. del Hoyo, A. Elliott, and J. Sargatal (eds.), *Handbook of the Birds of the World, Vol. 1: Ostrich to Ducks*, 140–160. Lynxs Editions, Barcelona.

Mathews, G.M. 1914. On the species and subspecies of the genus Fregata. *Australian Avian Record* 2: 117–121.

Mayr, G. 2004. Tertiary plotopterids (Aves, Plotopteridae) and a novel hypothesis on the phylogenetic relationships of penguins (Spheniscidae). *Journal of Zoological Systematics and Evolutionary Research* 43: 61–71.

Miller, J.F. 1778. *Various Subjects of Natural History, Wherein Are Delineated Birds, Animals and Many Curious Plants.* 10 pp. London.

Milne-Edwards, A. 1880. Expéditions scientifiques du Travailleur. *Annales des Sciences Naturelle* 6: 1–56.

Moreno, F.P. and 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.

Muizon, C. de and DeVries, T.J. 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). *Geologische Rundschau* 74: 547–563.

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

Nixon, K.C. 2002. *WinClada ver. 1.0000.* Published by the author, Ithaca, New York.

Nixon, K.C. and Carpenter, J.M. 1993. On outgroups. *Cladistics* 9: 413–426.

O' Hara, R. 1989. *Systematics and the Study of Natural History, with an Estimate of the Phylogeny of the Living Penguins (Aves: Spheniscidae).* Unpublished Ph.D. thesis. 171 pp. Harvard University, Cambridge, Massachusetts.

O'Hara, R. 1991. An estimate of the phylogeny of the living penguins (Aves: Spheniscidae). *American Zoology* 29: 11a.

Pycraft, W.P. 1898. Contributions to the osteology of birds, part. II. Impennes. *Proceedings of the Zoological Societu of London* 1898: 958–989.

Riva-Rossi, C.R., Gosztonyi, A.E., and Cozzuol, M.A. 2000. A Miocene cusk-eel (Ophidiiformes: Ophidiidae) from Península Valdés, Argentina. *Journal of Vertebrate Paleontology* 20: 645–650.

Scasso, R.A. and del Río, C.J. 1987. Ambientes de sedimentación, estratigrafía y proveniencia de la secuencia marina del Terciario superior de la región de Península Valdés, Chubut. *Revista de la Asociación Geológica Argentina* 42: 291–321.

Scasso, R.A., McArthur, J.M., del Río, C.J., Martínez, S., and Thirwall, M.F. 2001. $^{87}Sr/^{86}Sr$ late Miocene age of fossil molluscs in the "Entrerriense" of the Valdés Península (Chubut, Argentina). *Journal of South American Earth Sciences* 14: 319–329.

Sharpe, R.B. 1891. A review of recent attempts to classify birds. *Proceedings of the Second International Ornithological Congress*, 90. Budapest.

Sibley, C.G. and Monroe. B.1990. *Distribution and Taxonomy of the Birds of the World.* 1111 pp. Yale University Press, New Haven.

Simpson, G.G. 1946. Fossil penguins. *Bulletin of the American Museum of Natural History* 87: 1–100.

Simpson, G.G. 1971. A review of the pre-Pliocene penguins of New Zealand. *Bulletin of the American Museum of Natural History* 144: 321–378.

Simpson, G.G. 1972. Conspectus of Patagonian fossil penguins. *American Museum Novitates* 2488: 1–37.

Simpson, G.G. 1981. Notes on some fossil penguins, including a new genus from Patagonia. *Ameghiniana* 18: 266–272.

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

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., and Giraldo, A. 2003. Una nueva especie de Spheniscidae del Mioceno tardío de la Formación Pisco, Perú. *Bulletin de l'Institut Français d'Etudes Andines* 32: 361–375.

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

Tambussi, C.P., Acosta Hospitaleche, C., Reguero, M., and Marensi, S. 2006. Late Eocene penguins from West Antarctica: systematics and biostratigraphy. *In*: D. Pirrie, J.E. Francis, and J.A. Crame (eds.), Cretaceous–Tertiary High-Latitude Palaeoenvironments, James Ross Basin, Antarctica. *Geological Society of London. Special Publications* 258: 145–161.

Tonni, E.P. 1980. The present state of knowledge of the Cenozoic birds of Argentina. *Natural History Museum, Los Angeles, Contributions in Science* 330: 105–114.

Van Tuinen, M., Butvill, D.B., Kirsh, J.A., and Hedges, S.B. 2001. Convergence and divergence in the evolution of aquatic birds. *Proceedings of the Royal Society of London B* 268: 1345–1350.

Vieillot, L. 1816. *Analyse d'une nouvelle ornithologuie élémentaire*. 70 pp. d'Éterville, Paris.

Wagler, J.G. 1832. Mittheilungen über einige merkwürdige Thiere. II Vögel. *Isis, oder Encyclopaedische Zeitung, von Oken* 25: 1– 281.

Walsh, S.A. and Hume, J.P. 2001. A new Neogene marine avian assemblage from north-central Chile. *Journal of Vertebrate Paleontology* 21: 484–491.

Zinsmeister, W., Marshall, L.G., Drake, R., and Curtis, R. 1981. First radio-isotope (Potassium-Argon) age of marine Neogene Río Negro beds in northeastern Patagonia, Argentina. *Science* 212: 440.

Zusi, R.L. 1975. An interpretation of skull structure in penguins. *In*: B. Stonehouse (ed.), *The Biology of Penguins*, 59–84. Macmillan Press, London.

Appendix 1

Catalogue numbers for museum specimens examined in the construction of the character dataset.

Comparative material used in this study included the following specimens: *Spheniscus magellanicus*: MLP A2 (skull), MLP A3 (skull), MLP A31 (skull, tarsometatarsus), MLP A34 (skull, humerus, femur); MLP A35 (skull, humerus, tarsometatarsus), MLP A466 (humerus, femur), IAA5 (skull), IAA6 (skull), IAA7 (skull), IAA23 (skull), MACN 52767 (skull, humerus, femur, tibiotarsus, tarsometatarsus), MACN 54681 (complete skeleton), MACN 54682 (complete skeleton), MACN 54683 (skull), MACN 54685 (skull), MEF 0063 (complete skeleton), AMNH 8823 (complete skeleton). *Spheniscus humboldti* AMNH 4920 (complete skeleton). *Spheniscus demersus* AMNH 22678 (complete skeleton). *Pygoscelis adeliae*: MLP A36 (humerus, tibiotarsus, femur), MLP A414 (humerus, femur, tibiotarsus, tarsometatarsus), MLP A415 (skull), MLP A416 (skull), MLP A417 (skull), MLP A418 (skull), MLP A419 (skull), MLP A420 (skull), MLP A421 (skull), MLP A422 (skull), MLP A423 (skull), MLP A424 (skull), MLP A425 (skull), MLP A426 (skull), MLP A427 (skull), MLP A428 (skull), MLP A429 (skull), MLP A430 (skull), MLP A431 (skull), MLP A432 (skull), MLP A433 (skull), MLP A434 (skull), MLP A464 (humerus, femur, tibiotarsus, tarsometatarsus), MLP A469 (humerus, femur, tibiotarsus, tarsometatarsus), MLP A471 (humerus), IAA18 (skull), IAA21 (skull), MACN 52363 (humerus, femur, tibiotarsus, tarsometatarsus). *Pygoscelis papua*: MLP A38 (humerus, femur, tibiotarsus, tarsometatarsus), MLP A449 (skull), MLP A450 (skull), MLP A451 (skull), MLP A452 (femur, tibiotarsus, tarsometatarsus), MLP A463 (complete skeleton), MLP A468 (humerus, femur, tibiotarsus, tarsometatarsus), IAA13 (humerus), IAA14 (humerus), IAA15 (humerus), MACN 52364 (humerus, femur, tibiotarsus, tarsometatarsus), AMNH 5973 (complete skeleton). *Pygoscelis antarctica*: MLP A37 (humerus, femur, tibiotarsus, tarsometatarsus), MLP A435 (skull), MLP A436 (skull), MLP A437 (skull), MLP A438 (skull), MLP A439 (skull), MLP A440 (skull), MLP 441 (skull), MLP A442 (skull), MLP A443 (skull), MLP A444 (skull), MLP A445 (skull), MLP A446 (skull), MLP A447 (skull), MLP A448 (complete skeleton), MLP A465 (humerus, femur, tibiotarsus, tarsometatarsus), MLP A470 (humerus, femur, tibiotarsus), IAA8 (skull), IAA10 (femur), IAA11 (femur), IAA12 (humerus), IAA16 (tibiotarsus), IAA17 (tibiotarsus), IAA19 (skull), IAA20 (skull), IAA22 (skull). *Eudyptes crestatus*: MLP A39 (complete skeleton), IAA 1 (skull), IAA 2 (skull), IAA 3 (skull), IAA 4 (skull), MACN 53556 (skull), AMNH 5912 (complete skeleton). *Aptenodytes patagonicus*: IAA 9 (skull), AMNH 2611 (complete skeleton). *Aptenodytes forsteri*: AMNH 3745. *Eudyptula minor* AMNH 6257 (complete skeleton). Complete skeletons of *Diomedea exulans* AMNH 5109, *Podilymbus podiceps* AMNH 1050, *Fregata magnificens* AMNH 21469, and *Gavia immer* AMNH 10759 were used in the character state polarization.

The fossils *Paraptenodytes antarcticus* MLP 20-2, 4, 6 (femur, tibiotarsus and tarsometatarsus; holotype), AMNH 3338 (near complete skeleton), *Paraptenodytes biloculata* AMNH 3341 and AMNH 3346 (humerus), and MPEF-PV 1729 (partial skeleton) were also included in the matrix. The holotypes of the following species were examined: *Arthrodytes grandis* (= *A. andrewsi*) MLP M-606 (cast of humerus), MLP M-607 (cast of coracoid), MLP M-608 (cast of scapula), *Paleospheniscus gracilis* MLP M-611 (cast of tarsometatarsus), *P. bergi* MLP 20-81 (tarsometatarsus), *P. patagonicus* MLP 20-34 (tarsometatarsus), *P. wimani* (= *P. menzbieri*) MLP 20-62 (tarsometatarsus), *Paraptenodytes brodkorbi* (= *Isotremornis nordenskjoeldi*) MLP M-601 (cast of femur) and MLP M-603 (cast of humerus), *Eretiscus tonii* MLP 81-VI-26-1 (tarsometatarsus). Characters of *Paraptenodytes robustus* BM (NH) A/591 (humerus) were taken from Simpson (1972).

Appendix 2

Character list and character states employed in the phylogenetic analysis.

Mandible

1. Shape of the mandibles: decurved (0); recurved (1). After O'Hara (1989, character 7). Shape of outgroup *Fregata* and *Gavia* mandibles are no comparable (Acosta Hospitaleche 2004, character 0).

2. Cranial fenestra of the mandible: small or imperforate (0); well developed (1). Modified from O'Hara (1989, character 8) and following Acosta Hospitaleche (2004, character 1) and Bertelli and Giannini (2005, character 99).

3. Caudal fenestra of the mandible: closed (0); open (1). After Bertelli and Giannini (2005, character 100) coded close as 1 and open as 0. O'Hara (1989, character 9) and Acosta Hospitaleche (2004, character 2) included three states, closed, polymorphic or open indeed our two states

4. Retroarticular process compared to the articular fossa in dorsal view: subequal broad (0); narrower and moderately long (1); slender and very long (2). After Bertelli and Giannini (2005, character 105). The out groups are not comparable.

5. Medial process of the mandible: not hooked (0); hooked (1). After Bertelli and Giannini (2005, character 104). The presence of a conspicuous hook in the medial process is a synapomorphy of the penguins.

Skull

6. Postorbital process: ventrolaterally projected (0); ventrolaterally and posteriorlly projected (1). Simpson (1946: 11) described this as a distinctive feature for *Paraptenodytes*.

7. Supraoccipital with paired grooves for the exit of the *venae occipitalis externae*: poorly developed (0); deeply excavated (1). After Bertelli and Giannini (2005, character 74).

8. Foramen for the external ophthalmic artery (*rami occipitalis*) on the squamosal: small or vestigial (0); well-developed (1). After Bertelli and Giannini (2005, character 78).

9. Pterygoid shape: narrow and rod-like (0); expanded as a thin horizontal plate (1). O'Hara (1989) considered no variation of the pterygoid within penguins; Bertelli and Giannini (2005, character 89) coded this character considering it like a well known synapomorphy of the Sphenisciformes, but they only included living species in the in-group. Simpson (1946: 12) recognized a great disparity in the shape of this bone in *Paraptenodytes*; for that reason we decide to include this character in our analysis.

10. Lacrimal (= prefrontal): perforated (0); unperforate (1). After O'Hara (1989, character 11), Acosta Hospitaleche (2004, character 5) and Bertelli and Giannini (2005, character 81)

11. Shape of processes of the nasal and premaxillary bones: narrow enough to see the nasal fossa in dorsal view (0); wide and hiding the nasal fossa (1). After O'Hara (1989, character 6), Acosta Hospitaleche (2004, character 6) and Bertelli and Giannini (2005, character 85).

12. Location of the caudal end of the nasal aperture: over the orbitonasal foramen (0); rostral to the orbitonasal foramen (1). After O'Hara (1989, character 5), Acosta Hospitaleche (2004, character 7) and Bertelli and Giannini (2005, character 84).

13. Configuration of the temporal fossa: deeper posteriorly and joined to the opposite one in the sagittal line (0); does not reach the sagittal line (1). After Zusi (1975) and Acosta Hospitaleche (2004, character 8). States (0) and (1) in Bertelli and Giannini (2005, character 76) correspond to states (1) and (0) of the present work, respectively.

14. Temporal crest: well developed (0); poorly developed or absent (1). Pycraft (1898: 963 discussed this character in relationship with the depth of the posterior region of the temporal fossa. After Acosta Hospitaleche (2004, character 13) Depth is coded by Bertelli and Giannini (2005, character 77).

15. Jugal arch: strongly curved (0); weakly curved or straight (1). After Acosta Hospitaleche (2004, character 10). We do not follow Bertelli and Giannini (2005, character 93) that identified four states of this character, neither Zusi (1975) that distinguished only three because we accommodate all variation into two states.

16. Supraorbital edge: narrower near to the nasal bones (0); constant in width (1); absent (2). Modified from O'Hara (1989, character 10) and Acosta Hospitaleche (2004, character 10). We do not agree with Bertelli and Giannini (2005, character 75) who did not consider the observed variation in the degree of development of the supraorbital edge to be justification for an additional state.

17. Width of temporal crests respect to the nasal bones: wider (0); similar (1). After Acosta Hospitaleche (2004, character 12).

18. Transversal occipital crest: well-developed (0); poorly developed (1).

19. Plane that contains the basitemporal plate and the tomial crests: parallel (0); non-parallel (1). Character described by Zusi (1975) and coded by Acosta Hospitaleche (2004, character 14).

20. Disposition of tomial crests: approximately at the same level of the basitemporal plate (0); dorsal at the level of the basitemporal plate (1). This two distinctive morphologies were recognized by Zusi (1975: 69) and coded by Bertelli and Giannini (2005, character 97).

21. Ventral border of the otic process of the quadrate: absent (0); present as a ridge (1); present as a tubercle (2). After Bertelli and Giannini, 2005 (character 96).

Postcranium

22. Atlas hypapophyses: absent or sligthly developed (0); well developed, with a prominent ridge (1). After Bertelli and Giannini (2005, character 108). The condition of *Madrynornis* is like the *Spheniscus*. The condition of *Paraptenodytes* is described by Simpson (1946: 13): "ventral longitudinal ridge terminating posteriorly in a small but distinct hypapophysis".

23. Sternal rostrum: present (0); absent (1). After O'Hara (1989, character 13), Acosta Hospitaleche (2004, character 16) and Bertelli and Giannini (2005, character 15).

24. Medial margin of the coracoid: complete (0); incomplete (1); absent (2). After Acosta Hospitaleche (2004, character 17) and Bertelli and Giannini (2005, character 119). This feature was described by Zusi (1975) and followed by O'Hara (1989, character 14) who considered only two states.

Humerus

25. Configuration of the trochlear processes of the humerus: non-*Spheniscus* type (0); *Spheniscus* type (1). We follow O'Hara (1989, character 15) and Acosta Hospitaleche (2004, character 18). Bertelli and Giannini (2005, character 128) identified similar states in this character. Mayr (2004, character 37) coded the presence or absence of the trochlear processes in a very different context, analyzing the relationships of the penguin with another birds, e.g., Plotopteridae.

26. Tricipital fossa of the humerus: bipartite with a small septum (0);

bipartite with a high septum (1); no bipartite (2). After Acosta Hospitaleche (2004, character 19).

27. Preaxial angle of the humerus: smaller than 20° (0); equal to or larger than 20° (1). After Acosta Hospitaleche (2004, character 20).

28. Shaft-trochlear angle of the humerus: large (0); small (1). After Acosta Hospitaleche (2004, character 21).

Pelvis

29. Ilioschiatic fenestra in relation to the acetabulum: smaller (0); similar to larger (1). After O'Hara (1989 character 16), Acosta Hospitaleche (2004, character 38) and Bertelli and Giannini (2005, character 132).

Femur

30. More proximal extension of the femur: corresponding to the head (0); corresponding to the trochanter (1). After Acosta Hospitaleche (2004, character 22)

31. Patella: shallow groove (0); deep groove (1), perforated (2). After Bertelli and Giannini (2005, character 135) who recognized these three states. O'Hara (1989, character 18), Acosta Hospitaleche (2004, character 39) and Mayr (2004, character 43) recognized only two states.

Tibiotarsus

32. Tibiotarsal tuberosity for insertion of the popliteus tendon: present (0); absent (1). After Acosta Hospitaleche (2004, character 23) and Bertelli and Giannini (2005, character 137).

33. Flexor fossa of the tibiotarsus: present (0); absent (1). After Acosta Hospitaleche (2004, character 24).

34. Tibiatarsus fibular crest: rounded (0); quadrangular (1). After Acosta Hospitaleche (2004, character 25).

35. Supratendinous bridge: narrow (0); wide (1). After Acosta Hospitaleche (2004, character 26).

36. Tubercle where the retinaculi musculi fibularis attaches: present (0); absent (1). After Acosta Hospitaleche (2004, character 27).

37. Shape of the lateral condyle of the tibiotarsus: circular (0); elongate (1). After Acosta Hospitaleche (2004, character 28).

38. Indentation of edge of medial condyle of the tibiotarsus: present (0); absent (1). After Acosta Hospitaleche (2004, character 29).

39. Relative distal extension of the condyles of the tibiotarsus (in caudal view): lateral condyle more extended than the medial (0); medial condyle more expanded than the lateral (1); similar extension in both of them (2). After Acosta Hospitaleche (2004, character 32).

Tarsometatarsus

40. Medial proximal vascular foramen: present (0); absent (1). After Acosta Hospitaleche (2004, character 33) and modified from O'Hara (1989, character 20) and Bertelli and Giannini (2005, character 139).

41. Lateral proximal vascular foramen in posterior view: present (0); absent (1). After Acosta Hospitaleche (2004, character 34). Modified from O'Hara (1989, character 19) and Bertelli and Giannini (2005, character 140).

42. Tibial tuberosities of the tarsometatarsus: flat (0); mounted (1). After Bertelli and Giannini (2005, character 142).

43. Number of hypotarsal crests: two (0); three (1); four (2). After Acosta Hospitaleche (2004, character 36).

44. Hypotarsal channel: present (0); absent (1). After Acosta Hospitaleche (2004, character 37) and Bertelli and Giannini (2005, character 141).

Comments.—We discarded character 73 proposed by Bertelli and Giannini (2005) because this character does not show any variation among the species here analyzed (see O'Hara 1989). According to O'Hara (1989), we believe that character 79 from Bertelli and Giannini (2005) exhibits variation in the population and we do not use it in our analysis.

Characters 80, 82, 83, 88, 90–92, 94, 95, 98, and 103 of Bertelli and Giannini (2005) cannot be seen in *Madrynornis* and were therefore omitted. We also did not include their character 106 because we think it is redundant with their character 105 (number 3 in our matrix). Characters 109-125 and 129 (Bertelli and Giannini 2005) were not included because of the impossibility to score them on the fossil materials. Characters 86, 87, 126, 130, 131, 133, 134, and 138 of Bertelli and Giannini (2005) were discarded because we observed no variation among penguins, while character 127 was not taken into account due to its redundancy with character 128.

Appendix 3

Character matrix used in the phylogenetic analysis. a = 0,1. Asterisks indicate fossil species.

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                                  1 1111111112 2222222223 3333333334 4444
                         1234567890 1234567890 1234567890 1234567890 1234
Gavia                    ?11?001000 a0011000?1 0102?2??11 ?01000001? 1100
Diomedea                 011?000001 1101111111 0002?2??10 ?111110000 1000
Fregata                  ?00?00?001 11011211?1 ??0??2??11 ?010010020 1020
Pygoscelis adeliae       1010101110 0011000101 1001011101 2001101111 0121
Pygoscelis antarctica    1000101010 0011000101 1001011101 2011001111 0121
Pygoscelis papua         1010100111 0011010101 1001011101 1111001111 0121
Megadytes antipodes      1001100011 a011001000 1000011100 100???11?0 01?1
Eudyptes chrysocome      1011100011 a011000110 2000010101 1101111110 1111
Eudyptes chrysolophus    1001100011 a011000110 200001??01 11????11?0 11?1
Eudyptes pachyrrhynchus  1011100011 1011010110 200a01??01 11????11?0 11?1
Eudyptes minor           1011101011 a011120010 1001110010 1000111120 11?1
Spheniscus demersus      1012101011 1100110000 200001??10 11???111?0 11?1
Spheniscus humboldti     1012101011 1100120000 200011?11a 11???111?0 11?1
Spheniscus magellanicus  1012101011 1100120000 200011011a 1101011120 1121
Spheniscus mendiculus    1012101011 1100120000 200011?110 11????11?0 11?1
Aptenodytes forsteri     0110101110 0011000100 1111011001 0110001110 00?1
Aptenodytes patagonicus  0110101110 0011000111 1111010001 0101001110 00?1
Palaeospheniscus biloculata (*)  ?????????? ?????????? ????0010?? ??????11?1 0111
Madrynornis mirandus (*)         1012100011 101112000? 2000000101 1110111120 1111
Paraptenodytes antarcticus (*)   ?????1010? ??01?200?? 11??1201?1 ?1?1001110 1101
Spheniscus urbinai (*)           10??????? 11000201?0 2??01?111? ?????????0 0???
Spheniscus megarhamphus (*)      10011010?? 1100?201?? ?????????? ?????????? ????
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