

## NOTA PALEONTOLOGICA

# A NEW EARLY MIOCENE PENGUIN SKULL FROM PATAGONIA: TAXONOMIC AND PALEOBIOLOGICAL VALUE



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**Palabras clave.** Pingüino fósil. *Spheniscus*. Cráneo. Patagonia. Mioceno.

As in birds in general, penguin skulls provide morphological features that are important from systematic and paleobiological points of view. In modern penguins, the arrangement of the nuchal crests is distinct for each genus (Acosta Hospitaleche and Canto, 2005; Acosta Hospitaleche *et al.*, 2006). This character, together with the morphology of the salt-gland grooves, allows defining a variety of forms between two extreme adaptive types (Acosta Hospitaleche and Tambussi, 2006). One extreme form is the *Pygoscelis* type, characterized by a wide nasal gland depression limited by well-defined edges, with small foramina aligned along the groove for the passage of blood vessels, a shallow temporal fossa, and poorly developed temporal nuchal crests. The other extreme configuration is the *Spheniscus* type, which is characterized by a laterally open nasal gland depression devoid of edges, less developed vascular foramina (with blood vessels extending laterally to the orbit), a deep temporal fossa, and well-developed temporal nuchal crests. These two morphotypes can also be recognized in fossil penguins and provide information about feeding strategies and food preferences.

In this work, a new skull (MLG 3400) exhumed from the Chenque Formation (early Miocene of Santa Cruz Province, Argentina) (Fig. 1) is assigned to Spheniscidae cf. *Spheniscus* Brisson, 1760 (Fig. 2). The significance of this finding is that it increases the penguin fossil record in the area, which is scant and consisting of only isolated remains.

## MATERIALS AND METHODS

Comparative materials are housed in the **AMNH**, American Museum of Natural History, New York, United States; **MEF-PV**, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; **MLG**, Museo del Lago Gutiérrez, San Carlos de

Bariloche, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MUSM**, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Perú; **SGO-PV**, Museo Nacional de Historia Natural, Santiago, Chile.

The analyzed specimens comprise the following taxa: *Madrynormis* Acosta Hospitaleche, Tambussi, Donato and Cozzuol, 2007: MEF-PV 100; *Paraptenodytes antarcticus* (Moreno and Mercerat, 1891): cast MLP from AMNH 3338; *Spheniscus urbinai* Stucchi, 2002: MUSM 401; *S. megaramphus* Stucchi, Urbina and Giraldo, 2003: MUSM 175; *Pygoscelis calderensis* Acosta Hospitaleche, Chávez and Fritis, 2006: SGO-PV 790; *Icadyptes* Clarke, Ksepka, Stucchi, Urbina, Giannini, Bertelli, Narváez and Boyd, 2007: data from Ksepka *et al.*, 2008; *Perudyptes* Clarke, Ksepka, Stucchi, Urbina, Giannini, Bertelli, Narváez and Boyd, 2007: data from



**Figure 1.** Location of the outcrops of the early Miocene Chenque Formation at Pico Truncado, Santa Cruz Province, Argentina/ Mapa de ubicación de los afloramientos de la Formación Chenque (Mioceno temprano) en Pico Truncado, Provincia de Santa Cruz, Argentina.

Clarke *et al.*, 2007; *Aptenodytes* Miller, 1778: MLP 478; *Spheniscus magellanicus* Forster, 1781: MLP 873, MLP 874; *S. humboldti* Meyen, 1834: MLP 686; *Pygoscelis adeliae* (Hombron and Jacquinot, 1841): MLP 464; *P. antarctica* Forster, 1781: MLP 470; *P. papua* Forster, 1781: MLP 38; *Eudyptes chrysochome* (Forster, 1781): MLP 39; *Palaeospheniscus?* Moreno and Mercerat, 1891: SGO-PV 1063.

A sample was analyzed comprising all extinct and living penguin species from southernmost South America with known skulls. Results were interpreted in the context of the morphotypes established by Acosta Hospitaleche and Tambussi (2006) with the goal of testing the position of the new skull MLG 3400.

Ten landmarks (shown in Fig. 3.1) were chosen for shape analysis (see Acosta Hospitaleche, 2009). The dorsal view was preferred because it allows a better analysis of the configuration of the nuchal crests and shape of the rostrum. The differences in size, orientation, and position of the salient features were removed from the dataset by Procrustean superimposition (Rohlf and Slice, 1990). With this technique, centroid size is scaled to 1 (square root of the summed squared distances from all landmarks to the configuration centroid). The position is normalized by translation of all configurations so that the centroids are located at the origin. Orientation is es-

tablished by rotation of all configurations about an optimum angle. These steps minimize the sum of squared distances between corresponding landmarks. The generalized Procrustes superimposition (Rohlf and Slice, 1990) allows calculation of mean shapes from the samples. The computer graphics used here are thin plate splines, whose function minimizes the energy required during transformation. A relative warps analysis is reported as the joint distribution of weighted scores together with the diagrams of grid deformations corresponding to the eigenvectors that generated those scores.

## SYSTEMATIC PALEONTOLOGY

Order SPHENISCIFORMES Sharpe, 1891

Family SPHENISCIDAE Bonaparte, 1831

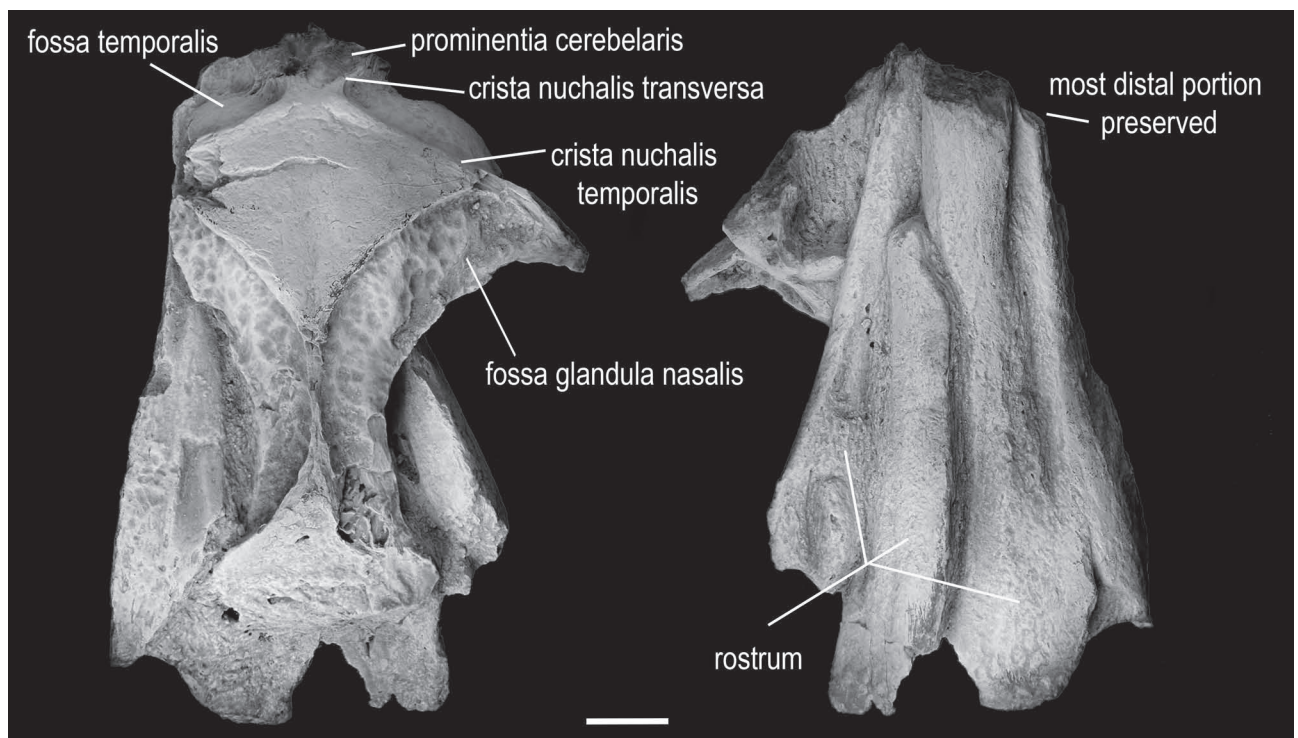
?Genus *Spheniscus* Brisson, 1760

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

cf. *Spheniscus* Brisson, 1760

### Figure 2

*Referred material.* MLG 3400, fragmentary skull. The caudalmost portion is preserved, including both *fossae glandulae nasales* and the *calvaria*. The *processus postorbitalis* and the *fossa temporalis* are complete on the left side, but they are both



**Figure 2.** Skull MLG 3400 cf. *Spheniscus*. 1, dorsal view; 2, palatal view/ Cráneo MLG 3400 de cf. *Spheniscus*. 1, vista dorsal; 2, vista palatal. Scale bar/ escala: 10 mm.

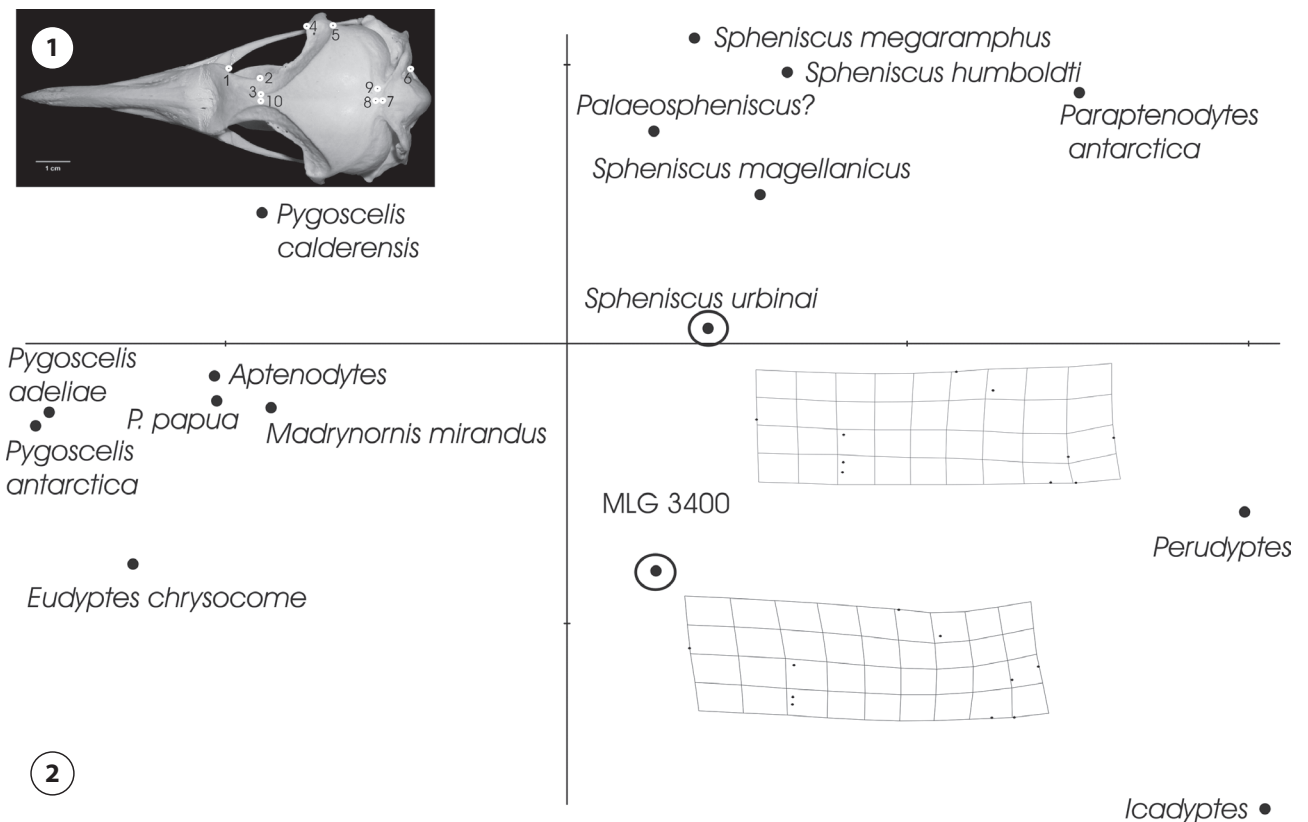
partial on the right side, along with the proximal portion of the *crista nuchalis transversa* and fragments of the associated rostrum.

**Locality and horizon.** The locality is situated in Bahía Lángara, near Pico Truncado, 22 km south of Caleta Olivia, Santa Cruz Province, Argentina (at 46°37'1.20"S–67°19'1.20"W) (Fig. 1). The strata are assigned to the Chenque Formation, which has been correlated, at least in part, with the Monte León and Gaiman formations. Such correlation is based on stratigraphic relationships (Malumián, 1999), volcanic ash and biogenic silica (Riggs, 1978), and fossil evidence (Cione, 1986; Cione and Expósito, 1980). For stratigraphic sections of the Chenque Formation at neighboring localities see Barreda and Palamarczuk (2000).

The age of this unit has been determined mainly on the

basis of its fossil content, stratigraphic relationships, and sea level curves. Analyses of dinoflagellates and pollen content indicate that the main part of the unit is early Miocene (Barreda, 1992, 1996). Barreda and Palamarczuk (2000) suggested a marine transgression beginning during the late Oligocene, which might have become more extensive toward the early Miocene. Additionally, the increase in megathermal elements has been recognized during the deposition of this unit (Palmazzesi and Barreda, 2007), according to the fossil pollen record and isotopic data (Zachos *et al.*, 2001).

**Description and comparisons.** MLG 3400 is medium-sized, larger than any of the living species of *Spheniscus* and *Paraptenodytes antarcticus*, but smaller than *Perudyptes*, *Icadyptes*, and *S. urbinai*. Braincase globosity is intermediate between the rounded *Pygoscelis* Wagler, 1832, and the winged *Sphenis-*



**Figure 3. 1,** Landmarks chosen for the skull shape analysis. Landmark 1 is located at the most cranial point of the suture between lachrymal and nasal bones. Width of the *fossa glandulae nasalis* is indicated by landmarks 2 and 3 located in the interorbital region, and by landmarks 4 and 5 at the most caudal level. Landmark 6 indicates the site where the cerebellar prominence contacts the skull. Landmarks 7 and 8, placed on the sagittal line, indicate the presence and extension of the sagittal nuchal crest. The dorsalmost end of the temporal fossa is indicated by landmark 9. Landmark 10, placed on the sagittal line, shows the distance between both *fossae glandulae nasales*. Scale bar= 10 mm; **2,** Relative warps analysis and deformation grids corresponding to the skull under study and *Spheniscus urbinai*, the morphologically closest species/ **1,** Landmarks seleccionados para el análisis morfométrico del cráneo. El landmark 1 está ubicado en el punto más cranial de la sutura entre los lacrimales y los nasales. El ancho del *fossa glandulae nasalis* está indicado por los landmarks 2 y 3, ubicados en la región interorbital, y por los landmarks 4 y 5 a nivel caudal. El landmark 6 indica la unión de la prominencia cerebelar al cráneo. Los landmarks 7 y 8, ubicados en la línea sagittal muestran el grado de desarrollo de la cresta sagittal. El extremo más dorsal de la fosa temporal es señalado por el landmark 9. El landmark 10, emplazado sobre la línea sagittal, muestra la distancia entre ambas *fossae glandulae nasales*. Escala= 10 mm; **2,** Análisis de deformaciones relativas y grillas de deformación correspondientes al cráneo bajo estudio y *Spheniscus urbinai*, la especie morfológicamente más cercana.

cus. It is cranio-caudally shorter than *Perudyptes*, which seems to have undergone deformation.

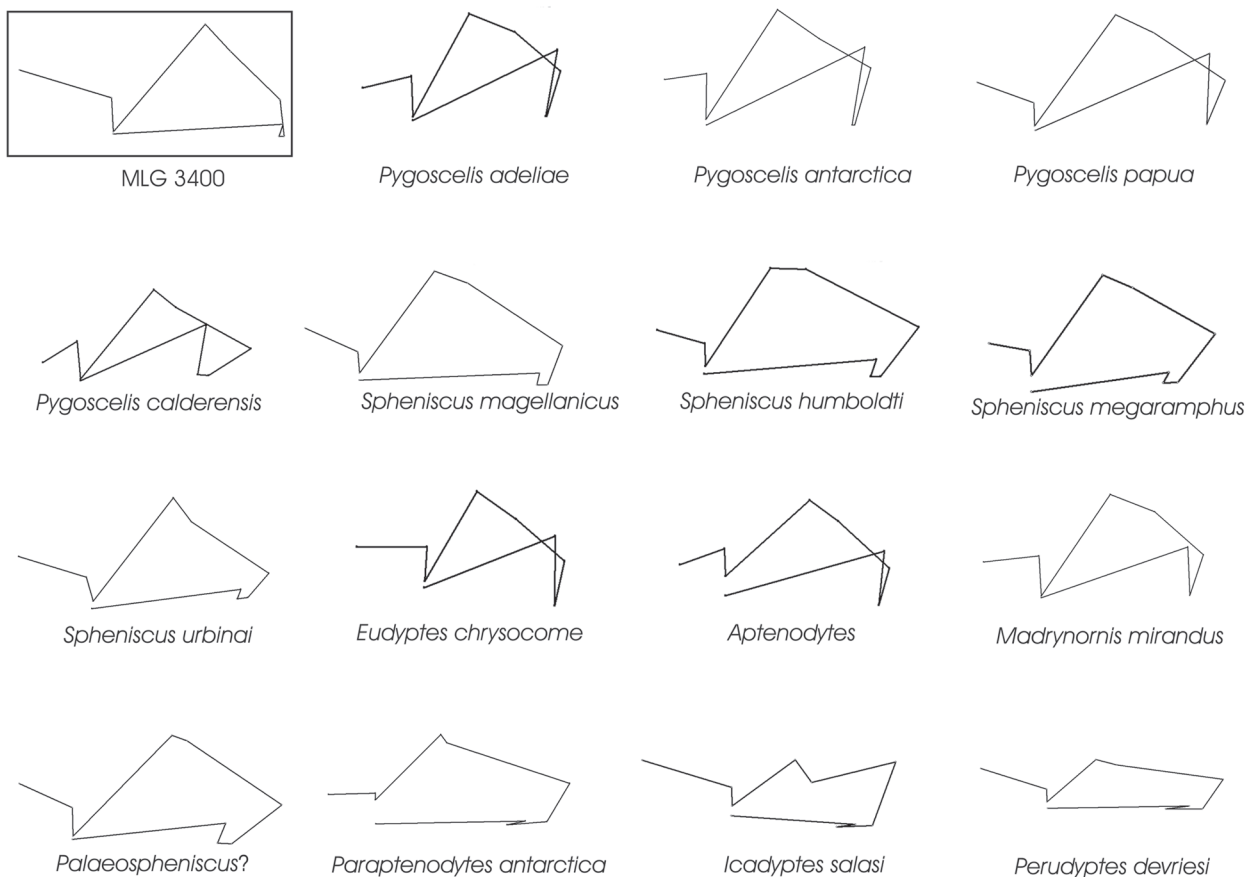
The roof of the newly described skull is rhomboidal, similar to those of the fossil species of *Spheniscus*. Measurements could not be taken in MLG 3400 because only the left side of the skull region is complete.

As in *Madrynornis* and all species of *Pygoscelis*, the frontals of MLG 3400 are shaped as 1 mm wide bars. Contrarily, in living *Spheniscus* the width of the frontals between the *fossa glandulae nasalis* is variable. The narrower portion reaches 2 mm in *S. demersus* and 8 mm in *S. mendiculus*. In the Peruvian fossils, the frontals narrow at the cranial end, reaching a minimum width of 4–5 mm in *S. urbinai*, 3 mm in *S. megaramphus*, 7 mm in *Perudyptes*, 10 mm in *Icadyptes*, and 11 mm in *Parapterodytes antarcticus*.

The *fossa glandulae nasalis* is not bounded by a supra-orbital edge as in all the *Spheniscus*-type skulls, including *Spheniscus*, *Icadyptes*, *Perudyptes*, *Madrynornis*, and *Paraptero-*

*dytes antarcticus*. Only the fossil and living species of *Pygoscelis* develop a supraorbital edge. The *fossa glandulae nasalis* is narrower rostrally as in most *Spheniscus* and the Peruvian Eocene species. The broader portion of the fossa (13 mm) is wider than in *Parapterodytes antarcticus* (3 mm), *S. magellanicus* (6 mm), *S. humboldti* (7 mm), *S. megaramphus* (9 mm), *Perudyptes* (9 mm), and *Icadyptes* (4 mm). The width of the grooves is uniform in *S. urbinai* and *Pygoscelis* (about 11 mm), and *Madrynornis* (15 mm).

The nuchal crests are weak in comparison to those of *Spheniscus* and *Icadyptes*, but more developed than in *Pygoscelis* and *Madrynornis*. The *cratae nuchalis temporales* are moderately developed and reach the sagittal line dorsally. In *Spheniscus*, the *crata nuchalis transversa* is expanded like wings, while in *Madrynornis* and *Parapterodytes antarcticus* it is little extended and not developing wing-like expansions. The sagittal nuchal crest is undeveloped in MLG 3400, *Spheniscus*, *Madrynornis*, and *Pygoscelis*. On the contrary, this crest is very



**Figure 4.** Schematic landmark configurations of the species included at the present analysis/ Configuración esquemática de los landmarks de las especies incluidas en el presente análisis.



well developed in *Paraptenodytes antarcticus* (7 mm length) and *Icadyptes* (13 mm).

The *fossa temporalis* is wide and rounded at the dorsal end, as in *S. megaramphus*, *S. urbinai*, *Paraptenodytes antarcticus*, and *Perudyptes*; it is triangular in modern *Spheniscus* and *Madrynornis*, and quadrangular in *Icadyptes*. The fossa of MLG 3400 is deeper than that of *Pygoscelis*, but shallower than that of *Spheniscus*. Both fossae are separated from each other by 6 mm in MLG 3400 and *S. urbinai*, 3 mm in *S. humboldti*, 8 mm in *S. megaramphus*, 12 mm in *S. demersus*, 14 mm in *Pygoscelis*, and 28 mm in *Madrynornis*.

The rostrum (Fig. 2.2) is partially preserved. It is more robust than those of the living species of *Spheniscus* but it seems to be as strong as in fossil species of this genus. The fragmentary state hinders detailed comparison with other species.

### MORPHOMETRIC ANALYSIS

According to this analysis, the first two components (Fig. 3.2) define a group formed by all the *Pygoscelis* skulls, close to *Madrynornis*, *Aptenodytes*, and *Eudyptes chrysocome*. At the opposite extreme, the *Spheniscus* type is represented by the modern and fossil species of *Spheniscus* together with *Palaeospheniscus?*, while *Paraptenodytes antarcticus* and the Eocene genera *Perudyptes* and *Icadyptes* are far from all the other skulls. MLG 3400 is closer to *Spheniscus urbinai* than to any other species.

When the taxa are plotted in the space corresponding to the second and third components, the location of MLG 3400 with respect to the other species remains unchanged. The similarities with *Spheniscus urbinai* are also noticed when the landmark configuration is visualized in detail (Fig. 4). In addition, Figure 4 illustrates the close morphology shared by modern and fossil species of *Pygoscelis*.

### DISCUSSION AND CONCLUSIONS

No striking differences in size (Acosta Hospitaleche and Gasparini, 2006) or shape (Acosta Hospitaleche and Tambussi, 2006; Acosta Hospitaleche, 2009) have been found between the skulls of living penguin species belonging to the same genus. Consequently, the same pattern was assumed for congeneric fossil species.

Even though MLG 3400 is not a complete skull, the preserved portion is very informative. The *fossae glandulae nasales* and the *cristae nuchalis* are directly related to the development of the nasal gland and the muscle *adductor mandibulae externus* respectively. Although the presence of a salt gland is not a relevant character for taxonomic purposes (Ibañez, 2009), the *fossae glandulae nasales* are fundamental for interpreting

the systematics and paleobiology of the group. As expected, the size of the salt gland is greater in marine species than in other birds. However, its degree of development is not directly related to that of the *fossa glandulae nasalis* (see Marples, 1932; Ibañez *et al.*, 2010). In penguins, whose salt gland is always supraorbital, the grooves are prominent and run from the contact between the lachrymal and the cranial end of the frontal to the postorbital processes (Herbert, 1975). All penguin species have a *fossa glandulae nasalis*, but only the *Pygoscelis* type develops a lateral margin.

The nuchal crests are attachment points for the deeper neck muscles, and their morphology allows inferences about habits related to diet and food catching (Zusi, 1975). The degree of development of each crest and their interrelationships determine particular configurations useful for systematic purposes. The muscle *adductor mandibulae externus* consists of several aponeuroses, and its three main subdivisions are involved in elevating the mandible. The *pars rostralis* has two different origins, *i.e.*, orbital and temporal, attached to the *crista nuchalis transversa* (see Baumel and Witmer, 1993).

The morphology of MLG 3400 resembles that of *Spheniscus* —particularly *S. urbinai*— because of the similar configuration of the nuchal crests, *fossa glandulae nasalis*, and *fossa temporalis*. Future research based on more complete material may confirm the presence of *Spheniscus* in the Miocene of Patagonia. Notwithstanding, the specimen described here represents a starting point in the review of the Miocene penguin associations from Patagonia (Argentina). All the currently known Patagonian fossil penguins are referred to extinct genera. The new material described herein —albeit with some reservations about the taxonomic determination— could represent the first specimen assigned to a modern penguin genus in Patagonia.

Morphological differences between the ecological types represented by the ichthyophagous *Spheniscus* and the krill-eating *Pygoscelis* could be useful to predict the habits of extinct forms (Acosta Hospitaleche and Tambussi, 2006). MLG 3400 is interpreted as a medium-sized penguin, morphologically closer to the *Spheniscus* type than to the *Pygoscelis* type, with a primarily ichthyophagous diet. The degree of development of the nuchal crests suggests a powerful skull mechanism for mandibular depression and upper jaw protraction. MLG 3400 shows an extensive area for muscle attachment on the braincase that could indicate great strength during jaw closure. This would be consistent with the need for adequate force production during dives for pursuit-capture purposes, consistent with the predicted diet.

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