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# A small penguin cranium (Aves, Spheniscidae) from the Late Miocene of Bahía Inglesa Formation, Atacama Desert, Northern Chile

Carolina ACOSTA HOSPITALECHE & Sergio SOTO-ACUÑA

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# A small penguin cranium (Aves, Spheniscidae) from the Late Miocene of Bahía Inglesa Formation, Atacama Desert, Northern Chile

**Carolina ACOSTA HOSPITALECHE**
División Paleontología Vertebrados, Museo de La Plata, Universidad Nacional de La Plata,
Paseo del Bosque s/n., B1900FWA La Plata (Argentina)
*and* Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET),
C1425FQB Buenos Aires (Argentina)
acostacaro@fcnym.unlp.edu.ar (corresponding author)

**Sergio SOTO-ACUÑA**
Red Paleontológica U-Chile, Laboratorio de Ontogenia y Filogenia, Departamento de Biología,
Facultad de Ciencias, Universidad de Chile, Las Palmeras 3425, Ñuñoa, Santiago (Chile)
*and* KayTreng Consultores SpA, José Domingo Cañas 1640,
Apartment 1502, Ñuñoa, Santiago (Chile)
*and* Escuela de Geologia, Facultad de Ciencias, Universidad Mayor,
Manuel Montt 367, Providencia, Santiago (Chile)
sesotacu@ug.uchile.cl

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## ABSTRACT

A new cranium of penguin from the Late Miocene of the Bahía Inglesa Formation (Northern Chile) is described here. Specimen SGO.PV.22245 exhibits a unique combination of characters that suggests it belongs to a new species of either *Eudypula* Bonaparte, 1856, *Spheniscus* Brisson, 1760, or more probably to a more basal taxon related to them. The specimen is notably smaller than the fossil species of *Spheniscus* and more similar in size to the extant *Spheniscus*. The *fossa glandulae nasalis* narrows caudally, the *crista nuchalis transversa* and the *crista temporalis* are expanded like short wings, and a short *crista nuchalis sagittalis* connects with the rounded and cranially projected *eminentia cerebellaris*. The *fossa temporalis* is subtriangular and deeper caudally and the cranial roof is widely expanded. All these features approach the condition to some species of *Spheniscus* and *Eudyptula*. However, because of the incompleteness of the material and the fact that it cannot be compared with some fossil species of *Spheniscus* only known through postcranial material, we are not able to provide a more accurate assignment.

KEY WORDS
*Eudyptula*,
*Spheniscus*,
Neogene,
South America.

**RÉSUMÉ**

*Un petit crâne de manchot (Aves, Spheniscidae) de la fin du Miocène de la formation Bahía Inglesa, désert d'Atacama, Nord du Chili.*

Un nouveau crâne de manchot du Miocène supérieur de la Formation de Bahía Inglesa (Nord du Chili) est décrit ici. Le spécimen SGO.PV.22245 présente une combinaison unique de caractères qui suggère qu'il appartient à une nouvelle espèce d'*Eudypula* Bonaparte, 1856, de *Spheniscus* Brisson, 1760, ou plus probablement à un taxon plus basal qui leur est apparenté. Le spécimen est nettement plus petit que les espèces fossiles de *Spheniscus* et plus similaire en taille au *Spheniscus* existant. La *fossa glandulae nasalis* qui se rétrécit caudalement, la *crista nuchalis transversa* et la *crista temporalis* sont élargies comme des ailes courtes, et une courte *crista nuchalis sagittalis* se connecte à l'*eminentia cerebellaris* arrondie et crânienne projetée. La fosse temporale est sous-triangulaire et plus profonde caudalement et le toit crânien est largement élargi. Toutes ces caractéristiques rapprochent l'état de ce fossile de certaines espèces de *Spheniscus* et d'*Eudyptula*. Cependant, en raison du caractère incomplet du matériel et du fait qu'il ne peut être comparé à certaines espèces fossiles de *Spheniscus* connues uniquement par le biais de matériel post-crânien, nous ne sommes pas en mesure de fournir une attribution plus précise.

**MOTS CLÉS**
*Eudyptula*,
*Spheniscus*,
Néogène,
Amérique du Sud.

## INTRODUCTION

Penguins (Aves, Sphenisciformes) are a group of seabirds extensively represented in the fossil record. The oldest report dates back to the Paleocene, a time of early diversification for the group (Slack *et al.* 2006; Mayr *et al.* 2020; and references cited there) that was followed by an uninterrupted spread and radiation of species in the Southern Hemisphere oceans.

In Southern South America, fossil penguins are recorded in Argentina, Chile, and Perú. The Argentinian record includes the middle Eocene Leticia Formation (Clarke *et al.* 2003; Acosta Hospitaleche & Olivero 2016), the Oligocene San Julián Formation (Acosta Hospitaleche 2005), the Early Miocene Gaiman Formation, Chenque Formation, and Monte León Formation (Acosta Hospitaleche 2003, 2007, 2011; Acosta Hospitaleche *et al.* 2008; Cione *et al.* 2011; and numerous references cited there), and the Middle-Late Miocene Puerto Madryn Formation (Acosta Hospitaleche *et al.* 2007). The Peruvian assemblages containing penguins are restricted to the middle Eocene Paracas Formation and Otuma Formation (Acosta Hospitaleche & Stucchi 2005; Clarke *et al.* 2007, 2010), the Early Miocene Chilcatay Formation (Acosta Hospitaleche & Stucchi 2005; Stucchi 2007) and the Middle Miocene-Pliocene Pisco Formation (Stucchi 2002, 2007; Stucchi *et al.* 2003). Finally in Chile, penguins are recorded in the contemporaneous middle-late Eocene Río Turbio and Man Aike formations, together with the late Eocene Loreto Formation (Sallaberry *et al.* 2010), the Middle Miocene-Pliocene Bahía Inglesa Formation (Acosta Hospitaleche *et al.* 2006a; Walsh & Suárez 2006; Chávez-Hoffmeister 2007; Acosta Hospitaleche *et al.* 2021), the Middle Miocene-Pleistocene Coquimbo Formation (Acosta Hospitaleche *et al.* 2006b), the Pliocene La Portada Formation (Emslie & Guerra Correa 2003), and the Late Pliocene Horcón Formation (Chávez-Hoffmeister *et al.* 2014) (Fig. 1A).

Although these Neogene South American assemblages are not coetaneous, at least one faunistic element is shared between the Atlantic and Pacific coasts (Fig. 1A). *Spheniscus urbinai* Stucchi, 2002 is undoubtedly found in Argentina (Acosta Hospitaleche 2011; Acosta Hospitaleche *et al.* 2021), Chile (Yury-Yáñez *et al.* 2009; Chávez-Hoffmeister 2014), and Peru (Stucchi 2002). Beyond that, and without exceptions, all these units contain a penguin fauna more closely related to the extant forms than those reported from the Paleogene formations. In fact, at least seven extinct species assigned to the extant genera *Pygoscelis* Wagler, 1832, *Spheniscus* Brisson, 1760, and *Eudyptes* Vieillot, 1816 lived on the Pacific coasts (Chile and Peru) during Mio-Pliocene times (see below).

We examined a new partial cranium of penguin (SGO.PV.22245) collected from the Late Miocene strata of the Bahía Inglesa Formation, outcropping in the Mina Fosforita locality (Fig. 2). The known penguin fauna of this unit is composed of *Spheniscus urbinai*, *S. megaramphus* Stucchi, Urbina & Giraldo, 2003, *S. muizoni* Göhlich, 2007 and *Pygoscelis calderensis* Acosta Hospitaleche, Chávez-Hoffmeister & Fritis, 2006 in the Late Miocene levels (Acosta Hospitaleche *et al.* 2006b; Chávez-Hoffmeister 2008a; Yury-Yáñez *et al.* 2009, 2013; see however Benson 2015), *Pygoscelis grandis* Walsh & Suárez, 2006, and possibly *S. chilensis* Emslie & Guerra Correa, 2006 in the Early Pliocene ones (Walsh & Suárez 2006; Chávez-Hoffmeister 2008a). The configuration of the nuchal crests, the nasal gland fossa, and the cranial roof indicates that specimen SGO.PV.22245 is not a procellariform and belongs to a member of Spheniscidae. It exhibits an intermediate morphology between *Spheniscus* and *Eudyptula*. The development of temporal crests expanded like wings and reaching the midline of the skull, temporal fossae narrowing dorsally, and nasal gland sulci running along the entire supraorbital extension preclude the assignment to a procellariform.

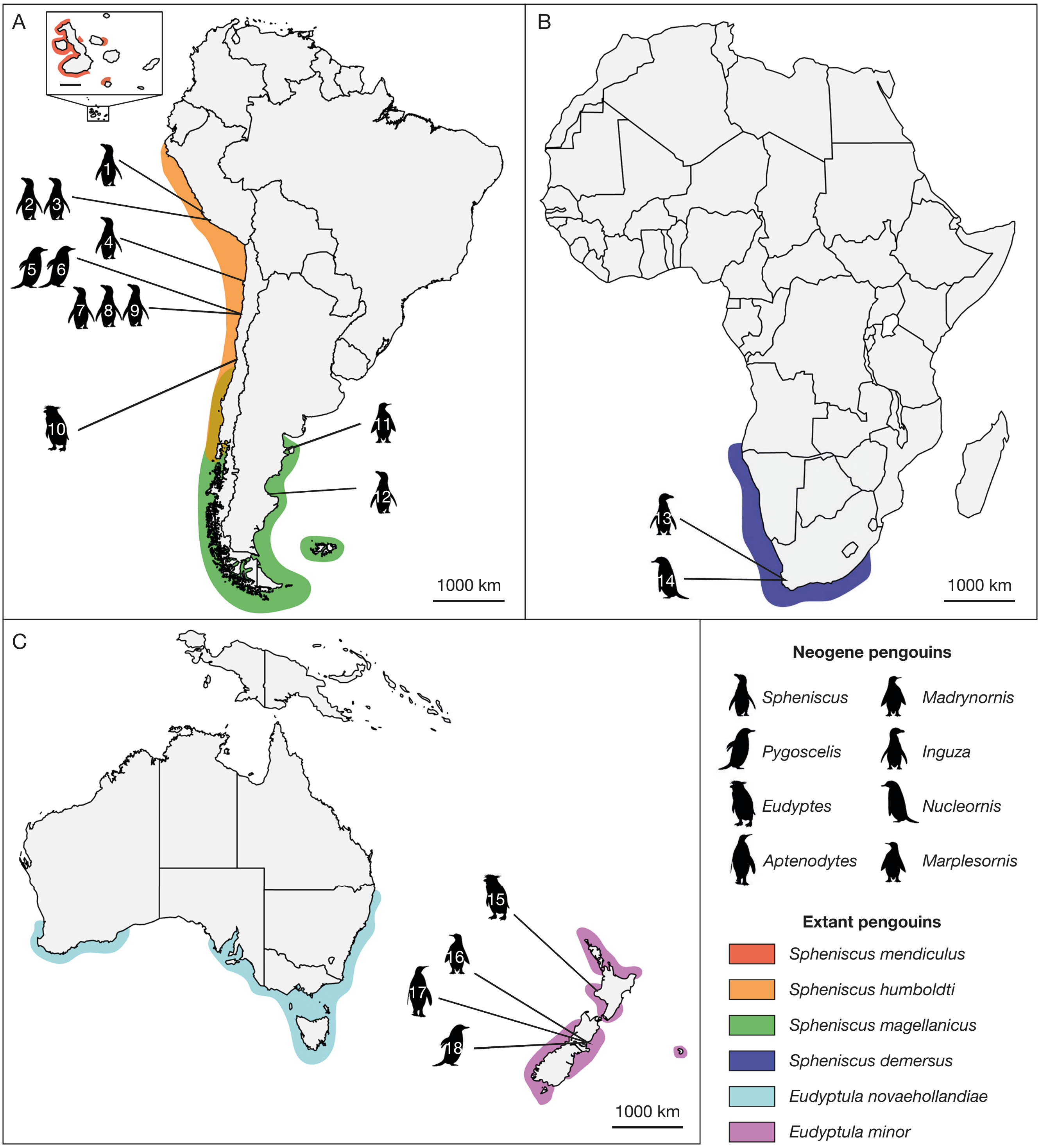

FIG. 1. — Map of Southern continents with the distribution of extant species of the genera *Eudyptula* Bonaparte, 1856 and *Spheniscus* Brisson, 1760 together with fossil species of crown Sphenisciformes: **A**, South America; **B**, Africa; **C**, Oceania. Numbers: **1**, *Spheniscus muizoni* Gohlich, 2007, Pisco Formation (Middle Miocene); **2**, *Spheniscus megaramphus* Stucchi, Urbina & Giraldo, 2003, Pisco Formation (Late Miocene); **3**, *Spheniscus urbinai* Stucchi, 2002, Pisco Formation (Late Miocene-Early Pliocene); **4**, *Spheniscus chilensis* Emslie & Correa, 2003, La Portada Formation (Pliocene); **5**, *Pygoscelis calderensis* Acosta Hospitaleche, Chávez & Fritis, 2006, Bahía Inglesa Formation (Late Miocene); **6**, *Pygoscelis grandis* Walsh & Suarez, 2006, Bahía Inglesa Formation (Pliocene); **7**, *Spheniscus muizoni* Gohlich, 2007, Bahía Inglesa Formation (Late Miocene); **8**, *Spheniscus urbinai* Stucchi, 2002, Bahía Inglesa Formation (Late Miocene); **9**, *Spheniscus megaramphus*, Bahía Inglesa Formation (upper Miocene); **10**, *Eudyptes calauina* Chavez Hoffmeister, Carrillo-Briceño & Nielsen, 2014, Horcón Formation (Late Pliocene); **11**, *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato & Cozzuol, 2007, Puerto Madryn Formation (Middle-Late Miocene); **12**, *Spheniscus urbinai* Stucchi, 2002, Chenque Cruz Formation (Early Miocene); **13**, *Inguza predemersus* (Simpson, 1971), Varswater Formation (Early Pliocene); **14**, *Nucleornis insolitus* Simpson, 1979, Varswater Formation (Early Pliocene); **15**, *Eudyptes atatu* Thomas, Tennyson, Scofield, Heath, Pett & Ksepka, 2020, Tangahoe Formation (Late Pliocene); **16**, *Marplesornis novaezealandiae* (Marples, 1960), Greta Sandstone? (Middle-Late Miocene?); **17**, *Aptenodytes ridgeni* Simpson, 1972, Greta Sandstone? (Middle-Late Miocene?); **18**, *Pygoscelis tyreei* Simpson, 1972, Greta Sandstone? (Middle-Late Miocene?).

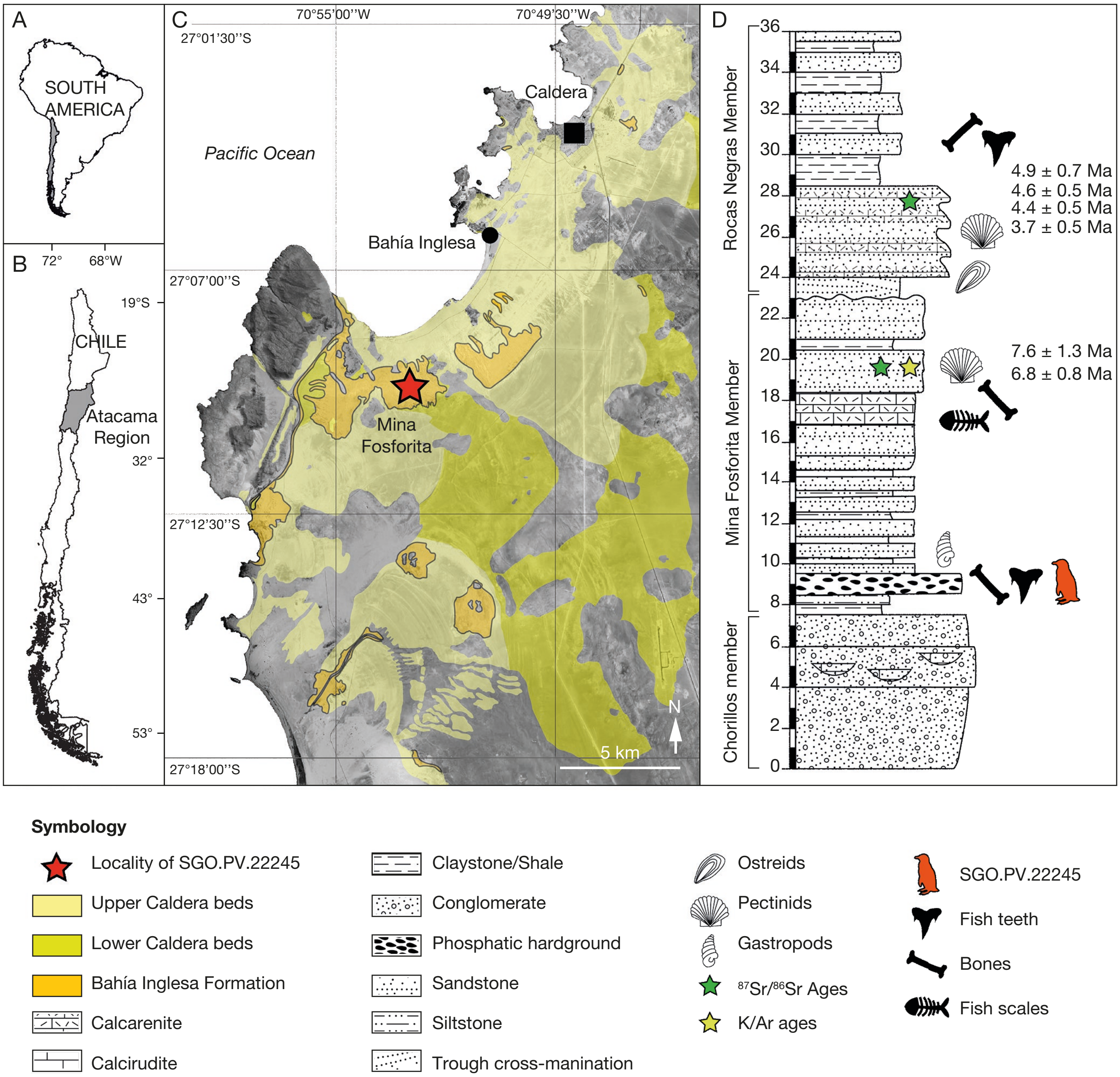

Fig. 2. — Geographic and geological precedence of SGO.PV.22245: **A**, **B**, location of Atacama Region in Northern Chile; **C**, map of Caldera Basin indicating the main Neogene lithological units and the fossiliferous locality; **D**, generalized stratigraphic column of the upper section of Bahía Inglesa Formation, indicating the fossil horizon (modified from Le Roux *et al.* 2016: fig. 4).

The genus *Spheniscus* is represented today by four species: *S. magellanicus* (Forster, 1781) from Argentina and Chile (Martínez *et al.* 2020a), *S. humboldti* Meyen, 1834 from Chile and Peru (Martínez *et al.* 2020b), *S. mendiculus* Sundevall, 1871 from the Galapagos Islands (Carlson & Townsdin 2020), and *S. demersus* (Linnaeus, 1758) from South Africa and Namibia (Martínez *et al.* 2020c). Four fossil species of *Spheniscus* inhabited the same areas during the Neogene: *Spheniscus urbinai* and *S. megaramphus* were recorded in the Late Miocene-Pliocene Miocene of Peru (Stucchi 2002; Stucchi *et al.* 2003), the Late Miocene of Chile (Chávez-Hoffmeister 2005; Yury-Yáñez *et al.* 2009) and the Early Miocene of Argentina (Acosta Hospitaleche 2011; Acosta Hospitaleche *et al.* 2021). *Spheniscus muizoni* is recorded in the Middle Miocene of Peru (Göhlich 2007), and possibly the Late Miocene of Chile (Yury-Yáñez *et al.* 2013). Finally, *S. chilensis* was only reported from the Pliocene of Chile (Emslie & Guerra Correa 2003), and the alleged fifth species *S. anglicus* Benson, 2015 (specimen P2001.10.2) is presumably also from the Miocene of Chile (Benson 2015) (Fig. 1). We wish to call attention to this fifth species of *Spheniscus*, based on a specimen bought and taken out of the country illegally, violating the laws for the protection of paleontological heritage in Chile.

In this context, its geographical and stratigraphic origin is not reliable, and besides, the characters used for its diagnosis are not adequate.

*Eudyptula minor* (Forster, 1781) was originally described within *Aptenodytes* based on a specimen from the South Island (New Zealand), and after that a second species was named *E. albosignata* Finsch, 1874 from a Banks Peninsula specimen (Turbott 1990). A taxonomic reappraisal reclassified *Eudyptula* into a single species containing six subspecies differentiable by the plumage coloration and external morphometric measurements (Kinsky & Falla 1976). In this way, *Eudyptula minor* would be represented by *E. m. novaehollandiae* (S Australia and Tasmania), *E. m. iredalei* (North I, New Zealand), *E. m. variabilis* (S North I, Cook Strait, New Zealand), *E. m. albosignata* (E South I, New Zealand). *E. m. minor* (W and S South I, Stewart I), and *E. m. chathamensis* (Chatham Is., New Zealand) (Martínez *et al.* 2020d). However, more recent analyses using mitochondrial markers (Banks *et al.* 2008; Peucker *et al.* 2009) found differences in two deeply divergent lineages, supporting the establishment of two species of *Eudyptula* (Grosser *et al.* 2015, 2016). A comprehensive morphometric analysis of skeletal elements provides quantitative evidence ratifying the taxonomic distinction between *E. minor* (Forster, 1781) from New Zealand and *E. novaehollandiae* (Forster, 1781) from Australia (Grosser *et al.* 2017). *Eudyptula minor* is also known from the Late Pleistocene of the South Island, New Zealand (Worthy & Grant-Mackie 2003) (Fig. 1).

The main goal of the present contribution is the report of a new penguin in the Bahía Inglesa Formation (Fig. 2). The fossil cranium SGO.PV.22245 (Fig. 3) was comparatively described with a broad sample of penguin specimens (Fig. 4), in particular with *Spheniscus* and *Eudyptula* taxa based on the morphological similarities detected.

## MATERIAL AND METHODS

### MATERIAL

Specimen SGO.PV.22245 is permanently housed in the Paleontology Area of the Museo Nacional de Historia Natural in Santiago (Chile), and it was mechanically prepared in the Red Paleontológica U.Chile Laboratory in Santiago (Chile) to remove part of the surrounding sediment. The comparative material includes the following fossils: *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato and Cozzuol, 2007 (MEF-PV 100), *Paraptenodytes antarcticus* Moreno and Mercerat, 1891 (AMNH 3338), *Pygoscelis calderensis* (SGO.PV 792), *Spheniscus urbinai* (MLG 3400, MPC 12002, MUSM 269, MUSM 401, SGO.PV 21327, SGO.PV 21328, SGO.PV 1063), *Spheniscus megaramphus* (SGO.PV.22222, MUSM 175), *S. anglicus* (P2001.10.2), and *Eudyptula*? (MPC 1096, from Chávez-Hoffmeister 2008b); and extant species *Spheniscus magellanicus* (MLP-597, MLP-611, MLP-614, MLP-642, MLP-643, MLP- O-14357, MLP-O-14439, MLP-O-14464, MLP-O-14894, MLP-O-14895, MLP-O-15091, MLP-O-15184, MLP-O-15185, MLP-O-15186, MLP-O-15187;), *S. humboldti* (MLP 686, NRM 20106577, NRM 557824, NRM 619823), *S. demersus* (UF 21341, from Triche 2005), *S. mendiculus* (UF 22275), *Eudyptula minor -sensu lato-* (BMNH 1952.3.143, BMNH 1966.51.1, BMNH 2002.2.1, BMNH 1896.2.16.38), *E. m. albosignata* (UF 31924 from Triche 2006), *E. m. iredalei* (unnumbered specimen available at http://shearwater.nl/index.php%3Ffile=kop12.php.html), *Eudyptes sclateri* (NRM 1652.1.38), *Eudyptes chrysolophus* NRM 928173, NRM 928174), *Eudyptes pachyrhynchus* (NRM 1972.1.26), *Eudyptes chrysolocome* (NRM 1323), *Aptenodytes forsteri* (MLP-O-15035, MLP-O-15188, NRM 1330, NRM 1846.4.15.26, BMNH 1846.4.15.27, BMNH 1846.4.15.28, BMNH 2011.14.1, MBNH 1972.1.25, BMNH 1905.12.30.419), *Aptenodytes patagonicus* NRM 886041, NRM 928157, NRM 928152, NRM 928159, NRM 928160, NRM 928171, NRM 928172, *Megadyptes antipodes* (BMNH 1852.1.17.11, BMNH 2006.31.26), *Pygoscelis adeliae* (MLP 32, MLP 33, MLP 415, MLP 416, MLP 417, MLP 418, MLP 419, MLP 420, MLP 421, MLP 422, MLP 423, MLP 424, MLP 425, MLP 426, MLP 427, MLP 428, MLP 429, MLP 430, MLP 431, MLP 432, MLP 433, MLP 434.MLP 464), *P. papua* (MLP 38, MLP 449, MLP 451, MLP 463, MLP 468), *P. antarctica* (MLP-O-14670, MLP-O-14671, MLP-O-14672, MLP-O-14673, MLP-O-14674, MLP-O-14675, MLP-O-14676, MLP-O-14677, MLP-O-14678, MLP-O-14679, MLP-O-14703, MLP-O-14704, MLP-O-14705, MLP-O-14706, MLP-O-14707, MLP-O-14708, MLP-O-14709, MLP-O-14710, MLP-O-14717, MLP-O-14737, MLP-O-14831, MLP-O-14905, MLP-O-14916, MLP-O-14947, MLP-O-15189, MLP-O-15190, MLP-O- 15191, MLP-O-15211, MLP 470).

### INSTITUTIONAL ABBREVIATIONS

| | |
|---|---|
| MEF-PV | Museo Paleontológico Egidio Feruglio,Trelew; |
| MLG | Museo del Lago Gutiérrez, Bariloche; |
| MLP | División Paleontología Vertebrados del Museo de La Plata, La Plata; |
| MPC | Museo Paleontológico de Caldera, Caldera; |
| MUSM | Museo de la Universidad San Marcos, Lima; |
| P | Paleontology collection of the Science Museum of Minnesota, Minnesaota; |
| SGO-PV | Área de Paleontología del Museo Nacional de Historia Natural, Santiago; |
| UF | Florida Museum of Natural History, Gainesville. |

### METHODS

Osteological terms proposed by Baumel & Witmer (1993) are followed in the comparative description, and the measurements (expressed in millimeters) were taken with a Caliper Vernier with a precision of 0.01 mm. The postorbital width in SGO.PV.22245 was estimated as twice the distance between the tip of the *processus postorbitalis* and the sagittal line because the left side is broken. The systematic classification for modern species follows Winkler *et al.* (2020) and was updated with Grosser *et al.* (2015) for *Eudyptula* species. The stratigraphic scheme concurs with the work of Le Roux *et al.* (2016), who divided the Bahía Inglesa Formation into eight members.

## LOCALITY AND GEOLOGICAL SETTING

The specimen SGO.PV.22245 (Fig. 3) was recovered in the Mina Fosforita locality, which is located 12 km SW of Caldera, in Copiapó Province, Atacama Region, Northern Chile (Fig. 2A-C). The outcrop of provenance is part of the Mina Fosforita Member (*sensu* Le Roux *et al.* 2016) from Bahía Inglesa Formation (Rojo 1985). This is a siliciclastic semiconsolidated unit, dominated by coquinas, conglomerates, sandstones, siltstones and phosphorites, interpreted as a continental slope to shallow marine system (Marquardt *et al.* 2000; Godoy *et al.* 2003). The Bahía Inglesa Formation overlies Jurassic plutonic rocks in erosive discordance, and underlies the Pleistocene Caldera Beds (Marquardt 1999), and the age of the entire unit ranges from the Middle Miocene to Pliocene (Guzmán *et al.* 2000; Marquardt *et al.* 2000; Marchant *et al.* 2000; Godoy *et al.* 2003; Achurra 2004; Le Roux *et al.* 2016).

In particular, the Mina Fosforita Member comprises a succession of medium-to-fine sandstones, siltstones, and shales with nodular phosphate hardground in the basal portion (Le Roux *et al.* 2016; Fig. 2D). This basal section was previously referred to in the literature as 'the bonebed' (Walsh & Hume 2001; Walsh & Suárez 2005). From this unit more than 60 species have been described (Gutstein *et al.* 2008) including cartilaginous fishes (Long 1993; Suárez *et al.* 2004; Suárez 2015; Villafaña *et al.* 2019), bony fishes (Long 1993; Oyanadel-Urbina *et al.* 2021), crocodyliforms (Walsh & Suárez 2005; Soto-Acuña *et al.* 2015), pinnipedians (Walsh & Naish 2002), cetaceans (Gutstein *et al.* 2009, 2015) and seabirds (Walsh & Hume 2001; Sallaberry *et al.* 2007; Chávez-Hoffmeister 2008b; Sallaberry *et al.* 2008). K-Ar date obtained from El Morro locality, from an ash layer above the phosphatic bonebed, gives an age of 7.6 ± 1.3 Ma (Godoy *et al.* 2003). On the other hand, $^{87}$Sr/$^{86}$Sr stable isotopes obtained from pectinids indicate an age of 6.8 ± 0.8 Ma in the same unit (Henríquez 2006). Accordingly, considering that the overlapping error brackets yield a range of 6.3-7.6 Ma, a mean value of 7.0 for the deposition of Mina Fosforita Member can be inferred (Le Roux *et al.* 2016). Therefore, the phosphatic bonebed can be constrained to a Tortonian-Messinian age.

## SYSTEMATIC PALEONTOLOGY

### Order SPHENISCIFORMES Sharpe, 1891
### Family SPHENISCIDAE Bonaparte, 1831

### Spheniscidae gen. et sp. indet.
(Figs 3; 4)

MATERIAL. — SGO.PV.22245, partial cranium lacking the rostrum, the palate and most of the occipital portion (Figs 3; 4A).

LOCALITY AND HORIZON. — Mina Fosforita locality, Caldera, Atacama Region, Northern Chile. Mina Fosforita Member, Bahía Inglesa Formation, Tortonian-Messinian age (Fig. 2).

MEASUREMENTS. — Postorbital width 48.46 mm in SGO.PV.22245 (50.4 mm in *S. demersus* UF 21341, 64.3 mm in *S. magellanicus* MLP 643).

DESCRIPTION
According to the configuration and relative development of the *crista nuchalis*, the *fossa glandulae nasalis*, and the morphology of the cranial roof, features described below in detail, SGO.PV.22245 is assigned to Spheniscidae. The attribution of SGO.PV.22245 to any Paleogene penguin species (e.g. *Icadyptes*, *Perudyptes*, *Anthropornis*, *Waimanu*) can easily be ruled out based on differences in morphology. In addition to the Paleogene penguins having skulls notably larger than that of the specimen described here, and other morphological differences separate them. Paleogene penguins have a more elongated crania, stronger nuchal crests (and a larger *crista sagittalis*), and broader *fossae temporalis*. Differences with the Neogene species and particularly the extant genera are subtler and will be treated in more detail.

The *fossa glandulae nasalis* is narrow (Fig. 3A, B) like in *Eudyptula*, *Megadyptes*, and *Paraptenodytes* whereas in *Eudyptes*, some species of *Spheniscus*, *Pygoscelis*, *Aptenodytes*, and *Madrynornis* is significantly broader (Fig. 4). This fossa narrows caudally and is not laterally delimited, like in *Eudyptula*, *Spheniscus, Aptenodytes*, and *Paraptenodytes*, whereas a supraorbital edge appears in *Eudyptes*, *Megadyptes*, and *Pygoscelis* (Fig. 4). The left and right *fossa glandulae nasalis* leave a narrow interorbital region in between (Fig. 3A, B), like in *Eudyptula*, *Eudyptes*, *Pygoscelis*, *Spheniscus* and *Madrynornis*. This area is wider in *Aptenodytes*, *Megadyptes,* and *Paraptenodytes* (Fig. 4).

The *crista nuchalis transversa* and the *crista temporalis* (Fig. 3A, E) are expanded like short wings like in most of the modern penguins with the single exception of *Spheniscus*, in which these cristae are more extensively projected. A short *crista nuchalis sagittalis* (shorter than in *Paraptenodytes*) connects the *crista nuchalis transversa* with the *eminentia cerebellaris*, which is rounded and caudally projected (Fig. 3A, C, E).

The *fossae temporales* are subtriangular and deeper caudally (Fig. 3C), completely distinguishable from *Paraptenodytes* (Fig. 4B), in which the fossae are quadrangular and dorsally sub-rounded. The dorsal extension of each fossa is intermediate between *Eudyptula* (in which the fossae are mostly laterally developed) and most of the *Spheniscus* species (in which the left and right fossae meet dorsally near the sagittal line), approaching the condition of the latter (Fig. 4I-Q). This feature, however, can vary intra-specifically (Ksepka & Bertelli 2006).

The cranial roof is more expanded than in most penguin species (Fig. 3A, C, D), and it only matches *Eudyptula* in its morphology. The *depressio frontalis* is barely marked like in *Eudyptula*, whereas it differentially develops in the *Spheniscus* species (Fig. 4I-Q).

The *processus postorbitales* (only the right one is preserved) are ventrolaterally projected (Fig. 3A-C), like in the fossil species of *Spheniscus*, whereas in living *Spheniscus* and *Eudyptula*, the process is mostly ventrally projected (Fig. 4). Although the *processus postorbitales* observed in *Eudyptula* varies among

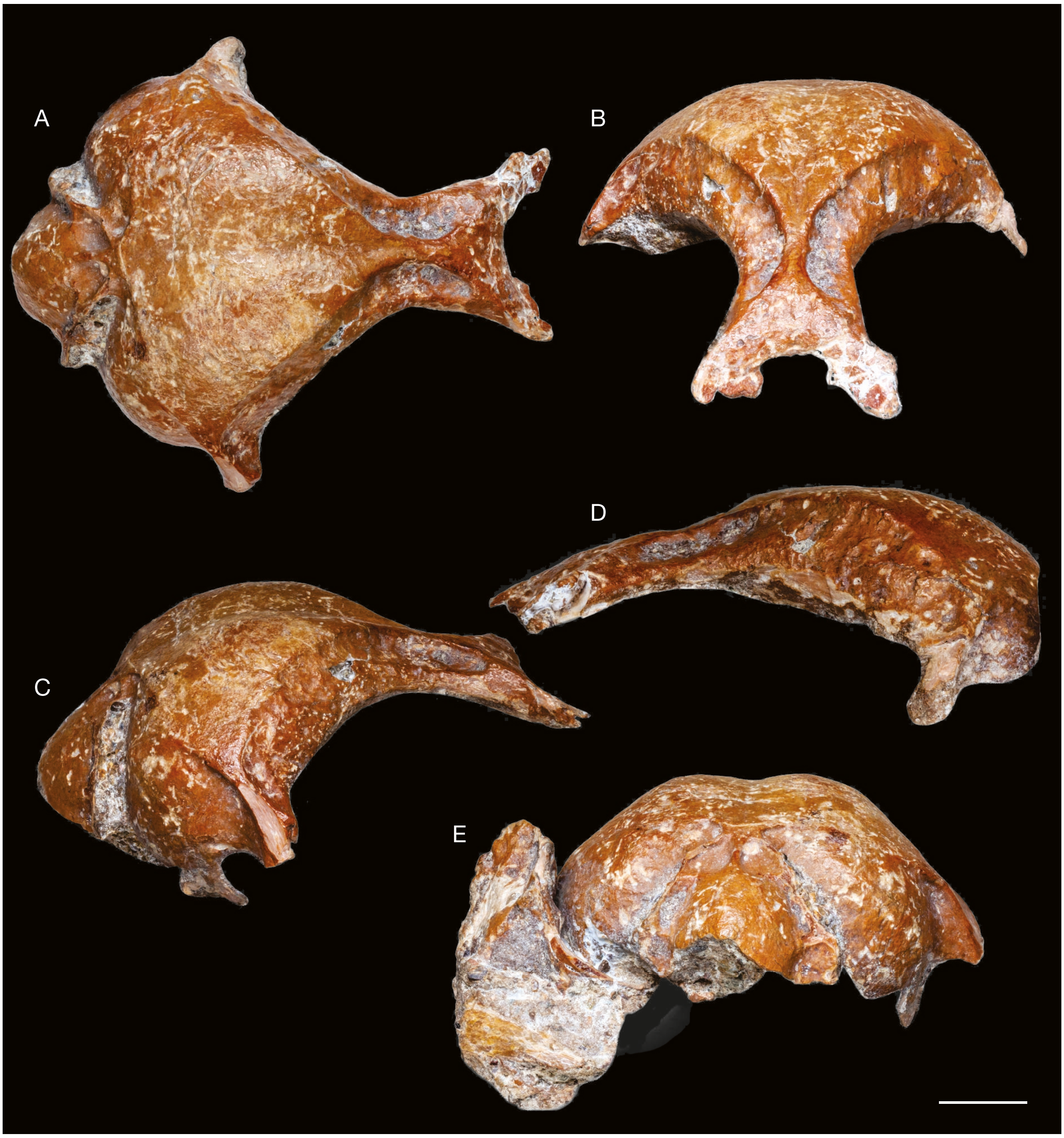

FIG. 3. — Spheniscidae gen. et sp. indet. SGO.PV.22245 in: **A**, dorsa; **B**, rostro-dorsal; **C**, latero-caudal (right side); **D**, lateral (left side); and **E**, occipital views (the sediment that surround the fossil was digitally removed in A-D). Scale bar: 1 cm.

individuals (slightly inclined cranially in *E. novaehollandiae*, and more caudally in *E. minor*), it never projects laterally like in SGO.PV.22245 and is rounded and barely projected in *Eudyptes*, *Pygoscelis*, *Aptenodytes*, *Megadyptes*, and *Madrynornis*, rostrally and slightly laterally in *Paraptenodytes* (Fig. 4).

The *prominentia cerebellaris* is caudally extended (Fig. 3C), and its tip is rounded like in *Eudyptula*, *S. megaramphus*, and *Eudyptes*, whereas it is more acute in *S. urbinai* and all the remaining modern species (Fig. 4). The *prominentia cerebellaris* is ventrally broken and the whole occipital region is crushed. Two shallow and symmetrical depressions are dorsally located on the *prominentia cerebellaris*, a similar condition is observed in some specimens like *Spheniscus demersus* and *Eudyptula novaehollandiae*. Unfortunately, the cranial foramina are not visible because of the poor preservation.

## DISCUSSION AND FINAL COMMENTS

Specimen SGO.PV.22245 is medium in size compared to the extant species and presents a barely expanded *crista nuchalis*, a notably dorsally expanded cranial roof, narrow *fossae glandulae nasalis,* and narrow interorbital region, that give it a globose appearance, like in *Eudyptula* and *Spheniscus*.

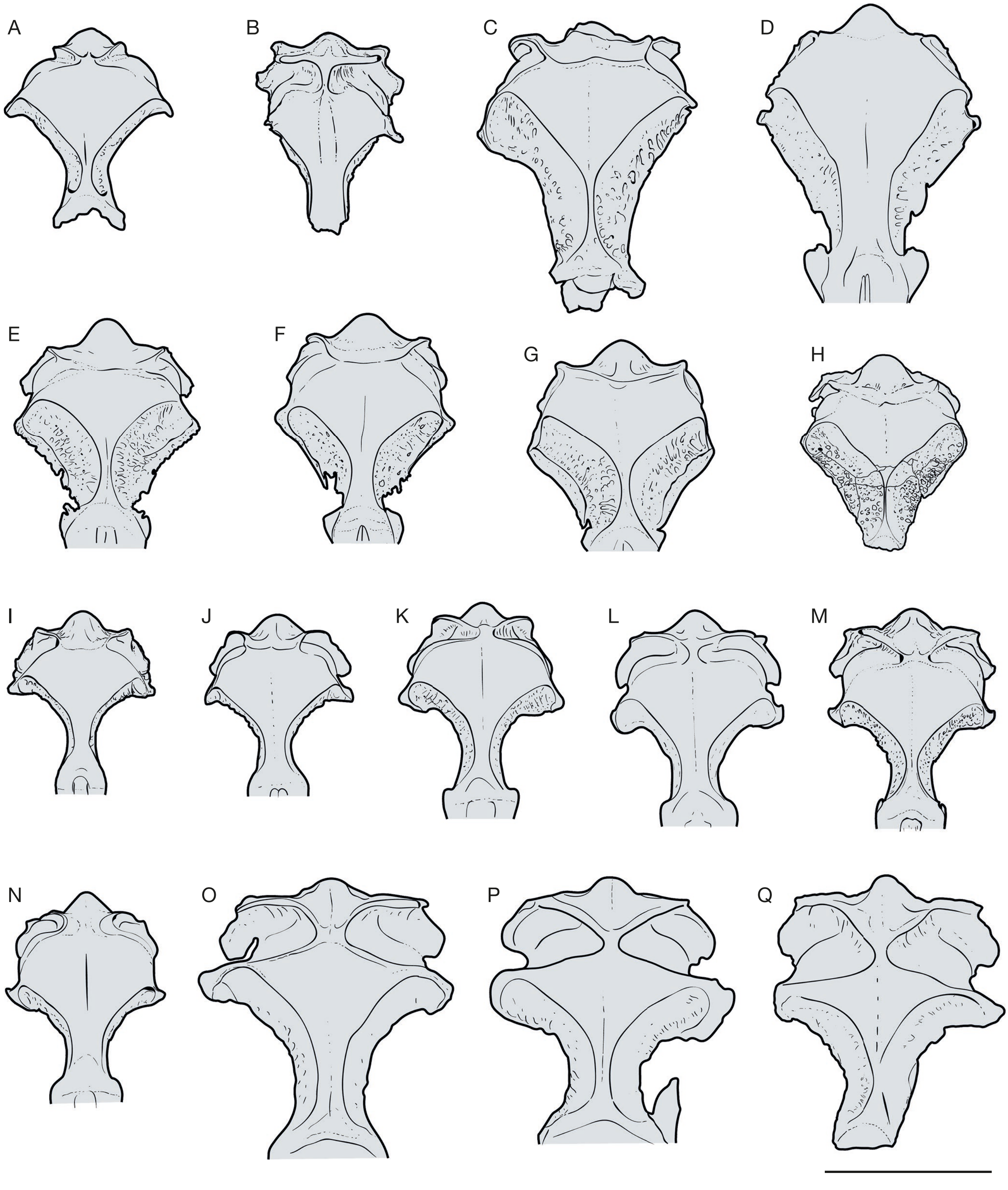

Fig. 4. — Schematic comparison of crania from Neogene and extant penguins in dorsal view: **A**, SGO.PV.22245; **B**, *Paraptenodytes antarcticus* (Moreno & Mercerat, 1891); **C**, *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato & Cozzuol, 2007; **D**, *Aptenodytes forsteri* Gray, 1844; **E**, *Eudyptes chrysolophus* (Brandt, 1837); **F**, *Megadyptes antipodes* (Hombron & Jacquinot, 1841); **G**, *Pygoscelis adeliae* (Hombron & Jacquinot, 1841); **H**, *Pygoscelis calderensis* Acosta Hospitaleche, Chávez-Hoffmeister & Fritis, 2006; **I**, *Eudyptula minor* (Forster, 1781); **J**, *Eudyptula novaehollandiae* Eudyptula Bonaparte, 1856; **K**, *Spheniscus magellanicus* (Forster, 1781); **I**, *Spheniscus humboldti* Meyen, 1834; **M**, *Spheniscus demersus* (Linnaeus, 1758); **N**, *Spheniscus mendiculus* Sundevall, 1871; **O**, *Spheniscus megaramphus* Stucchi, Urbina & Giraldo, 2003; **P**, *Spheniscus urbinai* Stucchi, 2002; **Q**, *Spheniscus anglicus* Benson, 2015. Scale bar: 5 cm.

Beyond the discrepancies in the taxonomic classification of *Eudyptula*, something worthy to note in the context of the present contribution is the small magnitude of the morphological differences found between *E. minor* and *E. novaehollandiae* (Grosser *et al.*, 2017) (see also Fig. 4I, J), which diverged from each other relatively recently (*c.* 3 Ma in Cole *et al.* 2019). Only the summation of the small metric differences along the whole skeleton between the two species allows the allocation of the skeletons through a principal component analysis. In other words, the two extant *Eudyptula* species cannot be distinguished from each other using only a single measurement. However, taking for example the postorbital width as a single measurement, SGO.PV.22245 is notably larger than all the extant *Eudyptula* (48.46 mm in SGO.PV, 36.69 in *Eudyptula minor* BMNH 1896.2.16.38, 38.73 mm in BMNH 1966.51.1, 40 mm in BMNH 2002.2.1, and 40.6 mm in BMNH 1952.3.143), precluding attribution to any of the living species of this genus.

The presence of a new species of *Eudyptula* in this assemblage was already proposed since the discovery of a set of bones smaller than those of *S. humboldti*, among which the cranium MPC 1096 of *c.* 42 mm of postorbital width was collected (Chávez Hoffmeister 2008b). These materials, however, have not yet been formally described. Accidental records of *E. novaehollandiae* have been reported from central and southern Chile (Valverde & Oyarzo 1996; Brito 2000; Wilson *et al.* 2000; Barros 2015), although there are no known records of breeding pairs or nests for this species in South America.

Besides, the cranium SGO.PV.22245 had been considered morphologically close to *S. urbinai* (*in schedis*), and so the material was preliminarily labeled under that name when it was entered into the official repository. However, after the direct comparison of specimen SGO.PV.22245 with all the extinct and extant species of *Spheniscus*, it seems unlikely. The dorsal expansion of the *fossa temporalis*, without reaching the sagittal plane, the presence of a short *crista sagittalis*, and the shape of the *fossae glandularum nasales* are more similar to the living species of *Spheniscus*, although the width of the interorbital region resembles *S. urbinai* (and some individuals of *Eudyptula minor iredalei*).

We cannot eliminate the possibility that SGO.PV.22245 belongs to *Inguza predemersus* Simpson, 1975, a new species of *Spheniscus* still unnamed, or to any of the fossil species of *Spheniscus* whose crania are still unknown (e.g. *S. chilensis* and *S. muizoni*). *S. muizoni*, described from the Middle Miocene of the Pisco Formation in Perú (Göhlich 2007) and later preliminarily reported from the Late Miocene of the Bahía Inglesa Formation (Yury-Yáñez *et al.* 2013), is exclusively known from postcranial material. *S. muizoni* was described as the smallest of the extinct species of *Spheniscus* (including the alleged *S. anglicus*), although it is almost identical in size to *S. chilensis*, and close in size to *Spheniscus demersus* and *S. magellanicus* based on postcranial measurements (Göhlich 2007). Our measurements of the postorbital width indicate that the new fossil was smaller than the compared species.

Unfortunately, the incompleteness of this fossil makes the comparison of several features of the rostrum and the palate impossible. The unique combination of characters observed in different species of *Spheniscus* and *Eudyptula* is not surprising due to the close relationship between them (Ksepka & Ando 2011; Thomas *et al.* 2020; Vianna *et al.* 2020). Indeed, genomic studies estimate that in the mid-Miocene, the lineage leading to the *Spheniscus*/*Eudyptula* ancestor colonized the South American coast (Vianna *et al.* 2020). Accordingly, SGO.PV.22245 could represent a new species, either of *Eudyptula*, *Spheniscus,* or more probably according to our observations, to a new genus that could be ancestral to both. However, we prefer to be cautious and restrict the taxonomic assignment until new and/or more complete materials are available for a further examination.

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## Author statements

CAH and SSA conceived of the presented idea, examined, and compared the material. CAH and SSA wrote the manuscript, prepared the figures, and approved the final version of the manuscript.

## Conflict of interests

The authors declare that there is no conflict of interest.

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