



New crania from Seymour Island (Antarctica) shed light on anatomy of Eocene penguins

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Abstract: Antarctic skulls attributable to fossil penguins are rare. Three new penguin crania from Antarctica are here described providing an insight into their feeding function. One of the specimens studied is largely a natural endocast, slightly damaged, and lacking preserved osteological details. Two other specimens are the best preserved fossil penguin crania from Antarctica, enabling the study of characters not observed so far. All of them come from the uppermost Submeseta Allomember of the La Meseta Formation (Eocene–?Oligocene), Seymour (Marambio) Island, Antarctic Peninsula. The results of the comparative studies suggest that Paleogene penguins were long-skulled birds, with strong nuchal crests and deep temporal fossae. The configuration of the nuchal crests, the temporal fossae, and the parasphenoidal processes, appears to indicate the presence of powerful muscles. The nasal gland sulcus devoid of a supraorbital edge is typical of piscivorous species.

Key words: Antarctica, Sphenisciformes, crania, La Meseta Formation, late Eocene.

Introduction

Penguins (Aves, Sphenisciformes) are the best represented Paleogene Antarctic seabirds. This is probably so because of the intrinsic features of their skeletons, dense and heavy bones increase the chance of fossilization, and the presumably gregarious habit, typical of extant species. The oldest penguin record is known from the Paleocene of New Zealand (Slack *et al.* 2006). In the Antarctic Peninsula region, penguins have a continuous record in the James Ross Basin, spanning the Late Paleocene to the Eocene–?earliest Oligocene (for stratigraphic details see Marenssi *et al.* 2012).

Skulls of extinct penguins are rare, even in Antarctica where thousands of fossil specimens have been collected on Seymour Island (Reguero *et al.* 2013). Most of the known remains are non-articulated bones and a vast majority of holotypes of penguin species from Antarctica are either tarsometatarsi (Myrcha *et al.* 2002;

Jadwiszczak 2006; Tambussi *et al.* 2006) or humeri (Tambussi and Acosta Hospitaleche 2007). Unfortunately, no cranium has been unequivocally assigned to any known Antarctic species.

So far, three deformed “neurocrania” have been the only large fragments of penguin braincases reported from Antarctica, all of them collected within the uppermost unit (Submeseta Allomember) of the Eocene La Meseta Formation (Seymour Island). A specimen housed at the University of California Museum of Paleontology (UCMP 321265) contains the posterior portion of the cranium, including much of the occipital, temporal, and interorbital regions (Ksepka and Bertelli 2006). A specimen from the University of Białystok IB/P/B-0346 is an incomplete and deformed “neurocranium” (Jadwiszczak 2006). A specimen from the División Paleontología de Vertebrados, Museo de La Plata, MLP 84-II-1-10, preserves part of the calvaria, occipital region, nuchal crests, temporal fossa, posterior end of the left *fossa glandulae nasalis* and some other part of the “neurocranium” (Acosta Hospitaleche and Haidr 2011). Other isolated cranial elements from Antarctica are represented by interorbital fragments (MLP 78-X-26-158 and MLP 92-II-2-250 in Haidr and Acosta Hospitaleche 2012; UCMP 321208 and UCMP 321223 in Ksepka and Bertelli 2006); a left quadrate (MLP 94-III-15-413 in Acosta Hospitaleche and Haidr 2011), and pieces of a penguin braincase and upper jaw (IB/P/B-0167 in Jadwiszczak 2006, 2011).

The purpose of this contribution is to provide a thorough comparative description of three new crania of extinct penguins. Two of them are the best preserved skulls attributable to Antarctic fossil penguins, offering a unique chance to further anatomical knowledge on these birds.

Material and methods

Three fossil penguin crania (MLP 12-I-20-1, MLP 12-I-20-2, and MLP 12-XI-1-1) here described were surface-collected during two consecutive summer field trips of the Geomarambio Group of the Instituto Antártico Argentino (IAA) and are housed at the Division Paleontología de Vertebrados (MLP), Museo de La Plata, La Plata, Argentina. The comparative material includes the following fossil skulls: *Waimanu* (CM zfa 33, data taken from Slack *et al.* 2006, and images kindly provided by David Penny); *Perudyptes devriesi* MUSM 889; *Icadyptes salasi* MUSM 897, and photographs generously taken by Rodolfo Salas Gismondi; *Paraptenodytes antarctica* cast MLP AMNH 3338 (Moreno and Mercerat 1891); *Madrynornis mirandus* MEF-PV 100 (Acosta Hospitaleche *et al.* 2007); Spheniscidae indet. MLG 3400; *Marplesornis novaezealandiae* (data taken from Marples 1960); *Spheniscus urbinai* MUSM 269, MUSM 401, MUSM 403 (Stucchi 2002); *Spheniscus megaramphus* MUSM 175, MUSM 362, MUSM 363 (Stucchi *et al.* 2003); *Pygoscelis calderensis* SGO-PV 790, SGO-PV 791, SGO-PV 792 (Acosta Hospitaleche *et al.* 2006); and the Antarctic specimens UCMP 321265 (Ksepka and Bertelli

2006), IB/P/B-0346 (Jadwiszczak 2006), and MLP 84-II-1-10 (Acosta Hospitaleche and Haidr 2011).

Anatomical nomenclature (Fig. 1) follows that of Baumel (1993). Measurements were taken using a 0.01 mm increment Vernier Caliper (Table 1).

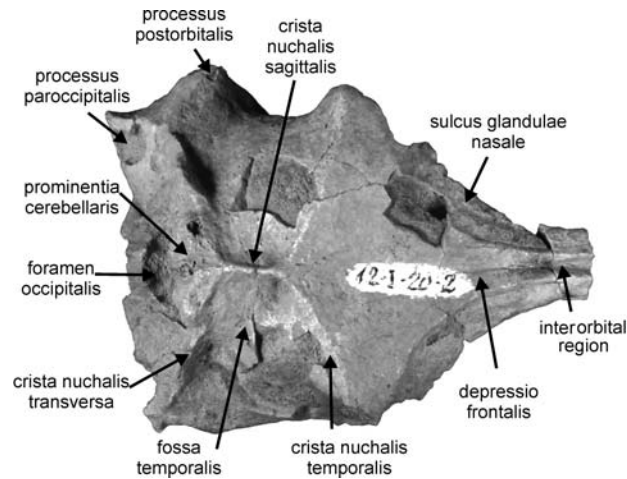


Fig. 1. Neurocranium; osteological terms used in comparative descriptions (after Baumel 1993).

Table 1
Measurements taken in the Antarctic crania studied herein.

	MLP 12-I-20-1	MLP 12-I-20-2	MLP 12-XI-1-1
Interorbital width (including the <i>sulcus glandulae nasalis</i>)	15	11.8	
Interorbital width (without the <i>sulcus glandulae nasalis</i>)	7.7	4.5	
Height from <i>lamina parasphenoidalis</i> to the roof	44.1	39	35.7
Width of the <i>condylus occipitalis</i>	13	–	
Height of the <i>condylus occipitalis</i>	6.8	–	
Width of <i>lamina parasphenoidalis</i>	33.4	30.5	29
Width of <i>ala parasphenoidalis</i>	4.3	–	
Length of <i>ala parasphenoidalis</i>	16	–	
Length of <i>crista n. sagittalis</i>	9.1	11.8	

Abbreviations. — MLP (División Paleontología de Vertebrados, Museo de La Plata, Argentina). MEF-PV 100 (Museo Paleontológico Egidio Feruglio, Trelew, Argentina). MLG 3400 (Museo del lago Gutiérrez Rosendo Pascual, San Carlos de Bariloche, Argentina). MUSM (Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad de San Marcos, Lima, Peru). SGO-PV (Sección Paleontología, Museo Nacional de Historia Natural, Santiago, Chile). UCMP (Canterbury Museum). UCPM (University of California, Museum of Paleontology, Berkeley, USA). IB/P/B (Institute of Biology, University of Białystok, Poland).

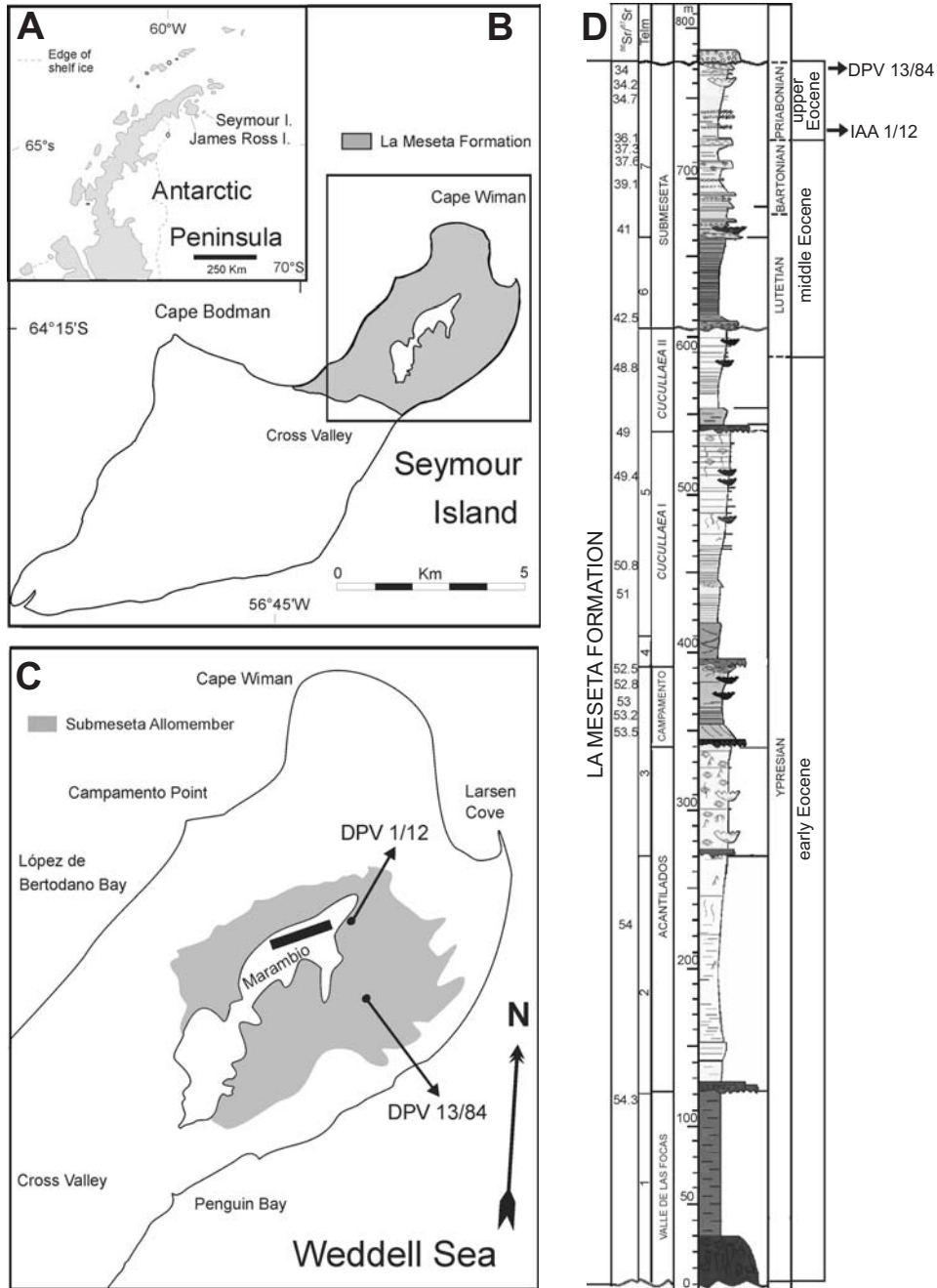


Fig. 2. **A.** Map showing the location of Antarctic Peninsula, Antarctica. **B.** Location of the La Meseta Formation in Seymour Island (= Marambio). **C.** Sketch map of the northern part of Seymour Island showing the distribution of the Submeseta Allomember and the fossil penguin-bearing localities in which the crania were found. Modified from Marenssi *et al.* (1998a). **D.** Stratigraphic section of the La Meseta Formation (modified from Reguero *et al.* 2013). Fossil localities are indicated.

Geological setting

The fossils presented here come from the La Meseta Formation, exposed along the slopes of the plateau of Seymour Island, James Ross Basin, Antarctic Peninsula (Fig. 2A–C). The La Meseta Formation (La Meseta Alloformation of Marensi *et al.* 1998a) is an unconformity-bounded unit (Elliot and Trautman 1982; Ivany *et al.* 2006) deposited between the early Eocene and probably the earliest Oligocene (Montes *et al.* 2010). This unit is approximately 720 meters thick and fills a 7 km wide valley cut down into older sedimentary rocks constituting the island; its current location is the product of regional uplift and tilting of the Paleocene and Marambio Group beds (Reguero *et al.* 2013).

The La Meseta Formation (Fig. 2D) includes mudstones and sandstones with interbedded conglomerates and is organized into six erosionally-based units (Marensi *et al.* 1998a). These are named, from the base to the top, Valle de Las Focas, Acantilados, Campamento, *Cucullaea* I, *Cucullaea* II and Submeseta Allomembers (Telm 1–7 according to Sadler 1988). The La Meseta Formation mostly comprises poorly consolidated siliclastic fine-grained sediments deposited in deltaic, estuarine and shallow marine environments as part of a tectonically-controlled incised valley system (Marensi 1995; Marensi *et al.* 1998b; Porębski 1995, 2000).

The fourteen species of fossil penguins have been described from this unit (Acosta Hospitaleche *et al.* 2013; see also Jadwiszczak 2006, who recognized ten species, and further remarks in Jadwiszczak 2008). These taxa are not necessarily coetaneous, but all occur in the late Eocene Submeseta Allomember.

The three fossil crania described herein were found within strata referred to the Submeseta Allomember. Specimens MLP 12-I-20-1 and the MLP 12-XI-1-1 come from locality DPV 13/84 (at the bottom of level 38, Sergio Santillana, personal commun.). This is an important site from where a very complete skeleton of *Palaeudyptes klekowskii* Myrcha, Tatur and del Valle 1990, was recovered (Acosta Hospitaleche 2013). Specimen MLP 12-I-20-2 was collected at IAA 1/12 (at the top of the level 38 following Sergio Santillana, personal communication), not far from locality DPV 13/84.

Systematic paleontology

Aves

Order Sphenisciformes Sharpe, 1891

Family Spheniscidae Bonaparte, 1831

(Figs 3–5)

Material. — MLP 12-I-20-1, the partial cranium missing part of the rostrum, preserving the almost completely *sulcus glandulae nasale*, the interorbital region, the complete *calvaria*, both *fossae temporalia*, the almost complete *cristae nuchalis* (the end of the *crista nuchalis temporalis* is missing), the most cranial

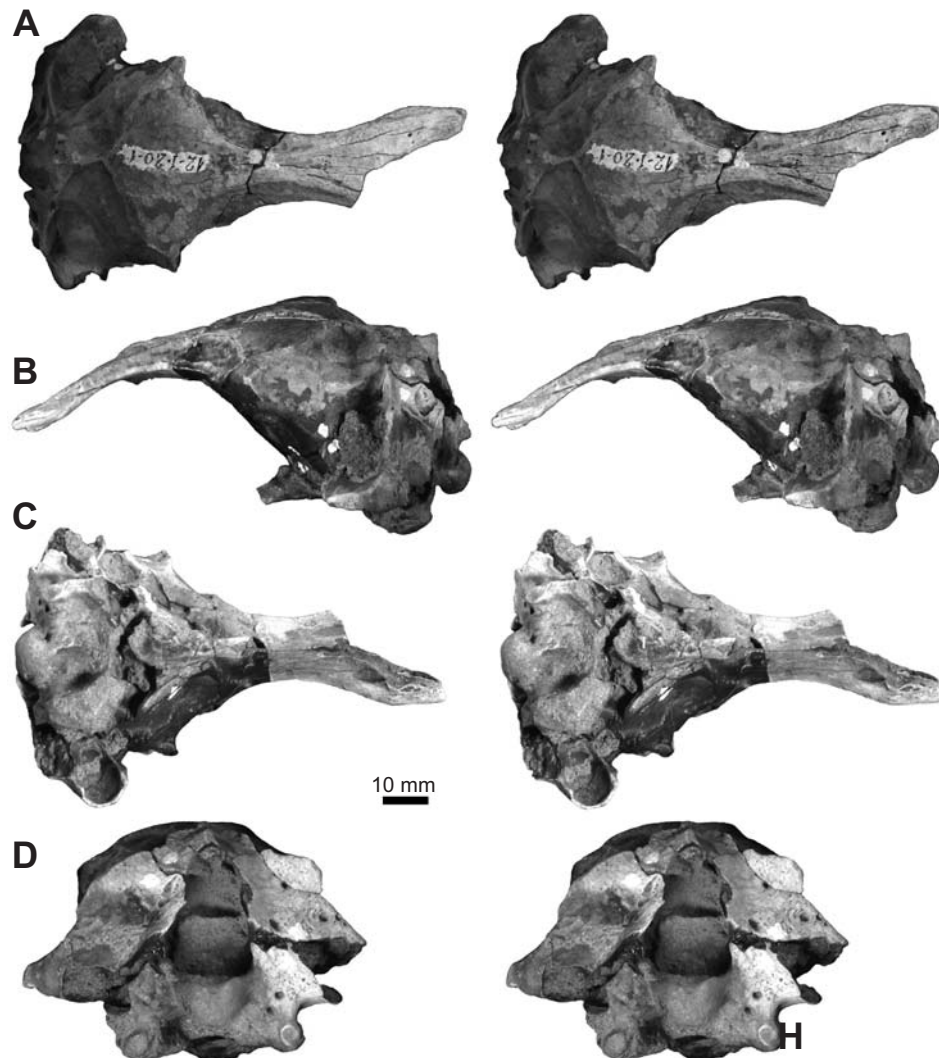


Fig. 3. Penguin skull MLP 12-I-20-1. Stereoscopic photographs in dorsal (A), lateral (B), palatal (C) and occipital (D) views.

part of the *prominentia cerebellaris*, the *condylus occipitalis*, part of the *processus paroccipitalis* and the *processus postorbitalis*, the whole *lamina parasphenoidalis* and the basal part of the *rostrum parasphenoidalis* (Fig. 3).

MLP 12-I-20-2, the partial cranium missing the rostrum and preserving the posterior half of the interorbital region, the *sulcus glandulae nasale*, the complete *calvaria*, both *fossae temporalia*, the *cristae nuchalis* (missing the end of the *crista nuchalis temporalis*), the part of the occipital region, including the *foramen occipitalis*, and the *processus postorbitalis* and the *processus paroccipitalis* broken (Fig. 4).

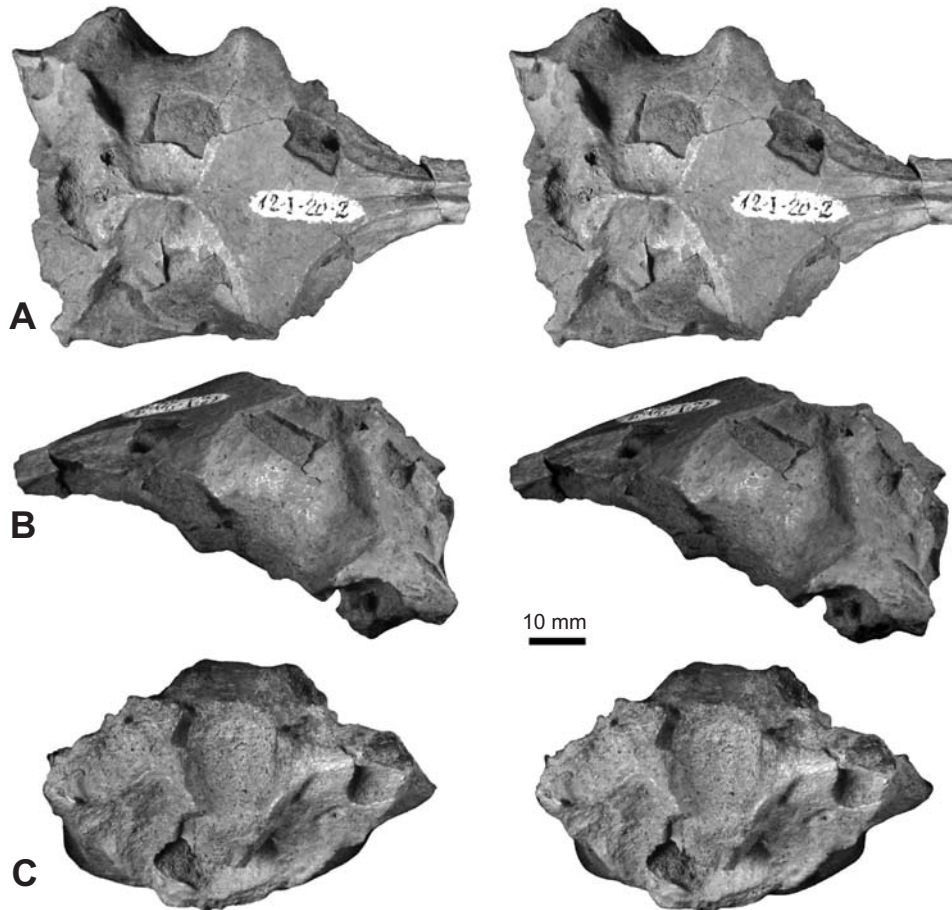


Fig. 4. Penguin skull MLP 12-I-20-2. Stereoscopic photographs in dorsal (A), lateral (B) and occipital (C) views.

MLP 12-XI-1-1, the partial roof of the cranium compressed dorsoventrally due to deformation, preserving the part of the occipital region and the *processus paroccipitalis*; the remaining part is represented by a slightly damaged natural endocast (Fig. 5).

Measurements. — See Table 1.

Locality. — DPV 13/84 (MLP 12-I-20-1 and 12-XI-1-1), IAA 1/12 (MLP 12-I-20-2); level 38 within the Submeseta Allomember (late Eocene), La Meseta Formation, Seymour Island (Antarctic Peninsula).

Comparative description. — Specimens MLP 12-I-20-1 and MLP 12-XI-1-1 are medium-sized, slightly larger than the extant *Pygoscelis papua* (Gentoo Penguin), whereas MLP 12-I-20-2 is larger compared to the largest modern penguins, such as *Aptenodytes forsteri* or the Emperor Penguin (Table 1). MLP 12-I-20-2 is similar to MLP 84-II-1-10, UCPM 321265 and IB/P/B-0346. The latter resembles

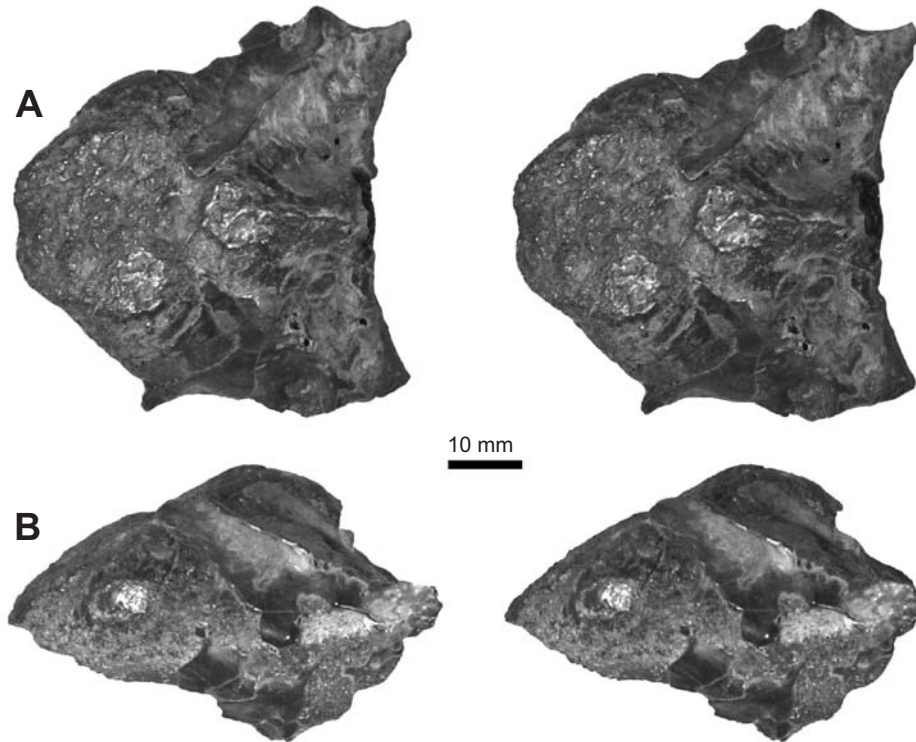


Fig. 5. Penguin skull MLP 12-XI-1-1 in dorsal (A) and lateral (B) views.

the “neurocranium” of the extant *Aptenodytes* (albeit is larger). These crania are more globose than those of *Icadyptes*, *Perudyptes*, and *Inkayacu* from the Eocene of South America, which are extremely elongated. Unfortunately, the actual shape of the Antarctic specimen UCMP 321265 cannot be used for comparison because of the high post-mortem compression it underwent.

The roof of the skull is relatively narrow in MLP 12-I-20-1 and MLP 12-I-20-2 (poorly preserved in MLP 12-XI-1-1) and similar to that in specimens attributable to fossil species of *Spheniscus* (UCMP 321265 and MLP 84-II-1-10). On the other hand, the roof in the Peruvian Eocene species of *Waimanu* (from the Paleocene of New Zealand, see Slack *et al.* 2006) is very slender, with large emarginations along the orbital and postorbital regions.

The *depressio frontalis* is conspicuously developed along the roof of MLP 12-I-20-2, at the caudal part of the skull and also at the interorbital region. This depression is slightly marked at the anterior end of the *crista nuchalis sagittalis* in MLP 12-I-20-1.

The *sulcus glandulae nasale* is well developed in MLP 12-I-20-1 and MLP 12-I-20-2, in comparison with specimen UCMP 321265, where its counterparts are very poorly marked. The sulci (left and right) become narrower toward the anterior

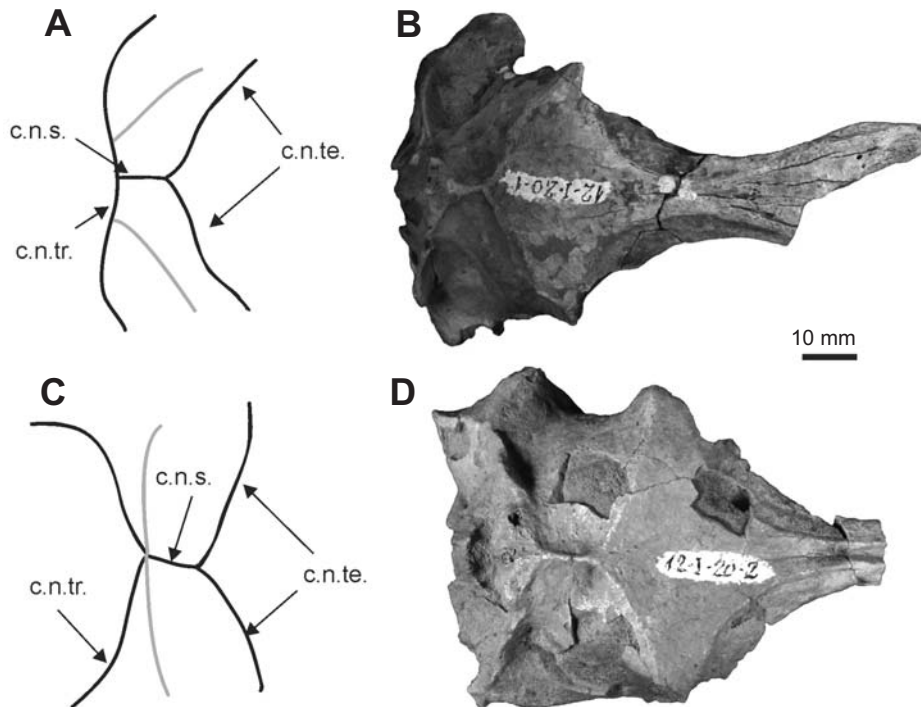


Fig. 6. Cranial crista configurations in: MLP 12-I-20-1 (A, B) and MLP 12-I-20-2 (C, D). C.n.tr.: *crista nuchalis transversa*, c.n.s.: *crista nuchalis sagittalis*, c.n.t. *crista nuchalis temporalis*.

end and leave in between them a small interorbital rod-like area constituted by the frontals. The absence of the supraorbital edge in the crania here examined is a feature shared with *Parapterodytes*, *Icadyptes*, *Perudyptes*, *Inkayacu*, and *Waimanu* among the fossil species, and *Spheniscus* among the living genera.

The *cristae nuchalis* are strongly developed in MLP 12-I-20-1 and MLP 12-I-20-2, but not so much as in the Peruvian Eocene species of *Perudyptes* and *Inkayacu*, whereas MLP 12-XI-1-1 exhibits a weaker *crista nuchalis sagittalis* (although it may have resulted from post-mortem deformation). The three crania are similar regarding the nuchal crest configuration, although some features suggest they may have belonged to different species (Fig. 6). For example, in MLP 12-I-20-2, the *crista nuchalis temporalis* is concave with respect to the *fossa temporalis*, as in MLP 84-II-1-10, whereas it is convex in MLP 12-I-20-1, *Icadyptes*, *Perudyptes*, and *Inkayacu*. In MLP 12-XI-1-1 the *cristae* configuration is deformed and poorly preserved.

The *crista nuchalis transversa* in all these specimens is almost straight and perpendicular to the *crista nuchalis sagittalis*. However, slight differences have been noticed here. In MLP 12-I-20-2, MLP 84-II-1-10, and UCMP 321265 it is slightly convex respect of the *fossa temporalis*. Contrarily, in MLP 12-I-20-1 it is concave, slightly more than in the three Peruvian Eocene species.

Beyond its curvature, the *crista nuchalis temporalis* is near perpendicular to the *crista nuchalis sagittalis* in the Antarctic specimens, forming a sharp crest, like in *Marplesornis novaezealandiae*, *Parapterodytes antarcticus*, *Spheniscus urbinai*, and *Spheniscus megaramphus*. In most penguins this crest is curved toward the anterior region.

The *crista nuchalis sagittalis* connecting the *cristae nuchalis temporalis* and the *cristae nuchalis transversa* is present in the three crania described herein and skulls of other Eocene penguins compared above, but is not developed in *Waimanu*. The peculiarity observed in specimen MLP 12-I-20-1 is its extension over the *prominentia cerebellaris*, at least at the anteriormost preserved part. The MLP 12-XI-1-1 is represented almost entirely by a natural endocast. For that reason, the *cristae nuchalis* are not preserved, and anatomical details are hard to distinguish.

In the three skulls here studied the *fossa temporalis* deeply incises the roof, like in UCMP 321265, IB/P/B-0346, and MLP 84-II-1-10, *Parapterodytes*, and *Perudyptes*. Its dorsal end is wide and quadrangular in the Antarctic specimens, whereas is sharp in *Spheniscus* (both extinct and extant species). In majority of modern species the dorsal end of the *fossa temporalis* is triangular and it does not reach the *crista nuchalis sagittalis*. Each fossa reaches its counterpart at the *crista nuchalis sagittalis*, like in all the Antarctic crania, becoming deeper at the posterior end, like in *Spheniscus* (fossil representatives), *Perudyptes*, *Waimanu* and *Parapterodytes*, whereas in *Pygoscelis*, *Aptenodytes*, and *Madrynornis* the fossa is notably shallower.

The posterior wall closes the fossa, projecting the *crista nuchalis transversa* into wings, like in both modern species of *Spheniscus* and the Eocene specimens. Two areas are defined in the *fossa temporalis*, the posteriormost being deeper than the anterior part (Fig. 6). Boundaries between these two parts are poorly marked, but in specimen MLP 12-I-20-2 the anterior limit is convex, whereas in MLP 12-I-20-1 it is concave. In specimen MLP 12-XI-1-1 this feature is not preserved. In MLP 84-II-1-10 the *fossa temporalis* does not show different parts and, unfortunately, it cannot be observed in specimens UCMP 321265 and IB/P/B-0346 because of their poor preservation.

The *processus postorbitalis* appears to be short in specimen MLP 12-I-20-1 (although it is not complete) in comparison with those in *Perudyptes*, *Icadyptes* and, especially, *Inkayacu*, in which they are particularly slender and long. There is an emargination between them and the *sulcus glandulae nasale* in MLP 12-I-20-1. In specimens MLP 12-I-20-2 and MLP 12-XI-1-1 they are broken.

The *squamosus* is flabelliform in MLP 12-I-20-1; the surface is concave and leaning posteriorly. It extends laterally, ending in a sharp *processus zygomaticus*. The *prominentia cerebellaris* is broken in the three crania here studied, preserving just a little part in each one. In MLP 12-I-20-1 the dorsal part is preserved, showing the extension of the *crista nuchalis sagittalis* over it. The outline of the *foramen occipitalis* is not preserved, although it seems narrow at the dorsal half. In specimen MLP 12-I-20-2 the *foramen occipitalis* is oval in shape, like in IB/P/B-0346.

The occipital region is trapezoidal in specimens MLP 12-I-20-1, MLP 12-I-20-2 and MLP 12-XI-1-1, as in MLP 84-II-1-10 and *Paraptenodytes*, while it is more quadrangular in the modern species and *Madrynornis*. Specimens IB/P/B-0346 and UCMP 321265 are poorly preserved in this area. In MLP 12-I-20-2 the occipital area is wider than in MLP 12-I-20-1 at the level of the *prominentia cerebellaris* and the *foramen occipitalis*. The *foramen vena occipitalis externa* is not extended as a sulcus in specimen MLP 12-I-20-1. More laterally – and at the same vertical level as the latter – opens the *foramen rami occipital arteriae ophtalmica*. Another opening, likely a vein foramen, is located dorsally to the one described before and probably corresponds to the dorsal head vein or the rostral middle cerebral vein. This foramen is not present in modern penguin crania (Fig. 7).

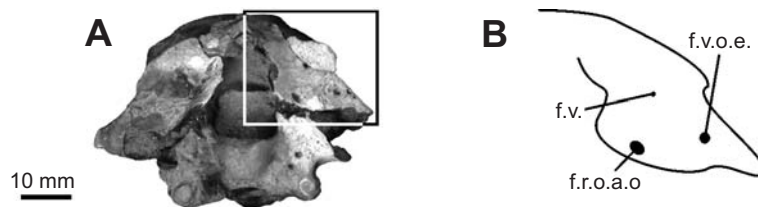


Fig. 7. Details of the cranial foramina in occipital view: **A.** MLP 12-I-20-1. **B.** Schematic detail of the sector pointed by the square: f.r.o.a.o. – *foramen rami occipitalis arteriae ophtalmica*, f.v. – *foramen vein*, f.v.o.e. – *foramen vena occipitalis externa*.

The *condylus occipitalis* is larger and stronger than that of specimen UCMP 321265, suggesting that MLP 12-I-20-1 belonged to a robust bird. It is reniform and ventrodorsally compressed, with the *incisura mediana condyli* well-marked, whereas it is rounded in MLP 84-II-1-10, the Miocene species, the extant *Pygoscelis adeliae*, *P. papua* and *Eudyptes*. In *Spheniscus* and *Aptenodytes* it is oblong.

The *condylus occipitalis* extends further ventrally to the *lamina parasphenoidalis* in specimen MLP 12-I-20-1, like in MLP 84-II-1-10 and UCMP 321265. The *fossa subcondylaris* is well defined in MLP 12-I-20-1, similar to that of MLP 84-II-1-10, but deeper than in *Paraptenodytes antarcticus* and even more so than in specimen UCMP 321265.

In specimens MLP 12-I-20-1 and MLP 12-I-20-2 the *processus paroccipitalis* is ventrally projected (the end is broken in bones) beyond the *condylus occipitalis*, whereas bifid processes are produced both ventro-laterally and posteriorly in IB/P/B-0346.

The laterosphenoid is well ossified in specimen MLP 12-I-20-1, and a small part of the mesethmoid is preserved. The *lamina parasphenoidalis* is deeply concave in MLP 12-I-20-1 and projects anteriorly through the well-developed *rostrum parasphenoidale*. Worth noting is development of strong *alae parasphenoidalia*, which are anteroposteriorly enlarged, like in specimen MLP 84-II-1-10. They are strikingly weaker in extant and Miocene penguins.

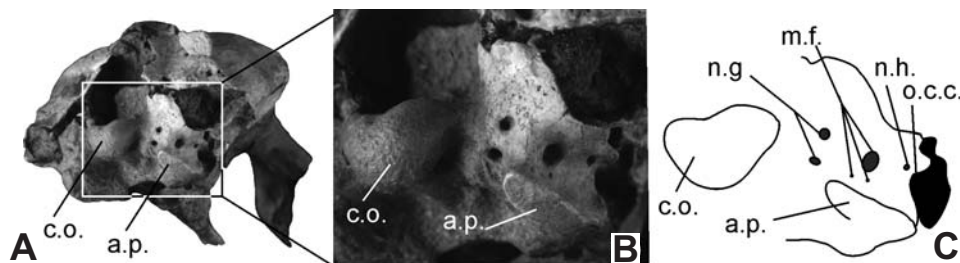


Fig. 8. Details of the cranial foramina at the base of the skull: **A.** MLP 12-I-20-1 in occipito-ventro-lateral view. **B.** Close up of the sector pointed by the square. **C.** Schematic detail: a.p. – *ala parasphenoidalis*, c.o. – *condylus occipitalis*, m.f. – metotic foramen, n.g. – *nervi glossopharyngeus*, n.h. – *nervi hypoglossus*, o.c.c.: *ostium canali carotici*.

Specimen MLP 12-I-20-1 shows two posteroventrally located large foramina for passage of the *nervi glossopharyngeus* (XII), opening medially to the *ala parasphenoidalis*. Besides and lateral to the *ala parasphenoidalis* – in MLP 12-I-20-1 – open two additional large foramina. The caudalmost one, besides two other small foramina barely perceptible, is the metotic foramen for passage of the *nervi vagus* (X), *nervi accesorius spinalis* (XI) and the *vena jugularis externa*; the other one is the foramen for *nervi hypoglossus* (IX) that in penguins opens separately (Fig. 8). In specimens MLP 12-I-20-1 and UCMP 321265 a small portion of the *tuba auditiva communis* is preserved.

Taxonomic remarks. — It is ironic that although crania are the most informative element in avian systematics, it is still not possible to assign them to definite species or even genera. For many years, the fossil representatives have been represented exclusively by appendicular elements, and consequently the significant systematic features in penguins have been established on the basis of tarso-metatarsal characters. The situation is changing nowadays; several species have been diagnosed based on more complete skeletons (Slack *et al.* 2006; Acosta Hospitaleche *et al.* 2007; Clarke *et al.* 2007, 2010; Göhlich 2007) and, in a few cases, crania (Stucchi 2002; Stucchi *et al.* 2003; Acosta Hospitaleche *et al.* 2006).

Interpretations and discussion

The *depressio frontalis* seems to be more related to the development of the suture between both halves of the skull than to muscle attachment (see Baumel 1993).

The strong *alae parasphenoidalia* observed in specimen MLP 12-I-20-1 that serve as insertion of cervical muscles, principally the *M. rectus capitis dorsalis*, and were also observed in other fossil and extant birds (*e.g. Morus, Hesperornis*), indicate the development of long skulls (see Baumel 1993).

The *sulcus glandulae nasale* accommodates the *glandula nasalis* that secretes the salt consumed with the food. Nevertheless, the size and structure of the sulcus is

not necessarily related to the development of the nasal gland (a detailed study in birds, including Spheniscidae can be consulted in Ibáñez *et al.* 2010 and literature cited therein). Moreover, the gland is ecologically sensitive to abrupt changes, while the sulcus is more conservative in its structure (see for example Cornelius 1982; and Woodin *et al.* 2008 for a discussion about variation in size of the salt gland). However, the absence of a supraorbital edge is in some way related to piscivorous habits, at least in extant penguin species (*e.g.* species of *Spheniscus*, *Aptenodytes*; Williams 1995) in which ecological and biological data were studied for comparison. Regarding fossil species, recent studies suggest that *Paraptenodytes* (in which the supraorbital edge is not developed, among other cranial features) would be also a specialist fish-eating penguin (Haidr and Acosta Hospitaleche 2013).

The presence of a strong *crista nuchalis sagittalis* is a character usually used in vertebrates for the inference of dietary preferences. This crest provides attachment for the sheet of deep fascia separating both sides (left and right) of dorsal neck muscles (a stronger insertion is shown in specimen MLP 12-I-20-2, where this crest surmounts the *prominentia cerebellaris*). The presence of the *crista nuchalis sagittalis* indicates a piscivorous habit in seabirds. The *crista nuchalis transversa* also serves for insertion of neck musculature.

The deeply excavated *fossa temporalis* dorsally reaching the median plane of the skull indicates the location of powerful jaw muscles inside. It is consequent with the degree of development of the *cristae nuchalis* and the *sulcus glandulae nasale* and the derived implications regarding dietary preferences.

Conclusion

Even though the material here described cannot be taxonomically identified beyond family level, it is very important in the context of avian studies. These skulls constitute the best preserved neurocranial remains from Antarctica, allowing a comparative description of characters not observed so far. Specimen MLP 12-XI-1-1 is slightly damaged, and the post mortem deformation renders it uninformative in terms of anatomy. However, the configuration of the *fossa temporalis*, the *eminentia cerebellaris* and the *processus paroccipitalis* allow its assignment to Sphenisciformes. From the detailed comparison with the available skulls, including those from Neogene and Paleogene species, the following observations can be noted:

1. All the Eocene skulls known so far have strong *cristae nuchalis* projected as sharp ridges or wings (*Icadyptes*, *Perudyptes*, *Inkayacu*, specimens UCMP 321265, MLP 84-II-1-10, MLP 12-I-20-1, and MLP 12-I-20-2). However, this cranial configuration is not exclusive of Paleogene taxa and can be found, for instance, in the Miocene and modern species of *Spheniscus*.
2. Even developing the same general pattern of cranial *cristae* configuration (see above), differences in the concavity and convexity of the *crista nuchalis*

transversa and the *cristae nuchalis temporalis* were observed among different Eocene penguin species.

3. The deeply excavated *fossa temporalis* contacting the counterpart at the *crista nuchalis sagittalis* was a common cranial pattern – if not the only configuration – present in Eocene penguins.

4. The supraorbital edge closing the lateral side of the *sulcus glandulae nasalis* was not developed in any of the Paleogene species compared, and was known to occur only since the Miocene. Neogene skulls show different cranial configurations: *Pygoscelis calderensis* (Acosta Hospitaleche *et al.* 2006) and *Madrynornis mirandus* (Acosta Hospitaleche *et al.* 2007) have *sulcus glandulae nasalis* laterally closed by a supraporbital edge. On the contrary, the Patagonian skull MLG 3400 (Acosta Hospitaleche 2011) and the fossil species of *Spheniscus* (Stucchi 2002; Stucchi *et al.* 2003) do not have this edge. Doubtlessly, it is an anatomical feature intrinsic to each species, and not dependent on taphonomic issues. The occurrence of the second pattern, associated with a crustacivorous diet (see also Ksepka and Ando 2011) could have been related to different ecological conditions developed in the Miocene, probably occasioned by paleogeographical events such as the opening of the Drake Passage and the establishment of the Antarctic Circumpolar Current.

The new anatomical data are important for functional morphology studies such as muscular reconstruction, estimation of bite-strength, inference of dietary preferences, and mandibular mechanics. Eocene remains discussed here highlight the first appearance of several adaptive features in Eocene penguins, so far reported only for Miocene crania and widespread in living species.

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