Penguin cranial remains from the Eocene La Meseta Formation, Isla Marambio (Seymour Island), Antarctic Peninsula

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Abstract: Widely accepted ideas about trophic preferences of early penguins suggest that all Eocene sphenisciforms were piscivorous. However, recent findings from the La Meseta Formation (Eocene) of Antarctica, support the presence of at least two different morphotypes that may have evolved as a niche partitioning strategy, which is consistent with the high diversity recorded. The first of them corresponds to a medium–large sized penguin, resembling the Neogene species in configuration. Another morphotype is represented by extremely large penguins with very long and slender bills, clearly linked to fish catching habits.

Introduction

The La Meseta Formation (Eocene), Antarctic Peninsula, is a highly fossiliferous unit in terms of the quantity and diversity of remains. The invertebrate taxa include bivalves, gastropods (Stilwell & Zinsmeister 1992, Bitner 1996), bryozoan colonies (Hara 2001), crinoids (Rasmussen 1979, Baumiller & Gaździcki 1996), ophiuroids (Aronson *et al.* 1997, Blake & Aronson 1998), and echinoids (McKinney *et al.* 1988). Within the vertebrates, fishes (Jerzmańska 1988, Jerzmańska & Świdnicki 1992), whales (Wiman 1905, Borsuk-Białynicka 1988, Fordyce 1989), a sparnotheriodontid mammal (Vizcaino *et al.* 1997), a ratite bird (Tambussi *et al.* 1994) and penguins (Myrcha *et al.* 2002, Jadwiszczak 2006a, Hospitaleche & Reguero 2010 and references cited therein) have been described.

Penguins (Aves, Sphenisciformes) are particularly abundant in this unit. Even though knowledge of this group has increased greatly in the past few years, there are still many unanswered questions, especially regarding penguin anatomy and functional morphology. Due to the fact that the systematics of Sphenisciformes relies on the morphology and proportions of the tarsometatarsi, and sometimes humeri, few Antarctic studies have been performed regarding other skeletal elements. Only in a few cases elements other than the tarsometatarsi and humeri have been described (Hospitaleche & Reguero 2010), and analysed in detail (Hospitaleche & Di Carlo 2010, see also Jadwiszczak 2006a, 2006b).

The first Antarctic penguin skull to be described was a very fragmentary bill assigned by Olson (1985) to ?*Palaeeudyptes* sp. Other isolated remains including cranial elements have been described (Myrcha *et al.* 1990) and more recently re-studied (Jadwiszczak 2003, 2006a).

Additional remains from the Submeseta Allomember were described and treated as problematic specimens (Jadwiszczak 2006a) due to their poor preservation and lack of comparable material. In spite of this, Jadwiszczak's valuable contribution has provided the basis for advancing the knowledge of morphological aspects that might be useful in systematic and palaeobiological studies. According to their general morphology and size, some of these remains have been assigned to *Palaeeudyptes gunnari* (Wiman, 1905) (Jadwiszczak 2006a), although previous studies assigned them to *Anthropornis* sp. or *Palaeeudyptes* sp. Jadwiszczak (2000, 2003) and to ?*Palaeeudyptes* sp., probably *P. klekowskii* Myrcha, Tatur & del Valle, 1990 (Jadwiszczak 2006a, see also Myrcha *et al.* 1990). Other specimens studied by Jadwiszczak (2006a) were assigned to *P. gunnari* or *Archaeospheniscus wimani* (Marples, 1953) or were too fragmentary for identification according to Jadwiszczak (2006a). Only one of them corresponds to an incomplete and deformed neurocranium and constitutes until today the only reference to a Palaeogene Antarctic cranium (Jadwiszczak 2006a). All of them come from the Submeseta Allomember.

More recently, new findings from La Meseta Formation were described and at least three species were identified on the basis of size differences (Ksepka & Bertelli 2006), although the fragmentary state of the material does not allow their systematic assignment.

The above seems to indicate that the preservation of craniums and mandibles is improbable. They are easily destroyed and only small fragments can be recovered from the sediments.

In this context of patchy information, even minor skull characteristics that can be detected will be useful for: 1) increasing the knowledge of the anatomy of penguin
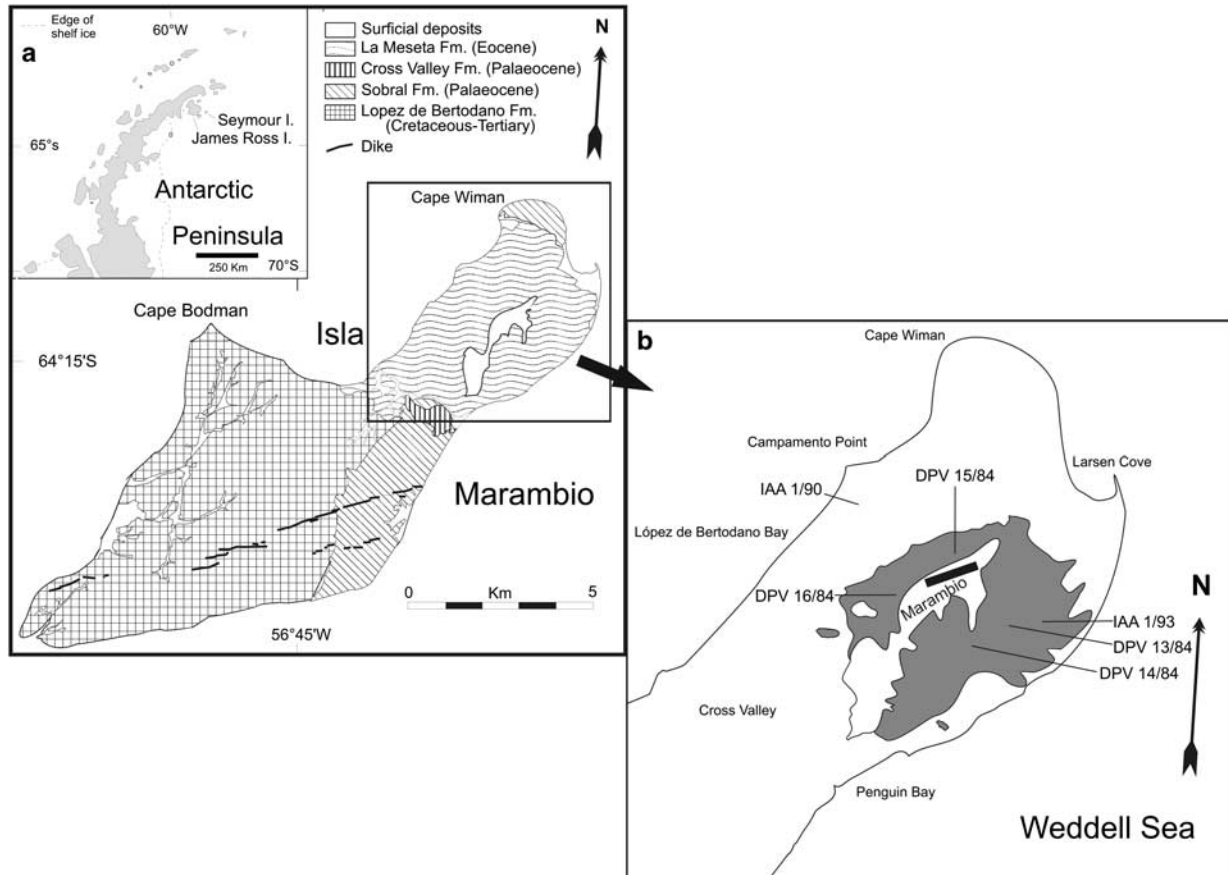
Fig. 1. a. Map showing the location of Isla Marambio (Seymour Island), Antarctic Peninsula. **b.** Sketch map of the northern part of Isla Marambio showing the distribution of the Submeseta Allomember and the fossil penguin bearing localities cited in the text.

skulls, in particular of Sphenisciformes from Antarctica, 2) elucidating, as much as the material allows and within the limitations imposed by its preservation state, their trophic habits, and 3) analysing the faunal changes detectable from the specimens studied here.

In the present contribution, several cranial and mandibular penguin remains from La Meseta Formation (Eocene) of the Antarctic Peninsula are studied, including the oldest penguin neurocranium from Antarctica. A comparative description including modern and fossil species is given in order to identify the presence of different morphotypes in this penguin assemblage.

Abbreviations

DPV (División Paleontología Vertebrados del Museo de La Plata, Argentina), IAA (Instituto Antártico Argentino), MEF-PV (Museo Paleontológico Egidio Feruglio, Argentina), MLP (Museo de La Plata, Argentina), RNP (Rae Natalie Prosser, The R. Natalie P. Goodall Foundation, Argentina), RV (University of California at Riverside, USA), UCPM (University of California Museum of Paleontology, USA).

Geological and geographical setting

The La Meseta Formation (Rinaldi et al. 1978, Elliot & Trautman 1982, Marenssi et al. 1998a) crops out on Isla Marambio (Seymour Island) and Cockburn Island, close to the northern tip of the Antarctic Peninsula (Fig. 1). This unit has been assigned to the Eocene and is composed of sandstones and mudstones with interbedded shell rich conglomerates, organized into six erosionally based internal units. They are from base to top: Valle de Las Focas, Acantilados, Campamento, *Cucullaea* I, *Cucullaea* II and Submeseta Allomembers (Telms 1–7 according to Sadler 1988). These units were deposited during the Eocene in deltaic, estuarine and shallow marine settings, mostly within a NW–SE trending valley (Marenssi et al. 1998a, 1998b).

In particular, penguins are one of the most abundant groups, represented throughout the sequence by 14 species (Tambussi et al. 2006, see also Jadwiszczak 2006a). The oldest penguin from La Meseta Formation appears in the Valle de las Focas Allomember or the Acantilados Allomember (Telm 1-2 according to Jadwiszczak 2006b) and is represented by an indeterminate genus and species. One species was collected in the Campamento Allomember,
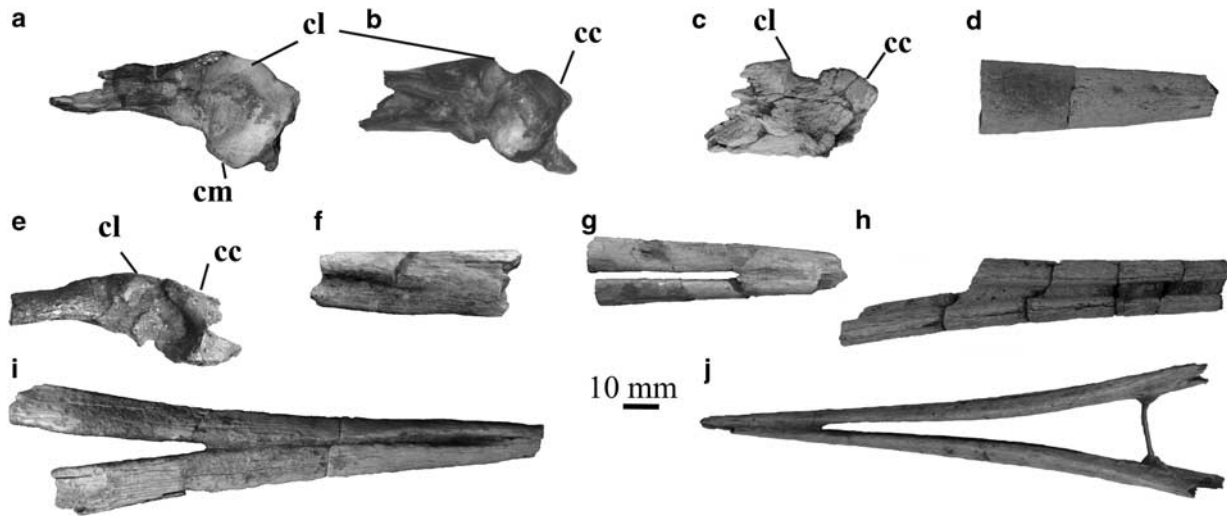
Fig. 2. **a.** Dorsal view of articular region (MLP 96-I-6-48). **b.** Dorsal view of articular region (MLP 92-II-2-115a). **c.** Dorsal view of articular region (MLP 91-II-4-223). **d.** Lateral view of symphysis (MLP 96-I-6-48). **e.** Dorsal view of articular region (MLP 92-II-2-108). **f.** Medial view of right *ramus mandibularis* (MLP 78-X-26-143). **g.** Ventral view of fragmentary mandible (MLP 78-X-26-144). **h.** Dorsal view of *rami mandibularis* (MLP 92-II-2-195). **i.** Ventral view of *rami mandibulae* (MLP 91-II-4-221). **j.** Dorsal view of *rami mandibulae* (MLP 78-X-26-2). cl = *cotyla lateralis*, cm = *cotyla medialis*, cc = *cotyla caudalis*. Scale bar = 10 mm.

whereas the diversity increases in the highest levels of the formation. At least eight species are known from the *Cucullaea* I Allomember, six species from *Cucullaea* II, and in the Submeseta Allomember, at the top of the sequence, 14 species are present (see however Jadwiszczak 2006a, 2006b, 2008, 2010).

Twelve facies were described by Marenssi *et al*. (1998a), three of which are present in the La Meseta Formation. Facies Association I extends from the Valle de Las Focas, through the Acantilados and Campamento allomembers. The Formation represents valley-confined deposition in progradational/agradational tide dominated and wave influenced delta front/delta plain environments at the beginning of the infill of the incised valley. Energy increased as the delta built up to sea level. The incision of third order surfaces in the upper part of the Acantilados Allomember indicates the change from a wave reworked delta front to a tide dominated delta plain environment. Only a few fragments of penguin bills have been described from these levels (Jadwiszczak 2006b).

Facies Association II is the intermediate element, and includes the *Cucullaea* I, *Cucullaea* II and the lower part of the Submeseta Allomembers. A diverse and abundant macrofauna has been found here, corresponding to a valley confined estuary mouth to inner estuary complex. Tidal channels and mixed flats, tidal inlets and deltas, and washover and beach environments represent the interfingering of high and low energy environments (Marenssi *et al*. 1998a). Within the vertebrates, several penguin remains including MLP 96-I-6-48, MLP 92-II-2-115a, MLP 92-II-2-108, MLP 92-II-2-250 and MLP 92-II-2-203 of the material here described, come from this facies.

The uppermost Facies Association III is characterized by a more uniform sandy lithology that represents non-confined tide and storm influenced nearshore environments. A sea level rise is suggested on the top of the Submeseta Allomember. Thin shell beds, gravel beds and clay levels are intercalated (Marenssi *et al*. 1998a). Most of the remains described in this contribution, including the neurocranium, come from this level.

Systematic palaeontology

Aves
Sphenisciformes
Fig. 2

Material: MLP 96-I-6-48 (several fragments of a mandible, Fig. 2a–d).

Provenance: *Cucullaea* I Allomember (Telm 5).

Locality: IAA 1/90.

Description: The anterior end of the *pars symphysialis* is broken. Its ventral surface is straighter than in living species. The height of the *rami mandibulae* increases in anterior–posterior direction. Although the material is fragmentary and lacks most of the *ramus mandibularis*, the symphysis shows latero-medial compression as opposed to 91-II-4-221 and 78-X-26-2 (mentioned below), both of which show a stronger curvature on the lateral side.

The articular region is narrower cranio-caudally than in living penguins. Its *processus mandibularis medialis*

Table I. Measurements (mm) taken on the *fossa articularis quadratica* of the materials under study and the comparison specimens.

Specimen	Species	Length (L)	Width (W)	Index (L/W)
MUSM 175	*Spheniscus humboldti*	0.811	1.643	0.493
MLP 873	*Spheniscus magellanicus*	0.9	1.16	0.775
RNP A-1836	*Pygoscelis adeliae*	0.76	1.17	0.649
RNP A-767	*Pygoscelis adeliae*	0.77	1.12	0.687
RNP A-1652	*Pygoscelis adeliae*	0.77	1.06	0.726
MLP 38	*Pygoscelis papua*	0.69	1	0.69
MLP 464	*Pygoscelis adeliae*	0.72	0.96	0.75
RNP A-426	*Pygoscelis antarctica*	0.76	1.08	0.703
RNP A-425	*Pygoscelis antarctica*	0.67	0.92	0.728
RNP A-414	*Pygoscelis antarctica*	0.71	1.04	0.682
RNP A-532	*Pygoscelis antarctica*	0.87	1.11	0.783
RNP A-766	*Pygoscelis antarctica*	0.84	1.03	0.815
RNP A-420	*Pygoscelis antarctica*	0.92	1.12	0.821
RNP A-1875	*Pygoscelis antarctica*	0.76	0.91	0.835
RNP A-531	*Pygoscelis antarctica*	0.99	1.09	0.908
RNP A-806	*Pygoscelis papua*	1.08	1.12	0.964
RNP A-2023	*Aptenodytes patagonicus*	1.16	1.27	0.913
RNP A-2024	*Aptenodytes patagonicus*	1.03	1.12	0.919
RNP A-2019	*Aptenodytes patagonicus*	1.24	1.28	0.968
RNP A-2021	*Aptenodytes patagonicus*	1.15	1.14	1.008
Cast AMNH 3338	*Paraptenodytes*	1.8	2	0.9
MEF-PV 100	*Madrynornis mirandus*	0.88	1.33	0.661
MLP 96-I-6-48	Fossil under study	2.04	2.6	0.784
MLP 92-II-2-108	Fossil under study	1.83	1.97	0.928
MLP 92-II-2-115a	Fossil under study	1.98	2.07	0.956

extends posteriorly; its end is slightly damaged, only the tip of the process is broken. The margin of the *cotyla medialis* is sub-quadrangular and extends further medially, more than in UCMP 321057 described by Ksepka & Bertelli (2006). The *tuberculum pseudotemporale* is well developed as in those described by Ksepka & Bertelli (2006), and sharper than in modern taxa (also developed in Ksepka & Bertelli 2006). The *crista transversa fossa* is elevated and sharp, similar to that of *Spheniscus magellanicus* (Forster, 1781) and *Pygoscelis*, whereas in *Eudyptes chrysocome* (Forster, 1781) this crest is less pronounced. The *processus retroarticularis* seems not to be developed, although the material is badly damaged in this region. The *cotyla caudalis* and the *cotyla lateralis* are merged, whereas they are separated by a crest in modern penguins. They form a fossa deeper than in the modern penguins. The attachments of the *membrana postmeatica* and *ligamentum occipitomandibulare* form a rounded tubercle as in modern species. A well-marked *sulcus intercotylaris*, deeper than in modern and Miocene species, occurs between the *cotyla lateralis* and the *cotyla medialis*. The *fossa articularis quadratica* has no distinguishing features. The posterior end of the *fossa aditus canalis mandibulae* is more rounded than in living and Miocene species.

The articular region is similar in shape to *Paraptenodytes antarcticus* (Moreno & Mercerat, 1891). The proportion of the articular surface (length from beginning of *processus lateralis* to end of *processus caudalis* if possible or to the most caudal end of the *processus lateralis*/width from the most medial point of the *cotyla medialis* to the most lateral point of the *cotyla lateralis*) is similar to that of *Pygoscelis* and also to *Paraptenodytes antarcticus*, although MLP 96-I-6-48 is slightly wider than the latter (see Table I).

Material: MLP 92-II-2-115a (articular region of the right *ramus mandibularis*, Fig. 2b).

Provenance: *Cucullaea* I Allomember (Telm 5).

Locality: IAA 1/90.

Description: It is less robust, 2.95% smaller in length and 20.4% in width than MLP 96-I-6-48 (see Table I), although the processus *mandibularis medialis* is similarly extended in both. The edge of the *cotyla medialis* is more rounded and less extended medially than in MLP 96-I-6-48, *Madrynornis*, and the living species of *Spheniscus* and *Eudyptes*, while it is similar to that of *Pygoscelis*.

The *tuberculum pseudotemporale* is very well developed, much more than in the materials described by Ksepka & Bertelli (2006) and even more prominent than in MLP 96-I-6-48. The *crista trasversal fossa* is less elevated with respect to the articular surface than in MLP 96-I-6-48, but more than *Madrynornis* and the modern species. The *processus retroarticularis* seems not to be developed, although the material is badly damaged in this region, showing irregular edges that might indicate a missing end. The *cotyla caudalis* and the *cotyla lateralis* are clearly

separated, as in the living penguins and *Spheniscus megaramphus* Stucchi, Urbina & Giraldo, 2003. The *cotyla lateralis* is well separated from the rest of the articular surface, rounded in shape and concave. The attachments of the *membrana postmeatica* and *ligamentum occipitomandibulare* do not show any particular feature. The *sulcus intercotylaris* between the *cotyla lateralis* and the *cotyla medialis* is almost half the length of that of MLP 96-I-6-48 and one third narrower than that of MLP 92-II-2-108, it is around the same size than *Pygoscelis antarctica* (Forster, 1781) and *Aptenodyptes patagonicus* Miller, 1778. The foramen located anterior to the *cotyla lateralis*, described by Ksepka & Bertelli (2006) in Antarctic materials, is present here. The *fossa articularis quadratica* is shallower than in MLP 96-I-6-48 and *Pygoscelis papua* Forster, 1781, but similar to that of the other modern species. The posterior end of the *fossa aditus canalis mandibulae* is rounded. The proportion of the articular surface is similar to that of *Aptenodyptes patagonicus* and MLP 92-II-2-108 (see below).

Material: MLP 92-II-2-108 (articular region of the right *rama mandibularis*, Fig. 2e).

Provenance: *Cucullaea* I Allomember (Telm 5).

Locality: DPV 6/84.

Description: The proportion of the articular surface is around 6% smaller than MLP 92-II-2-115a (see Table I) but very similar in shape, even though the specimen is not as well preserved as the former. No significant differences were observed, however the *tuberculum pseudotemporale* seems to be less developed, as in UCMP 321057 (Ksepka & Bertelli 2006). Concerning the proportion of the articular surface, this specimen is similar to *A. patagonica* and to MLP 92-II-2-115a, as stated before.

Material: MLP 91-II-4-223 (articular region of *ramus mandibulae*, Fig. 2c).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 15/84.

Description: This specimen is eroded and badly damaged. Only the articular surface is preserved, but not its processes or its most ventro-caudal region. As in MLP 92-II-2-108 and MLP 92-II-2-115a, the cotyla caudalis is divided from the cotyla lateralis, which is concave and very well developed.

Material: MLP 94-III-15-409 (articular region of left mandible).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 13/84.

Table II. Measurements (mm) taken on the mandibles under study and the comparison specimens. LS = length of symphysis. WM = width of mandible at the union of both *rami mandibulae*. LRM = length of the *ramus mandibularis* from the tip to the *fenestra rostro mandibularis*. WRS = width of the ramus mandibularis right at the caudal end of the symphysis.

Specimen	Species	LS	WM	LRM	WRS
IB/P/B-0617e	*Spheniscidae* indet.	34	9	-	-
MUSM 897	*Icadyptes salasi*	11	6	78	3
RNP A-2024	*Aptenodytes patagonicus*	17	5	76	2.5
RNP A-426	*Pygoscelis antarctica*	7	5	51	2
RNP A-806	*Pygoscelis papua*	9	5	62	2
RNP A-1652	*Pygoscelis adeliae*	6	6	45	3
78-X-26-2	Fossil under study	30	8	118	3
78-X-26-144	Fossil under study	26	13	-	7
92-II-2-195	Fossil under study	-	-	-	5
91-II-4-221	Fossil under study	-	8	-	4

Description: The fragment is badly damaged, which does not permit comparison of features. The only one visible is the foramen already observed in MLP 92-II-2-115 and described by Ksepka & Bertelli (2006).

Material: MLP 78-X-26-2 (*rami mandibulae*, Fig. 2i)

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 14/84.

Description: This *ramus mandibularis* is 118 mm length (see Table II), it is 40 mm longer than that of the modern species, and similar in length to the one studied by Jadwiszczak (2006a), *Waimanu* (Slack *et al.* 2006) and *Icadyptes salasi* Clarke, 2007. Both *rami mandibulae* are joined through the symphysis, lacking their articular region. The symphysis is more than twice the length of mandibles of living representatives (see Table II) and the tip is not curved. Each *ramus mandibularis* is stout and slender. Its height is nearly constant (about 10 mm) along its entire length, scarcely increasing gradually towards the caudal end, a feature also present in UCMP 321057 (Ksepka & Bertelli 2006), *Perudyptes devriesi* Clarke, 2007 (Clarke *et al.* 2007), *Spheniscus megaramphus* (Stucchi *et al.* 2003) and *Icadyptes salasi* (Ksepka *et al.* 2008). The lateral side of the mandible is concave, whereas it is flat in modern and Neogene species. The ventral outline is straight, as in all Palaeocene and Eocene penguins. The vascular foramina covering the external surface of the tip of the mandible are present as in all penguins (see Ksepka *et al*. 2008).

Material: MLP 78-X-26-143 (fragment of right *ramus mandibulae*, Fig. 2f) and MLP 78-X-26-144 (fragment of mandible, Fig. 2g).

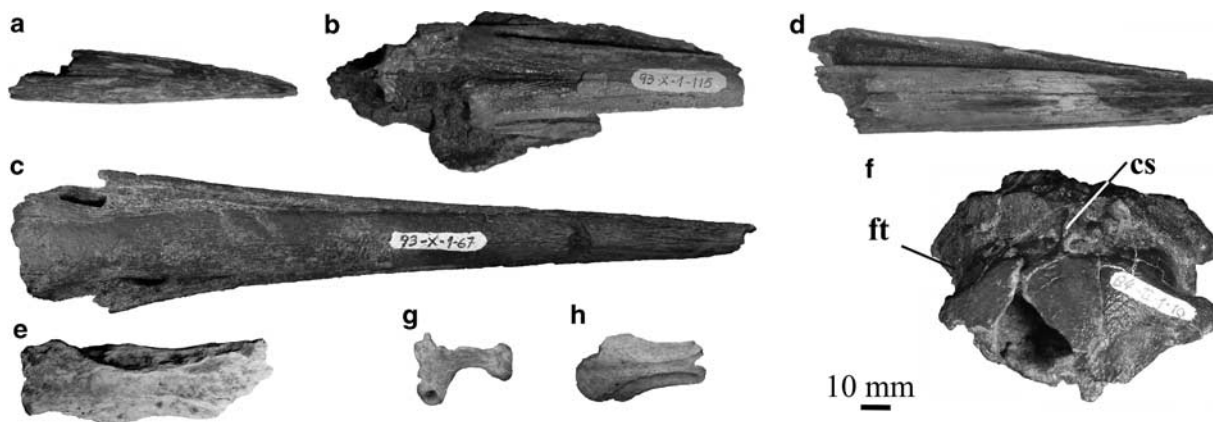*Provenance*: Submeseta Allomember (Telm 7).

Locality: DPV 14/84.

Fig. 3. **a.** Lateral view of bill (MLP 92-II-4-202). **b.** Dorsal view of proximal portion of bill (MLP 93-X-1-115). **c.** Dorsal view of bill (MLP 93-X-1-67). **d.** Dorsal view of *rami mandibularis* without the tip or proximal portion (MLP 93-X-1-91). **e.** Dorsal view of interorbital region (MLP 78-X-26-158). **f.** Dorsal view of posterior portion of skull (MLP 84-II-1-10). **g.** Lateral view of left quadrate (MLP 94-III-15-413). **h.** Dorsal view of interorbital region (MLP 92-II-2-250). ft = *fossa temporalis*, cs = *crista nuchalis sagittalis*. Scale bar = 10 mm.

Description: The symphysis of the 78-X-26-144 is similar in length (26 mm) but more robust than that of MLP 78-X-26-2 (30 mm). The rest of the features resemble the former in terms of the concave lateral surfaces and the straightness of the entire *ramus*. MLP 78-X-26-143 is very fragmentary and shows the end of the insertion of the ramphoteca on its medial surface.

Material: MLP 93-X-1-68 (fragment of right *rami mandibulae*, without articular region or symphysis).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 14/84.

Description: The specimen is deformed, therefore measurements could not be taken. The inner surface shows the insertion of the ramphoteca.

Material: MLP 92-II-2-203 (fragment of right *ramus mandibulae*, without the articular region or symphysis).

Provenance: *Cucullaea* II Allomember (Telm 6).

Locality: IAA 1/93.

Description: The material is badly damaged and does not present particular characters.

Material: Several fragments of mandibles: MLP 92-II-2-195 (right and left *ramus mandibulae* joined by sediment, but without the articular region or symphysis, Fig. 2(h), MLP 92-II-2-197 (fragment of left? *ramus mandibularis*), MLP 92-II-2-198 (small fragment of the left *ramus madibularis*), MLP 92-II-2-199 (fragment of the left *ramus madibularis*),

MLP 92-II-2-200 (fragment of the *ramus madibularis*), MLP 92-II-2-201 (fragment of the right *ramus madibularis*).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 14/84.

Description: Most of the remains are very fragmentary; MLP 92-II-2-195 is the most complete. It is larger in size, considering the width of the *ramus mandibularis* (Table II), than MLP 78-X-26-2, *Icadyptes* and extant penguins. However, it is slender and stout as the other remains described here.

Material: MLP 93-X-1-67 (whole bill with missing distalmost tip, Fig. 3c).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 14/84.

Description: The bill is 179 mm long and slender, gradually narrowing toward the tip. As in *Icadyptes*, there is no indication of a downturned tip, whereas the end is slightly curved in the materials described by Jadwiszczak (2006b) and even more recurved or decurved in modern and Miocene penguins.

The nares extend through most of the length of the bill and are wider posteriorly. In dorsal view they are well differentiable as in the living *Spheniscus*, *Eudyptes*, *Eudyptula* and *Pygoscelis*. The nasal-premaxillar suture seems not obliterated like in modern and Miocene species, and unlike *Perudyptes*.

Material: MLP 91-II-4-202 (distal end of bill, Fig. 3a).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 16/84.

Description: Distal end of bill similar to MLP 93-X-1-67 described above. The length is 70 mm, the most proximal section is 15 mm width, larger than that described by Jadwiszczak 2006a (see Table II).The dorsal outline is rounded, but the cross section is sub-triangular. Tomial edges are straight. Laterally the dorsal and ventral surfaces form an angle of approximately 10°.

Material: MLP 93-X-1-115 (proximal portion of bill, Fig. 3b).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 13/84.

Description: Similar in size to MLP 93-X-1-67, the nasal fossae present the same configuration as well.

Material: MLP 93-X-1-91 (fragment of bill without the tip or proximal portion, Fig. 3d).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 14/84.

Description: Similar in size to MLP 93-X-1-67. Particular features are not observable because of the degree of deformation.

Material: MLP 91-II-4-221 (fragment of *ramus mandibularis* with the symphysis broken and without the articular region, Fig. 2i).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 15/84.

Description: Right and left *rami mandibulae* joined by symphysis as well as by sediment. The fossil remain lacks the articular region and the tip of the mandible as well.

On lateral view vascular foramina are present. The ramus appears to be long and slender similar to MLP 78-X-26-2. Measurements cannot be taken because the mandible is not complete. Although MLP 91-II-4-221 resembles MLP 78-X-26-2 in shape, it seems remarkably larger than the latter, but smaller than MLP 96-I-6-48 and MLP 78-X-26-4. MLP 91-II-4-221 is similar to MLP 78-X-26-2 in that they both show a marked curvature on the lateral side of the *ramus mandibulae*, while this is straight in MLP 96-I-6-48.

Material: MLP 84-II-1-10 (posterior portion of skull, Fig. 3f).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 14/84.

Description: This skull is slightly larger than those of living *Spheniscus* and UCPM 321265 (Ksepka & Bertelli 2006) and preserves part of the calvaria, occipital region, nuchal crests, temporal fossa, posterior end of the left fossa *glandulae nasalis* and part of the neurocranium. It is more globose than those of *Icadyptes* and the Antarctic UCPM 321265, which is slender and more elongated antero-posteriorly.

The *fossa temporalis* is well developed, reaching the sagittal nuchal crest dorsally, as in *Paraptenodytes* and UCMP 321265 (Ksepka & Bertelli 2006). The dorsal end of this fossa is wider antero-posteriorly than in fossil and living species of *Spheniscus*. In the other modern species compared, the fossa ends in a triangular shape and does not reach the sagittal crest. The *fossa temporalis* is similar in size and shape to that of the Peruvian fossil *Perudyptes*, and to the Antarctic skull UCPM 321265.

The temporal crest is almost perpendicular to the sagittal crest, while in most penguins this crest is curved toward the anterior region. The sagittal crest is prominent as in *Paraptenodytes* and comparatively shorter.

The occipital region is trapezoidal as in *Paraptenodytes*, while it is more quadrangular in modern species and *Madrynornis*. The occipital condyle is robust and rounded as in the Miocene species, *Pygoscelis adeliae* (Hombron & Jacquinot), *P. papua* and *Eudyptes*; it is oblong in *Spheniscus*, *P. papua* and *Aptenodytes*. The occipital condyle is smaller than that of UCMP 321265 (Ksepka & Bertelli 2006), but it is wider than high in both. The subcondylar fossa is deeper and more defined than in *Paraptenodytes antarcticus* and even more so than in UCMP 321265.

The tubercles of the *lamina parasphenoidalis* are stronger than those of the living and Miocene species, and elongated as in *Paraptenodytes*.

Material: MLP 94-III-15-413 (left quadrate, Fig. 2p).

Provenance: Submeseta Allomember (Telm 7).

Locality: DPV 13/84.

Description: The *processus orbitalis* is broken. The quadrate forms a more concave angle between the otic and *squamosal capitula* of the *condylus caudalis* than in *Spheniscus*, *Pygoscelis*, and similar to *Aptenodytes* and *Eudyptes*. The tubercle for attachment of the *adductor mandibulae externus* described by Clarke *et al*. (2007) in *Icadyptes*, and also present in Miocene and modern species, is absent in this material.

The *condylus lateralis* is proportionally smaller than in living species and similar to that of *Paraptenodytes* and *Madrynornis*, the compared Miocene species. A wide sulcus

separates the otic and squamosal capitula, as in all penguins. The *condylus caudalis* is flat and less pronounced than in *Icadyptes* and similar to that of modern and Miocene species.

In palatal view, the pterygoid condyle is not so rounded as in *Madrynornis, Paraptenodytes* and modern penguins. This condyle is located more antero-medially than the *cotyla medialis* as well, as in Miocene and modern penguins. However, the sharp tip of the pterygoid condyle points medially as opposed to the extant and Miocene penguins whose *cotyla medialis* points antero-medially. The quadratojugal articulation is deep and rounded, similar to that of all penguins.

Material: MLP 78-X-26-158 (fragment of skull including interorbital region, Fig. 3e).

Provenance: La Meseta Formation (upper levels).

Locality: DPV 2/84.

Description: The preserved fragment includes both frontals and a portion of the *sulcus glandulae nasalis*. The interorbital region is 90% wider than in *Madrynornis* and *Pygoscelis* (these taxa present stick-like frontals), similar to that of *Spheniscus, Aptenodytes*, and *Paraptenodytes* and 10% narrower than in 321223 (Ksepka & Bertelli 2006).

The *sulcus glandulae nasalis* is narrower towards the anterior end, as in *Spheniscus* and *Paraptenodytes*. The supraorbital edge is also absent in these three taxa. The lateral edges of the fossa glandulae nasalis curve ventrally, as in UCMP 321223 (Ksepka & Bertelli 2006).

Material: MLP 92-II-2-250 (fragment of skull including interorbital region, Fig. 3h).

Provenance: *Cucullaea* I Allomember (Telm 5).

Locality: IAA 1/90.

Description: It is less than half the size of MLP 78-X-26-158 and exhibits basically the same features.

Discussion and conclusions

Little background information exists about the functional morphology of Antarctic penguins. In the oldest species, improved diving capability may have been linked to the development of stronger bones and probably muscular structures enabling them to endure greater forces operating in water (see Hospitaleche & Di Carlo 2010). Such robust structures would not have been optimal for speed swimming. This idea was explored by Jenkins (1985), who based on the morphology of the flippers, considered that *Anthropornis nordenskjoeldi* Wiman, 1905, one of the "giant penguins",

would have been a slow swimmer. Even more, it was suggested that its long neck probably favoured the capture of motile prey (fishes) rather than krill and small squids (Tambussi *et al*. 2006).

Although the available cranial materials are too fragmentary to make a morphometric analysis, some considerations about their functional morphology can be advanced. A set of skull characters were evaluated in living penguins and showed promise as good indicators of trophic preferences and life habits (see Acosta Hospitaleche & Tambussi 2006 and references therein).

With respect to the neurocranium, only two previously reported Antarctic specimens are available for comparisons (Jadwiszczak 2006a, Ksepka & Bertelli 2006). MLP 84-II-1-10 studied here comes from the Submeseta Allomember in the upper levels of the unit. The configuration of the temporal fossa suggests a wide and well-developed temporal portion of the adductor mandibulae externus muscle. This muscle depresses the mandible and protracts the upper jaw. The extensive attachment area could indicate great forces acting to close the jaws (see Acosta Hospitaleche & Tambussi 2006). Although the temporal fossae are shallow, the presence of a long sagittal nuchal crest supports the idea of powerful muscles acting in this area. This morphology suggests a piscivorous habit.

On the other hand, most of the previously described mandibular remains from Antarctica come from the Submeseta Allomember (see Jadwiszczak 2006a, Ksepka & Bertelli 2006). The articular regions here described were mainly from the lower and medium beds of the La Meseta Formation. One specimen (MLP 96-I-6-48) shows a peculiarity with respect to the *cotyla caudalis* and *lateralis*, which does not present a clear separation between them as opposed to the other articular regions, which show two different cotylae developed.

In addition, the *processus retroarticularis,* which is present in all extant penguins, was not observed in any of the material here described, in some cases due to lack of preservation, but in others it does not seem to had been developed.

Although fragmentary, these specimens always exhibit the same morphology, consisting of elongated and dagger-like bills. This morphology is closely associated to the capture of large prey such as fish or squids. This morphology is widely developed in medium and large Palaeogene species. Elongate and powerful bills have been also described for the Peruvian *Perudyptes*, *Icadyptes* and *Inkayacu* (Clarke *et al*. 2007, 2010), and the two New Zealand species of *Waimanu* (Slack *et al*. 2006). The single exception is a fragmentary *rostrum maxillare* (IB/P/B–0617e) studied by Jadwiszczak (2006b) that comes from the Acantilados Allomember. This upper jaw is basally wide and strongly narrowing toward the tip in dorsal view, a particular shape that implies an important advance in the knowledge of the Antarctic penguins. It is the first

evidence to suggest that not all the Eocene Antarctic penguins had long slender bills (Jadwiszczak 2006b).

The specimens MLP 96-I-6-48 and 92-II-2-203 here described, exhumed from the lower and middle units of the La Meseta Formation, are medium to large in size and partially resemble the shape observed in Miocene species. It means a mandible shape more similar to extant penguins than to those of the Eocene species. The former also shows a singular morphology in the articular region (see above). In contrast, the mandibles from the upper levels of the sequence are long and slender, similar to those classically used in giant penguin reconstructions, and probably belonged to taxa specialized in catching fish. These two morphotypes support the hypothesis proposed by Jadwiszczak (2003) about the co-existence of penguins with different trophic habits, and explain a possible strategy to avoid interspecific competition. Although the evidence is fragmentary, a niche partitioning like this is expected when the number of sympatric species is high, as in the case of the penguin assemblage of the late Eocene of Antarctica. Future research involving articulated skeletons or at least associated remains will be very useful to clarify these ideas.

Acknowledgments

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