Fossil penguin beaks from the Eocene of Antarctica: new materials from La Meseta Formation

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Running head: Fossil penguin beaks from the Eocene of Antarctica

Abstract: New materials coming from different levels of the La Meseta and Submeseta formations, including the most complete beak of a penguin (MLP 14-XI-27-27) from Antarctica, are described here. A new morpho-geometric approach, based on Principal Component Analysis, and Elliptic Fourier Analysis, was performed to analyze the articular area of the mandibles and maxilar remains, a skeletal correlate of dietary habits. As a result, we can infer that most of the penguins analyzed belong to the piscivorous morphotype. This corroborates the abundance of piscivores in the Eocene of Antarctica and provides more information regarding the morphological configurations of the predominantly crustacivore penguins.

Keywords: anatomy, geometric morphometry, rostrum, mandibles.

Resumen: Picos fósiles de pingüinos del Eoceno de Antártida: nuevos materiales de la Formación La Meseta. Nuevos materiales procedentes de diferentes niveles de las formaciones La Meseta y Submeseta, incluyendo el pico de pingüino más completo (MLP 14-XI-27-27) de Antártida son aquí descritos. Un nuevo enfoque morfogeométrico, basado en el Análisis de Componentes Principales, y en el Análisis de Contornos de Fourier, fue realizado para analizar el área articular de restos mandibulares y maxilares, correlatos óseos de los hábitos dietarios. Como resultado, podemos inferir que la mayoría de los pingüinos analizados pertenecen al morfotipo de los piscívoros. Esto corrobora la abundancia de pingüinos piscívoros en el Eoceno de Antártida y brinda más información respecto de las configuraciones morfológicas de los pingüinos predominantemente crustacívoros.
Palabras claves: anatomía, morfometría geométrica, rostrum, mandíbulas.

INTRODUCTION

Most of the Antarctic avian remains come from Seymour (=Marambio) Island (see however; Jadwiszczak *et al*., 2012), a small island located east of the northern Antarctic Peninsula (Fig. 1) that is known for its extraordinarily rich penguin fossil record. Although, Paleocene remains are very scarce and restricted, penguin bones are extremely numerous within Eocene sediments, although mainly through disarticulated and unassociated remains (Acosta Hospitaleche *et al*., 2013).

Morphological studies on trophic habits in birds have been mainly related to the length, width, and curvature of the beak with respect to the rest of the skull (Zusi, 1975; Myrcha *et al*., 1990). Although these are certainly quite good indicative features, the analysis of the articulation surfaces in the jaws also provides important information in this regard (see Bock, 1964, 1966; Haidr & Acosta Hospitaleche, 2012, 2014).

Previous analyses have enabled the recognition of different morphotypes related to piscivory, crustacivory, or generalist diets. For instance, small variations in the structure of the articulation surfaces of the jaws are indicative of the type of movements during opening and closing of the beak (Haidr & Acosta Hospitaleche, 2014). In this way, morphogeometric analyses bring us tools to visualize and measure the changes in the shape of the entire beak, and eventually enable the definition of the morphotypes.

The recent finding of an associated mandible and rostrum maxillare (MLP 14-XI-27-27) belonging to an Sphenisciformes, together with new abundant partial mandibles from the Eocene of Seymour Island, motivates the present contribution.

GEOLOGICAL SETTING

The James Ross Basin contains an almost complete sedimentary sequence, unique around the world that spans more than 40 My, from mid-Cretaceous to latest Eocene-?earliest Oligocene. In Seymour Island, located in the east of the northern Antarctic Peninsula, the Marambio Group and the Seymour Island Group are exposed (Fig. 1); the latter includes the Cross Valley Formation at the base, and the highly fossiliferous La Meseta and Submeseta formations at the top (Fig. 2). The late Paleocene-middle Eocene La Meseta Formation (Elliot & Trautman, 1982) crops out on Seymour and Cockburn islands. This unit is divided into six allomembers, from base to top: Valle de las Focas, Acantilado I, Acantilado II, Campamento, Cucullaea I, and Cucullaea II (Fig. 2). Materials here described come from Acantilado II (fossil locality IAA 1/13), Cucullaea I (fossil localities IAA 1/90, IAA 1/95, and DPV 6/84), and Cucullaea II (fossil locality IAA 1/93).

The middle Eocene- ?earliest Oligocene Submeseta Formation (according to Montes *et al*., 2013) is the topmost portion of the sedimentary fill of the James Ross Basin (del Valle *et al*., 1992) and is internally divided into three levels: Submeseta I, Submeseta II, and Submeseta III. The Submeseta Formation was redefined from the uppermost part of the former La Meseta Formation (Elliot & Trautman, 1982; Ivany *et al*., 2006), precisely the Submeseta Allomember in the sense of Marenssi *et al*. (1998a). This unit corresponds to the Facies Association III of Marenssi *et al*. (1998b), characterized by a uniform sandy lithology that represents a tidal shelf influenced by storms. The majority of penguin bones come from these levels that correspond to the Facies Association III of Marenssi *et al*. (1998b). Materials here studied come from Submeseta II (fossil localities DPV 13/84, DPV 14/84, and DPV 15/84), and Submeseta III (uppermost part of the fossil localities DPV 13/84, DPV 14/84, and DPV 16/84).

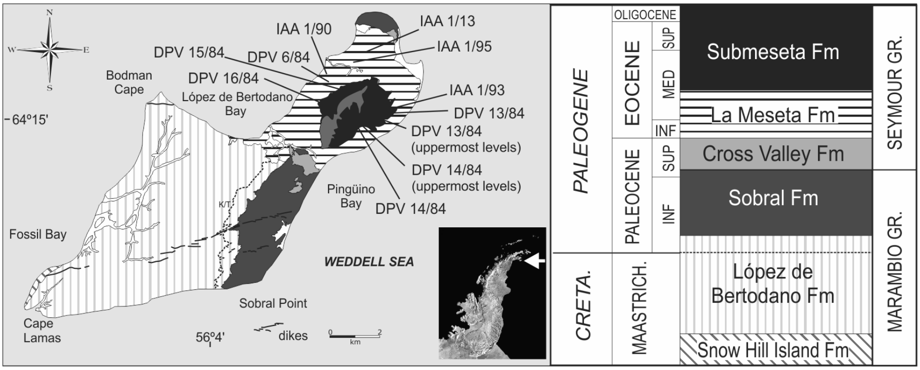

Fig. 1. Fossil localities where the studied materials were collected. In the table at the right are indicated the geological units. Modified from Montes et al. (2013).

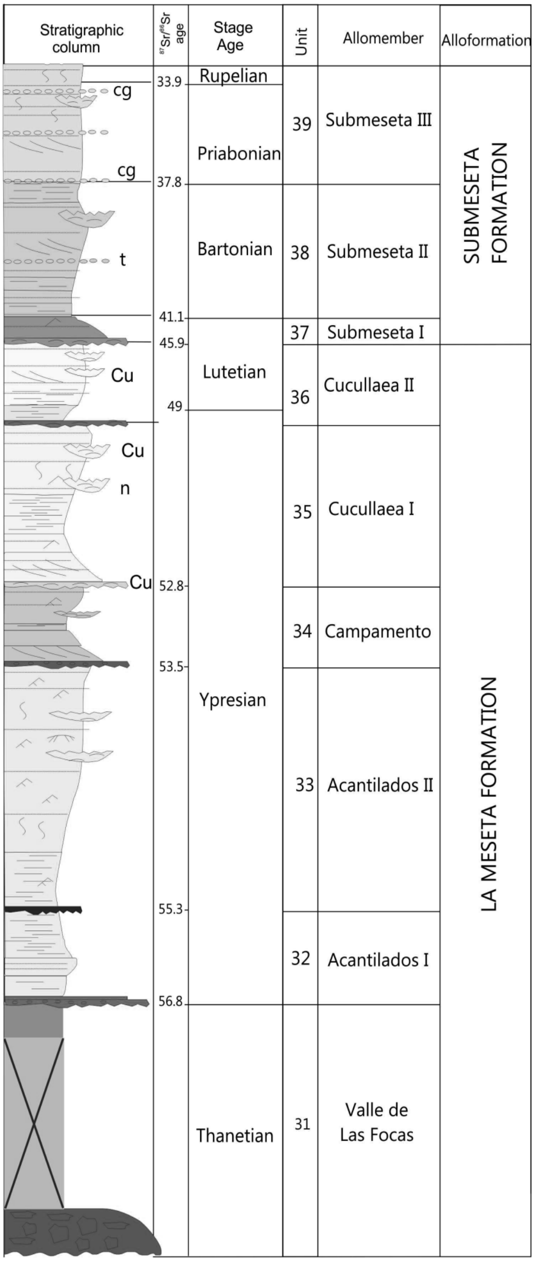

Fig. 2. Stratigraphic column showing the internal divisions in Allomembers of La Meseta Formation and Submeseta Formation. Modified from Montes et al. (2013).

MATERIAL AND METHODS

Materials

The fossils under study were collected during Argentinian summer campaigns between 1977 and 2014 in Seymour Island, and are housed at the División Paleontología Vertebrados, Museo de La Plata (MLP). Comparative modern skeletons belong to the osteological collections of the Sección Ornitología (MLP-O) and División Paleontología Vertebrados of the Museo de La Plata (MLP-PV), Argentina; Museo Acatushún, Fundación Natalie Goodall (RNP), Argentina; Departamento de Paleontología de Vertebrados of the Museo de Historia Natural; Museum of Natural History (MNH), and MNH at Tring, UK; and Naturhistoriska Riksmuseet (NRM), Sweden.

Descriptions of new materials are in agreement with the terminology proposed by Baumel & Witmer (1993). Measurements were taken using a 0.01 mm increment Vernier Caliper.

Analyses

Independent analyses were performed in order to define shape variations in the articular region of the mandibles, and beak shape. Landmark configurations and contours were obtained from pictures taken on dorsal view, from specimens of modern and Eocene Antarctic penguins upper and lower jaw. The set of fossil included those collected in the new campaigns and here described, but also materials previously reported (Table 1) (Acosta Hospitaleche & Haidr, 2011), and placed in the MLP; in all three analyses, MLP 14-XI-27-27 was included.

For the lower jaw (n=130, See

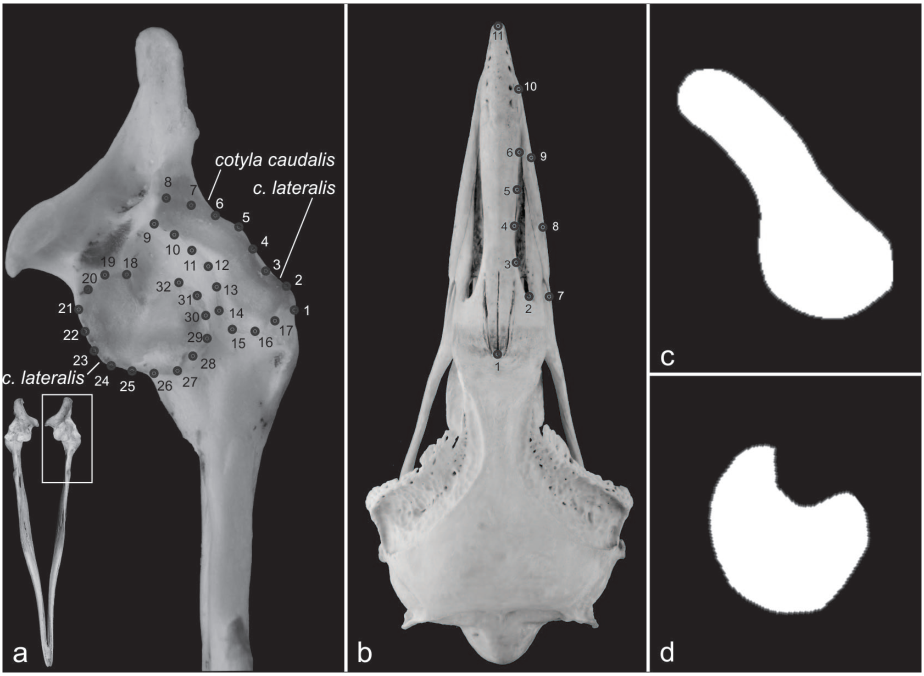

Fig. 3. Configurations analyzed: a-b Morpho-geometric analyses: a. Landmarks on mandibles, b. Landmarks on beaks; c-d Elliptic Fourier Analysis: c. Outline of *cotyla lateralis*, d. Outline of *cotyla medialis*.

Appendix 1), a landmark configuration was established for the articulation *cotylae* (*cotyla medialis*, *c. lateralis*, and *c. caudali*s) including five landmarks types one and two, and 27 semilandmarks (Fig. 3a, See Appendix 2 for detail on landmarks). Partially broken *cotylae medialis* of some of the fossils were reconstructed to be included in the analysis. For the upper jaw (n=110, See Appendix 3) landmarks configuration (See Fig.3b, Appendix 4) was established to point out general shape of beak including the tomial edge, nostril, and total length relative to width. Landmarks configurations were digitized with TPS Pack (Rohlf, 2016), analyses were performed in MorphoJ 1.06d (Klingenberg, 2011) and differences in size, orientation, and position were removed using Full Generalized Procrustes Analysis (GPA).

The subtle variations in shape of the *cotyla lateralis* (Fig. 3c) and the *cotyla medialis* (Fig. 3d) of the mandibles were sorted using Elliptic Fourier Analysis (EFA) of contour coordinates (Rohlf & Archie, 1984), carried out with the software package Shape (Iwata & Ukai, 2002). Specimens were evaluated using the same photographic sample, and outlines were digitally redrawn to highlight their contrasts, to then be converted into black-and-white using ChainCoder (Freeman, 1975). For each of the 129 specimens, 2500 coordinates of the outline were obtained and twenty five harmonics were sufficient to characterize the outline in detail. Elliptic Fourier descriptors were subsequently normalized to be invariant with respect to size, rotation, and starting point, with normalization based on the ellipse of the first harmonic (Kuhl & Giardina, 1982) using Chc2Nef. The effective information contained in these coefficients (see Rohlf & Archie, 1984) was summarized through a PCA, performed with PrintComp (Iwata & Ukai, 2002). Variation in shape accounted for by each principal component was represented through the software PrintPrint. Finally, the scores for the PCA

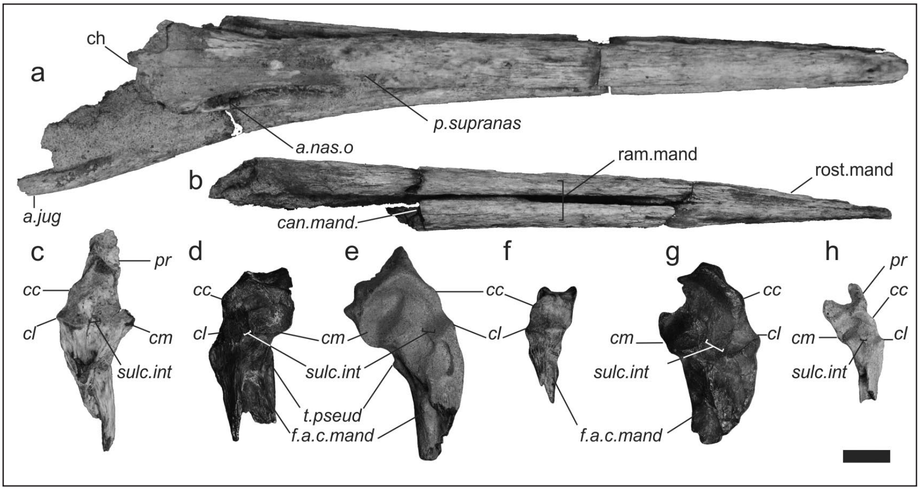

Fig. 4. Fossils under study:, a, upper jaw, b, rama mandibulae, and c, left articular end of ramus mandibulae of MLP 14-XI-27-27; and articular end of ramus mandibulae of, d, MLP 13-XI-28-199; e, MLP 13-XI-28-135; f, MLP 92-II-2-251;g, MLP 91-II-4-204;h, MLP 90-I-20-10. Abbreviations: a.jug., *arcus jugalis*; a.nas.o., *apertura nasi ossea*; can.mand., *canalis mandibulae*; ch, charnella; cc, *cotyla caudalis*; cl, *cotyla lateralis*; cm, *cotyla medialis*; f.a.c.mand., *fossa aditus canalis mandibulae*; pr, *processus retroarticularis*; p.supranas, *pila supranasalis*; ram.mand., *rami mandibulae*; rost.mad., *rostrum mandibulae*; sulc.int., *sulcus intercotylaris*; t.pseud., *tuberculum pseudotemporale*. Scale bar: 10 mm.

were exported to the software Past (Hammer et al., 2001) where clouds of data were visualized in a biplot graph.

Interpretation of the results was framed in morphotypes definition after Haidr & Acosta Hospitaleche (2012). Principal Component Analyses (PCA) were used for the three configurations, as an exploratory method to see the differences among individuals in both modern and fossil penguins.

RESULTS
SYSTEMATIC PALEONTOLOGY

Aves Linnaeus, 1758
Sphenisciformes Sharpe, 1891
Indeterminate genus and species
Fig. 4

Material. MLP 14-XI-27-27 (left articulated mandible and rostrum maxillare) (Fig. 4a,b,c).

Procedence. DPV 14/84 (uppermost levels, Submeseta III Allomember (level 39).

Remarks. The *ramus mandibulae* is a little stouter in cross section, and the *crista tomialis* is straight. The *canalis mandibulae* is shallow and the *pars symphysialis* (46.2 mm length) is sharp like other Antarctic specimens (Fig. 4b). The *rostrum maxillare* is approximately 162.6 mm (tip is lacking), and the *aperturae nasale ossea* (107.3 mm length) open dorsally oriented (Fig. 4a). This configuration represents an intermediate condition among the specimens already known. The *pila supranasalis* presents a variable width, broadening at different points (Fig. 4a). No distinctive characters can be described in palatines, which are partially preserved, as well as the *arcus jugalis,* whose cranialmost portion connects with the *maxillare*. At the articular end of the mandible, the *cotyla lateralis* and *c. caudalis* (15 mm length and 17.1 mm width respectively) can be differentiated from each other though they are united like in *Spheniscus* (Fig. 4c). The *cotyla lateralis* is rhomboidal, similar in shape to others Antarctic Eocene penguins of the piscivorous morphotype, like the extant *Spheniscus* and *Aptenodytes*. The medial portion of the *cotyla medialis* is lacking, and the *processus retroarticularis,* although partially preserved, is clearly caudally enlarged. It is the attachment surface of the *m. depressor mandibularis*, and a sign of trophic habit.

Material. MLP 13-XI-28-199 (right articular end of mandible) (Fig.4d).
Procedence. Locality IAA 2/13, Cucullaea I Allomember, La Meseta Formation.
Remarks. This mandibular *pars caudalis* is intermediate in size between the largest mandibular remains found for Antarctica and the smallest one represented by MLP 90-I-20-10, with a *cotyla fossae articularis* width of 1.56mm, and length of 1.34mm. The *tuberculum pseudotemporalis* develops as a crest (Fig. 4d), that extends dorsally towards the ventral margin of the *fossa aditus canalis mandibulae*, and ventrally towards the mandibular ventral medial line. This crest might have acted as an extra point of attachment for the *m. pterygoideous*. The *cotyla caudalis* is clearly differentiated from the *c. lateralis*; the latter has an oval shape and does not extend completely to the medial border as in most Eocene mandibles.

Material. MLP 13-XI-28-135 (left articular end of mandible) (Fig. 4e).
Procedence. Locality DPV 6/84 Cucullaea I Allomember (level 35), La Meseta Formation.
Remarks. The caudal portion of *fossa aditus canalis mandibulae* is present, with a *canalis neurovascularis mandibulae* on the caudalmost portion of the fossa. The *tuberculum pseudotemporale* is robust and visible in dorsal view. A *canalis vascularis* is placed anterior to the *cotyla lateralis*. The *sulcus intercotylaris* is wide (3 mm). *Cotyla medialis* has an irregular kidney shape, similar to modern species, and *cotyla lateralis* can be differentiated from *c. caudalis*.

Material. MLP 92-II-2-251 (right articular end of mandible) (Fig. 4f).
Procedence. Seymour Island, Submeseta Formation (probably level 38).
Remarks. This material belongs to a small size mandible, smaller than most extant penguins. It has a *pars caudalis* almost complete, lacking only the retroarticular process. The sulcus for insertion of *m. pterygoideuos* is much excavated and presents a crest that is divided in two; this division is coincident dorsally with the line of maximal convexity of the *cotyla medialis*.

Material. MLP 91-II-4-204 (left articular end of mandible) (Fig. 4g).
Procedence. Locality IAA 1/93. Cucullaea II Allomember (La Meseta Formation).
Remarks. It has a robust and tall *pars caudalis* 22.2 mm height. *Cotyla medialis* is partially broken, and has a semicircular shape. The lateral *cotylae fossae articularis* are very well differentiated, *c. caudalis* is rectangular, and *c. lateralis* is teardrop shaped. The medial margin of both *cotylae* forms a wide angle of approximately 107.44°. The *sulcus intercotylaris* is 4.78 mm wide. The *tuberculum pseudotemporalis* is comparatively not well developed. The *processus retroacticularis* is not preserved, and the surface of attachment for the *m. pterygoideus* is less profound than in the other remains previously described.

Material. MLP 90-I-20-10 (left articular end of mandible) (Fig. 4h).
Procedence. DPV 6/84. Cucullaea I Allomember (level 35) La Meseta Formation.

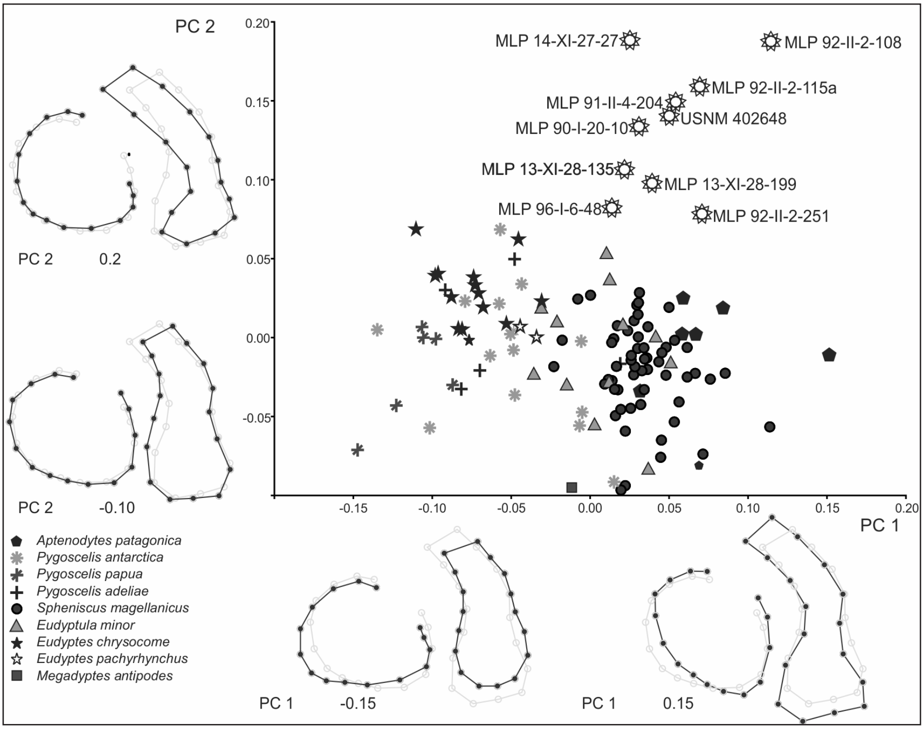

Fig. 5. Principal Component Analysis of the mandibular articulation *cotylae*. Biplot of the analysis, shape changes were represented through a wireframe set at the extreme point of each principal component.

Remarks. This material represents the smallest caudal portion of a *ramus mandibulae* ever found for the Eocene of Antarctica. The *fossa aditus canalis mandibularis* is 8 mm long and 10 mm wide. On the *facies medialis* the *tuberculum pseudotemporalis* is barely differentiated probably due to erosion. The articular surface presents a *cotyla medialis* with a semicircular shape and a deep sulcus. The *cotyla lateralis* and *c. caudalis* are separated and their medial line forms an angle of 72.69°. The *processus retroarticularis* is partially broken.

Morphogeometric analysis of mandibles

PCA (Fig. 5). The first three principal components explain 57.673 % of the variance. The PC1 (27.304 % of variance) accounts for the difference in length of the *cotyla lateralis*/*caudalis*, the subdivision of these *cotylae*, and the variations on the elongation of the *cotyla medialis*. Those individuals in the positive numbers develop a longer *cotyla* that extends farther caudally and rostrally, and have a more evident division between the *c. lateralis* and the *c. caudalis*. The *cotyla medialis* develops a medial conspicuous projection in the individuals placed on the negative numbers and is rather farther relative to the *cotyla lateralis* in those same individuals. Therefore, the general morphology tends to be more quadrangular, with a length and width of similar range. This component separates the group formed by the modern piscivorous penguins from those that range from having mixed diets to being almost exclusively crustacivores. Positive values aggregate *Spheniscus magellanicus*, *Aptenodytes patagonicus*, MLP 92-II-2-108, MLP 92-II-2-115a, MLP 92-II-2-251, USNM 402648,

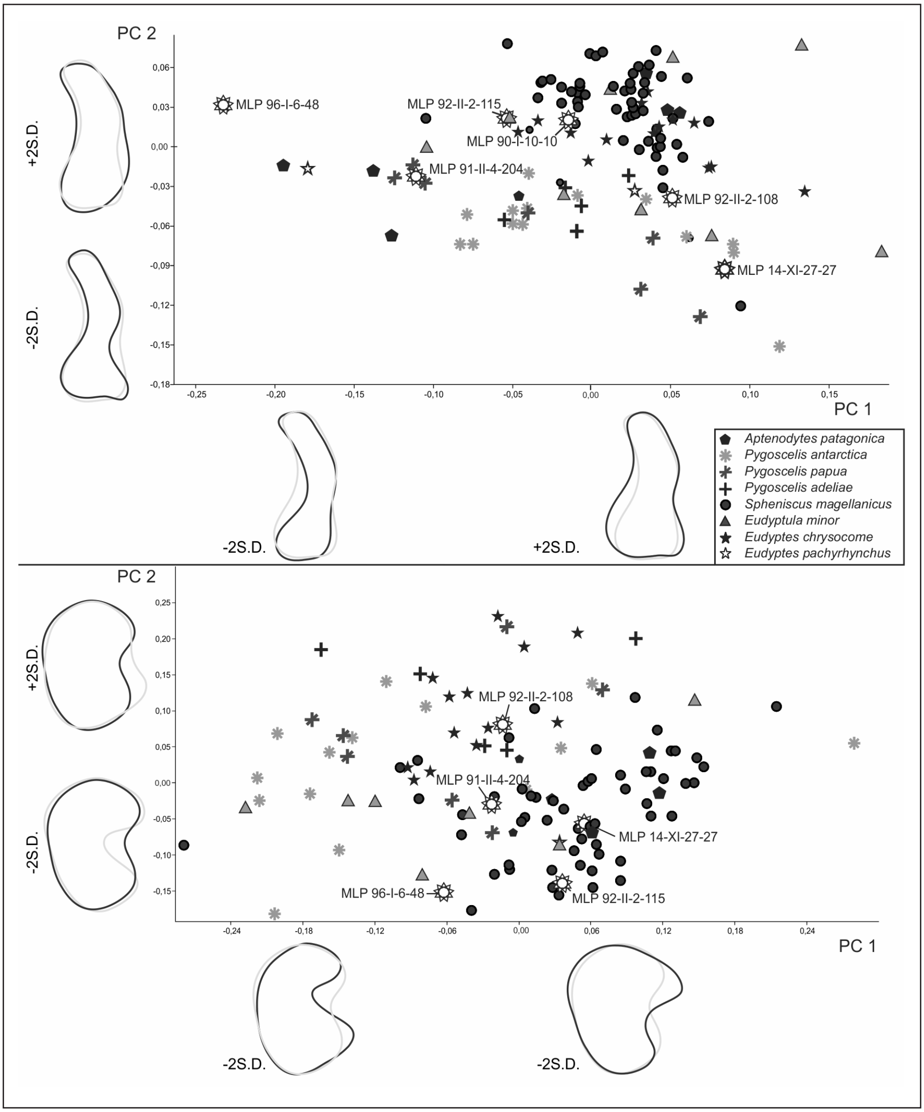

Fig. 6. Elliptic Fourier analyses: a, biplot of the PCA with the outlines of the *cotyla lateralis*, b, biplot of the PCA with the outline analysis of *cotyla medialis*

MLP 13-XI-28-199, MLP 90-I-20-10; MLP 13-XI-28-135, MLP 14-XI-27-27, and MLP 96-I-6-48 are also within this range but closer to the negative values and therefore to the crustacivore forms. Negative values aggregate *Eudyptes*, and *Pygoscelis*. In the midrange, at both sides of the zero value, we found *Eudyptula*, and *Megadyptes*; MLP 13-XI-28-135, MLP 14-XI-27-27, and MLP 96-I-6-48, could be also considered within this group since they occupy the lowest positive values.

The PC2 (21.125% of variance) divides fossils from modern penguins. The group formed by the Eocene penguins is characterized by a clear separation between the *cotyla lateralis* and the *c. caudalis,* typical configuration found in penguins from La

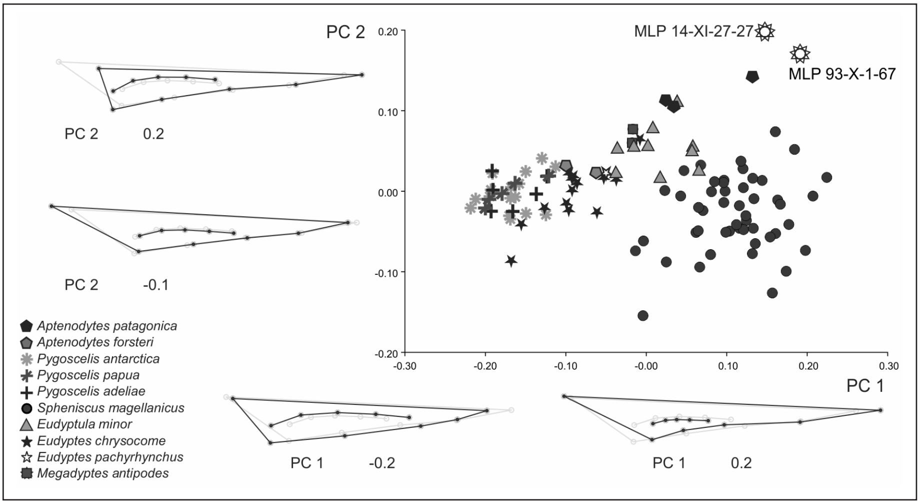

Fig. 7. Principal Component Analysis of beaks. Biplot of the analysis, shape changes were represented through a wireframe set at the extreme points of each principal component.

Meseta Formation; the latter reaches farther posteriorly and medially, ending up in an acute curvature, between both *cotylae*. The *cotyla medialis* for these values develops its main axis antero-posteriorly and the *sulcus intercotylaris* is twice as long. The tendency in the negatives values of the biplot is toward a non-differentiation of the *cotyla caudalis* from the *cotyla lateralis*. The caudal portion of *c. lateralis* does not extend medially, keeping the same direction of the main axis. The *c. medialis* is closer to the *c. lateralis,* and its main axis is latero-medially developed.

Elliptic Fourier analysis (EFA) of mandible (Fig. 6). Outline analysis of *cotyla lateralis* permits a clear distinction between *Pygoscelis antarctica*, *P. papua*, and *P. adeliae*, located at the lower part of the biplot, from *Spheniscus* that occupies the upper part of the graph. *Aptenodytes patagonicus* and *Eudyptula minor* are placed in between both groups and *E. chrysocome* is included within the cloud delimited by *Spheniscus*.

Regarding the first component, Eocene Antarctic specimens are not densely distributed. Taking into account the second component, fossils analyzed here are in the range of *Spheniscus*, *Eudyptes*, *Aptenodytes,* and *Eudyptula*, except for MLP 14-II-27-27 which are on the negative values, on the range of pygoscelid penguins.

Outline analysis of *cotyla medialis* appears a little vague since there is no clear differentiation between *Pygosceli*s and *Spheniscus*, as with the *cotyla lateralis*. None of the first components allows grouping the taxa in a single cloud. The penguins from La Meseta formation are scattered on the biplot with no particular aggrupation.

Morpho-geometric analysis of upper jaw

PCA (Fig. 7). The first three principal components explain 96.473% of the variance. The PC1 itself explains the 81.272% of the variation, and separates those penguins with a stouter and shorter beak, and a longer and convex *apertura nasi ossea* on the negative values (*Pygoscelis*, *Eudyptes*, and *Aptenodytes forsteri*), from those with a longer and slender beak, and a much shorter *apertura nasi ossea* (*Spheniscus magellanicus*, *A. patagonicus*, MLP 93-X-1-67, and MLP 14-XI-27-27) in the positive values. *Eudyptula* and *Megadyptes* are placed in between the negative and positive values but closer to *Spheniscus magellanicus*.

PC 2 with a 15.201% of the variance explained congregates all extant penguins together, while separating the fossils in the extreme positive values. Extant penguins present a farther posteriorly extended charnella with respect to the *apertura nasi ossea* than the fossil forms. The biplot, PC1 vs PC2, aggregates the two fossil upper jaws together and closer to *Spheniscus* and to *Aptenodytes patagonicus*, the most piscivorous forms among extant penguins, with features typical of fish eating animals such as long and flat beaks and small nasal apertures, resulting in a gracile structure.

DISCUSSION AND CONCLUSIONS

The MLP 14-XI-27-27 (Fig. 4 a, b, and c) constitutes the most complete beak known from Antarctica and, together with the other materials analyzed here, provides a more accurate idea about the composition of these penguin assemblages in terms of their dietary preferences.

Analyses confirm the predominance of penguins that prey on fish over the generalists and the crustacivore species for the Eocene of Antarctica. On the upper jaw PCA, MLP 14-XI-27-27 was found closer to the piscivorous forms, while in the mandibular articulation PCA, the MLP 14-XI-27-27 was found in the midrange of both dietary groups. MLP 14-XI-27-27, MLP 96-I-6-48, and MLP 13-XI-28-135 were the ones closer to the extant crustacivore group, whereas all the others fossils from La Meseta Formation were closer to the piscivorous group constituted by the extant penguins in the analysis of the mandibular articulation.

Given the results obtained from previous morpho-geometric analysis, and since this method allows the comparison of subtle variations of the surface, we expected EFA to give a better resolution of groups. However, only the analysis of the *cotyla lateralis* was successful in sorting the variation according to the trophic habits in modern taxa and allowed discrimination of the most piscivorous (*Aptenodytes* and *Spheniscus*) from the most crustacivorous penguins (*P. adeliae*, *P. papua*, and *P. antarctica*).

The results were clearer when both *cotylae* were analyzed together (Fig. 5), probably implying that the articulation surface works as a single structure, and each *cotyla* closely depends on the other in form and function.

Considering the results of the different analyses, it is possible to conclude that a longer *cotyla lateralis*, with a subdivision into two *cotylae*, might provide a greater mobility of the quadratum/mandibular articulation, and therefore a larger aperture of the mandible with greater points of stabilizations as proposed by previous works (see Haidr & Acosta Hospitaleche, 2014). The independent *cotyla lateralis*, with a *c. caudalis* axis extended farther medially, might have been a different way of coping with great forces for part of the piscivorous forms in the Eocene, with the addition of a longer and therefore less stable beak. In this way, the articulation might have had greater points of stabilizations anteriorly and posteriorly. The upper jaw would also be a good indicative of feeding habits, having those with shorter and stouter beaks with longer and wider nostrils, a greater capacity for krill catching and filtration of the water; whereas long and slender beaks would be more related to fish catching. Some features that could not be included in the analyses such as the *tuberculum pseudotemporale* (MLP 13-XI-28-199, and MLP 13-XI-28-135) and the area of insertion of the *m. pterygoideus* (MLP 92-II-2-251), indicate greater and stronger areas of insertion for muscles implied in closing both the lower (*m. pseudotemporalis*) and upper jaw (*m. pterygoideus*).

On the past few years, the La Meseta Formation cranial and mandibular record have increased significantly (see also Acosta Hospitaleche & Haidr, 2011; Acosta Hospitaleche, 2013). The MLP 14-XI-27-27 constitutes the first record of an associated upper and lower jaw, and together with the other remains here described, is meaningful in the understanding of feeding habits of the penguins in the past assemblages.

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