Feeding habits of Antarctic Eocene penguins from a morpho-functional perspective

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With 6 figures

Abstract: Cranial and mandibular penguin remains from the Eocene of Antarctica were studied in order to determine their feeding habits and food item preferences. Their osteology and musculature were compared with those of modern taxa. Different morphotypes were recognized based on their skull, configuration of the articular region of the mandible and bill shape. The results point to a variety of trophic habits and food preferences consistent with the known taxonomic diversity for this unit. For the middle Eocene, large sized penguins were interpreted as fish and crustacean eaters, whereas for the late Eocene, taxonomic diversity and number of individuals in the colonies during the late Eocene seems to increase. This colony could be reconstructed as being composed of medium-sized generalist penguins, piscivorous large- and medium-sized species, and also large penguins with a diet based on crustaceans and squids.

Key words: Fossil Spheniscidae, Antarctica, anatomy, osteology, musculature.

1. Introduction

Eocene Antarctic penguins are characterized by a high specific and morphological diversity. While fourteen species (but see Jadwiszczak 2006a) have been described for La Meseta Formation, little is known about their feeding habits and food preferences. They are known through a large amount of materials, but few of the latter correspond to skulls and jaws. Recent works have dealt with these fossils (Ksepka & Bertelli 2006; Jadwiszczak 2006b; Acosta Hospitaleche & Haidr 2011), but only from a descriptive point of view (see also Jadwiszczak 2010).

The available evidences suggested that Paleocene and Eocene penguins were birds with long and thin beaks, consistent with a piscivorous diet (Clarke et al. 2007, 2010; Slack et al. 2006). However, recent contributions have revealed a variety of cranial and mandibular remains that include not only medium- and large-sized fish-eating forms, but also taxa with shorter and wider rostra (Jadwiszczak 2006b; Acosta

Hospitaleche & Haidr 2011). As in modern penguins, these small differences in bill shape can reflect not only the feeding habits, but minor divergences in the adaptiveness of closely related forms (Bock 1966).

Cranial and mandibular remains from the Eocene of Antarctica were here studied in order to determine their feeding habits and food item preferences. Most of the elements are badly preserved, so they were first reconstructed and then analyzed from a morpho-functional point of view. Previous works suggest that the development of jaw muscles must be related to feeding habits, as well as the shape of the bill and structure of the palate (George & Berger 1966). A holistic approach integrating osteological morphology and estimated muscular development was used for the first time to study Antarctic fossil penguins.

Musculature dissections were done using skulls and mandibles of modern penguins, and the subsequent muscular reconstructions for the Eocene penguins were used to propose a new hypothesis about their feeding habits.
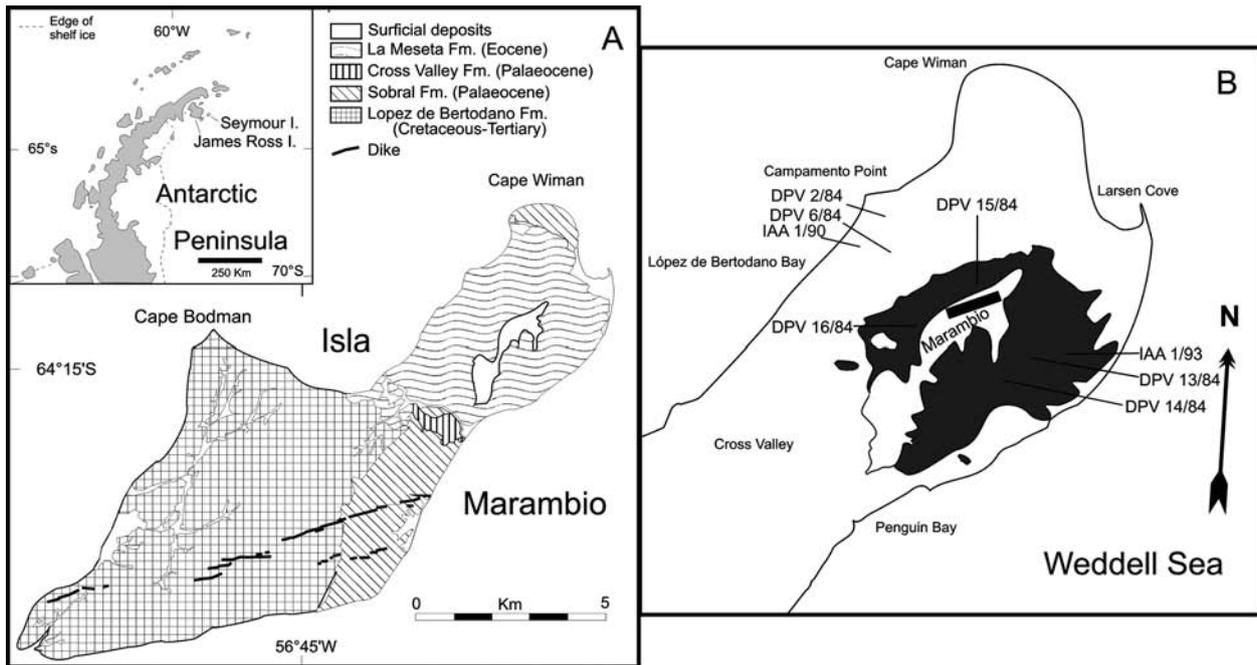
Fig. 1. A – Map showing the location of Seymour Island, Antarctic Peninsula. **B** – Sketch map of the northern part of Seymour Island showing the distribution of the Submeseta Allomember and the fossil penguin-bearing localities cited in the text.

2. Material and methods

The studied material is housed in the Museo de La Plata (MLP), La Plata, Argentina. They were collected from the Eocene La Meseta Formation (RINALDI et al. 1978; ELLIOT & TRAUTMAN 1982; MARENSSI et al. 1998a) that crops out in the Seymour and Cockburn islands, close to the northern tip of the Antarctic Peninsula (Fig. 1).

Fossils were measured with a Vernier caliper (0.01 mm resolution), and described using the terminology proposed by BAUMEL & WITMER (1993). Major associated muscles were reconstructed based on observations made from modern penguin species.

Different morphotypes were recognized from the configuration of the articular region of the mandible and the shape of the bill. Most of the beaks and mandibles are isolated, so the correspondence between them could not be ascertained. In every case, they were treated as different individuals.

Reconstructions were based on extant and fossil specimens housed in the Museo de la Universidad de San Marcos (MUSM), Perú, American Museum of Natural History (AMNH), United States, and MLP. For the first mandibular morphotype (MLP 96-I-6-48 and MLP 11-II-20-04) *Pygoscelis adeliae* was taken into account because of its krill-eating habit (Fig. 2E-F). For the second mandibular morphotype (MLP 92-II-2-115a and MLP 92-II-2-108), the living fish-eating *Aptenodytes patagonica* was used, and the Peruvian *Icadyptes salasi* (MUSM 897, CLARKE et al. 2007), *Perudyptes devriesi* (MUSM 889,

CLARKE et al. 2007) and *Inkayaku paracasensis* (MUSM 1444, CLARKE et al. 2010) were considered for mandible proportions (Fig. 3A-B). Finally, reconstruction of the skull (MLP 84-II-1-10) was based on *Eudyptes*, *Spheniscus*, the Eocene *Perudyptes*, and the Patagonian *Paraptenodytes antarcticus* (AMNH 3338, SIMPSON 1946), which show a similar morphology (Fig. 4A-B).

The muscle reconstruction of the skull was based on dissection made in *Spheniscus magellanicus* and on data by ZUSI (1975) (Fig. 5).

3. Systematic paleontology

Aves LINNAEUS, 1758
Sphenisciformes SHARPE, 1891

Material: MLP 96-I-6-48 (several fragments of a mandible, Fig 2A-D); MLP 92-II-2-115a (articular region of the right ramus mandibulae Fig 3C-D); MLP 92-II-2-250 (fragment of skull including interorbital region) all from Locality IAA 1/90, *Cucullaea* I Allomember (Telm 5).

MLP 92-II-2-108 (articular region of the right ramus mandibulae), from Locality DPV 6/84, *Cucullaea* I Allomember (Telm 5).

MLP 92-II-2-203 Fragment of right ramus mandibulae, without the articular region or symphysis, from Locality IAA 1/93, *Cucullaea* II Allomember (Telm 6).
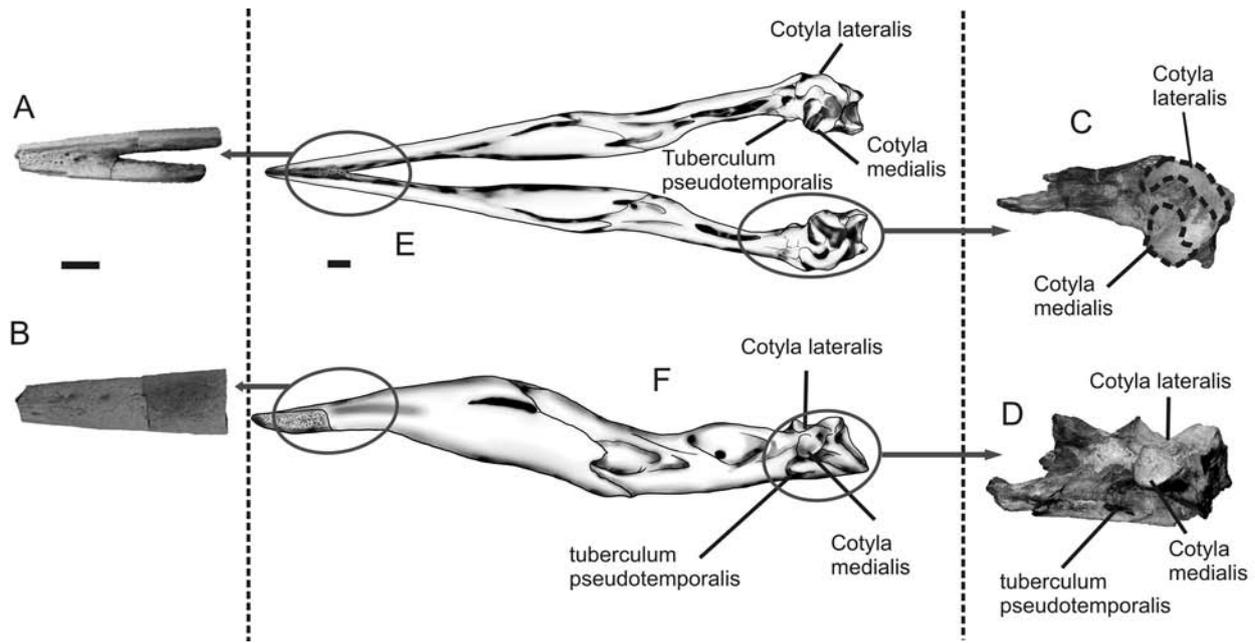
Fig. 2. First mandibular morphotype MLP 96-I-6-48: **A** – Symphysis in dorsal view, **B** – symphysis in lateral view, **C** – articular region in dorsal view, **D** – articular region in medial view, **E-F** – schematic reconstruction based on extant and fossil specimens. Scale bar equals 10 mm.

MLP 78-X-26-158 (fragment of skull including interorbital region), from Locality DPV 2/84, Submeseta Allomember (Telm 7).

MLP 94-III-15-409 (articular region of left mandible); MLP 93-X-1-115 (proximal portion of bill); MLP 94-III-15-413 (left quadrate); MLP 11-II-20-03 (articular region of right mandible); MLP 11-II-20-04 (articular region of left mandible), all from Locality DPV 13/84, Submeseta Allomember (Telm 7).

MLP 78-X-26-2 (ramus mandibulae); MLP 78-X-26-143 (fragment of right ramus mandibulae) and MLP 78-X-26-144 (fragment of mandible); MLP 93-X-1-68 (fragment of right ramus mandibulae, without articular region or symphysis); Several mandible fragments: MLP 92-II-2-195 (right and left ramus mandibularis joined by sediment, but without the articular region or symphysis), 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); MLP 93-X-1-67 (whole bill with missing distalmost tip); MLP 93-X-1-91 (fragment of bill without tip or proximal portion); MLP 84-II-1-10 (posterior portion of skull, Fig. 4C), all from Locality DPV 14/84, Submeseta Allomember (Telm 7).

MLP 91-II-4-223 (articular region of ramus mandibularis); MLP 91-II-4-221 (fragment of ramus mandibularis with symphysis broken and without articular region), from Locality DPV 15/84, Submeseta Allomember (Telm 7).

MLP 91-II-4-202 (distal end of bill), from Locality DPV 16/84, Submeseta Allomember (Telm 7).

4. Results and discussion

Only one single skull (MLP 84-II-1-10) could be included in this study. Although the rostrum is not preserved, useful information could be recovered from the posterior region, particularly from the configuration of the nuchal crests and temporal fossa. The crista nuchalis transversa is moderately developed in comparison with that of modern species. This specimen also presents a well developed crista nuchalis sagittalis, which constitute a wide origin for the m. depressor mandibulae and the adductor mandibulae externus, whose functions are the opening and closing of the bill, respectively. The m. depressor mandibulae is directly associated to the elevation of the upper jaw. According to Bock (1964), in birds that possess a postorbital ligament, when the m. depressor mandibulae is depressing the lower jaw, the force of the system acts vertically on the quadrate. This causes the quadrate to move forward while raising the upper
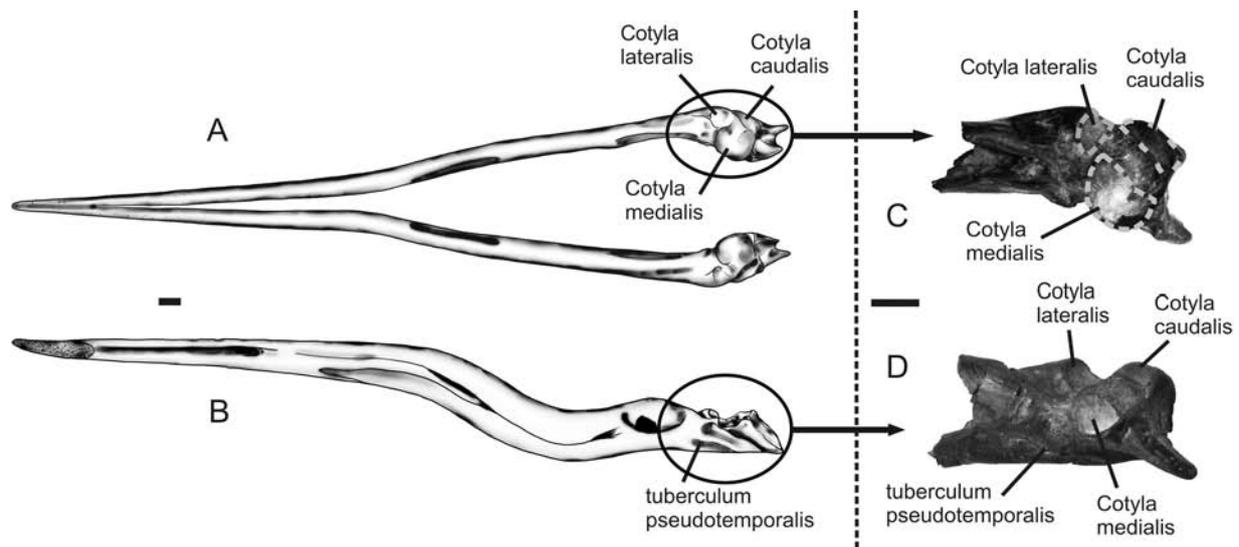
Fig. 3. Second mandibular morphotype MLP 92-II-2-115a: **A-B** – Reconstruction of the mandible based on living fish-eating and Peruvian Eocene penguins. **C** – Articular region of the right ramus mandibularis in dorsal view, **D** – articular region in medial view. Scale bar equals 10 mm.
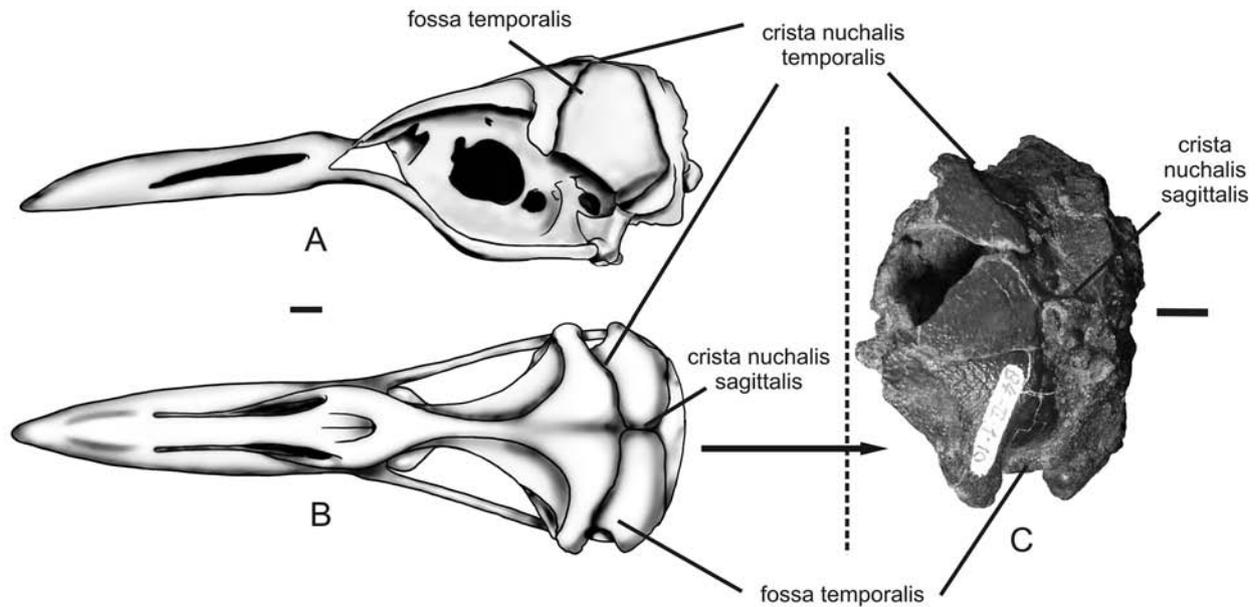

Fig. 4. Skull MLP 84-II-1-10: **A-B** – Reconstruction of the skull based on living and fossil species. **C** – Posterior portion of skull in dorsal view. Scale bar equals 10 mm.

jaw. The postorbital ligament is present in extant penguins, in which it is located backwards, beyond the orbit restricting mandibular depression (BOCK 1964).

We subdivided the mandibles into two groups. The first one is represented by the specimens MLP 96-I-6-48 and MLP 11-II-20-04, and is characterized by the robust and latero-medially depressed rami mandibulae and strong articular regions. Although the articular region presents a wide surface, the merge of the cotyla lateralis and the cotyla dorsalis would reduce the
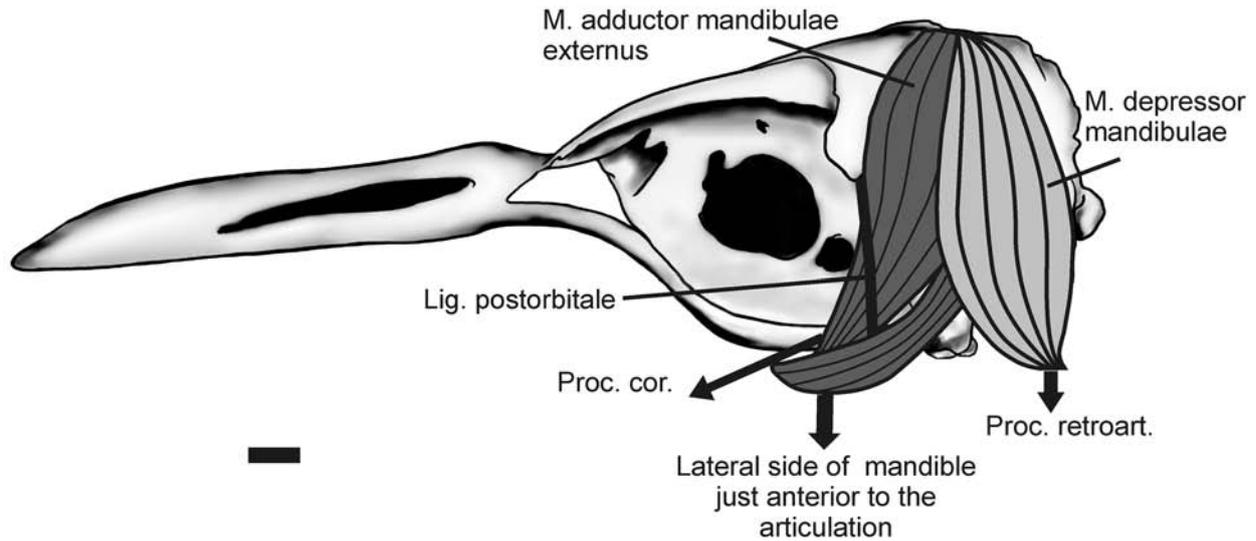
Fig. 5. Schematic reconstruction of the skull MLP 84-II-1-10, showing the main muscles involved in the preserved areas. Arrows point of muscles insertion. Proc. Cor. = Processus coronoideus, Proc. Retroart = Processus retroarticularis, Lig. Postorbitale = Ligamentum postorbitale. Scale bar equals 10 mm.

number of contact points, and therefore, the stabilization at this joint. This is because the increment in number of separate contact points in a mobile joint reduces the chances of elements disarticulation during movement. A particular feature of these mandibles is the great development of the tuberculum pseudotemporalis, different from the condition in the other morphotype described here or any other extant penguin. This process is the site of attachment for the tendon of m. pseudotemporalis, which is in charge of closing the jaws. Its great development would imply capability to bear strong forces, suggesting a diet similar to that of the recent species *Pygoscelis adeliae* (HOMBRON & JACQUINOT, 1841) and *P. antarctica* (FORSTER, 1781) (based mainly on crustaceans approximately 30 mm long, and small fishes).

The second group was recognized on the basis of specimens MLP 92-II-2-115a and MLP 92-II-2-108. Their articular surfaces are more quadrangular in shape and less robust than those of the first group, with well-separated cotyla lateralis and cotyla caudalis. These multiple points of contact between the fossa articularis quadratica and the quadrate would stabilize the articulation as in modern penguins *Spheniscus* BRISSON 1760, *Aptenodytes* MILLER, 1778 with predominantly fish-eating diets. Based on this assump-

tion, this morphotype could represent piscivorous birds. Accordingly, their skulls would have deep fossae temporales for the location of powerful muscles to catch and hold prey, specially the m. adductor mandibularis during pursuit diving.

On the other hand, isolated remains such as MLP 93-X-1-67 and other smaller fragments correspond to more elongated and graceful bills, similar to those of *Aptenodytes*, *Spheniscus,* and *Eudyptula* BONAPARTE, 1856. As the Paleocene *Waimanu tuatahi* (SLACK et al. 2006) from New Zealand and the Eocene *Perudyptes devriesi*, *Icadyptes salasi*, and the recently described *Inkayacu paracasensis* from Peru, the specimen MLP 93-X-1-67 would have preferred large-sized fishes. In addition, and according to HOFER (1945), the straight crista tomialis would help to reduce the risk of fracture under conditions of increased forces during the capture of fast prey (see BOCK 1966). These long and slender bills are not suitable for the development of large tongues as those of plankton-eating penguins (ZUSI 1975). This feature indicates a feeding habit based on fish rather than on krill.

Based on the robustness and size of the remains, it is likely that these bills match the articular regions of the second group. However, only the study of more complete forms will allow contrast of these hypotheses.

Fig. 6. Stratigraphic units of La Meseta Formation at the Peninsula Antarctica, Antarctica (modified from MARENSSI 2006) and the penguin trophic habits inferred for each level in this study.

5. Conclusions

The results obtained here point to a variety of trophic habits and food preferences consistent with the known taxonomic diversity for this unit. The presence of fourteen taxa (or ten according to JADWISZCZAK 2006a) is understandable only in an ecosystem with a high niche partition. Each species of penguins may have preyed on different items and exploited different prey sizes. They could have performed their foraging trips at different times of the day and at different distances from the coast as well.

In this sense, KSEPKA & BERTELLI (2006) proposed that early penguins were primarily piscivorous and that specializations for catching smaller prey such as crustaceans and mollusks evolved later. However, a poorly preserved tip of an upper jaw from the lower levels of the La Meseta Formation was interpreted as a wide beak (JADWISZCZAK 2006b). It would indicate crustacean-eating habits or at least a non fish-catching penguin.

The remains studied here were interpreted as large- and medium-sized piscivorous penguins, large-sized crustacean eaters and medium-sized generalist birds. Across the levels of the La Meseta Formation, these morphotypes were found associated in different ways.

On the basis of the available evidence, it is possible to recreate different penguin breeding colonies for each level (Fig. 6).

In the lowest levels only a fragmentary beak corresponding to a penguin with presumably crustacean and squid food preferences was described by JADWISZCZAK (2006b), whereas in the middle Eocene, large-sized penguins were interpreted as fish and crustacean eaters. Finally, for the late Eocene, both the taxonomic diversity and the amount of members of the colony would have been larger. This colony could be reconstructed as formed by middle-sized generalist penguins, piscivorous large and middle-sized species, and also large penguins with a diet based on crustaceans and squids.

However, it is important to consider here the limitations of the fossil record. Although, the penguin assemblage of this unit is very abundant, most of the remains are disarticulated and fragmented. These biases only allow the recovery of partial data, particularly from the lowest levels of the La Meseta Formation, from where only few remains are known. Main part of the remains, including the scarce articulated skeletons, comes from the Sumbeseta Allomember (late Eocene), at the top of the sequence.

Acknowledgements

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