

Miocene Patagonian penguins: craniomandibular morphology and functional mechanics

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Fossil penguins (Aves, Spheniscidae) are widely recorded throughout the Southern Hemisphere and are especially well represented from the Eocene to present in Patagonia. There are currently three Miocene specimens that include preservation of part of the skull and mandibles: *Paraptenodytes antarcticus*, *Madrynornis mirandus* and MLG 3400 (cf. *Spheniscus*). Osteological appraisals relative to extant taxa and a morphometric analysis were employed to infer possible dietary preferences. The results suggest that *Paraptenodytes antarcticus* and cf. *Spheniscus* were piscivores but used different strategies for prey capture. *Madrynornis*, on the other hand, might have had a mixed diet comprising both small fish and crustaceans.

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PENGUINS (Aves, Spheniscidae) are wing-propelled diving birds whose oldest records occur in the Paleocene of New Zealand (Slack *et al.* 2006) and Antarctica (Tambussi *et al.* 2005). They are widely distributed in the Southern Hemisphere throughout the Cenozoic. Their Patagonian fossil record in particular (Fig. 1) comprises numerous species, including *Madrynornis mirandus* from the middle Miocene Puerto Madryn Formation (Acosta Hospitaleche *et al.* 2007) and *Paraptenodytes antarcticus* Moreno & Mercerat, 1891 from the lower Miocene Gaiman Formation (Acosta Hospitaleche 2005). The remains assigned to these taxa are exceptionally well preserved and include postcranial skeletons with associated skull and mandibular elements. In addition, a poorly preserved skull (MLG 3400) from the early Miocene Chenque Formation, recently reported by Acosta Hospitaleche (2011, 2012), has been tentatively assigned to *Spheniscus* Brisson, 1760 and may correspond to *S. urbinai* Stucchi, 2002, although the fragmentary nature of this material hinders a more definite taxonomic assignment (Acosta Hospitaleche 2011).

Previous studies of Patagonian fossil penguins have explored their systematic relationships (Simpson 1946, Bertelli *et al.* 2006, Acosta Hospitaleche *et al.* 2007, 2011), the endocranial structures of *Paraptenodytes antarcticus* (Ksepka *et al.* 2012) and taphonomy (Cione

et al. 2010). In contrast, their trophic habits and dietary preferences remain unclear. Zusi (1975) and Livezey (1989) examined dietary correlates in cranio-mandibular structures, and Ksepka *et al.* (2006) discussed cranial character state evolution relative to feeding: these studies concluded that early penguins were piscivores. However, at least three morphotypes have been identified recently from fossils found in the Eocene La Mesa Formation of Antarctica (Haidr & Acosta Hospitaleche 2012a), which show variation consistent with dietary diversity. The first morphotype has a rectangular cotyla medialis, which narrows on the most medial section. The cotyla lateralis and c. caudalis are merged (forming a continuous joint surface and enhancing mobility of the mandible) and the ramus mandibulae are mediolaterally compressed, flat and stout. Morphotype two has quadrangular cotylae, slender and cylindrical ramus mandibulae (inferring a narrow bill and tongue), and shows a clear separation between the cotyla lateralis and c. caudalis (creating greater contact with the quadrate and thus enhanced stabilization), equivalent to the morphology of *Aptenodytes* or *Spheniscus* (Haidr & Acosta Hospitaleche, 2012a). The third morphotype was based on skull morphology of a single specimen, MLP 84-II-1-10, which showed a long crista nuchalis sagittalis and wide, shallow fossa temporalis, presumably accommodating development of substantial jaw musculature.

Following previous approaches, we carried out a detailed analysis of cranio-mandibular morphology in



Fig 1. Map showing the fossil localities: 1, locality of *Paraptenodytes antarcticus*, Playa Villarino, Peninsula Valdés, Chubut Province; 2, locality of *Madrynornis mirandus*, Bryn Gwyn, Chubut Province; 3, locality of MLG 3400 cf. *Spheniscus*, Pico Truncado, Santa Cruz Province, Argentina.

the Neogene taxa *Madrynornis mirandus*, *Paraptenodytes antarcticus* and a taxonomically indeterminate specimen, MLG 3400 Spheniscidae cf. *Spheniscus*, with the goal of identifying characters that reflect dietary preferences.

Institutional abbreviations. MLG (Museo del Lago Gutiérrez Dr. Rosendo Pascual); MLP (Museo de La Plata), IAA (Instituto Antártico Argentino); RNP (Rae Natalie Prosser, Museo Acatushún), Argentina; NRM (Naturhistoriska Riksmuseet), Sweden; and AMNH (American Museum of Natural History), United States of America.

Penguin diets and trophic habits

Modern penguins have a varied diet that includes fish, crustaceans and molluscs (Wilson 1995, Boersma & Stokes 1995 and references cited therein). This variation includes not only differences in prey preferences between species, but also intraspecific influences related to environment and access to prey: e.g., pressures from neighboring colonies, or placement of the breeding colony on island or continental areas (Lescroël & Bost 2005). Dietary plasticity must, therefore, be taken into account when defining morphotypes (see Emslie & Patterson 2007). At least two broad dietary categories can, nonetheless, be recognized: piscivores and crustaci-vores (Acosta Hospitaleche & Tambussi 2006). Although most species do not feed exclusively on a single prey type, the contrasting proportions do offer an ecological discriminator (see Williams, 1995 and references therein cited).

Spheniscus and *Aptenodytes* Miller, 1778 are among the most piscivorous of extant penguins (Williams 1995). They capture their prey by pursuit diving and ingest more than 50% fish, or 96% in weight respectively. The beaks of these taxa are long and thin, especially in *Aptenodytes* (Zusi, 1975). Crustaci-vores, on the other hand, which consume primarily krill, possess higher, shorter and wider beaks, together with a fleshy tongue (e.g., *Pygoscelis* Wagler, 1832; see Zusi 1975). Pygoscelid penguins may include as much as 86% by weight of crustaceans in their gastric masses (see Williams 1995).

Acosta Hospitaleche & Tambussi (2006) and Acosta Hospitaleche (2011) also evaluated penguin cranial morphogeometrics as a quantitative indicator of dietary habits and, recently, complemented this with similar assessments of the articular region in the mandible (Haidr & Acosta Hospitaleche 2012a, 2012b). These methodologies not only identified the standard piscivore

Repository	Species	Diet
MEF PV 100	<i>Madrynornis mirandus</i>	mixed diet
MLP M- AMNH 3338	<i>Paraptenodytes antarctica</i>	Piscivore
RNP A-2019	<i>Aptenodytes patagonicus</i>	Piscivore
RNP A-2020	<i>Aptenodytes patagonicus</i>	Piscivore
RNP A-2021	<i>Aptenodytes patagonicus</i>	Piscivore
RNP A-2022	<i>Aptenodytes patagonicus</i>	Piscivore
RNP A-2023	<i>Aptenodytes patagonicus</i>	Piscivore
RNP A-2024	<i>Aptenodytes patagonicus</i>	Piscivore
NRM 886,041	<i>Aptenodytes patagonicus</i>	Piscivore
NRM 928,157	<i>Aptenodytes patagonicus</i>	Piscivore
NRM 928,152	<i>Aptenodytes patagonicus</i>	Piscivore
NRM 928,171	<i>Aptenodytes patagonicus</i>	Piscivore
RNP A-27	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-42	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-103	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-171	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-482	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-483	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-496	<i>Eudyptes chrysocome</i>	mixed diet

(Continued)

Table 1. (Continued).

Repository	Species	Diet
RNP A-511	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-518	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-637	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-642	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-707	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-708	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-727	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-733	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-850	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-897	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-1001	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-1014	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-1072	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-1085	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-1115	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-1116	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-1182	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-1636	<i>Eudyptes chrysocome</i>	mixed diet
RNP A-767	<i>Pygoscelis adeliae</i>	Crustacivore
RNP A-1652	<i>Pygoscelis adeliae</i>	Crustacivore
RNP A-1836	<i>Pygoscelis adeliae</i>	Crustacivore
MLP 435	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 436	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 437	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 439	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 440	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 442	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 443	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 444	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 446	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 447	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 455	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 704	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 705	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 706	<i>Pygoscelis antarctica</i>	Crustacivore
RNP A-420	<i>Pygoscelis antarctica</i>	Crustacivore
RNP A-426	<i>Pygoscelis antarctica</i>	Crustacivore
RNP A-531	<i>Pygoscelis antarctica</i>	Crustacivore
RNP A-766	<i>Pygoscelis antarctica</i>	Crustacivore
RNP A-1875	<i>Pygoscelis antarctica</i>	Crustacivore
MLP 450	<i>Pygoscelis papua</i>	Crustacivore
MLP 451	<i>Pygoscelis papua</i>	Crustacivore
MLP 454	<i>Pygoscelis papua</i>	Crustacivore
MLP 703	<i>Pygoscelis papua</i>	Crustacivore
MLP 708	<i>Pygoscelis papua</i>	Crustacivore
RNP A-125	<i>Pygoscelis papua</i>	Crustacivore
RNP A-804	<i>Pygoscelis papua</i>	Crustacivore
RNP A-806	<i>Pygoscelis papua</i>	Crustacivore
RNP A-1804	<i>Pygoscelis papua</i>	Crustacivore
MLP 35	<i>Spheniscus magellanicus</i>	Piscivore
MLP 611	<i>Spheniscus magellanicus</i>	Piscivore
MLP 614	<i>Spheniscus magellanicus</i>	Piscivore
MLP 642	<i>Spheniscus magellanicus</i>	Piscivore
MLP 686	<i>Spheniscus magellanicus</i>	Piscivore
MLP 717	<i>Spheniscus magellanicus</i>	Piscivore
MLP 727	<i>Spheniscus magellanicus</i>	Piscivore
MLP 728	<i>Spheniscus magellanicus</i>	Piscivore
MLP 756	<i>Spheniscus magellanicus</i>	Piscivore
MLP 789	<i>Spheniscus magellanicus</i>	Piscivore
MLP 791	<i>Spheniscus magellanicus</i>	Piscivore
MLP 847	<i>Spheniscus magellanicus</i>	Piscivore
MLP 873	<i>Spheniscus magellanicus</i>	Piscivore
MLP 922	<i>Spheniscus magellanicus</i>	Piscivore
MLP 985	<i>Spheniscus magellanicus</i>	Piscivore

Table 1. Inferred diets of 88 adult penguins from nine fossil and extant species used in the morphometric analysis.

and crustacivore dietary categories, but further recognized a third generalist grade, which manifested a more mixed prey composition (Haidr & Acosta Hospitaleche 2012a, 2012b).

Material and methods

A morphometric analysis was carried out on the articular surface of the mandible from 88 adult individuals representing nine modern and fossil species of penguins (Table 1): *Spheniscus magellanicus* Forster, 1781 (15), *Pygoscelis papua* Forster, 1781 (9), *P. adeliae* Hombron & Jacquinot, 1841 (3), *P. antarctica* Forster, 1781 (19), *Aptenodytes patagonicus* Miller, 1778 (11), *Eudyptes chrysocome* Forster, 1781 (25), *Madrynornis mirandus* (1) and *Paraptentodytes antarcticus* (1). MLG 3400 was not included because the mandible was not preserved. Five landmarks and 11 semi-landmarks (Fig. 2) were established, and shape changes were assessed through an analysis of deformations using the TPS software package (Rohlf 2010). This followed the approach of Pérez *et al.* (2006) and was evaluated against the feeding morphotypes established by Haidr & Acosta Hospitaleche (2012a). Landmark 1 represents the anterior initiation of the cotyla lateralis, and semi-landmarks 2, 3, 4 and 5 are located between landmarks 1 and 6, the latter of which is placed at the greatest point of the concavity formed by the merger of the cotyla lateralis and c. caudalis (or at the greatest point of concavity of the cotyla lateralis when the cotyla caudalis is not differentiated). Semi-landmarks 7 and 8 are placed between landmarks 6 and 9. The latter is positioned at the most caudal point of the cotyla caudalis (or c. lateralis when c. caudalis is not developed). Landmark 10 is at the most caudal end of the cotyla medialis, whereas landmark 16 is located at the most cranial contact point between the cotylae medialis and c. lateralis. Semi-landmarks 11, 12, 13, 14 and 15 are located between the latter two landmarks (Fig. 2).

Additional material used for comparative descriptions includes *Eudyptula minor* Bonaparte, 1856, *Eudyptes chrysocome*, *Pygoscelis adeliae*, *P. antarctica*, *P. papua*, *Spheniscus magellanicus* and *Aptenodytes patagonica*. Dissections of *Spheniscus magellanicus* were also undertaken in order to identify muscle origins and insertions together with articular surfaces. Description of these soft tissue structures follows the terminology of Zusi (1975) and Baumel (1993).

Results and discussion

Morphometric analyses

Results of the morphogeometric analyses (Fig. 3) indicate that the first principal component (PC1) adequately differentiates crustacivores (*Pygoscelis* and *Eudyptes* Vieillot, 1816) from piscivores (*Spheniscus*, *Aptenodytes*) and places the extinct *Paraptentodytes* with *Aptenodytes*,

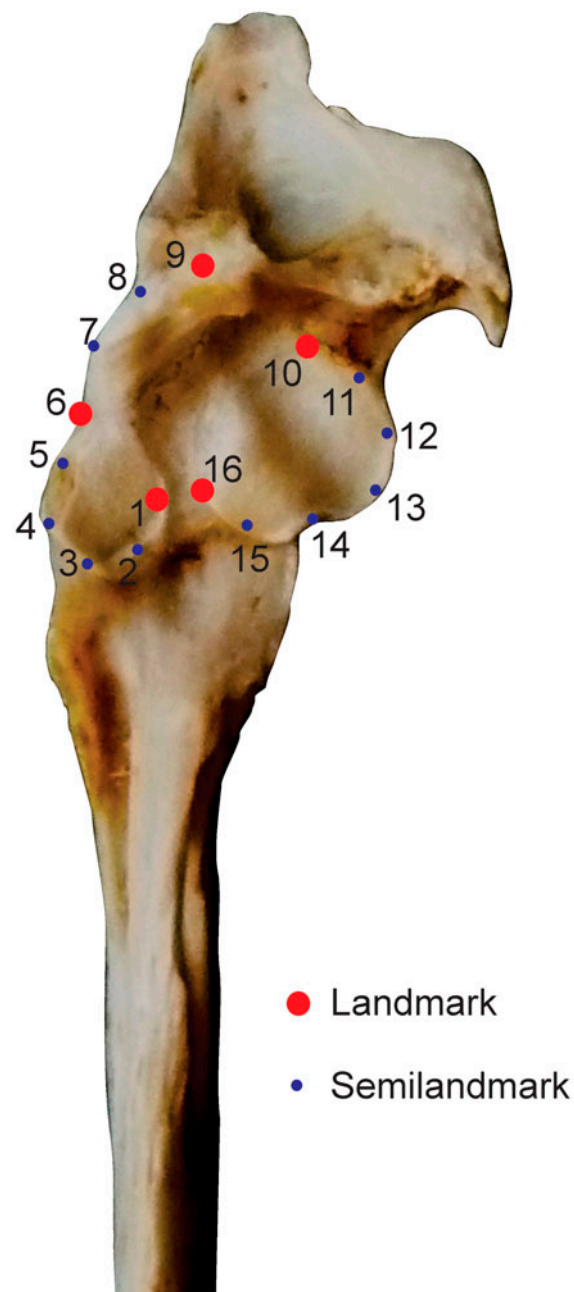


Fig 2. Articular surface from a *Aptenodytes patagonicus* mandible, showing landmarks and semilandmarks used in the morphometric analysis.

and *Madrynornis* closer to *Spheniscus* and some specimens of *Eudyptes*. PC1 also shows the morphological change in articulation shape, from a surface that is wider than long (right quadrants), to one that is more quadrangular in outline (left quadrants), and the corresponding trend towards rounding of the cotyla medialis, with a short gap separating it from the cotyla lateralis. The continuous edge of the cotylae lateralis and c. caudalis likewise becomes progressively straighter toward the right quadrant. The cotylar configuration found in the left quadrants, therefore, helps in the stabilization of the mandibular articulation. It works as a caudal and anterior stop, during the opening and closing

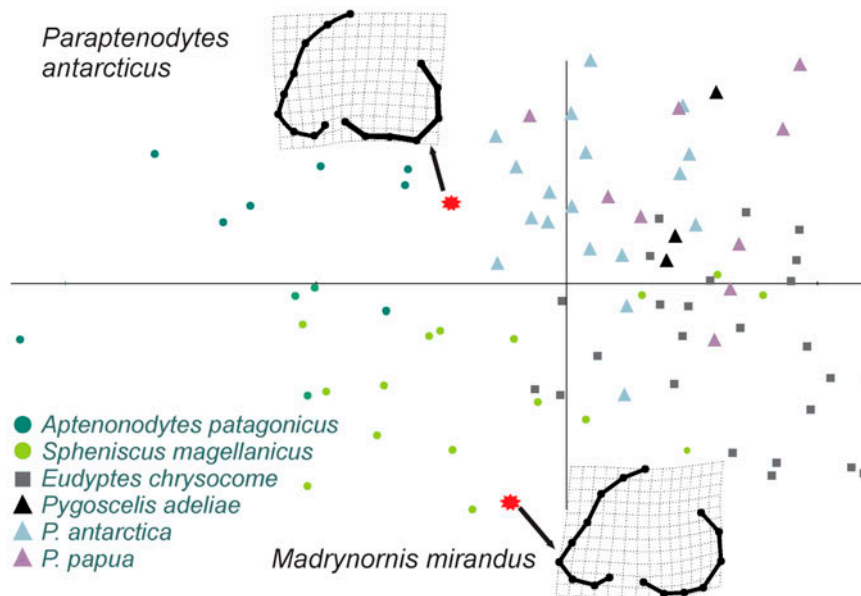


Fig 3. Results of the morphometric analysis of articular surfaces of mandibles. Deformation grids show the landmark and semilandmark configuration in *Madrynornis mirandus* and *Paraptenodytes antarcticus*.

movements of the bill, which has great importance during the capture of large and slippery prey.

The second principal component (PC2) shows the progression from a concave outline represented by landmarks 13 to 15 towards a convex one in the lower quadrants, and the widening of the gap between cotyla lateralis and medialis.

Comparative descriptions of the fossils

Madrynornis mirandus (MEF-PV 100). This species (Fig. 4A, 5B) is represented by a large portion of the cranium, a rostral mid-section, and the posterior part of the left mandibular ramus (Acosta Hospitaleche *et al.* 2007). The development of the fossa temporalis is intermediate between the conditions in *Spheniscus* and *Eudyptes*, and it occupies a lateral position similar to that of *Eudyptula*. The posterior portion of the fossa adjacent to the crista nuchalis transversa is deeper and narrower than that found in *Spheniscus*. In dorsal view, the fossa temporalis is triangular as in all living penguins, and differs from the condition in the indeterminate Spheniscidae (MLP 84-II-1-10) from the Eocene of Antarctica (Haidr & Acosta Hospitaleche 2012a) and from *Paraptenodytes*. The crista nuchalis sagittalis is not differentiated. The processus postorbitalis is thin and well developed, and extends ventrally.

The aperturæ nasi ossea are visible in dorsal view as in *Pygoscelis* and *Eudyptes* (the proportions and shape are particularly reminiscent of *P. papua*), which could indicate a similarly broad beak (and is related to feeding on krill: Zusi 1975, Ksepka & Bertelli 2006). The mandibular ramus is also laterally compressed as in all living penguins, but noticeably dissimilar to Eocene fossil penguins for which a piscivorous diet has been

inferred (Haidr & Acosta Hospitaleche 2012a). The processus coronoideus, upon which inserts the aponeurosis of the m. adductor mandibulae externus pars rostralis (an elevator of the mandible), resembles that of *Spheniscus* (Fig. 4A). The tuberculum pseudotemporale, located medially on the caudal region of the mandibular ramus, shows the same degree of development as in all modern species. The processus retroarticularis (Fig. 5B) has medial and lateral projections developed to a degree intermediate between *Spheniscus* and *Eudyptes*, and provides attachment for the m. depressor mandibularis (Fig. 4A). The processus retroarticularis in *Spheniscus* and *Eudyptes* extends further caudally than in *Pygoscelis papua*, presumably increasing the length of the lever arm for this muscle.

The fossa articularis quadratica is shallow, and the proportions of the joint are similar to those of ‘morphotype 1’ from the Eocene of Antarctica, which is interpreted to have been a potential crustacivore (Haidr & Acosta Hospitaleche 2012a). The cotyla lateralis and c. caudalis also appear to be fused as in ‘morphotype 1’ (Haidr & Acosta Hospitaleche 2012a), functioning as a single articulation surface, although this component of the mandible is incomplete in MEF-PV 100. The cotyla medialis is large, medially extended and rectangular, whereas it is quadrangular in ‘morphotype 2’ (see Haidr & Acosta Hospitaleche 2012a). The sulcus intercotylaris is weakly developed as in *Paraptenodytes antarcticus*, unlike the Eocene morphotypes, and is again consistent with modern crustacivores such as *Pygoscelis* or *Eudyptes* (Haidr & Acosta Hospitaleche, 2012a). The general morphology and proportions of the articular and post articular surfaces including the processus retroarticularis have an overall resemblance to *Eudyptes chrysocome* and *Spheniscus*.

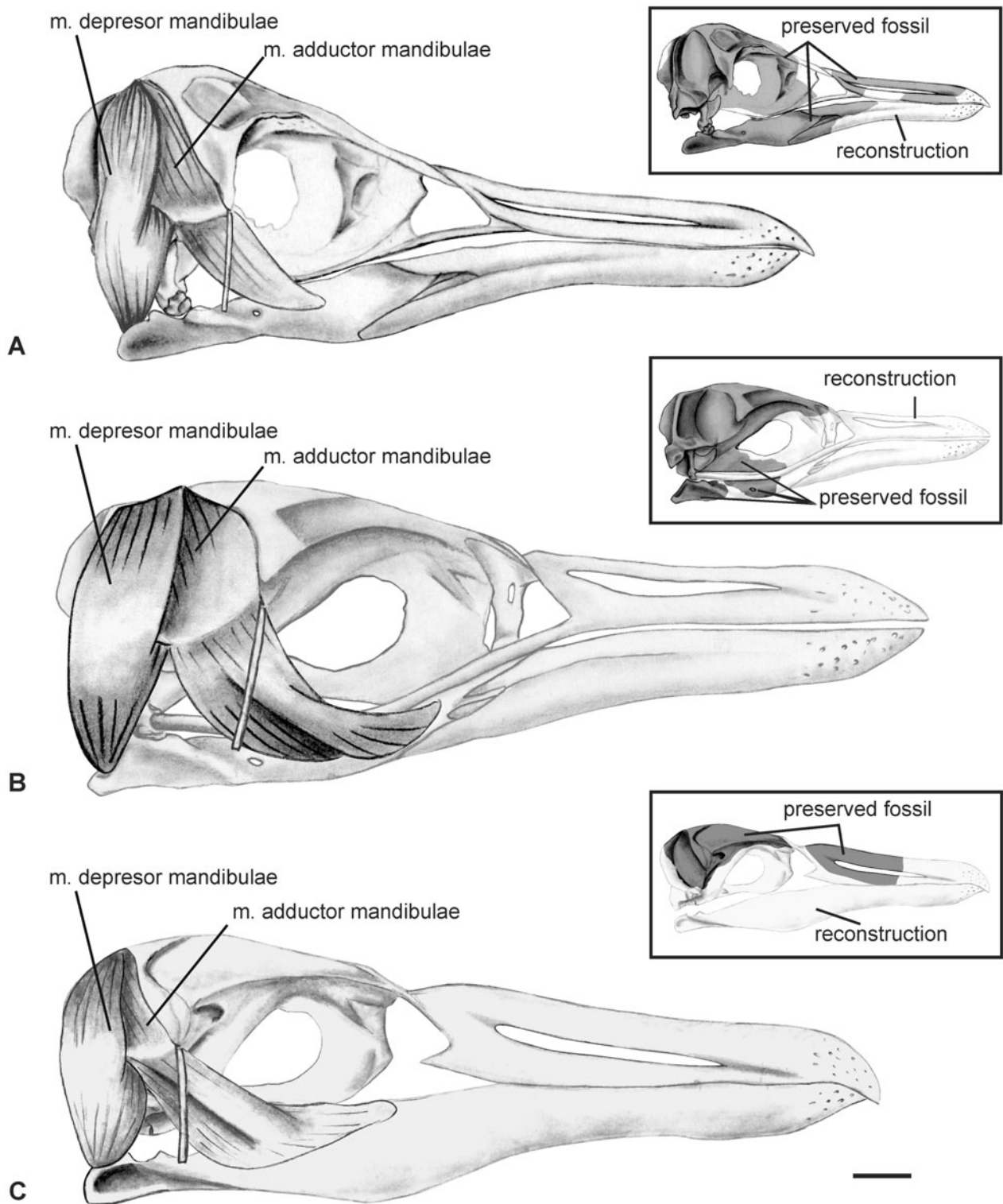


Fig 4. Schematic reconstruction of the fossil material and the associated musculature. **A**, *Madrynornis mirandus*; **B**, *Paraptenydytes antarcticus*; **C**, *Spheniscidae cf. Spheniscus*. Scale bar = 10 mm.

Paraptenydytes antarcticus (MLP cast of AMNH 3338). Remains include a partial skull and fragments of the left mandibular ramus (Bertelli *et al.* 2006, figs 1–3). The taxon is characterized by an exceptionally deep fossa temporalis and a well-developed crista nuchalis sagittalis. The *m. adductor mandibulae externus* of *Paraptenydytes* (Fig. 4B) has a more dorsal

origin from the fossa temporalis than in *Madrynornis* (Fig. 4A) and MLG 3400 (Fig. 4C). The presence of a crista nuchalis sagittalis provides a larger attachment surface allowing the development of a more voluminous musculature (Fig. 4B). The crista nuchalis transversa extends to the sagittal crest, providing an extensive line of origin for the *m. depressor mandibulae* (Fig. 4B).

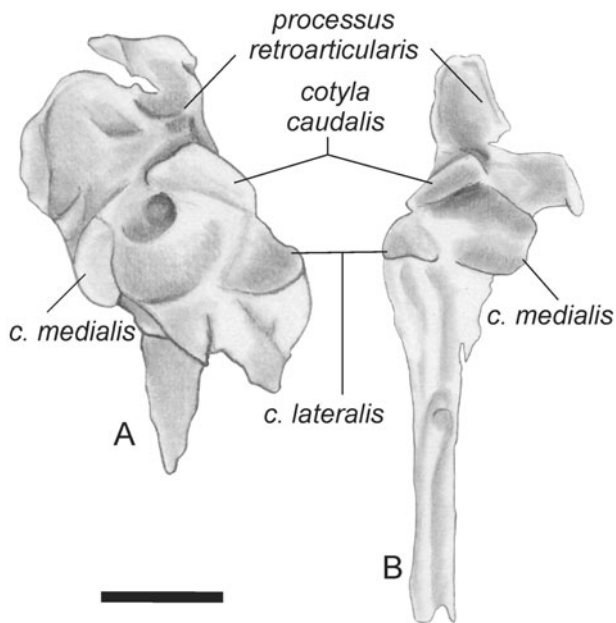


Fig 5. Schematic reconstruction of the fossil mandibles. **A**, *Paraptenodytes antarcticus*; **B**, *Madrynornis mirandus*. Scale bar = 10 mm.

The posterior margin of the fossa temporalis, which contacts the crista nuchalis transversa, is deeper and wider than in *Madrynornis* and *Spheniscus*, and could be related to the development of musculature involved in the capture and manipulation of large prey items.

The mandible of AMNH 3338 (Fig. 5A) is not well preserved. The ratio of length to width of the articular surface is similar to that of *Aptenodytes*. The cotyla lateralis is wide and similar to that of ‘morphotype 2’ and *Spheniscus magellanicus* (Haidr & Acosta Hospitaleche, 2012a). The cotyla caudalis and c. lateralis form two separate articulation surfaces. This, together with the cotyla medialis, presumably imparted stability for the quadrate articulation.

The processus retroarticularis is damaged but conforms to that of *Pygoscelis papua* (it is wider and less projected than in the living taxa compared). The fossa retroarticularis is shallow (see Bertelli *et al.* 2006).

Spheniscidae cf. *Spheniscus* (MLG 3400; Acosta Hospitaleche 2012, fig. 2). This specimen is slightly smaller than *Aptenodytes*. The fossa temporalis has a compatible shape and rounded dorsal tip like that of *Spheniscus magellanicus*. The merger of the crista nuchalis temporalis and c.n. transversa occurs dorsally, forming a short crista nuchalis sagittalis. The fossa temporalis is as deep as in *Spheniscus*, and is likewise triangular in dorsal view. This structure, together with the merged cristae, attachment of the m. adductor mandibulae, suggests increased leverage and a powerful bite (Acosta Hospitaleche 2011, 2012), and is unlike the condition in *Madrynornis* where both cristae merge laterally rather than dorsally (Acosta Hospitaleche *et al.* 2007). The processus postorbitalis extends laterally to a much greater degree than that seen in extant species and Miocene Patagonian taxa, and implies that the ligamentum

postorbitale formed an acute angle between the processus postorbitalis and its vertical insertion point on the mandible. This potentially facilitated a wider gape of the mandible and ingestion of larger prey.

Conclusions

The Patagonian fossil penguin fauna is represented through two stratigraphical intervals: the lower and upper middle Miocene. Taxa occurring in the older assemblages include *Paraptenodytes antarcticus* and the indeterminate MLG 3400, whereas *Madrynornis mirandus* appears, and probably *Paraptenodytes antarcticus* persists, further up-sequence (Acosta Hospitaleche 2003, 2005).

The cranial and mandibular morphology of *Paraptenodytes antarcticus* implies powerful musculature and possibly the ability to catch larger-bodied prey, including fish. Its mandible is also compatible in form with extant piscivorous species, and Eocene remains found in Antarctica (Haidr & Acosta Hospitaleche 2012a). Thus, our morphometric analyses indicate an affinity with *Aptenodytes*, which is a specialized piscivore (Fig. 3).

MLG 3400, tentatively assigned to *Spheniscus* (Acosta Hospitaleche, 2011), might also have been piscivorous, but differences in muscle insertion areas and overall osteology relative to *Paraptenodytes* imply a potentially contrasting feeding strategy.

In summary, it can be inferred that during the early Miocene, Patagonian penguin assemblages comprised fish-eating species that potentially partitioned their food resources by selecting prey of different sizes. By the middle Miocene, however, mixed diet forms can be recognized.

The cranial osteology of *Madrynornis mirandus* implies lesser development of the mandibular musculature (adductor and depressor) than in *Paraptenodytes*. Although this skull condition is shared with *Aptenodytes patagonica*, which is a piscivore, the thin and slender beak and mandible typical of most piscivorous animals is absent in *Madrynornis mirandus*. Rather, it has a broad beak much like *Pygoscelis papua*, which consumes both krill and a significant component of small fish (Williams 1995). In addition, the similar shape of the processus retroarticularis relative to *Eudyptes* is suggestive of a tendency towards the capture of small fish, as opposed to crustacevory. These morphological features are complemented by the results of the morphometric analysis, which placed *Madrynornis* in a position close to both *Spheniscus* and *Eudyptes*. We, therefore, propose that *M. mirandus* might have had a broad diet involving opportunistic predation upon small-bodied fish, cephalopods and crustaceans.

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