

# Skull shape analysis and diet of South American fossil penguins (Sphenisciformes)

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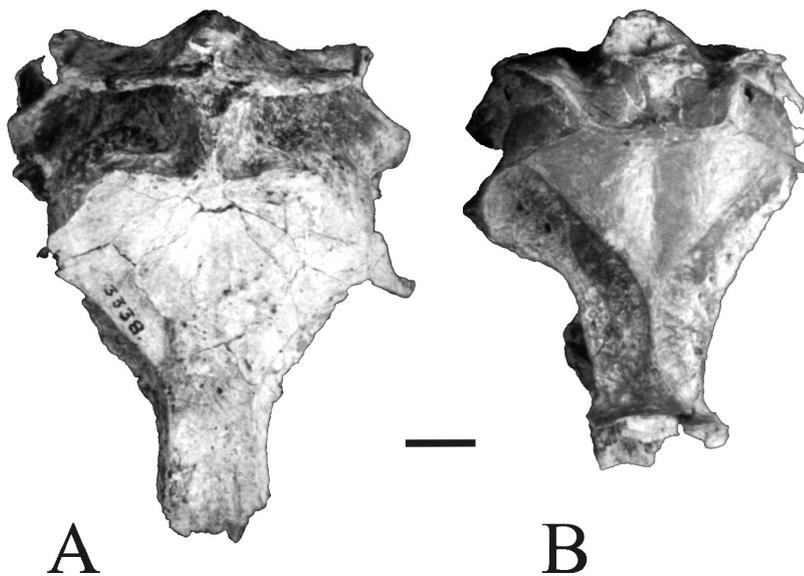
**ABSTRACT** – Form and function of the skull of Recent and fossil genera of available Spheniscidae are analysed in order to infer possible dietary behaviors for extinct penguins. Skull shapes were compared using the Resistant-Fit Theta-Rho-Analysis (RFTRA) Procrustean method. Due to the availability and quality of the material, this study was based on six living species belonging to five genera (*Spheniscus*, *Eudyptula*, *Eudyptes*, *Pygoscelis*, and *Aptenodytes*) and two Miocene species: *Paraptenodytes antarticus* (Moreno and Mercerat, 1891) and *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato & Cozzuol. Seventeen landmark from the skull were chosen, including homologous and geometrical points. Morphological similarities among RFTRA distances are depicted using the resulting dendrograms for UPGMA (unweighted pair-group method using arithmetic average) cluster analysis. This shape analysis allows the assessment of similarities and differences in the skulls and jaws of penguins within a more comprehensive ecomorphological and phylogenetic framework. Even though penguin diet is not well known, enough data supports the conclusion that *Spheniscus* + *Eudyptes* penguins specialize on fish and all other taxa are plankton-feeders or fish and crustacean-feeders. We compared representative species of both ecomorphological groups with the available fossil material to evaluate their feeding strategies. Penguins are the most abundant birds, indeed the most abundant aquatic tetrapods, in Cenozoic marine sediments of South America. The results arising from this study will be of singular importance in the reconstruction of those marine ecosystems.

**Key words** - *Spheniscidae*, skull shape analysis, ecomorphology, South America, fossil and living penguins.

## Analyse de la forme du crâne et régime alimentaire des manchots (Sphenisciformes) fossiles d'Amérique du Sud

- La forme et la fonction du crâne des genres récents et fossiles de Spheniscidés disponibles sont analysées dans le but de savoir si les possibles comportements alimentaires des pingouins éteints pourraient être inférés à partir de cette analyse. Les formes du crâne ont été comparées en utilisant la méthode de l'Analyse Procrustéenne "Resistant-Fit Theta-Rho-Analysis (RFTRA)". En raison de la disponibilité et de la qualité du matériel, cette étude a été basée sur six espèces vivantes appartenant à cinq genres (*Spheniscus*, *Eudyptula*, *Eudyptes*, *Pygoscelis* et *Aptenodytes*) et deux espèces miocènes: *Paraptenodytes antarticus* (Moreno et Mercerat, 1891) et *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato & Cozzuol 2007. Dix-sept points remarquables du crâne ont été choisis, y compris les points homologues et géométriques. Les similitudes morphologiques parmi les distances de RFTRA sont dépeintes en utilisant les dendrogrammes résultants pour UPGMA employant l'analyse de groupement. Cette analyse permet l'évaluation des similitudes et des différences entre les crânes et les mâchoires des manchots dans une analyse écomorphologique et phylogénétique plus complète. Même si le régime alimentaire des manchots n'est pas bien connu, il existe certaines données indiquant que les manchots *Spheniscus* + *Eudyptes* ont un régime spécialisé de poissons et les autres taxa se nourrissent de plancton ou de poissons et crustacés. Nous avons comparé des espèces représentatives des deux groupes écomorphologiques aux matériaux fossiles disponibles dans le but d'évaluer leurs stratégies d'alimentation. Les pingouins sont les oiseaux les plus abondants, en fait les tétrapodes aquatiques les plus abondants, dans les sédiments marins cénozoïques de l'Amérique du Sud. Les résultats de cette étude auront sans doute une importance singulière dans la reconstruction de ces écosystèmes marins.

**Mots clés** - *Spheniscidae*, analyse de forme du crâne, écomorphologie, Amérique du Sud, manchots fossiles et vivants



**Figure 1** - Skull in dorsal view of (A) *Paraptenodytes antarctica* AMNH 3338, and (B) *Madrynornis mirandus* MEF PV=100. Scale bar equals 1 cm.

## INTRODUCTION

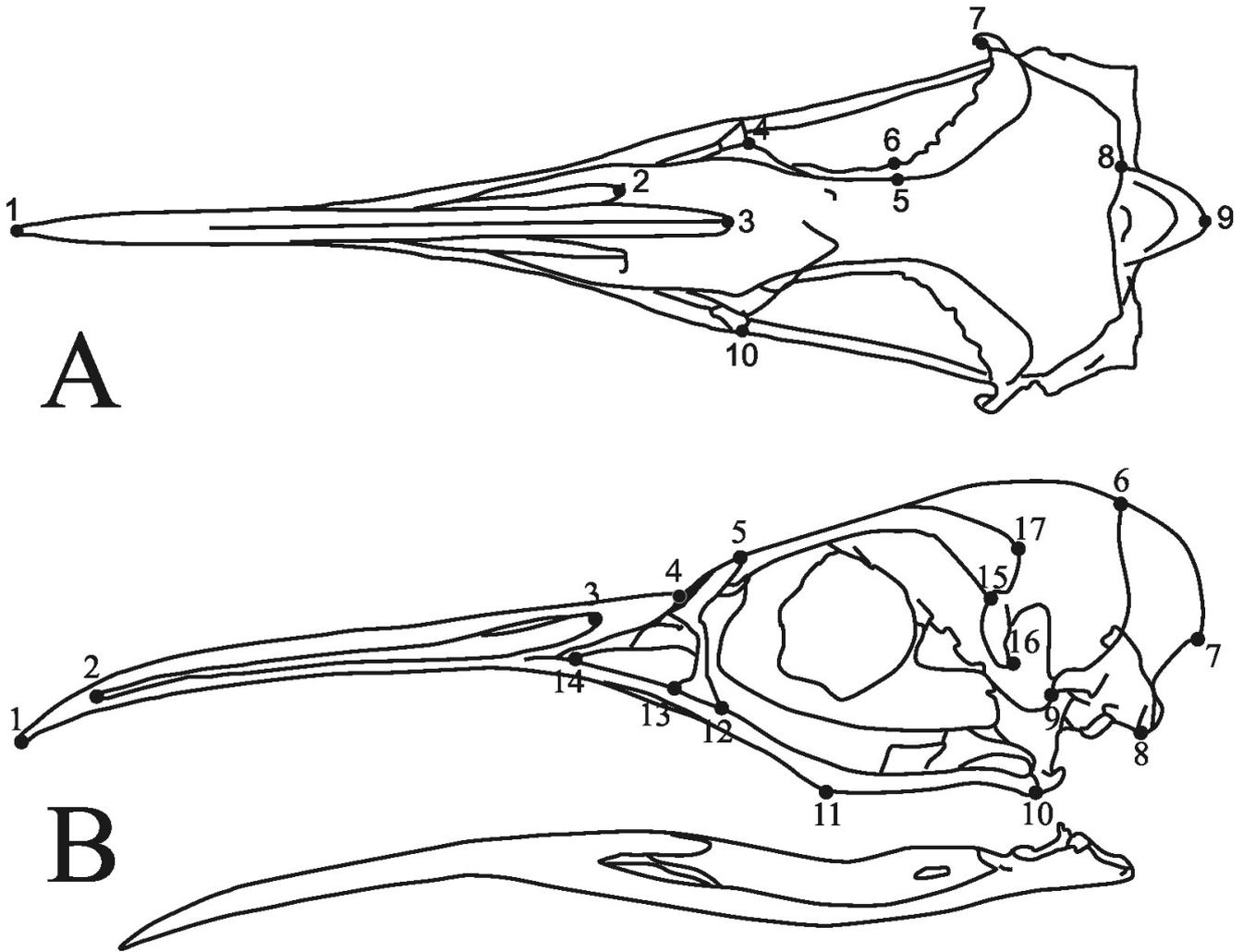
The ability of organisms to perform specific ecological activities, such as escaping predators or capturing their food, implies better feasibility in survival, reproduction and growth (Waingwright, 1994). Consequently, there will exist a critical relation between morphology, performance and habitat uses. Additionally, an understanding of the ecological context in which the organisms use their maximal capability is necessary to be able to recognize why a trait evolved (Irschick & Losos, 1998). Numerous field and laboratory studies of different vertebrates are known that attempt to make predictions of actual movements from the analysis of movement potentialities. Irschick & Losos (1998) in reference to the speed of *Anolis*, affirm that only field performance studies could say exactly if the total inferred capacity is used by the animal. Therefore, a conjunction of field and laboratory studies is indispensable to make appropriate inferences about the relationship between design and abilities. Nevertheless, when the objects of study are fragments of extinct organisms, the inferences on capacities and patterns are severely restricted. This situation, which is, by the way, well known of any paleontologist, restricts us to a profound analysis of the only objects available: bones and muscular insertions in cases when they have been preserved. This work is the first of a series that tries to analyse comparatively the skull design of fossil and living penguins and to contrast the results with data on trophic capabilities derived from other sources.

Penguins (Sphenisciformes) are the best adapted, wing propelled divers among birds. The fusiform or bobbin-shaped body, and the short legs situated in the posterior part of the body, confer them a highly hydrodynamic design. They are important top consumers in the food chains of temperate to cold marine water ecosystems and apparently, this has been so since their earliest records (Late Paleocene, Tambussi et al., 2005).

Considerable effort has been made in the last decade to study penguins, particularly their underwater energetics, metabolism and food preferences (Bannasch, 1992; Bannasch et al. 1994), but still little is known of the basic skeletal adaptations of penguins and their prey-capture efficiency. Despite the relatively long history of descriptive anatomy (Watson, 1883; Pycraft, 1898; Shufeldt, 1909; Lowe, 1933; Schreiweis, 1972), studies of the morphology of Recent and fossil penguins using quantitative techniques are few (see for example Livezey, 1989 or Jadwiszczak, 2001). Two studies covering the topic, “avian cranial diversity” (Zusi, 1993) and evolution of trophic patterns in birds (Zweers et al., 1997) were published, and particularly, we know a single work in which skull structure is interpreted with respect to different food and feeding behaviour in living penguins (Zusi, 1975, see also Stonehouse, 1993). However, none of these works applied any morphometric tools, such as those used here. According to Zusi, the goal of his work is not “concerned with classification and phylogeny” (Zusi, 1975: p 59) although he recognizes two phyletic lines. This position will be further discussed later on.

We examined the shape of the skull of Recent genera of available Spheniscidae and two fossil genera. Due to the accessibility and quality of the material, this study was based on six living species belonging to five genera (*Spheniscus magellanicus*, *Eudyptula minor*, *Eudyptes chrysosome*, *Pygoscelis papua*, *Aptenodytes forsteri* and *A. patagonicus*) and all the skulls of fossil species known from Argentina: *Paraptenodytes antarcticus* (Moreno & Mercerat, 1891) (fig. 1A) and a second specimen *Madrynornis mirandus* Acosta Hospitaleche, Tambussi, Donato & Cozzuol 2007 (fig. 1B). We then compared these data with those about diet and prey-capture mode obtained from the literature.

We addressed the following hypotheses: (1) the shape of the skull gives an idea of the animal’s trophic pref-



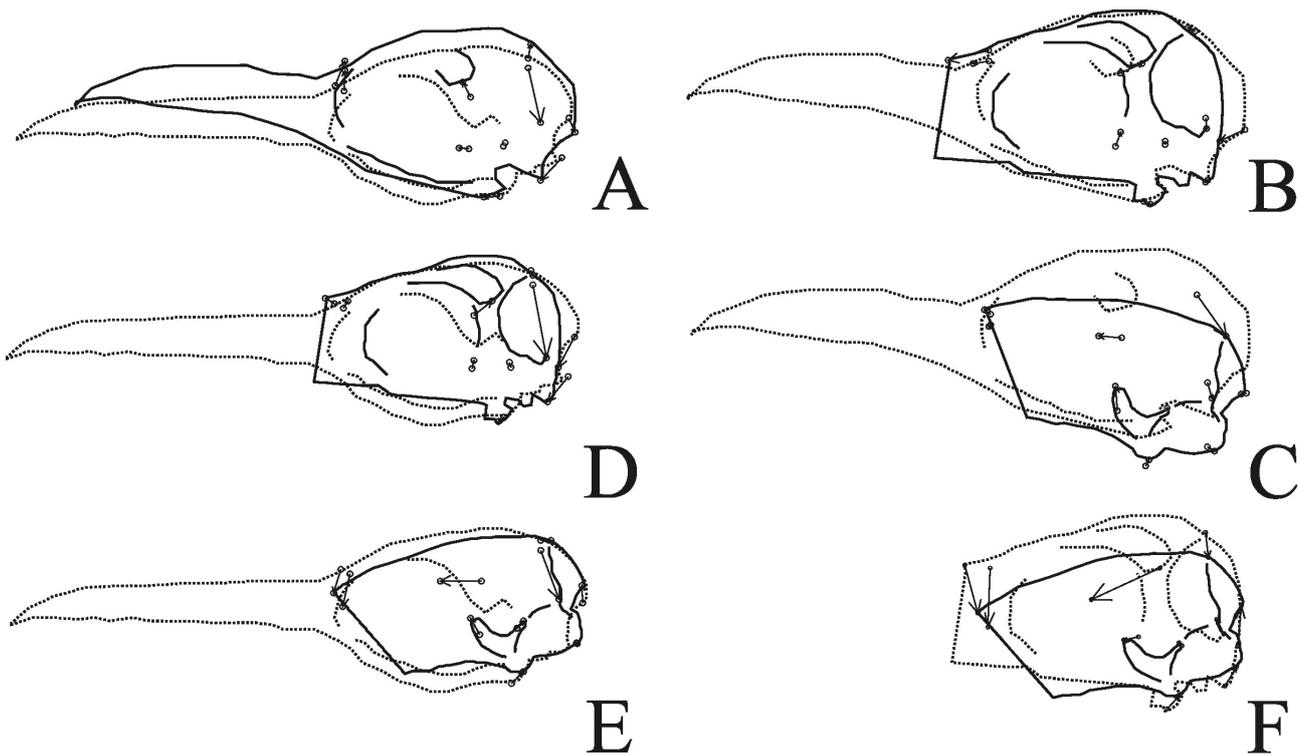
**Figure 2** - Skull of *Aptenodytes patagonica* showing landmarks used for RFTRA in dorsal and lateral views. (A) skull in dorsal view: 1. tip of the bill; 2. posterior end of the nasal fossa; 3. end of nasal process of os premaxillare; 4. dorsal part of os lacrimale; 5. internal edge of fossa glandulae nasalis at interorbital region; 6. external edge of fossa glandulae nasalis at interorbital region; 7. post-orbital process; 8. dorsal end of fossa temporalis; 9. posterior end of prominentia cerebellaris; 10. anterior point of arcus jugalis. (B) skull in lateral view: 1. tip of the bill; 2. anterior end of nasal fossa; 3. posterior end of nasal fossa; 4. lacrimal-nasal contact point; 5. lacrimal-frontal contact point; 6. most posterodorsal point of fossa temporalis; 7. posterior end of prominentia cerebellaris; 8. condyle; 9. tip of zygomaticus process (os squamosum); 10. suture between arcus jugalis and quadratum; 11. point of maximum curvature of arcus jugalis; 12. posterior suture between lacrimal and arcus jugalis; 13. anterior suture between lacrimal and arcus jugalis; 14. anterior point of fossa antorbitalis; 15. external edge of nasal fossa; 16. tip of postorbital process; 17. internal edge of nasal fossa.

erences and (2) the shape of the skull and jaw allows the differentiation of ecomorphic assemblages.

As we mentioned previously, the present work is part of a more ambitious project that attempts to integrate functional and ecomorphological, paleontological and phylogenetic studies to develop hypotheses on penguin trophic strategies and evolution. Although preliminary, our results offer more reliable data for the construction of paleobiological hypotheses and the reconstruction of extinct marine ecosystems.

**BACKGROUND**

Fossil penguins are an attractive group for examining questions concerning locomotor performance (Bannasch, 1986 and the literature cited therein; Whitehead, 1989; Green et al., 2003) and feeding behaviour (Williams, 1995; Stonehouse, 1975). Penguins are entirely planktonic or nektonic feeders. Their main prey groups include fishes, crustaceans and cephalopods (Simpson, 1976). Although the various authors who have investigated the matter differ in their accounts



**Figure 3** - Results of RFTRA of the skull in lateral view of (A) *Pygoscelis* (base specimen) and *Spheniscus*, (B) *Spheniscus* (base specimen) and *Madrynornis mirandus* MEF PV=100, (C) *Spheniscus* (base specimen) and *Paraptendytes*, (D) *Pygoscelis* (base specimen) and *Madrynornis mirandus* MEF PV=100, (E) *Pygoscelis* (base specimen) and *Paraptendytes*, (F) *Madrynornis mirandus* MEF PV=100 (base specimen) and *Paraptendytes*.

of the feeding behaviour of the diverse penguin species or the amount of items they ingest, relative consensus exists for accepting that *Spheniscus* sp [comprising four species: the African penguin (*S. demersus*), the Humboldt penguin (*S. humboldti*), the Magellanic penguin (*S. magellanicus*), and the Galapagos penguin (*S. mendiculus*)], the Emperor penguin (*Aptenodytes forsteri*), King penguin (*Aptenodytes patagonicus*), and Little penguin (*Eudyptula minor*) are the most carnivorous (feeding on fish and squid) of all living species (Williams, 1995; Simpson, 1976). On the other hand, the species of *Pygoscelis*, such as the Chinstrap penguin (*Pygoscelis antarctica*), the Adelie penguin (*P. adeliae*) and the Gentoo (*P. papua*) feed especially on krill.

As we have stated earlier, the field of skeletal anatomy produced various contributions. Studies of skulls such as Zusi's (1975), and O'Hara's (1989), the latter including some important characters of the whole skeleton, were basic for the elaboration of the present paper. In her thesis, Acosta Hospitaleche (2004) included detailed descriptions of the skeleton of the different species of penguins that inhabit the Patagonian and Antarctic coasts. Bertelli et al. (2006) and Acosta Hospitaleche et al. (2007) showed relevant characters of *Paraptendytes antarticus* from the early Miocene and *Madrynornis mirandus* from the early Late Miocene of Patagonia respectively.

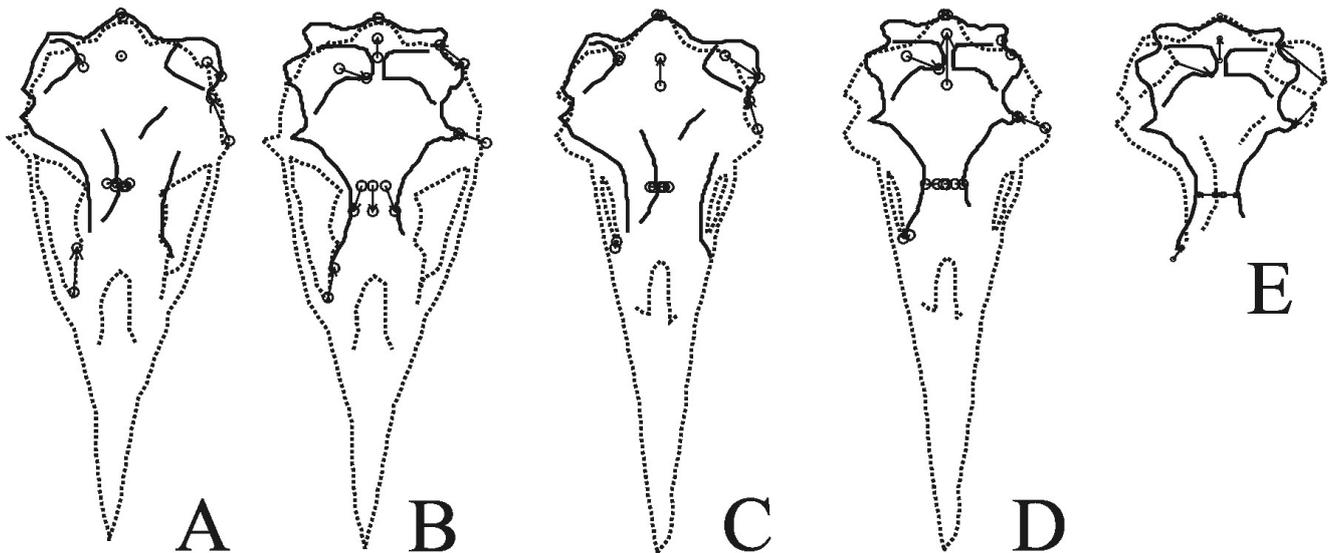
The contributions of the classic works of Simpson

(1946, 1972) to these topics are invaluable and although his goal was the study of fossil penguins, he included detailed osteological descriptions. Additionally, Schreiweis (1972) and Bannasch (1986) made comparative studies of the muscular system of living penguins.

Ecomorphological (relation between ecology, morphology and behavior of an organism) and biomechanical (relation between morphology and function of a structure) analyses offer useful tools for ecomorph identification and niche inference. Valuable contributions have been made concerning Passeriformes (Polo & Carrascal, 1999; Barbosa & Moreno, 1999), but few studies of this kind have been performed on other groups of birds. For instance, Noriega (2001, 2002) published certain biomechanic considerations about an extinct Pelecaniformes. No holistic and comparative studies on penguins to discern adaptive and/or evolutionary characters that reflect their way of life have been undertaken until now.

## METHODS

Skull shapes were compared using the Procrustean method Resistant-Fit Theta-Rho-Analysis (RFTRA). Procrustes methods allow the analysis of morphology through superimposition of one morphology onto another using landmarks. RFTRA (software made by R. Chapman 1990) was



**Figure 4.** Results of RFTRA of the skull in dorsal view of (A) *Spheniscus* (base specimen) and *Madrynornis mirandus* MEF PV=100, (B) *Spheniscus* (base specimen) and *Paraptenodytes*, (C) *Pygoscelis* (base specimen) and *Madrynornis mirandus* MEF PV=100, (D) *Pygoscelis* (base specimen) and *Paraptenodytes*, (E) *Madrynornis mirandus* MEF PV=100 (base specimen) and *Paraptenodytes*.

developed to identify and measure the homologous regions of shape change by establishing congruence among those that have not changed.

Comparisons between dorsal and lateral views of the skulls were made. Seventeen landmarks for the skull were chosen, including homologous and geometrical points (fig. 2). In the case of living species, landmarks were distributed on the whole of the skull, but they were restricted to the posterior part of the skull in the fossil species, because they are the only region that was preserved and could be compared with the other materials.

Morphological similarities among RFTRA distances are depicted using the resulting dendrograms for UPGMA (unweighted pair-group method using arithmetic average) cluster analysis.

Photographs and drawings of the dorsal and lateral aspect of the cranium were made for each species, and subsequently scanned into the computer. The scanned images were then used to digitalize the outlines of each specimen using the computer program tpsDig version 1.4 written by James Rohlf.

The examined specimens belong to the collections of Museo de La Plata (MLP), Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN), Museo Paleontológico Egidio Feruglio (MEF-PV), and American Museum of Natural History (AMNH).

Osteological terminology follows Baumel & Witmer (1993) and, when necessary, Simpson (1946) and O'Hara (1989).

## RESULTS

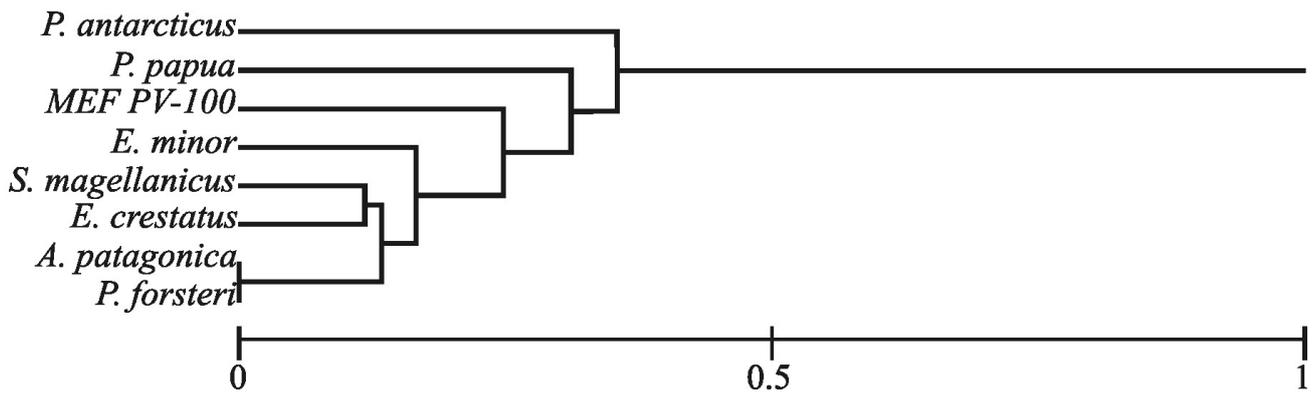
Comparisons of all available skulls corresponding to living species were made. Because only the posterior part of the skull has been preserved in the fossils, fewer landmarks were used than in the case of the living penguins.\*

Skulls were analysed in lateral, dorsal, and ventral views; however, the conformation of groups in relation to trophic habits was fundamentally based on the lateral view, which was most informative.

Because the main goal of this work was to try to establish relationships between shape and habit so as to infer way of life in fossils, we emphasized the analysis of species that have been assigned to quite different habits: krill-feeders represented by *Pygoscelis papua* and ichthyophagous forms represented by *Spheniscus magellanicus*.

Differences in skull shape among these two living species are mainly due to the extreme curvature of the anterior portion of the jugal bar and the elevated position of the base of the upper jaw relative to the basitemporal plate (Zusi, 1975, Acosta Hospitaleche & Tambussi, 2006) in *Pygoscelis*. Additionally, *Pygoscelis papua* differs from *Spheniscus* by the following characters: lower prominentia cerebellaris (fig. 3A), less extended fossa temporalis, more ventral foramen magnum, more dorsally extended nasal processes of the premaxillae and lacrimals, less laterally expanded nasal glands and more ventral and anterior processus paroccipitalis.-

The postorbital region of *Madrynornis mirandus* is shorter than in *Spheniscus* (figs. 3B, 4A,4B), larger and wider than in *Paraptenodytes* (figs. 3C, 4C), but narrower



**Figure 5** - Dendrogram resulting from UPGMA cluster analysis using RFTRA distances of skulls of selected spheniscids.

than in *Aptenodytes*; the interorbital region is narrower than in *Aptenodytes* and *Paraptenodytes* (fig. 3F) but wider than in *Eudyptula*; also, the orbital region is broader than in *Aptenodytes* and *Eudyptes*, and the occipital region is globe-shaped and more caudally projected than in *Aptenodytes* and *Pygoscelis* (fig. 3D) but less so than in *Eudyptes* (for more details, see Acosta Hospitaleche & Tambussi, 2006). Morphologically, the general skull shape resembles *Spheniscus*, due to characters such as the delicate curvature of the jugal bar or the position of the basitemporal plate. RFTRA confirms many of the observations made from visual examination, such as the postorbital region shorter than in *Spheniscus*, or the markedly globe-shaped occipital region, but also shows that *Madrynornis* possesses a narrower interorbital region than other species. These differences are explained by the fact that neither the skull of this species nor that of *Paraptenodytes* show similarities with any of the living species in dorsal view.

*Paraptenodytes antarcticus* shows a more extended postorbital area than *Pygoscelis* (fig. 4D), *Eudyptes*, *Eudyptula*, and *Aptenodytes*; the interorbital region is broader than in *Pygoscelis* and *Spheniscus*; the orbital region is narrower and more depressed than in *Eudyptes*, and narrower than in *Eudyptula*; the occipital region is less caudally projected than in *Eudyptes*. The skull is higher than in *Spheniscus*. Morphologically, the general shape of the skull of *Paraptenodytes* is not similar to any of the specimens used in the comparisons but shows a deep fossa temporalis as in *Madrynornis mirandus*.

A dendrogram grouping skull shapes (fig.5) indicated that, as expected, both *Aptenodytes forsteri* and *A. patagonicus* are clearly discriminated. This should not be surprising since the bill-cranium proportions of these two species seem to be very different from those of the others. *Eudyptes chrysosome* and *Spheniscus magellanicus* are most similar to each other ( $D = 0.11$ ), followed by *Eudyptula minor* ( $D = 0.13$ ), *Madrynornis mirandus* ( $D = 0.25$ ), *Pygoscelis papua* ( $D = 0.31$ ) and finally, by the extinct *Paraptenodytes antarcticus* ( $D = 0.37$ ).

## DISCUSSION AND CONCLUDING REMARKS

Spheniscidae includes seventeen species of living penguins and more than two dozen extinct taxa, distributed exclusively in the Southern Hemisphere. Concerning the South American fossil taxa, three taxonomic groups have been recognized (Simpson, 1946): Paraptenodytinae, Palaeospheniscinae and Spheniscinae. Nowadays, this scheme is not supported by phylogenetic analysis.

*Paraptenodytes antarcticus* is considered as the sister taxon of all extant taxa (Bertelli et al., 2006) and both fossil and living forms (Acosta Hospitaleche et al., 2007). The genus *Paraptenodytes* is known from the lower Miocene Gaiman Formation of Patagonia (Simpson, 1946) and recently was reported from the upper middle-lower Upper

Miocene Puerto Madryn Formation, the same level from which *M. mirandus* was recovered (Acosta Hospitaleche, 2003).

*Madrynornis mirandus*, for which almost the entire skeleton is known, early Late Miocene in age, is the first species described from Argentinean rocks that is closely related to the living forms (Acosta Hospitaleche et al., 2007).

Procrustes methods are not specifically practical in constructions of phylogenetic schemes due to the manner of selection of common landmarks between different taxa (Chapman, 1990). Nevertheless, they are very useful tools because they allow studies of morphological tendencies in a previously established phylogenetic scheme. Our analysis of spheniscids was based mainly on homologous landmarks. Only two landmarks from the dorsal view of the skull and four from the lateral view among a total of seventeen points were strictly geometric and the dendrograms (fig. 5) generated from distance matrices show similar patterns for both fossils. It is possible that this dendrogram reflects phylogenetic relationships, at least partially. According to Acosta Hospitaleche et al. (2007) *Paraptenodytes antarcticus* belongs to a different clade, basal within Spheniscidae. RFTRA analysis shows that the general skull shape of the *Paraptenodytes*

tiniae should be regarded as a different kind of spheniscid skull shape (neither *Spheniscus*-like nor *Pygoscelis*-like) and dendrograms could be showing a more distant hypothetical relationship between *Paraptenodytes* and the remaining species.

Zusi (1975) recognized two different lineages in the modern Spheniscidae based on skull morphology: one characterized by having the processus retroarticularis similar in size to the fossa articularis quadratica and the crista tomialis of the rostrum subparallel to the plane of the lamina parasphenoidalis; this group includes *Pygoscelis* and *Aptenodytes* species. The second lineage is characterized by the possession of a processus retroarticularis smaller than the fossa articularis quadratica and the crista tomialis situated on an oblique plane with respect to the lamina parasphenoidalis; it includes *Spheniscus*, *Eudyptula*, *Eudyptes* and *Megadyptes* species.

The results achieved with our geometric analysis demonstrated different arrangements because *Aptenodytes* is located far distant with respect to *Pygoscelis*, while *Spheniscus* presents greater shape affinity with *Eudyptes*. This is not coincident with the phylogenetic analysis (Acosta Hospitaleche et al., 2007) in which an *Aptenodytes* + *Pygoscelis* clade is recognized.

Penguins have been described as plankton and nekton feeders (Simpson, 1976) and their prey items range from small fishes to tiny euphausiids. Clearly, many birds are able to subsist on food that is not their favourite diet or that does not generally form the main food item. The more relevant aspect of this work is the identification of extreme types of habits or at least, types or ecomorphs that may be easily recognized within penguins. In this sense, it has been considered appropriate to distinguish two extreme types: the nekton feeder and the ichthyophagous types. As previously pointed out, *Spheniscus* prefers fishes and squids whereas *Pygoscelis* favours krill, and both taxa were selected as representative of these two different behavioural patterns.

The first one, represented by *Spheniscus magellanicus*, shows a more elongated and slender cranium, very little curvature of the anterior part of the jugal arch and a more ventral basitemporal plate. The second type, represented by *Pygoscelis*, is characterized by a short and wide skull, a postorbital region less extended than in *Spheniscus*, with strong curvature of the anterior part of the jugal arch and a high basitemporal plate.

*Madrynornis mirandus* MEF PV-100 bears a strong general resemblance to the first type, that has been considered as essentially ichthyophagous, but it is not possible to assert that this taxon fed exclusively on fishes. The skull shape of *Paraptenodytes* differs from that of *Spheniscus*, e.g. the skull is lower and the postorbital region is longer, but also from *Pygoscelis*, e.g. the skull is higher and the postorbital region is longer than in *Pygoscelis*.

Unfortunately, the present analysis of the skull of *Paraptenodytes* does not give us information about its feeding preferences and rather it seems to show that it does not belong to either of the suggested types. Speculations seem to

be premature and must wait for a more complete analysis.

So far, no study has explored the shape components of penguin skull and mandible using geometric morphometric techniques, on a subsample of living and fossil skulls. It is to be hoped that the comparison with more species and the possibility of including other fossil skulls may provide important information on their feeding mechanisms and also, in combination with other evidence (e.g. paleoclimate, comparisons with other extant forms), insightful data on the paleobiology of these extinct organisms.

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## ADDENDUM

At the time when this work was made only two fossil skulls were available. At least four new fossil skulls were published in the last two years, which could not be included in our analysis. See for example Stucchi et al (2003), Acosta Hospitaleche et al. (2006), Clarke et al. (2007) and Stucchi (2007).

## REFERENCES

- Acosta Hospitaleche, C. 2003. *Paraptenodytes antarcticus* (Aves: Sphenisciformes) en la Formaci n Puerto Madryn (Mioceno tard o temprano), provincia de Chubut, Argentina. *Revista Espa ola de Paleontolog a*, 18: 179-183.
- Acosta Hospitaleche, C. 2004. *Los ping inos (Aves, Sphenisciformes) f siles de Patagonia. Sistem tica, biogeograf a y evoluci n*. PhD Thesis, Facultad de Ciencias Naturales y Museo, UNLP, La Plata, 321 pp.
- Acosta Hospitaleche, C., Chavez, M. & Fritis, O. 2006. Ping inos f siles (*Pygoscelis calderensis* sp. nov.) en la Formaci n Bah a Inglesa (Mioceno Medio-Plioceno), Chile. *Revista Geol gica de Chile*, 33, 327-338
- Acosta Hospitaleche, C. & Tambussi, C. 2006. Skull morphometry of *Pygoscelis* (Sphenisciformes): inter and intraspecific variations. *Polar Biology*, 29:728-734.
- Acosta Hospitaleche, C., Tambussi, C., Donato, M. & Cozzuol, M. 2007. A new fossil penguin from Patagonia and a phylogenetic analysis of living and fossil species. *Acta Paleontologica Polonica*, 52:299-314.
- Bannasch, R. 1986. Morphologic-functional study of the locomotor system of penguins as a general model

- of movement in under-water flight. I. *Gegenbaurs Morphologisches Jahrbuch*, 132 (5): 645-679.
- Bannasch, R. 1992. Hydrodynamics of penguins: an experimental approach. *2<sup>nd</sup> International Conference on Penguins, Abstracts*, 138. Cowes, Phillip Island, Australia, 24-28 August, 1992.
- Bannasch, R., Wilson, R. & Culik, B. 1994. Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *Journal of Experimental Biology*, 194, 83–96.
- Bertelli, S., Giannini, N. & Ksepka, D. 2006. Redescription and Phylogenetic Position of the Early Miocene Penguin *Paraptenodytes antarcticus* from Patagonia. *American Museum Novitates*, 3525: 1-36.
- Barbosa, A. & Moreno, E. 1999. Evolution of foraging strategies in waders: an ecomorphological approach. *The Auk*, 116: 712-725.
- Baumel, J. & Witmer, L. 1993. Osteologia; pp. 45-132. In: Baumel, J., King, A.,
- Chapman, R. 1990. Conventional Procrustes approaches; pp.251-267. In: Rolph, F. & Bookstein, F. (eds), *Proceedings of the Michigan Morphometrics Workshop*. Special Publication 2. University of Michigan, Ann Arbor.
- Clarke J., Ksepka, D. Stucchi, M., Urbina, M., Giannini, N., Bertelli, S., Narva, Y. & Boyda, C. 2007. Paleogene equatorial penguins challenge the proposed relationship between biogeography, diversity, and Cenozoic climate change. *Proceedings of the National Academy of Science*, 104: 11545–11550.
- Green, J.A., Butler, P.J., Woakes, A.J. & Boyd, I.L. 2003. Energetics of diving in macaroni penguins. *Journal of Experimental Biology*, 206: 43-57.
- Irschick, D. & Losos, J. 1998. A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution*, 52 (1): 219-226.
- Jadwiszczak, P. 2001. Body size of Eocene Antarctic penguins. *Polish Polar Research*, 22: 147-158.
- Livezey, B. 1989. Morphometric patterns in Recent and fossil penguins (Aves, Sphenisciformes). *Journal of Zoology*, 219: 269-307.
- Lowe, P. 1933. On the primitive characters of the penguins and their bearing on the phylogeny on the ostrich and its allies. *Proceeding of the Zoological Society of London*, 1: 185-247.
- Moreno, F. & Mercerat, A. 1891. Catálogo de los pájaros fósiles de la República Argentina conservados en el Museo de La Plata. *Anales del Museo de La Plata (Paleontología Argentina)*, 1, La Plata: 7-71.
- Noriega, J. 2001. Body mass estimation and locomotion of the Miocene peleciform bird *Macranhinga*. *Acta Paleontologica Polonica*, 46 (2): 115-128.
- Noriega, J. 2002. Additional material of *Macranhinga paranensis* Noriega 1992 (Aves: Pelecaniformes: Anhingidae) from the “Mesopotamian” (Ituzaingó Formation; Upper Miocene) of Entre Ríos Province, Argentina; pp. 51-81. In Zhou, Z. & Zhang, F. (eds.): *Proceedings of the 5th International Meeting of the Society of Avian Paleontology and Evolution*, Beijing 2000, China Science Press.
- O’ Hara, R. 1989. *Systematics and the study of Natural History, with an estimate of the phylogeny of the living penguins (Aves: Spheniscidae)*. PhD thesis. Harvard University, Cambridge, 171 pp.
- Polo, V. & Carrascal, L. 1999. Shaping the body size distribution of Passeriformes: habitat use and body size are evolutionarily and ecologically related. *Journal of Animal Ecology*, 68:324-337.
- Pycraft, W.P. 1898. Contributions to the osteology of birds, Part II. Impennes. *Proceedings of the Zoological Society of London*, 15: 458-989.
- Rohlf, J. 1999. *TPSDIG*. Version 1.18 Department of Ecology and Evolution, State University of New York, Stony Brook, NY. Website: <http://life.bio.sunysb.edu/morph>
- Schreiweis, D. O. 1972. *A comparative study of the appendicular musculature of the Order Sphenisciformes*. PhD thesis. Washington State University, Pullman.
- Shufeldt, R.W. 1909 *Osteology of birds*. *New York State Museum Bulletin*, 130: 1-381.
- Simpson, G. G. 1946. Fossil penguins. *Bulletin of the American Museum of Natural History*, 87: 1-100.
- Simpson, G.G. 1972. Conspectus of Patagonian Fossil Penguins. *American Museum Novitates*, 2488: 1-37.
- Simpson, G.G. 1976. *Penguins. Past and present, here and there*. Yale University press New Haven, London: 150 pp.
- Stonehouse, B. 1967. The general biology and thermal balances of penguins. *Advances in Ecological Research*, 4: 131-196.
- Stonehouse, B. 1975. Introduction: The Spheniscidae; pp. 1-15. In: Stonehouse, B. (ed.). *The biology of penguins*. London & Basingstoke, Macmillan Press.
- Stucchi, M. 2002. Una nueva especie de Spheniscus (Aves: Spheniscidae) de la Formación Pisco, Perú. *Boletín de la Sociedad Geológica del Perú*, 94: 19-26.
- Stucchi, M., Urbina, M. & Giraldo, A. 2003. Una nueva especie de Spheniscidae del Mioceno tardío de la Formación Pisco, Perú. *Bulletin de l’Institut Français d’Etudes Andines*, 32: 361-375.
- Tambussi, C., Reguero, M., Marensi, S. & Santillana, S. 2005. *Crossvallia unienwillia*, a new Spheniscidae (Sphenisciformes, Aves) from the Late Paleocene of Antarctica. *Geobios*, 38: 557-675.
- Wainwright, P. 1994. Functional morphology as a tool in ecological research; pp. 42-59. In Wainwright, P.C. & Reilly, S.M. (ed). *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago.
- Watson, M. 1883. Report on the anatomy of the Spheniscidae collected during the voyage of H.M.S. Challenger.

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- Whitehead, M.D. 1989. Maximum diving depths of the Adelie penguin, *Pygoscelis adeliae*, during the chick rearing period, in Prydz Bay, Antarctica. *Polar Biology*, 9: 329- 332.
- Williams, T. D. 1995. *The penguins, Spheniscidae*. Birds families of the world. Oxford University Press, 295pp.
- Zusi, R. L. 1975. An interpretation of skull structure in penguins; pp. 59-84. *In*: Stonehouse, B. (ed). *The biology of penguins*. Macmillan Press, London & Basingstoke.
- Zusi, R.L. 1993. Patterns and diversity in the avian skull; pp. 391-437. *In*: Hanken, J. & Hall, B.K. (eds). *The skull*. University of Chicago Press, Chicago.
- Zweers, G., Vandenberghe, J. & Berkhoudt, H. 1997. Evolutionary patterns and avian trophic diversification. *ZACS (Analysis of complex systems) Zoology*, 100: 25-57.