THE CORACOIDS IN FUNCTIONAL AND MORPHOLOGICAL STUDIES OF PENGUINS (AVES, SPHENISCIDAE) OF THE EOCENE OF ANTARCTICA

CAROLINA ACOSTA HOSPITALECHE [1] & ULISES DI CARLO [2]

Abstract. The partial articulated skeleton MLP 77-V-10-1 comes from the upper levels of La Meseta Formation (Seymour Island, Antarctica) at the southwestern slope of the plateau. These remains were found in the Submeseta Allomember, within the *Anthropornis nordenskjoeldi* Biozone, dated at 34.2 Ma using strontium isotope ratios from shells. MLP 77-V-10-1 is a giant penguin, probably the largest ever described, whose coracoids are strikingly wide at the distal surface. The present contribution is a study of this new fossil penguin, with particular emphasis on the coracoids. The osteography and associated muscles are described. Functional connotations of coracoid morphology are thoroughly discussed and its implications on the mechanics of diving are explored. We concluded that the coracoid morphology suggests a change in diving strategy from the earliest penguins until the living representatives. In the oldest penguins, the improvement of diving capacity would have been linked to the development of stronger bone and probably muscular structures enabling endurance of greater forces operating in a denser medium. In contrast, the Neogene penguins would have optimized the force action of the flight apparatus by developing more precise movements, adjusting the angle of attack of each of the effective forces.

Riassunto. Lo scheletro di pinguino MLP 77-V-10-1 parzialmente articolato è stato rinvenuto nei livelli superiori della Formazione La Meseta (Seymour Island, Antartide) sul pendio sudovest del plateau. Questi resti sono stati trovati nell'Allomembro Submeseta entro la Biozona ad *Anthropornis nordenskjoeldi*, datata a 34.2 Ma, in base ai rapporti isotopici dello stronzio misurati nelle conchiglie. MLP 77-V-10-1 è un pinguino gigante, probabilmente il più grande mai descritto, i cui coracoidi sono particolarmente larghi nella loro superficie distale. Questo articolo è dedicato allo studio di questo nuovo reperto, con particolare enfasi sui coracoidi. Vengono descritti l'osteografia ed i muscoli associati. Le connotazioni funzionali della morfologia dei coracoidi sono discusse in dettaglio e vengono analizzate le implicazioni in rapporto alla meccanica del nuoto: concludiamo che la morfologia del coracoide suggerisce un mutamento nella strategia delle immersioni, dai rappresentanti più antichi di pinguini sino alle forme attuali. Nei pinguini più antichi, i miglioramenti nella capacità di nuoto e immersione sarebbero stati connessi con lo sviluppo di ossa più robuste e probabilmente di strutture muscolari che consentivano maggiore resistenza nell'operare in un mezzo più denso. I pinguini neogenici, invece, avrebbero ottimizzato la forza d'azione dell'apparato di volo, sviluppando movimenti più precisi e migliorando l'angolo di inserzione di ciascuna forza effettiva.

Introduction

The sternum, coracoids, scapulae and furcula are an essential locomotory complex for volant birds, and also for penguins, which use their flippers to move under water. These structures provide the site of articulation for the humerus and attachment surfaces for "flight muscles". Because of their close relation, it is feasible to make inferences for one of these elements based on the others. A feature common to all birds is that the sternocoracoid articulation is the only mobile joint of the pectoral girdle.

Penguins are characterized by the peculiarly marked curvature of the *facies articularis sternalis*, a character already observed in fossil species which drew Simpson's (1975) attention to the possible functional meaning of this feature. Previous studies indicate that such curvature substantially limits wing abduction, defined as the movement from dorsomedial to ventrolateral position (Sy 1936). Complementary, the adduction movement in penguins was described as the exact opposite to the previous abduction (Bannasch 1986b).

In this contribution a partially articulated penguin skeleton from La Meseta Formation of the late Eocene at Seymour Island (Antarctica) is studied. Its coracoid

1   División Paleontología Vertebrados, Museo de La Plata, Paseo del Bosque s/n, B1900FWA La Plata, Argentina. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). E-mail: acostacaro@museo.fcnym.unlp.edu.ar
2   Ulises Di Carlo. Instituto Superior Juan N. Terrero. B1900FWA La Plata, Argentina.

osteography is analyzed in detail, the action of associated muscles is briefly discussed and its functional morphology compared to other fossil and living species is analyzed. Additionally, a rough estimate of the height of this penguin species is provided.

Materials and methods

MLP 77-V-10-1 is housed at the División Paleontología Vertebrados of Museo de La Plata, La Plata, Argentina. Comparative material included skeletons of fossil and modern species from the collections of Museo de La Plata (MLP), Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Ciudad Autonoma de Buenos Aires, Museo Paleontológico "Egidio Feruglio" (MEF), Trelew, R. Natalie P. Goodall Foundation at the Museo Acatushún, (RNP), Tierra del Fuego, Argentina.

They include the skeleton of the modern species: *Aptenodytes patagonica* (RNP A-1937, RNP A-1896, RNP A-2024, RNP A-1676), *Aptenodytes forsteri* (RNP A-018), *Spheniscus magellanicus* (MLP 873), *Spheniscus humboldti* (data taken from Stucchi 2002), *Pygoscelis adeliae* (MLP 464), *Pygoscelis antarctica* (MLP MLP 874), *Pygoscelis papua* (MLP 38), and *Eudyptes chrysocome* (MLP 39); and the fossil *Palaeospphenicus biloculata* (MEF-PV 1729), *Palaeospheniscus* sp (MLP 20-355, MLP 20-356), *Paraptenodytes antarcticus* (cast of the holotype housed at MEF), *Madrynornis mirandus* (MEF-PV 100), *Spheniscus muizoni* (Göhlich 2007), *Spheniscus urbinai* (data taken from images provided by Marcelo Stucchi), *Icadyptes* (data taken from *Ksepka* et al 2008), *Waimanu tuatahi* (data taken from Slack et al. 2006).

Osteologic and muscular terminology follows Baumel & Witmer (1993) and George & Berger (1966) when necessary. Measurements were taken using Vernier callipers (0.01 mm accuracy).

The shape of the sternocoracoid surface was studied through elliptic Fourier analysis of the contour coordinates (Rohlf & Archie 1984), performed with the software package shape (Iwata & Ukai 2002). This method performs an orthogonal decomposition of a curve into a sum of harmonically related ellipses.

Each specimen was photographed with the same focal distance using a digital camera, and the outline was digitally redrawn to highlight its contrast with respect to the background. Once the best contrast between objects and background was achieved, the image was converted into a black-and-white image using the software ChainCoder (Freeman 1975).

For each of ten specimens, 3000 coordinates of the outline were obtained and twenty 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 the software Chc2Nef. The efective information contained in these coefficients (see Rohlf & Archie 1984) was summarized through a principal component analysis, performed with the software PrintComp (Iwata & Ukai 2002) based on the variance-covariance matrix. Variation in shape accounted for by each principal component was represented with the software PrintPrint, which reconstructs the contour shape on each component from the calculated coefficients by inverse Fourier transformation.

Finally, the scores from the principal components analysis were exported to the software Past (Hammer et al. 2001) where clouds of data were visualized in a biplot graph.

Provenance

MLP 77-V-10-1 comes from the upper La Meseta Formation at the southwestern slope area of the plateau in Seymour Island, Antarctica (Fig. 1). La Meseta Formation is composed of sandstones and mudstones with interbedded shell-rich conglomerates, organized into six erosionally-based internal units, named from base to
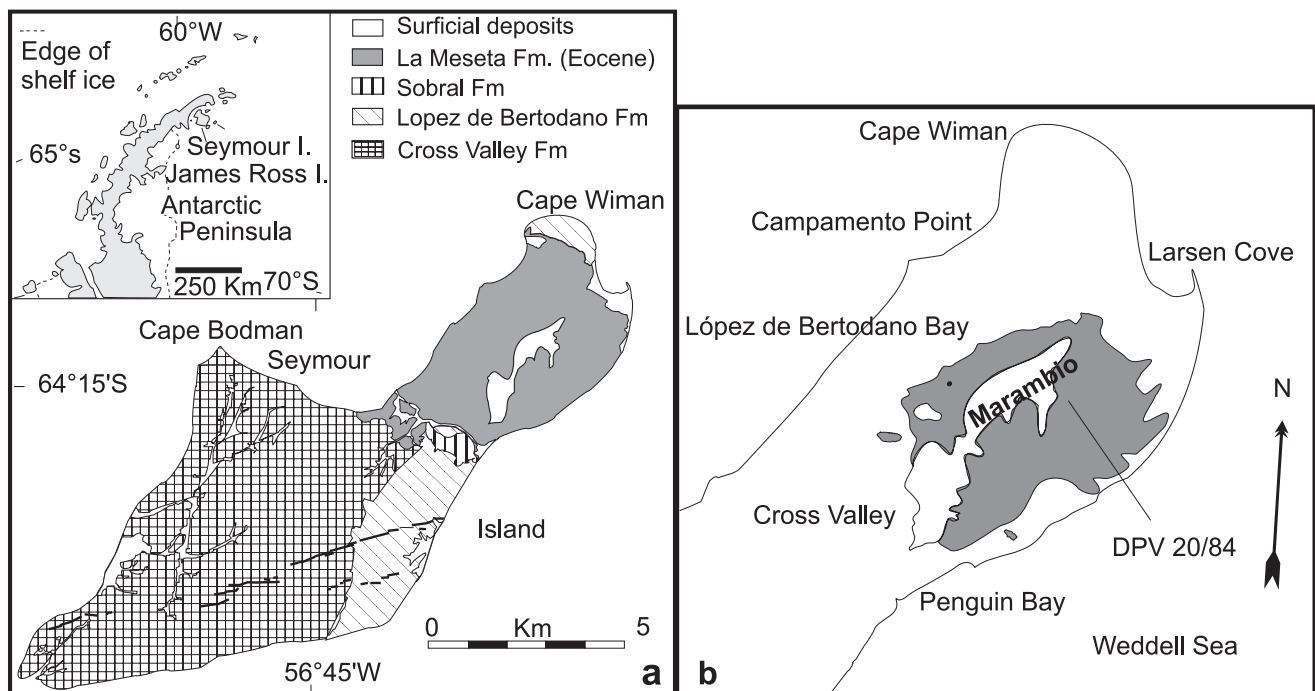

Fig. 1   - Detailed location map showing: a- Seymour Island, Antarctic Peninsula, b- the northern part of Seymour Island with detailed distribution of the Submeseta Allomember and the locality DPV 20/84 where MLP 77-V-10-1 was found. A-B measured section (stratotype) of the *Anthropornis nordenskjoeldi* Biozone.
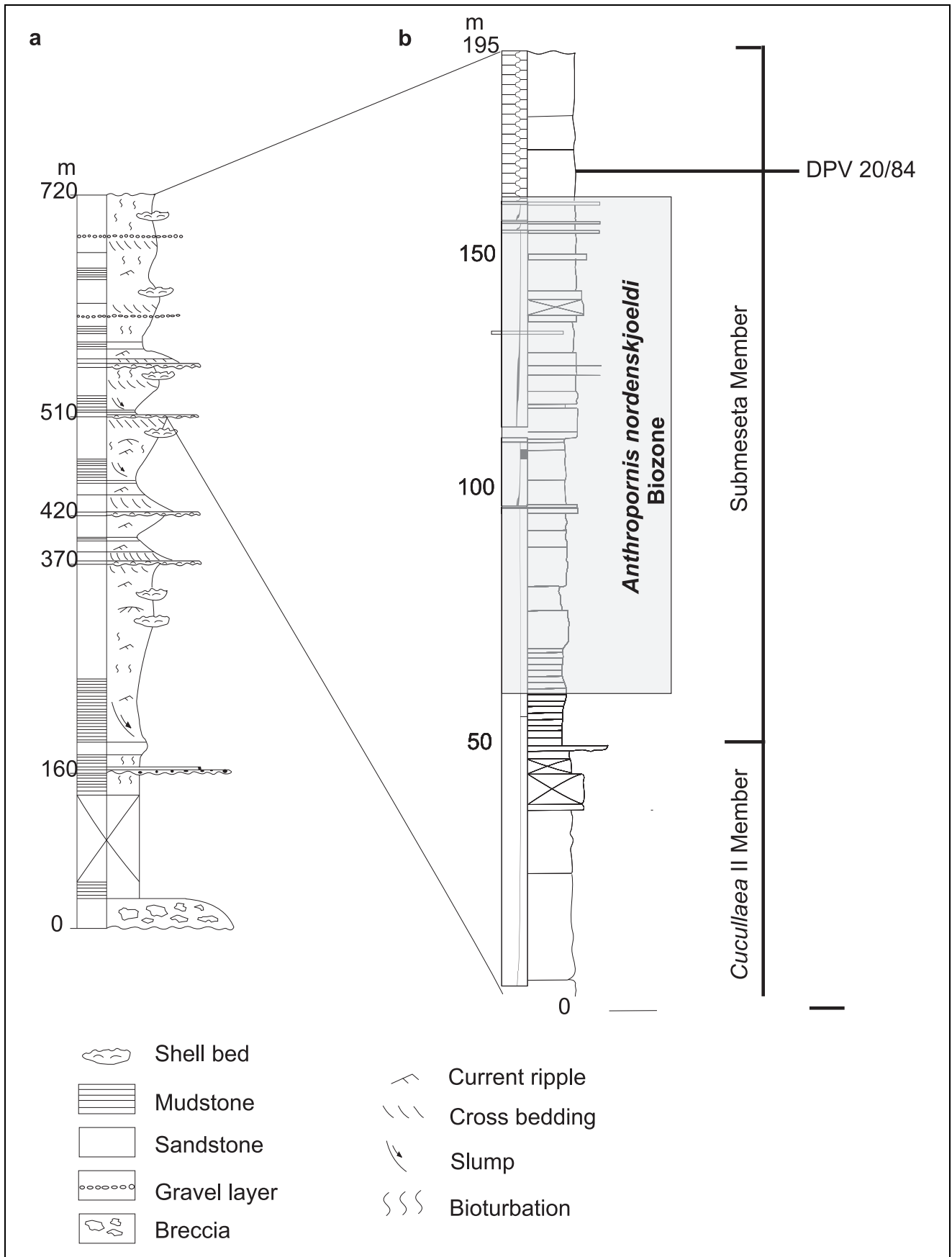
Fig. 2 - Stratigraphic section of: a- La Meseta Formation, Seymour Island, Antarctic Peninsula (modified from Reguero et al. 2002), b- Measured section from the eastern flank of the plateau (stratotype of the *Anthropornis nordenskjoeldi* Biozone) showing stratigraphic levels of the *Cucullaea* II and Submeseta members (modified from Marenssi et al. 1998a) and the level corresponding to the locality DPV 20/84. Shaded rectangular area delimits the *Anthropornis nordenskjoeldi* Biozone.

top Valle de Las Focas, Acantilados, Campamento, *Cucullaea* I, *Cucullaea* II and Submeseta Allomembers. These units were deposited during the Eocene in deltaic, estuarine and shallow marine settings, mostly within a northwest-southeast trending valley (Marenssi et al. 1998 a, b).

Almost all the vertebrate fossil specimens collected from the Submeseta Allomember (or Telm 7) have been found within a single horizon, easily distinguishable by the massive occurrence of penguin bones and the phospatic brachiopod "*Lingula*", within the *Anthropornis nordenskjoeldi* Biozone. A detailed list of the fauna occurring in this biozone was provided by Tambussi et al. (2006). Age of the horizons was established by Dingle & Lavelle (1998) at 34.2 Ma using strontium isotope ratios from shells. DPV 20/84 lies about 30 m above this rich vertebrate-bearing horizon within the Submeseta Allomember (Fig. 2).

Penguin coracoids

The coracoids are the most massive elements in the pectoral girdle of penguins (Fig. 3). They are relatively long bones (Fig. 4) whose *facies dorsalis* extends towards the middle of the dorsal surface and becomes concave caudally forming the *impresio m. sternocoracoidei*. The *facies ventralis* is correspondingly convex. The *processus acrocoracoideus* is very long in comparison to that of flying birds and a ventromedial curve is present forming the *facies articularis clavicularis*.

The *sulcus m. supracoracoidei* is very large and *the processus procoracoideus* is particularly strong, representing the second surface that participates in a syndesmotic joint with the furcula and the scapular acromion. The sternal section of the coracoid is very wide and develops a conspicuous *processus lateralis*. The *facies articularis sternalis* presents a great curvature that forms an "arc" in living and Mio-Pliocene penguins (and also in the only known coracoid from the Oligocene of Patagonia, see Acosta Hospitaleche 2005, Acosta Hospitaleche et al. 2007), but is sigmoid or "S-shaped" in the Eocene materials (Fig. 5).

One variable feature is the ossification that develops between the *processus procoracoideus* and the *angulus medialis*, which determines closure of the *incisura n. supracoracoidei* over the *margo medialis* forming a foramen. Because this ossification results in significant widening of the coracoid, it is important from a myological viewpoint (Fig. 4).

New fossil MLP 77-V-10-1

While the preservation of this skeleton is far from being perfect (Fig. 6) and it does not include any of the
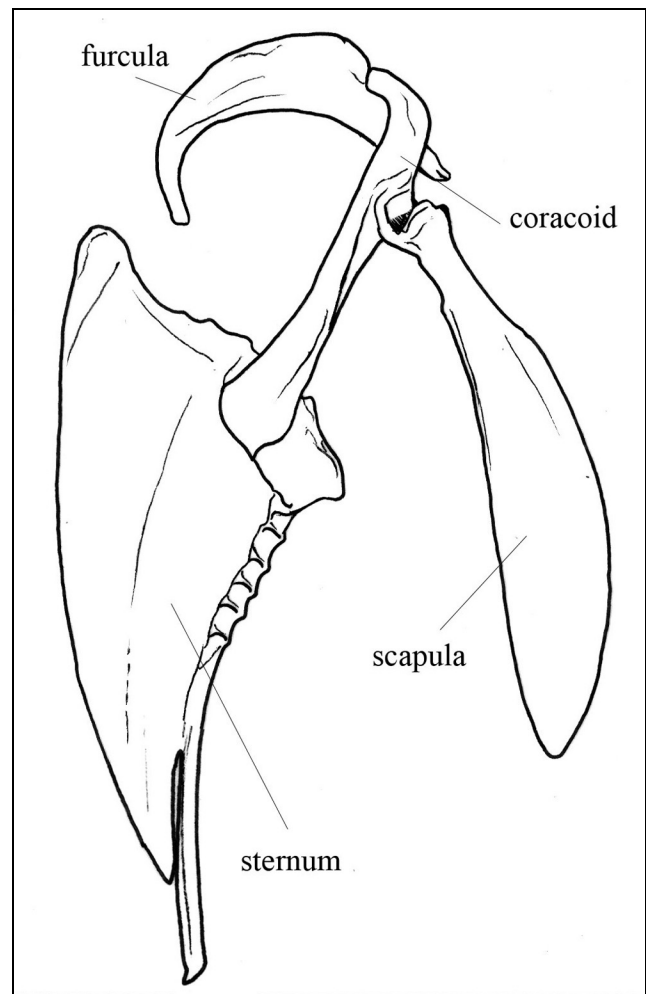

Fig. 3 - Schematic drawing of penguin pectoral girdle, which forms the essential locomotory complex during swimming. Main elements are indicated.

elements traditionally regarded as diagnostic for the group (humeri and tarsometatarsi), the extremely large size of its coracoid is noteworthy and suggests a number of interesting considerations. MLP 77-V-10-1 (Fig. 6) consists of an articulated segment of vertebral column, whose poor preservation makes difficult to establish the exact number of vertebrae preserved. Both coracoids with damaged proximal ends have also been preserved. Although the coracoids are not complete, their distal ends are well preserved allowing study of the sternocoracoid surface, essential in diving kinematics.

Coracoid 77-V-10-1 (Fig. 6) is 187 mm long lacking its proximal end, most probably reaching ca. 200 mm with the complete omal end. Its flabelliform aspect in anterior view is similar to the coracoid of other Eocene species. The *incisura n. supracoracoidei* is open and thus does not develop a foramen *supracoracoidei* over the *margo medialis*.

In distal view, the *facies articularis sternalis* is S-shaped, 107.4 mm long and with a constant anteroposterior width of about 10 mm.

Fig. 4 - Penguin coracoids and terminology employed in comparisons and descriptions. Left and right drawings represent the two basic shapes of modern coracoids (at the left: *Palaeospheniscus* sp., at the right *Pygoscelis* sp.).

Processus acrocoracoideus

Facies articularis scapularis

Sulcus m. supracoracoidei

Fenestra supracoracoidei

Processus lateralis

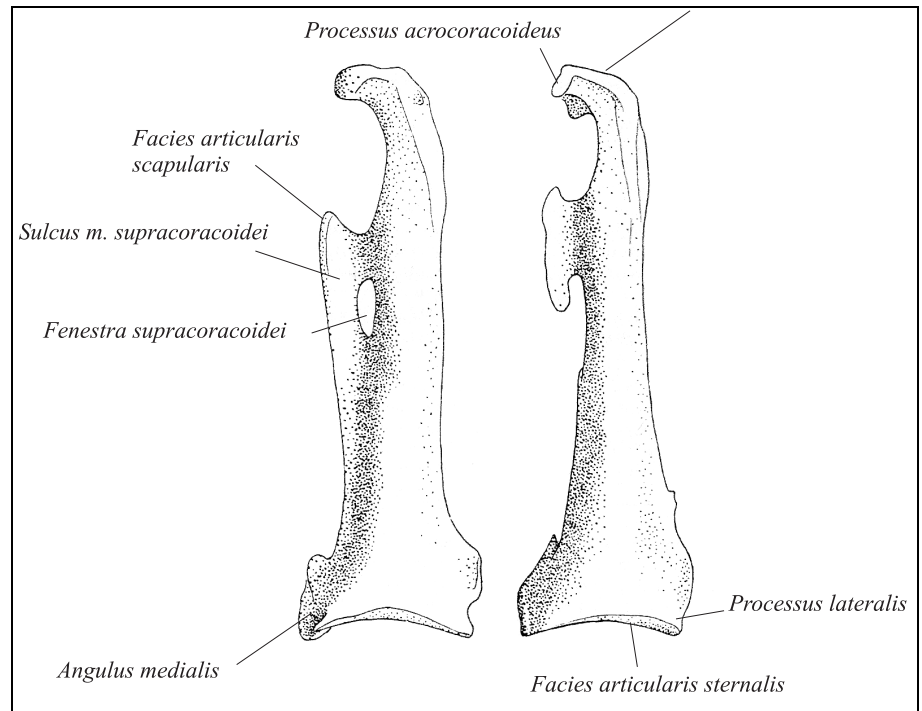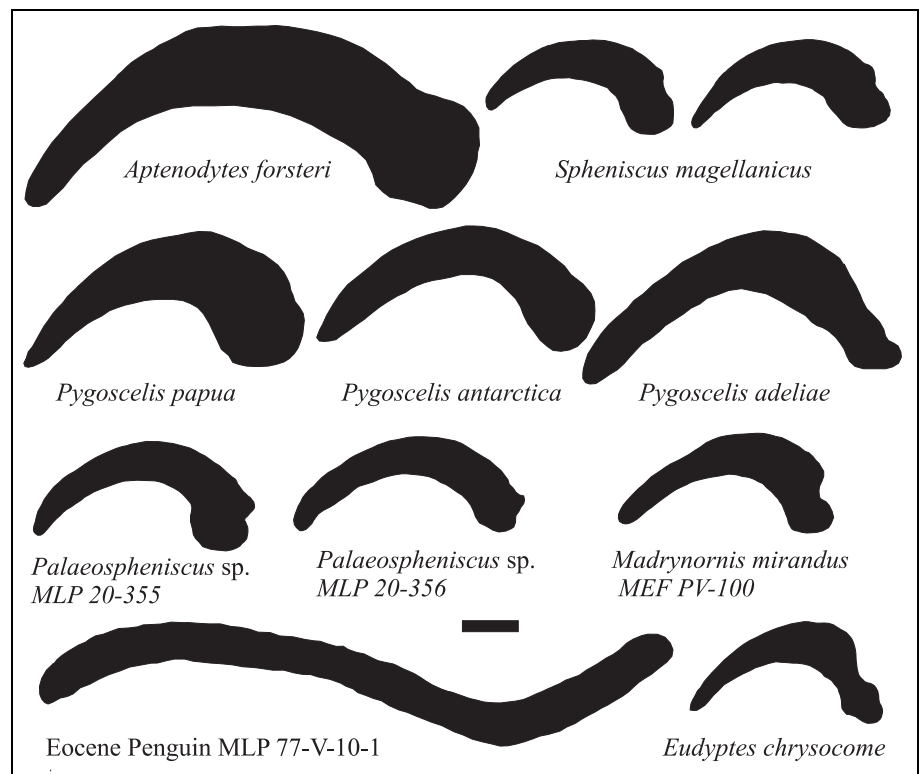*Angulus medialis*

Facies articularis sternalis

Fig. 5 - Diagram of the different coracoids studied in distal view, showing the C-shape of Miocene and modern penguins and the S-shape of MLP 77-V-10-1. Scale bar: 10 mm.

Aptenodytes forsteri

Spheniscus magellanicus

Pygoscelis papua

Pygoscelis antarctica

Pygoscelis adeliae

Palaeospheniscus sp. MLP 20-355

Palaeospheniscus sp. MLP 20-356

Madrynornis mirandus MEF PV-100

Eocene Penguin MLP 77-V-10-1

Eudyptes chrysocome

Musculature associated to the coracoids

Classically, it has been suggested that the wing muscles of penguins that lift the wings should be specially strong due to the higher density of the aquatic environment compared with air. In this sense, Owen (1866) argued that hypertrophy of *m. supracoracoideus* with respect to *m. pectoralis* (upstroke muscle vs. downstroke muscle) is required. These two muscles are the major wing movers during underwater flight and Schreiweis (1982) described the very strongly developed supracoracoideus in relation to the pectoralis. However, Bannasch (1986a) demonstrated in his dissections that differential development of both muscles is not necessary in penguins. This is linked to the fact that "underwater flight" also involves an active upward thrust, for which the wing is placed at a hydrodynamically efficient angle (see details in Bannasch 1986a).
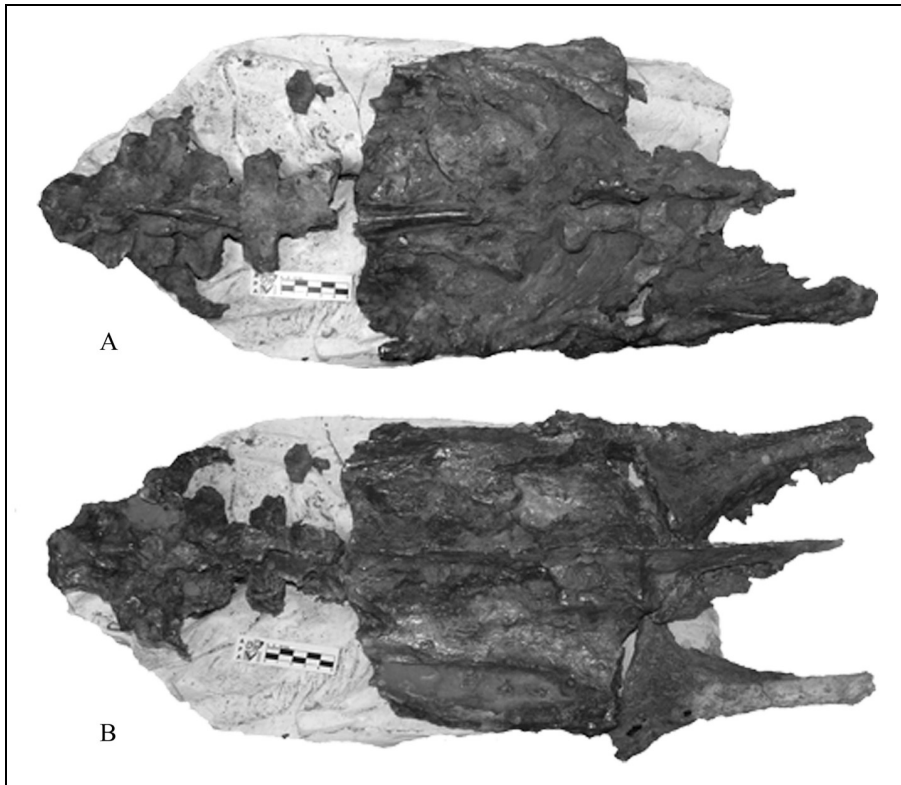
Studies of diving kinematics in penguins indicate that body size would not be a determining factor in the degree of relative development of associated musculature (Bannasch 1986a). Therefore, differential development of muscular attachment surfaces of bones in larger-sized penguins such as MLP 77-V-10-1 with respect to living species is not expected.

Those muscles mainly used to produce the necessary forces to move the wing are divided into strong isotonic muscles (which perform the movement itself), and predominantly isometric muscles (those that maintain an appropriate plane of movement and transfer the propulsive forces generated by isotonic muscles to the body). Some muscles of this group can also produce rotation forces that are considerable, although not determinant, or take part in small-scale adjustments to the angle of force transference. They act as antagonists or as synergists with respect to the muscles in the first group. Hereinafter these isometric muscles will be called "position muscles" as proposed by Bannasch (1987).

Muscles inserted in the coracoid exert forces that participate both in the movement during diving and in the position of the coracoid itself (Poore et al. 1997). *M. supracoracoideus* is essentially the wing lifter; and its great development in penguins relative to its antagonist, the pectoral, is only comparable to hummingbirds among flying birds (Bannasch 1986b). Although this seems striking, these two groups share other myological characteristics, such as muscle fiber ultrastructure and enzymatic activity (Mill & Baldwin 1983).

This is quite probably related to the fact that both birds produce a significant upward thrust during wing flapping. Particularly in penguins, muscle fiber diameter is similar in both *m. pectoralis* and *m. supracoracoideus* (Mill & Baldwin 1983). *M. supracoracoideus*, primarily involved in humerus lift, has its origin in the *facies muscularis sterni* (sternum) and the coracoid base, and runs through a wide tendon the *canalis triosseus* to finally insert onto the humerus (Bannasch 1986b).

Another main muscle is the small tendinous *m. coracobrachialis cranialis*, arising from the craniolateral surface of the *processus acrocoracoideus* and inserted onto the *facies ventralis* of the humerus (Sandoval Arias 2004). It is the smallest muscle in the scapular girdle that plays a role in wing position. An additional muscle, *m. coracobrachialis caudalis,* is inserted on the *processus craniolateralis sterni* (sternum) and the *processus lateralis* of the coracoid, as well as on the facies of the *supracoracoideus* muscle. A powerful tendon joins *m. coracobrachialis caudalis* to the *fossa tricipitalis* and the *tuberculum ventrale* of the humerus (Sandoval Arias 2004). This muscle caudally pulls the humerus and constitutes an important synergist of the *supracoracoideus* muscle. It rotates backwards the humeral head (around the ligament insertion point) and at the same time downwards, accomplishing wing supination. However, and because of its small mass, it is considered a position muscle with virtually no participation in the production of the power stroke that achieves wing movement (Bannasch 1986b, though see also Watson 1883). Other smaller

muscles such as the *subcoracideus, sternocoracoideus* and *subcoracoscapulares* also act as complements to achieve positioning of girdle elements (Bannasch 1987).

The coracoid in reconstructions

Preliminary studies conducted on different living penguin species point to allometric relationships between elements of the pelvic and thoracic limbs, while demonstrating relative uniformity between the proportions of elements in the same limb (Balseiro et al. 2004). As mentioned above, the coracoid forms a functional complex with the wing, and it is possible to establish metric relationships between them.

Body size estimations in penguins have been classically calculated from tarsometatarsus, femur and humerus lengths (Simpson 1946, 1971, 1975, 1976) and more recently, on the basis of regressions using the lengths of appendicular elements (Kirkwood et al. 1989; Rising & Somers 1989; Senar & Pascual 1997; Campbell & Marcus 1992), long bone circumference (Anderson et al. 1985) and body size of extant species (Livezey 1989). More recently, heights of Eocene penguins have been calculated from lengths and diameters of long bones. According to that, the average body sizes are greater in fossil species than in living ones (Jadwiszczak 2001). Four fossil species (eg. the Antarctic species) were larger than Emperor Penguin *Aptenodytes forsteri*, the largest penguin inhabiting Antarctica today (Livezey 1989).

Besides, height can be also estimated from the size of the coracoid. Livezey (1989) analyzed several elements of the skeleton and established that the width of the coracoid base is less variable intraspecifically than between different species. We have observed that measurements in different species show direct correlation between the size of humerus and coracoid. This relationship can greatly restrict the range of possibilities for the systematic allocation of MP-77 V-10-1.

While it is common for penguin coracoids to be heavily eroded or even fractured at the *processus lateralis* and the *angulus medialis* levels, both coracoids studied here have an undamaged distal end, whose width is more than twice that of any coracoid described or figured until now (see Jadwiszczak 2006).

The relationship between maximum humeral length and width of coracoid base can be represented by an index which ranges between 2.8 and 3.5 in current penguins; 2 to 3. 12 in Miocene penguins and 2.5 in the Paleocene specimen *Waimanu tuatahi*.

Since the distal coracoid width of MLP 77-V-10-1 is 107.4 mm, application of this index indicates that its humerus would have been between 214.8 and 343.68 mm long. Even considering that the calculated size

range is large, it is possible to assert that this would be the largest specimen studied so far, whose size in taxonomic terms is closer to *Anthropornis*. Moreover, application of the index obtained for the only Paleogene species *Waimanu tuatahi* with available data (2.5) yields a possible maximum humerus length of 268.5 mm.

The largest known humeri correspond to those of *A. grandis* (194.2 mm) and *A. nordenskjoeldi* (182.8 mm) according to Tambussi et al. (2006), and to *Anthropornis nordenskjoeldi* (152.2 mm), *Palaeeudyptes klekowski* (150.4 – 158) and *P. gunnari* (144-142.2) as stated by Jadwiszczak (2006). All of them are smaller than the value estimated for the specimen under study.

The height and mass of several penguin species have been estimated based on regressions of hind limb measurements. For instance, *Anthropornis nordenskjoeldi* (1.66-1.99 m and 81.7-97.8 kg, respectively) and *Palaeeudyptes klekowskii* (1.47-1.75 m and 56.0-65.7 kg) are among the largest species (Jadwiszczak 2001). Humeral dimensions indicate that the holotype of *I. salasi* would be intermediate in size between these two taxa, yielding a conservative minimum standing height of 1.5 m (Clarke et al. 2007).

Even ignoring the size and robustness that the humeri of MLP 77-V-10-1 would have had, the observation of its coracoids allows assuming that the material under study belonged to a giant bird. This would be the largest penguin known to date.

Given the large amount of material from the Eocene of Antarctica that has been studied and the repeated taxonomic revisions of these associations, the systematic scenario was not expected to be much more different than was hitherto known. This implies that MLP 77-V-10-1 corresponds to one of the abovementioned species, probably *Anthropornis nordenskjoeldi*. However, this skeleton could also belong to a species not yet described, although the material available for this study does not allow precise systematic assignation to any of the known species and is insufficient for the foundation of a new taxon.

Discussion

In mechanical terms, the complex formed by the wing and the pectoral girdle acts as a lever system. For the purpose of simplification, and considering that the rest of the forces acting on the system are negligible or compensated, it is possible to narrow down the analysis to two levers (as major system components): the coracoid and the wing. In this system, the humerus alternately pulls and pushes the coracoid at its contact point (Fig. 7a) subjecting it to a series of forces whose resultants are a longitudinal force that tends to pull on the
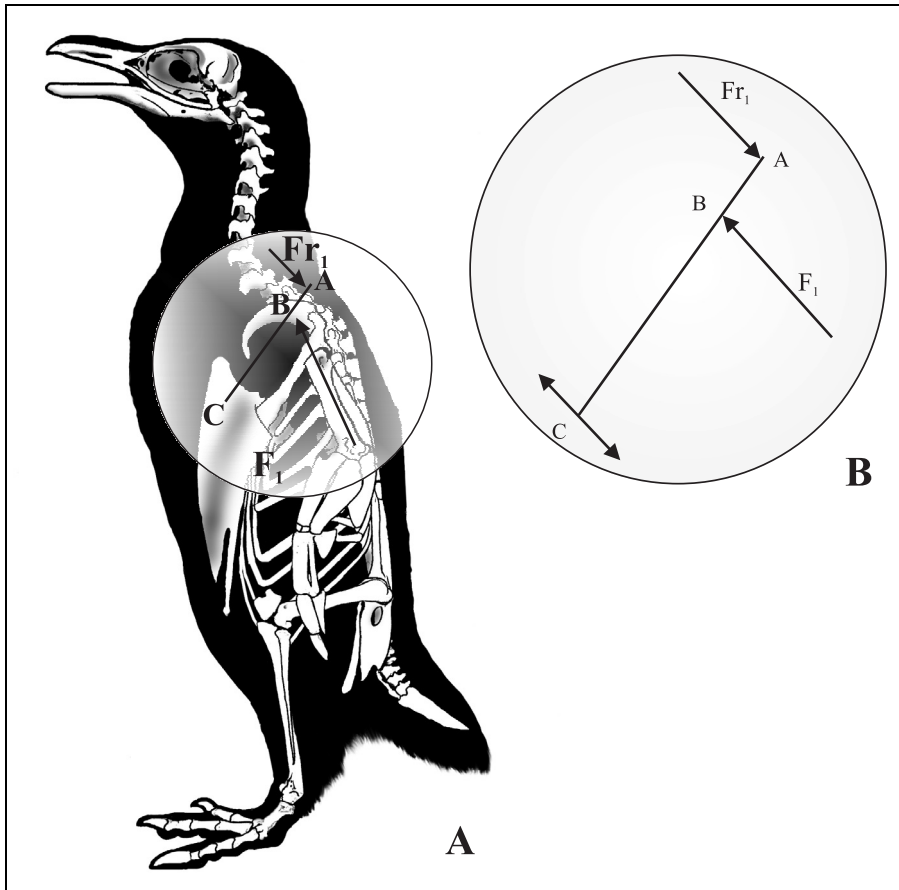
coracoid and a torque force (Young & Freeman 2003) that tends to rotate the latter (Fig. 7b).

The forces at the proximal end of the coracoid are mostly exerted symmetrically by both left and right wings (on both coracoids) and cancel each other out or are annulled by the furcula (Fig. 7b). The forces that are not compensated or annulled add longitudinal components in both directions along the main coracoid axis; thus, it is possible to perform a morpho-functional analysis of the distal end of the coracoid without taking into account the forces at its proximal end.

In this way, the analysis of the articulation between the coracoid base and the sternum allows making some considerations regarding its ideal morphology. The sternocoracoidal articulation is a contact area that must be capable of withstanding the forces transmitted by wing movement. To achieve this the joint must be strong enough but cannot be rigid, so that it can absorb the force peaks while preventing relative displacement of the elements. Considering the static friction forces (see Young & Freeman 2003 for details about these force types) that exist between coracoid and sternum, the coracoid base would be expected to develop a larger sternocoracoidal surface or present an optimized morphology in penguins compared to flying birds. The higher density of water with respect to air results in higher forces exerted at this point.

Eocene penguins, such as the Antarctic species, possess the coracoids with widest distal end (see for example Jadwiszczak 2006). The widening of this surface is due largely to the expansion of the *angulus medialis* and the *processus lateralis*, and not the *facies articularis sternalis*. Thus, in terms of the functional morphology of the coracoid generates a duality regarding the optimization of the structure. On one hand, the position muscles acting on this area have a wider surface area for attachment, which facilitates the development of more voluminous muscle masses. The thrust that allows to the penguin moving forward during diving (product of the sum of longitudinal forces from different sources) would also be optimized. Thus, by increasing the sternocoracoidal surface, the risk of detachment of the coracoid from the sternum or the breaking of the *sulcus articularis coracoideus* is minimized.

Again, the expansion of the *angulus medialis*, and especially that of the *processus lateralis*, result in an S-shaped sternocoracoidal surface in distal view. This presupposes an increase in the coefficient of static friction, which in turn assists the coracoid in maintaining its position, reducing the relative displacement between the coracoid and sternum. This morphology is highly suitable to keep the coracoid in position, resisting the torque forces tending to rotate it. However, this configuration would also restrict small-scale movements tending to adjust and refine the angle of attack.

The analysis of the accompanying spheniscofauna shows that all Eocene coracoids regardless of size exhibit a morphology very similar to that of MLP 77-V-10-1, with an S-shaped sternocoraoidal articulation, larger in size compared to that of the Miocene and current species. So, the morphology of coracoid can not be related to diving capability.

Since the coracoid is a key element in this system and because the success of wing movements highly depends on it, it is possible to assume that the diving kinematics of Eocene penguins was similar for all species. Given the extension of their distal surface, the Eocene coracoids such as MLP 77-V-10-1, would be suitable to withstand thrust forces of high magnitudes. Under this assumption, several ideas about coracoid morphology and its implications can be explored.

At first, the fact that they were able to withstand higher thrust force magnitudes could be related to higher water density, as compared to the density of the medium in which penguins dive today. Density is an important property of sea water, since it determines the existence of oceanic currents (Antonov et al. 2006), but in practice, it does not vary significantly. Still, its value depends on three variables: salinity, temperature and pressure. Due to environmental characteristics, Antarctic fossil penguins such as MLP 77-V-10-1 inhabited denser waters compared to both Miocene and present-day species that occur in more temperate climate zones. However, this idea can be easily discarded given that the current Antarctic species share the same coracoidal morphology with modern species of more temperate climates.

On the other hand, this feature could also be related to the acquisition of the ability to dive to greater depths. This would provide a larger area for muscle attachment, supporting efficient coracoid stabilization with increasing pressure. If living penguins are regarded as a *proxy* group in which the largest species present greater diving capabilities, it is possible to suggest that the specimen under study is very well adapted to deep diving. Nevertheless, the presence of morphological differences among current species with dissimilar diving habits has been discarded. In both extremes of variation, the Emperor Penguin, inhabitant of Antarctic waters, can dive up to 450 m depth where the pressure exerted by the water column is much higher than on the surface, and the *Eudyptes* species usually do not exceed 100 m. Both species have a similar morphology of the coracoid distal end (Fig. 5).

Some living species are very well adapted to deep diving, and they can make extensive trips over great distances. In particular, several penguin species have specialized in pursuit diving, which involves precise manoeuvres tending to prey capture (Williams 1995). For this purpose, improved function of the sternocoracoidal surface would be required. This would entail reduction of the surface area of this joint without decreasing its efficiency; i.e., development of osseous and probably muscular structures equally efficient but less bulky. In mechanical terms, this would be possible even when reducing the articulation area, if the angle of attack of the forces is optimized by a more effective positioning of the coracoid.

Precisely in Neogene species, concomitantly with the morphological change of the coracoid base, the convexity of the curve that defines the "C" in distal view also changes (Fig. 5). The formation of this smaller surface has probably entailed the development of less bulky musculature without impairing its efficiency.

If this were the adaptive strategy adopted by Neogene penguins, the arc formed by the coracoid base would be expected to have become more specialized

Fig. 8 - Diagram of the Principal Components Analysis based on the outlines of the coracoids in distal view. Fossil species are indicated with an asterisk (*).
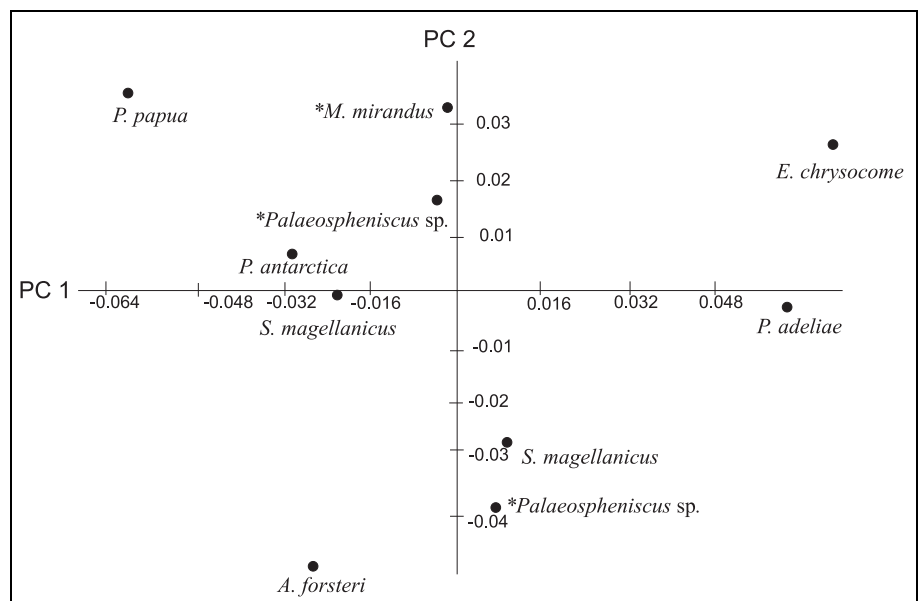
through time. Actually, the analysis of outlines shows some minor differences in shape between modern and Miocene species. The diagram of figure 8 shows a central group formed by all the fossil materials included in the analysis (the early Miocene *Palaeospheniscus* and the late Miocene *Madrynornis* forms from Patagonia), while the living species are located at both sides. The species to the right of the fossil forms are the Rockhopper Penguin *Eudyptes chrysocome* and the Adelie Penguin *Pygoscelis adeliae,* which are rather generalized divers, while at the left, the species Gentoo Penguin *Pygoscelis papua* and *Aptenodytes forsteri* are represent speed- and depth-specialized divers.

Conclusions

Eocene penguin coracoids are characterized by being longitudinally elongated structures with a transversely elongated sternocoracoidal articulation surface. This first character would have facilitated bearing the high-magnitude thrust forces exerted by the flippers during diving movements. Furthermore, the extensive distal surface would have helped to prevent the coracoid from detaching from the sternum, but it would also have resulted in immobilization of the joint. The Eocene penguin coracoids would not have been able to absorb the movements tending to rotation and thus their locomotive movements would have been less accurate.

The C-shaped coracoid base found in most modern penguin species allows small rotation movements, which would have achieved optimization of the angle of attack (of the forces), thus requiring weaker forces to obtain the same results. This makes the system more flexible, and at the same time, allows a reduction of the articular surface while maintaining the same resistance against the detachment of the *facies articularis sternalis* from the *sulcus articularis coracoideus.*

This suggests a change in diving strategy. In the oldest penguins, the improvement of diving capacity would have been linked to the development of stronger bone and probably muscular structures enabling endurance of greater forces operating in a denser medium. In contrast, the Neogene penguins would have optimized the force action of the flight apparatus by developing more precise movements, adjusting the angle of attack of each of the effective forces.
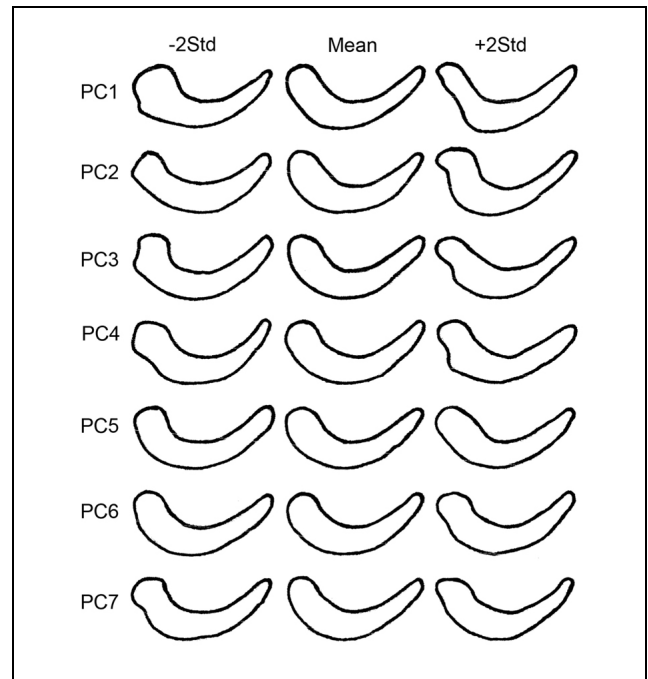

Fig. 9 - Outlines of the coracoids in distal view reconstructed along each component of the PCA by inverse Fourier transformation. The coefficients of the elliptic Fourier descriptors were calculated, letting the score for a particular principal component be equal to the mean plus or minus two times the standard deviation. This visualization helps for understanding the morphological mean of the variation evaluated by each principal component.

Considering the Neogene species, a subtle difference in shape was found between Miocene and living species, which would surely be related to the different diving strategies. In species more specialized in depth and speed diving, the coracoid has a more prominent *angulus medialis*, while species less specialized in this sense present a coracoid with an elongated and more slender *angulus medialis* (Fig. 9).

R E F E R E N C E S

Acosta Hospitaleche C. (2005) - Systematic revision of *Arthrodytes* Ameghino, 1905 (Aves, Sphenniscidae) and its assignment to the Paraptenodytinae. *Neues Jahrb. Geol. P.-A.*, 7: 404-414.

Acosta Hospitaleche C., Tambussi C., Donato M. & Cozzuol M. (2007) - A new miocene penguin from Patagonia and its phylogenetic relationships. *Acta Paleontol. Pol.*, 52: 299-314.

Anderson S.E., Hall-Martin A. & Russell D.A. (1985) - Long-bone circumference and weight in mammals, birds and dinosaurs. *J. Zool.*, 207: 53-61.

Antonov J.I., Locarnini R.A., Boyer T.P., Mishonov A.V. & Garcia H.E. (2006) - Salinity. In: Levitus S. (Ed.) - World Ocean Atlas 2005 V. 2. Ed. NOAA Atlas NESDIS 62, U.S. Government Printing Office, 182 pp.

Balseiro D., Halpern K. & Sferco E. (2004) - Interpretación morfométrica del esqueleto de Pingüinos (Aves, Sphennisciformes). IX Congreso Argentino de Ciencias Morfológicas: 8.

Bannasch R. (1986a) - Morphologisch-funktionelle Untersuchung am Lokomotionsapparat der Pinguine als Grundlage fur ein allgemeines Bewegungsmodell des "Unterwasserfluges", teil I. *Gegenbaurs Morphol. Jahrb.*, 132: 645-679.

Bannasch R. (1986b) - Morphologisch-funktionelle Untersuchung am Lokomotionsapparat der Pinguine als Grundlage fur ein allgemeines Bewegungsmodell des "Unterwasserfluges", teil II. *Gegenbaurs Morphol. Jahrb.*, 132: 757-817.

Bannasch R. (1987) - Morphologisch-funktionelle Untersuchung am Lokomotionsapparat der Pinguine als Grundlage fur ein allgemeines Bewegungs- modell des "Unterwasserfluges", tell III. *Gegenbaurs Morphol. Jahrb.*, 133: 39-59.

Baumel J. & Witmer L.M. (1993). Osteologia. In: Baumel J.J., King A.S., Lucas A.M., Breazile J.E. & Evans H.E. (Eds) - Handbook of Avian Anatomy, Nomina Anatomica Avium. Cambridge University Press, 45-132.

Campbell K. & Marcus L. (1988) - The relationship of hindlimb bone dimensions to body weight in birds. *Sci. Ser. Nat. Hist. Mus.*, 36: 395-412.

Clarke J.A., Ksepka D.T., Stucchi M., Urbina M., Giannini N., Bertelli S., Narváez Y. & Boyd C.A. (2007) - Paleogene equatorial penguins challenge the proposed relationship between biogeography, diversity, and Cenozoic climate change. *PNAS*, 104: 11545-11550.

Dingle R.V. & Lavelle M. (1998) - Late Cretaceous Cenozoic climatic variations of the northern Antarctic Peninsula: new geochemical evidence and review. *Palaeogeogr. Palaeoclimatol. Palaeocol.*, 141: 215-232.

Freeman, H. (1975) - Computer processing of line drawing images. *C. Sur.*, 6: 57-97.

George J.C. & Berger A.J. (1966) - Avian Myology. V. of 500 pp. Academic Press, New York.

Göhlich U. (2007) - The oldest fossil record of the extant penguin genus *Spheniscus*, a new species from the Miocene of Peru. *Acta Palaeontol. Pol.*, 52: 285-298.

Hammer O., Harper D. & Ryan P. (2001) - Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.*, 4: 9.

Iwata H. & Ukai Y. (2002) - SHAPE: a computer program package for quantitative evaluation of biological shapes based on elliptic Fourier descriptors. *J. Hered.*, 93: 384-385.

Jadwiszczak P. (2001) - Body size of Eocene Antarctic penguins. *Pol. Polar Res.*, 22: 147-158.

Jadwiszczak P. (2006) - Eocene penguins of Seymour Island, Antarctica: Taxonomy. *Pol. Polar Res.*, 27: 3-62.

Kirkwood J., Duignan P., Kember N., Bennet P. & Price D. (1989) - The growth rate of the tarsometatarsus bone in birds. *J. Zool.*, 217: 403-416.

Kuhl F. P. & Giardina C. R. (1982) - Elliptic Fourier features of a closed contour. *Comput. Graph. Image Process.*, 18: 236-258.

Livezey B. C. (1989) - Morphometric patterns in recent and fossil penguins (Aves, Sphennisciformes). *J. Zool.*, 219: 269-307.

Marenssi S. A., Santillana S. N. & Rinaldi C. A. (1998a) - Stratigraphy of La Meseta Formation (Eocene), Marambio Island, Antarctica. In: Casadío S. (Ed.) - *Paleógeno de América del Sur y de la Península Antártica. RAGA, Publicación Especial* 5: 137-146.

Marenssi S. A., Santillana S.N. & Rinaldi C.A. (1998b) - Paleoambientes sedimentarios de la Aloformación La Meseta (Eoceno), Isla Marambio (Seymour), Antártida. *Instituto Antártico Argentino, Contribución*, 464, 51 pp.

Mill G. & Baldwin J. (1983) - Biochemical correlations of swimming and diving behavior in the little penguin *Eudyptula minor*. *Physiol Zool*, 56: 242-254.

Owen R. (1866) - On the anatomy of Vertebrates, Vol. 2 of 121 pp. Longmans Green, London.

Poore S., Ashcroft A., Sánchez-Haiman A. & Goslow G.E., Jr. (1997) - The contractile properties of the *m. supracoracoideus* in the pigeon and starling: a case for long-axis rotation of the humerus. *J. Exp. Biol.*, 200: 2987-3002.

Reguero M.A. Marenssi S.A. & Santillana S.N. (2002) - Antarctic Peninsula and Patagonia Paleogene terrestrial environments: biotic and biogeographic relationships. *Palaeogeogr. Palaeoclimatol. Palaeocol.*, 2776: 1-22.

Rising J. & Somers K. (1989) - The measurements of overall body size in birds. *Auk*, 106: 666-674.

Rohlf F. J. & Archie J.W. (1984) - A comparison of Fourier methods for the description of wing shape in mosquitoes (Ritera Culicidae). *Syst. Zool.*, 33: 302-317.

Sandoval Arias, G.A. (2004) - Miología del tronco y del miembro posterior de *Sicalis luteola* (Aves: Passeriformes: Emberizidae). Tesis de grado. Facultad de

Ciencias, Pontificia Universidad Javeriana, 108 pp., Bogotá.

Schreiweis D. (1982) - A comparative study of the appendicular musculature of penguins (Aves: Sphenisciformes). V. of 46 pp. Smithsonian Institution Press, Washington.

Senar J. & Pascual J. (1997) - Keel and tarsus length may provide a good predictor of avian body size. _Ardea_, 85: 269-274.

Simpson G.G. (1946) - Fossil penguins. _Bull. Am. Mus. Nat. Hist._, 87: 7-99.

Simpson G.G. (1971) - A review of the pre-Pleistocene penguins of New Zealand. _Bull. Am. Mus. Nat. Hist._, 144: 319-378.

Simpson G.G (1975) - Fossil penguins. In: Stonehouse B. (Ed.) - The biology of the penguins. London: 19-42.

Simpson G.G. (1976) - Penguins. Past and present, here and there. V. of 150 pp., Yale University press New Haven, London.

Sy M. (1936) - Funktionell-anatomische Untersuchungen am Vogelflugel. _J. Ornithol._, 84: 199-296.

Stucchi M. (2002). - Una nueva especie de _Spheniscus_ (Aves: Spheniscidae) de la Formación Pisco, Perú. _Bol. Soc. Geol. Perú_, 94: 17-24.

Tambussi C., Acosta Hospitaleche C., Reguero M. & Marenssi S. (2006) - Late Eocene penguins from West Antarctica: systematics and biostratigraphy. In: Francis J.E., Pirrie D. & Crame J.A. (Eds) - Cretaceous-Tertiary High-Latitude Palaeoenvironments, James Ross Basin, Antarctica. _Spec. Pub. Geol. Soc. Lond._, 258: 145-161.

Watson M. (1883) - Report on the anatomy of the Spheniscidae collected during the voyage of H. M. S. Challenger. In: Murray J. (Ed.) - Report on the Scientific Results of the Voyage of H. M. S. Challenger During the Years 1873-1876, vol. 7, 244 pp., Neill and Company, Edinburgh.

Williams T. D. (1995) - The penguins. Spheniscidae. Birds families of the world. V. of 295 pp., Oxford University Press, Oxford.

Young H. & Freedman R. (2003) - Sears and Zemansky's University Physics with Modern Physics with Mastering Physics, 12th Edition, Mastering Physics Series. V of 1714 pp., Addison Wesley.