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FUNCTIONAL IMPLICATIONS OF A SINGULAR PENGUIN SCAPULA (AVES, SPHENISCIFORMES) FROM THE EOCENE OF ANTARCTICA

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

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Abstract. Penguins have peculiar modifications in their skeletal anatomy as a consequence of their extremely specialized diving habit. Morphological specialization is particularly evident in the forelimb. However, the kinematics of the pectoral girdle appears to be key to the locomotion of penguins. Penguin scapulae have an unusual morphology among birds. Modern penguins have a very large (especially broad) scapula, whereas this bone is long but narrower in basal fossil species. The recent finding of an incomplete scapula with a singular acromion in the Upper Eocene Submeseta Allomember of the La Meseta Formation in the Antarctic Peninsula reveals a scapula proportionally narrower than those of modern penguins but similar to that of *Waimanu* and possibly other Eocene species. Osteological comparisons and muscular dissections of modern penguins show that the most striking feature is the curvature of the acromion, and the consequent enlargement of the *facies articularis clavicularis.* The configuration of the acromion and the *corpus scapula* reflects a lack of functional optimization in terms of the resistance to forces transverse to the body axis. The scapula's general morphology suggests it belonged to a medium to large-sized penguin species with no so specialized diving skills.

Riassunto. I pinguini hanno delle modificazioni peculiari nel loro scheletro dovute alla loro modalità di immersione, estremamente specializzata. La specializzazione morfologica e' particolarmente evidente nell'arto anteriore: la cinematica del cinto pettorale rappresenta la chiave della locomozione dei pinguini. Le scapole dei pinguini hanno una morfologia del tutto inusuale tra gli uccelli. I pinguini attuali hanno una scapola molto grossa (soprattutto larga), mentre questo osso è lungo e sottile nelle forme fossili più antiche. Il recente ritrovamento di una scapola incompleta con un acromion singolare nell'Allomembro La Meseta Formation (Eocene superiore) della Penisola Antartica rivela una scapola proporzionalmente più sottile di quelle dei pinguini attuali, ma simile a quella di *Waimanu* e possibilmente anche di altre specie dell'Eocene. Confronti osteologici e dissezioni muscolari di pinguini attuali mostrano che la caratteristica più saliente consiste nella curvatura dell'acromion, con conseguente espansione della *facies articularis clavicularis.* La configurazione dell'acromion e il *corpus scapula* riflettono una carenza di ottimizzazione funzionale in termini di resistenza contro le forze che agiscono trasversalmente all'asse del corpo. La morfologia della scapola nel suo complesso suggerisce l'appartenenza ad un esemplare di grandezza medio-grande, senza una particolare attitudine al nuoto subacqueo.

Introduction

Penguins have peculiar modifications in their anatomy as a consequence of their diving habit. Among them, the hydrodynamic shape of the body plays a crucial role for energetic economy during locomotion, in addition to other skeletal and muscular adaptations. The forelimb is probably one of the structures where morphological changes are more evident. The bones are dorsoventrally flattened, and the articulations are immobile, generating a flipper-shaped structure. The peculiarity of this "underwater flight" is that penguins also exert an active upward thrust, for which the wing is positioned at an efficient hydrodynamic angle. In addition to the resistance component in the direction of flow, there is also a transversal forces component, perpendicular to the first one. The resultant force can thus be divided into a thrust component in the direction of movement of the animal, and an elevation component perpendicular to the former (Bannasch 1986a).

In large-sized penguins, in addition to the mandatory wing torsion, there is a clear strong elastic deformation in the transverse plane. In the upward stroke, the wing tip bends down; in the downward stroke, it is curved in the opposite direction. Particularly, in the acceleration phase there is strengthening in the down-

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[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@fcnym.unlp.edu.ar

[2] Instituto Superior Juan N. Terrero, B1900FWA La Plata, Argentina. E-mail: ulilaplata@gmail.com

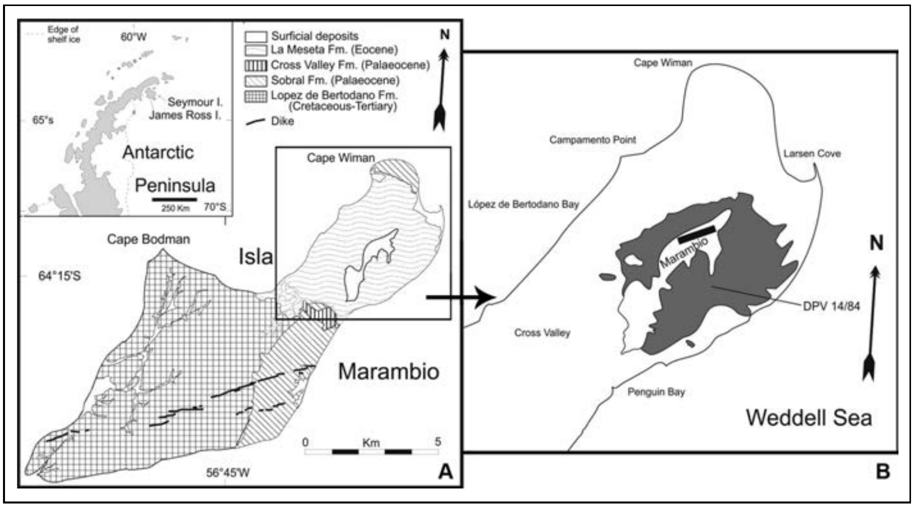


Fig. 1 - A) Map showing the location of Seymour Island, Antarctic Peninsula; B) Sketch map of the northern part of Seymour Island showing the distribution of the Submeseta Allomember and the fossil penguin-bearing locality cited in the text.

ward stroke, and often the flapping plane is not exactly perpendicular to the body axis (Bannasch 1986a).

The kinematics of the pectoral girdle appears to be a central point in the locomotion of penguins, as the wing elevator muscles work in a denser medium acting against pressure from the water column (see discussion in Bannasch 1994; Acosta Hospitaleche & Di Carlo 2010). While each of these elements is characteristic of penguins, the scapula is of particular interest, as its paddle-shape, unique among birds, was for many years considered as a synapomorphy of the Sphenisciformes (O'Hara 1989, 1991). However, recent discoveries showed that it is not a paddle-shape structure in earliest penguins (Slack et al. 2006; Ksepka et al. 2008, 2012).

Because of its development from the dermomyotome, similar to that of trunk musculature (Christ et al. 1977; Christ & Wilting 1992), some authors consider that the scapular body would not be a skeletal element, but simply part of the ossified musculature (Huang et al. 2000). However, its role as a support element for muscle attachment clearly justifies its consideration as a part of the skeleton, criterion followed in this paper.

Variations in the morphology of the scapula of living penguins were analyzed in detail by Schreiweis (1982). After a careful comparative analysis of the 14 species (currently considered as 17 different species, see Williams 1995), he concluded that there existed relative morphological homogeneity. Subtle differences were also found among scapular body outlines (Watson 1883), allowing grouping the species. However, further studies with a larger sample are still necessary. Variations of the morphology of the acromion or head of the scapula have not been yet described for penguins. Only the corpus scapula has been scored (see for example Bertelli & Giannini 2005; Ksepka & Clarke 2010) considering if it is widely expanded or narrow.

The recent finding of a partially complete scapula (MLP 11-II-20-05) with a morphological singular acromion in the Eocene La Meseta Formation, Peninsula Antarctica (Fig. 1) has motivated the present work. Its main anatomical features and their functional implications are discussed. Osteological and muscular analyses of the scapula allow advancing further assumptions about its role in the kinematics of the pectoral girdle and its involvement in the respiratory mechanics of penguins. A detailed account of its comparative morphology is given below.

Materials and Methods

The studied material is housed at the Museo de La Plata (MLP), Argentina. Comparison remains include skeletons from the collections of Museo de La Plata, Instituto Antártico Argentino, both from Argentina, and data taken from published species accounts (Stucchi 2002; Stucchi et al. 2003; Slack et al. 2006; Ando 2007; Clarke et al. 2007, 2010; Göhlich 2007; Fordyce & Thomas 2011).

Direct observation of the involved musculature was made through the dissection of two specimens of the modern penguin *Spheniscus magellanicus*. Anatomical terms follow Baumel (1993).

Systematic Paleontology

Order **Sphenisciformes** Sharpe, 1891

Family Spheniscidae Bonaparte, 1831

Fig. 2

Assigned material: MLP 11-II-20-05

Provenance: Locality DPV 14/84. James Ross Basin, Antarctic Peninsula, Antarctica (Fig. 1). Submeseta Allomember (Telm 7 according to Sadler 1988). La Meseta Formation, Late Eocene.

Description. The scapulae of penguins show an unusual morphology among birds. In all penguins, the scapula is very large (and it is particularly wide in living and Neogene species), a feature related to the great development of scapular muscles. The scapula is formed by a *corpus* separated from the proximal end by a *collum scapula* (Fig. 3).

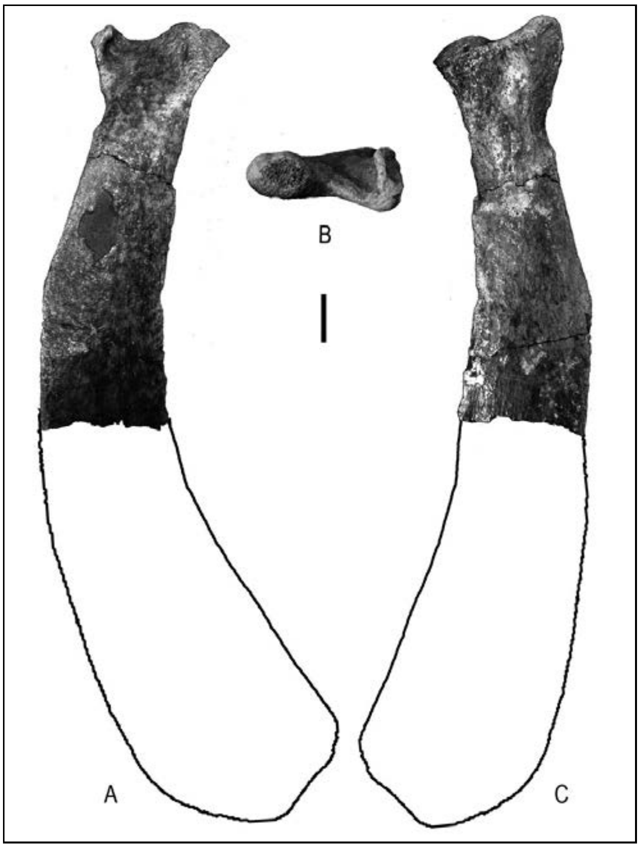


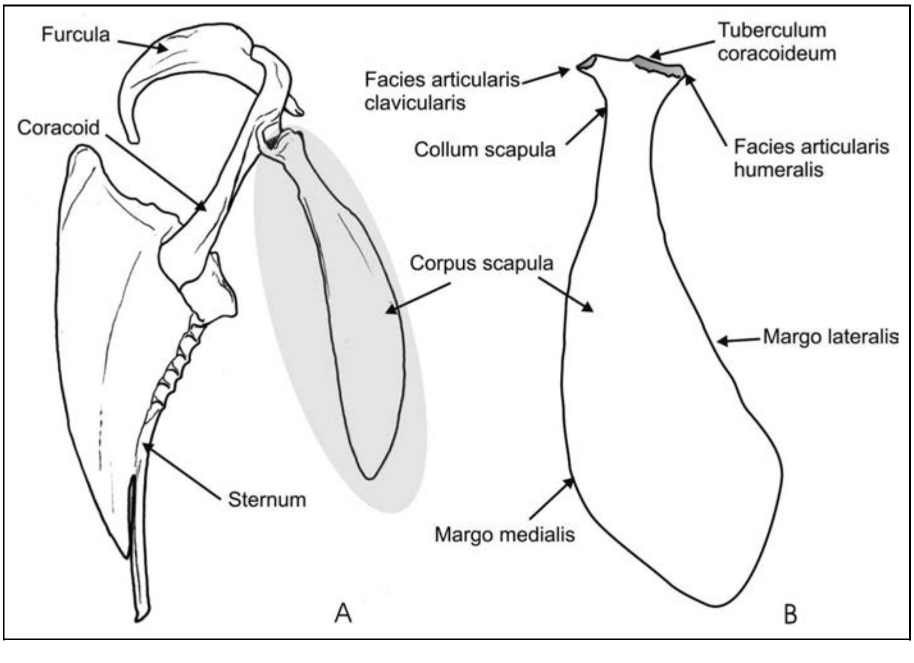
Fig. 2 - Penguin scapula MLP 11-II-20-05 from the Late Eocene Submeseta Allomember, La Meseta Formation, Antarctic Peninsula (Antarctica): A) dorsal view; B) proximal view; C) ventral view. Scale bar: 10 mm.

The *corpus scapula* is thin and distinctly paddle-shaped in modern species, in comparison with other birds, although it is intermediate in shape in the more primitive forms (see Slack et al. 2006; Simpson 1946; Clarke et al. 2007; Ksepka & Clarke 2010; Ksepka et al. 2006, 2008, 2012). Regarding its position in the body, the scapulae are parallel to each other at their more proximal portion, but gradually became more separated toward the broadened distal end, reaching the eighth rib. An interesting feature related to the mechanics of the scapula is that the dorsal margin is oriented along the same plane in penguins and flying modern birds (Stephan 1979).

The proximal end comprises two articular facets separated by a shallow notch, as in all birds. The inner facet or *facies clavicularis articularis* is developed on the acromion, and it contacts with the clavicle. In all the described fossil penguin taxa, the acromion is more or less elongated, but always unbent, in the Paleogene representatives (Slack et al. 2006; Clarke et al. 2007, 2010; Ksepka & Clarke 2010; Ksepka et al. 2008, 2012; Sallaberry et al. 2010) and the Miocene ones (Acosta Hospitaleche et al. 2007; Gölich 2007; Cione et al. 2010). However, in the specimen here described, the acromion shows a particular and unusual morphology among penguins. In all penguins, the outer facet is divided into two portions by a small ridge. Of these two parts, the internal one is set on the *tuberculum coracoideum* and contacts with the coracoids. This tubercle is developed as a hemispherical projection, similar to that one of *Icadyptes* (see Clarke et al. 2010). The external part is the *facies articularis humeralis* and contributes to the formation of the *cavitas glenoidalis*. The *facies articularis humeralis* is subcircular, rather than ovoid as in most extant penguins (see Ksepka & Clarke 2010).

The range of variation of the scapula was widely studied by Watson (1883), who determined that modern penguins can be differentiated on the basis of the mor-

Fig. 3 - A) Schematic drawing of penguin pectoral girdle, which forms the essential locomotory complex during swimming. Main elements are indicated; B) Penguin scapula and terminology employed in comparisons and descriptions.



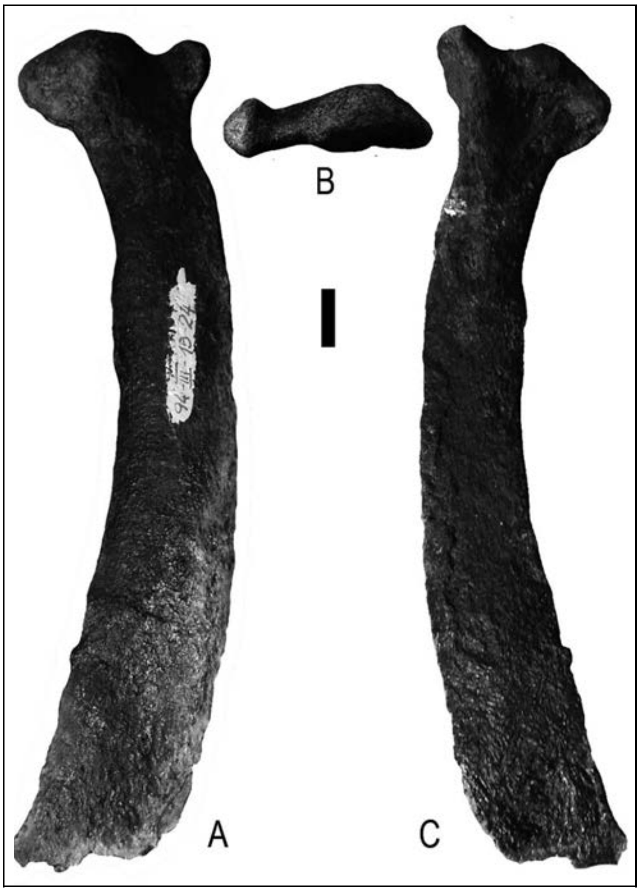


Fig. 4 - Penguin scapula MLP 94-III-15-24 from the Late Eocene Submeseta Allomember, La Meseta Formation, Antarctic Peninsula (Antarctica): A) dorsal view; B) proximal view; C) ventral view. Scale bar: 10 mm.

phology of the *corpus scapula* (see also Ksepka & Clarke 2010), while the proximal end would remain invariable.

The MLP 11-II-20-05 has a bent acromial process with a *facies clavicularis articularis* developed over a surface proportionally larger in comparison to all other known penguins, including fossil and living described species. Eocene penguin scapulae from Antarctica were compared, and little variation in acromion morphology was found. The morphologically most similar material is MLP 94-III-15-24 (Fig. 4). It has a slightly curved acromion in comparison with the other comparative materials, although not as curved as in the case of MLP 11-II-20-05 here described. The *collum scapula* is long and the *corpus scapula* is narrow, at least in the preserved part.

Musculature involved. According to the principle of action, and as suggested by Bannasch (1987), two groups of muscles were distinguished and considered in the present contribution. The first one consists of strong isotonic muscles that produce the necessary forces for locomotion, and isometric muscles that fix the corresponding plane of movement. They also transfer and redirect the forces produced by the isotonic muscles. The second group consists of position muscles that make precise adjustments in the plane of action of the forces. These are small muscles with very short lever arms, acting through their proximal insertion, as well as antagonists or synergists for the muscles of the first group, almost entirely in regard to the rotational component of the forces.

The musculature of penguins, mainly reduced to tendons, is not comparable to that of any other group of birds, in the sense it is really different because of the strong modifications. Most of the muscles acting across the shoulder joint are very well developed, a reflection of the peculiar action of the wings during underwater flight. For example, the *m. supracoracoideus* is very strongly developed in relation to the *m. pectoralis*. They both are the primary movers of the wing during underwater flight.

A complex set of muscles maintains the stiffness of the pectoral girdle and is responsible for the movements of the humerus in the *cavitas glenoidalis*. Among them, the following are connected to the scapula: the *m. latissimus dorsi, pars cranialis* is attached to its lateral border, the *m. rhomboideus superficialis* is inserted on about the anterior half of its vertebral border, the *m. serratus profundus* is inserted on about the caudal half of the costal surface near the vertebral border, the *m. serratus superficialis, pars cranialis* is mostly fleshy and inserted on the lateral border, the *m. serratus superficialis, pars caudalis* is also mostly fleshy and inserts on the ventrolateral border of approximately the posterior fifth of the scapula, the *m. scapulohumeralis caudalis* has an extensive origin from approximately the posterior two-thirds of the dorsal and lateral surfaces, the *Mm. coracoscapulares* (*m. subcoracoideus* fused with the *m. subscapularis* according to Furbringer 1888), which arises fleshy from about the proximal third of the costal surface of the scapula, the *m. deltoideus, pars major* and the *m. deltoideus, pars minor*, the *m. scapulotriceps* and the *m. humerotriceps* (fused in a common tendon) attached to the acromial process of the scapula.

Among those muscles, the *Mm. rhomboidei superficialis* (MRS), *Mm. rhomboidei profundus* (MRP), *Mm. serrati superficialis* (MSS), and the *Mm. serrati profundus* (MSP) are not directly related with the wing movements. However, they have influence on the relative lateral position of the scapula with respect to the pectoral girdle and the sternum, connecting also the ribs and the spine.

The MRS is inserted onto the last one to two cervical vertebrae and the first three to four thoracic ones, spreading cranially toward the anterior half of the *margo dorsalis scapulae* and the *extremitas omalis claviculae*. The MRS pulls the scapula backward, up and down, bringing the coracoid to the pronated position. While the MRS acts on one MSS face, the *Mm. scapulohumeralis caudalis, supracoracoideus* and *pectoralis* act on the other one. However, traction of the *m. pectoralis* decreases the abductor effect of the coracoid, or may even eliminate it. The MRP originates on the *processus spinosi* of five to six thoracic vertebrae, and extends to the *margo dorsalis* of the scapula. It moves the scapula forward, as a long lever, up and down. When the scapula is firm and contraction is synergistic, both muscles pull the spine ventrally. In the upright position, the *Mm. rhomboidei* should transfer most of the weight of the rib cage to the spine (see details in Bannasch 1986b).

The MSS is divided in two parts. The most cranial one originates in the last cervical ribs and the first thoracic ones, and extends obliquely forward and upward, reaching the *collum scapulae* and separating the lateral and medial head of the *m. subscapularis*. The most caudal head develops three muscle bellies, which rise from the second, third and fourth thoracic rib respectively, below the *processus uncinatus*, reaching the caudal part of the *margo ventralis* and the *margo caudalis* of the scapula. They both pull the scapula downwards or the rib upwards (Bannasch 1986b).

The MSP is completely covered by the scapula. It originates from the *processus uncinatus* of the two posterior cervical ribs and the first two thoracic ribs, and inserts dorsocaudally on the caudal half of the *facies ventralis* of the scapula. It pulls the ribs backward and downward (Sy 1936).

Only the *deltoideus, pars major* (DMA), the *deltoideus, pars minor* (DMI), the *scapulotriceps* (ST) and the *humerotriceps* (HT) are linked to the acromion and participate together in the elevation, abduction and adduction of the wing, as well as in humeral rotation and stabilization of the pectoral girdle during diving.

The DMA (Figs 5a, 6c) is a tiny triangular muscle attached to the acromial process of the scapula, the distal end of the clavicle and the humerus through a short tendon. It extends disto-caudally toward the dorsal surface of the humerus, where it inserts by means of a thin broad tendon next to the tendon of *m. supracoracoideus*.

The development of the DMA in penguins presents some variation. It is shortest in *Aptenodytes* and *Megadyptes*, longest in *Eudyptes* and intermediate in *Spheniscus*, *Eudyptula*, and *Pygoscelis*. Its tendon is shortest in *Eudyptes* and *Spheniscus*, longest in *Megadyptes* and *Pygoscelis*, and intermediate in *Eudyptula* and *Aptenodytes* (Schreiweis 1982). This muscle elevates and retracts the humerus, and assists the *m. supracoracoideus* in the elevation of the wing (Dial 1992). The *m. deltoides pars major* is well developed in flying birds, and is together with the *m. supracoracoideus* the main antagonist for *m. pectoralis* (Sy 1936). Only in the case of *A. forsteri* the DMA muscle is somewhat more developed (Schreiweis 1982), so that in that case there may be some small anterior traction for pronation and elevation of the humerus. The DMI (Fig. 5b) is a short muscle with two heads, of which the dorsal one is attached to the acromial process of the scapula and the coracoscapular ligament. The action of this muscle would be expected to be negligible because of its small size (Bannasch 1986b). With the exception of *Eudyptes* and *Eudyptula*, the DMI also originates inside the *canalis triosseum*, from the clavicular process of the coracoids (Schreiweis 1982). It assists the shoulder in the protraction of the humerus during flexion movements (Meyers 1997).

From a functional point of view, the DMI (Figs. 5b, 6b) is closely associated with the ventral head of the *m. supracoracoideus*. It can pull the humeral head into the articular cavity backward and downward, strengthening the effect of the *supracoracoideus* supinator, which is especially important in the last phase of upward movement of the wing. As a position muscle, it is a synergist of the *coracobrachialis* and an antagonist of the *pectoralis*.

Compared with the two previously described muscles, the ST (Figs. 5c, 6b-c) is a large muscle formed by two different heads. The dorsal head is the largest, arising from the acromial process of the scapula and the clavicle. A strong tendon is common to both heads, and fuses with the tendon of the *humerotriceps*. This muscle extends the elbow during both upstroke and downstroke movements.

Finally, the HT (Figs 5d, 6a-c) is a smaller muscle also formed by two heads that exchange fibers between them (Schreiweis 1982; Watson 1883). The dorsal and largest head ends on the common tendon of the ST and HT. It is relatively longer in *Aptenodytes*, *Eudyptula*, and *Spheniscus*, shorter in *Pygoscelis*, and intermediate in size *Eudyptes* and *Megadyptes* (Schreiweis 1982). The ST and HT extend and stabilize the elbow during wing movements (Dial 1992).

Discussion and conclusions

From the comparative analysis of the scapula and its associated musculature, it is possible to affirm that the acromion is indeed a highly conservative structure in fossil and living penguins. On the contrary, the *corpus scapula* is particularly broad in the neogene and living species, but not in the paleocene forms.

The assignment of both specimens MLP 11-II-20-05 and MLP 94-III-15-24 to Sphenisciformes is doubtless. However, the configuration of their acromion appears to be an unusual feature among penguins. The enlarged *facies articularis clavicularis* resulting from the curvature of the acromion provides a more stable

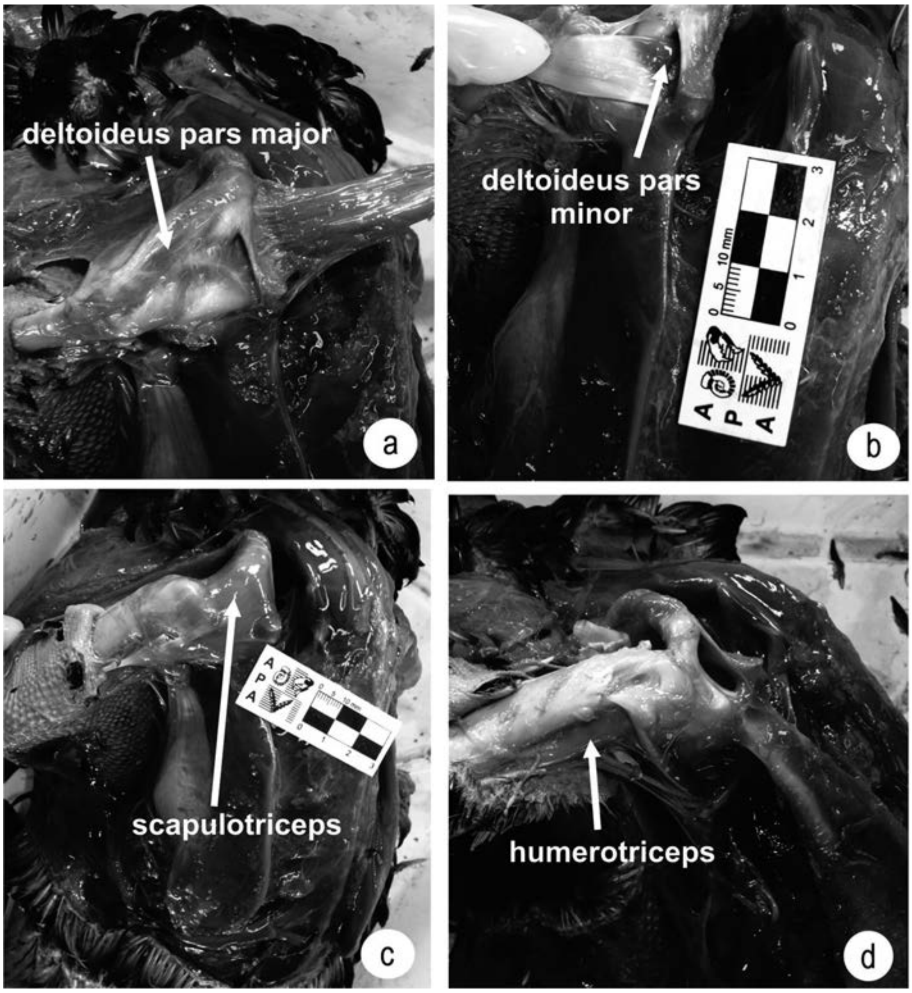


Fig. 5 - Dissection of *Spheniscus magellanicus* showing the muscles linked to the acromion: A) deltoideus, pars major; B) deltoideus, pars minor; C) scapulotriceps; D) humerotriceps.

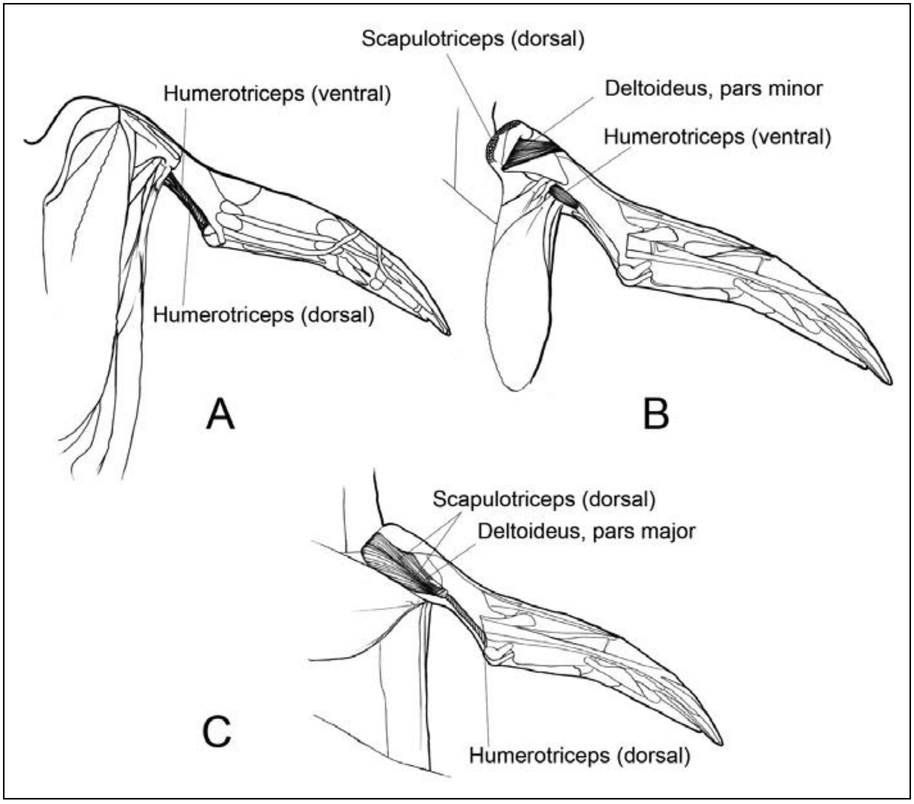


Fig. 6 - Schematic draw of the muscles showed in dissections: A) ventral view of the second layer of muscles of the wing; B) dorsal view of deepest muscles of the wing; C) dorsal view of superficial muscles of the wing.

surface for the contact with the clavicles. At the same time, this feature generates a better defined channel for the running of the supracoracoid tendon. This configuration would be able to withstand greater forces than in modern penguins.

According to the observations made here and the data given by Schreiweis (1982, and literature therein cited), the primary function of the scapula, linked to the skeletal- muscle system, is to provide stiffness to the rib cage and an attachment point for the muscles that move the wing during swimming.

However, the scapula seems to participate to some extent in the mechanics of breathing. In birds with strong flight power, the scapula extends about the level of the last ribs. In penguins, it is even longer. This relates to the fact that the scapula provides the surface for insertion of the rhomboid and serratus muscles, which are involved in inspiratory and expiratory movements, as they are responsible for the relative ascent and descent of the ribs. Due to its length, and although the relative displacement of the ribs is minimal, the scapula allows a substantial change in the volume of the thoracic cavity. Similarly, a very recent work has claimed that the *uncinate processes* of the ribs, whose function was traditionally believed to be purely supportive, also participates in the breathing mechanics (Zimmer 1935). Moreover, the morphology of the *uncinate processes* has been observed to be directly related to locomotor habit. These processes are more elongated in diving birds than in others, facilitating the inspiratory and expiratory movements of the ribs and sternum, and reducing energetic costs of these movements (Tickle et al. 2007, 2009). Thus, it is possible to consider the elements of the shoulder girdle and rib cage together as a module in terms of respiratory mechanics and underwater locomotion.

In comparison with that of other birds, the scapula of penguins provides an enlarged attachment area for the muscles involved in respiratory mechanics (even more in modern species in comparison with the primitive forms), while giving greater stiffness to the rib cage. Consequently, penguins would benefit by acquiring greater resistance to strengths transversal to the body axis, compared to the rod-shaped scapulae of other birds.

Another factor to consider, which denotes the importance of the morphology and relative development of the scapula with respect to diving skills, is provided by direct observations in chicks and sub-adult penguins. Young penguins have functional limitations as a consequence of their immature skeletal-muscle development. They present a total lack of ossification of the sternum and the distal half of the scapula. Therefore, the associated muscles have not yet reached their full extension (Bannasch 1987). Thus, they cannot make underwater excursions like the adult birds, and are limited to swimming without diving, with a narrower range of wing flapping (Bannasch 1987).

Two implications arise from the morphofunctional analysis of the acromion of MLP 11-II-20-05. On the one hand, the enlarged *facies articularis clavicularis* provides greater resistance against potential joint dislocation. On the other hand, this enlargement of the contact surface area results in an exponential reduction of the maneuverability and refinement of possible movements.

The preserved portion of the scapula MLP 11-II-20-05 allows the reconstruction of a *corpus scapula* proportionally narrower than those of modern penguins. This would reflect a lack of functional optimization in terms of the resistance to forces transversal to the body axis.

Given these parameters, we would expect the scapula MLP 11-II-20-05 to belong to a medium- to large-sized penguin, with limited diving skills. This would mean that this penguin could dive under water, as extant penguins do, but only by means of non refined movements. Modern spheniscids have developed a diving strategy based mainly on the refinement and adjustment of the angle of attack of the forces involved in these movements. Comparatively, MLP 11-II-20-05 would represent a penguin that exerted more powerful forces for diving and swimming, and undoubtedly also for breathing movements. These results are in agreement with those obtained through the analyses of the coracoid (Acosta Hospitaleche & Di Carlo 2010). Penguins displaying these features are the primitive forms (see Ksepka & Clarke 2010 for a phylogenetic discussion).

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