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New data on the humerotriceps of penguins and its implications in the evolution of the fossa tricipitalis

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ABSTRACT

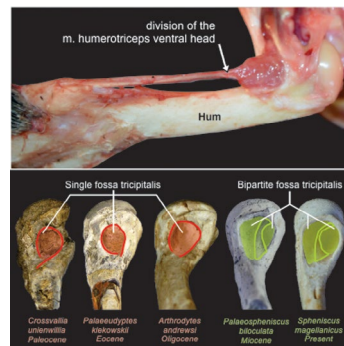
A paddle-shaped wing, the general morphology of the humerus, and the muscles involved in wing movement are among the most characteristic adaptations to diving in penguins. Particularly, the humeral fossa tricipitalis and the musculus humerotriceps are clear examples of muscular rearrangement accompanying skeletal changes. In extant Spheniscidae, we were able to identify two heads of this muscle attaching within a different compartment of the bipartite fossa. Since the partition of the fossa appeared as a novelty during the Miocene, we propose that this might have had implications for underwater flight contributing to wing-propelled diving efficiency.

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Introduction

Penguins' anatomy is highly derived, with characteristic bone, musculature, and paddle-shaped wings adapted to a diving habit. The humerus, for instance, is a short and cranio-caudally flat bone with stout muscle insertions, and with a fossa pneumotricipitalis (fossa tricipitalis) that lacks pneumatic function. This fossa is an important character used in penguins systematic (e.g. Bertelli and Giannini 2005), regarding depth, relative volume, and the presence/absence of a bipartition within it.

The oldest penguin fossil record corresponds to *Waimanu manneringi* from the late early Paleocene and *W. tuatahui* from the late Paleocene of New Zealand (Slack et al. 2006). These taxa present primitive wings in comparison with other Paleogene penguins, and a deep and single fossa tricipitalis. For Antarctica, *Crossvallia unienwillia* (Tambussi et al. 2005), a species recorded for the latest Paleocene, presents a small fossa with respect to the humeral head, in comparison with the later species, shallow and with no partition (Figure 1).

For the Eocene, an incipient partition of the fossa tricipitalis was described only for small humeri from Seymour Island, Antarctica, which was assigned to either of the smallest Antarctic species *Delphinornis*, *Mesetaornis*, or *Marambiornis* (see Jadwiszczak 2006). However, in those cases, the development of the partition is not comparable to that of extant species. The rest of the Paleogene species from Antarctica (e.g. Fordyce and Thomas 2011; Jadwiszczak et al. 2013; Acosta Hospitaleche 2014) have a fossa with no partition.

Paleogene species are also known from the middle Eocene of Peru: *Perudyptes devriesi*, *Icadyptes salasi* (Clarke et al. 2007) and *Inkayacu paracacensis* (Clarke et al. 2010); *Palaeudyptes* from the Late Eocene, *Kairuku*, *Archaeospheniscus*, and *Platydyptes* from late Oligocene (Ksepka et al. 2012); Australia: *Palaeudyptes* sp, and *Pachydyptes simpsoni* from the late Eocene Park and Fitzgerald (2012); and Argentina: *Arthrodytes andrewsi* and *Paraptendytes robustus* from the late Oligocene (Acosta Hospitaleche 2005; Chattian,

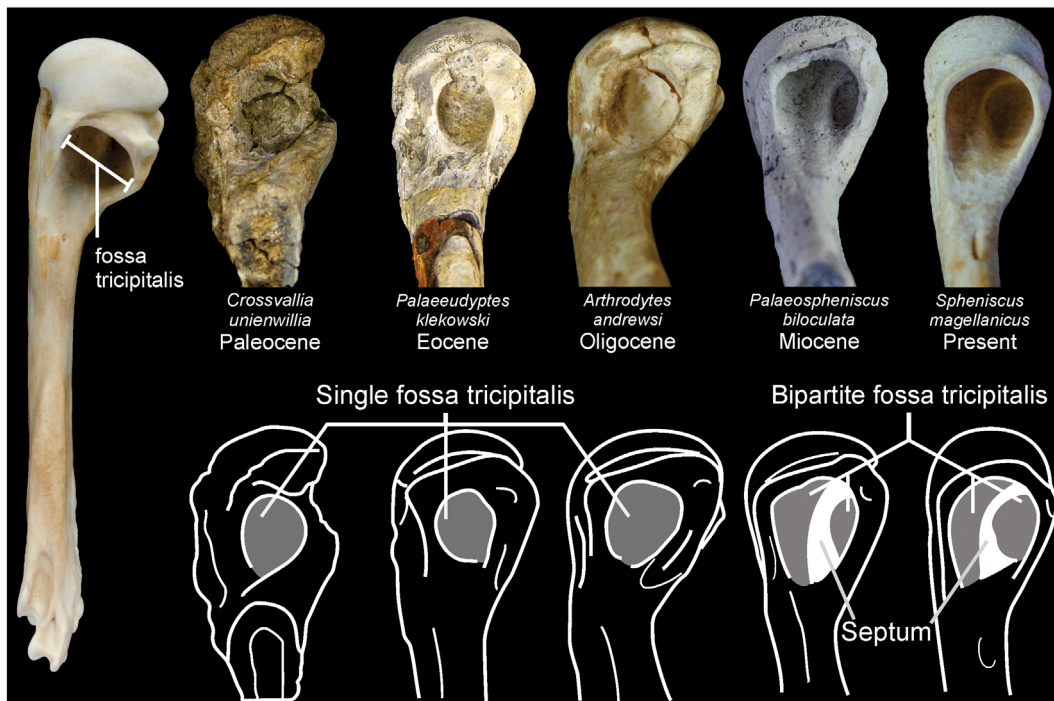


Figure 1. The fossa tricipitalis in fossil and extant penguins. Pictures are not to scale.

according to Parras et al. 2008); all these species have a single fossa.

Regardless of the high diversity of penguins during the Eocene, which ranges from tiny to giant species, all of them have a single fossa tricipitalis with no internal partitions (Figure 1). On the contrary, the high diversity of species worldwide during the Miocene (see reviews of penguin species in Stucchi et al. 2003 and Göhlich 2007 for Peru; Acosta Hospitaleche et al. 2007, 2008 for Argentina; Acosta Hospitaleche et al. 2006 and Chávez-Hoffmeister 2014 for Chile; Ksepka and Thomas 2012 for Africa; Park and Fitzgerald 2012; Thomas and Ksepka 2013 for Australia; Simpson 1972 for New Zealand; Jadwiszczak et al. 2012 for Antarctica) comprises penguins with a bipartite fossa tricipitalis, with the single exception of the Patagonian *Parapterodonytes antarctica* (see above), a condition that persists in living penguins (Figure 1) and is actually a synapomorphy of crown Spheniscidae (Ksepka et al. 2006).

In modern penguins the bipartite fossa tricipitalis (Figure 1), appears in late stages of the post-hatching ontogeny (e.g. *Spheniscus magellanicus*, see Austin 2015). The septum that divides the fossa is topographically coincident with the sulcus incisurae transversus which is placed cranial to the caput humeri. This fact has led to the interpretation that the bipartition might be a product of internal bony reabsorption at both of its sides, with the resultant of an articulation surface increment and a structure for extra support for the insertion of the ligamentum acrocoracohumerale (Austin 2015).

As presented before, the fossa tricipitalis has been extensively used for systematics, however, a functional interpretation has been seldom attempted.

Schreiweis (1982), in a detailed manuscript on penguin myology, describes, among others, the m. humerotriceps (one of the

two parts of the m. triceps brachii). In particular, the ventral head of this muscle originates fleshy from the region of the pneumatic foramen of the humerus (within the fossa tricipitalis), its belly develops near the origin and then continues mostly as a tendon. This tendon fuses to that of the m. triceps scapularis throughout most of its extension, both connect to two sesamoid bones at the elbow, and then they reach the ulna independently.

Since the fossa tricipitalis is the place of insertion of the m. humerotriceps, we consider that the study of this muscle will help understand the appearance and functional meaning of the bipartition of the fossa, as a novelty in penguins. This contribution constitutes the first attempt to analyze the morphology of the fossa tricipitalis and the m. humerotriceps in penguins from an integrative perspective.

Materials and methods

Materials for dissection (*Pygoscelis adeliae*, n 13, and *Spheniscus magellanicus*, n 3) were collected during summer Antarctic expeditions of the Instituto Antártico Argentino and in Patagonia, and are now deposited in the Ornithology Section of the Museo de La Plata (MLP). The penguins used for dissections were kept frozen, except for one specimen of *Pygoscelis adeliae* (used in Figure 2) which was preserved in formalin. In most of the cases, only one wing (left) could be dissected due to the increasing rotten of the animal after many hours of dissection.

Fossils used to illustrate (*Crossvallia unienwillia* MLP 00-I-10-1, *Palaeoudyptes klekowskii* MLP 11-II-20-207, *Arthrodytes andrewsi* cast holotype MLP M-606, *Palaeospheniscus biloculata* MLP 77-XII-22-1) the different conditions of the fossa tricipitalis are permanently housed at the Vertebrate Paleontology Division of the MLP. Anatomical nomenclature follows Baumel (1993).

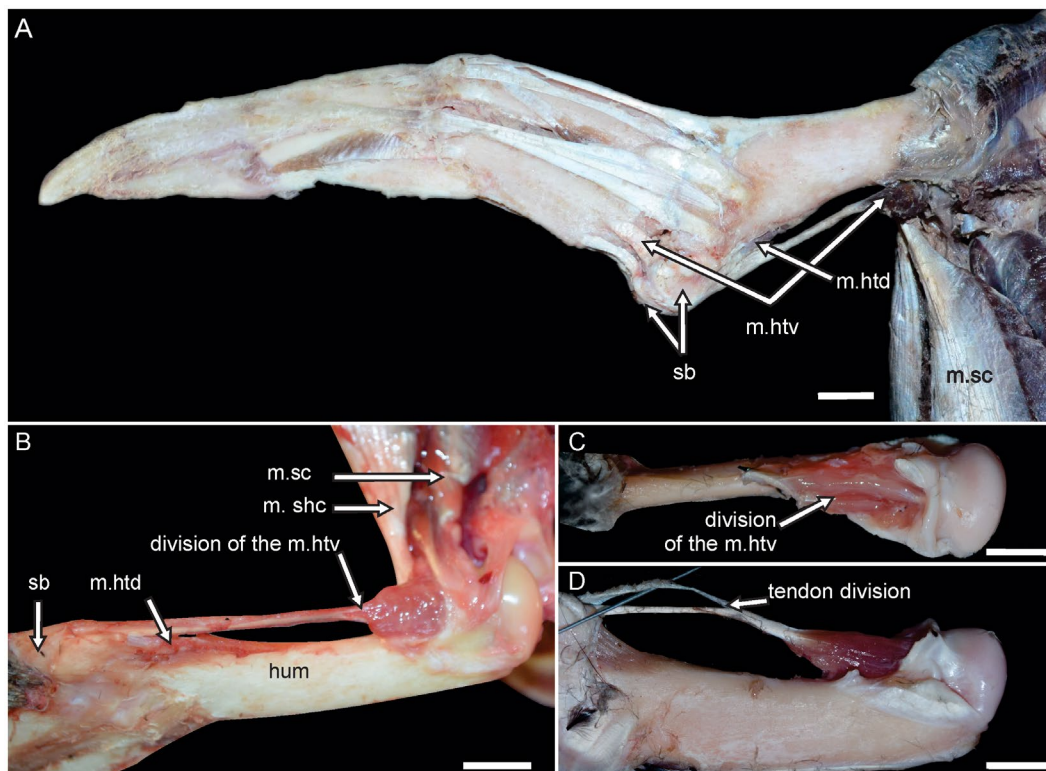


Figure 2. Muscular dissections of two penguin wings. **A**, dissection showing a complete wing of *Pygoscelis adeliae*; **B**, wing of *Spheniscus magellanicus* showing the division of the m. humerotriceps; **C**, division of the m. humerotriceps belly in *Spheniscus magellanicus*; **D**, division of the tendon of the m. humerotriceps in *Spheniscus magellanicus*. Abbreviations: hum, humerus; m.htd, dorsal head of musculus humerotriceps; m.htv, ventral head of m. humerotriceps; m.sc, musculus subcoracoideus; m.shc, musculus scapulohumeralis caudalis; sb, sesamoid bone. Scale bar: 10 mm.

Results

The m. triceps brachii comprises two parts: the m. scapulo-triceps and the less voluminous m. humerotriceps. Tendons of both muscles are connected with sesamoids at the elbow articulation (see Bannasch 1986) that articulate with the humeral proc. flexororum. The m. scapulo-triceps has a dorsal and a ventral head. The dorsal head of the m.t. scapulo-triceps originates on the clavicle, the ligamentum coracoescapularis, and the scapular acromion, and the smaller ventral head of the m.t. scapularis ventralis originates on the scapula. Both muscle bellies converge into a tendon that continues towards the cranial sesamoid ulnar bone to finally insert on the ulna.

The m. humerotriceps has also both dorsal and ventral heads (Figure 2(A)), which are not particularly well developed in penguins, and are much smaller than those of flying birds (George and Berger 1966). We found that the ventral head of the m. humerotriceps, is divided in two parts (Figure 2(B)), and that each one of these separated heads inserts in a different subdivision of the fossa. This division of the ventral head, that we nominate as cranial and caudal portions (Figure 2(B), (C)), has never been described before in any contribution.

In the species under study, the origin of each one of these heads is coincident with a different compartment of the fossa tricipitalis. Fibers of these two heads run obliquely toward two tendons, then join the sesamoid bone, and finally reach the ulna (Figure 2).

Discussion and conclusions

For the Paleogene single fossa condition, we could infer that the ventral head of the m. humerotriceps would had been a single structure with no divisions just like the fossa and, therefore, that the muscle complexity has been evolving together with the fossa and as a consequence of its growing complexity.

The fossa has undergone diverse modifications throughout penguin evolution. The first novelty was the loss of its pneumaticity and its modifications toward becoming solely a site of muscular insertion. This, however, might have happened before the diversification of penguins, since the oldest known Sphenisciform already lacks a pneumatic foramen (Slack et al. 2006), as well as its sister clade, the Procellariiformes (Baumel 1993). The second significant change occurred in the Miocene, when the fossa became partitioned in two. Generally, Paleogene species not only present a different skeletal pattern regarding robustness and proportions, but also an invariably single fossa tricipitalis (see above). We have found during dissections that the presence of this partition is coincident with a two-headed muscle that has independent attachments in each subdivision of the fossa. For this reason, we propose that this partition has functional implications in the muscle exertion made by the ventral head of the m. humerotriceps.

The division of a single muscle into two heads implies a new disposition of its fiber bundles that now run obliquely towards the tendon. This derives in a greater number of fibers in cross-section, and therefore in a more powerful muscle.

During dissection we found that by pulling the tendon of the ventral head of the m. humerotriceps, the elbow movement tending to rotation was disabled. We propose that this disposition of two heads, for this specific muscle head, with two different origins would increase the resultant force as opposed to a just one-headed muscle with a single simple origin. The action of these confluent paired heads could cause contraction without significant shortening of the muscle, and therefore, without elongation of the antebrachium. During contraction, the sesamoids are firmly attached to the articulation, making it more rigid and contributing in avoiding rotation of the elements of the zeugopodium.

Without this post-Miocene arrangement, the elbow articulation might not be as stable as that of modern penguins. This certainly does not imply that they were not able to dive; in fact, there are wing-propelled divers such as *Fratercula*, whose wings do not present such extreme adaptations as the paddle-shaped ones of penguins. However, we might assume that the bipartition of the fossa would represent an advantage for diving in modern forms, conferring a greater stability to the wing during propulsion. For that reason, species with a bipartite fossa tricripitalis, and the corresponding muscle arrangement, would have been positively selected during penguin evolution.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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