



***Aprosdokitos mikrotero* gen. et sp. nov., the tiniest Sphenisciformes that lived in Antarctica during the Paleogene**

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With 5 figures and 1 table

Abstract: A small humerus from Eocene levels of Seymour Island, Antarctica is assigned here to *Aprosdokitos mikrotero* sp. and gen. nov. (Aves, Sphenisciformes), based predominantly on its small size. An ontogenetic series based on *Pygoscelis antarctica* was established for comparative purposes, and evaluation of pathological conditions was also carried out in order to rule out other possible sources of size variation.

Key words: Spheniscidae, Seymour Island, Eocene, humerus.

1. Introduction

Penguins were and are a successful group of seabirds that have conquered different ecological niches, occupying marine coasts in diverse cold and temperate environments around the world. As a group, they are viewed as conservative because their morphology shows little change since the Paleocene, although body size appears to be a variable feature both temporally and geographically.

Antarctic penguins are mainly represented by large and giant species, although in fact, the high diversity found during the Eocene in Seymour Island includes a wide spectrum of sizes. Small-sized penguins are represented in Antarctica by *Delphinornis*, *Mesetaornis* and *Marambiornis*, diagnosed from tarsometatarsi without associated humeri (MYRCHA et al. 2002).

Other tiny species are recorded also outside Antarctica, such as *Eretiscus tonni* from the early Miocene of Argentina, and the Hakataramea penguin (FORDYCE & JONES 1990), subsequently nominated by ANDO (2007) as “*Pakudyptes hakataramea*” in his unpublished dissertation, from the latest Oligocene-earliest Miocene

of New Zealand, besides the living *Eudyptula minor*, found in New Zealand, Australia, Chatham Is., and Tasmania (MARTÍNEZ 1992). However, size is the only similarity shared among these species (see description below for details).

Although most penguin species have been diagnosed based on their tarsometatarsi, the systematic importance of the humerus has been repeatedly highlighted. An extensive list of humeral characters has been proposed to analyze the relationships between Paleogene taxa, although it has not been possible yet to score them in the smallest Antarctic species due to the absence of comparable elements (see CHAVEZ-HOFFMEISTER 2014).

The present contribution is motivated by the finding of two very small Antarctic humeri belonging to penguins in the Eocene La Meseta Formation and Submeseta Formation, Seymour (Marambio) Island, Antarctic Peninsula (Fig. 1). Because of the strikingly small size of these bones, three issues are addressed here: 1. Ontogenetic stage, 2. Comparative morphology, including possible anomalies, and 3. Systematic assignment.

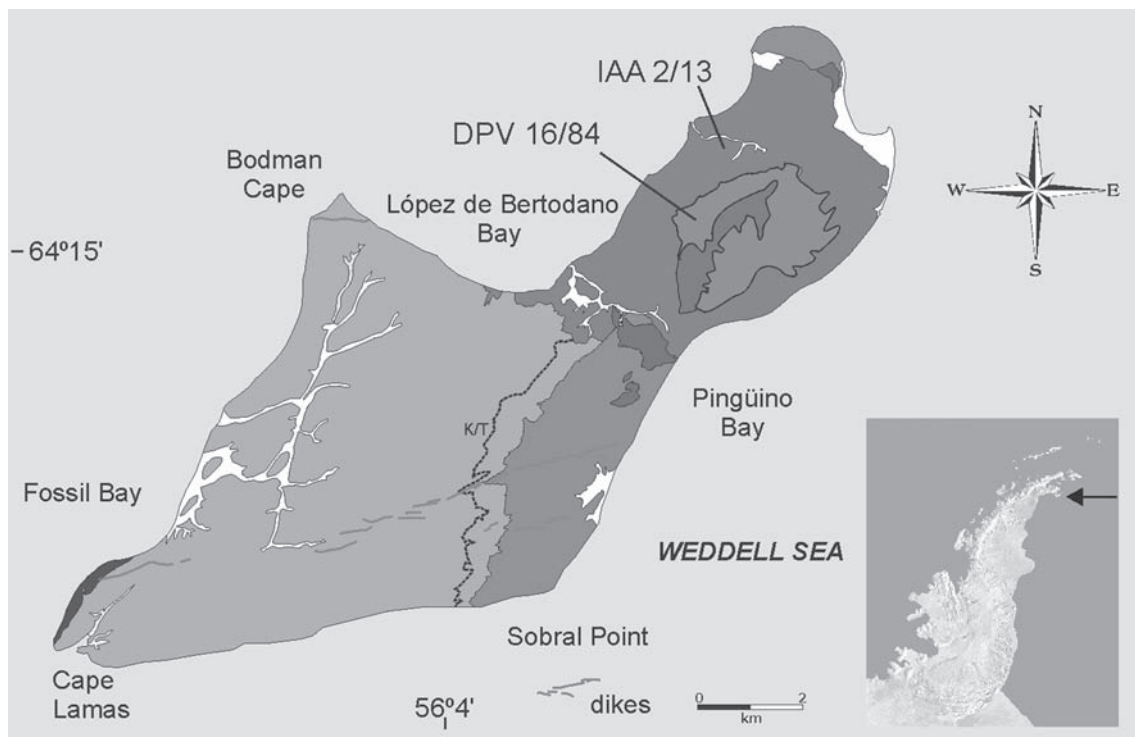


Fig. 1. Map of Seymour Island (Antarctic Peninsula, West Antarctica), pointing the fossil localities DPV 16/84 and IAA 2/13 where the humeri described here were found. At the right, the arrow is showing the location of Seymour Island, near the tip of the Peninsula.

2. Material and methods

Humeri were collected during summer campaigns of Instituto Antártico Argentino (Dirección Nacional del Antártico) and are housed in the División Paleontología de Vertebrados of Museo de La Plata (MLP), Argentina.

A complete ontogenetic series based on skeletons of the modern Antarctic penguin *Pygoscelis antarctica*, including chicks, juveniles, sub-adults and adult specimens was established for comparative purposes (see Table 1). For the fossil specimens, as well as for each skeleton of the series, degree of ossification, development of structures and textural aging was compared following TUMARKIN-DERATZIAN et al. (2006).

Once the ontogenetic stage of fossils had been determined, the possibility of abnormal development of the wing was considered. Different pathologies were considered by comparison with descriptions published in the literature (RAIDAL et al. 2006).

Comparative material includes 400 humeri from the Eocene of Antarctica, which are currently under study, belonging to the Argentinean collection at the Museo de La Plata and those described in JADWISZCZAK (2006) and TAMBUSI et al. 2006. Terminology follows the proposals of BAUMEL & WITMER (1993) and LIVEZEY & ZUSI (2006). Measurements were taken using a Vernier caliper (0.01 mm increments).

Table 1. Ontogenetic series based on *Pygoscelis antarctica* established for comparative purposes.

Repository number	Age
1769	newborn
790	7 days old
805	10 days old
788	2 weeks old
786	2 weeks old
789	3 weeks old
787	4 weeks old
817	5 weeks old
809	6 weeks old
812	8 weeks old
807	10 months old
806	1 year old

3. Geographic and stratigraphic provenance

The Seymour Island Group includes the middle-late Paleocene Cross Valley Formation, the latest Paleocene- middle Eocene La Meseta Formation, and the middle Eocene-?Oligocene Submeseta Formation. The

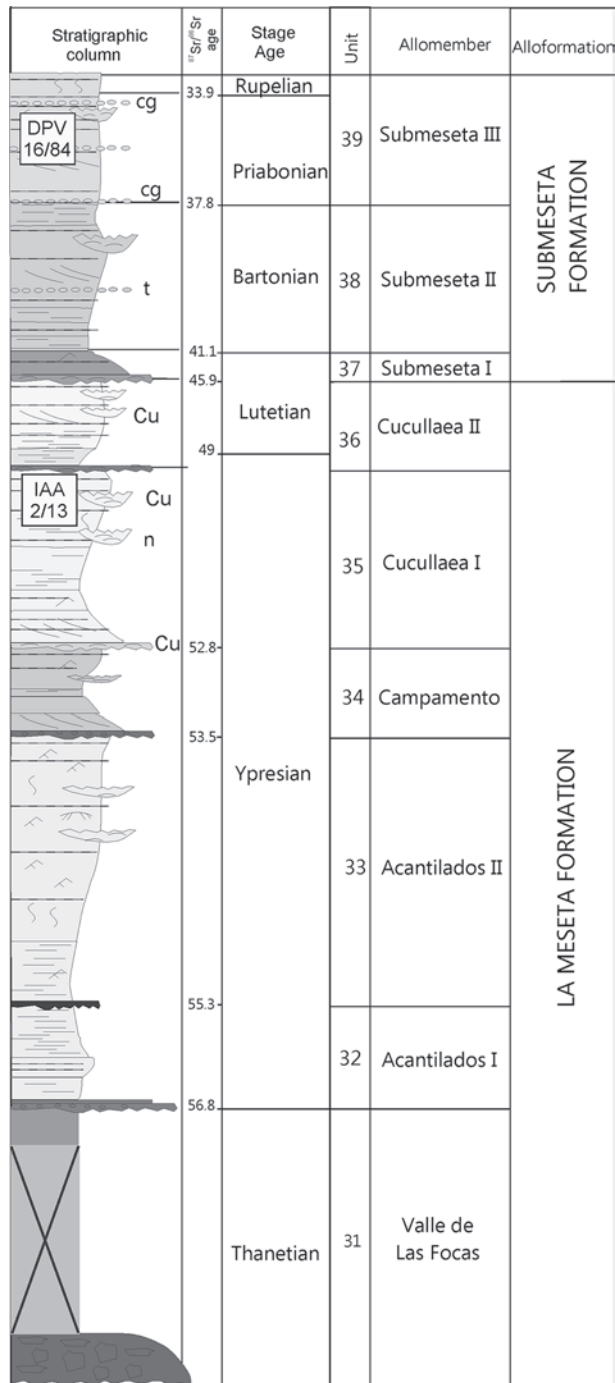


Fig. 2. Stratigraphic column showing the fossil localities in the sequence. References: cg, conglomerates, t, *Turritella* bank, Cu, *Cucullaea coquina*, n, Naticid bank.

La Meseta and Submeseta formations are the main Cenozoic strata of the James Ross Basin, exposed around the northern part of Seymour Island (DEL VALLE et al. 1992) (Fig. 1).

The La Meseta Alloformation (Fig. 2), *sensu* MARENSSI et al. 1998a (= La Meseta Formation) includes mudstones and sandstones with interbedded conglomerates. It is internally organized in six lens-shaped units that represent different sedimentation stages related to sea level fluctuations (MARENSSI et al. 2002). These erosionally-based allomembers, named Valle de Las Focas, Acantilado I, Acantilado II, Campamento, Cucullaea I, and Cucullaea II (MONTES et al. 2013), were deposited in deltaic, estuarine and shallow marine environments (PORĘBSKI 1995; MARENSSI et al. 1998b). The humerus MLP 13-IX-28-385 was collected at the fossil locality IAA 2/13 (also informally known as “Simil RV”) which encompasses outcropping levels of Cucullaea I Allomember (Ypresian). These beds are correlated with DPV 6/84 (= RV 8200 for WOODBURN & ZINSMEISTER, 1984), belonging to levels deposited above to the Naticid gastropods levels.

The middle Eocene-earliest Oligocene Submeseta Formation (MONTES et al. 2013) is divided into three levels (Fig. 2), named, from base to top, “Submeseta I”, “Submeseta II”, and “Submeseta III” (MONTES et al. 2013), and represents the uppermost part of the marine sedimentary sequence of the Basin (MARENSSI et al. 1998a). The humerus MLP 00-I-1-19 comes from the Submeseta III levels (Priabonian); it was collected at the locality DPV 16/84, with the latest deposits of the cycle.

These levels correspond to the Facies Association III, characterized by a uniform sandy lithology that represents a tidal shelf influenced by storms (MARENSSI et al. 1998b).

4. Ontogenetic determination

Due to the extreme small size of the remains, their ontogenetic stage was thoroughly analyzed. Both materials were compared with humeri of an ontogenetic series comprising twelve age categories based on specimens of *Pygoscelis antarctica* (Fig. 3), from a sample spanning from newborn chicks to one-year-old juveniles.

The comparative analysis of materials shows that the humerus does not acquire recognizable morphology in chicks younger than 15 days (Fig. 3A-D); the degree of flattening of the diaphysis being variable and increasing constantly with age. Adult morphology of the humeral diaphysis is achieved in chicks that are at least 20 days old (Fig. 3E-F). Ossification of the proximal epiphysis starts in 30-day-old birds (Fig. 3G); in addition, the humeral head becomes cranio-caudally broader and continues expanding until the juvenile



Fig. 3. Ontogenetic series constituted by *Pygoscelis antarctica*. **A**, MLP 1769 (newborn), **B**, MLP 790 (7 days old), **C**, MLP 805 (10 days old), **D**, MLP 788 (2 weeks old), **E**, MLP 786 (2 weeks old), **F**, MLP 787 (4 weeks old), **G**, MLP 817 (5 weeks old), **H**, MLP 809 (6 weeks old), **I**, MLP 812 (8 weeks old), **J**, MLP 807 (ten months old), **K**, MLP 806 (1 year old). Each line of photographs has its own scale. Scale bar = 10 mm.

stage (Fig. 3L). The impressions of the pectoral and supracoracoideus muscles become clearly differentiated between the third and fourth month (Fig. 3J-K). These muscles are closely related with wing movements during diving. The appearance of their scars in the fourth month of life (Fig. 3J) is consistent with the age at which penguins begin their incursions into the ocean. In juveniles that are only barely smaller than adults, the head of the humerus is almost completely developed, and the *tricipital fossa* is formed, whereas the distal epiphysis is still not ossified (Fig. 3L). Ossification of the distal end is completed in one-year-old individuals, when the bird reaches adult size, and only textural aging allows clear distinction between these two age categories (Fig. 3L).

The fossils present complete ossification of the epiphyses (Fig. 4), which only occurs in adult and sub-adult penguins that have already reached adult size. This ossification is particularly evident in the distal end of the humerus MLP 00-I-1-19 (Fig. 4A-D) and allows its confident assignment to an adult penguin, and in the proximal end of MLP 13-IX-28-385 (Fig. 4E-G), which shows a completely developed *caput humerus*. In chicks and young juveniles, the distal epiphysis is rounded, neither the *condyla* nor the *sulci m. humerotricipitalis* and *scapulotricipitalis* are recognizable (Fig. 3), and the head is not developed. In the fossils under study, all these structures and the *processus flexorius* (in MLP 00-I-1-19) are well developed (Fig. 4).

Textural aging is another feature that can easily indicate juvenile and sub-adult states of specimens because of incomplete ossification of the periosteal bone (TUMARKIN-DERATZIAN et al. 2006, see also WATANABE 2016.). Thus, non-adult specimens are more susceptible to breakage and weathering. The surface of specimen MLP 00-I-1-19 is somewhat eroded, which could be mistakenly identified as the textural aging of a sub-adult bird, but in fact reflects only weathering. The surface of specimen MLP 13-IX-28-385 doubtlessly corresponds to an adult penguin.

5. Concerning possible anomalous conditions of the humeri

Congenital musculoskeletal disorders and deformities are rare in wild populations of birds, or possibly rarely recorded due to the individuals not surviving and anomalous characters not being passed on to new generations. In addition, such abnormalities are rare in the fossil record, and indeed no cases of penguins with this type of deformity have ever been reported.

However, some interesting pathologies have been described in birds, occurring in isolated individuals (see SCHMIDT et al. 2003). Most studies refer to poultry and only in a few cases involve penguins (POURLIS 2011). Particularly regarding pathologies affecting the flipper, two cases of micromelia have been reported for the living species *Eudyptula minor* (RAIDAL et al. 2006). These cases represent rare events, resulting from random non-heritable genetic defects that occur during limb development, or possibly caused by exposure to teratogenic toxins. In both specimens, the affection was unilateral and the wing was significantly shortened. In cases of micromelia such as these, the humerus is also abnormally developed, and this condition can be easily detected. None of these cases consisted simply of reduction of bone size; they also involved noticeable distortions in shape. This is not the case of the fossils studied here, whose only abnormality is their size. In summary, the specimens MLP 00-I-1-19 and MLP 13-IX-28-385 are completely ordinary in terms of their morphology and there is no reason to consider that they represent an abnormal condition.

6. Systematic paleontology

Order Sphenisciformes
Genus *Aprosdokitos* nov.

Type species: *Aprosdokitos mikrotero* sp. nov., monotypic.

Etymology: From Ancient Greek “aprosdóki_tos” meaning “unexpected”, in reference to the unexpected finding of a new genus in the Eocene of Antarctica.

Diagnosis: As for type species.

Aprosdokitos mikrotero sp. nov.
Figs. 4A-D, 5A

Material: MLP 00-I-1-19 (right humerus).

Etymology: Specific epithet *mikrotero* from the Greek word “mikrótero”, meaning “the smallest”, in reference to the very small size of the assigned humerus, the most striking feature of the specimen.

Type locality and age: DPV 16/84 Fossil site, Seymour Island (Antarctic Peninsula), Submeseta III, Submeseta Formation (Priabonian-Rupelian?).



Fig. 4. A-D – *Apros dokitos mikrotero*, MLP 00-I-1-19 (holotype, left humerus) A, cranial, B, medial, C, distal, and D, caudal views. E-G – *Spheniscidae* indet., MLP 13-IX-28-385 (right humerus) E, cranial, F, medial, and G, caudal views. Ammonium chloride powder was sublimated for fossil whitening. Scale bar = 10 mm.

Measurements: Total length: 50.8 mm, distal width 9.5 mm, width of diaphysis (taken proximally to the *angulus preaxialis*): 6.8 mm, width of diaphysis (taken distally to the *angulus preaxialis*): 8.2 mm, antero-posterior width of diaphysis: 3.9 mm, antero-posterior width of distal epiphysis: 6.2 mm.

Diagnosis: Very small humerus (ca. 50.8 mm), with diaphysis broader distally to the *angulus preaxialis* and single *fossa tricipitalis*. *Condylus dorsalis humeralis* larger than the *ventralis*, which is located over the dorsal edge. *Processus flexorius* narrow and ventro-distally extended, cranial end of *sulcus m. scapulotricipitalis* curved caudally, and completely separated from the *sulcus m. humerotricipitalis* by an intermediate trochlear ridge.

Description: The humerus is small and slender. The diaphysis is almost completely straight (barely sigmoid), and the *angulus preaxialis* is well marked, dividing the shaft into a broader distal part and a narrower proximal part.

The proximal epiphysis is badly preserved, but some features are observable. The *fossa tricipitalis* is typically single and oval, with its main axis oriented proximo-distally. The *caput humeris* and the *incisura capitis* are broken, the *crista bicipitalis* is weakly developed. Only the distal fragment of the *crista deltopectoralis* is preserved, unfortunately without any portion of the *impressio m. pectoralis*.

The angle between the main axis and the tangent of the condylae is small, ca. 17°. The *condylus dorsalis humeralis* is larger than the *condylus ventralis*, which is located over the dorsal edge. Both condylae are spheroidal and conspicuous.

The *processus flexorius* is narrow and extended ventro-distally, ending in a rounded tip that is directed distally. The cranial end of the *sulcus m. scapulotricipitalis* is curved caudally, and completely separated from the *sulcus m. humerotricipitalis* by an intermediate trochlear ridge. The *sulcus m. humerotricipitalis* is deeper than the *sulcus m. scapulotricipitalis*. The *fossa m. brachialis* is shallow.

In caudal view, a distal concavity separates the proximo-caudal margin of the middle and ventral trochlear ridge from the edge of the shaft. The dorsal trochlear ridge barely surpasses the ventral margin of the shaft.

Spheniscidae indet.

Fig. 4E-G

Material: MLP 13-IX-28-385 (half of the shaft and part of the proximal epiphysis of left humerus).

Provenance: IAA 2/13 Fossil site, Seymour Island (Antarctic Peninsula). *Cucullaea* I, La Meseta Formation (Ypresian).

Measurements: Width of diaphysis (taken proximally to the *angulus preaxialis*): 5.1 mm, antero-posterior width of diaphysis: 3.2 mm.

Description: This humerus is slightly smaller than MLP 00-I-1-19 and the shaft is slender and barely sigmoid. Like in *Aprosdokitos mikrotero*, the proximal epiphysis is globose and the *fossa tricipitalis* is single.

The *crista deltopectoralis* is ridge-like and the *impressio m. deltopectoralis* is shallow. At the broken part, the section of the bone shows marked pachyostosis. Its general morphology resembles MLP 00-I-1-19.

Systematic remarks: Assignment of MLP 00-I-1-19 and MLP13-IX-28-385 to the living *Eudyptula minor*, or to the fossil species *Eretiscus tonni* or the Hakataramea penguin (“*Pakudyptes hakataramea*” in ANDO 2007) can be easily rejected. The *fossa tricipitalis* is bipartite in those species as it is in all the Neogene and modern taxa (ACOSTA HOSPITAL-ECHE et al. 2006: fig. 1; HAIDR & ACOSTA HOSPITAL-ECHE 2015), whereas it is single in the materials studied here (Fig. 4).

The general morphology of the humeri described here is shared with other Paleogene penguins. For instance, in all these taxa the *fossa tricipitalis* is deep, single, and lacks a pneumatic foramen. A distal concavity separates the proximo-caudal margin of the middle and ventral ridge from the margin of the shaft, as noted by CHÁVEZ-HOFFMEISTER (2014) in most basal penguins.

Considering the known Paleogene species, the correspondence of these specimens to any of the medium-sized, large or giant species can be ruled out. The huge difference in size precludes the assignment of MLP 00-I-1-19 and MLP 13-IX-28-385 to any species of *Tonniornis*, *Archaeospheniscus*, *Palaeedyptes*, or *Anthropornis*. Therefore, only detailed comparisons to the smallest Antarctic fossil penguin species, i.e. *Marambiornis*, *Mesetaornis*, and *Delphinornis* (see table of humeri measurements for Antarctic species in JADWISZCZAK 2006) are worth considering.

Even though these three species were described from their tarsometatarsi, several humeri were later assigned to them (see JADWISZCZAK 2006 and TAMBUSI et al. 2006). Although it has some degree of uncertainty, this systematic determination seems reasonable based on size and robustness. Moreover, in other cases, such tentative assignments based mainly on proportions and measurements were later confirmed through findings of more complete and articulated specimens (e.g., *Palaeedyptes gunnari* and *P. klekowski* in ACOSTA HOSPITAL-ECHE & REGUERO 2010, 2014).

The humeri assigned to *Marambiornis*, *Mesetaornis* and *Delphinornis* are considerably larger (Fig. 5) than those of MLP 00-I-1-19 and MLP 13-IX-28-385. The former taxa were described from tarsometatarsi that are approximately 45 mm long (MYRCHA et al. 2002: table 1), and their humeri were estimated to be more than 90 mm long (see JADWISZCZAK 2006: table 14; TAMBUSI et al. 2006). This is almost twice the length of the materials here described, which does not allow assignment of these humeri to any of these previously described species.

Fifteen humeri from the Polish collection have been indistinctly assigned to these three species (see JADWISZCZAK 2006: table 14). Considering the observed variation, those small humeri were divided into two major groups, one of them with two sub-groups, although none of them could be directly related to those species (JADWISZCZAK 2006). The groove between the *margo caudalis* and the hollow limited by the articular surface of the *caput humeri*, *facies m. supracoracoidei* and *f. m. coracobrachialis caudalis* mentioned by JADWISZCZAK (2006) as one of the diagnostic characters and illustrated for specimen IB/P/B-0132, is also observed in



Fig. 5. Comparative scheme of: **A**, *Apros dokitos mikrotero* MLP 00-I-1-19 and materials assigned genera of small-sized penguins: *Delphinornis* sp. and/or *Mesetaornis polaris* and/or *Marambiornis exilis* by JADWISZCZAK (2006: fig. 19, table 4); **B**, IB/P/B-0398 (mirrored image), **C**, IB/P/B-0132, **D**, IB/P/B-0382 (mirrored image). Images B, C, and D were taken from JADWISZCZAK (2006) and re-drawn with his permission. Scale bar = 10 mm.

MLP 00-I-1-19 (MLP 13-IX-28-385 is broken in this region). The major differences with respect to previously described materials seem to be related to size and robustness. Both materials described here are extremely small and slender, with weak, compressed and barely sigmoid shafts.

7. Discussion and conclusions

The preparation of an ontogenetic series from extant penguins was extremely important not only for comparison of the elements assigned here to *Apros dokitos*, but also for the study of other remains. The most distinctive feature of *Apros dokitos mikrotero* is its small size, which is about half of that of other known fossil Eocene

penguins of Antarctica; thus, establishing whether the individuals were adult was a crucial step in this study.

Abnormalities and known pathologies affecting the wing were also discarded, particularly those that could result in shortening of the long bones. Both materials correspond to normal adult penguins.

Previously known Antarctic humeri were grouped into fourteen species by TAMBUSI et al. (2006) and alternatively, into ten species by JADWISZCZAK (2006). In any case, regardless of the number of species recognized, the result of this study is the same. After direct comparison with more than 400 specimens, MLP 00-I-1-19 and MLP 13-IX-28-385 cannot be assigned to any known species.

Both new fossils have a single *fossa tricripitalis*, whereas in all living species as well as in the small Neogene penguin *Eretiscus tonni* and the Hakataramea penguin, this fossa is bipartite. The tiny size precludes assignment to any of the giant, large and medium-sized species, and thus only *Marambiornis*, *Mesetaornis* and *Delphinornis* were considered for further comparisons. Based on tarsometatarsal measurements, these three taxa, as well as the unnominate materials mentioned by JADWISZCZAK (2006), would be larger than MLP 00-I-1-19 and MLP 13-IX-28-385. These new humeri are extremely slender, and their diaphyses are slightly curved and only weakly sigmoid.

Even though both humeri were found isolated, and most penguin taxa are currently diagnosed from partial skeletons, or at least by the presence of a tarsometatarsus, the specimens MLP 00-I-1-19 and MLP 13-IX-28-385 can be differentiated from every known fossil and living penguin species, reason enough to consider them as a new taxon. The MLP 00-I-1-19 is assigned here to *Aprosdokitos mikrotero*, the smallest Antarctic species ever described. The MLP 13-IX-28-385 shares its size and others similarities with *A. mikrotero*, although we prefer to keep it as an indeterminate species due its fragmentary condition.

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