Enigmatic morphological disparity in tarsometatarsi of giant penguins from the Eocene of Antarctica

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Abstract: The only record of the Paleogene Antarctic Sphenisciformes comes from the Eocene La Meseta Formation (Seymour Island, Antarctic Peninsula). The analysis of tarsometatarsi attributed to the genus *Anthropornis* ("giant" penguins) from the Argentine, Polish and Swedish collections revealed an intriguing heterogeneity within these taxonomically important elements of the skeleton. The unique hypotarsal morphology challenges the current systematics of large-bodied penguins and sheds new light on their evolution.

Key words: Antarctic Peninsula, Eocene La Meseta Formation, penguins, *Anthropornis*, tarsometatarsi.

Introduction

Penguins (Aves: Sphenisciformes), one of the most distinctive and highly specialized orders of birds, evolved presumably in the late Mesozoic, and the earliest published fossils come from the late early Paleocene (62–61 Ma; Slack *et al.* 2006). It is widely accepted that some Paleogene (65.5–23.0 Ma) sphenisciforms reached impressive dimensions. Such "gigantism" became particularly widespread during the Eocene epoch (55.8–33.9 Ma), and individuals assigned to at least nine species from Antarctica, Australia, New Zealand and South America were clearly larger than the recent penguins (Jadwiszczak 2009; Clarke *et al.* 2010). The Eocene record of Antarctic penguins, known solely from the La Meseta Formation, Seymour Island (Antarctic Peninsula) (Fig. 1), includes *Anthropornis nordenskjoeldi* Wiman, 1905, the largest sphenisciform ever, as well as *A. grandis* (Wiman, 1905) – its smaller (though still impressive in size) congeneric (Jadwiszczak 2001). Their type specimens are isolated tarsometatarsi which is typical of all distinct La Meseta penguins (Myrcha *et al.* 2002).
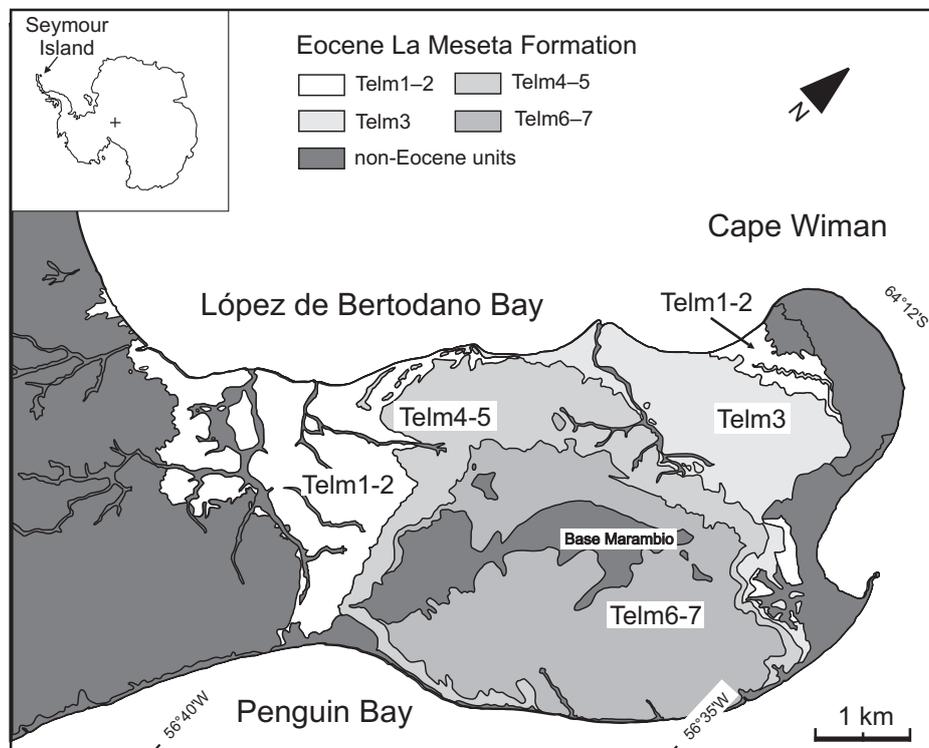
Fig. 1. Location map of units of the La Meseta Formation on Seymour Island (according to Sadler 1988).

The purpose of this paper is to report on the existence of intriguing morphologic heterogeneity within those important elements of the hind-limb skeleton of *Anthropornis*. Our finding sheds new light on systematics and evolution of early penguins.

Material and geological setting

A total of 19 isolated tarsometatarsi assigned to the genus *Anthropornis* were analyzed. Only eight of them were complete enough to use in this study. They come from Seymour Island, a small ice-free scrap of land located east of the northern end of the Antarctic Peninsula at 64°17'S, 56°45'W. The early Eocene–latest late Eocene La Meseta Formation (Elliot and Trautman 1982) crops out in the northeastern part of the island (Fig. 1). It represents a sequence (*ca* 800 m thick and richly fossiliferous at numerous horizons) of shallow marine, mostly poorly consolidated siliciclastic fine-grained sediments (Porębski 1995, 2000; Jadwiszczak 2006 and references cited therein). Sadler (1988) mapped the formation in terms of seven major lithofacies Telm1–Telm7, whereas Marenssi *et al.* (1998) proposed six erosionally-based units (allomembers). Specimens discussed here were buried in sediments within the unit Telm4 and Telm7 (the Cucullaea I and Submeseta Allo-
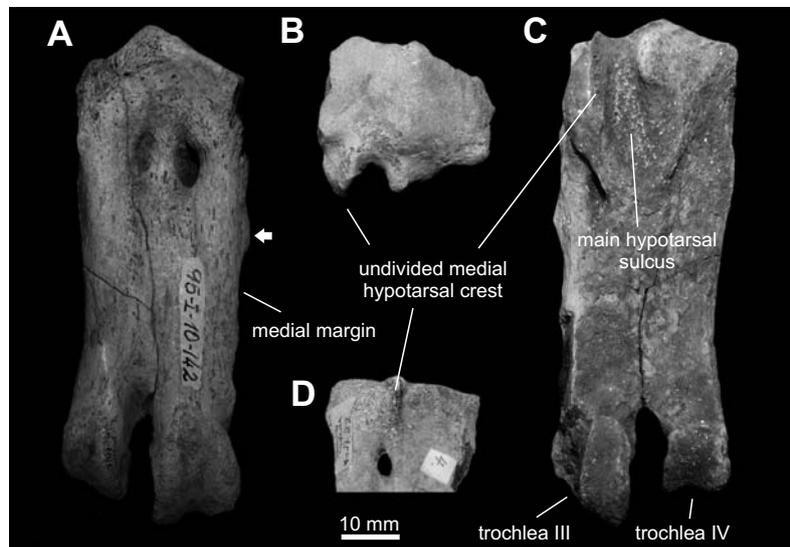
Fig. 2. Right tarsometatarsi of *Anthropornis grandis* (**A–C**. MLP 95-I-10-142, **D**. NRM-PZ A.22) from the La Meseta Formation (Seymour Island, Antarctic Peninsula) representing bones with a single medial hypotarsal crest. **A**. Dorsal view. **B**. Proximal view. **C**. Plantar (ventral) view. **D**. Ventromedial view. The white arrow points to the medial convexity characteristic of all but one tarsometatarsus assigned to the genus *Anthropornis*.

member respectively). They are housed at the Institute of Biology, University of Białystok, Białystok (Poland), Museo de La Plata, Ciudad de La Plata (Argentina) and the Swedish Museum of Natural History, Department of Palaeozoology, Stockholm (Sweden); abbreviated: IB/P/B, MLP and NRM-PZ respectively.

Results

We found that tarsometatarsi attributed to *Anthropornis* can be divided into two groups that differ in the morphology of the hypotarsus (synonymy: calcaneus), a conspicuous structure present on the posterior (plantar in penguins) side of the bone (Figs 2, 3). Its sulci (in numerous bird species accompanied by canals) conduct flexor tendons of the pedal digits (Baumel and Witmer 1993). The first group is represented by six specimens with an undivided medial hypotarsal crest (Fig. 2): NRM-PZ A.22 (a holotype of *A. grandis*; Wiman 1905, plate 2, fig. 6; Fig. 2D), IB/P/B-0483 (Myrcha *et al.* 2002, fig. 6), MLP 95-I-10-142 (Fig. 2A–C), MLP 95-I-10-156 (the last three bones assigned to *A. grandis* by Myrcha *et al.* [2002]), MLP 84-II-1-7 (*A. nordenskjoeldi* in Myrcha *et al.* 2002), and MLP 94-III-15-356 (*Anthropornis* sp., assignment based on CAH's personal observation).

The second set comprises two specimens, huge MLP 83-V-20-50 (*A. nordenskjoeldi* in Myrcha *et al.* 2002) and intriguingly small MLP 84-II-1-9 (*Anthropornis* sp. in Myrcha *et al.* 2002; Fig. 3), both having the medial crest of the hypotarsus di-
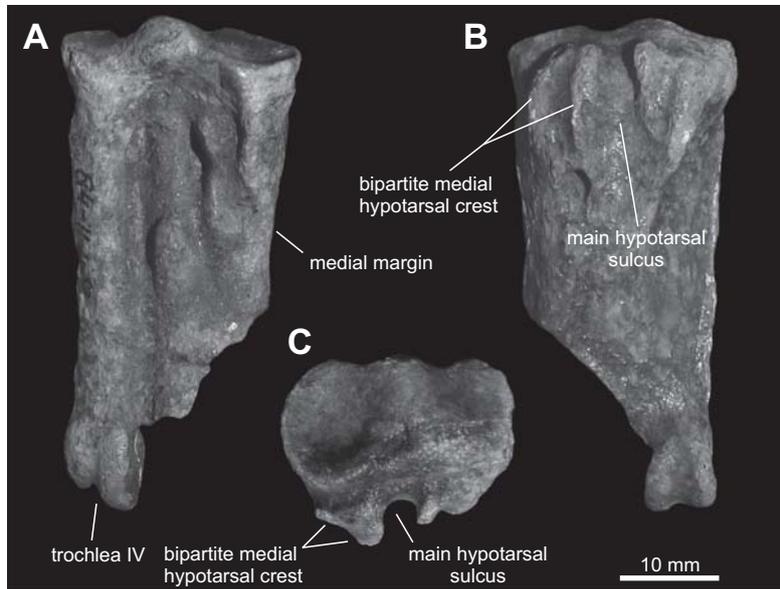
Fig. 3. Right tarsometatarsus of *Anthropornis* sp. (specimen MLP 84-II-1-9) from the La Meseta Formation (Seymour Island, Antarctic Peninsula) representing bones with a bipartite medial hypotarsal crest. **A**. Dorsal view. **B**. Plantar (ventral) view. **C**. Proximal view.

vided into two clearly separated ridges (Fig. 3B; for measurements, see Myrcha *et al.* 2002, table 1). Moreover, MLP 84-II-1-9, unlike other bones listed here, is devoid of a convexity (Fig. 2A) on its medial margin (Fig. 3). Hypotarsi of other specimens are too abraded to compare.

Discussion

The results presented above uncover an intriguing aspect of diversity in penguins. Studying fossil sphenisciforms for years, we have never had to deal with such heterogeneity within an otherwise well-defined genus. The hypotarsal morphology is important in fossil penguin systematics, and the number of calcaneal ridges has appeared to be conservative at generic level (Myrcha *et al.* 2002).

In our opinion, the most obvious difference between two species of *Anthropornis* is hypotarsal morphology, not linear dimensions, and accepting this approach would require updating the specific diagnoses. The main drawback of this explanation is that it does not take into account the considerable size disparity between MLP 83-V-20-50 and MLP 84-II-1-9 (35.5% for the proximal width; Myrcha *et al.* 2002, table 1). The latter is the smallest tarsometatarsus assignable to *Anthropornis*, however, it is definitely an element of the hind-limb skeleton of an adult bird (no remnants of intermetatarsal sutures can be found). Maybe it reflects the extreme case of the sexual size dimorphism (Jadwiszczak and Mörs 2011), but

the sample is too small to enable further examination of this issue. Anyway, their stratigraphical distance seems not to play any role here – both specimens come from "vertically" adjacent localities (DPV14/84 and DPV 13/84, respectively; Myrcha *et al.* 2002, fig. 2) within Telm7 unit or the Submeseta Allomember. Interestingly, systematically heterogeneous bones from the group possessing an undivided medial crest were found as low as Telm4 or Cucullaea I Allomember (MLP 95-I-10-142 and MLP 95-I-10-156) and as high as Telm7 (Myrcha *et al.* 2002, table 2, fig. 2). Such distribution suggests that the "simplified" hypotarsal morphology (medial crest undivided) represents, in the case of *Anthropornis*, the ancestral condition persisting through the time. Intriguingly, the more complex hypotarsi (characterized by the divided medial crest) appeared close to the Eocene/Oligocene transition and the onset of continental glaciation (Jadwiszczak 2010a).

An apparently similar situation, though with the reversed polarity of character states, *i.e.* the bipartite state of the medial hypotarsal crest being geologically older than the undivided one, was reported in *Spheniscus* (Göhlich 2007). *Spheniscus muizoni* Göhlich, 2007 from the Miocene of Peru (the earliest known representative of this genus), unlike its congenerics (both extinct and extant), has "a second very week crest" laterally attached to the medial hypotarsal crest ("along its distal half"), see Göhlich (2007, p. 295). In our estimation, however, the actual status of this feature seems to be debatable. The above mentioned second crest is indeed poorly developed and we are not convinced it deserves its name (Göhlich 2007, fig. 3C$_2$).

The lack of the convexity on the medial margin of MLP 84-II-1-9 most probably results from the small size of this bone (and obviously the rest of a skeleton it belonged to). We interpret such a swelling present in all but one tarsometatarsus assigned to *Anthropornis* as a supportive mass-related structure (see also Jadwiszczak 2010b, and Jadwiszczak and Mörs 2011).

To conclude, the fossil record testifies to the existence of two distinct morphotypes within hypotarsi of *Anthropornis* that is a unique feature questioning the validity of the current intrageneric systematics of giant penguins. In our opinion, these morphotypes represent, in fact, two species, and the next step would normally be to analyze the type specimens (*i.e.* NRM-PZ A.22 and NRM-PZ A.45; Wiman 1905) in terms of their hypotarsal morphology. However, since the proximal part of the holotype of *A. nordenskjoeldi* (NRM-PZ A.45), unlike its counterpart in *A. grandis* (Fig. 2D), is too poorly preserved (PJ's personal observation), the formal revision of the genus, requires availability of more complete specimens (preferably skeletons; Acosta Hospitaleche and Reguero 2010).

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