An enigmatic fossil penguin from the Eocene of Antarctica

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**ABSTRACT**

Tarsometatarsi are key skeletal elements in penguin palaeontology. They constitute, among others, type specimens of all 10 widely accepted species of fossil penguins from the Eocene La Meseta Formation on Seymour Island (Graham Land, Antarctic Peninsula). Here, we report on a recently collected large-sized tarsometatarsus from this formation that represents a new morphotype. We are convinced that the morphotype corresponds to a new species, but the material is too scarce for a taxonomic act. Undoubtedly, the bone discussed here is a valuable addition to our knowledge on diversity of early penguins.

**KEYWORDS**

Antarctic Peninsula; La Meseta Formation; Paleogene; Sphenisciformes; tarsometatarsus; new morphotype

Eocene (56–34 Mya) penguins (Aves, Sphenisciformes) have a remarkably extensive fossil record, especially in contrast to their earlier relatives known from the Paleocene (66–56 Mya) (Jadwiszczak 2009). At present, various scientific institutions house thousands of Eocene penguin bones, collected within several localities scattered throughout the Southern Hemisphere. Most of these specimens, albeit very rarely in the form of articulated partial skeletons (e.g., Acosta Hospitaleche & Reguero 2010), were recovered from the Eocene La Meseta Formation on Seymour Island, Antarctic Peninsula (Fig. 1; Myrcha et al. 2002; Jadwiszczak 2009; Jadwiszczak & Mörs 2011; Reguero et al. 2013).

Holotypes of all 10 undisputed species assigned to six genera of early penguins from that formation are tarsometatarsi (Myrcha et al. 2002; Reguero et al. 2013; Chávez Hoffmeister 2014). Importantly, a number of previous studies, also including those focused on tarsometatarsi (e.g., Jadwiszczak 2008), have already demonstrated that the list of actual species (possibly also genera) is not exhaustive. Herein, we report on a penguin tarsometatarsus that expands on the existing knowledge of the Eocene penguin diversity.

**Material and methods**

The bone considered here was collected in 2012 by TM in the upper part of the La Meseta Formation on Seymour Island (James Ross Basin, northern Antarctic Peninsula). It was found in the unit Telm7 (or Submeseta Allomember; see Marenssi 2006), traditionally regarded as Late Eocene in age, (e.g., Marenssi 2006), within the Swedish locality NRM 5 (64°14.490'S, 56°37.215'W) (Fig. 1). This locality corresponds to the Submeseta II Allomember or level 38 of Montes et al. (2013) that they interpreted as late Middle Eocene (Bartonian) in age. According to some recent sources (e.g., Buono et al. 2016; Kriwet et al. 2016), level 38 is of Late Eocene (Priabonian) age.

The fossil bone was found in situ while surface collecting. The site is a small, isolated plateau and it can be confidently excluded that the material has been transported by solifluction down from higher levels. The specimen derives from a fossiliferous horizon (Fig. 1) that is very rich in vertebrate remains, especially penguins and teleosts, and has also produced a few chondrichthyan teeth (e.g., Kriwet et al. 2016). The fossil specimen is housed in the collections of the Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm, Sweden (NRM-PZ).

The specimen was mechanically cleansed of remnants of the matrix material by PJ in 2016. The graphical reconstruction of the medial margin (Fig. 2d), following the preparation of the fossil, was based on the shape of its preserved parts, especially of the position of its maximum concavity. Relevant tarsometatarsi of Eocene Antarctic penguins from rich collections held by the authors’ institutions — the University of Białystok, Poland (IB/P/B) and the Swedish Museum of Natural History, Stockholm — also helped to (virtually) recreate the margin. Data for present-day Aptenodytes penguins (Table 1) are based on specimens from the Natural History Museum at Tring (UK), studied by PJ as part of the project GB-TAF-4610 (SYNTHESYS programme). The measurement categories follow those used by Myrcha et al. (2002).
Results and discussion

The analysed specimen (Fig. 2) represents the tarsometatarsus, a taxonomically important bone (Myrcha et al. 2002) of an early penguin that exhibits an unusual combination of character states. The latter observation precludes its assignment to any known species of these birds, hence the taxonomic position can be summarized as follows.

Class Aves Linnaeus, 1758
Order Sphenisciformes Sharpe, 1891
Family Spheniscidae Bonaparte, 1831 (but see Clarke et al. 2003)
Spheniscidae gen. et sp. indet.

Material examined

The incomplete left tarsometatarsus, NRM-PZ A.856, of an adult individual (Fig. 2).

Description

The fossil specimen is from a large penguin (see Jadwiszczak & Chapman 2011), in the size range of Palaeudyptes gunnari (Wiman, 1905) and Anthropornis grandis (Wiman, 1905), from the La Meseta Formation (Table 1; see also table 1 in Myrcha et al. 2002). It is elongate and missing portions of the medial margin, whereas other affected parts, the proximal epiphysis as well as trochlea, are of minor importance. The intercotylar eminence is prominent. Both proximal vascular foramina are small in dorsal view (unlike in Anthropornis and Palaeudyptes), located at the same level relative to the main axis. The lateral one is better developed (unlike in Anthropornis) and its opening is located much deeper. In plantar view, the openings are located inside the wider bony vestibules, the lateral one is more proximal. The proximal metatarsal III is strongly lowered in dorsal view (unlike in Palaeudyptes and other result in concavity is clearly separated from the raised surface of the proximal epiphysis (unlike in Anthropornis). The lateral intermetatarsal sulcus is well-developed and becomes shallower (smoothly, unlike in Palaeudyptes) towards its distal end which is lacking in a distal vascular foramen. The short medial sulcus has two conspicuous oval-shaped tubercles, insertion sites of the extensor retinaculum, situated mesiodistally and distally to the medial vascular foramen (unlike in Palaeudyptes and Anthropornis). The insertion scar
for the cranial tibial muscle is conspicuous, slightly elongated and, unlike in *Anthropornis* and *Palaeudyptes*, rounded in profile. The distal metatarsal III possesses a characteristic, subtly elevated triangular surface in dorsal view. There is also a conspicuous sharp and oblique crest just proximal to the trochlea II. Both structures, together with the medial plantar crest, form a uniquely well-developed passage for the tendon of the abductor muscle for the digit II (see Jadwiszczak 2015). The intermediate hypotarsal crests are distinctly separated. The adaxial one is low, oblique and smoothly weakens, losing its height, distally (unlike in *Anthropornis*). The hypotarsal sulcus is narrow. Distally to the medial hypotarsal crest, there is a raised rim with a slightly elevated, flat and oval-shaped, ligament/tendon attachment point. The lateral bone margin forms a long sharp edge, the lateral plantar crest. The origin site of the abductor muscle for the digit IV, located between the hypotarsus (and its distal bony continuation) and lateral plantar crest (see

**Figure 2.** Tarsometatarsi of Eocene penguins for Seymour Island, Antarctic Peninsula. (a–g) Left-side bone, NRM-PZ A.856, representing a new morphotype: (a, d) dorsal; (b) lateral; (c) plantar; (e) medial; (f) proximal; and (g) distal views of the specimen; (d) showing the reconstruction of its medial margin. (h–k) Tarsometatarsi (dorsal view) representing ‘giant’ penguins from the Eocene of Seymour Island. Left-side bones: (h) IB/P/B-0483 and (i) IB/P/B-0457; reversed right-side bones: (j) NRM-PZ A.22 and (k) NRM-PZ A.7.
Table 1. Measurements of a new specimen as well as tarsometatarsi assignable to ‘giant’ fossil penguins from the Eocene of Seymour Island and the living emperor penguin (Aptenodytes forsteri G.R. Gray, 1844). Data are introduced as medians, ranges and numbers of specimens. Asterisks mark samples with small-sized bones underrepresented, because of their incompleteness. All values are in millimetres.

| Specimen/taxon                   | Total length | Length to the groove of trochlea III | Mediolateral width of shaft (narrowest part) | Dorsoplantar thickness of trochlea III along its groove | References                      |
|----------------------------------|--------------|--------------------------------------|---------------------------------------------|-----------------------------------------------------|---------------------------------|
| NRM-PZ A.856 (a new morphotype) | 64.2         | 61.6                                 | 22.7                                        | 14.1                                                | This study                      |
| Anthropornis                     | 78.6         | 76.3                                 | 26.6                                        | 19.4                                                | Myrcha et al. (2002, table 1)   |
| Palaeeudyptes                     | 74.7–88.1 (6)*| 72.8–86.0 (6)*                       | 21.4–31.5 (9)                               | 17.0–21.0 (6)*                                      | Myrcha et al. (2002, table 1)   |
| | 68.6         | 66.8                                 | 28.4                                        | 19.4                                                | Myrcha et al. (2002, table 1)   |
| Palaeudyptes                      | 59.0–81.5 (29) | 57.9–79.0 (31)                       | 22.4–32.8 (31)                               | 15.8–33.3 (41)                                      | Jadwiszczak (unpublished data)  |
| Aptenodytes forsteri             | 46.4         | 45.0                                 | 28.7                                        | 13.8                                                |                                 |
|                                  | 415–48.7 (7) | 40.0–47.3 (7)                        | 26.9–30.5 (7)                               | 13.1–14.5 (7)                                       |                                 |

Jadwiszczak 2015), is relatively broad, like in other similarly sized penguin tarsometatarsi. The lateromedially narrowest part of the bone shaft is located distally to the level of the midpoint of the metatarsal II and the trochlea II is only moderately medially deflected (unlike in Palaeudyptes).

Remarks

The specimen NRM-PZ A.856 (Fig. 2) is clearly longer (ca. 30%) than its counterparts in the largest living Sphenisciformes assignable to the emperor penguin (Aptenodytes forsteri G.R. Gray, 1844), having a comparably massive trochlea III (Table 1). Although its medial width is similar to that in the second largest modern sphenisciform, the king penguin (A. patagonicus J.F. Miller, 1778), this is obviously because of the stronger fusion of all three metatarsals in the fossil bone (see also Myrcha et al. 2002), and overall it looks more robust than those in Aptenodytes (Jadwiszczak, pers. obs.). In our estimation, it can therefore be assigned to the large-sized penguins or, with a high level of confidence, even to the smaller of the so-called giant sphenisciforms (Jadwiszczak & Chapman 2011).

The reported specimen differs in many respects from the available similarly sized tarsometatarsi of Eocene Antarctic penguins and a vast majority of described traits were, according to our assessment, conservative in early Sphenisciformes. Hence, we are convinced that this unique combination of character states renders the discussed bone particularly interesting as a sole representative of a new (skeletal) morphotype of these grand birds, probably representing a new species. However, a taxonomic act would require more specimens to account for variability (see also Jadwiszczak 2008) and they are currently unavailable.

To conclude, we have showed that the diversity of the early Antarctic penguins, already regarded as considerable, is as yet only incompletely understood. This finding, together with a number of other recent reports (such as Buono et al. 2016), substantiates the abiding importance of the La Meseta Formation on Seymour Island for the studies of fossil vertebrates that inhabited Antarctica before the final break-up of Gondwana.

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Disclosure statement

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