Antarctic Science 26(3), 279–280 (2014) © Antarctic Science Ltd 2013 doi:10.1017/S0954102013000631

Short Note
First report on hind-toe development in Eocene Antarctic penguins

PIOTR JADWISZCZAK[1] and ANDRZEJ GAŹDZICKI[2]

[1]*Institute of Biology, University of Białystok, Świerkowa 20B, 15-950 Białystok, Poland*
[2]*Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warszawa, Poland*
piotrj@uwb.edu.pl

Received 22 May 2013, accepted 24 August 2013, first published online 15 October 2013

Introduction

Penguins (Aves: Sphenisciformes), wing-propelled diving seabirds, use their hind limbs mainly for steering underwater and walking on land. They are digitigrade animals, although can be plantigrade in slow motion or when at rest (Simpson 1946). Their metatarsal I and two phalanges forming the hallux or hind-toe are vestigial (Fig. 1a & b). Sphenisciformes may have existed in the Cretaceous, but the oldest known fossils are from the Palaeocene. Penguins became diversified and widely distributed by the Late Eocene (Jadwiszczak 2009). Thousands of Eocene penguin bones, assignable to at least ten species, come from Seymour (Marambio) Island, Antarctic Peninsula. Other fossils from this epoch are from South America, New Zealand and Australia (Jadwiszczak 2009).

The single most important bone in fossil penguin taxonomy is undoubtedly the tarsometatarsus (Myrcha *et al*. 2002, Jadwiszczak 2008). This characteristic and morphologically complex skeletal element is the most common choice as a type specimen, especially when the fossil record consists of isolated bones (e.g. Myrcha *et al*. 2002). Despite the volume of papers on the penguin tarsometatarsus (Myrcha *et al*. 2002, Jadwiszczak 2008, 2009), there are still many interesting challenges to be explored. One of the most neglected, though greatly important, issues is the existence of the metatarsal I and its continuation, the hallux, in early Sphenisciformes. Presented here are tarsometatarsi of penguins from the Late Eocene of Antarctica that allow the recognition of previously unknown details of their plantar morphology and shed new light on foot evolution in these highly specialized birds.

The material discussed here comes from the unit Telm7 or Submeseta Allomember (?Late Middle to Late Eocene) of the Eocene La Meseta Formation on Seymour Island (Antarctic Peninsula; 64°17'S, 56°45'W; Myrcha *et al*. 2002). The specimens presented below are housed at the Institute of Biology, University of Bialystok, Poland (IB/P/B).

Results

The vast majority of large-sized tarsometatarsi from the Eocene of Antarctica (i.e. bones assignable to genera *Anthropornis*, *Archaeospheniscus* and *Palaeeudyptes*) have no preserved (or clearly developed) attachment surface for the metatarsal I. The most prominent exception is the specimen IB/P/B-0290 (*Palaeeudyptes* sp. in Myrcha *et al*. 2002), which possesses a conspicuous, wide and slightly convex scar on the plantar side of its metatarsal II, located mediodistally to the medial intermetatarsal foramen (Fig. 1e).

The majority of the smaller representatives of the Eocene Antarctic penguins (i.e. those within the size range of most of the present-day species) have recognizable attachment scars situated either distally or mediodistally to the above-mentioned foramen (Fig. 1c & d). Interestingly, these small penguins can be divided into two groups. The first group is characterized by the presence of a long, narrow and slightly elevated attachment surface (e.g. specimens IB/P/B-0279a [Fig. 1d], 0484 and 0547; classified to the genus *Delphinornis*). The second group comprises a single bone probably belonging to a juvenile individual, IB/P/B-0279b, identified by Myrcha *et al*. (2002) as *Mesetaornis* sp. Its attachment scar forms a large (long and wide) surface (Fig. 1c).

The tarsometatarsus IB/P/B-0970 (Fig. 1f & g) deserves separate consideration. This specimen is undoubtedly a skeletal element of a relatively young bird (evident by the slight intermetatarsal suture in dorsal view and sharp edges of the trochleae), although it is too incomplete to be unequivocally assigned to any species. Nevertheless, the most striking characteristic of this bone is the presence of a protruding, long and narrow crest located distally to the medial intermetatarsal foramen (Fig. 1f & g). Slight sutures are also visible along its contact with the metatarsal II.

Discussion

In modern Sphenisciformes, the first metatarsal bone has a ligamentous junction to the second metatarsal (Schreiweis 1982, Baumel & Witmer 1993). In tarsometatarsi of extant penguins, the attachment surface is either barely visible (Stephan 1979) or, most often, not detectable (authors' observation). As we reported above, a number of Eocene bones clearly differ from their modern counterparts in this regard. Furthermore, the oldest known stem penguin, Palaeocene *Waimanu manneringi* Jones, Ando & Fordyce, 2006 from New Zealand, seems to possess a spindle-shaped

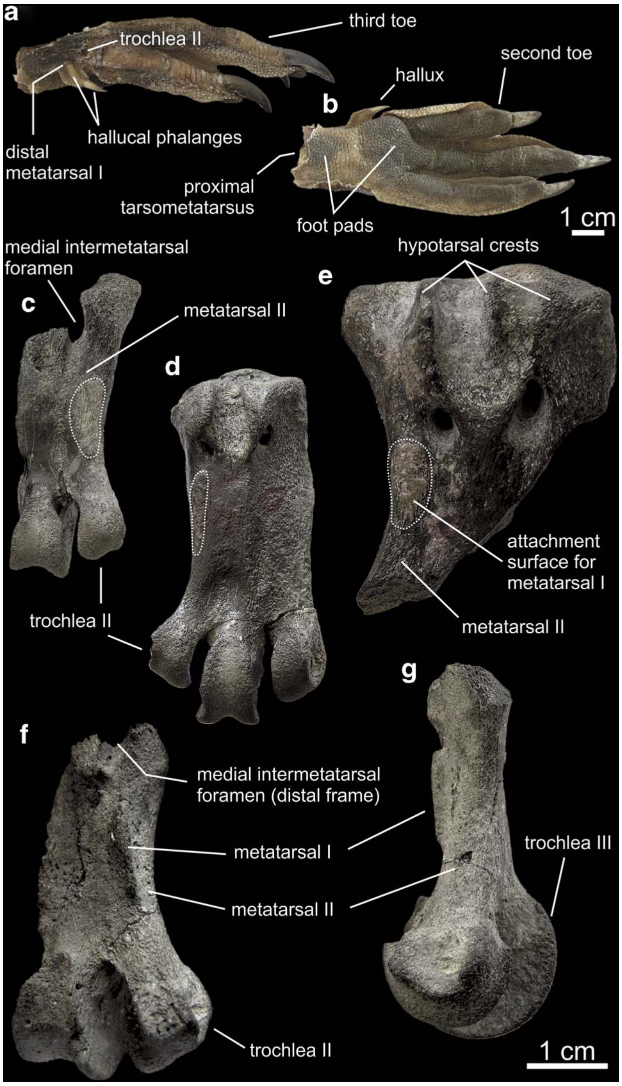

Fig. 1. Foot of the extant penguin *Pygoscelis adeliae* (Hombron & Jacquinot, 1841) and tarsometatarsi of Eocene penguins from the La Meseta Formation, Seymour Island. **a. & b.** *Pygoscelis adeliae*. **c.** *Mesetaornis* sp., IB/P/B-0279b. **d.** *Delphinornis gracilis* Wiman, 1905, IB/P/B-0279a. **e.** *Palaeeudyptes* sp., IB/P/B-0290. **f. & g.** Unassigned specimen, IB/P/B-0970. (**a. & g.** side view, **b.–f.** plantar view).

flat structure that can be interpreted as such a surface (based on photos provided by D. Ksepka). However, regardless of the geological age, the actual location of the junction appears to be similar (Fig. 1; Schreiweis 1982, fig. 17).

In our estimation, the distinct scar and its relatively large area in two of the fossil specimens (Fig. 1c & e), especially in that classified as *Mesetaornis* sp. (IB/P/B-0279b), testify to the existence of a more developed hallux than in modern penguins. Interestingly, these tarsometatarsi belonged to individuals that were significantly different in size. The clearly narrower attachment surfaces in *Delphinornis* (e.g. IB/P/B-0279a; Fig. 1d) possibly reflect the presence of weaker halluces.

However, the most unique specimen is IB/P/B-0970. The position and shape of a prominent and well delineated bony crest (Fig. 1f & g) suggests that this represents the metatarsal I, so far unseen in Sphenisciforme fossils. Moreover, it may in fact be an ossicle coalesced with the metatarsal II and, if our interpretation is correct, this would be the only such case recognized in penguins. A similar finding has been reported for Diomedeoididae (an extinct group of tubenoses) by Mayr (2009) and the vestigial metatarsal I can be observed in some extant tridactyl (hallux absent) auks (authors' observation). Thus, it appears to be quite probable that some Eocene penguins also lacked hallucal phalanges.

Unexpectedly diverse hallux-related tarsometatarsal morphology strongly suggests the existence of considerable plasticity in foot design, much greater than that discussed previously (e.g. Myrcha *et al.* 2002) and observed in living penguins. This could have resulted from a combination of phylogenetic constraints, biomechanical solutions and ecological factors, but further investigations require more complete fossils.

Acknowledgements

We are grateful to D. Ksepka (USA) for sharing the photographs of *Waimanu* that enabled examination of morphology of the plantar tarsometatarsus in Palaeocene penguins. C. Acosta Hospitaleche and S. Emslie are thanked for their helpful reviews.

References

Baumel, J.J. & Witmer, L.M. 1993. Osteologia. *In* Baumel, J.J., *ed. Handbook of avian anatomy: Nomina anatomica avium*. Cambridge, MA: Nutall Ornithological Club, 45–132.

Jadwiszczak, P. 2008. An intriguing penguin bone from the Late Eocene of Seymour Island, Antarctic Peninsula. *Antarctic Science*, **20**, 589–590.

Jadwiszczak, P. 2009. Penguin past: the current state of knowledge. *Polish Polar Research*, **30**, 3–28.

Mayr, G. 2009. Notes on the osteology and phylogenetic affinities of the Oligocene Diomedeoididae (Aves, Procellariiformes). *Fossil Record*, **12**, 133–140.

Myrcha, A., Jadwiszczak, P., Tambussi, C.P., Noriega, J.I., Gaździcki, A., Tatur, A. & Del Valle, R.A. 2002. Taxonomic revision of Eocene Antarctic penguins based on tarsometatarsal morphology. *Polish Polar Research*, **23**, 5–46.

Schreiweis, D.O. 1982. A comparative study of the appendicular musculature of penguins (Aves: Sphenisciformes). *Smithsonian Contributions to Zoology*, **341**, 1–46.

Simpson, G.G. 1946. Fossil penguins. *Bulletin of the American Museum of Natural History*, **87**, 1–99.

Stephan, B. 1979. Vergleichende Osteologie der Pinguine. *Mitteilungen aus dem Zoologischen Museum Berlin*, **55**(Supplement Annalen für Ornithologie 3), 3–98.