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The earliest fossil record of a medium-sized penguin

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Abstract: The fossil record of Antarctic Sphenisciformes dates as early as the late Palaeocene Cross Valley Formation, Seymour Island, Antarctic Peninsula. However, the best known Antarctic locality for early penguin remains (mainly isolated bones) is the Eocene La Meseta Formation that outcrops in the northeast of Seymour Island. The analysis of an unstudied set of specimens collected there by members of the British Antarctic Survey in 1989 has resulted in identification of a distal humerus from the unit Telm3 (early Eocene) of the formation that is the oldest known bone attributable to a medium-sized (in the context of the entire Cainozoic era) penguin. This find suggests that the origin of these birds, in conjunction with an increase in taxonomic diversity of the Eocene Sphenisciformes, was related to the Early Eocene Climatic Optimum (EECO) or, more probably, the early phase of subsequent cooling.

Key words: Antarctic Peninsula, La Meseta Formation, Telm3, early Eocene, Sphenisciformes, humerus.

Introduction

Penguins (Aves: Sphenisciformes) are highly specialized seabirds grouped into six extant genera and 17 species. They range from 40–45 cm in length, in the Little Penguin (*Eudyptula minor* [J.R. Forster, 1781]) to 100–130 cm in the Emperor Penguin (*Aptenodytes forsteri* G.R. Gray, 1844) (Fig. 1; Williams 1995). The oldest sphenisciforms are represented by well-defined fossils from the Palaeocene of New Zealand dating to about 62 million years ago (Ma), and the record of penguins from this epoch is limited to two genera and three species from Antarctica (Tambussi *et al.* 2005) and New Zealand (Slack *et al.* 2006). All of them attained considerable body sizes, comparable to those of recent *Aptenodytes* (Slack *et al.* 2006) or larger (Tambussi *et al.* 2005). Large-sized penguins became much more numerous and widespread during the Eocene epoch (Fig. 1); their re-

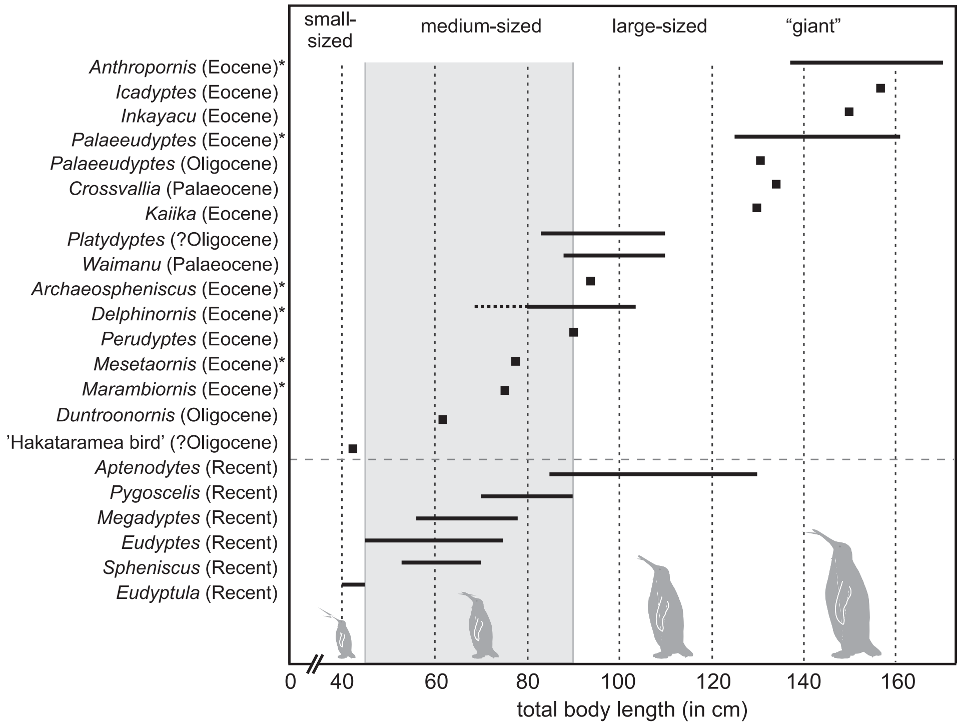

Fig. 1. Comparison of body-size ranges for recent and selected Palaeogene penguins (genus level; details and references in text). Asterisks denote birds from the La Meseta Formation, Seymour Island.

mains are known from Antarctica, Australia, New Zealand and South America (Myrcha *et al.* 2002; Jadwiszczak 2006a, b, 2009; Tambussi *et al.* 2006; Clarke *et al.* 2007, 2010; Sallaberry *et al.* 2010; Acosta Hospitaleche and Jadwiszczak 2011; Fordyce and Thomas 2011; Jadwiszczak and Mörs 2011). Small or *Eudyptula*-like Sphenisciformes are not known before the latest Oligocene (Fordyce and Jones 1990; Jadwiszczak 2009).

The first formally documented medium-sized[1] penguin, *i.e.* a representative of sphenisciforms ranging in their total length between 45–58 cm (recent *Eudyptes chrysocome* [J.R. Forster, 1781]) and 75–90 cm (recent *Pygoscelis papua* [J.R. Forster, 1781]), comes from the ?late early–middle Eocene of the Antarctic Peninsula (Jadwiszczak 2001, 2006a; Myrcha *et al.* 2002), and a number of such specimens are known from the middle Eocene of southern Chile (Sallaberry *et al.* 2010). Here, we report on the earliest record of a medium-sized penguin from the early Eocene of the La Meseta Formation, Seymour Island (Antarctic Peninsula).

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[1] This term is widely used throughout the literature devoted to present-day taxa, *e.g.* Williams 1995; Fig. 1.

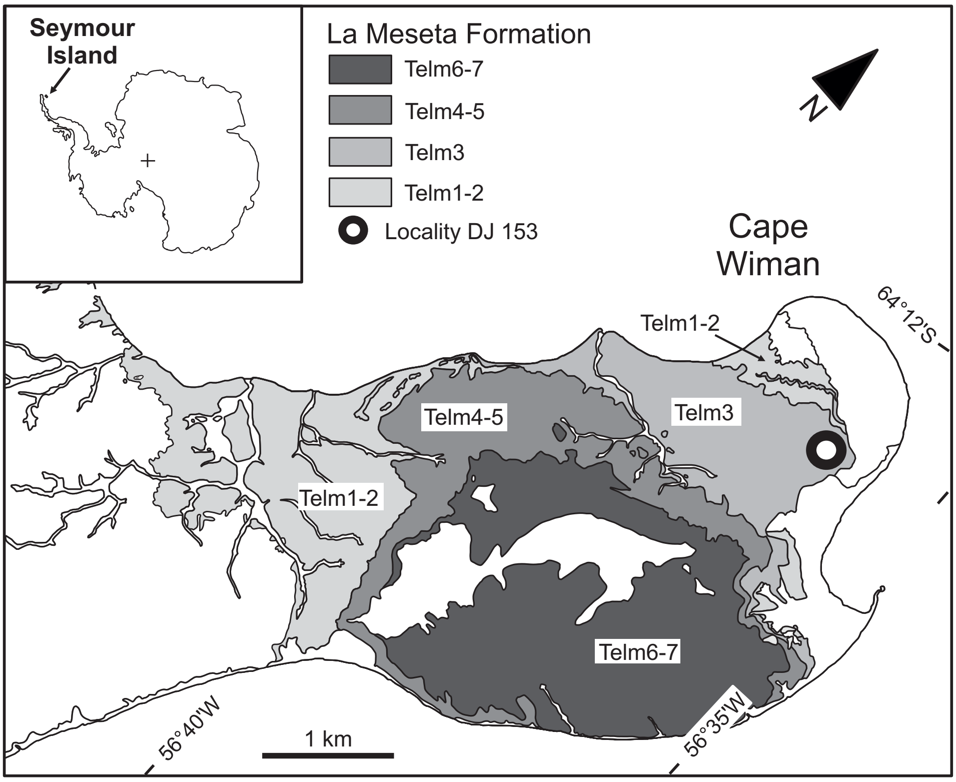

Fig. 2. Location map of units of the La Meseta Formation on Seymour Island (according to Sadler 1988) and the collecting locality DJ 153.

Geologic setting, sedimentology and stratigraphy

Seymour Island is an ice-free island located east of the northern tip of the Antarctic Peninsula at 64°17'S, 56°45'W. The early Eocene–latest Eocene La Meseta Formation (Elliot and Trautman 1982) outcrops in the northeastern part of the island (Fig. 2). 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; Marenssi 2006). Sadler (1988) mapped the formation in terms of seven major lithofacies Telm1–Telm7 and this system is adopted here.

According to Ivany *et al.* (2008, table 2) deposition of the Telm2–Telm5 units took place between the early Eocene and the earliest middle Eocene (based on $^{87}Sr/^{86}Sr$ ratios from mollusk shells). This sequence is only partly in line with Marenssi's (2006, fig. 5) opinion that the base of the La Meseta Formation (Telm1) is close to the Paleocene/Eocene boundary and the early/middle Eocene transition should be sought within the lowermost Telm5. Moreover, Ivany *et al.*

(2008, fig. 9) provided δ^{18}O data testifying to temperatures of up to 15˚C near the base of Telm3, at least 4–5°C warmer than those inferred from earlier (Telm2) and later (the remainder of Telm3, Telm4 and Telm5) samples. Most probably this event corresponds to the Early Eocene Climatic Optimum (EECO; see Zachos *et al.* 2001, fig. 2; Bohaty and Zachos 2003, fig. 2; Jadwiszczak 2010a, fig. 2).

Material and methods

The specimen discussed here is a left distal humerus of a fossil penguin (Figs 3, 4) collected at Cape Wiman, Seymour Island (La Meseta Formation, Telm3, B.A.S. locality DJ 153; Fig. 2) by J.J. Hooker, a member of the British Antarctic Survey Expedition, in 1989. It is permanently housed at the Natural History Museum (London) and catalogued as NHMUK BAS A2481. Comparative material

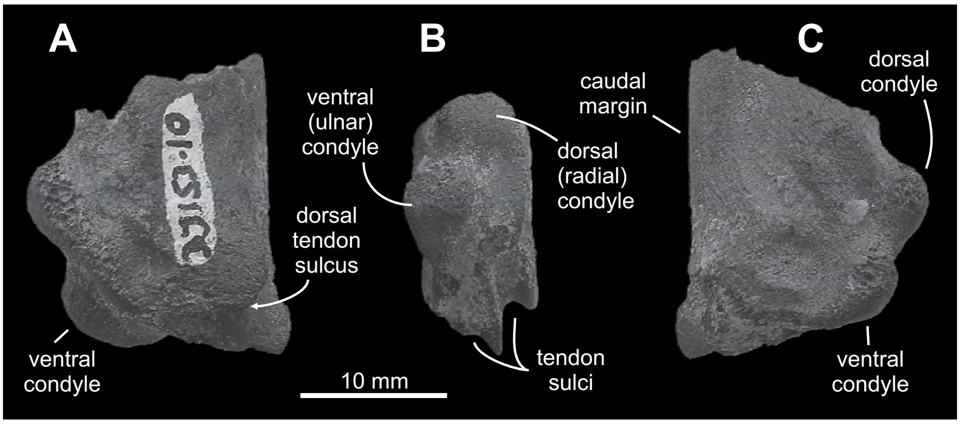

Fig. 3. Distal left humerus (specimen NHMUK BAS A2481) from the unit Telm3 of the La Meseta Formation (Seymour Island, Antarctic Peninsula); in dorsal (**A**), distal (**B**) and ventral (**C**) views.

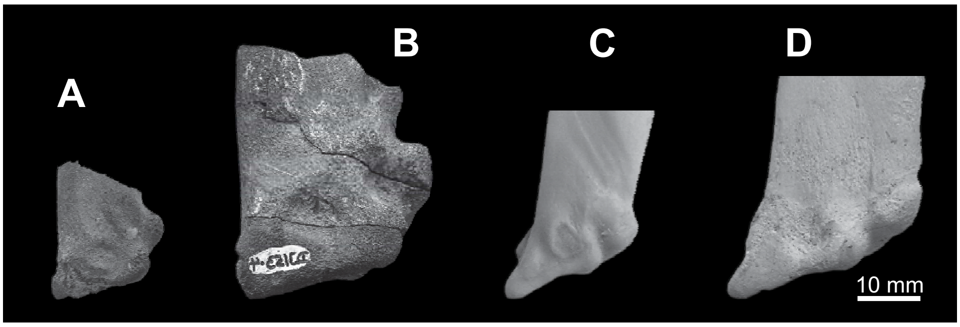

Fig. 4. Comparison of distal humeri of undetermined early Eocene Antarctic penguins: NHMUK BAS A2481 (**A**) and NHMUK BAS A2475 (**B**) and recent Antarctic penguins: *Pygoscelis adeliae* (**C**) and *Aptenodytes forsteri* (**D**); in ventral views.

Table 1

Measurements (in mm) of distal humeri of fossil and extant Antarctic penguins. Abbreviations: THW, total craniocaudal width; HW, craniocaudal width (between dorsal condyle and sulcus); HB, dorsoventral breadth; DCB, breadth of dorsal condyle (for details, see text).

Specimen/species		Measurements				Indices	
		THW	HW	HB	DCB	HW/HB	DCB/HB
fossil	**NHMUK BAS A2481** (this study)	**20.8**	**16.8**	**9.7**	**6.2**	**1.73**	**0.64**
	IB/P/B-0382 (group B of problematic humeri[1])	21.4	18.1	10.2	7.5	1.77	0.74
	IB/P/B-0176 (*Archaeospheniscus wimani*)	27.9	24.1	12.4	9.7	1.94	0.78
	IB/P/B-0199 (undetermined species)	15.5	–	–	4 5.0	–	–
	IB/P/B-0584[2] (undetermined species)	27.3	22.5	12.0	–	1.88	–
	MLP 93-I-6-3 („*Tonniornis minimum*”[3])	25.5	–	–	–	–	–
	MLP 93-X-1-145 („*Tonniornis mesetaensis*”[4])	27.3	–	–	–	–	–
	NHMUK BAS A2475 (undetermined species[5])	–	–	17.6	–	–	–
extant	*Aptenodytes forsteri* (juvenile)	33.1	26.1	12.2	9.1	2.14	0.75
	Pygoscelis papua	24.7	19.9	8.2	7.1	2.43	0.87
	Pygoscelis adeliae	20.7	16.7	6.6	5.7	2.53	0.86
	Eudyptes chrysolophus	23.1	18.1	7.4	5.8	2.45	0.78

[1] See Jadwiszczak 2006a.

[2] The oldest distal humerus from the La Meseta Formation (Telm1; Jadwiszczak 2006b).

[3, 4] For discussion on doubtful validity of this taxon (erected by Tambussi *et al.* 2006), see Jadwiszczak 2006b.

[5] From locality DJ 153 (Telm3; see text).

(single representatives of two named and two undetermined extinct [abbreviated IB/P/B], and four extant penguin species; see Table 1 and Fig. 4) comes from the collection housed at the Institute of Biology, University of Białystok (Białystok, Poland). A single undetermined bone from the locality DJ 153, much larger than those above (Table 1 and Fig. 4), belongs in the Natural History Museum, London (abbreviated NHMUK). Measurements for two fossil specimens from the collection located at the Museo de la Plata, La Plata, Argentina (abbreviated MLP; Table 1) are after Tambussi *et al.* (2006, table 1).

A system of size-based categories we use in this work (see above and Fig. 1) is a combination of schemes available for both modern (a core and a reference point for extinct penguins) and fossil (a “giant” class) taxa. Data for Fig. 1 were compiled from the following sources: Simpson 1975 (Oligocene *Palaeeudyptes*, *Duntroonornis* and *Platydyptes*), Fordyce and Jones 1990 (“Hakataramea bird”), Williams 1995 (recent genera), Jadwiszczak 2001 (*Anthropornis*, Eocene *Palaeeudyptes*, *Archaeospheniscus*, *Delphinornis*, *Mesetaornis* and *Marambiornis*), Tambussi *et al.* 2005 (*Crossvallia*), Slack *et al.* 2006 (*Waimanu*), Clarke *et al.* 2007 (*Icadyptes* and *Perudyptes*), Clarke *et al.* 2010 (*Inkayacu*), and Fordyce and Thomas 2011 (*Kaiika*). Although the actual taxonomical status of Eocene Antarctic species assigned to *Archaeospheniscus* and *Palaeeudyptes* (*i.e.* genera whose type species are known from the Oligocene of New Zealand) is debatable (*e.g.*

Ksepka and Clarke 2010), we decided not to abandon the conservative approach to this issue (Myrcha *et al.* 2002; Jadwiszczak 2006a).

We used the following measurement categories (abbreviations below correspond to those in Table 1; see also Fig. 3B):

1. Total craniocaudal width of the distal humerus (between the dorsal condyle and caudalmost point on the bony crest separating both tendon sulci) (THW).
2. Craniocaudal width of the distal humerus measured between the dorsal condyle and dorsal tendon sulcus (HW).
3. Dorsoventral breadth of the distal humerus measured at the level of the ventral condyle (HB).
4. Dorsoventral breadth of the dorsal condyle (DCB).

Additionally, we defined two indices resulting from the above measurements: a craniocaudal elongation index of humeral distal aspect (proximal view; HW/HB) and a relative breadth of the dorsal condyle (DCB/HB). Direct measurements were taken using digital callipers and rounded to the nearest 0.1 mm. Unfortunately any considerations regarding the trochlear-shaft angle (an important determinant of wing shape) are not justified due to the small portion of the shaft preserved. Anatomical nomenclature (Fig. 3) follows that of Baumel and Witmer (1993).

Results

The specimen NHMUK BAS A2481 (Fig. 3) is clearly smaller than its counterparts in both the recent Emperor Penguin (*Aptenodytes forsteri*; Fig. 4D) and fossil *Archaeospheniscus wimani* (Marples, 1953) (Table 1). Its craniocaudal width (measurement THW and HW) is very close to that in the recent Adélie Penguin (*Pygoscelis adeliae* [Hombron *et* Jacquinot, 1841]), though its dorsal condyle is relatively narrower (index DCB/HB; Table 1) and the distal aspect of the bone (Fig. 3B) is less elongated craniocaudally (*i.e.* relatively broader; index HW/HB; Table 1, Fig. 4C). In our opinion, however, this humerus undoubtedly was a part of the wing skeleton of a medium-sized penguin (see above and Figs 1, 4). As it was collected within the unit Telm3, it can be assigned to the early Eocene (see Ivany *et al.* 2008, fig. 9).

Discussion

The vast majority of medium-sized bones of Eocene Antarctic penguins originate from the upper part of the La Meseta Formation (Myrcha *et al.* 2002; Jadwiszczak 2006a, 2008), thus they are of middle or (predominantly) late Eocene age (Ivany *et al.* 2008; Marenssi 2006). Myrcha *et al.* (2002) and Jadwiszczak (2006a) reported several such bones from Telm5 (middle and upper part) and Unit

II *sensu* Elliot and Trautman (1982) which corresponds to Telm4–Telm6 (three tarsometatarsi and a single radius respectively). Even though one or more of these specimens are in fact older than middle Eocene (which is uncertain), the humerus NHMUK BAS A2481 here described precedes them in terms of geological time (Telm3 is more basal than Telm4; *e.g.* Myrcha *et al.* 2002, fig. 2).

The taxonomic affinities of NHMUK BAS A2481 are obscure. Distal humeri of suitable dimensions and age (Eocene) are rare, some poorly preserved or documented, and only tentatively (if at all) assigned to species (*e.g.* Jadwiszczak 2010b). A provisional classification of medium-sized (isolated) humeri proposed by one of the authors (Jadwiszczak 2006a) was limited to morphotypes and entirely based on proximal parts of these bones. The only complete specimen was IB/P/B-0382 from Telm7 (attributed to group B of problematic humeri; Jadwiszczak 2006a, table 4, fig. 19; Table 1). It is slightly larger (Table 1) and clearly younger than NHMUK BAS A2481. It also differs from the latter (among others) in having a more pointed dorsal margin of the dorsal tendon sulcus and the relatively broader dorsal condyle (Table 1).

The above results, supported by data from Telm1–Telm2 (solely remains of large or “giant” penguins found; Jadwiszczak 2006b; see also Table 1), testify to the EECO (base of Telm3) or, more probably, early post-EECO (remainder of Telm3; Ivany *et al.* 2008) origin of medium-sized Sphenisciformes, at least in the Antarctic Peninsula region. Such a level of uncertainty results from the sampling scheme adopted by Ivany *et al.* (2008). Two vertical sections that were sampled within Telm3 by Ivany *et al.* (2008, fig. 3) are distant from the sampling station DJ 153 (Fig. 1).

Taking into account quite large dimensions of other penguin remains from DJ 153[2] as well as assuming that the body size diversification amongst sympatric bird species can decrease the strength of competition (Leyequién *et al.* 2007), our results suggest the earliest evidence of such an evolutionary strategy in penguins. The comparison with the much younger specimen, IB/P/B-0199 from Telm7, clearly smaller than NHMUK BAS A2481 (Table 1), indicates that the bone reported here does not represent the smallest penguin known from the Eocene of Seymour Island.

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[2] Housed at the Natural History Museum, London (including partial humeri [Fig. 4B] and tarsometatarsi; personal observation).

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