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Eocene penguins of Seymour Island, Antarctica: The earliest record, taxonomic problems and some evolutionary considerations

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Abstract: Penguin bones from the La Meseta Formation (Seymour Island, Antarctic Peninsula) are the only record of Eocene Antarctic Sphenisciformes. Being an abundant component of the youngest unit of the formation (Telm7), they are not so common in earlier strata. Here, I present the oldest penguin remains from the La Meseta Formation (Telm1–Telm2), often bearing close resemblance to their counterparts from younger units. Addressing the recent findings in fossil penguin systematics, I suggest there is too weak a basis for erecting new Eocene Antarctic taxa based on non-tarsometatarsal elements of penguin skeletons, and considering Oligocene species part of the studied assemblage. Finally, I conclude if the common ancestor of extant Sphenisciformes lived in the Eocene Antarctic (as suggested recently), penguins referred to *Delphinornis* seem to be prime candidates to that position.

Key words: Antarctica, La Meseta Formation (Eocene), paleontology (penguins), taxonomy, evolution.

Introduction

Penguins (Aves: Sphenisciformes) are flightless birds from the Southern Hemisphere, superbly adapted to an aquatic life (Simpson 1976; Williams 1995). They are sorted into seventeen extant species (Williams 1995), ecologically and behaviorally heterogeneous (Croxall and Davis 1999), but their monophyly seems to be beyond question (*e.g.* Bertelli and Giannini 2005; Ksepka *et al*. 2006). There are also several dozens of fossil species of penguins – the precise number depends on the researcher (Jadwiszczak 2006 and references cited therein). Although studied for some 150 years (Huxley 1859), the evolutionary history of penguins is only partially understood despite several significant recent studies (Bertelli and Giannini 2005; Mayr 2005; Baker *et al.* 2006; Bertelli *et al.* 2006; Ksepka *et al*. 2006; Slack *et al*. 2006).

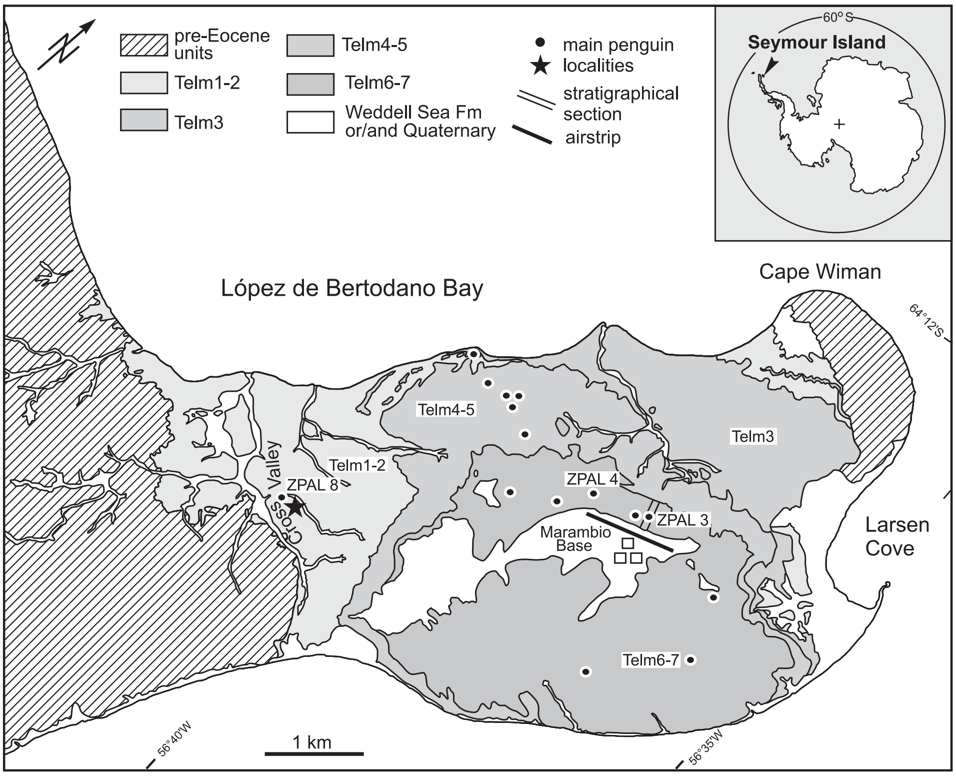


Fig. 1. Penguin locality index map of the La Meseta Formation on Seymour Island. Asterisk indicates the oldest *in situ* finding of penguin bones in the Telm2s. Distribution of lithostratigraphical units according to Sadler (1988). Arrow of inset shows the location of Seymour Island in the northern Antarctic Peninsula (revised from Myrcha *et al.* 2002, fig. 1).

Simpson (1946), one of the fathers of evolutionary systematics, assigned all penguin species, both extinct and extant, to a single family – Spheniscidae (see also Simpson 1971a, b; 1975). Clarke *et al*. (2003), preferring the phylogenetic nomenclature, suggested the name "Spheniscidae" for the penguin crown clade only, leaving Paleogene penguins outside this clade. They (Clarke *et al*. 2003) introduced the term "Pansphenisciformes" to encompass all taxa that are more closely related to living penguins than to any other extant birds (although compare the recommendation for the form of panclade names in the subsequent June 2006 draft of the PhyloCode, Article 10.3), and those pansphenisciforms that share the evolutionary ancestry of the loss of the aerial flight with modern-day penguins were termed "Sphenisciformes". As this requires wing bones to be preserved (or even more in some cases[1]), many fossil penguins cannot be assigned to Sphenisciformes

[1] Total wing to estimated body mass might also be important in taxa with morphologies corresponding to transitional volant/non-volant phases.

Fig. 2. View of the locality ZPAL 8 (arrowed; from Kriwet and Gaździcki 2003, fig. 2). Asterisk shows the location of the oldest *in situ* penguin bones in the Telm2s. *Photograph by A. Gaździcki, February 1994.*

(*sensu* Clarke *et al*. 2003) until more complete skeletons are found (see also "Taxonomic note" in Ksepka *et al*. 2006).

Recently, Slack *et al*. (2006) published the results of the cladistic analysis showing that *Waimanu* Jones, Ando and Fordyce, 2006 from the Paleocene of New Zealand (the oldest penguins, grouped in two species) belongs to Sphenisciformes (*sensu* Clarke *et al*. 2003). This crucial finding allows us to place all more derived penguins in that clade.

Other recent contributions to the debate on penguin evolution have been made by Baker *et al.* (2006) and Ksepka *et al*. (2006; partially rooted in the authors' other studies, *e.g.* Bertelli and Giannini 2005; Bertelli *et al*. 2006). The former strongly suggests an Antarctic origin of extant taxa, the latter emphasizes the importance of the Subantarctic regions (including Antarctic Peninsula). Nevertheless, both approaches locate ancestors of *Aptenodytes* (the most basal extant taxon; Baker *et al*. 2006; Ksepka *et al*. 2006) and *Pygoscelis* in the Antarctic Peninsula region (Ksepka *et al*. 2006 suggest wider geographical range). Molecular dating by Baker *et al.* (2006, multiple gene evidence) shows the common ancestry of modern-day taxa dates back to the Eocene epoch. These results are contrary to former conclusions (*e.g.* Simpson 1975; Clarke *et al*. 2003) that the existence of parts of the extant radiation of penguins in Miocene and older beds is unlikely. Ksepka *et al*. (2006) predict the origin of Spheniscidae (*sensu* Clarke *et al*. 2003) "by the

Fig. 3. Stratigraphical distribution of penguin remains within rock column of the Eocene La Meseta Formation on Seymour Island. Locality numbers (ZPAL, DPV, IAA) at the right of the columns mark the horizons from which penguin bones were collected (asterisk shows the location of the oldest *in situ* penguin bones in the Telm2s). Revised from Myrcha *et al.* 2002, fig. 2.

Miocene" – timing based on the fossils described in papers by Stucchi (2002) and Stucchi *et al*. (2003).

The La Meseta Formation (Seymour Island, Antarctic Peninsula; Figs 1–3) is the only place in the Antarctic where Eocene penguins have been found (Wiman 1905a, b; Marples 1953; Simpson 1971a; Cione *et al*. 1977; Myrcha *et al*. 1990, 2002; Jadwiszczak 2006; Tambussi *et al*. 2006; for the Paleocene record see Tambussi *et al*. 2005). Because of its geological age, location and diversity of described penguin species (see references cited above), the formation seems to be a suitable place for the search for the ancestors of extant Spenisciformes.

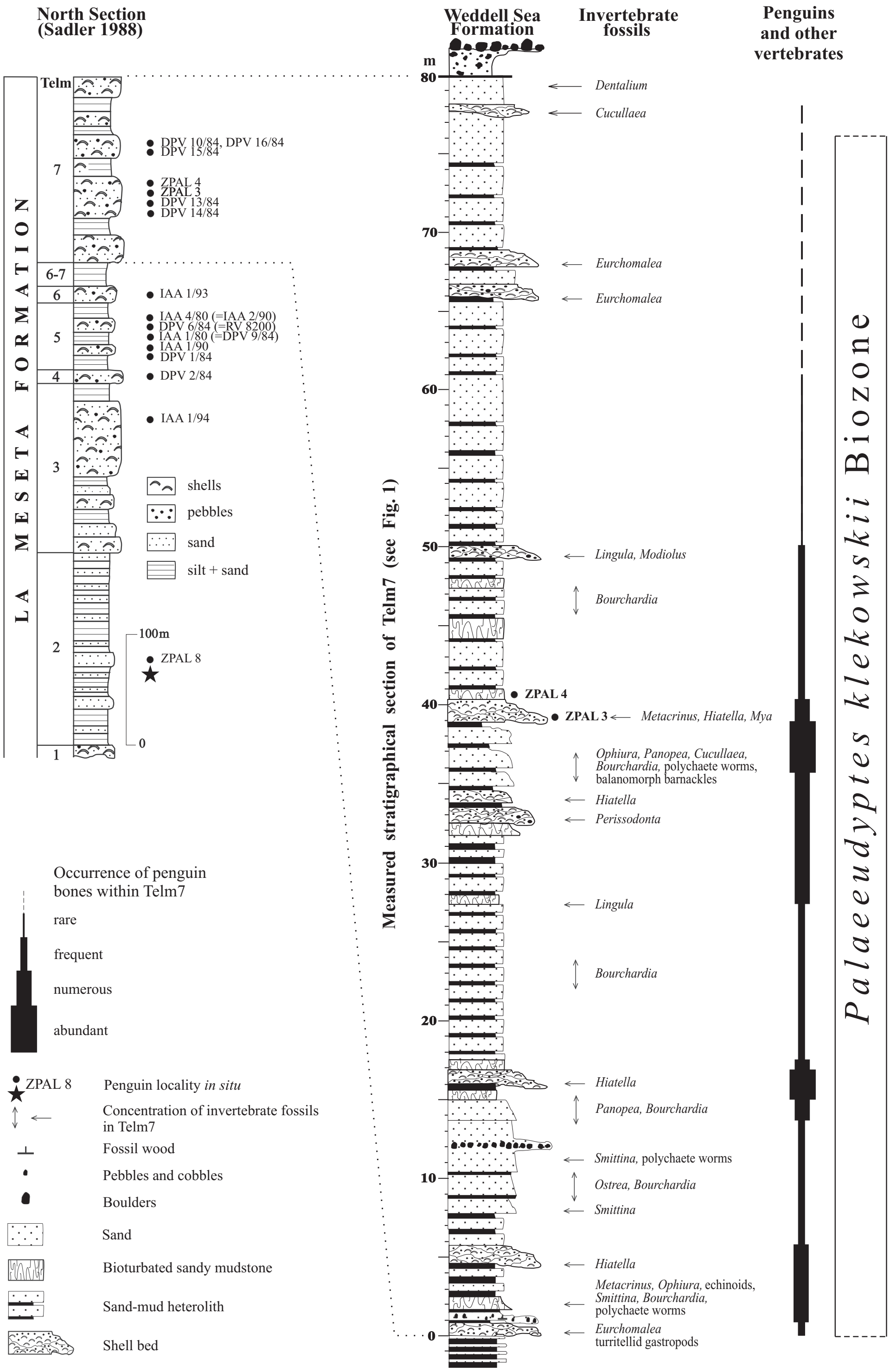
The purpose of this paper is to present the oldest penguin bones from the La Meseta Formation, and to clarify the disconcordance that arose recently as a result of taxonomic analyses of two largest collections of fossil penguins from the formation (Jadwiszczak 2006; Tambussi *et al*. 2006). The ultimate objective is to review recognized taxa in the context of the possible ancestry of the crown penguins.

Material and methods

This paper follows a recent article on the taxonomy of the Late Eocene penguins from the La Meseta Formation (Seymour Island, Antarctica) (Jadwiszczak 2006), which was a complement of an earlier work by Myrcha *et al*. (2002). The base for considerations presented here is the Polish collection of penguin remains from that formation (housed at the Institute of Biology, University of Białystok, abbreviated IB/P/B; Myrcha and Tatur 1986; Myrcha *et al*. 1990, 2002; Jadwiszczak 2000, 2001, 2003, 2006).

The majority of specimens are from the unit Telm7[2], the youngest part of the La Meseta Formation (Late Eocene; Fig. 3; Myrcha *et al*. 2002; Jadwiszczak 2006; Tambussi *et al*. 2006). The oldest, though rare, bones are from the units Telm1 and Telm2 (late Early Eocene according to Cocozza and Clarke 1992, and Dutton *et al*. 2002, or Early Eocene according to Marenssi 2006; see also Dingle *et al*. 1998). The oldest *in situ* findings come from the unit Telm2s (*sensu* Sadler 1988; vicinity of the ZPAL 8 locality; Figs 1–3; A. Gaździcki and A. Tatur *personal commun.*; see also Myrcha *et al*. 2002: fig. 1). All bones from the lower part of the La Meseta

[2] The formation was subdivided by Sadler (1988) into seven lithofacies units (Telm1–Telm7) and this division is adopted here. For different subdivision schemes and their stratigraphic correlation see Marenssi *et al.* (1998: fig. 4) and Marenssi (2006: fig. 5).


North Section
(Sadler 1988)
Weddell Sea
Formation
Invertebrate
fossils
Penguins
and other
vertebrates
L A M E S E T A F O R M A T I O N
Telm
7
6-7
6
5
4
3
2
1
DPV 10/84, DPV 16/84
DPV 15/84
ZPAL 4
ZPAL 3
DPV 13/84
DPV 14/84
IAA 1/93
IAA 4/80 (=IAA 2/90)
DPV 6/84 (=RV 8200)
IAA 1/80 (=DPV 9/84)
IAA 1/90
DPV 1/84
DPV 2/84
IAA 1/94
shells
pebbles
sand
silt + sand
100m
ZPAL 8
0
Occurrence of penguin
bones within Telm7
rare
frequent
numerous
abundant
ZPAL 8
Penguin locality in situ
Concentration of invertebrate fossils
in Telm7
Fossil wood
Pebbles and cobbles
Boulders
Sand
Bioturbated sandy mudstone
Sand-mud heterolith
Shell bed
Measured stratigraphical section of Telm7 (see Fig. 1)
m
80
70
60
50
40
30
20
10
0
Dentalium
Cucullaea
Eurchomalea
Eurchomalea
Lingula, Modiolus
Bourchardia
ZPAL 4
ZPAL 3
Metacrinus, Hiatella, Mya
Ophiura, Panopea, Cucullaea,
Bourchardia, polychaete worms,
balanomorph barnackles
Hiatella
Perissodonta
Lingula
Bourchardia
Hiatella
Panopea, Bourchardia
Smittina, polychaete worms
Ostrea, Bourchardia
Smittina
Hiatella
Metacrinus, Ophiura, echinoids,
Smittina, Bourchardia,
polychaete worms
Eurchomalea
turritellid gastropods
Palaeeudyptes klekowskii Biozone

Formation (Telm1–Telm2) were collected in 1994 by A. Gaździcki and A. Tatur (both from the Polish Academy of Sciences). For more details on the Polish collection as well as the geological and stratigraphical setting, see Figs 1–3; Myrcha *et al*. 1990, 2002; Jadwiszczak 2006 and the bibliography therein. The unpublished photographs of several specimens from the Argentine collection discussed here (Museo de La Plata accession numbers: MLP 93-I-6-3, 93-X-1-145, 93-X-1-146 and 93-X-1-147) were used with permission from Claudia P. Tambussi (Museo de La Plata, Argentina).

Here, anatomical nomenclature follows the convention adopted by Myrcha *et al*. (2002) and Jadwiszczak (2006). Measurements were taken with digital calipers and rounded to the nearest 0.1 mm.

New material: the oldest (Early Eocene) penguin bones from the La Meseta Formation (Telm1–Telm2)

Class Aves
Order Sphenisciformes Sharpe, 1891
(also "Sphenisciformes" *sensu* Clarke *et al*. 2003)
Gen. et spec. indet.
(Figs 4–5)

Material. — Eighteen specimens. Damaged tip of (most likely) an upper jaw (*i.e. rostrum maxillare* component), IB/P/B-0617e (Fig. 4a, c); two very incomplete shafts of humeri, IB/P/B-0576a (Fig. 5c, e), 0586c; incomplete head of right humerus, IB/P/B-0583a (Fig. 5b, d); distal left humerus (damaged), IB/P/B-0584 (Fig. 5g, h); nearly complete head of left humerus, IB/P/B-0585 (Fig. 5a, f); incomplete right *os metacarpale majus*, IB/P/B-0576b (Fig. 4d); very incomplete shaft of femur, IB/P/B-0576e; very incomplete shaft of tibiotarsus, IB/P/B-0583b; incomplete shaft of tibiotarsus, IB/P/B-0617b; distal shaft of right tibiotarsus, IB/P/B-0617c (Fig. 4e); two unidentifiable fragments of long bones (most likely tibiotarsi), IB/P/B-0576c, 576d; three complete phalanges, IB/P/B-0586a (*digitus* III *phalanx* 2; Fig. 4g), 0586b (*digitus* IV *phalanx* 1; Fig. 4f), 0617a (*digitus* IV *phalanx* ?2–4); two tiny unidentifiable fragments, IB/P/B-0576f, 0617d.

Measurements (in mm). — IB/P/B-0617e: proximal width 11.6; IB/P/B-0584: extreme cranio-caudal width of the distal end ca. 28.4, dorso-ventral thickness of *condylus ventralis* ca. 5.2; IB/P/B-0585: dorso-ventral diameter of *fossa pneumatica* (between inner/outer sides of its rim) 11.4/21.3, extreme length of the articular surface of *caput humeri* 34 (estimated), caudal (=largest) width of the articular surface of *caput humeri* 25.3; IB/P/B-0576b: cranio-caudal width at the center (of the preserved fragment) 13.8; IB/P/B-0617c: medio-lateral width at the center (of the preserved fragment) 18.8; IB/P/B-0586a, 0586b, 0617a: length along the long axis of the bone (dorsal side) ca. 32.7, 29.8, 21.9.

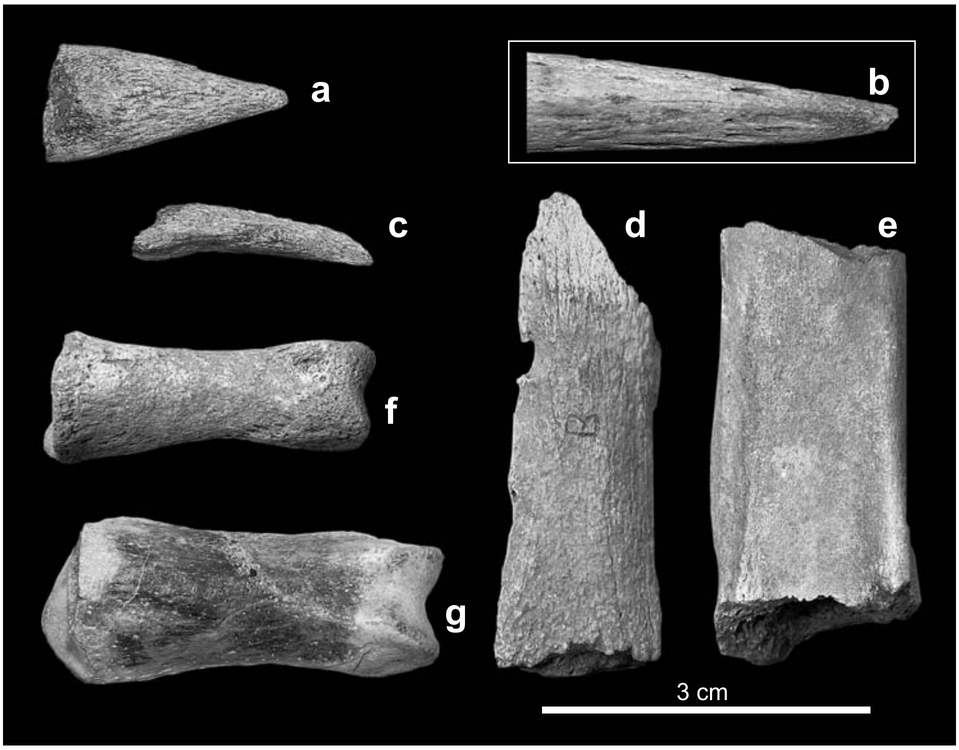


Fig. 4. Selected penguin bones from the lower part of the La Meseta Formation (Telm2–Telm2s) and a single specimen (indicated by the white square) from the upper part (Telm7) of the formation. Damaged tip of (most likely) an upper jaw (specimen IB/P/B-0617e; a – dorsal view, c – side view), tip of an upper jaw of *Anthropornis* sp. or *Palaeeudyptes* sp. (specimen IB/P/B-0167; b – dorsal view; see also Myrcha *et al.*1990: fig. 5; Jadwiszczak 2003: fig. 2), phalanges (specimens IB/P/B-0586b, 0586a; f, g – dorsal view), partial carpometacarpus (specimen IB/P/B-0576b; d – ventral view) and partial tibiotarsus (specimen IB/P/B-0617c; e – cranial view).

Description. — Fragmentary *rostrum maxillare* (IB/P/B-0617e) wide basally and strongly narrowing toward tip in dorsal view, and only slightly curved in lateral view. Both humeral heads (IB/P/B-0583a, 0585) medium-sized (see "Remarks"), with undivided and relatively small *fossa pneumatica*. *Facies musculi supracoracoidei* (insertion of *pectoralis secundus sensu* Marples 1952) well developed, roughly parallel to the long axis of the bone. *Tuberculum ventrale* well developed. *Incisura capitis* deep, *sulcus ligamentosus transversus* undivided (both features preserved in specimen IB/P/B-0585). Both fragments of humeral shafts (IB/P/B-0576a, 0586c) as well as distal left humerus (IB/P/B-0584) medium-sized, flattened. *Condylus ventralis* and *condylus dorsalis* of the latter specimen probably quite slender. *Os metacarpale majus* (IB/P/B-0576b) flattened, relatively large. Other identified specimens (hind-limb skeleton, see "Material") of typical (*i.e.* penguin-like) shape, medium- or large-sized.

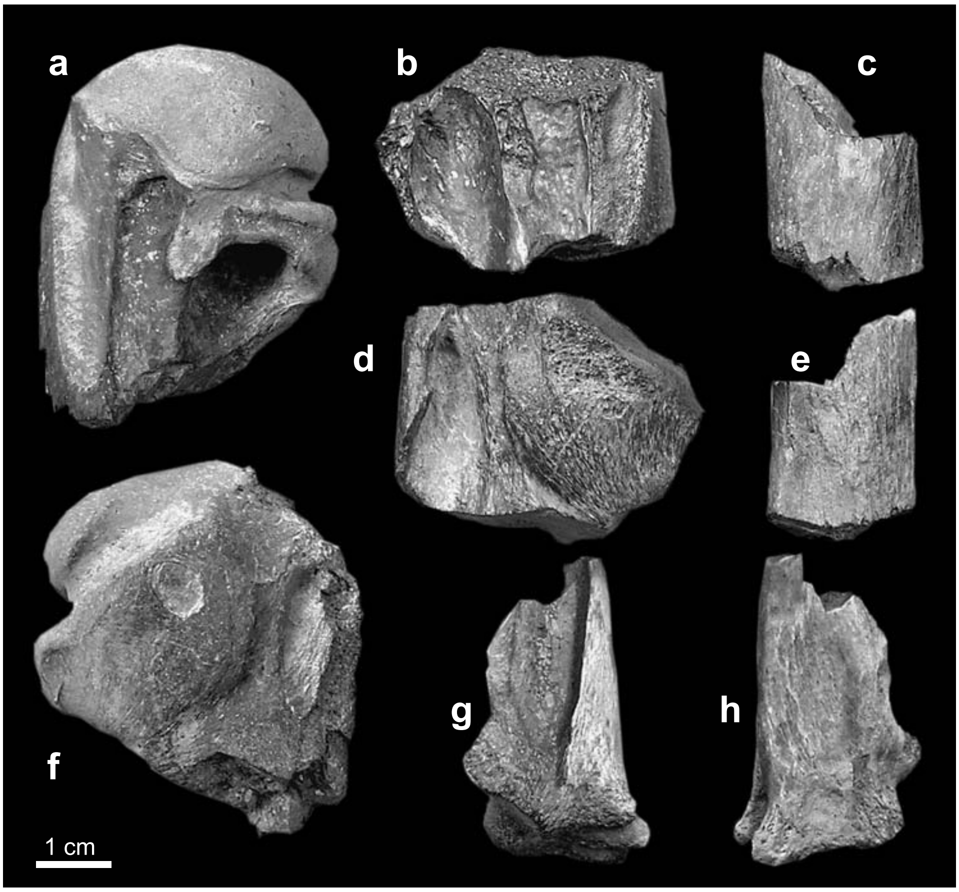


Fig. 5. Penguin humeri from the lower part of the La Meseta Formation (Telm1–Telm2). Complete head (specimen IB/P/B-0585; a – dorsal view, f – ventral view), damaged head (specimen IB/P/B-0583a; b – dorsal view, d – ventral view), partial shaft (specimen IB/P/B-0576a; c – dorsal view, e – ventral view) and damaged distal end (specimen IB/P/B-0584; g – dorsal view, h – ventral view).

Remarks. — Assuming correct anatomical identification of the specimen IB/P/B-0617e (made by direct comparison with the upper jaws of fossil and extant penguins), its shape suggests relatively wide (dorsally) bill, more like that in Recent *Eudyptes pachyrhynchus* or *Pygoscelis adeliae*, than in Recent *Aptenodytes forsteri* (see Zusi 1975: fig. 4.5) or Eocene *Anthropornis*/*Palaeeudyptes* (Fig. 4b; Olson 1985: fig. 11; Myrcha *et al.*1990: fig. 5; Jadwiszczak 2003: fig. 2; taxonomic position after Jadwiszczak 2006). Both humeral heads closely resemble those of *Palaeeudyptes gunnari* (Wiman 1905b: figs 3, 3a, 8 and 8a; Marples 1953: figs 5 and 6; Simpson 1971a: fig. 5; Jadwiszczak 2006: fig. 9a–c; not photographed specimens IB/P/B-0066 and 0573 from the Polish collection). The only distal humerus is similar to that of *Archaeospheniscus wimani* in terms of the overall size (Jadwiszczak 2006: fig.12a–b). However, both of its condyles appear more slender than in *A. wimani* (see Jadwiszczak 2006), even after taking erosion into consideration. Partial carpometacarpus is most likely similar in terms of its shape and size to its counterparts in *Palaeeudyptes klekowskii* (Jadwiszczak 2006: fig. 7c). The phalanges are, without doubt, skeletal elements of large birds, maybe *Palaeeudyptes* and/or *Anthropornis*. Other specimens are even less characteristic, but clearly belonged to medium and large-sized penguins (*Archaeospheniscus*, *Palaeeudyptes* and *Anthropornis* size categories).

The above-described fragments are very similar to specimens recovered from younger units of the La Meseta Formation (*cf.* Jadwiszczak 2006), some better preserved parts (*e.g.* humeral heads) could be even directly assigned to known species. However, they come from the units deposited during very warm period in relation to later paleoclimatic history of the formation (Gaździcki *et al*. 1992; Dingle *et al*. 1998), and tarsometatarsi (the most characteristic bones of fossil penguins; *e.g.* Myrcha *et al*. 2002) are not known from these strata. In my opinion, specimens discussed here, because of the above-mentioned factors and the fragmentary nature of most material, constitute too weak a basis for taxonomic assignment.

Occurrence. — Seymour Island, La Meseta Formation (Eocene): Telm1 (IB/P/B-0583a, 0583b, 0584), Telm2 (IB/P/B-0585), Telm2s (IB/P/B-0576a–f, 0586a–c, 0617a–e). The only *in situ* findings are those from Telm2s (Myrcha *et al*. 2002; A. Gaździcki and A. Tatur *personal commun*.). Other bones are probably also not allochthonous in their origin (A. Gaździcki and A. Tatur *personal commun*.).

Remarks on recent problems in systematics of Middle–Late Eocene Antarctic penguins

Two papers on taxonomy of fossil penguins from the La Meseta Formation have been published recently – mine (Jadwiszczak 2006) and the work by Tambussi *et al*. (2006). Both are continuations of an earlier analysis by Myrcha *et al*. (2002) devoted solely to tarsometatarsi. I analyzed all non-tarsometatarsal skeletal elements from the Polish collection, Tambussi *et al*. (2006) studied humeri from the Argentine collection. The numbers of recognized species agree (ten in both cases), though I termed my result “a minimal reliable estimate” (Jadwiszczak 2006) and Tambussi *et al*. (2006) placed a number of humeri with unique features in the “Spheniscidae *incertae sedis*” group. However, resulted taxonomic listings differ remarkably, that is, I (Jadwiszczak 2006) confirmed previous taxonomic conclusions (Myrcha *et al*. 2002; Jadwiszczak 2006: table 1), whereas Tambussi *et al*. (2006) did not include four species (*Archaeospheniscus wimani*, *Delphinornis gracilis*, *Marambiornis exilis* and *Mesetaornis polaris*) recognized by Myrcha *et al*. (2002), added two species (*Palaeeudyptes antarcticus* and *Archaeospheniscus lopdelli*) so far known from the Oligocene of New Zealand, and erected a new genus, *Tonniornis* (with two species: *T. mesetaensis* and *T. minimum*). Having the opportunity to compare specimens from the Polish collection with the photographs of some bones from the Argentine set (see "Material and methods"), I was able to make a number of taxonomic clarifications and remarks.

Two nearly complete specimens assigned by Tambussi *et al*. (2006) to *Delphinornis larseni*, MLP 93-X-1-146 and 93-X-1-147, seem to share characteristic features of the humeral head morphology with their counterparts from my "B" group of small humeri – IB/P/B-0382 and 0471 (see Jadwiszczak 2006). Additionaly, their overall sizes are very similar to that of IB/P/B-0382, the best preserved small humerus from the Polish collection (Jadwiszczak 2006: fig.19c–d). There are, however, some differences in overall shaft shape between the Argentine specimens and IB/P/B-0382: the former is narrow proximally and does not possess, possibly due to abrasion, the preaxial angle. Distal ends of both specimens discussed by Tambussi *et al*. (2006) are too damaged to compare with IB/P/B-0382.

The holotype of *Tonniornis mesetaensis* (MLP 93-X-1-145), the type species of the genus erected by Tambussi *et al*. (2006), closely resembles (*e.g.* overall size, undivided *fossa pneumatica*) the partial humerus IB/P/B-0176 assigned by me (Jadwiszczak 2006) to *Archaeospheniscus wimani*. Hence I am not convinced that the former assignment is correct. Moreover, I question the generic assignment of specimens referred to *Tonniornis minimum*. Some features from the generic diagnosis cannot be observed as specimens assigned to *T. minimum* are lacking of either whole or large parts of humeral heads (*cf.* Tambussi *et al*. 2006: fig. 6c–d). Additionally, MLP 93-I-6-3 (a holotype) somewhat resembles (*e.g.* overall size, shaft shape, the size and location of *facies musculi supracoracoidei*) the specimen IB/P/B-0382. In my opinion, there is no justification for erecting new taxa based solely on bones other than tarsomatetarsi as long as we study isolated bones and the material suggests the presence of several species of similar size (see Myrcha *et al*. 2002 and Jadwiszczak 2006). Facing problems similar to those of Tambussi *et al*. (2006), I simply sorted small humeri into several groups based on morphology (A1, A2, B and "other specimens"; see Jadwiszczak 2006).

According to Tambussi *et al*. (2006), the fossil penguin assemblage from the La Meseta Formation (from the unit Telm7) includes two species so far known exclusively from the Oligocene of New Zealand: *Archaeospheniscus lopdelli* and *Palaeeudyptes antarcticus*. The former species is represented in the Argentine collection by ten specimens (the only complete bone is MLP 94-III-15-17), the latter – by a humerus (MLP 84-II-1-1) missing the proximal epiphysis. Even ignoring the geographic and, more importantly, stratigraphic differences, there is no basis for comparison as there are no humeri from New Zealand assigned to *P. antarcticus* (Simpson 1971a, b; see also Ksepka *et al*. 2006). In the case of *A. lopdelli*, the objections are similar to those above, with the exception that the validity of this New Zealand species is open to question, and the humerus is represented by a poorly preserved distal end (Simpson 1971b). Some measurements of specimens referred by Tambussi *et al*. (2006) to *A. lopdelli* most closely match those of *Palaeeudyptes* sp. in Jadwiszczak 2006. Interestingly, the oblique *facies musculi supracoracoidei* (or "*pectoralis secundus*"), the feature mentioned in specimens' description (Tambussi *et al*. 2006), is indeed typical of *Archaeospheniscus* (*A. lowei* and *A. wimani*), not *Palaeeudyptes* (Simpson 1971b; Jadwiszczak 2006). Photographs of specimens referred by Tambussi *et al*. (2006) to these species as well as measurements for *P. antarcticus* have been neither published nor available to me.

Tambussi *et al*. (2006) defined the *Anthropornis nordenskjoeldi* Biozone, a biostratigraphic unit within Telm7 (Submeseta Allomember *sensu* Marenssi *et al*. 1998), characterized, among others, by the numerous penguin bones (the highest concentration within the formation, all species represented). I must notice, however, that *A. nordenskjoeldi* seems to be neither restricted to that zone nor the numerically predominant penguin species (Case 1996; Myrcha *et al*. 2002; Jadwiszczak 2006), and would be better to name this zone as the *Palaeeudyptes klekowskii* Biozone (Fig. 3). Although the stratigraphic range of occurrence of *P. klekowskii* is also not restricted to that unit (Jadwiszczak 2006; Tambussi *et al*. 2006), this species of large-sized penguins is more abundant than *A. nordenskjoeldi* (Case 1996; Myrcha *et al*. 2002; Jadwiszczak 2006), and hence superior to the latter as an index fossil.

Potential ancestors of extant penguin lineages

Baker *et al.* (2006) located the common ancestry of extant penguins in the Eocene of the Antarctic. This triggers an intriguing question: if their finding is correct, then which fossil species should be considered as possible ancestors (for context see "Introduction")? The most obvious feature that would eliminate taxa from such a list (or at least make them clearly less probable candidates) is the extremely large overall body size (see Peters 1983 and references cited therein). The impressive size of some Eocene penguins (Jadwiszczak 2001) was certainly a case of (extreme) specialization (*e.g.* Simpson 1975), and most likely these forms (*Anthropornis* and *Palaeeudyptes*) were in the evolutionary cul-de-sac (but see Ksepka *et al*. 2006). The former genus became extinct probably close to the Eocene/Oligocene boundary, the latest remains referred to the latter are known from the Oligocene of New Zealand (Marples 1952; Simpson 1971b).

The body size attained by *Archaeospheniscus wimani* was similar to that of *Aptenodytes* (Jadwiszczak 2001), the largest modern-day penguins. Such dimensions seem to be not too limiting for an evolutionary change (see Williams 1995: p. 143). The last representatives of *Archaeospheniscus* were found in the Oligocene of New Zealand (Marples 1952; Simpson 1971b), and they (*A. lowei* and *A. lopdelli*) were larger than *A. wimani* (*e.g.* Simpson 1975). A relatively short, compared to other Paleogene Sphenisciformes, tarsometatarsus with well developed *foramina*

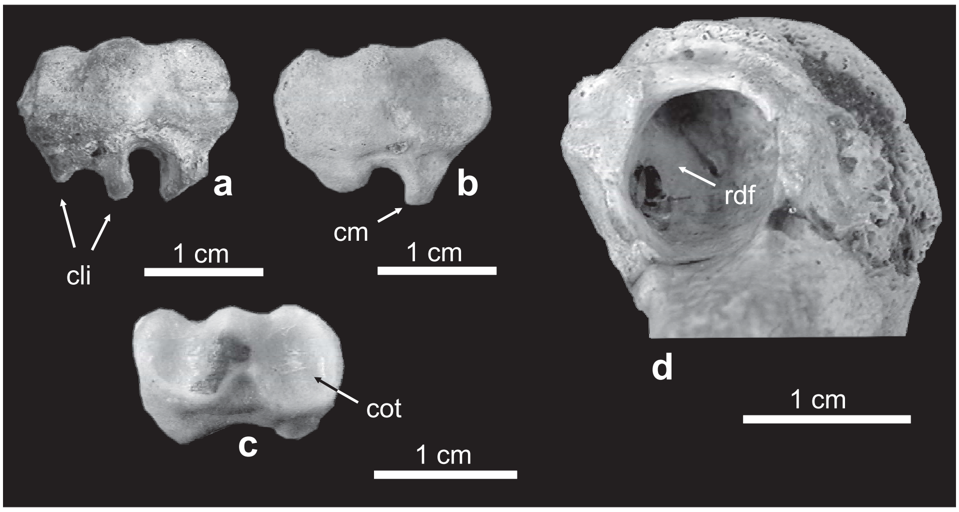


Fig. 6. Proximal tarsometatarsi of Eocene (a, b) and Recent (c) penguins, and Eocene humeral pneumatic fossa (d) from Seymour Island showing derived features of some fossil specimens (b, d; see text for details). a – *Marambiornis exilis*, specimen IB/P/B-0490 (holotype, reversed); b – *Delphinornis arctowskii*, specimen IB/P/B-0484 (holotype); c – Recent *Pygoscelis adeliae*; d – gen. sp. (group B; see Jadwiszczak 2006), specimen IB/P/B-0382. Abbreviations: cli, *crista lateralis + cristae intermediae hypotarsi*; cm, *crista medialis hypotarsi*; cot, *cotyla medialis*; rdf, osseous ridge dividing the *fossa pneumatica*.

vascularia proximalia is characteristic of these penguins (Marples 1952: plate 8, fig. 5; Simpson 1971b: fig. 19a; Myrcha *et al.* 2002: p. 26 and fig. 9). These features are also conspicuous in *Aptenodytes*, and both genera show in this respect some degree of resemblance (Wiman 1905b: plate II, figs 1, 7; and references cited above). Another taxonomically important bone, the humerus, differs much in both genera (Marples 1952: fig. 6; Jadwiszczak 2006: fig. 12a, b), including (but not limited to) the morphology of *fossa pneumatica* (an evolutionarily important feature – see Ksepka *et al*. 2006). On the other hand, the oblique *facies musculi supracoracoidei*, which is typical of extant penguins (Marples 1952; Simpson 1971b), is also one of the diagnostic features of *Archaeospheniscus* (Jadwiszczak 2006).

Small penguins from the Eocene of Antarctica (*Delphinornis*, *Marambiornis* and *Mesetaornis*) are promising candidates for ancestors of extant Sphenisciformes. The number of described taxa (three genera, five species), the clear possibility of the existence of unrecognized ones, and the fact that four species are known solely from the uppermost unit of the La Meseta Formation (Myrcha *et al*. 2002; Jadwiszczak 2006; Tambussi *et al*. 2006), suggest the group[3] was evolutionarily dynamic during

[3] I do not suggest *Delphinornis*, *Marambiornis* and *Mesetaornis* form a clade (but notice the low Bremer support values in Ksepka *et al.* 2006: figs 2–3), rather an ecological or size group that included evolutionarily dynamic genera.

the Late Eocene. All well preserved pneumatic fossae of small humeri are (weakly) bipartite (Fig. 6d; Jadwiszczak 2006; larger specimens have undivided fossae), the condition observed in those of extant penguins, though there is much variation in the latter group (Marples 1952; Ksepka *et al*. 2006). An intriguing feature of some Eocene tarsometatarsi (*Delphinornis*) is the simplified hypotarsus – *crista lateralis* and *cristae intermediae* form a single tubercle rather than high crests (Fig. 6b; Myrcha *et al*. 2002: figs 10–12). This is close to the condition met in all extant penguins (Fig. 6c; Slack *et al*. 2006). Although most small tarsometatarsi are relatively elongated (Myrcha *et al*. 2002), which is a primitive trait (*e.g.* Slack *et al*. 2006), there is an exception – *Delphinornis arctowskii* (Myrcha *et al*. 2002: fig. 12). Several modern-day specimens studied by me for this study (*Pygoscelis adeliae*, *Eudyptes chryslophus*) are only a little bit less elongated than the holotype of *D. arctowskii* (the elongation index, EI, was defined in Myrcha *et al*. 2002). In my opinion, tarsometatarsi assigned to this Eocene species could be difficult to separate from some of their recent counterparts for an untrained eye.

The presence of the *foramen vasculare distale* in all tarsometatarsi referred to *Delphinornis* (and other small penguins) seems to be the most serious challenge to the pattern described above. This clearly plesiomorphic feature (*e.g.* Slack *et al.* 2006) is not observed in large Eocene penguins (Myrcha *et al*. 2002), but whether it is a by-product of their body size or a real phylogenetic signal, is difficult to prove. Unfortunately, the phylogeny of penguins (and any other taxon) can never be known with certainty.

Concluding remarks

- The oldest penguin bones from the La Meseta Formation (Seymour Island) come from the two lowermost units (Telm1 and Telm2), *i.e.* they are probably Early Eocene in age. These specimens belonged to skeletons of medium- and large-sized birds, and some of them bear very close resemblance to taxa known from younger strata of the La Meseta Formation (Middle and Late Eocene genera: *Anthropornis*, *Archaeospheniscus* and *Palaeeudyptes*).
- Assuming correct anatomical and taxonomical identification, a poorly preserved tip of (most likely) an upper jaw could be the first Eocene fossil suggesting not all large penguins had elongated and dagger-like bills.
- The comparison of results yielded by two recent analyses of Eocene Antarctic penguins (Jadwiszczak 2006 and Tambussi *et al*. 2006) suggests too weak a basis for erecting new taxa based on non-tarsometatarsal skeletal elements as well as considering Oligocene New Zealand species part of Eocene Seymour Island assemblage.
- The name of the *Anthropornis nordenskjoeldi* Biozone proposed by Tambussi *et al*. (2006) should be replaced by *Palaeeudyptes klekowskii* as an index fossil.

- Assuming the common ancestor of extant penguins lived in the Eocene Antarctic (see Baker *et al*. 2006), penguins referred to *Delphinornis* seem to be prime candidates.

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