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Aspects of diversity in early Antarctic penguins

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Penguin bones from the Eocene La Meseta Formation (Seymour Island, Antarctic Peninsula) constitute the only extensive fossil record of Antarctic Sphenisciformes. Here, we synonymize some of the recognized genera (*Anthropornis* with *Orthopteryx*, *Delphinornis* with *Ichtyopteryx*) and species (*Anthropornis nordenskjoeldi* with *Orthopteryx gigas*, *Delphinornis gracilis* with *Ichtyopteryx gracilis*). Moreover, we suggest that Antarctic species of *Anthropornis* and *Palaeeudyptes*, so-called giant penguins, may in fact comprise only one species each instead of two, based on evidence of well-marked sexual dimorphism. We also present new estimates of body mass based on femora testifying to the impressive scope of interspecific body-size variation in Eocene Antarctic penguins.

Key words: Aves, Sphenisciformes, systematics, sexual dimorphism, body mass, Eocene, Antarctic Peninsula.

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Introduction

Penguins (Aves: Sphenisciformes) are highly marine seabirds confined in their distribution to the Southern Hemisphere. The oldest record of penguins is represented by a partial skeleton from the late early Paleocene of New Zealand (Slack et al. 2006). The earliest known Antarctic sphenisciform is late Paleocene in age, and its remains are much less complete—just three poorly preserved bones found within the Cross Valley Formation of Seymour Island, Antarctic Peninsula (Tambussi et al. 2005). In contrast, thousands of bones have been recovered from the Eocene La Meseta Formation of Seymour Island, and this is the oldest record of high diversity in Sphenisciformes.

Based on collections acquired from the La Meseta Formation, fifteen species assigned to ten genera have been erected since 1905 (Wiman 1905a, b; Marples 1953; Simpson 1971; Myrcha et al. 1990, 2002; Jadwiszczak 2006a, 2008, 2009; Tambussi et al. 2006; and references cited therein), but only six genera and ten species seem to be taxonomically distinct (Simpson 1971; Myrcha et al. 2002; Jadwiszczak 2006b). These are: *Anthropornis grandis* (Wiman, 1905), *Anthropornis nordenskjoeldi* Wiman, 1905, *Archaeospheniscus wimani* (Marples, 1953), *Delphinornis arctowskii* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur, and del Valle, 2002, *Delphinornis gracilis* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur, and del Valle, 2002, *Delphinornis larseni* Wiman, 1905, *Marambiornis exilis* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur, and del Valle, 2002, *Mesetaornis polaris* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur, and del Valle, 2002, *Palaeeudyptes gunnari* (Wiman, 1905), and *Palaeeudyptes klekowskii* Myrcha, Tatur, and del Valle, 1990 (see also Jadwiszczak 2008). Their type specimens are tarsometatarsi, bones from the hindlimb skeleton (Wiman 1905a, b; Marples 1953; Simpson 1971; Myrcha et al. 1990, 2002; see also Walsh et al. 2007). Other named species were based either on very fragmentary material (*Ichtyopteryx gracilis* Wiman, 1905) or on non-tarsometatarsal features (e.g., *Orthopteryx gigas* Wiman, 1905). Interestingly, most (if not all) of the above-mentioned species were probably synchronous (and surely sympatric) during the late Eocene time period (Simpson 1975; Case 1996; Jadwiszczak 2006a), an unusual situation (in terms of taxonomic diversity) compared to "recent standards" (e.g., Case 1992). Such a situation occurred twice more in fossil penguins from younger epochs (Jadwiszczak 2009). Moreover, estimated body-size parameters (body mass and total length) indicate that individuals from at least four (distinct) species were larger than extant Emperor Penguins (*Aptenodytes forsteri* Gray, 1844) (Livezey 1989; Jadwiszczak 2001).

Here, we investigate three aspects of diversity of early Antarctic penguins: systematics of the smallest and largest representatives of these birds, body mass, and sexual size dimorphism in "giant" species (from the genera *Palaeeudyptes* and *Anthropornis*). This work aims to refresh the list of distinct taxa and to review, using samples from wider taxonomic ranges, unexplored (by students of Eocene sphenisciforms) models corresponding to the relations between femoral diameter and circumference, and body mass. The cross-sectional measurements of the femur (a bone sensitive to mass-related forces) are closely related to body mass in living terrestrial vertebrates (Anderson et al. 1985) and can also

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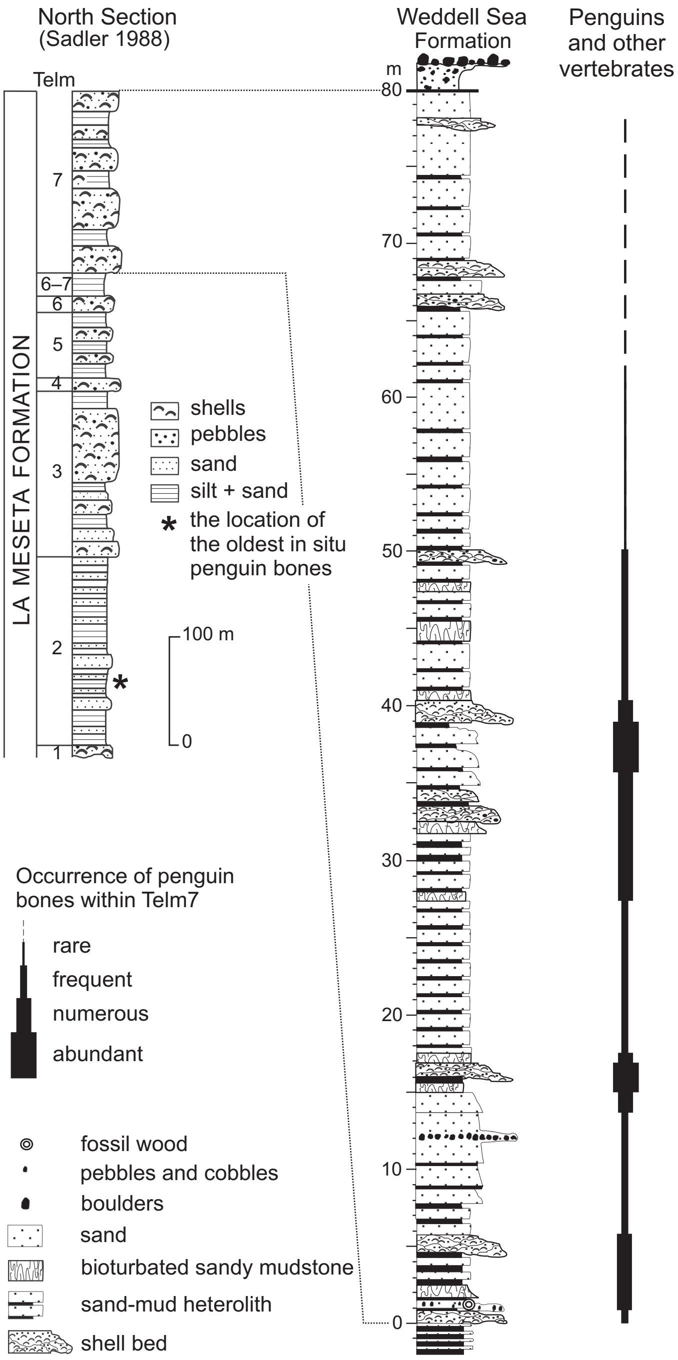

Fig. 1. The rock column of the La Meseta Formation (Seymour Island, Antarctica) showing the concentration of penguin bones in Telm7 and the oldest penguin locality in situ (modified from Myrcha et al. 2002: fig. 2).

be treated as approximate measures of body size in birds (e.g., Campbell and Marcus 1992). Moreover, due to the recent advances in the study of osteology and systematics of early Antarctic penguins (assignment of isolated bones to taxa or groups of taxa; Jadwiszczak 2006a) as well as the size of the studied sample, such data can be used to verify previous estimates (see above).

Institutional abbreviations.—BMNH, Natural History Museum, London, UK; IB/P/B, Institute of Biology, University of Białystok, Białystok, Poland; MLP, Museo de La Plata, Ciudad de La Plata, Argentina; NRM-PZ, Department of Palaeozoology, Swedish Museum of Natural History, Stockholm, Sweden; NRM-VE, Department of Vertebrate Zoology, Swedish Museum of Natural History, Stockholm, Sweden; SAMA, South Australian Museum, Adelaide, Australia.

Other abbreviations.—CV, coefficient of variation; N, number of specimens; P, P-value, a measure of the strength of evidence against the null hypothesis; SSD, sexual size dimorphism (skeletal sexual dimorphism).

Material and methods

A total of 41 tarsometatarsi, 30 femora and three synsacra of Eocene Antarctic penguins from Seymour Island (Antarctic Peninsula) were used for this study (Appendix 1). They are housed at the IB/P/B, MLP and NRM-PZ. Morphology of bones from the IB/P/B and NRM were studied directly. Data for femora from the IB/P/B and tarsometatarsi from the IB/P/B (except two measurement categories, see below) and MLP were taken from Jadwiszczak 2006a and Myrcha et al. 2002, respectively, whereas measurements for bones from the NRM (tarsometatarsi, femora and synsacra) and selected measurements (distal width and thickness of shaft) for tarsometatarsi from the IB/P/B were taken by PJ (using digital callipers with an accuracy of 0.1 mm). Taxonomic assignment of bones from the IB/P/B and MLP follows that of Myrcha et al. (2002) and Jadwiszczak (2006a), the systematics of specimens from the NRM (Wiman 1905a, b; Marples 1953; Simpson 1971) was revised by PJ (based on size and/or morphology; see below). The material consists solely of isolated skeletal elements.

Symmetry of distribution (skewness = 0) was tested by means of classical Student's t-tests, whereas testing for normality was performed using Shapiro-Wilk's W test. Elongation indices were compared by means of a two-sided randomization test (10000 randomizations). The coefficient of variation (CV), a standardized measure of variation, was expressed in a form of the standard deviation as a percentage of the mean. CVs for extant penguins were calculated using data from Livezey (1989). The scaling model of Campbell and Marcus (1992), used for body mass estimation, was derived from the logarithmic relationship between selected skeletal measurements and body masses of birds (89 families). Here, we utilized data only for the "Swimmers" subgroup (including, but not limited to, Spheniscidae or penguins). Another model we used, that of Cubo and Casinos (1997), was based on the long-bone allometry, and resulted in regressions with body mass as the independent variable (so inverse prediction was needed). Unlike the previous approach, this one concentrated mainly on Palaeognathiformes (running birds) and penguins, although several non-flying species from other orders were also considered (Cubo and Casinos 1997).

Geological and stratigraphical setting

The La Meseta Formation (Elliot and Trautman 1982) is an unconformity-bounded unit exposed in the north-eastern part of Seymour Island (James Ross Basin, Antarctic Peninsula) that spans most of the Eocene epoch (Marenssi 2006). It comprises up to 720 m of richly fossiliferous and mostly poorly consolidated siliciclastic fine-grained sediments (Fig. 1) deposited in deltaic, estuarine and shallow marine environments as part of a tectonically controlled incised valley system, in a back-arc basin (Borsuk-Białynicka 1988; Feldmann and Woodburne 1988; Fordyce 1989; Jerzmańska and Świdnicki 1992; Long 1992; Stilwell and Zinsmeister 1992; Porębski 1995, 2000; Doktor et al. 1996; Woodburne and Case 1996; Gandolfo et al. 1998; Reguero et al. 1998, 2002; Dzik and Gaździcki 2001; Marenssi et al. 2002; Myrcha et al. 2002; Fostowicz-Frelik 2003; Goin et al. 2006; Jadwiszczak et al. 2008). These clastics contain evidence of Paleogene cooling and the first appearance of ice (Gaździcki et al. 1992; Dingle et al. 1998; Francis et al. 2008; see also Birkenmajer et al. 2005).

Sadler (1988) subdivided the formation into seven major lithologic units, Telm1–Telm7, and this system is adopted here (Fig. 1; for different subdivision schemes and their correlation see Marenssi et al. 1998). The material studied was collected from the Eocene La Meseta Formation, mostly from its youngest unit, i.e., Telm7 (late Eocene; for details see Appendix 1; Myrcha et al. 2002; Jadwiszczak 2006a, 2008 [the Argentine and Polish collections]; Sadler 1988; Marples 1953; Myrcha et al. 1990 [the Swedish collection; most probably entirely from Telm6–7]).

Systematic palaeontology

Order Sphenisciformes Sharpe, 1891

Family Spheniscidae Bonaparte, 1831

Genus *Delphinornis* Wiman, 1905

Type species: *Delphinornis larseni* Wiman, 1905; Seymour Island, Antarctic Peninsula; La Meseta Formation, Eocene.

Delphinornis gracilis (Wiman, 1905) comb. nov.

Fig. 2.

1905 *Ichtyopteryx gracilis* sp. nov.; Wiman 1905a: 251, pl. 12: 4.

2002 *Delphinornis gracilis* sp. nov.; Myrcha et al. 2002: 30–31, fig. 11; new synonymy.

Holotype: NRM-PZ A.20, incomplete right tarsometatarsus.

Type locality: NE Seymour Island (Antarctic Peninsula).

Type horizon: La Meseta Formation, Telm6–7 of Sadler (1988; see also Marples 1953: fig. 1 ["Swedish locality"], and Myrcha et al. 2002: fig. 1), late Eocene.

Material.—IB/P/B-0279a (complete right tarsometatarsus; type specimen of *Delphinornis gracilis* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur, and del Valle, 2002), IB/P/B-0492 (incomplete left tarsometatarsus), IB/P/B-0549 (incomplete left tarsometatarsus), IB/P/B-0408 (incomplete left tibiotarsus) and IB/P/B-0130 (incomplete right femur).

Emended diagnosis.—Tarsometatarsus small and slender (Table 1; Myrcha et al. 2002: table 1). The medial hypotarsal crest sloping towards the medial margin of the bone, but the slope steeper than in *Delphinornis larseni*, though not than in *Delphinornis arctowskii* (Myrcha et al. 2002: figs. 10–12). It also differs from *D. larseni* in having the intercondylar eminence narrow and prominent and trochleae not massive. The distal vascular foramen poorly developed in comparison with that of *D. larseni* (Wiman 1905b: pl. 2: 2; Myrcha et al. 2002: fig. 10a; Ksepka et al. 2006: fig. 15). The articular surface of the trochlea III, unlike its counterpart in other species of *Delphinornis*, markedly narrowing towards the plantar surface of the shaft in plantar view (Wiman 1905b: pl. 2: 5a and Myrcha et al. 2002: figs. 11b, 12b).

Remarks.—Wiman (1905a, b) erected six monotypic genera of Sphenisciformes from the La Meseta Formation, Seymour Island. Type specimens for five species are tarsometatarsi, *Ichtyopteryx gracilis* (Fig. 2A) and *D. larseni* being decidedly the smallest penguins within this assemblage. *Ichtyopteryx gracilis* was placed by Simpson (1971) in "dubious taxa", because of the badly preserved holotype (distal tarsometatarsus). Myrcha et al. (2002) supplemented the genus *Delphinornis* with two species: *D. gracilis* and *D. arctowskii*, both based on tarsometatarsi (Fig. 2B, C) and representing small-bodied fossil penguins. Myrcha et al. (2002) proposed also a new generic diagnosis for *Delphinornis* based on features of the proximal tarsometatarsus. Unfortunately, this part is not preserved in Wiman's (1905) specimen assigned to *I. gracilis*. Additionally, tarsometatarsi belonging to *Delphinornis* share a characteristic shape of a distal part of the

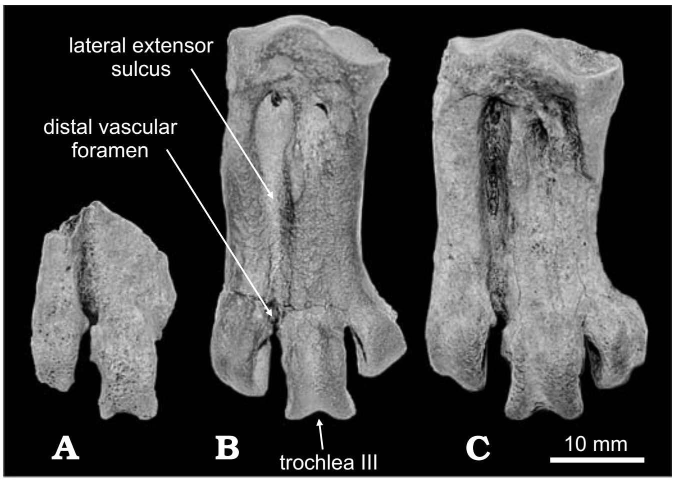

Fig. 2. Tarsometatarsi assigned to the sphenisciforms from the late Eocene, upper La Meseta Formation of Seymour Island, in dorsal view. Assignments as proposed in this paper. **A**, **B**. *Delphinornis gracilis* (Wiman, 1905) comb. nov.; NRM-PZ A.20 (**A**), IB/P/B-0279a (**B**). **C**. *Delphinornis arctowskii* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur and del Valle, 2002, IB/P/B-0484 (reversed to facilitate comparison).

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Table 1. Metric comparisons of the sphenisciform *Delphinornis gracilis* (Wiman, 1905) comb. nov. with other species of small-sized penguins from the Eocene La Meseta Formation, Seymour Island.

Species	Specimen	Tarsometatarsal measurements (mm)			
		Total length	Dorso-plantar thickness of trochlea III	Distal width of shaft	Distal thickness of shaft
Delphinornis gracilis	NRM-PZ A.20	–	ca. 8.2	14.1	4.2
	IB/P/B-0279a	41.5	8.8	14.4	5.1
Delphinornis arctowskii	IB/P/B-0484	40.2	10.6	16.9	5.3
	MLP 93-X-1-92	43.8	10.6	–	–
Delphinornis larseni	IB/P/B-0062	47.8	10.3	18.9	6.0
	MLP 84-II-1-79	48.9	12.0	–	–
Mesetaornis polaris	IB/P/B-0278	49.6	11.5	ca. 16.3	6.0
	IB/P/B-0490	46.0	10.5	16.3	5.9

lateral extensor (intermetatarsal) sulcus (Fig. 2): it is generally well marked with a U-shaped cross-section (slight in *Marambiornis*, moderately marked and V-shaped in *Mesetaornis*) (PJ's personal observation; see also Myrcha et al. 2002). Interestingly, this feature is also conspicuous in *I. gracilis*.

The specimen assigned to *I. gracilis*, like those of *D. arctowskii* and *D. gracilis*, possesses a poorly developed distal vascular foramen. This is contrary to the condition (a specific feature; Myrcha et al. 2002) observed in *Delphinornis larseni*. Tarsometatarsi of *D. larseni* are also clearly larger than their counterparts in the above-mentioned taxa. Further investigation of tarsometatarsi assigned to *D. gracilis* and *Ichtyopteryx gracilis* revealed that they are closest to each other in terms of dimensions (Table 1). They also share a unique shape of the articular surface of the trochlea III in plantar view and this is the only new feature added to the specific diagnosis by Myrcha et al. (2002; see above). The assumption of their conspecificity is the most parsimonious explanation, hence the synonymisation (*I. gracilis* has priority at specific level, *Delphinornis* has priority at generic level). Interestingly, the specific names in the above-mentioned binominals are homonyms (secondary homonymy; ICZN 1999: Art. 53.3 and 57.3).

Genus *Anthropornis* Wiman, 1905

Type species: *Anthropornis nordenskjoeldi* Wiman, 1905; Seymour Island, Antarctic Peninsula; La Meseta Formation, Eocene.

Anthropornis nordenskjoeldi Wiman, 1905

Fig. 3.

1905 *Anthropornis nordenskjöldii* sp. nov.; Wiman 1905a: 249, pl. 12: 6.

1905 *Orthopteryx gigas* sp. nov.; Wiman 1905b: 27–28, pl. 8: 2–2b; new synonymy.

Holotype: NRM-PZ A.45, incomplete left tarsometatarsus.

Type locality: NE Seymour Island (Antarctic Peninsula).

Type horizon: La Meseta Formation, Telm6–7 of Sadler (1988; see also Marples 1953: fig. 1 ["Swedish locality"], and Myrcha et al. 2002: fig. 1), late Eocene.

Material.—IB/P/B-0070, IB/P/B-0085, IB/P/B-0287, MLP 84-II-1-7, MLP 83-V-20-50, MLP 83-II-1-19, BMNH A3358 (incomplete tarsometatarsi); IB/P/B-0091, IB/P/B-0092, IB/P/B-0307, IB/P/B-0478, IB/P/B-0711, NRM-PZ A.37, MLP 93-X-1-4, MLP 82-IV-23-4, MLP 83-I-1-190, MLP 88-I-1-463, BMNH A3338, SAMA P14157b, SAMA P14157c, SAMA P14158a (incomplete humeri), IB/P/B-0119, NRM-PZ A.43 (nearly complete humeri); NRM-PZ A.23 (incomplete synsacrum, type specimen of *O. gigas* Wiman, 1905).

Diagnosis.—Tarsometatarsal features as listed by Myrcha et al. (2002) (but see the "Skeletal sexual dimorphism and fossil penguins" section).

Remarks.—Wiman (1905b), by erecting *Orthopteryx gigas*, had departed from his principle of basing fossil penguin species on tarsometatarsi, and this led to long lasting confusion in the systematics of this group (Simpson 1946, 1971; Jadwiszczak 2009). In his opinion (Wiman 1905b), the type specimen of *O. gigas*, a partial synsacrum being the sole member of the so-called Group 1, was too large to belong to *Anthropornis nordenskjoeldi* (another "giant" penguin he

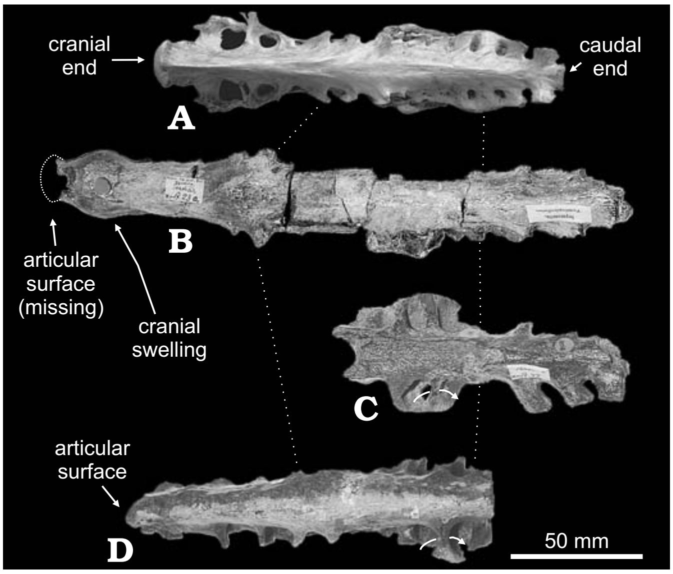

Fig. 3. Synsacra (in ventral views) of the Recent sphenisciform and fossil penguins. **A**. Recent *Aptenodytes forsteri* Gray, 1844, NRM-VE A611330. **B**–**D**. Fossil penguins from the Eocene La Meseta Formation, Seymour Island. Assignments as proposed in this paper. **B**. *Anthropornis nordenskjoeldi* Wiman, 1905, NRM-PZ A.23. **C**. ?*Anthropornis* sp., NRM-PZ A.47. **D**. ?*Palaeeudyptes* sp., NRM-PZ A.9.

described, placed in Group 3), and due to other morphological details, was rather doubtfully spheniscid.

The total length of specimen NRM-PZ A.23 is 212 mm, and taking into account its missing ends, was originally somewhat longer (approximately 230 mm long, Simpson 1946). For comparison, the complete synsacrum of the extant *Aptenodytes forsteri* (NRM-VE A611330; Fig. 3A) is 177 mm long (data for *A. nordenskjoeldi* do not exist, because no other synsacrum can be reasonably assigned to this species; see previous paragraph). However, the length of a synsacrum depends, in part, on the number of vertebrae within it. According to Pycraft (1898), one to three caudal vertebrae can be included in the synsacrum of modern penguins, depending on age. Moreover, Wiman's (1905b) arguments for the uncertain status of *O. gigas* as a penguin species are not too serious (as stated by Simpson [1946], and we agree with this statement). First, specimen NRM-PZ A.23 originally comprised at least 14 vertebrae; too many according to Wiman (1905b), but present-day sphenisciforms have between 12 and 14 synsacral vertebrae (Pycraft 1898; Simpson 1946; Stephan 1979). Although *Waimanu* Jones, Ando, and Fordyce, 2006 (the basal penguin from the Palaeocene of New Zealand) had 11 fused synsacral vertebrae (Slack et al. 2006), it would be premature to conclude that the primitive state was to have a lower number of such skeletal elements. Even so, *O. gigas* is considerably younger in terms of geologic time than *Waimanu*. Second, the lack of a dorsal keel is arguable, as it is conspicuous in the preserved fragment of the dorsal surface (Wiman 1905b: pl. 8: 2). On the other hand, the lack of a ventral keel was considered by Simpson (1946: 39) as a sole "really distinctive" feature (to some degree, at least), and placed in the generic diagnosis of the "dubious taxon" *Orthopteryx* (see Simpson 1971). However, the ventral keel, as noticed by Simpson (1946), is not equally well developed in all modern penguins, and is usually restricted to the cranial part of the synsacrum. A reduced ventral keel is also observed in the Eocene penguins, but some specimens (e.g., IB/P/B-0102 and IB/P/B-0149) possess the keel extending to the caudal part of the bone (PJ personal observation; Jadwiszczak 2006a: fig. 18e). In the Palaeocene *Waimanu*, the synsacrum does not form such a structure but keeps a columnar shape (Slack et al. 2006: fig. 1; Tatsuro Ando, personal communication).

The cranial part of specimen NRM-PZ A.23 is clearly elongated. Additionally, there is a conspicuous swelling of the bone, just caudal to the (missing) articular surface (Fig. 3B). It seems to be a structure supporting the cranial end of the synsacrum, evolved to compensate for the huge body mass of the bird. Interestingly, such a swelling is also observed in the Palaeocene *Waimanu* ("large robust birds"; Slack et al. 2006: fig. 1). The only Eocene penguin known to have analogous supportive structures, but within its hind-limb skeleton (evolutionarily sensitive to mass-related forces), is *Anthropornis nordenskjoeldi*. Birds assigned to this species had massive tarsometatarsi with well pronounced convexity in the centre of their (otherwise concave) medial margins (e.g., Wiman 1905b: pl. 2: 3, 6; Myrcha et al. 2002: 17).

In our opinion premises discussed above justify the synonymisation of *Orthopteryx gigas* with *Anthropornis nordenskjoeldi* (the latter having priority). Neither the synsacral length of *O. gigas* is inconsistent with that of holotype tarsometatarsus of *A. nordenskjoeldi* nor the lack of the ventral keel in *O. gigas* does not exclude the species from sphenisciforms.

We agree with Simpson's (1971) view that the synsacrum NRM-PZ A.9 (Fig. 3D), assigned by Wiman (1905b) to his Group 3 (the one containing the holotype of *A. nordenskjoeldi*), could have belonged to a clearly smaller bird, most probably from the genus *Palaeeudyptes*. The systematic position of the synsacrum from Wiman's (1905b) Group 2 (NRM-PZ A.47; Fig. 3C) remains open to question, however.

Skeletal sexual dimorphism and fossil penguins

Two genera of the largest Eocene Antarctic penguins, *Anthropornis* and *Palaeeudyptes*, comprise two species each. *Palaeeudyptes klekowskii* and *Palaeeudyptes gunnari* as well as *A. nordenskjoeldi* and *A. grandis* differ primarily in their dimensions (Simpson 1971; Myrcha et al. 1990, 2002), with other features possibly being size-related. The exploratory analysis of tarsometatarsi assigned to *Palaeeudyptes* (relatively large sample available) revealed an intriguing pattern. The distribution of tarsometatarsal lengths for *P. gunnari* (smaller birds) was slightly left-skewed (skewness = -0.894, N = 11), whereas that for *P. klekowskii* was significantly right-skewed (skewness = 1.148, N = 21; t = 2.290, df = 20, P = 0.033). Combined

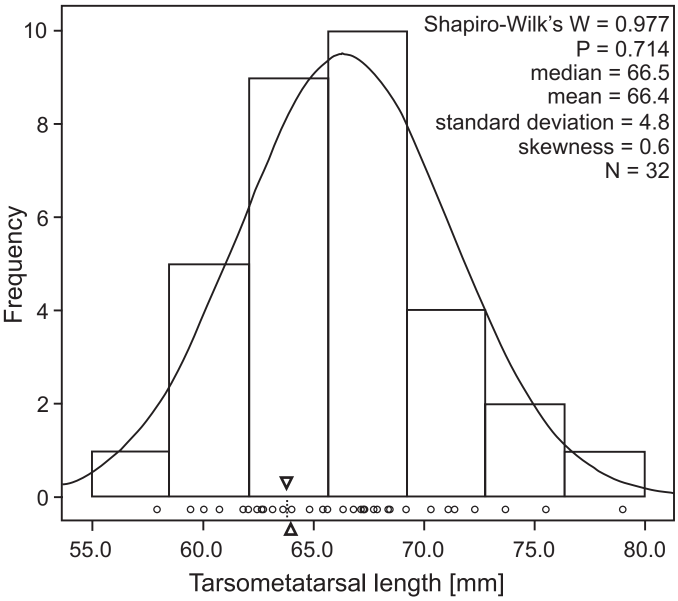

Fig. 4. Distribution of tarsometatarsal lengths within the Antarctic branch of the sphenisciform genus *Palaeeudyptes*; details of testing for normality and the normal curve fitted. Open arrows at the base of the histogram separate data values for *Palaeeudyptes gunnari* (Wiman, 1905) (left) and *Palaeeudyptes klekowskii* Myrcha, Tatur, and del Valle, 1990.

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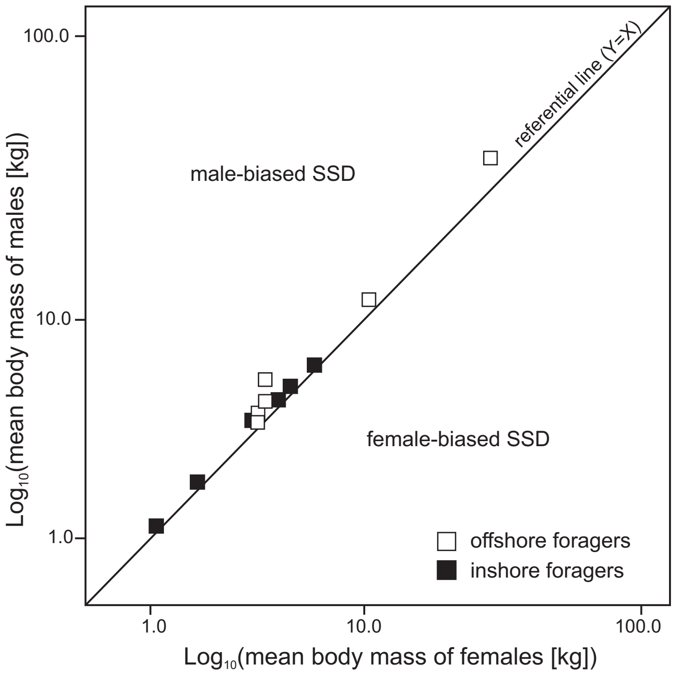

Fig. 5. Sexual size dimorphism (SSD) in present-day penguins. Based on data for 16 species compiled by Davis and Renner (2003).

samples exhibited a relatively small degree of skewness (departure from symmetry mainly due to a single outlier; Fig. 4), not statistically significant (t = 1.331, df = 31, P = 0.193). Interestingly, the distribution of examined values did not depart from normality (Fig. 4).

The statistically insignificant level of asymmetry can be observed in a relatively large (representative) sample taken from a population of tarsometatarsal lengths of a single species (based on data for 50 unsexed adult Wilson's Storm Petrels, *Oceanites oceanicus* Kuhl, 1820 [PJ, unpublished data] and 40 Great Northern Loons, *Gavia immer* (Brunnich, 1764) [Gatesy and Middleton 1997]; see also Livezey 1989: table 3—the standard deviation used as a measure of variability suggests the existence of symmetry within large samples representing seven Recent penguin species). The left-skewness in *P. gunnari* and right-skewness in *P. klekowski* may result from the incorrect approach used to assign specimens to both taxa (i.e., the size criterion), while in fact distributions of bone lengths may be partly overlapping. The alternative and more probable explanation of the observed pattern seems to be the sexual size dimorphism (SSD; to be more precise, skeletal sexual dimorphism) within a single species of *Palaeeudyptes* (*P. gunnari* has priority; the rule of parsimony). As the tarsometatarsal morphology is (in this case) quite homogeneous at the generic level, specific names used within the above considerations can be safely replaced with the "male" and "female" terms. Moreover, because we found juvenile features in some large tarsometatarsi (e.g., there is a conspicuous suture between metatarsals III and IV in IB/P/B-0551), the age factor does not seem to be dominant here. The effect of another potential confounder, the relative elongation of a bone (the index of elongation, a measure of robustness, was defined by Myrcha et al. [2002]), can also be excluded, as its value is not related to the taxonomic position within Antarctic *Palaeeudyptes* (mean difference = 0.014, N_1 = 13, N_2 = 9, P = 0.79). This may be also applicable to the genus *Anthropornis* (see data in Myrcha et al. 2002: table 1), but the sample is too small to conduct more detailed analyses.

Comparing variation adjusted for means, we observed that tarsometatarsal lengths for *Palaeeudyptes* (both species combined) were more dispersed in relation to the mean value (CV = 7.2, N = 32) than those for the most variable extant species (*Eudyptula minor* [Forster, 1781]; CV = 5.6, N = 34). On the other hand, the difference between *E. minor* and the least variable extant species (*Megadyptes antipodes* [Hombron and Jacquinot, 1841]; CV = 2.5, N = 30) does considerably exceed that for *Eudyptula* and *Palaeeudyptes* (3.1 and 1.6, respectively). Thus, in our opinion, such a situation does not preclude the existence of the large scope of size-related variability within a single species rather than the presence of two species.

Body mass of modern penguins is notoriously variable during the breeding season; however, males tend to be slightly larger (male-biased SSD; Fig. 5; Livezey 1989; Davis and Renner 2003). This difference is also present in skeletal measurements. Although Mahalanobis' distances differ considerably across six species (representing six genera) studied by Livezey (1989), all the intersexual differences were statistically significant (P<0.001). This makes sense because, among others, sexually dimorphic pairs can exploit a wider range of resources than monomorphic ones (Figuerola 1999), avoiding intersexual food competition (Selander 1966). According to so-called Rensch's rule, in taxa with male-biased dimorphism (such as penguins, Fig. 5) SSD increases with body size. Generally, in extant seabirds Rensch's rule exists as a trend devoid of statistical significance (Serrano-Meneses and Székely 2006). If fossil Sphenisciformes followed this rule, the giant penguins (unlike their present-day smaller relatives) were highly dimorphic, and this would be consistent with the pattern observed in *Palaeeudyptes* (and suggested for *Anthropornis*). Unfortunately, no statistical testing is possible in this case, because it is not possible to set the split line.

Body mass estimation

Body mass estimation for early Antarctic penguins using both Campbell and Marcus' (1992) scaling model with least shaft circumferences of the femora and the allometric equation by Cubo and Casinos (1997) with the femur transverse diameters yielded similar results (Table 2). These values are

Table 2. Predicted body masses (in kg) for fossil penguins from the Eocene La Meseta Formation, Seymour Island (a combined sample approach). Values were calculated using Campbell and Marcus' (1992) (CM) and Cubo and Casinos' (1997) (CC) methods, details in text.

Method	N	Mean	Minimum	Maximum
CM	29	11.69	2.6	26.4
CC	29	10.58	2.5	23.4

Table 3. Predicted body masses (in kg) for fossil penguins from the Eocene La Meseta Formation, Seymour Island. Values were calculated by means of adjusted Cubo and Casinos' (1997) allometric equation, details in text.

Taxon/taxa	N	Median	Mean	SD	Minimum	Maximum
Anthropornis sp. and/or *Palaeeudyptes* sp.	11	46.8	48.36	8.9080	34.4	67.7
Palaeeudyptes gunnari	5	32.7	32.08	4.3727	24.7	36.1
Archaeospheniscus wimani	3	24.3	24.96	3.5995	21.8	28.9
Small-bodied species	10	9.0	9.09	2.4703	6.3	12.4

decidedly lower than estimates reported by Livezey (1989) and Jadwiszczak (2001), who obtained their results by means of slightly different statistical techniques and/or other bones (estimated body masses for *A. nordenskjoeldi*: 81 kg [Livezey 1989] and 81–108 kg [Jadwiszczak 2001]).

Nevertheless, when we substitute both parameters of Cubo and Casinos' (1997: table II) equation with the lower endpoint values of their 95% confidence intervals, estimates become much more reasonable (Table 3). They were of course nothing more than just very rough assessments based on several assumptions, but for the largest extant penguin, *Aptenodytes forsteri*, the returned value is 31.8 kg (specimen NRM-VE A611330), which is within the range reported for this species (see Davis and Renner 2003). Interestingly, the range of body masses obtained for *Anthropornis* and *Palaeeudyptes* is shifted toward lower values in comparison with that obtained by Jadwiszczak (2001). Its lower limit (data for *P. gunnari*) seems to be underestimated (bones of this bird are larger than those of the Emperor Penguin). On the other hand, there is a sole specimen, IB/P/B-0701 (the largest one), so poorly preserved that the diameter cannot be measured or body mass (directly) estimated. It certainly belonged to *Anthropornis nordenskjoeldi* and suggests a higher upper limit for the body mass of fossil penguins than that reported in Table 3. Another discrepancy exists between values predicted for *Archaeospheniscus wimani*—estimates presented here (Table 3) are around twice as high as those reported by Jadwiszczak (2001).

Conclusions

Previous studies recognized six genera and ten species of well-established extinct penguins from Seymour Island. This is obviously the highest diversity known from any one small area (deposits of the La Meseta Formation fill a 7 km wide incised valley cut into older strata; e.g., Marenssi 2006). This diversity remains impressive even if it is partly based on sexual size dimorphism, supposedly well marked in the huge-bodied penguins. These results are pending on further investigations which require collecting much larger samples.

It seems clear that Eocene Antarctic penguins were more varied in terms of body size than their relatives are today. Nevertheless, relying on scaling models developed for taxonomically mixed groups of extant birds (such as "swimmers" or "flightless species"), in the case of fossil penguins, appears to result in too biased estimates of body mass, though the general pattern can still be observed.

Ichtyopteryx gracilis and *Delphinornis gracilis* as well as *Orthopteryx gigas* and *Anthropornis nordenskjoeldi* are doubtfully separable both generically and specifically. The synonymisation we formally propose clarifies the systematics of the group and allows the removal of the two dubious penguin taxa.

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Appendix 1

Specimens used for this study, either directly (as indicated in text) or in a form of measurements taken from literature.

Anthropornis nordenskjoeldi
IB/P/B-0675, IB/P/B-0701 (femora); NRM-PZ A.23 (synsacrum).

Aptenodytes forsteri (Recent species)
NRM-VE A611330 (femur and synsacrum).

Archaeospheniscus wimani
IB/P/B-0641, IB/P/B-0658, NRM-PZ A.32 (femora).

Delphinornis arctowskii
IB/P/B-0484, MLP 93-X-1-92 (tarsometatarsi).

Delphinornis gracilis comb. nov.
IB/P/B-0130 (femur); IB/P/B-0279a, NRMPZ A.20 (tarsometatarsi).

Delphinornis larseni
IB/P/B-0090 (femur); IB/P/B-0062, MLP 84-II-1-79 (tarsometatarsi).

?*Delphinornis* sp.
IB/P/B-0073 (femur).

Marambiornis exilis
IB/P/B-0434 (femur); IB/P/B-0490 (tarsometatarsus).

?*Marambiornis* sp.
IB/P/B-0458 (femur).

Mesetaornis polaris
IB/P/B-0215 (femur); IB/P/B-0278 (tarsometatarsus).

?*Mesetaornis* sp.
IB/P/B-0436 (femur).

Palaeeudyptes gunnari
IB/P/B-0103, IB/P/B-0430, IB/P/B-0504, IB/P/B-0655, IB/P/B-0699 (femora); IB/P/B-0072, IB/P/B-0112, IB/P/B-0277, IB/P/B-0487, MLP 82-IV-23-5, MLP 82-IV-23-6, MLP 84-II-1-124'{?}, MLP 87-II-1-45, MLP 91-II-4-222, MLP 94-III-15-16, NRM-PZ A.7 (tarsometatarsi).

Palaeeudyptes klekowskii
IB/P/B-0061, IB/P/B-0065, IB/P/B-0101, IB/P/B-0281, IB/P/B-0285, IB/P/B-0485, IB/P/B-0486, IB/P/B-0545, IB/P/B-0546, IB/P/B-0551, MLP 78-X-26-18, MLP 83-V-30-15, MLP 83-V-30-16, MLP 83-V-30-17, MLP 84-II-1-76, MLP 84-II-1-78, MLP 84-II-1-124, MLP 93-X-1-63, MLP 93-X-1-106, MLP 93-X-1-108, MLP 93-X-1-142, MLP 94-III-15-20 (tarsometatarsi).

?*Palaeeudyptes* sp.
NRM-PZ A.9 (synsacrum).

Anthropornis sp. and/or *Palaeeudyptes* sp.
IB/P/B-0227, IB/P/B-0230, IB/P/B-0342, IB/P/B-0457, IB/P/B-0496, IB/P/B-0509, IB/P/B-0643, IB/P/B-0740, IB/P/B-0743, NRM-PZ A.44 (femora).

Sphenisciformes gen. et sp. indet.
IB/P/B-0518, IB/P/B-0758, NRM-PZ A.236 (femora); NRM-PZ A.47 (synsacrum).

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