Taxonomic revision of Eocene Antarctic penguins based on tarsometatarsal morphology

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ABSTRACT: Eocene penguin remains from Seymour Island (Antarctica) are so far the oldest-known record of extinct Sphenisciformes. Rich Argentine and Polish collections of penguin bones from the La Meseta Formation are taxonomically revised on tarsometatarsal morphology. Two genera and four species are erected: *Mesetaornis polaris* gen. et sp. n., *Marambiornis exilis* gen. et sp. n., *Delphinornis arctowskii* sp. n. and *D. gracilis* sp. n. Moreover, the diagnoses of already described species: *Anthropornis nordenskjoeldi, A. grandis, Palaeeudyptes klekowskii, P. gunnari, Archaeospheniscus wimani* and *Delphinornis larseni* are revised as well. Gradual cooling of climate, changes of environment and trophic relationships, that lasted several millions years, were most probably responsible for the intense speciation and taxonomic diversification of the Middle–Late Eocene La Meseta penguins.

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

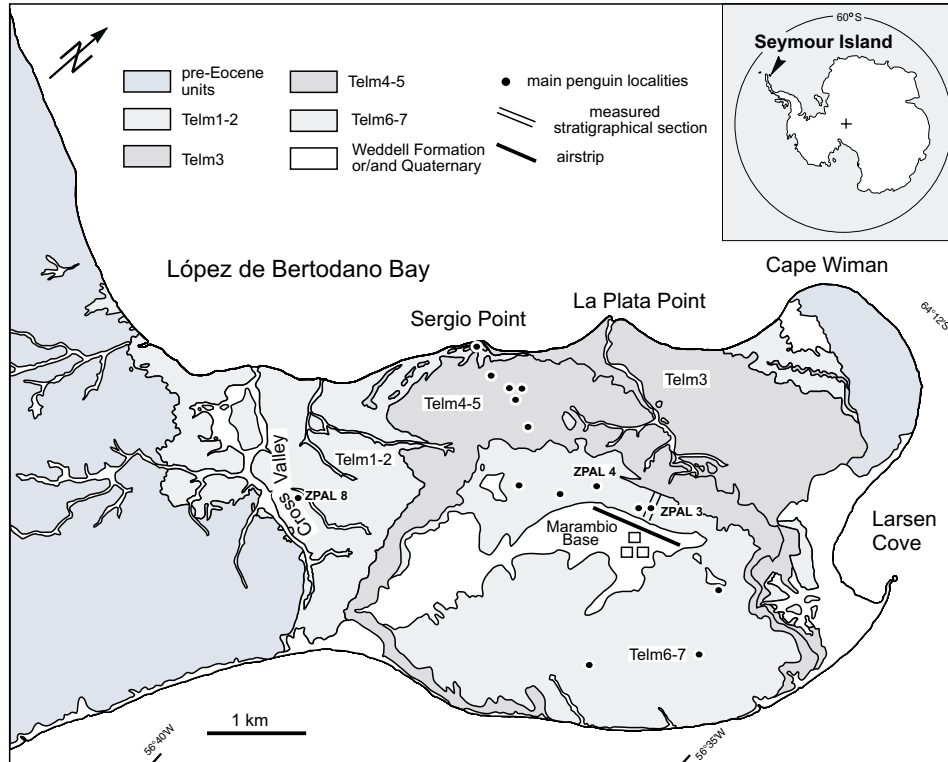†Andrzej MYRCHA passed away on October 28th, 1997

Fig. 1. Penguin locality index map of the La Meseta Formation on Seymour Island. Distribution of stratigraphical units according to Sadler (1988). Arrow of inset shows the location of Seymour Island in Antarctica.

Introduction

Penguins (Spheniscidae) form a sole family in the order Sphenisciformes. A great deal of data exists on their biology, ecology and physiology, but our understanding of the evolutionary history of the group is still very incomplete, despite having been studied for 150 years. The work *On the remains of birds from New Zealand* by Mantell (1850) *fide* Huxley (1859) was the earliest published notice concerning fossil penguin remains. Huxley (1859) was the first to describe an extinct Spheniscidae from an incomplete tarsometatarsus found near Kakanui, New Zealand. Simpson (1975, 1976) stated that most features basic to this family had probably developed by the Late Eocene and that these early penguins were very specialised.

Currently six sites in the Southern Hemisphere are famous for their fossil penguin bone-bearing localities. So far, the only site in Antarctica is Seymour Island (Isla Vicecomodoro Marambio on Argentine maps). This small scrap of land is situated off the north-eastern end of the Antarctic Peninsula (Fig. 1). Several collec-

tions of fossil penguin remains from the Eocene La Meseta Formation of Seymour Island are known: Swedish (Wiman 1905a, b; Simpson 1946, 1971a), English (Marples 1953, Simpson 1971a), Argentine (Cione *et al.* 1977, Simpson 1981, Bargo and Reguero 1998), United States (Elliot *et al.* 1975, Zinsmeister and Camacho 1982, Olson 1985, Case 1992) and Polish (Myrcha and Tatur 1986, Myrcha, Tatur and del Valle 1990, Jadwiszczak 2000, 2001).

The first collection of fossil penguin bones from Seymour Island was gathered by the members of the Swedish South Polar Expedition in 1901–1903. The earliest published systematics of the extinct Spheniscidae from that region (Wiman 1905a, b) distinguished six species of penguins. Each of them was the type species of a new genus. Simpson (1946) revised that analysis and postulated the existence of only four genera. Marples (1953), on the basis of the English collection of fossil material from Seymour Island, described four genera and species of extinct penguins, one genus and species for the first time. Both collections were thoroughly re-examined by Simpson (1971a), who distinguished five genera with six species of unquestionable validity and two genera and species defined as "dubious taxa". The successive decades resulted in several new collections of fossil penguins. One of them collected in the field by Myrcha, Tatur and Gaździcki and housed at the Institute of Biology, University of Białystok (Poland) enabled description of a new species of giant penguin – *Palaeeudyptes klekowskii* (Myrcha, Tatur and del Valle 1990). Millener (1988) suggested existence of up to seven genera and some fourteen species of Tertiary Spheniscidae from Seymour Island.

The purpose of this paper is to analyse the tarsometatarsi from the Polish and Argentine collections. These to complete a taxonomical revision and description of new taxa of the Eocene penguins from Seymour Island. The Polish collection is housed at the Institute of Biology, University of Białystok (formerly Warsaw University, Branch in Białystok; abbreviated IB/P/B). Tarsometatarsi from the Argentine collection are housed at the Museo de La Plata in La Plata (abbreviated MLP). These two collections comprise a total of 126 tarsometatarsi.

Geological and stratigraphical setting

The La Meseta Formation (Fig. 2) consists of poorly consolidated clastic sediments, approximately 800 m thick (Rinaldi *et al*. 1978, Elliot and Trautman 1982, Stilwell and Zinsmeister 1992, Marenssi, Santillana and Rinaldi 1998a) deposited during the Eocene, since the Ypresian (49.5 Ma) the low stand of sea level (Sadler 1988), to the latest Eocene (34.2 Ma), according to Sr isotope dating (Dingle and Lavelle 1998). The formation, originated largely within an incised valley system repeatedly developed above a major, linear NW-SE striking zone of fault-controlled subsidence (Porębski 1995, 2000). The predominantly marine-estuarine fill grades upwards into unconfined, tide- and wave-dominated shelf deposits

(Marenssi, Santillana and Rinaldi 1998a, and authors' personal observations). Sadler (1988) on the basis of extensive mapping, subdivided the formation into seven major lithofacies Telm1–Telm7 (acronyms for Tertiary Eocene La Meseta), often also grouped into three larger depositional sequences marking channelised transgressive-regressive cycles (Elliot and Trautman 1982, Porębski 1995, 2000; Marenssi, Santillana and Rinaldi 1998b). The La Meseta Formation is formed mainly by sands interbedded with bioturbated sandy muds, and sand/mud hetheroliths in several parts rich in marine and terrestrial fossils (Feldmann and Woodburne 1988, Stilwell and Zinsmeister 1992; Gaździcki 1996, 1998, 2001) concentrated often in shell conglomerates lithified by calcareous cement. The results of geochemical analyses of fossil shell material from the La Meseta Formation suggest a considerable cooling event (Gaździcki *et al*. 1992) at the time of deposition of the upper part of the formation (Telm6–Telm7).

Penguin bones in the La Meseta Formation

Until now, the Eocene penguin remains have been collected in Antarctica exclusively from the La Meseta Formation on Seymour Island (Simpson 1976, Fordyce and Jones 1990, Noriega *et al*. 1995). A few undetermined specimens of penguin bones were already found in the lower part of the formation, in scree covering Telm1 and Telm2. However, the oldest and single *in situ* findings (including humerus) come from the ZPAL 8 locality (see Fig. 1) *i.e.* Telm2s *sensu* Sadler (1988). Many more specimens, including numerous tarsometatarsi, were collected by Argentine paleontologists in the upper part of Telm3 (locality IAA 1/94), Telm4 (locality DPV 2/84), and especially in Telm5 at localities DPV 1/84, IAA 1/90, IAA 1/80 (= DPV 9/84), DPV 6/84 (=RV 8200) known as "Mammal Site", and IAA 4/80 (= IAA 2/90), see (Fig. 2 and Marenssi *et al.* 1994, Bargo and Reguero 1998, Reguero *et al.* 1998). These localities, beside diversified marine invertebrates (see Stilwell and Zinsmeister 1992), contain remains of diverse fossil terrestrial vertebrates with small and medium – size mammals (Marenssi *et al.* 1994; Woodburne and Case 1996; Vizcaino *et al.* 1998; Reguero, Marenssi and Santillana *in press*). Marine vertebrates also are present. Among them penguin remains as well as ichthyofauna represented by numerous isolated shark teeth were recovered (Long 1992a, b; Cione and Reguero 1994) The depositional setting of these beds is a shallow marine environment; mammal-bearing strata are in reworked, moderate to high energy subtidal facies (Marenssi *et al*. 1994).

Fig. 2. Stratigraphical distribution of penguins 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.

North Section (Sadler 1988)

Weddell 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
	sill + sand

100m

- ZPAL 8

0

Measured stratigraphical section of Telm7 (see Fig. 1)

m

80 ← Dentalium
   ← Cucullaea

70

← Eurchomalea
← Eurchomalea

60

50 ← Lingula, Modiolus
   ↕ Bourchardia

● ZPAL 4
● ZPAL 3 ← Metacrinus, Hiatella, Mya
40
   ↕ Ophiura, Panopea, Cucullaea,
     Bourchardia, polychaete worms,
     balanomorph barnacles
   ← Hiatella
   ← Perissodonta
30
   ← Lingula

   ↕ Bourchardia
20
   ← Hiatella
   ↕ Panopea, Bourchardia
   ← Smittina, polychaete worms
10 ↕ Ostrea, Bourchardia
   ← Smittina

   ← Hiatella
   Metacrinus, Ophiura, echinoids,
   ← Smittina, Bourchardia,
     polychaete worms
0 ← Eurchomalea
     turritellid gastropods

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
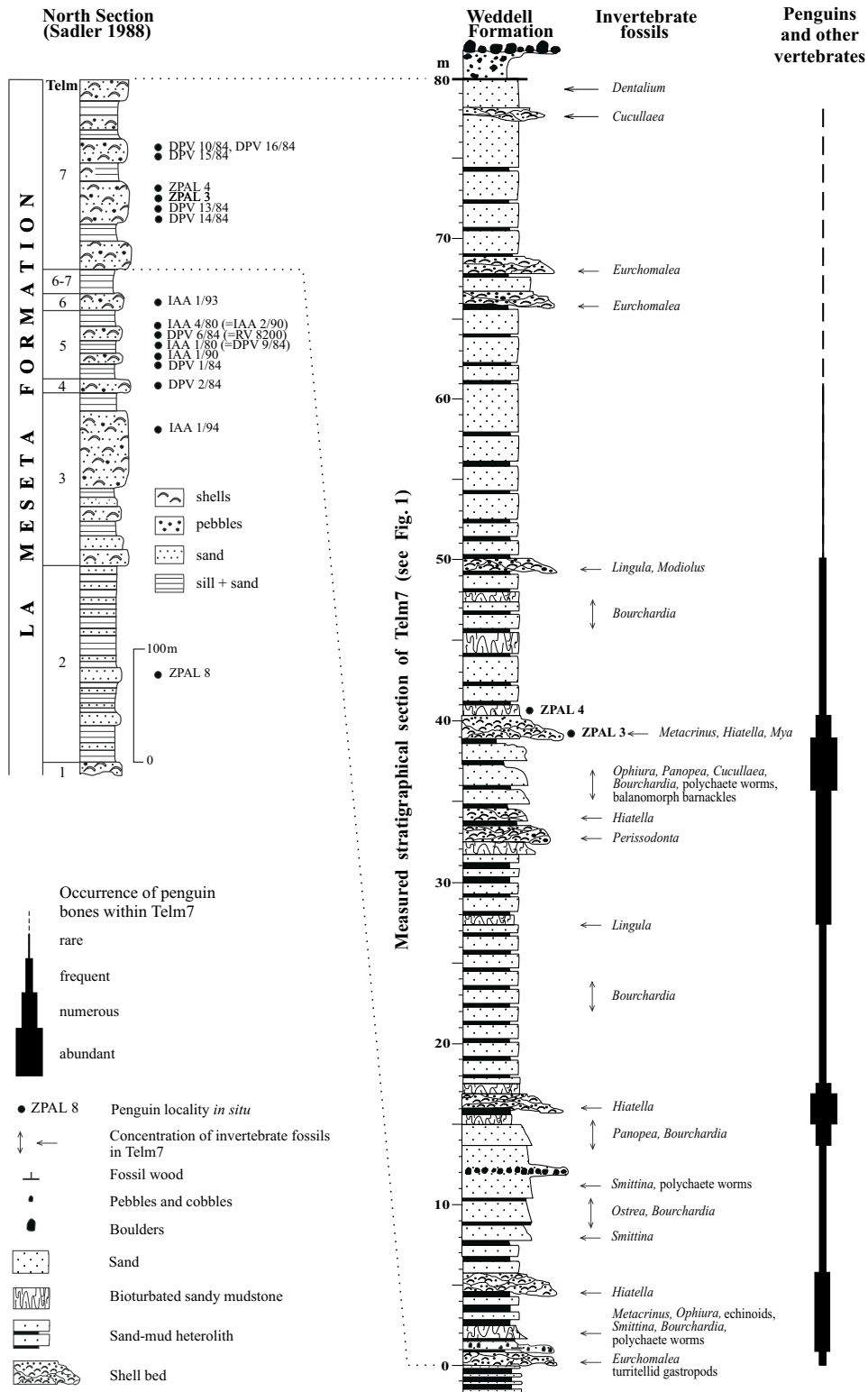
Sand-mud heterolith

Shell bed

Fig. 3. View of the top of meseta along the north-western side and the upper units of the La Meseta Formation where the numerous penguin bones have been collected in Telm7. Bodman Point and James Ross Island are in background. *Photograph by A. Gaździcki, January 1992.*

The highest numbers of tarsometatarsi were collected from Telm7 along NNW slope of the meseta (Figs 2, 3). Exceptionally abundant were localities: ZPAL 3 and ZPAL 4, DPV 10/84, DPV 15/84 and DPV 16/84. Minor findings come from the Telm7 and Telm6 exposed on the SE slope of the meseta in sites: DPV 13/84, DPV 14/84, and IAA 1/93, see also (Bargo and Reguero 1998, Reguero *et al.* 1998).

The most abundant remains of marine vertebrates (fishes, penguins and whales) were collected primarily in the lower and middle part of the Telm7 unit (Fig. 2). These fossils occurred from the basal gastropod turritellid shell bank to the horizons bearing bivalved and gastropod molluscs *Panopea*, *Hiatella*, *Perissodonta*, brachiopods *Lingula*, and *Bouchardia* (see also Stilwell and Zinsmeister 1992, Bitner 1996), as well as very often in horizons bearing bryozoan *Smittina* colonies (Hara 2001), crinoids *Metacrinus* (Rasmussen 1979, Baumiller and Gaździcki 1996), ophiuroid *Ophiura* (Aronson, Blake and Oji 1997, Blake and Aronson 1998), and echinoid *Abatus* (McKinney, McNamara and Wiedman 1988). Remains of *Mesetaichthys* fish (Jerzmańska 1988, Jerzmańska and Świdnicki 1992), Archaeoceti whale bones (Wiman 1905a, Borsuk-Białynicka 1988, Fordyce 1989), tarsometatarsus of a ratite bird (Tambussi *et al.* 1994) and tooth of a sparnotheriodontid mammal (Vizcaino *et al.* 1997) co-occur with penguin bones. Abundance of vertebrate remains occasionally covered by balanomorph barnackles (Zullo, Feldmann and Wiedman 1988), as-

sociated with fossilized wood infested by teredid bivalves, and numerous trace fossils (Wiedman and Feldmann 1988), indicate a nearshore tidal and wave-dominated environment (Myrcha, Tatur and del Valle 1990). This sedimentary environment may have developed near the mouth of an estuary (Porębski 1995, fig. 54; Marenssi, Santillana and Rinaldi 1998a).

The age of the penguin tarsometatarsi examined here probably ranges from 49.5 Ma (Porębski 2000) or 42.0 Ma (Marenssi *et al*. 1994) to 34.2 Ma (Dingle, Marenssi and Lavelle 1998). Thus the fossil penguins remains from the upper part of Telm3 may be up to 15 million years older than those from the uppermost part of the Telm7 (see Fig. 2).

Eocene climatic fluctuation

Globally extensive Late Paleocene–Early Eocene Cenozoic optimum of climate is also recognized in the late Early Eocene sediments (Telm1–2) of Seymour Island by paleontological and geochemical evidences of a very warm, wet, non-seasonal climate which persisted until the middle Middle Eocene (Askin 1988, 1992; Doktor *et al*. 1996, Dingle, Marenssi and Lavelle 1998, Dzik and Gaździcki 2001). Studies of paleoflora collected from Telm3–5 suggest a change to strongly seasonal climate, becoming cooler (cold-temperate) and wetter during the Middle Eocene (Case 1988, Askin 1997, Gandolfo, Marenssi and Santillana 1998). Evidence for a gradual cooling of climate towards the top of the La Meseta Formation (Telm6–7) is evidenced by marine bottom fauna (Zinsmeister and Camacho 1982, Zinsmeister 1991, Stilwell and Zinsmeister 1992, Aronson and Blake 2001, Hara 2001), stable isotopes in fossil shell material (Gaździcki *et al*. 1992) and by sedimentological and geochemical evidences (Dingle, Marenssi and Lavelle 1998). During the deposition of the uppermost part of the La Meseta Formation (top of Telm7) climate was relatively cold and dry (Dingle, Marenssi and Lavelle 1998; Dingle and Lavelle 2000). Progressive climate cooling and ice-sheet growth in the Southern Ocean is inferred from sediment and stable isotope data at the Eocene–Oligocene boundary (Barrera and Huber 1993, Salamy and Zachos 1999).

Material and methods

The tarsometatarsus is a characteristic bone of the hind limb skeleton of birds. It is formed as a result of fusion of several elements: the lower row of tarsal bones and three metatarsal elements. Penguin tarsometatarsi differ a great deal from their counterparts in other birds. The difference is particularly pronounced in their shortening and dorso-plantar flattening; these involved other morphological modifications (Fig. 4). In most cases, however, an anatomical identification of characteristic morphological features of the bones is not difficult. This possibility is of particular importance
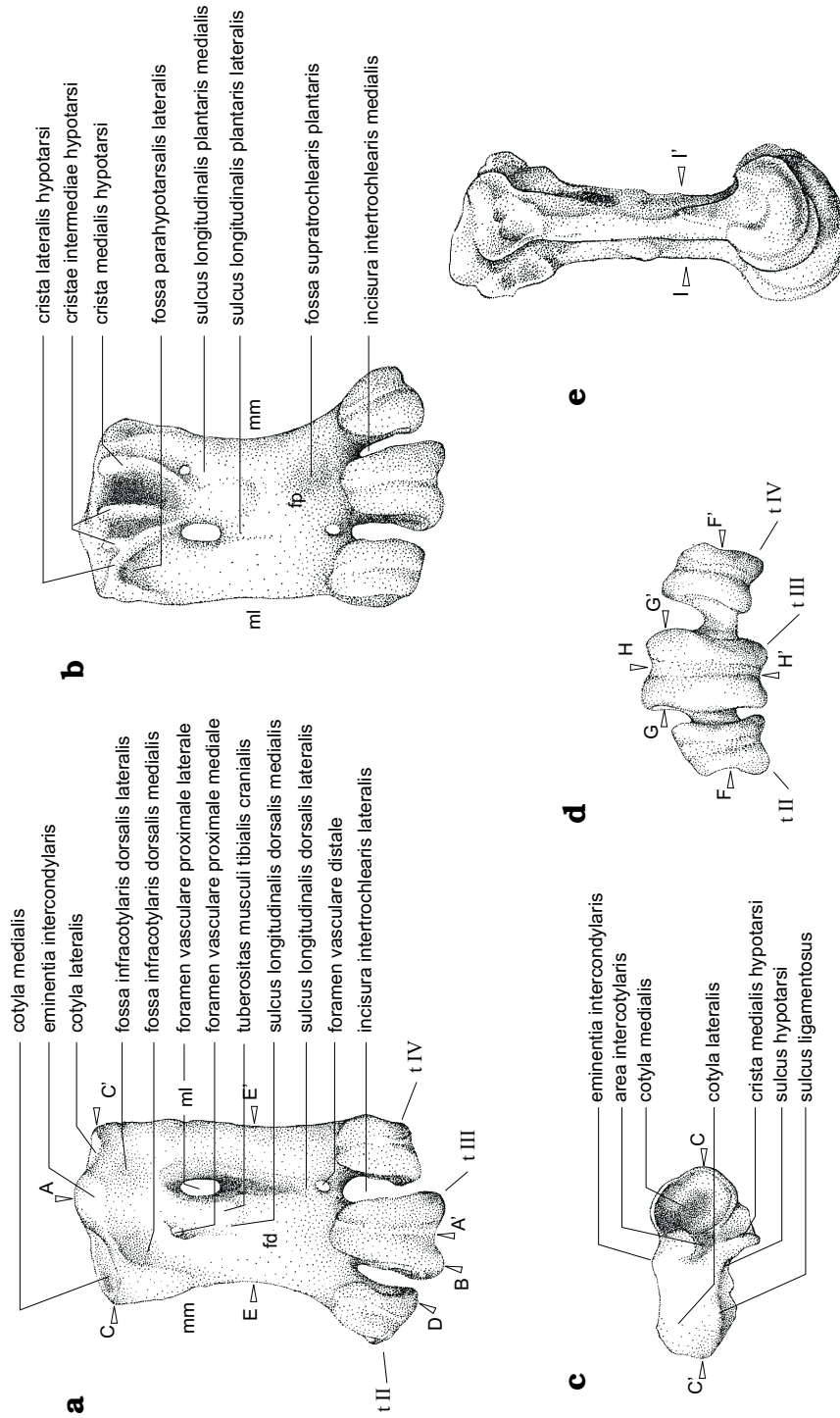
Fig. 4. Morphology and measurement points of the spheniscid tarsometatarsus: **a** – dorsal aspect, **b** – plantar aspect, **c** – proximal aspect, **d** – distal aspect, **e** – side aspect. Abbreviations: mm – margo medialis, ml – margo lateralis, fd – facies dorsalis, fp – facies plantaris, t II, III, IV – trochlea metatarsi II, III, IV; A–I – measurement points.

because the majority of Tertiary penguin species have been described on the basis of tarsometatarsi (Wiman 1905a, b; Marples 1953, Simpson 1971a, Myrcha, Tatur and del Valle 1990). Furthermore, fossils of Spheniscidae appear almost exclusively as single, isolated skeletal elements (Simpson 1975, 1981; Fordyce and Jones 1990) and this is particularly true with regard to the fossil material from Seymour Island (Marples 1953, Jadwiszczak 2000, 2001; authors' personal observation).

Here, anatomical nomenclature follows *Nomina Anatomica Avium* (Baumel *et al.* 1979), though some modifications were necessary. We introduced terms: "metatarsale" (after Stephan 1979), "margo medialis" and "margo lateralis" (because of dorso-plantar flattening of the bone). We distinguished "foramen vasculare proximale mediale" and "f. v. p. laterale". The characteristic structure of the proximal end of the bone required more additional terms: "fossa infracotylaris dorsalis medialis" and "f. i. d. lateralis", instead of "fossa infracotylaris dorsalis". In the case of the intermetatarsal groove nomenclature we applied alternative names listed by Baumel *et al.* (1979): "sulcus longitudinalis dorsalis" and "sulcus longitudinalis plantaris". These terms describe the tarsometatarsal morphology of the penguins more completely. Moreover, it was necessary to distinguish the intermetatarsal grooves by using "lateralis" and "medialis" adjectives.

We used the following measurement categories (for measurement points, here presented in brackets, see Fig. 4, for data – see Table 1):

1. Length from eminentia intercondylaris to the groove of trochlea III (A–A').

2. Total length from eminentia intercondylaris to the medial edge of trochlea III (A–B).

3. Proximal width from the more lateral (in relation to the main axis of the bone) edge of cotyla medialis to the more lateral (in relation to the main axis of the bone) edge of cotyla lateralis, in the most extreme points of the preserved articular surfaces (C–C').

4. Medial width between margo medialis and lateralis, in the narrower point of the shaft (E–E').

5. Distal width from the more lateral (in relation to the main axis of the bone) edge of trochlea II to the more lateral (in relation to the main axis of the bone) edge of trochlea IV (F–F').

6. Maximal width of trochlea III between its lateral and medial edges (G–G').

7. Dorso-plantar thickness of trochlea III (H–H').

8. Dorso-plantar thickness of the bone from the central point of tuberositas musculi tibialis cranialis to the corresponding point of the plantar side (I–I').

The elongation index (EI) is defined as a ratio of the length of the bone (A–A') to its medial width (E–E').

Numbers of categories correspond to those in Table 1. All measurements are in millimetres with 0.1 mm accuracy.

Based on the available material, we describe six genera and ten species of fossil penguins from the La Meseta Formation of Seymour Island. These descriptions

were possible due to clear differences in morphology of tarsometatarsi. The Argentine specimen MLP 83-V-20-96 which had been originally labelled as *Ichtyopteryx gracilis* Wiman, 1905 (the eleventh species) was excluded from our taxonomic considerations. This incomplete bone was the smallest tarsometatarsus in the collections. As Wiman's (1905a, b) holotype of *I. gracilis* was incomplete and therefore difficult to compare with other specimens, we did not include it in this study.

Table 1

Measurements of tarsometatarsi from the studied collections. Measurement categories was defined in the "Material and methods" chapter. The letters "EI" symbolize the elongation index. All measurements are presented in millimeters. Other explanations: * at the level of the tuberosity on margo medialis, ** at the level of the tuberosity on margo medialis – 31.7.

Measurements / Specimen	1	2	3	4	5	6	7	8	EI
Anthropornis nordenskjoeldi									
IB/P/B-0070	86.0	88.1	–	–	–	16.0	20.9	12.7	–
IB/P/B-0085a	–	–	–	–	49.6	18.0	21.0	–	–
IB/P/B-0287	–	–	–	36.4*	–	–	–	12.8	–
MLP 84-II-1-7	80.9	81.4	–	–	–	–	20.8	12.8	–
MLP 83-V-20-50	–	–	39.1	–	–	–	–	13.6	–
MLP 84-II-1-19	–	–	>34.4	31.2	–	–	–	12.1	–
Anthropornis grandis									
IB/P/B-0483	72.8	74.7	>36.3	28.7**	–	13.8	17.2	10.7	2.54
MLP 83-V-20-84	74.0	77.5	–	–	–	15.8	–	12.2	–
MLP 84-II-1-12	–	–	–	26.6	–	–	–	10.7	–
MLP 86-V-30-19	–	–	–	31.5	–	–	–	–	–
MLP 84-II-1-66	–	–	–	–	–	–	–	10.1	–
MLP 95-I-10-142	76.0	78.5	–	25.0	–	–	17.0	11.1	3.04
MLP 94-III-15-178	76.6	78.7	–	26.0	–	15.9	18.1	11.6	2.95
MLP 95-I-10-156	–	–	–	28.0	–	–	–	12.6	–
MLP 93-X-1-149	–	–	–	25.3	–	–	–	9.8	–
Anthropornis sp.									
IB/P/B-0293	–	–	–	33.3*	–	–	–	13.1	–
MLP 84-II-1-9	–	–	25.2	21.4	–	18.3	–	8.9	–
Palaeeudyptes klekowskii									
IB/P/B-0065	73.7	76.4	–	–	–	17.7	23.3	12.1	–
IB/P/B-0061	64.0	66.6	–	–	–	14.1	17.8	10.8	–
IB/P/B-0081	–	–	>33.0	–	–	–	–	11.3	–
IB/P/B-0093	–	–	–	–	–	14.2	20.8	11.1	–
IB/P/B-0101	65.6	68.4	–	–	–	–	19.0	11.0	–
IB/P/B-0142	–	–	–	–	–	16.7	22.4	12.1	–
IB/P/B-0077	–	–	>38.0	–	–	–	–	11.4	–
IB/P/B-0276	–	–	–	29.8	43.4	15.8	20.6	10.5	–
IB/P/B-0281	71.4	73.8	>36.0	–	–	17.0	21.7	11.4	–

IB/P/B-0285	66.8	68.5	–	–	–	15.5	–	–	–
IB/P/B-0485	68.4	71.0	>33.9	29.9	41.8	15.8	20.3	11.2	2.29
IB/P/B-0486	72.3	74.4	>31.4	<29.0	–	14.4	21.5	–	–
IB/P/B-0545	75.5	78.5	>37.0	31.4	47.6	–	22.3	12.4	2.4
IB/P/B-0546	70.3	72.6	37.9	30.5	44.0	16.8	20.0	11.7	2.3
MLP 93-X-1-142	68.5	69.4	37.0	29.0	43.4	15.2	19.7	11.1	2.36
MLP 84-II-1-78	65.4	67.4	35.6	27.3	41.7	15.1	19.1	10.3	2.4
MLP 93-X-1-63	67.2	69.5	35.8	28.7	43.8	15.6	19.9	–	2.34
MLP 93-X-1-6	–	–	–	30.4	44.8	15.9	20.7	–	–
MLP 84-II-1-5	–	–	27.3	–	–	–	–	10.2	–
MLP 84-II-1-76	67.7	69.5	–	27.0	–	–	20.4	10.7	2.51
MLP 93-X-1-106	67.8	69.5	–	28.4	–	14.2	19.1	–	2.39
MLP 93-X-1-108	67.2	68.6	–	28.4	–	–	–	10.0	2.37
MLP 84-II-1-49	–	–	–	–	–	15.0	20.0	10.9	–
MLP 94-III-15-4	–	–	–	–	–	–	19.6	9.2	–
MLP 78-X-26-18	66.3	–	–	–	–	–	–	10.1	–
MLP 94-III-15-18	–	–	–	–	–	–	19.6	9.8	–
MLP 93-X-1-65	–	–	–	–	–	–	19.7	8.8	–
MLP 94-III-15-20	79.0	81.5	40.1	32.4	50.0	15.6	21.4	12.8	2.44
MLP 83-V-30-15	71.1	73.2	–	32.8	–	14.9	19.7	12.8	2.17
MLP 83-V-30-16	69.2	72.5	–	29.8	–	–	18.9	11.0	2.32
MLP 83-V-30-17	64.8	–	–	–	–	–	18.7	8.7	–
MLP 84-II-1-124	67.1	68.8	37.8	29.9	46.3	14.0	20.8	9.7	2.24
Palaeeudyptes gunnari									
IB/P/B-0072	60.7	62.5	>30.0	27.9	38.8	13.3	18.0	11.0	2.18
IB/P/B-0112	62.6	64.5	>31.0	>27.0	39.2	14.5	17.7	–	–
IB/P/B-0277	62.0	62.6	–	30.0	38.3	11.6	17.7	10.8	2.07
IB/P/B-0487	60.0	62.4	>30.5	24.6	36.6	14.0	17.2	10.0	2.44
IB/P/B-0124	–	–	33.4	–	–	–	–	10.5	–
IB/P/B-0286	–	–	>32.5	28.9	–	–	–	9.8	–
IB/P/B-0295	–	–	–	26.6	–	–	–	11.1	–
IB/P/B-0296	–	–	–	26.9	–	–	–	10.0	–
IB/P/B-0541a	–	–	>30.0	–	–	–	–	–	–
MLP 91-II-4-222	61.8	64.3	32.3	26.9	39.4	13.1	17.4	8.1	2.3
MLP 87-II-1-45	63.1	63.8	31.5	29.4	–	13.7	17.3	10.0	2.15
MLP 82-IV-23-6	57.9	59.0	–	23.3	–	12.0	17.3	8.6	2.48
MLP 94-III-15-16	59.4	60.0	–	23.4	–	12.4	–	7.5	2.54
MLP 82-IV-23-5	62.7	64.5	–	–	–	13.2	19.4	9.5	–
MLP 84-II-1-75	–	–	–	–	–	–	17.2	9.4	–
MLP 84-II-1-6	–	–	–	–	–	–	18.3	8.7	–
MLP 83-V-20-27	–	–	–	26.1	–	–	–	9.9	–
MLP 93-X-1-151	–	–	–	23.1	35.2	13.2	17.0	9.1	–
MLP 95-I-10-16	–	–	–	26.8	–	–	17.3	9.6	–
MLP 84-II-1-47	–	–	–	–	–	–	17.7	9.1	–
MLP 84-II-1-65	–	–	–	–	–	–	15.8	–	–

MLP 84-II-1-124'	62.4	64.4	–	26.0	–	13.4	18.6	8.0	2.4
MLP 83-V-20-41	–	–	–	22.4	–	–	–	–	–
MLP 83-V-20-34	–	–	–	25.2	–	–	–	–	–
Palaeeudyptes sp.									
IB/P/B-0221	–	–	>38.1	–	–	–	–	13.3	–
IB/P/B-0268	–	–	–	–	–	–	–	10.5	–
IB/P/B-0288	>60.0	>60.0	–	–	–	–	–	–	–
IB/P/B-0290	–	–	>34.5	–	–	–	–	11.0	–
Archaeospheniscus wimani									
IB/P/B-0284	–	–	–	–	–	–	–	7.6	–
IB/P/B-0289	–	–	–	–	–	10.3	14.9	–	–
IB/P/B-0491	52.4	>52.6	>22.6	23.4	–	10.1	13.5	7.5	2.24
MLP 91-II-4-173	–	–	19.3	17.5	–	–	–	5.4	–
MLP 90-I-20-24	44.2	45.5	22.6	20.7	27.1	10.1	11.5	6.9	2.14
Delphinornis larseni									
IB/P/B-0062	46.8	47.8	>19.7	16.8	24.7	8.9	10.3	8.3	2.78
IB/P/B-0280	–	–	–	–	22.4	8.3	10.3	–	–
IB/P/B-0299	–	–	–	16.8	–	–	10.8	8.1	–
IB/P/B-0547	44.3	45.6	–	14.8	–	8.1	10.6	7.1	2.99
IB/P/B-0548	42.3	43.5	–	15.7	22.1	8.1	11.0	7.2	2.69
MLP 84-II-1-79	48.1	48.9	18.4	15.5	–	9.0	12.0	7.6	3.1
MLP 91-II-4-174	47.7	48.6	–	17.0	22.8	8.5	11.3	7.9	2.81
MLP 83-V-20-5	49.7	51.0	19.5	17.4	23.3	8.8	11.4	–	2.86
Delphinornis gracilis sp. n.									
IB/P/B-0279a	40.6	41.5	16.5	13.6	19.0	7.1	8.8	6.5	2.98
IB/P/B-0492	–	–	–	14.6	–	–	–	6.7	–
Delphinornis arctowskii sp. n.									
IB/P/B-0484	38.9	40.2	>17.3	16.0	22.1	7.8	10.6	7.3	2.43
MLP 93-X-1-92	42.8	43.8	–	17.1	–	8.5	10.6	–	2.5
Delphinornis sp.									
IB/P/B-0068	–	–	–	15.5	–	7.5	11.1	–	–
IB/P/B-0282	–	–	>15.7	–	–	–	–	7.3	–
IB/P/B-0283	45.6	46.1	>15.1	14.7	–	6.6	9.7	6.5	–
MLP 93-X-1-155	–	–	16.6	13.7	–	–	–	5.3	–
MLP 88-I-1-353	38.1	39.1	–	–	–	–	9.0	–	–
Mesetaornis polaris sp. n.									
IB/P/B-0278	48.6	49.6	>18.6	16.1	22.6	8.2	11.5	6.3	3.02
Mesetaornis sp.									
IB/P/B-0279b	–	–	–	–	–	7.7	9.8	–	–
?*Mesetaornis* sp.									
MLP 88-I-1-484	–	–	–	–	–	–	10.4	–	–
Marambiornis exilis sp. n.									
IB/P/B-0490	45.2	46.0	>17.5	15.0	20.4	7.0	10.5	6.1	3.01
MLP 93-X-1-111	45.4	47.2	18.2	15.0	21.3	8.0	10.0	6.3	3.03

Systematic paleontology

<div align="center">

Class Aves
Order Sphenisciformes Sharpe, 1891
Family Spheniscidae Bonaparte, 1831
Anthropornis Wiman, 1905
</div>

1905a. *Anthropornis* n. g.; Wiman: p. 249.

1905a. *Pachypteryx* n. g.; Wiman: p. 250.

Type species: *Anthropornis nordenskjöldii* Wiman, 1905 (by monotypy).

Revised diagnosis. — Robust tarsometatarsus with a very characteristic, pronounced convexity on margo medialis (no convexity on margo medialis in *Palaeeudyptes*, *Archaospheniscus*, *Delphinornis*, *Mesetaornis* and *Marambiornis*). Foramen vasculare proximale laterale considerably smaller and more proximal than its medial counterpart or absent (reverse situation in *Palaeeudyptes*), and foramina vascularia proximalia separated by a quite wide proximal portion of metatarsale III. Moreover, the proximal end of metatarsale III clearly lowered in relation to metatarsalia II and IV. Tuberositas musculi tibialis cranialis wide, but less marked than in *Palaeeudyptes*. Crista medialis hypotarsi, subdivided (undivided in *Palaeeudyptes*).

Remarks. — Wiman (1905a, b) did not give a separate diagnoses for genus and species in *Anthropornis* and *Pachypteryx*. His work was limited to description of the holotype specimens of, as he thought, different genera. Later examinations of the material (Ameghino 1905, Lambrecht 1933, Simpson 1946, 1971a) focused mainly on the size and shape of the bone, and the size and location of foramina vascularia proximalia as well as the characteristic convexity on margo medialis. Though Simpson (1946) noted that *Anthropornis* was the most characteristic genus described by Wiman (1905a, b), the separate status of *Anthropornis* and *Pachypteryx* was maintained until Brodkorb (1963). Incorporation of *Pachypteryx* into *Anthropornis* was widely accepted thereafter (Simpson 1971a, 1975, 1976; Cione *et al*. 1977), and also was confirmed in our analysis. We revised these descriptions and provide a differential, comprehensive and explicit diagnosis with some important details of the morphology of the proximal end and dorsal surface of the tarsometatarsus (see previous section).

<div align="center">

Anthropornis nordenskjoeldi Wiman, 1905
(Fig. 5)
</div>

1905a. *Anthropornis Nordenskjöldii* n. g. et n. sp.; Wiman: p. 249, pl. XII, fig. 6.

Revised diagnosis. — Tarsometatarsus clearly larger than in *Anthropornis grandis* (Table 1), but differs by tuberositas musculi tibialis cranialis somewhat more distal in relation to foramen vasculare proximale mediale. Foramen v. p. laterale very small if present, and cotyla medialis higher and crista medialis hypotarsi more prominent than in *A. grandis.*
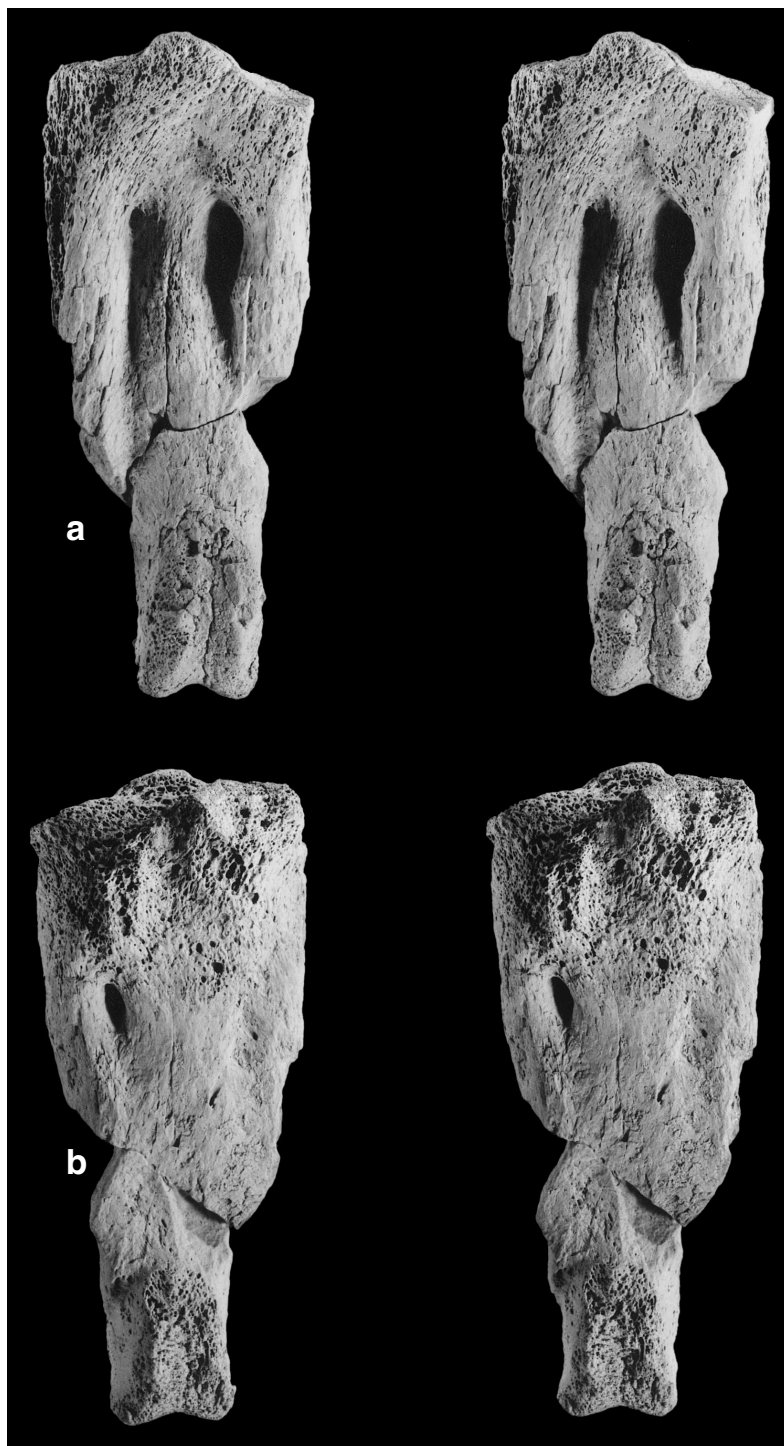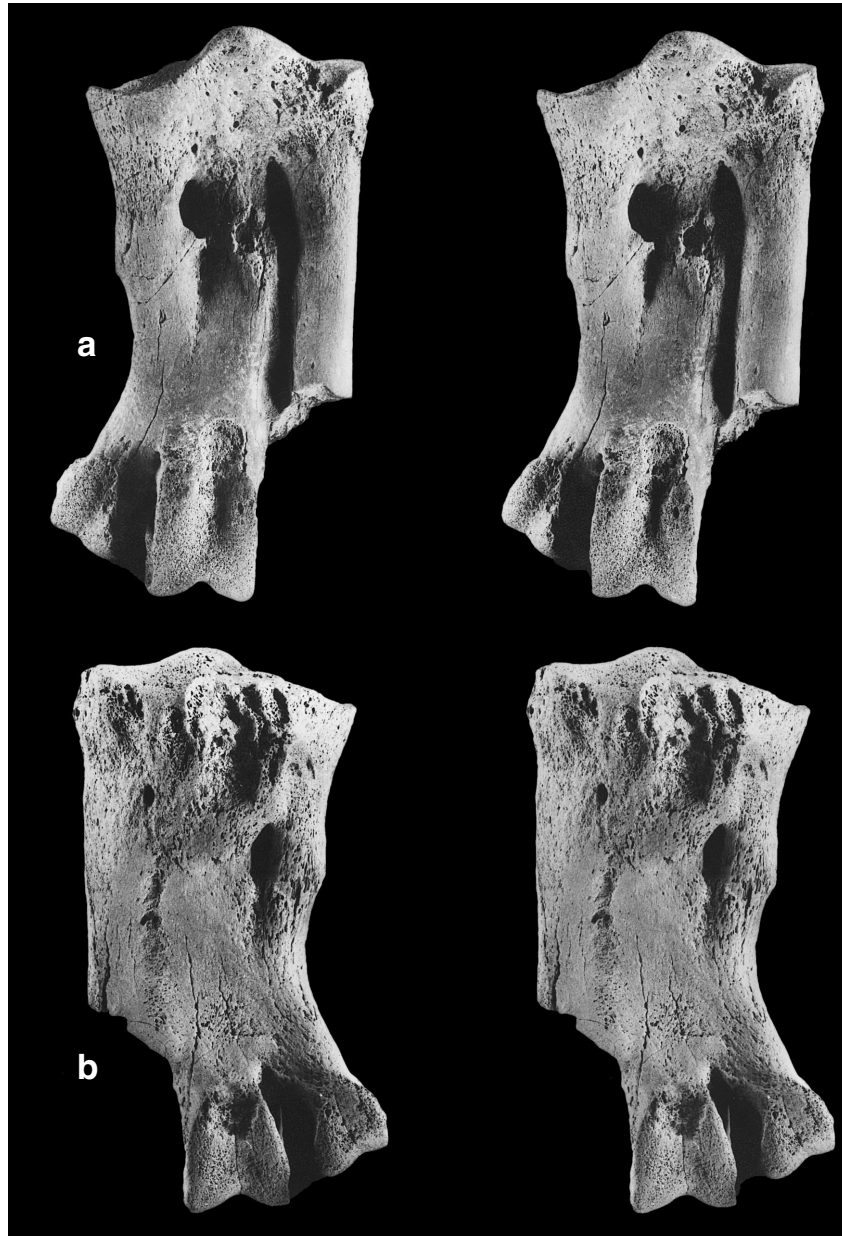
Fig. 5. Right tarsometatarsus of *Anthropornis nordenskjoeldi* Wiman, 1905; specimen IB/P/B-0070. Stereopairs: **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7 (scree).

Material. — Six specimens (for measurements see Table 1).

IB/P/B-0070 – incomplete and eroded, lacking trochleae II and IV as well as major parts of metatarsalia II and IV.

IB/P/B-0085a and b – two, distal and central, fragments of probably one bone.

IB/P/B-0287 – incomplete central shaft.

MLP 84-II-1-7 – incomplete, lacking lateral side and trochlea II.

MLP 83-V-20-50 – incomplete proximal end.

MLP 83-II-1-19 – incomplete and eroded proximal end.

Description. — Tarsometatarsus in the size range of Group 3 (probably also Group 1 and 2) of Wiman (1905b). Foramen v. p. mediale opened laterally (in relation to the main axis of the bone) or just distal to crista medialis hypotarsi. Sulcus longitudinalis dorsalis lateralis shallow, reaches incisura intertrochlearis. Sulcus l. d. medialis pronounced only at its proximal portion. Fossae infracotylaria dorsalia poorly developed.

Remarks. — *Anthropornis nordenskjoeldi* is the largest known fossil penguin from Seymour Island (*e.g.* Ameghino 1905). As some of diagnostic features for the tarsometatarsus listed by Wiman (1905a, b) were incorporated into the generic description (see "Remarks" at generic level), we provide a new specific diagnosis.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm7.

Anthropornis grandis (Wiman, 1905)
(Fig. 6)

1905a. *Pachypteryx grandis* n. g. et n. sp.; Wiman: p. 250, pl. XII, fig. 3.
1963. *Anthropornis grandis*; Brodkorb: p. 234.

Revised diagnosis. — Tarsometatarsus clearly smaller than in *Anthropornis nordenskjoeldi* (Table 1). Tuberositas musculi tibialis cranialis situated somewhat more proximally in relation to foramen vasculare proximale mediale than in *A. nordenskjoeldi*. Foramen vasculare proximale laterale tends to be better developed, cotyla medialis lower, and crista medialis hypotarsi less prominent than in *A. nordenskjoeldi*.

Material. — 10 specimens (for measurements see Table 1).

IB/P/B-0483 – incomplete, lacking trochlea IV and adjacent fragment of metatarsale.

MLP 83-V-20-84 – incomplete, lacking medial and lateral margins with trochleae.

MLP 95-I-10-142 – incomplete, lacking trochlea II with adjacent fragment of metatarsale.

MLP 94-III-15-178 – incomplete, lacking trochlea II and major parts of lateral margin with trochlea.

Other, less complete specimens:

MLP 84-II-1-12, MLP 86-V-30-19, MLP 84-III-1-176, MLP 84-II-1-66, MLP 95-I-10-156, MLP 93-X-1-149.

Fig. 6. Left tarsometatarsus of *Anthropornis grandis* (Wiman, 1905); specimen IB/P/B-0483. Stereo-pairs: **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7 (scree).

Description. — Tarsometatarsus in the size range of Group 4 of Wiman (1905b). Foramen v. p. mediale opened laterally (in relation to the main axis of the bone) or just distal to crista medialis hypotarsi. Sulcus longitudinalis dorsalis lateralis moderately deep, reaches incisura intertrochlearis. Sulcus l. d. medialis pronounced

only at its proximal portion. Fossae infracotylaria dorsalia poorly developed. Area intercotylaris large but shallow, connected with sulcus ligamentosus. The presence of a hollow just distal to trochlea III on the dorsal surface.

Remarks. — Wiman (1905a, b) comparing tarsometatarsi of *Anthropornis nordenskjoeldi* and "*Pachypteryx*" *grandis*, noted that in the latter specimen trochlea II was more strongly divergent, the bone above intermetatarsal foramina was not as thick, and the bone was not so strongly excavated anterior to the "intercondyloid tuberosity". Simpson (1971a) criticised these remarks and only stated that the bone was clearly smaller than in *A. nordenskjoeldi*. As we found several new diagnostic features, the revision of the previous diagnose was necessary.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm4, Telm5 and Telm7 (most frequently).

<p style="text-align:center">*Anthropornis* sp.</p>

Material. — Two specimens (for measurements see Table 1).
IB/P/B-0293 – incomplete, only shaft preserved.
MLP 84-II-1-9 – incomplete, lacking trochlea III, and II with adjacent fragment of metatarsale.

Remarks. — IB/P/B-0239, though unquestionably having features of tarsometatarsi of *Anthropornis* (convexity on margo medialis, features of preserved parts of intermetatarsal sulci and foramina), is too poorly preserved to assign it to any known species. MLP 84-II-1-9 also resembles other tarsometatarsi of this genus, but its size is too small and comparable to *Palaeeudyptes gunnari* rather than *Anthropornis grandis*.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm7.

<p style="text-align:center">*Palaeeudyptes* Huxley, 1859</p>

1859. *Palaeeudyptes*; Huxley: p. 675.
1905a. *Eosphaeniscus* n. g.; Wiman: p. 250.
Type species: *Palaeeudyptes antarcticus* Huxley, 1859 (by monotypy).

Revised diagnosis. — Massive tarsometatarsus with clearly concave margo medialis. Differs from *Anthropornis* in having foramen vasculare proximale laterale always present that is larger and often more distal than its medial counterpart. Sulcus longitudinalis dorsalis lateralis very deep proximally and dramatically weakening towards incisura intertrochlearis, a feature not observed in *Archaeospheniscus*. Surface of tuberositas musculi tibialis cranialis relatively smaller, though more pronounced, than in *Anthropornis* and *Archaeospheniscus*. The presence of a V-shaped groove in the proximal part of margo medialis (at least in bones from Seymour Island).

Remarks. — Huxley (1859) gave only a detailed description of the holotype specimen of *Palaeeudyptes antarcticus* from New Zealand. Wiman (1905a, b) also did not give a separate diagnosis of his genus *Eosphaeniscus* from Seymour Island and

limited his work to description of the holotype of *E. gunnari*. These two genera were synonimized by Simpson (1971a) who directly compared both holotype specimens and found no basis for separating the taxa. His diagnosis referred to the shape of the bone and features of foramina and sulci. Tarsometatarsi referred to this genus are the most numerous in both the Argentine and Polish collections. This rich material enabled revision of the generic diagnosis.

Palaeeudyptes klekowskii Myrcha, Tatur and del Valle, 1990
(Fig. 7)

1990. *Palaeeudyptes klekowskii* sp. nov.; Myrcha, Tatur and del Valle: p. 197–199, figs 2–4.

Revised diagnosis. — Tarsometatarsus massive, larger than in *Palaeeudyptes gunnari* (Table 1). Margo medialis relatively less concave than in *P. gunnari*; X/Y>7 (where X-measurement C–D, Y-distance between a culmination point of the concavity of margo medialis and its theoretical position on the chord linking measurement points "C" and "D").

Material. — 32 specimens characterised by a different degree of preservation (for measurements see Table 1).

The holotype: IB/P/B-0065 (Myrcha, Tatur and del Valle 1990) – incomplete, lacking lateral shaft, proximal end strongly eroded.

Paratypes (Myrcha, Tatur and del Valle 1990):
IB/P/B-0061 – incomplete, lacking lateral shaft.
IB/P/B-0081 – incomplete, lacking distal parts of metatarsalia with trochleae, strongly eroded.
IB/P/B-0093 – incomplete, lacking portion of proximal end and metatarsale IV with trochlea.
IB/P/B-0101 – incomplete, lacking portion of metatarsale II with trochlea, medial and lateral fragments of proximal end, strongly eroded.
IB/P/B-0142 – incomplete, lacking metatarsale IV and trochleae II, IV as well as portion of proximal end.

Other well-preserved specimens:
IB/P/B-0485 – complete, slightly eroded.
MLP 93-X-1-142 – complete, hypotarsus slightly eroded.
MLP 84-II-1-78, MLP 84-II-1-124 – complete specimens.
MLP 94-III-15-20 – complete, hypotarsus eroded.

Other specimens:
IB/P/B-0077, IB/P/B-0276, IB/P/B-0281, IB/P/B-0285, IB/P/B-0486, IB/P/B-0545, IB/P/B-0546, MLP 93-X-1-63, MLP 93-X-1-6, MLP 84-II-1-5, MLP 84-II-1-76, MLP 93-X-1-106, MLP 93-X-1-108, MLP 84-II-1-49, MLP 94-III-15-4, MLP 78-X-26-18, MLP 94-III-15-18, MLP 93-X-1-65, MLP 83-V-30-15, MLP 83-V-30-16, MLP 83-V-30-17.

Description. — Tarsometatarsus in the size range of Group 4 and (rarely) 3 of Wiman (1905b). Sulcus l. d. medialis slight if present. Fossa infracotylaris dorsalis

Fig. 7. Left tarsometatarsus of *Palaeeudyptes klekowskii* Myrcha, Tatur and del Valle 1990; specimen IB/P/B-0485. Stereopairs: **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7, ZPAL 4.

medialis and its lateral counterpart present. All trochleae relatively massive. The plantar opening of foramen vasculare proximale mediale situated somewhat more medially in relation to the main axis of the bone than crista medialis hypotarsi. The foramen separated from wide sulcus hypotarsi by a small osseous ridge. Crista

medialis hypotarsi slopes steeply towards margo medialis. The proximal end of metatarsale III quite thin in most cases.

Remarks. — Myrcha, Tatur and del Valle (1990) gave a detailed description of the tarsometatarsus of *Palaeeudyptes klekowskii*. However, not all features mentioned by them are of diagnostic importance.

In fact, *P. klekowskii* closely resembles its smaller relative (*P. gunnari*), but the range of linear dimensions (the difference between extreme cases exceeds 20%) as well as the relative concavity of margo medialis distinguish the two taxa of *Palaeeudyptes* from Seymour Island. The analysis of more extensive material resulted in a revision of the earlier diagnosis.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm7.

Palaeeudyptes gunnari (Wiman, 1905)

(Fig. 8)

1905a. *Eosphaeniscus Gunnari* n. g. et n. sp.; Wiman: p. 250, pl. XII, fig. 5.

1971a. *Palaeeudyptes gunnari*; Simpson: p. 374, figs. 1C, 5.

Revised diagnosis. — Tarsometatarsus relatively massive, though smaller than in *Palaeeudyptes klekowskii* (Table 1). Margo medialis relatively more concave than in *P. klekowskii* – X/Y<7 (see previous diagnosis for explanations).

Material. — 29 specimens, different degree of preservation (for measurements see Table 1).

MLP 91-II-4-222 – complete.

IB/P/B-0072, IB/P/B-0112, IB/P/B-0277, IB/P/B-0487 – almost complete.

Incomplete:

IB/P/B-0124, IB/P/B-0286, IB/P/B-0294, IB/P/B-0295, IB/P/B-0296, IB/P/B-0541a, MLP 87-II-1-45, MLP 82-IV-23-6, MLP 94-III-15-16, MLP 82-IV-23-5, MLP 84-II-1-75, MLP 84-II-1-6, MLP 83-V-20-27, MLP 93-X-1-151, MLP 95-1-10-16, MLP 84-II-1-47, MLP 84-II-1-65, MLP 84-II-1-124', MLP 83-V-20-41, MLP 83-V-20-34, MLP 93-X-1-84, MLP 84-II-1-24, MLP 93-X-1-112, MLP 93-X-1-117.

Description. — Tarsometatarsus in the size range of Group 5 of Wiman (1905b). Other features as in *Palaeeudyptes klekowskii*.

Remarks. — In respect to its size *Palaeeudyptes gunnari* resembles *Palaeeudyptes antarcticus* from New Zealand and Australia, but differs from it in some morphological features. *P. antarcticus* has smaller foramen vasculare proximale laterale and cristae intermediae hypotarsi with the presence of an osseous ridge reaching margo medialis.

Description of a new taxon of *Palaeeudyptes* from Seymour Island (Myrcha, Tatur and del Valle 1990) necessitated re-examination of available material and revision of the preceding diagnosis of *P. gunnari.*

Fig. 8. Right tarsometatarsus of *Palaeeudyptes gunnari* (Wiman, 1905); specimen IB/P/B-0072. Stereopairs: **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7 (scree).

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm3, Telm5 and Telm7.

Palaeeudyptes sp.

Material. — 20 incomplete specimens.
IB/P/B-0221, IB/P/B-0268, IB/P/B-0288, IB/P/B-0290, MLP 84-II-1-2, MLP 87-II-1-97, MLP 93-X-1-120, MLP 84-II-1-177, MLP 84-II-1-80, MLP CX-60-2/4, MLP 83-V-20-42, MLP 93-X-1-25, MLP 84-II-1-231, MLP

90-I-20-316, MLP 90-I-20-315, MLP 93-X-1-150, MLP 93-X-1-152, MLP 95-I-10-135, MLP 94-III-15-179, MLP 78-X-26-6.

Remarks. — These specimens possess features of *Palaeeudyptes*: the size and position of intermetatarsal foramina, morphology of intermetatarsal sulci, and width of proximal end of metatarsale III. Moreover, some of them have unique features. They are, however, too poorly preserved to assign them to any known species.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm7.

Archaeospheniscus Marples, 1952

1952. *Archaeospheniscus* gen. nov.; Marples: p. 40.

1953. *Notodyptes* gen. nov.; Marples: p. 11.

Type species: *Archaeospheniscus lowei* Marples, 1952.

Revised diagnosis. — Clearly distinguishable tarsometatarsus of moderate size, because of a small degree of elongation in shaft. Moreover, it differs from *Anthropornis* and *Palaeeudyptes* in having both foramina vascularia proximalia well developed and larger to at least moderate in size. Tuberositas musculi tibialis cranialis large but less prominent than in *Palaeeudyptes*. Sulcus longitudinalis dorsalis lateralis wide, but probably without (characteristic for *Palaeeudyptes*) clear weakening in a distal part.

Remarks. — Marples (1952) did not list diagnostic features of tarsometatarsus. The features listed by Simpson (1971b) also did not refer to this bone. In his later work (Simpson 1971a) synonimized *Archaeospheniscus* with *Notodyptes*, the latter taxon described by Marples (1953) and known from Seymour Island. Simpson (1971a) stressed, as did Marples (1953), that this genus is distinct by the shape of the tarsometatarsus and features of intermetatarsal foramina. The tarsometatarsus of the type species is not known and all diagnostic features of this bone were derived from tarsometatarsi of *A. lopdelli* (New Zealand species) and *A. wimani* (Seymour Island species) and we revised the diagnosis here.

Archaeospheniscus wimani (Marples, 1953)
(Fig. 9)

1953. *Notodyptes wimani* gen et sp. nov.; Marples: p. 11, pl. II, fig. 2.

1971a. *Archaeospheniscus wimani*; Simpson: p. 380, fig. 1D.

Revised diagnosis. — Tarsometatarsus smaller than in *Archaeospheniscus lopdelli* and probably *Archaeospheniscus lowei* (species known from New Zealand). The elongation index small, though bigger than in *A. lopdelli*. Trochlea II relatively less massive than in *A. lopdelli*. The presence of a characteristic concavity in the middle part of margo medialis.

Material. — Five specimens (for measurements see Table 1).

IB/P/B-0284 – incomplete, lacking lateral and distal portions of metatarsalia with trochleae.
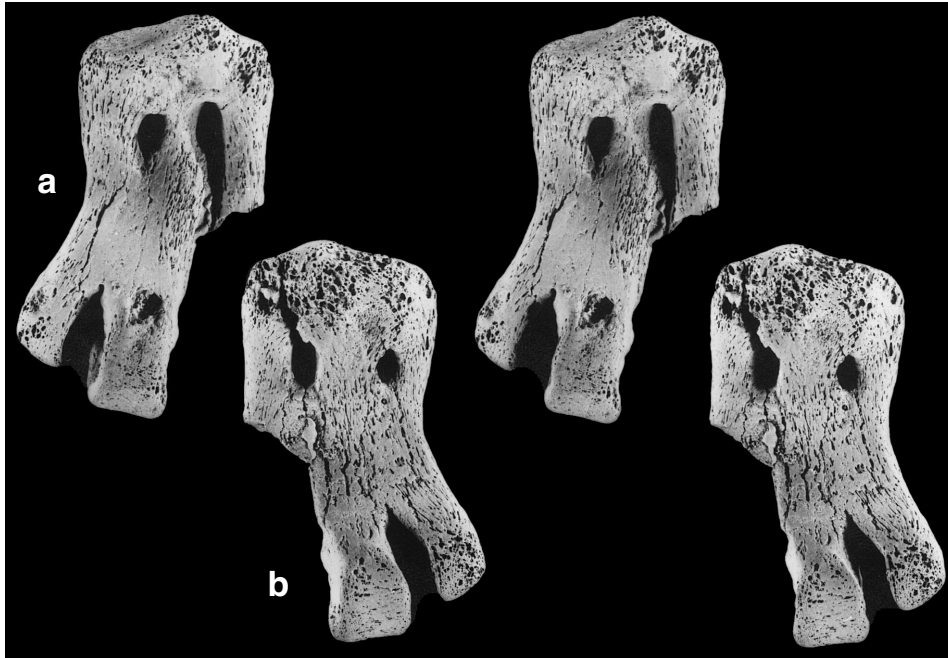
Fig. 9. Left tarsometatarsus of *Archaeospheniscus wimani* (Marples, 1953); specimen IB/P/B-0491. Stereopairs: **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7, ZPAL 4.

IB/P/B-0289 – incomplete, metatarsale II with trochlea and distal end of metatarsale III with trochlea preserved.

IB/P/B-0491 – incomplete, lacking distal end of metatarsale IV with trochlea, strongly eroded.

MLP 90-I-20-24 – complete, hypotarsus slightly eroded.

MLP 91-II-4-173 – incomplete, lacking trochlea III and IV with adjacent fragment of metatarsale.

Description. — Tarsometatarsus in the size range of Group 6 of Wiman (1905b). Metatarsale IV straight. Foramen vasculare proximale laterale larger than its medial counterpart, the separating fragment of metatarsale III wide or moderately wide. Foramen vasculare distale present. Sulcus longitudinalis dorsalis medialis slight if present. Eminentia intercondylaris relatively wide at its base. The plantar opening of foramen vasculare proximale mediale situated distally or somewhat more medially (in relation to the main axis of the bone) than crista medialis hypotarsi. In the latter case foramen separated from sulcus hypotarsi by a small osseous ridge. The presence of distinct pits just proximal to trochlea III and on the dorsal surface of trochlea II (near margo medialis).

Remarks. — *Archaeospheniscus wimani* is the smallest species in this genus. The comparison of dimensions of the holotype specimen (housed at the British Mu-

seum) accounts for the presence of considerable interspecific variability *e.g.* our specimen IB/P/B-0491 is c. 16 % longer than the holotype (measurement after Marples (1953)), but the difference could be exaggerated by erosion of the latter bone (compare Marples 1953: plate II, fig. 2) or measurement error.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm5 and Telm7.

<div align="center">

Delphinornis Wiman, 1905

</div>

1905a. *Delphinornis* n. g.; Wiman: p. 250–251.

Type species: *Delphinornis larsenii* Wiman, 1905.

Revised diagnosis. — The small tarsometatarsus differing from bones of other species of small penguins in having plantar opening of foramen vasculare proximale mediale situated more laterally (in relation to the main axis of the bone) than crista medialis hypotarsi or just distal to the crista (foramen situated more medially than crista medialis hypotarsi in *Mesetaornis* and *Marambiornis*). Furthermore, the following features are not present in *Mesetaornis* and *Marambiornis*. Cristae intermediae hypotarsi not separated by a groove. Crista medialis hypotarsi sloping towards margo medialis.

Remarks. — Description of new species in this genus, and new genera of small penguins, necessitated revision of the diagnosis.

<div align="center">

Delphinornis larseni Wiman, 1905

(Fig. 10)

</div>

1905a. *Delphinornis Larsenii* n. g. et n. sp.; Wiman: p. 250–251, pl. XII, fig. 1.

Revised diagnosis. — Size relatively large (Table 1). The degree of elongation variable, but shaft more elongated than in *Delphinornis arctowskii*. Crista medialis hypotarsi sloping towards margo medialis and a bone plane form a relatively sharp angle (angles larger substantially in *D. arctowskii* and *D. gracilis*). It also differs from *D. gracilis* in having all trochleae massive, eminentia intercondylaris wide and moderately prominent, and foramen vasculare distale well developed.

Material. — Eight specimens (for measurements see Table 1).

IB/P/B-0062 – complete.

IB/P/B-0280 – incomplete, lacking proximal end and portions of metatarsalia III and IV, dorsal aspect of foramen vasculare proximale mediale preserved.

IB/P/B-0299 – incomplete, lacking proximal end and trochlea II and IV, trochlea III partly broken.

IB/P/B-0547 – incomplete and eroded, lacking trochlea II.

IB/P/B-0548 – incomplete, strong erosion of proximal part and trochleae.

MLP 83-V-20-5 – complete, partly in matrix.

MLP 91-II-4-174 – almost complete, proximal end strongly eroded.

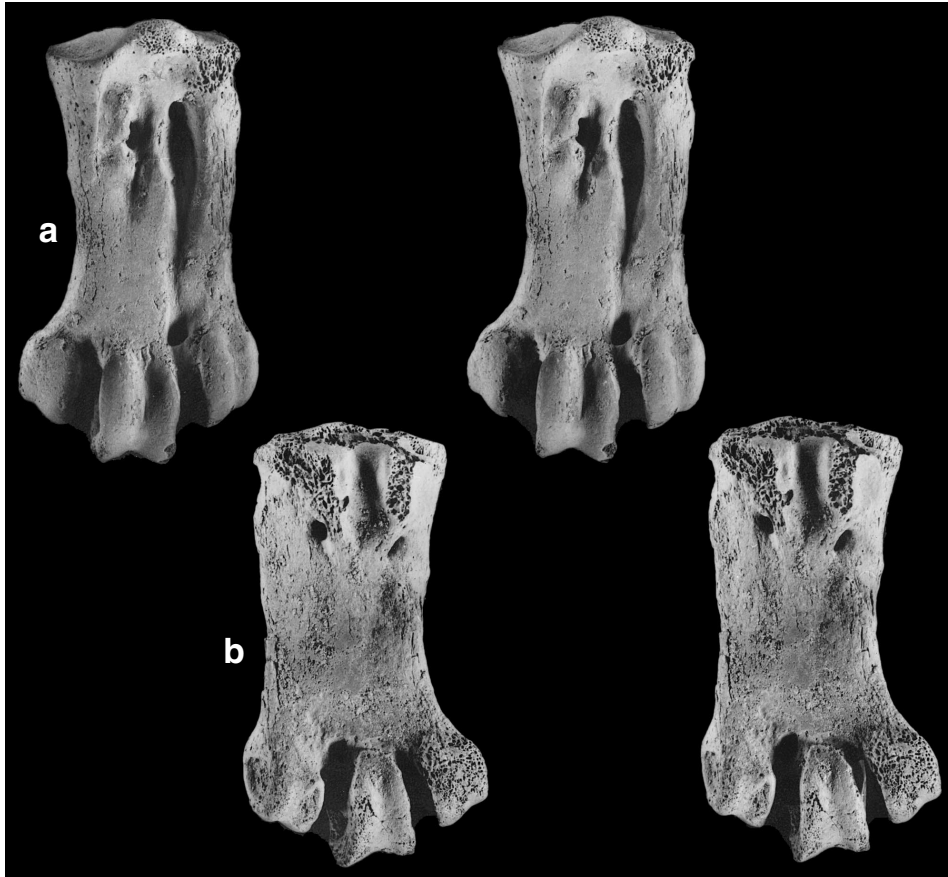MLP 84-II-1-79 – incomplete, lacking trochlea II.

Fig. 10. Left tarsometatarsus of *Delphinornis larseni* Wiman, 1905; specimen IB/P/B-0062. Stereopairs: **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7 (scree).

Description. — Tarsometatarsus in the size range of Group 7 of Wiman (1905b). The shape of tuberositas musculi tibialis cranialis variable, elongated to sub-elliptical. Foramen vasculare proximale laterale smaller than its medial counter-part. Sulcus longitudinalis dorsalis medialis short and shallow. Sulcus l. d. lateralis well developed. Area intercotylaris large and shallow (probably connected with sulcus ligamentosus). Foramen vasculare distale clearly isolated from incisura intertrochlearis lateralis by two osseous bridges (dorsal and plantar ones, dorsal bridge wider).

Remarks. — The number of available specimens and description of two addi-tional taxa within the genus necessitated revision of the diagnosis.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm5 and Telm7.
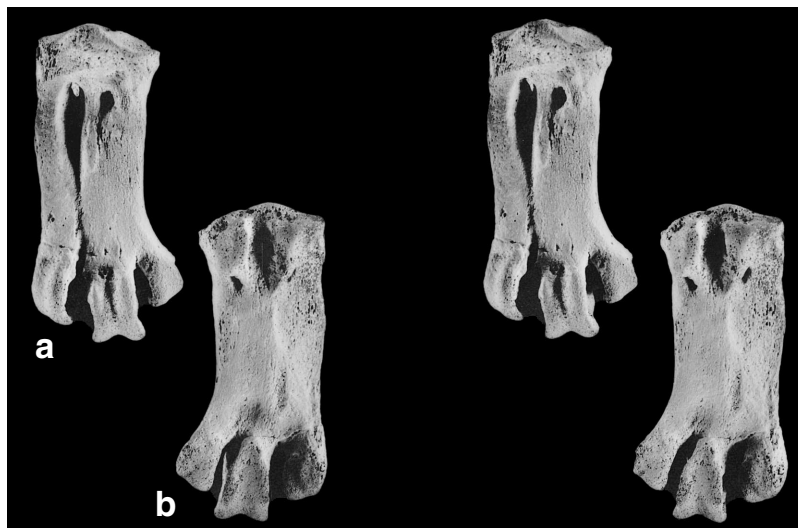
Fig. 11. Right tarsometatarsus of *Delphinornis gracilis* sp. n.; holotype specimen IB/P/B-0279a. Stereopairs: **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7 (scree).

Delphinornis gracilis sp. n.
(Fig. 11)

Holotype: IB/P/B-0279a, complete right tarsometatarsus.

Paratype: IB/P/B-0492, incomplete left tarsometatarsus, lacking proximal and distal ends.

Type horizon: Telm7, La Meseta Formation, Eocene.

Type locality: Seymour Island, Antarctic Peninsula.

Etymology: Latin for "slender".

Diagnosis. — Tarsometatarsus small and slender (Table 1). Crista medialis hypotarsi sloping towards margo medialis, but the slope steeper than in *Delphinornis larseni*. It also differs from *D. larseni* in having eminentia intercondylaris narrow and prominent, and trochleae not massive. Foramen vasculare distale poorly developed in comparison to *D. larseni*.

Description. — Tarsometatarsus in the size range of Group 8 of Wiman (1905b). Tuberositas musculi tibialis cranialis small and narrow. Foramen vasculare proximale laterale slightly longer and narrower than its medial counterpart, the plantar opening of the latter situated at margo medialis. Area intercotylaris deep and elongated, probably connected with sulcus ligamentosus. Sulcus longitudinalis dorsalis lateralis clearly widened proximally, gradually weakens towards incisura intertrochlearis with its medial counterpart slight if present. Fossa supratrochlearis distinct. The presence of an elongate hollow proximo-medial to this fossa. Fossa parahypotarsalis lateralis slight if present.

Remarks. — This species is the smallest within the genus and perhaps even within the entire fossil penguin fauna from Seymour Island. This general feature is the

most striking of the diagnostic characters. The holotype is well preserved and clearly differs from tarsometatarsi of other taxa of *Delphinornis*.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm7.

Delphinornis arctowskii sp. n.
(Fig. 12)

Holotype: IB/P/B-0484, complete left tarsometatarsus.
Paratype: MLP 93-X-1-92, incomplete left tarsometatarsus, lacking trochlea IV.
Type horizon: Telm7, La Meseta Formation, Eocene.
Type locality: Seymour Island, Antarctic Peninsula.
Etymology: after Henryk Arctowski (1871–1958), Polish explorer of Antarctica.

Diagnosis. — The shortest and least elongated, though relatively robust, tarsometatarsus within the genus (Table 1). Crista medialis hypotarsi, unlike in congenerics, slopes quite steeply towards margo medialis. The more lateral (in relation to the main axis of the bone) dorsal frame of foramen vasculare proximale mediale forms an osseous crista, the feature not observed in other species of *Delphinornis*.

Description. — Tarsometatarsus in the size range of Group 7 or 8 of Wiman (1905b). The foramen vasculare proximale mediale slightly larger than its lateral counterpart. The proximal widening of sulcus longitudinalis dorsalis lateralis less marked than in *Delphinornis gracilis*. Sulcus l. d. medialis short and shallow. Area intercotylaris deep, oval in shape and closed (without connectivity with sulcus ligamentosus). Tuberositas musculi tibialis cranialis subelliptical in shape, smaller than in *Delphinornis larseni*. Fossa supratrochlearis plantaris very slight. Trochleae relatively robust. Foramen vasculare distale separated from incisura intertrochlearis by a small osseous bridge (broken in the holotype).

Fig. 12. Left tarsometatarsus of *Delphinornis arctowskii* sp. n.; holotype specimen IB/P/B-0484. **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7, ZPAL 4.

Remarks. — The type specimens share a unique combination of features. The shape of the bones together with the character of crista medialis hypotarsi separate them from other species of *Delphinornis*. In respect to its size and proportions, the holotype resembles that of *Korora oliveri* from New Zealand (compare Marples 1952, p. 43), but differs from this species in several morphological features (*e.g.* in having foramen vasculare distale and massive trochleae).

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm7.

Delphinornis sp.

Material. — Five poorly preserved specimens: IB/P/B-0068, IB/P/B-0282, IB/P/B-0283; MLP 88-I-1-353, MLP 93-X-1-155.

Remarks. — These specimens possess features of tarsometatarsi of *Delphinornis* (*e.g.* the location of the plantar opening of foramen vasculare proximale mediale), but they are too poorly preserved (broken and/or strongly eroded) to assign them to any known species.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm5, Telm6 and Telm7.

Mesetaornis gen. n.

Type species: *Mesetaornis polaris* gen. et sp. n.
Etymology: From *ornis*, Greek, referring to "a bird from the Meseta".

Diagnosis. — Strongly elongated tarsometatarsus with quite large foramen vasculare proximale mediale (smaller in *Delphinornis* and *Marambiornis*). Differs from *Delphinornis* in having the plantar opening of the foramen situated more medially (in relation to the main axis of the bone) than crista medialis hypotarsi. Tarsometatarsus differs from *Marambiornis* in having cristae intermediae hypotarsi separated by a relatively narrow groove.

Remarks. — Morphology of hypotarsus, and position of the plantar opening of foramen vasculare proximale mediale in specimens assigned to this genus somewhat resemble features observed in tarsometatarsi of *Marambiornis*. However, considered with other characters *Mesetaornis* is distinct compared to tarsometatarsi of other genera of small penguins (i.e. *Delphinornis* and *Marambiornis*). The diagnostic importance of features of intermetatarsal foramina for both fossil and Recent penguins is widely accepted (Marples 1953, Simpson 1971a, Zusi 1975).

Mesetaornis polaris sp. n.
(Fig. 13)

Holotype: IB/P/B-0278, nearly complete left tarsometatarsus.
Type horizon: Telm7, La Meseta Formation, Eocene.
Type locality: Seymour Island, Antarctic Peninsula.
Etymology: From the Latin *polaris* – polar.

Fig. 13. Left tarsometatarsus of *Mesetaornis polaris* gen. et sp. n.; holotype specimen IB/P/B-0278. Stereopairs: **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7 (scree).

Diagnosis. — As for the genus.

Description. — Tarsometatarsus small (Table 1), in the size range of Group 7 (perhaps also 8) of Wiman (1905b). The presence of fossa parahypotarsalis lateralis, formed by a slight projection of margo lateralis. Foramen vasculare proximale laterale clearly smaller and more proximal than its medial counterpart. Sulcus longitudinalis dorsalis lateralis long (reaches foramen vasculare distale) and well developed. Sulcus l. d. medialis slight. Eminentia intercondylaris relatively wide at its base. Crista medialis hypotarsi narrow and sharp. The concavity of margo medialis weakly marked. Tuberositas musculi tibialis cranialis slight. Foramen vasculare distale opened distally.

Occurence. — Seymour Island, La Meseta Formation (Eocene), Telm7.

Mesetaornis sp.
(Fig. 14)

Material. — IB/P/B-0279b – incomplete, lacking metatarsale IV with trochlea, and major portion of the proximal end.

Description. — Tarsometatarsus small, in the size range of Group 8 of Wiman (1905b). Foramen vasculare distale and foramen vasculare proximale mediale well developed. Trochlea II relatively robust. Sulcus longitudinalis dorsalis medialis slight. The concavity of margo medialis marked weakly.
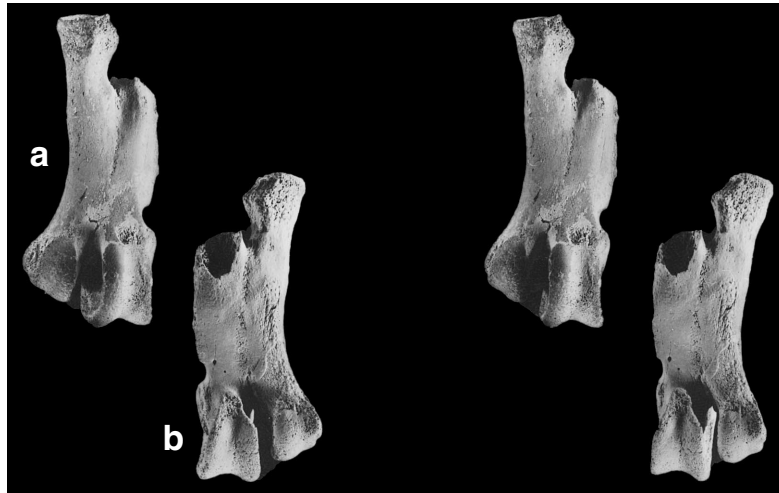
Fig. 14. Left tarsometatarsus of *Mesetaornis* sp.; specimen IB/P/B-0279b. Stereopairs: **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7 (scree).

Remarks. — This poorly preserved specimen shares diagnostic features with *Mesetaornis polaris*, but differs in smaller size, degree of elongation, and better development of foramen vasculare distale. Crista medialis hypotarsi appears shifted more towards margo lateralis than in tarsometatarsi of *M. polaris*. The degree of preservation of this specimen, however, does not support the establishment of a new species of *Mesetaornis*.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm7.

?*Mesetaornis* sp.

Material. — MLP 88-I-1-484 – incomplete, lacking lateral shaft, most of proximal end and trochlea II (for measurements see Table 1).

Description. — Tarsometatarsus small, in the size range of Group 7 of Wiman (1905b). Foramen vasculare proximale mediale well developed.

Remarks. — This specimen is very poorly preserved and in the degree of development of medial intermetatarsal foramen, it resembles tarsometatarsi of *Mesetaornis*.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm5.

Marambiornis gen. n.

Type species: *Marambiornis exilis* gen. et sp. n.

Etymology: From *ornis*, Greek, referring to "a bird from Marambio Island".

Diagnosis. — Strongly elongated tarsometatarsus with small foramina vascularia proximalia (larger in Mesetaornis). Differs from *Delphinornis* in having the plan-
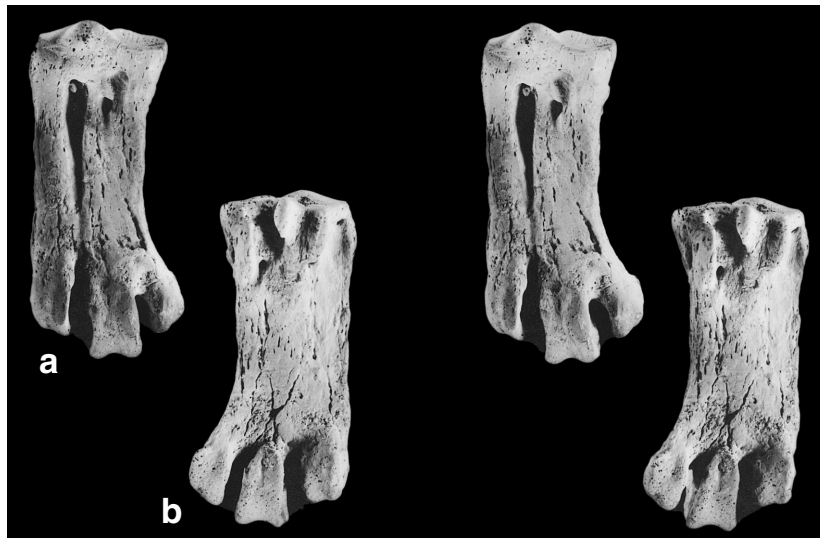
Fig. 15. Right tarsometatarsus of *Marambiornis exilis* gen. et sp. n.; holotype specimen IB/P/B–0490. Stereopairs: **a** – dorsal aspect, × 1; **b** – plantar aspect, × 1. La Meseta Formation, Telm7, ZPAL 4.

tar opening of foramen vasculare proximale mediale more medial (in relation to the main axis of the bone) than crista medialis hypotarsi. Cristae intermediae hypotarsi prominent and, unlike in *Delphinornis*, separated by a groove (clearly wider than in *Mesetaornis*). Sulcus hypotarsi narrower than in *Mesetaornis*.

Remarks. — see "Remarks" section of previously described genus.

Marambiornis exilis sp. n.
(Fig. 15)

Holotype: IB/P/B-0490, complete right tarsometatarsus.

Paratype: MLP 93-X-1-111, complete right tarsometatarsus, hypotarsus slightly eroded.

Type horizon: Telm7, La Meseta Formation, Eocene.

Type locality: Seymour Island, Antarctic Peninsula.

Etymology: From *exilis*, Latin, meaning "thin" and "narrow".

Diagnosis. — As for the genus.

Description. — Tarsometatarsus small (Table 1), in the size range of Group 7 of Wiman (1905b). Foramen vasculare distale open and connected with incisura intertrochlearis. Fossa parahypotarsalis lateralis conspicuous and very proximal. Eminentia intercondylaris narrow and prominent. Both intermetatarsal foramina small. Foramen vasculare proximale laterale larger and more proximal than its medial counterpart. Sulcus longitudinalis dorsalis lateralis shallow or moderate in depth, gradually weakens towards incisura intertrochlearis. Both dorsal proximal fossae present though shallow. Sulcus longitudinalis dorsalis medialis slight if

present. Trochlea IV clearly twisted but not diverged laterally. Tuberositas musculi tibialis cranialis narrow and elongated, moderately developed. Crista medialis hypotarsi well developed, but not as prominent as cristae intermediae hypotarsi.

Occurence. — Seymour Island, La Meseta Formation (Eocene), Telm7.

Table 2

Stratigraphic location of samples.

Taxon	Specimen	Unit	Locality
Anthropornis nordenskjoeldi	IB/P/B-0070	Telm7	Scree
Anthropornis nordenskjoeldi	IB/P/B-0085a	Telm7	Scree
Anthropornis nordenskjoeldi	IB/P/B-0287	Telm7	Scree
Anthropornis nordenskjoeldi	MLP 84-II-1-7	Telm7	DPV 14/84
Anthropornis nordenskjoeldi	MLP 83-V-20-50	Telm7	DPV 14/84
Anthropornis nordenskjoeldi	MLP 84-II-1-19	Telm7	DPV 13/84
Anthropornis grandis	IB/P/B-0483	Telm7	Scree
Anthropornis grandis	MLP 83-V-20-84	Telm7	DPV 14/84
Anthropornis grandis	MLP 84-II-1-12	Telm7	DPV 13/84
Anthropornis grandis	MLP 86-V-30-19	Telm7	Pt. 3
Anthropornis grandis	MLP 84-III-1-176	Telm7	DPV 14/84
Anthropornis grandis	MLP 84-II-1-66	Telm7	DPV 13/84
Anthropornis grandis	MLP 95-I-10-142	Telm4	DPV 2/84
Anthropornis grandis	MLP 94-III-15-178	Telm5	IAA 1/90
Anthropornis grandis	MLP 95-I-10-156	Telm4	DPV 2/84
Anthropornis grandis	MLP 93-X-1-149	Telm7	DPV 13/84
Anthropornis sp.	IB/P/B-0293	Telm7	Scree
Anthropornis sp.	MLP 84-II-1-9	Telm7	DPV 13/84
Palaeeudyptes klekowskii	IB/P/B-0065	Telm7	Scree
Palaeeudyptes klekowskii	IB/P/B-0061	Telm7	Scree
Palaeeudyptes klekowskii	IB/P/B-0081	Telm7	Scree
Palaeeudyptes klekowskii	IB/P/B-0093	Telm7	Scree
Palaeeudyptes klekowskii	IB/P/B-0101	Telm7	Scree
Palaeeudyptes klekowskii	IB/P/B-0142	Telm7	Scree
Palaeeudyptes klekowskii	IB/P/B-0077	Telm7	Scree
Palaeeudyptes klekowskii	IB/P/B-0276	Telm7	Scree
Palaeeudyptes klekowskii	IB/P/B-0281	Telm7	ZPAL 4
Palaeeudyptes klekowskii	IB/P/B-0285	Telm7	Scree
Palaeeudyptes klekowskii	IB/P/B-0485	Telm7	ZPAL 4
Palaeeudyptes klekowskii	IB/P/B-0486	Telm7	Scree
Palaeeudyptes klekowskii	IB/P/B-0545	Telm7	–
Palaeeudyptes klekowskii	IB/P/B-0546	Telm7	–
Palaeeudyptes klekowskii	MLP 93-X-1-142	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 84-II-1-78	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 93-X-1-63	Telm7	DPV 10/84

Palaeeudyptes klekowskii	MLP 93-X-1-6	Telm7	DPV 10/84
Palaeeudyptes klekowskii	MLP 84-II-1-5	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 84-II-1-76	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 93-X-1-106	Telm7	DPV 12/84
Palaeeudyptes klekowskii	MLP 93-X-1-108	Telm7	DPV 12/84
Palaeeudyptes klekowskii	MLP 84-II-1-49	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 94-III-15-4	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 78-X-26-18	–	–
Palaeeudyptes klekowskii	MLP 94-III-15-18	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 93-X-1-65	Telm7	DPV 10/84
Palaeeudyptes klekowskii	MLP 94-III-15-20	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 83-V-30-15	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 83-V-30-16	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 83-V-30-17	Telm7	DPV 13/84
Palaeeudyptes klekowskii	MLP 84-II-1-124	–	–
Palaeeudyptes gunnari	IB/P/B-0072	Telm7	Scree
Palaeeudyptes gunnari	IB/P/B-0112	Telm7	Scree
Palaeeudyptes gunnari	IB/P/B-0277	Telm7	Scree
Palaeeudyptes gunnari	IB/P/B-0487	Telm7	ZPAL 4
Palaeeudyptes gunnari	IB/P/B-0124	Telm7	Scree
Palaeeudyptes gunnari	IB/P/B-0286	Telm7	Scree
Palaeeudyptes gunnari	IB/P/B-0294	Telm7	Scree
Palaeeudyptes gunnari	IB/P/B-0295	Telm7	Scree
Palaeeudyptes gunnari	IB/P/B-0296	Telm7	Scree
Palaeeudyptes gunnari	IB/P/B-0541a	Telm7	ZPAL 4
Palaeeudyptes gunnari	MLP 91-II-4-222	Telm7	DPV 15/84
Palaeeudyptes gunnari	MLP 87-II-1-45	Telm5	DPV 1/84
Palaeeudyptes gunnari	MLP 82-IV-23-6	Telm7	DPV 14/84
Palaeeudyptes gunnari	MLP 94-III-15-16	Telm7	ZPAL 4
Palaeeudyptes gunnari	MLP 82-IV-23-5	Telm7	DPV 14/84
Palaeeudyptes gunnari	MLP 84-II-1-75	Telm7	DPV 13/84
Palaeeudyptes gunnari	MLP 84-II-1-6	Telm7	DPV 13/84
Palaeeudyptes gunnari	MLP 83-V-20-27	Telm7	DPV 14/84
Palaeeudyptes gunnari	MLP 93-X-1-151	Telm3	IAA 1/94
Palaeeudyptes gunnari	MLP 95-I-10-16	Telm5	RV 8200
Palaeeudyptes gunnari	MLP 84-II-1-47	Telm7	DPV 13/84
Palaeeudyptes gunnari	MLP 84-II-1-65	Telm7	DPV 14/84
Palaeeudyptes gunnari	MLP 84-II-1-124'	Telm7	DPV 14/84
Palaeeudyptes gunnari	MLP 83-V-20-41	–	–
Palaeeudyptes gunnari	MLP 83-V-20-34	–	–
Palaeeudyptes gunnari	MLP 93-X-1-84	Telm7	DPV 14/84
Palaeeudyptes gunnari	MLP 84-II-1-24	Telm7	DPV 14/84
Palaeeudyptes gunnari	MLP 93-X-1-112	Telm7	DPV 13/84
Palaeeudyptes gunnari	MLP 93-X-1-117	Telm7	DPV 13/84
Palaeeudyptes sp.	IB/P/B-0221	Telm7	Scree
Palaeeudyptes sp.	IB/P/B-0268	Telm7	Scree

|			
Palaeeudyptes sp.	IB/P/B-0288	Telm7	Scree
Palaeeudyptes sp.	IB/P/B-0290	Telm7	Scree
Palaeeudyptes sp.	MLP 84-II-1-2	–	–
Palaeeudyptes sp.	MLP 87-II-1-97	–	–
Palaeeudyptes sp.	MLP 93-X-1-120	–	–
Palaeeudyptes sp.	MLP 84-II-1-177	–	–
Palaeeudyptes sp.	MLP 84-II-1-80	–	–
Palaeeudyptes sp.	MLP CX-60-2/4	–	–
Palaeeudyptes sp.	MLP 83-V-20-42	–	–
Palaeeudyptes sp.	MLP 93-X-1-25	–	–
Palaeeudyptes sp.	MLP 84-II-1-231	–	–
Palaeeudyptes sp.	MLP 90-I-20-316	–	–
Palaeeudyptes sp.	MLP 90-I-20-315	–	–
Palaeeudyptes sp.	MLP 93-X-1-150	–	–
Palaeeudyptes sp.	MLP 93-X-1-152	–	–
Palaeeudyptes sp.	MLP 95-I-10-135	–	–
Palaeeudyptes sp.	MLP 94-III-15-179	–	–
Palaeeudyptes sp.	MLP 78-X-26-6	–	–
Archaeospheniscus wimani	IB/P/B-0284	Telm7	Scree
Archaeospheniscus wimani	IB/P/B-0289	Telm7	Scree
Archaeospheniscus wimani	IB/P/B-0491	Telm7	ZPAL 4
Archaeospheniscus wimani	MLP 91-II-4-173	Telm5	IAA 1/80
Archaeospheniscus wimani	MLP 90-I-20-24	Telm5	IAA 4/80
Delphinornis larseni	IB/P/B-0062	Telm7	Scree
Delphinornis larseni	IB/P/B-0280	Telm7	Scree
Delphinornis larseni	IB/P/B-0299	Telm7	Scree
Delphinornis larseni	IB/P/B-0547	Telm7	Scree
Delphinornis larseni	IB/P/B-0548	Telm7	Scree
Delphinornis larseni	MLP 84-II-1-79	Telm7	DPV 13/84
Delphinornis larseni	MLP 91-II-4-174	Telm5	IAA 1/80
Delphinornis larseni	MLP 83-V-20-5	Telm7	DPV 14/84
Delphinornis gracilis sp. n.	IB/P/B-0279a	Telm7	Scree
Delphinornis gracilis sp. n.	IB/P/B-0492	Telm7	ZPAL 4
Delphinornis arctowskii sp. n.	IB/P/B-0484	Telm7	ZPAL 4
Delphinornis arctowskii sp. n.	MLP 93-X-1-92	Telm7	DPV 14/84
Delphinornis sp.	IB/P/B-0068	Telm7	Scree
Delphinornis sp.	IB/P/B-0282	Telm7	Scree
Delphinornis sp.	IB/P/B-0283	Telm7	Scree
Delphinornis sp.	MLP 93-X-1-155	Telm6	IAA 1/93
Delphinornis sp.	MLP 88-I-1-353	Telm5	RV 8200
Mesetaornis polaris sp. n.	IB/P/B-0278	Telm7	Scree
Mesetaornis sp.	IB/P/B-0279b	Telm7	Scree
?*Mesetaornis* sp.	MLP 88-I-1-484	Telm5	RV 8200
Marambiornis exilis sp. n.	IB/P/B-0490	Telm7	ZPAL 4
Marambiornis exilis sp. n.	MLP 93-X-1-111	Telm7	DPV 13/84
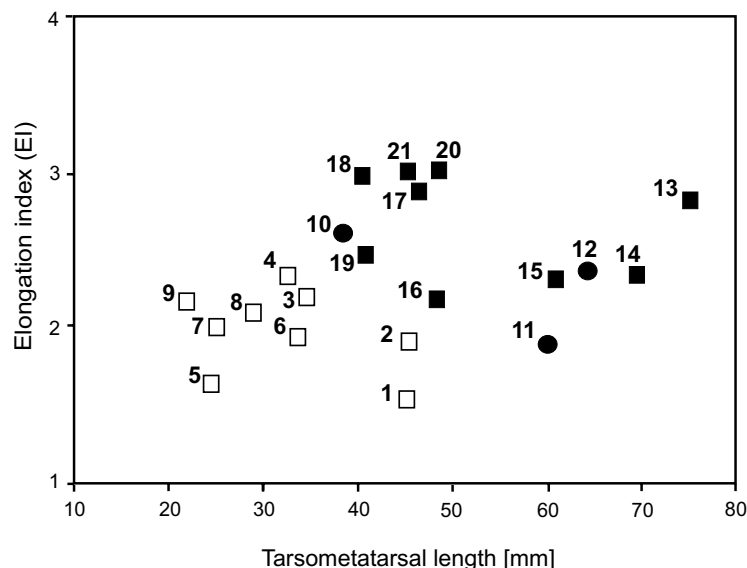
Fig. 16. Tarsometatarsal length plotted against the elongation index (EI, described in text) for a sample of Recent and fossil penguins. Open squares are mean values for Recent species (data from Stephan 1979); solid circles are values for holotypes of fossil penguins from the Eocene–Oligocene of New Zealand (data from Simpson 1971a); solid squares are mean values for fossil species from the Eocene of Seymour Island (this study, data from Table 1). Key to species (numbers of specimens in parentheses): **1** – *Aptenodytes forsteri* (3), **2** – *Aptenodytes patagonicus* (3), **3** – *Spheniscus humboldti* (2), **4** – *Spheniscus demersus* (8), **5** – *Spheniscus magellanicus* (4), **6** – *Pygoscelis papua* (9), **7** – *Eudyptes chrysolophus* (1), **8** – *Eudyptes chrysocome* (3), **9** – *Eudyptula minor*, **10** – *Korora oliveri* (1), **11** – *Archaeospheniscus lopdelli* (1), **12** – *Palaeeudyptes antarcticus* (1), **13** – *Anthropornis grandis* (3), **14** – *Palaeeudyptes klekowskii* (13), **15** – *Palaeeudyptes gunnari* (8), **16** – *Archaeospheniscus wimani* (2), **17** – *Delphinornis larseni* (6), **18** – *Delphinornis gracilis* (1), **19** – *Delphinornis arctowskii* (2), **20** – *Mesetaornis polaris* (1), **21** – *Marambiornis exilis* (2).

Comparative anatomy

The relative elongation of fossil tarsometatarsi in relation to those of recent penguins has been discussed by Wiman (1905b, 1942) and Simpson (1946, 1971b). Lowe (1933) had a diametrically opposed opinion about this feature. We completed a comparative analysis of available bones and found that tarsometatarsi of most extant species were relatively less slender than fossils from the Eocene La Meseta Formation of Seymour Island. Tarsometatarsi of most small fossil penguins (the size Group 7–8 of Wiman 1905b) are clearly more elongated than those of "giant" species, particularly *Palaeeudyptes* and *Archaeospheniscus* (Fig. 16).

The view that Eocene tarsometatarsi are characterised by the strong fusion of metatarsalia is widely accepted (Wiman 1905b, 1942; Simpson 1946, 1971b; Noriega and Tambussi 1989). We analysed small series of those bones, both fossil and Recent, and those illustrated by Wiman (1905b, 1942), Simpson (1946) and Stephan (1979). Our examination revealed that fossil tarsometatarsi from Seymour

Island are characterised by a stronger fusion of metatarsalia II and III than that observed in Recent forms. The degree of fusion of metatarsalia III and IV is probably comparable.

The most characteristic feature of the fossils from Seymour Island is the morphology of the hypotarsus. Cristae hypotarsi are slender, more prominent and clearly separated one from another in extinct compared to extant species. These features are particularly conspicuous in *Mesetaornis* and *Marambiornis*.

The fossil tarsometatarsi, with the exception of *Anthropornis* and *Palaeeudyptes*, possess foramen vasculare distale. The foramen is quite well developed in some cases (see above). With regard to the degree of elongation, the morphology of hypotarsus (except *Delphinornis*), and the presence of foramen vasculare distale, tarsometatarsi of *Mesetaornis*, *Marambiornis* and *Delphinornis* resemble those in Recent non-penguin members of class Aves.

Paleoecological implications

Hitherto, several thousand penguin bones have been collected from the Eocene strata of Seymour Island. Such a high accumulation of penguin remains occur only in the vicinity of penguin rookeries (Simpson 1976). The reworked terrestrial skeletal biota from rookeries may leave a paleontological record in near shore marine-estuarine sedimentary environments. Studies of the La Meseta coastal ecosystem supported evidence of this deposition (Feldmann and Woodburne 1988, Stilwell and Zinsmeister 1992; Gaździcki 1996, 1998). Eocene penguins had been breeding for 10–15 Ma on a land situated nearby, having a benefit from diversified and fertile shallow marine-estuarine environment. During that time the environment and biota changed: a delta evolved, climate deteriorated, and the structure of paleoecosystem and marine trophic levels changed (see also Case 1992, Aronson and Blake 2001). These factors may have accelerated evolution of penguins during the Eocene.

It is probable that a high number of penguin species are represented in sediments of the La Meseta Formation. Unfortunately, the mode of penguin bones occurrence, and a low frequency of small penguin tarsometatarsi specimens (mostly from Telm7) make it difficult to determine the stratigraphical range for each species. The largest species; *Anthropornis nordenskjoeldi* and *Palaeeudyptes klekowskii*, did not appeared until Telm7, but smaller representatives of the same genera; *Palaeeudyptes gunnari* and *Anthropornis grandis*, occurred from Telm3 toTelm7.

The oldest penguins are of Late Paleocene or Early Eocene age and are more primitive than any described species (see Fordyce and Jones 1990). Bones of the "Waipara Bird" differ in proportion from those of extant Sphenisciformes. Their characters suggest, however, a relationship with larger penguins as well as a volant bird ancestry (Fordyce and Jones 1990). This could testify for the Paleocene or

even Early Eocene origin of the order and subsequent rapid diversification of penguins as is shown by the fossil record.

The first Antarctic penguin remains were found in Telm2s of the La Meseta Formation and are probably the oldest-known specimens assignable to Spheniosciformes.The environment at that time was a warm, becoming cooler, wet, and strongly seasonal (middle part of Middle Eocene, paleoclimatic zone E2 of Dingle, Marenssi and Lavelle 1998). However, the majority of fossil tarsometatarsi are from Telm4–5 (upper part of Middle to early Late Eocene), when a cool, wet, non-seasonal period existed (paleoclimatic zone E3 of Dingle, Marenssi and Lavelle 1998) and from Telm7 (late Late Eocene), which is characterised as a cold, relatively dry period (paleoclimatic zone E4 of Dingle, Marenssi and Lavelle 1998). The paleontological record of penguin bones from these strata are locally productive and establish reliable taxonomic proposition covering probably all main species living in Antarctica during Middle–Late Eocene.

Co-occurrence of penguin bones together with fishes and abundant shark teeth was documented in the Telm3–5. Shark teeth were absent in Telm7, whereas bones of toothed whales (tooth evidence – Gaździcki and Tatur *personal commun.*) appeared beside penguins and fish remains. Fishes, penguins and whales (or sharks) are high-trophic marine species (Case 1992). The change of predator on the top of trophic pyramid by the newly evolved endothermic mammals that were well adapted to a cold marine environment may be correlated to deterioration of a climate between Middle and Late Eocene. Whales appeared in the Southern Hemisphere at the beginning of the Late Eocene (Fordyce 1989), also in concert with ecosystem changes due to gradual climate cooling. Exceptionally abundant penguin remains in Telm7 may indicate that during climate deterioration and accompanying ecosystem changes penguins found favourable marine conditions.

Concluding remarks

The tarsometatarsi reviewed here provide an evidence of a species-diverse assemblage of Eocene penguins from Seymour Island. The fossil bones were assigned to six known species: *Anthropornis nordenskjoeldi* Wiman, 1905, *A. grandis* (Wiman, 1905), *Palaeeudyptes klekowskii* Myrcha, Tatur and del Valle, 1990; *P. gunnari* (Wiman, 1905), *Archaeospheniscus wimani* (Marples, 1953) and *Delphinornis larseni* Wiman, 1905; and provide new features for the diagnoses of these taxa. Furthermore, this study has enhanced our knowledge of small-sized Eocene Antarctic penguins. Two new genera and species *Mesetaornis polaris* and *Marambiornis exilis*, are described as well as two new species of the genus *Delphinornis* (*D. arctowskii* and *D. gracilis*).

None of taxa established in this paper is known from other localities and *Palaeeudyptes* and *Archaeospheniscus* remain the only genera shared with other

regions (*i.e*. New Zealand and Australia). The stratigraphical range of known species is not uniform. Fossil bones of *Anthropornis nordenskjoeldi, Palaeeudyptes klekowskii, Delphinornis gracilis, D. arctowski, Mesetaornis polaris* and *M. exilis* were found exclusively in the Telm7 unit (the youngest one), whereas the range of other penguins encompasses Telm3–7.

Two species, *Ichtyopteryx gracilis* Wiman, 1905 and *Wimanornis seymourensis* Simpson, 1971, were not included here. The holotype of *I. gracilis* is so incomplete that it does not allow comparison with other specimens (Simpson 1971a, see also chapter "Material and methods"). *Wimanornis seymourensis* was described on the basis of a humerus (Simpson 1971a), and could not be compared here.

Taxonomic revision of the Middle–Late Eocene Antarctic penguins of Seymour Island should be considered as the first step towards the reconstruction and extent of fossil penguins in the Southern Ocean. As the affinity seems to be obvious between Antarctic and New Zealand penguins, detailed study both of them may give also important paleoecological information. Presented data support the opinion that Antarctica played an important role in penguin evolutionary history since the Eocene (see Fordyce and Jones 1990) and support the concept that phylogenetic roots of penguins preceded Cenozoic glaciation of Antarctica.

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