



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 nordenskjöldi*, *A. grandis*, *Palaeudyptes 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

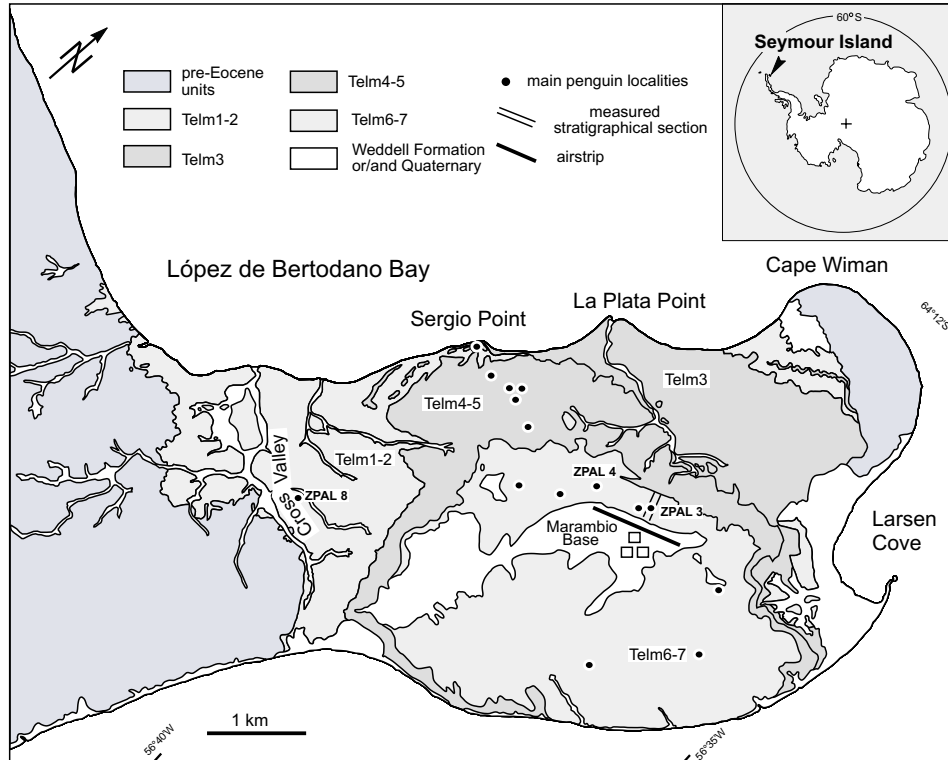


Fig. 1. Penguin locality index map of the La Meseta Formation on Seymour Island. Distribution of stratigraphical units according to Sadler (1988). Arrow of inset shows the location of Seymour Island in Antarctica.

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) *vide* 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 – *Palaeudyptes 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, Marensi, 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-dominated shelf deposits (Marensi,

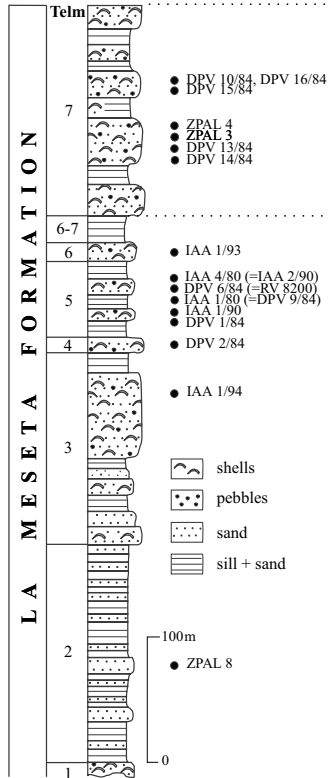
Santillana and Rinaldi 1998a, and authors' personal observations). Sadler (1988) on the basis of extensive mapping, subdivided the formation into seven major lithofacies Telm1–Telm7 (acronyms for Tertiary Eocene La Meseta), often also grouped into three larger depositional sequences marking channelised transgressive-regressive cycles (Elliot and Trautman 1982, Porębski 1995, 2000; Marensi, Santillana and Rinaldi 1998b). The La Meseta Formation is formed mainly by sands interbedded with bioturbated sandy muds, and sand/mud heteroliths 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

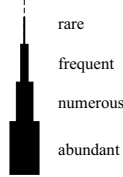
Until now, the Eocene penguin remains have been collected in Antarctica exclusively from the La Meseta Formation on Seymour Island (Simpson 1976, Fordyce and Jones 1990, Noriega *et al.* 1995). A few undetermined specimens of penguin bones were already found in the lower part of the formation, in scree 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 Marensi *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 (Marensi *et al.* 1994; Woodburne and Case 1996; Vizcaino *et al.* 1998; Reguero, Marensi 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 re-worked, moderate to high energy subtidal facies (Marensi *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)**



Occurrence of penguin bones within Telm7



- 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

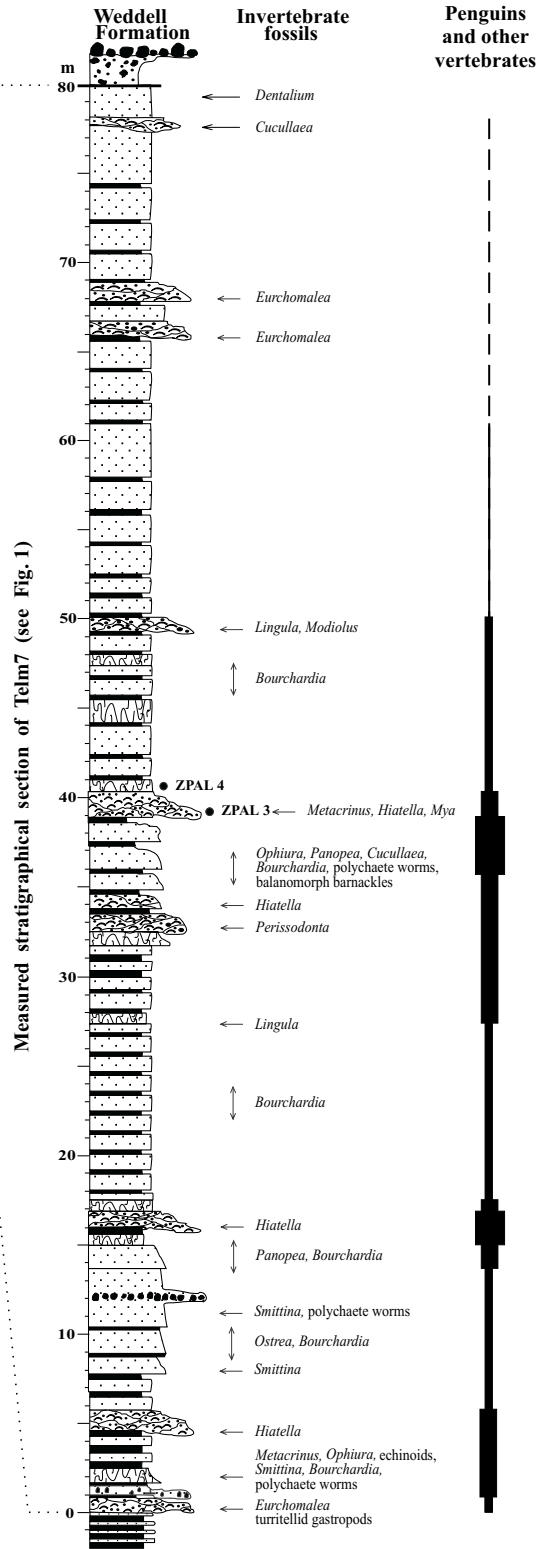




Fig. 3. View of the top of meseta along the north-western side and the upper units of the La Meseta Formation where the numerous penguin bones have been collected in Telm7. Bodman Point and James Ross Island are in background. *Photograph by A. Gaździcki, January 1992.*

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 turrnellid 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 (Porebski 1995, fig. 54; Marensi, Santillana and Rinaldi 1998a).

The age of the penguin tarsometatarsi examined here probably ranges from 49.5 Ma (Porebski 2000) or 42.0 Ma (Marensi *et al.* 1994) to 34.2 Ma (Dingle, Marensi 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, Marensi 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, Marensi 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, Marensi 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, Marensi 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 partic-

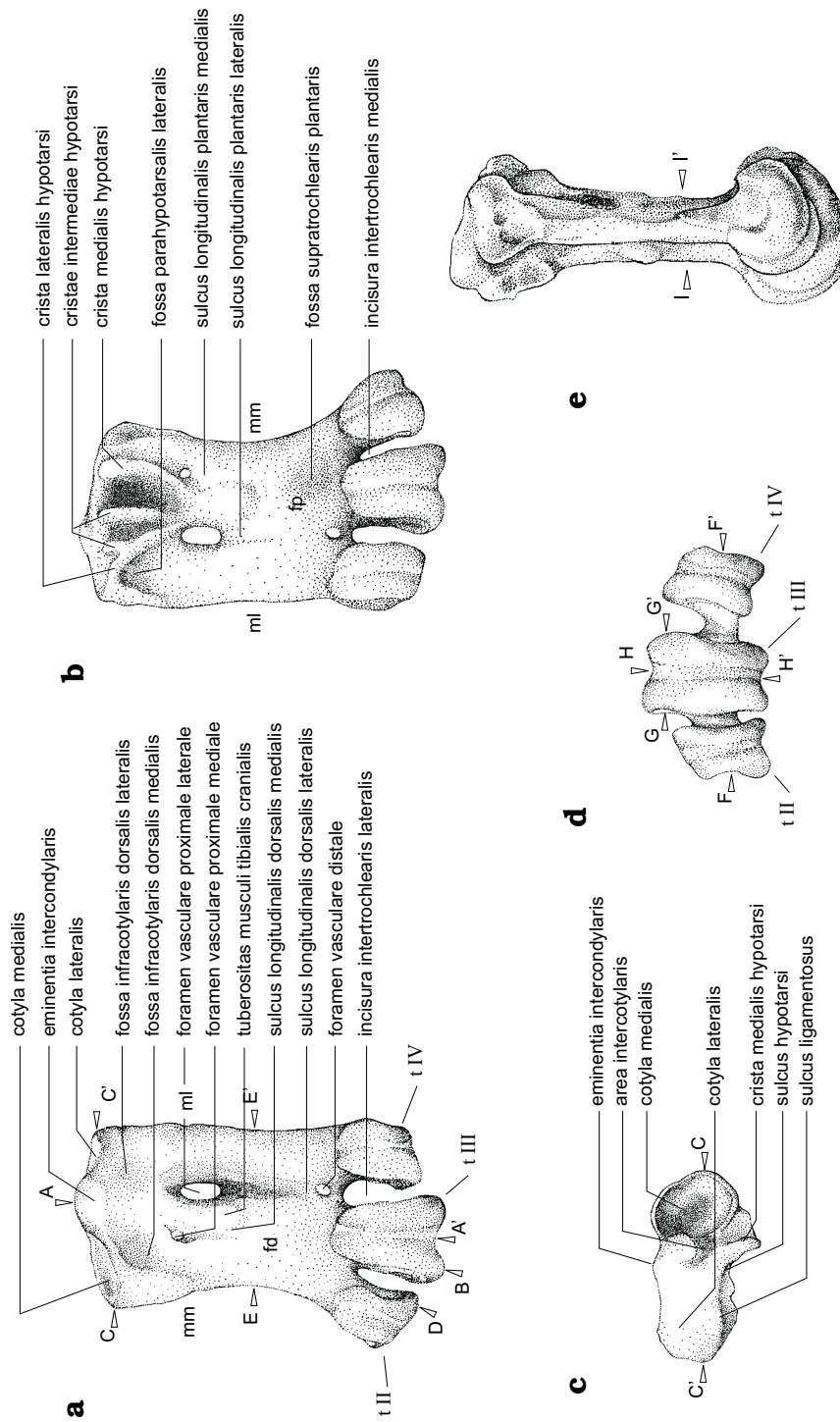


Fig. 4. Morphology and measurement points of the spheniscid tarsometatarsus: **a** – dorsal aspect, **b** – proximal aspect, **c** – plantar aspect, **d** – distal aspect, **e** – side aspect. Abbreviations: mm – margo medialis, ml – margo lateralis, fd – facies dorsalis, fp – facies plantaris, t II, III, IV – trochlea metatarsi II, III, IV; A–I – measurement points.

ular importance 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 Sey-

mour 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 were 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	1	2	3	4	5	6	7	8	EI
<i>Specimen</i>									
<i>Anthropornis nordenskjöldi</i>									
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	–
<i>Anthropornis grandis</i>									
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	–
<i>Anthropornis sp.</i>									
IB/P/B-0293	–	–	–	33.3*	–	–	–	13.1	–
MLP 84-II-1-9	–	–	25.2	21.4	–	18.3	–	8.9	–
<i>Palaeudyptes klekowskii</i>									
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
<i>Palaeudyptes gunnari</i>									
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	–	–	–	–	–
<i>Palaeodyptes</i> 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	–
<i>Archaeospheniscus wimani</i>									
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
<i>Delphinornis larseni</i>									
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
<i>Delphinornis gracilis</i> 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	–
<i>Delphinornis arctowskii</i> 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
<i>Delphinornis</i> 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	–	–
<i>Mesetaornis polaris</i> sp. n.									
IB/P/B-0278	48.6	49.6	>18.6	16.1	22.6	8.2	11.5	6.3	3.02
<i>Mesetaornis</i> sp.									
IB/P/B-0279b	–	–	–	–	–	7.7	9.8	–	–
<i>?Mesetaornis</i> sp.									
MLP 88-I-1-484	–	–	–	–	–	–	10.4	–	–
<i>Marambiornis exilis</i> 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

Class Aves

Order Sphenisciformes Sharpe, 1891

Family Spheniscidae Bonaparte, 1831

Anthropornis Wiman, 1905

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 *Palaeudyptes*, *Archaospheniscus*, *Delphinornis*, *Mesetaornis* and *Marambiornis*). Foramen vasculare proximale laterale considerably smaller and more proximal than its medial counterpart or absent (reverse situation in *Palaeudyptes*), 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 *Palaeudyptes*. Crista medialis hypotarsi, subdivided (undivided in *Palaeudyptes*).

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).

Anthropornis nordenskjoeldi Wiman, 1905

(Fig. 5)

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*.

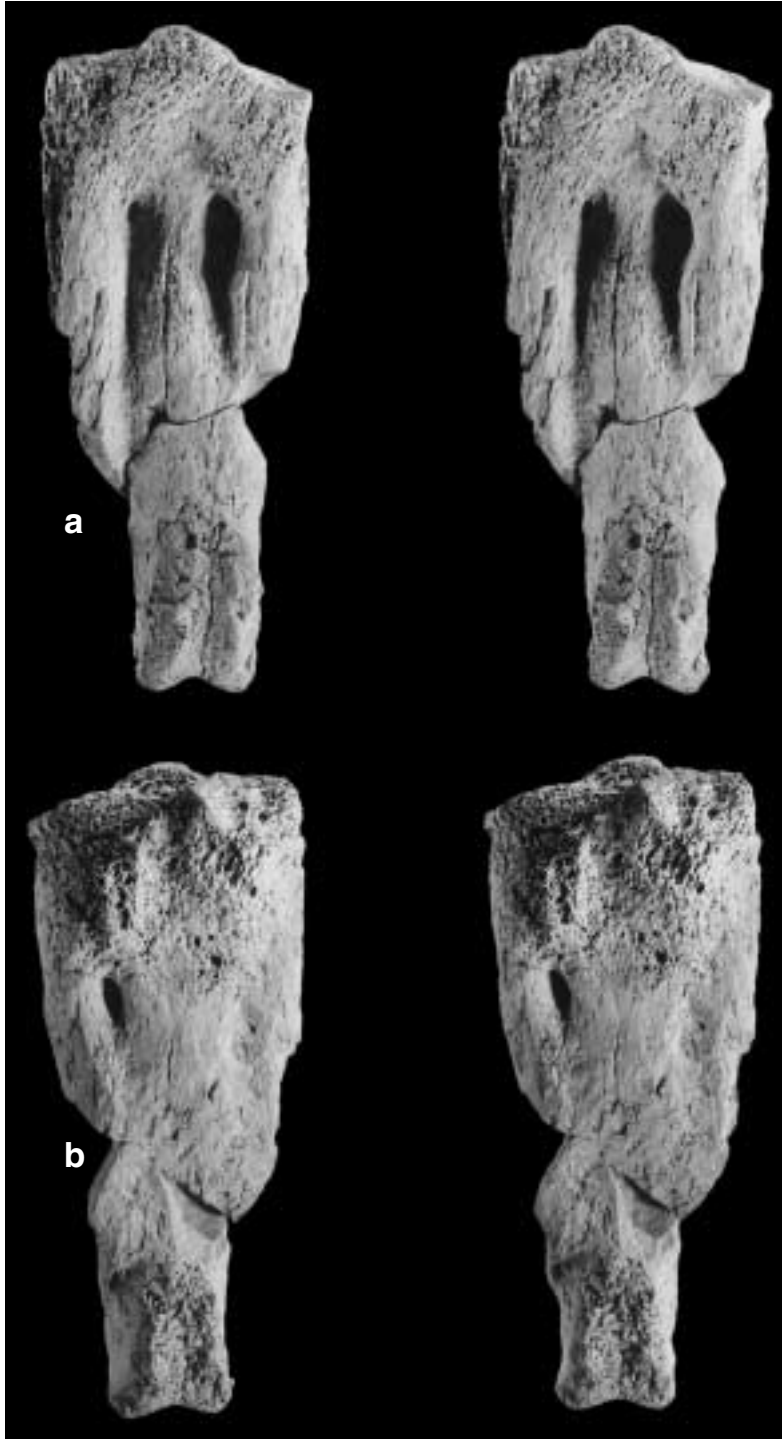


Fig. 5. Right tarsometatarsus of *Anthropornis nordenskoeldi* Wiman, 1905; specimen IB/P/B-0070. Stereopairs: **a** – dorsal aspect, $\times 1$; **b** – plantar aspect, $\times 1$. La Meseta Formation, Teln7 (screen).

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 infracotyliaria 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.

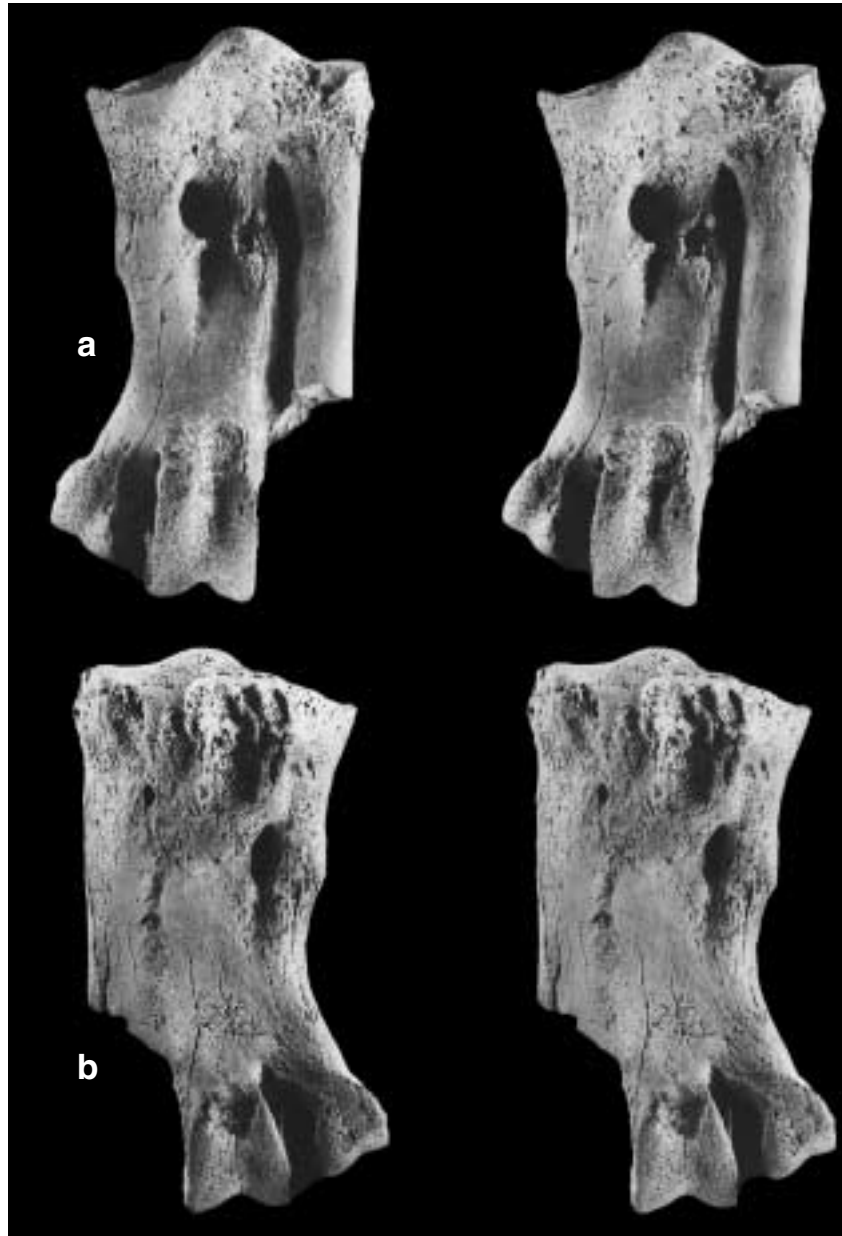


Fig. 6. Left tarsometatarsus of *Anthropornis grandis* (Wiman, 1905); specimen IB/P/B-0483. Stereo-pairs: **a** – dorsal aspect, $\times 1$; **b** – plantar aspect, $\times 1$. La Meseta Formation, Teln7 (screen).

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 nordenskjöldi* 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. nordenskjöldi*. 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).

Anthropornis sp.

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 *Palaeudyptes gunnari* rather than *Anthropornis grandis*.

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

Palaeudyptes Huxley, 1859

1859. *Palaeudyptes*; Huxley: p. 675.

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

Type species: *Palaeudyptes 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 *Palaeudyptes 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 synonymized 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.

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

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

Revised diagnosis. — Tarsometatarsus massive, larger than in *Palaeodyptes 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 infracotyloidalis dorsalis



Fig. 7. Left tarsometatarsus of *Palaeudyptes klekowskii* Myrcha, Tatur and del Valle 1990; specimen IB/P/B-0485. Stereopairs: **a** – dorsal aspect, $\times 1$; **b** – plantar aspect, $\times 1$. La Meseta Formation, Tlm7, 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 *Palaeodyptes 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 *Palaeodyptes* 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.

Palaeodyptes gunnari (Wiman, 1905)

(Fig. 8)

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

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

Revised diagnosis. — Tarsometatarsus relatively massive, though smaller than in *Palaeodyptes 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 *Palaeodyptes klekowskii*.

Remarks. — In respect to its size *Palaeodyptes gunnari* resembles *Palaeodyptes 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 *Palaeodyptes* from Seymour Island (Myrcha, Tatur and del Valle 1990) necessitated re-examination of available material and revision of the preceding diagnosis of *P. gunnari*.