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In Memory of Professor
Andrzej Myrcha
(1939–1997)

Eocene penguins of Seymour Island, Antarctica: Taxonomy

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Abstract: Skeletal remains of penguins from the Eocene La Meseta Formation (Seymour Island, Antarctica) constitute the only extensive fossil record of Antarctic Sphenisciformes. No articulated skeletons are known, and almost all fossils occur as single isolated elements. Most of the named species are based on tarsometatarsi (for which the taxonomy was revised in 2002). Here, 694 bones (from the Polish collection) other than tarsometatarsi are reviewed, and allocated to species. They confirm previous conclusions and suggest that ten species grouped in six genera are a minimal reliable estimate of the Eocene Antarctic penguin diversity. The species are: *Anthropornis grandis*, *A. nordenskjoeldi*, *Archaeospheniscus wimani*, *Delphinornis arctowskii*, *D. gracilis*, *D. larseni*, *Marambiornis exilis*, *Mesetaornis polaris*, *Palaeeudyptes gunnari* and *P. klekowskii*. Moreover, diagnoses of four genera (*Anthropornis*, *Archaeospheniscus*, *Delphinornis* and *Palaeeudyptes*) and two species (*P. gunnari and P. klekowskii*) are supplemented with additional, non-tarsometatarsal features. Four species of the smallest penguins from the La Meseta Formation (*D. arctowskii*, *D. gracilis*, *M. exilis* and *M. polaris*) seem to be the youngest taxa within the studied assemblage – their remains come exclusively from the uppermost unit of the formation. All ten recognized species may have co-existed in the Antarctic Peninsula region during the Late Eocene epoch.

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

Introduction

Penguins (Sphenisciformes: Spheniscidae) are highly specialized seabirds, restricted in their occurrence to the Southern Hemisphere. Today, they are represented by 17 species grouped in six genera (Williams 1995), whereas the number of extinct species exceeds 40 (Marples 1952, 1953; Simpson 1971a, b, 1972, 1973, 1979, 1981; Millener 1988; Fordyce and Jones 1990; Myrcha *et al*. 1990, 2002; Walsh and Hume 2001; Stucchi 2002; Emslie and Guerra Correa 2003; Stucchi *et*

al. 2003; Tambussi *et al.* 2005, and references cited therein). The oldest fossil bones referred to penguins come from the Late Paleocene or Early Eocene of New Zealand (Fordyce and Jones 1990) and the Cross Valley Formation (Late Paleocene) of Seymour Island, Antarctica (Tambussi *et al.* 2005), however, the fossil record of the present-day genera commences in the Late Miocene of Peru (Stucchi 2002; Stucchi *et al*. 2003).

The remains of extinct Sphenisciformes have been found in South America (Argentina, Chile and Peru), West Antarctica, southernmost Africa, Australia (Victoria and South Australia) and New Zealand (de Muizon and de Vries 1985; Fordyce and Jones 1990; Walsh and Hume 2001; Myrcha *et al.* 2002, and others). Only three places are known to have a locally productive record of synchronous or probably synchronous fossil penguin species (Simpson 1975, 1976; Fordyce and Jones 1990). The earliest such an assemblage comes from the Eocene of West Antarctica (Wiman 1905a, b; Marples 1953; Simpson 1971a, 1981; Cione *et al.* 1977; Myrcha *et al.* 1990, 2002). The other two are from the Oligocene of New Zealand (Marples 1952; Simpson 1971b; Fordyce and Jones 1990) and Late Oligocene and/or Early Miocene of Argentine Patagonia (Ameghino 1905; Simpson 1970, 1972, 1981; Tonni 1980).

Seymour Island (Isla Vicecomodoro Marambio on Argentine maps), situated at the tip of the Antarctic Peninsula (64°15'S, 56°45'W), is the only site in the Antarctic where the fossil remains of unquestionable penguin origin have been found (Simpson 1975; Fordyce and Jones 1990; Myrcha *et al.* 2002). These fossil bones constitute an extensive record of extinct penguins which documents the early stage of their evolution that took place just before the onset of the Paleogene continental glaciation in Antarctica (Myrcha *et al.* 2002; Gaździcki 2004).

The collections of fossil penguin bones from the Eocene La Meseta Formation of Seymour Island are scattered throughout the world – they are located in Argentina (Simpson 1972, 1981; Cione *et al.* 1977; Bargo and Reguero 1998), United States (Elliot *et al.* 1975; Zinsmeister and Camacho 1982; Olson 1985; Case 1992), New Zealand (Fordyce, *personal commun.*), Sweden (Wiman 1905a, b; Simpson 1946, 1971a), England (Marples 1953; Simpson 1971a) and Poland (Myrcha and Tatur 1986; Myrcha *et al.* 1990, 2002; Jadwiszczak 2000, 2001, 2003). Since 1905, thirteen species grouped in nine genera have been formally described from those collections, three species and genera are of doubtful distinctiveness (Table 1). Most species are based on one element from the hind-limb skeleton, the tarsometatarsus (Wiman 1905a, b; Marples 1953; Simpson 1971a; Myrcha *et al.* 1990, 2002). Wiman (1905b), the author of the first taxonomic approach to the fossil penguin fauna from Seymour Island, associated new taxa with size groups (Table 2). This association is still present in the paleontological literature (Simpson 1971a, Myrcha *et al*. 2002).

The latest large-scale re-examination of the Antarctic fossil penguin fauna included 126 tarsometatarsi from the Polish and Argentine collections (Myrcha *et al.*

2002). The intent of my work was to perform a comprehensive analysis of all fossil remains of Antarctic penguins from the former collection. The first part of the analysis is focused on the systematics supplementing the taxonomical revision by Myrcha *et al.* (2002; Table 1), and its result is presented in this paper.

Table 1

History of taxonomy of Eocene Antarctic penguins. *Orthopteryx gigas* is based solely on a synsacrum, *Wimanornis seymourensis* – on humeri. Other species are based on tarsometatarsi.

Wiman 1905a, b	Marples 1953	Brodkorb 1963[1]	Simpson 1971a	Myrcha *et al.* 1990	Myrcha *et al.* 2002
Orthopteryx gigas	considered to be synonymous with *Anthropornis nordenskjoldi*	distinct species (*Orthopteryx gigas*)	"dubious taxon"		species not confirmed by the analysis of tarsometatarsi
Anthropornis Nordens-kjöldii	distinct species (*Anthropornis nordenskjoldi*)	distinct species (*Anthropornis nordenskjoeldi*)	distinct species (*Anthropornis nordenskjoeldii*)		distinct species (*Anthropornis nordenskjoeldi*)
Pachypteryx grandis	considered to be synonymous with *Anthropornis nordenskjoldi*[2]	distinct species (*Anthropornis grandis*)	distinct species (*Anthropornis grandis*)		distinct species (*Anthropornis grandis*)
				Palae-eudyptes klekowskii[3]	distinct species (*Palaeeudyptes klekowskii*)
Eosphae-niscus Gunnari	distinct species (*Eosphaeniscus gunnari*)	distinct species (*Eosphaeniscus gunnari*)	distinct species (*Palaeeudyptes gunnari*[2])		distinct species (*Palaeeudyptes gunnari*)
			Wimanornis seymourensis		species not confirmed by the analysis of tarsometatarsi
	Notodyptes wimani	distinct species (*Notodyptes wimani*)	distinct species (*Archaeospheniscus wimani*[2])		distinct species (*Archaeospheniscus wimani*)
Delphinornis Larsenii	probably distinct species (*Delphinornis larsenii*)	distinct species (*Delphinornis larsenii*)	distinct species (*Delphinornis larsenii*)		distinct species (*Delphinornis larseni*)
					Delphinornis arctowskii[3]
					Delphinornis gracilis[3]
					Mesetaornis polaris[3]
					Marambiornis exilis[3]
Ichtyopteryx gracilis[4]	not considered	distinct species (*Ichtyopteryx gracilis*)	„essentially indeterminate at present"		"holotype (…) so incomplete that it does not allow comparison with other specimens"

[1] this is a catalogue of fossil birds

[2] change of a generic name

[3] holotype specimen belongs in the Polish collection

[4] very incomplete specimen

Table 2

Wiman's (1905b) size groups and corresponding species of fossil penguins from Seymour Island. Group no. 1 includes the largest specimens.

Group no.	Taxonomic position according to Wiman (1905b)	Present-day taxonomic position of Wiman's (1905a, b) holotypes (Simpson 1971a; Myrcha *et al.* 2002)
1	*Orthopteryx gigas*	probably *Anthropornis nordenskjoeldi*
2	unnamed	probably *Anthropornis nordenskjoeldi*
3[1]	*Anthropornis nordenskjoeldi*	*Anthropornis nordenskjoeldi*
4	*Pachypteryx grandis*	*Anthropornis grandis*
5[1]	*Eosphaeniscus gunnari*	*Palaeeudyptes gunnari*
6	unnamed	probably *Archaeospheniscus wimani*
7[1]	*Delphinornis larseni*	*Delphinornis larseni*
8	*Ichtyopteryx gracilis*	holotype too incomplete for taxonomical considerations

[1] Wiman (1905b) noted the existence of variant forms within this group

Geological and stratigraphical setting

The Eocene La Meseta Formation is exposed in the north-eastern part of Seymour Island (James Ross Basin, Antarctic Peninsula). It is composed of poorly consolidated clastic sediments (about 800 m thick) (Rinaldi *et al.* 1978; Elliot and Trautman 1982; Elliot 1988; Stilwell and Zinsmeister 1992; Marenssi *et al.* 1998; Myrcha *et al.* 2002), which are richly fossiliferous at numerous horizons (Borsuk-Białynicka 1988; Case 1988, 1992; Feldmann and Woodburne 1988; Fordyce 1989; Mitchell 1989; Jerzmańska and Świdnicki 1992; Long 1992; Stilwell and Zinsmeister 1992; Cione and Reguero 1994, 1998; Doktor *et al.* 1996; Gaździcki 1996, 1998, 2001, 2004; Askin 1997; Gandolfo *et al.* 1998; Vizcaino *et al.* 1998; Dzik and Gaździcki 2001; Myrcha *et al.* 2002; Fostowicz-Frelik 2003, and others).

The La Meseta 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 (Marenssi *et al.* 1998; Myrcha *et al.* 2002). Sadler (1988) subdivided the formation into seven major lithologic units Telm1–Telm7 and this system is adopted here (for different subdivision schemes and their correlation see Marenssi *et al.* 1998). According to results of palynological studies by Cocozza and Clarke (1992), the origin of the basal levels of the La Meseta Formation (Telm1) dates back to the late Early Eocene (just before 48.6 Ma; Gradstein and Ogg 2004). Based on $^{87}Sr/^{86}Sr$ ratios of molluscan aragonite, the uppermost part of the formation (top of Telm7) was deposited at *ca* 34.2 Ma (Dingle and Lavelle 1998) or *ca* 34.7 Ma (Dutton *et al.* 2002), *i.e.*, during the latest Eocene time period (Gradstein and Ogg 2004). These processes took place close to the final break-up of the supercontinent of Gondwana, the factor responsible for the development of the Antarctic Circum-polar Current (ACC) and, in an uncertain de-

gree (see discussion in Thomson 2004), the rapid expansion of continental ice sheets near the Eocene/Oligocene boundary (Lawver *et al.* 1992; Lawver and Gahagan 2003; Thomson 2004; Ivany *et al.* 2006; see also Birkenmajer *et al.* 2005).

Material and methods

The Polish collection was acquired in the field by Professor A. Myrcha (University of Białystok), Professor A. Gaździcki (Polish Academy of Sciences) and Dr A. Tatur (Polish Academy of Sciences) in 1985–94 on Seymour Island, and is housed at The Prof. A. Myrcha University Museum of Nature, University of Białystok, Poland (abbreviated IB/P/B). It consists of more than a thousand almost exclusively isolated bones and their fragments (917 database records) from the La Meseta Formation (several localities within the formation; for details see Myrcha *et al*. 2002). Most of them come from the Late Eocene sediments, from the Telm7 – the youngest unit within the formation (Myrcha *et al.* 2002: fig. 2). This set of fossil remains includes five holotype tarsometatarsi – a result of previous studies by Myrcha and colleagues (Myrcha *et al*. 1990, 2002).

Here, I analyze 694 anatomically identified bones (Fig. 1; not including tarsometatarsi – see Myrcha *et al.* 1990, 2002) from the Telm4–Telm7 units of the La Meseta Formation. "Material" subsections of the "Systematic paleontology" section contain solely specimens from the Polish collection, which I have added to the species' hypodigms. However, bones that are less characteristic (mainly due to their poor preservation) or problematic, but probably belong to a given species, are labeled as "other referred specimens" (*sensu* Simpson 1971a). Specimens without definite generic identification are sorted according to their location within skeleton and discussed in the "Problematic specimens" section. In some cases they are (due to their numbers) enumerated in tables (Tables 3–7).

Here, anatomical nomenclature follows, with slight modifications, that of Baumel and Witmer (1993). Latin or Latinized terms are italicized.

I used the following measurement categories (tables with measurements are placed in a separate section, "Measurements", which follows "Problematic specimens"):

I. Skull and face (*cranium et facies*; for measurements see Table 8).

1. Length from the tip of the bill to the rear edge of *apertura nasi ossea* (*naris*).
2. Width of *os frontale* in its narrowest part (not including *fossa glandulae nasalis*).
3. Width of *foramen magnum*.
4. Height of *foramen magnum*.
5. Width of *condylus occipitalis*.
6. Breadth (vertical) of *condylus occipitalis*.

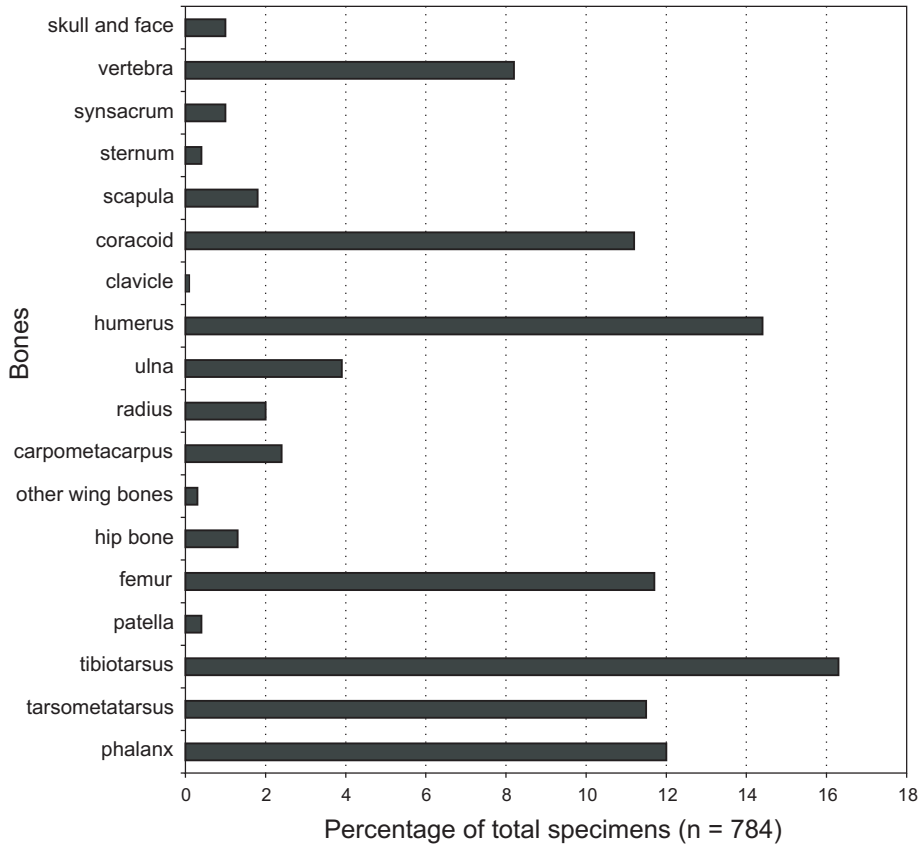

Fig. 1. Relative abundance of penguin bone categories recognized in the Polish collection (784 specimens, including tarsometatarsi – not examined here, from Telm4–Telm7 units of the La Meseta Formation, Seymour Island).

7. Width of the cerebral skull at the level of the even *processus paroccipitalis* (between midpoint concavities of both processes).
8. Width of *processus oticus* of *os quadratum* in its narrowest part.
9. Width of mandibular *facies articularis quadratica* between extreme points of *cotyla lateralis* and *cotyla medialis*.

II. Vertebra (*vertebra*; for measurements see Table 9).

1. Length of centrum (ventral side).
2. Length of *arcus vertebrae* (along the main axis of the bone).
3. Width of centrum in its narrowest part (dorsal view).
4. Distance between extreme points of both caudal articular processes.

III. Synsacrum (*synsacrum*; for measurements see Table 10).

1. Width of *corpus synsacri* between the last two vertebrae of the cranial part of the bone.

2. Width of *corpus synsacri* between the central and caudal part of the bone (just before *vertebra acetabularis*).
3. Height of *corpus synsacri* (width measured at right angles to the measurement no. 1).
4. Height of *corpus synsacri* (width measured at right angles to the measurement no. 2).

IV. Scapula (*scapula*; for measurements see Table 11).
1. Width of *collum scapulae* in its narrowest part, between dorsal and ventral edges of the bone.
2. Thickness of *collum scapulae* at right angles to the measurement no. 1.
3. Extreme thickness of the articular surface at the level of *tuberculum coracoideum*.

V. Coracoid (*coracoideum*; for measurements see Table 12).
1. Extreme length of the bone.
2. Distance between the central point of *facies articularis scapularis* along the main axis of the bone to *facies articularis sternalis*.
3. Medio-lateral width at the level of the upper edge of *facies articularis humeralis* at right angles to the main axis of the bone.
4. Medio-lateral width of the shaft in its narrowest part (at the level of the so-called *fenestra*, not including the precoracoid region).
5. Dorso-ventral thickness of the shaft at right angles to the measurement no. 4.
6. Length of *facies articularis humeralis*.
7. Width of *facies articularis humeralis.*
8. Diameter of *facies articularis scapularis*.

VI. Humerus (*humerus*; for measurements see Tables 13–14).
1. Length of the bone between the dome of *caput humeri* and *condylus ventralis humeri*.
2. Distance from the dome of *caput humeri* to the tip of preaxial angle (of the shaft).
3. Extreme length of the articular surface of *caput humeri*.
4. Dorso-ventral diameter of fossa *pneumatica* (between outer sides of its rim).
5. Cranio-caudal width of the shaft in the narrowest part of its proximal fragment.
6. Dorso-ventral thickness of the shaft at right angles to the measurement no. 5.
7. Cranio-caudal width of the shaft at the level of the preaxial angle.
8. Dorso-ventral thickness of the shaft at right angles to the measurement no. 7.
9. Extreme cranio-caudal width of the distal end.
10. Maximal dorso-ventral thickness of the distal end.
11. Dorso-ventral thickness of *condylus ventralis*.

VII. Ulna (*ulna*; for measurements see Table 15).
1. Extreme length of the bone.
2. Length of *cotyla ventralis* (proximal end of the bone).

3. Width of the proximal end of the bone (at right angles to previous measurement).
4. Extreme cranio-caudal width of the shaft (at the level of *olecranon*).
5. Dorso-ventral thickness of the shaft (at the level of *olecranon*).
6. Cranio-caudal width of the shaft 2/3 the length from the proximal end.
7. Dorso-ventral thickness of the shaft 2/3 the length from the proximal end.
8. Cranio-caudal width of the distal end of the bone.
9. Dorso-ventral thickness of the distal end of the bone.

VIII. Radius (*radius*; for measurements see Table 16).
1. Extreme length of the bone.
2. Length of *cotyla humeralis*.
3. Width of *cotyla humeralis*.
4. Cranio-caudal width of the shaft at the base of *caput radii*.
5. Dorso-ventral thickness of the shaft at the base of *caput radii*.
6. Cranio-caudal width of the shaft 2/3 the length from the proximal end.
7. Dorso-ventral thickness of the shaft 2/3 the length from the proximal end.
8. Cranio-caudal width of the distal end of the bone.
9. Dorso-ventral thickness of the distal end of the bone.

IX. Carpometacarpus (*carpometacarpus*; for measurements see Table 17).
1. Length of the bone between the proximal articular surface and the distal end of *os metacarpale majus*.
2. Cranio-caudal width of the proximal articular surface.
3. Dorso-ventral thickness of *os metacarpale majus* 1/2 the length of the carpometacarpus.

X. Hip/coxal bone (*os coxae*; for measurements see Table 18).
1. Diameter of *foramen acetabulum*.
2. Thickness of the shaft of *ischium* between *foramen obturatum* and *acetabulum*.
3. Thickness of the shaft of *ischium* between *foramen obturatum* and *foramen ilioischiadicum*.
4. Width of the preacetabular fragment of *ilium* in its narrowest part.
5. Width of *ilium* just cranial to *antitrochanter*.

XI. Femur (*femur*; for measurements see Table 19).
1. Length of the bone between *caput femoris* and *condylus medialis*.
2. Length of the bone between *trochanter femoris* and *condylus lateralis*.
3. Width of the proximal part of the bone (between the edge of *trochanter femoris* and femoral head).
4. Thickness of *trochanter femoris* (at right angles to previous measurement).
5. Medio-lateral diameter at the centre of the shaft (*i.e.*, at its narrowest part).
6. Medio-lateral width of the distal end of the bone.
7. Cranio-caudal thickness of *condylus lateralis* (at right angles to previous measurement).

XII. Tibiotarsus (*tibiotarsus*; for measurements see Table 20).
1. Length of the bone between the edge of the proximal articular surface (at the base of *crista cnemialis cranialis*) and *condylus medialis*.
2. Width of the proximal end of the bone between extreme points of *facies articularis medialis* and *f. a. lateralis*.
3. Medio-lateral width of the shaft at the level of *foramen interosseum distale* (approx. corresponds to 1/2 the length of the bone).
4. Cranio-caudal thickness of the shaft (at right angles to the previous measurement).
5. Width of the distal end of the bone (between cranio-distal portions of outer edges of both condyli).
6. Cranio-caudal thickness of *condylus medialis*.
7. Width of *pons supratendineus* at its centre.

Measurement categories for patella, *phalanx prox. digiti majoris*, clavicle and sternum (rare specimens) are defined in the text of next two sections, and values are also reported there. All ID numbers of measurement categories correspond to those in Tables 8–20. The measurement categories are also presented graphically – this supplementary material is available from the website of the Institute of Biology, University of Białystok (http://biol-chem.uwb.edu.pl/IP/ENG/biologia/mon.htm).

Most measurements are in millimeters with 0.1 mm accuracy (measured using digital calipers). Larger specimens were measured with a ruler with an accuracy of 1 mm.

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.

Revised diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002). Large and robust coracoid (Fig. 2) with a characteristic shallow and irregularly shaped depression on its corpus, limited by *facies articularis scapularis*, *facies a. humeralis*, *margo lateralis* and a conspicuous osseous crest sternal to both *facies*. This feature is not observed in *Palaeeudyptes*. Head of humerus massive with relatively smaller *fossa pneumatica* than in *Palaeudyptes klekowskii* (for details see "Remarks" section). Shaft of humerus robust (slender in *Palaeeudyptes*; Fig. 3), *margo caudalis* wide, without (unlike in *Palaeeudyptes*) well pronounced narrowing in the middle of its length (narrowing slight if any). *Facies musculi*

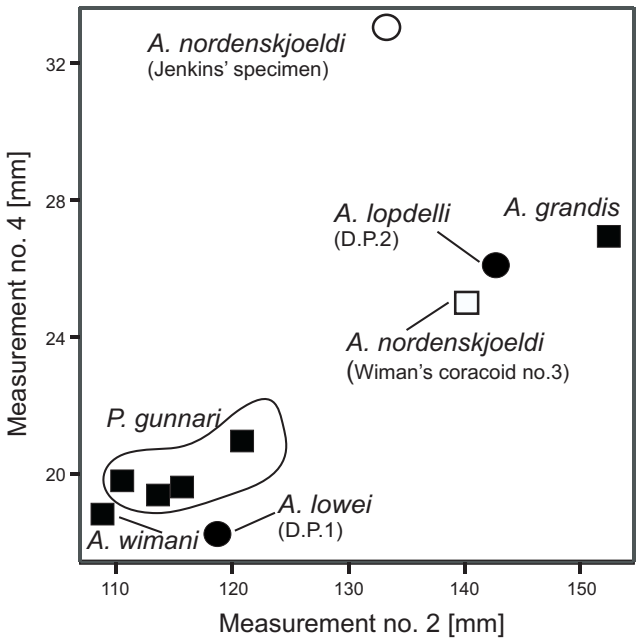

Fig. 2. Plot of coracoid measurements no. 2 and 4 (see "Material and methods") for specimens from the Polish collection (see text; black squares), Wiman's (1905b) specimen from the Eocene of Seymour Island (white square), Jenkins' (1974) specimen from the Eocene of Australia (white circle) and Marples' (1952) specimens from the Oligocene of New Zealand (black circles).

latissimus dorsi located quite close to the head of the bone (shifted distally in *Palaeeudyptes*), adjacent *foramen nutricium* situated, unlike in *Palaeeudyptes*, on *margo caudalis* or nearly so. *Facies musculi supracoracoidei* oblique in relation to the axis of the bone (parallel in *Palaeeudyptes*). Large ulna with conspicuous fossa (lacking in *Palaeeudyptes*) situated proximally on *facies ventralis*, between the main axis of the bone and *margo caudalis*. *Foramen nutricium* located proximally (at *margo caudalis*) always present (lacking in some ulnae attributed to *Palaeeudyptes*). Carpometacarpus robust and relatively broad (clearly slender in *Palaeeudyptes*). *Foramen interosseum proximale* (between robust tibiotarsus and fibula) weakly developed – the feature suggested by a slight concavity (well pronounced in *Palaeeudyptes*) of the proximal part of tibiotarsal *margo lateralis* (fibula is not present in the collection).

Remarks. — The diagnostic feature of the coracoid is evident only in one bone of this type from the examined set – referred here to *A. grandis* (specimens placed in *A. nordenskjoeldi* are too fragmentary to compare). Traces of the same structure can also be found in Jenkins' coracoid from Australia (Jenkins 1974: plate 37, fig. 1) that was identified as *A. nordenskjoeldi* (Jenkins 1985) and are probably lacking in Wiman's specimen from his Group 3 (Wiman 1905b: plate VII, fig. 3-3a). However, the Australian coracoid was discovered in the very close

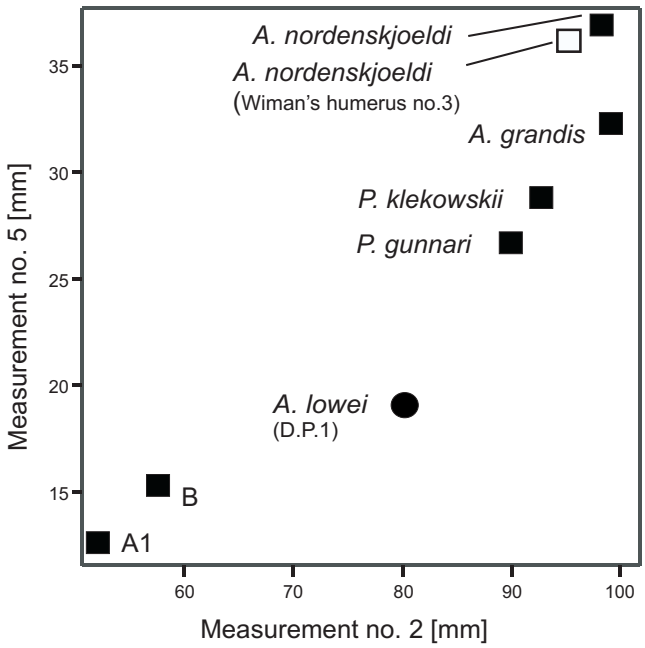

Fig. 3. Plot of humeral measurements no. 2 and 5 (see "Material and methods") for specimens from the Polish collection (see text; black squares), Wiman's (1905b) specimen from the Eocene of Seymour Island (white square) and Marples' (1952) specimen from the Oligocene of New Zealand (black circle).

vicinity of a characteristic humerus (and some other bones; Jenkins 1974), so it appears to be a much better candidate for inclusion into *Anthropornis* than Wiman's specimen.

The relative volume of *fossa pneumatica* (in humeri; see diagnosis) was calculated as (W/D)×100, where "W" is a weight of fine sand used to fill the fossa and "D" stands for the largest cranio-caudal width of the proximal end of humerus (compare Marples 1952). In *Anthropornis*, the value of this "index" ranges from 3.0 to 4.0 with median value of 3.5 (N = 3). A number of humeral features listed by Simpson (1971a), *i.e.*, some details of the shaft's shape and undivided form of *fossa pneumatica* are, in my opinion, of no diagnostic importance for this genus. Hence, I moved them to "Description" sections of constituent species. I agree with Simpson (1971a) that massive humeri of *Anthropornis* were characterized by large head and small *fossa pneumatica* as well as oblique *facies musculi supracoracoidei* ("*pectoralis secundus*" *sensu* Marples 1952 and Simpson 1971a).

Anthropornis nordenskjoeldi Wiman, 1905
(Figs 4–5)

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

Diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002).

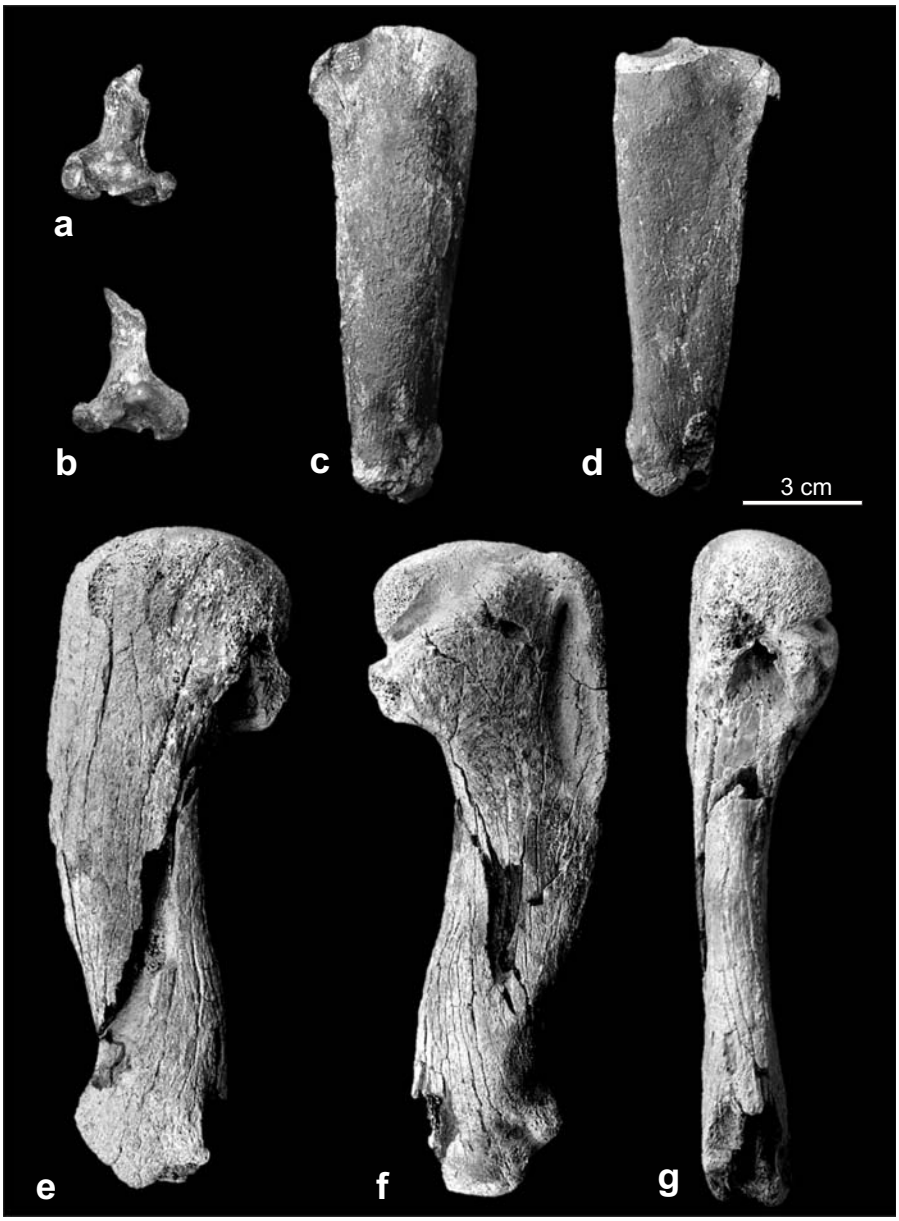

Fig. 4. Selected bones of *Anthropornis nordenskjoeldi* Wiman, 1905 from the Polish collection. Quadrate (specimen IB/P/B-0094a; a – rostral view, b – caudal view), ulna (specimen IB/P/B-0150; c – dorsal view, d – ventral view) and humerus (specimen IB/P/B-0119; e – dorsal view, f – ventral view, g – caudal view).

Material. — 27 specimens. Scapular portion of right coracoid, IB/P/B-0463; incomplete shaft of right coracoid, IB/P/B-0837; proximal right humerus, IB/P/B-0091; distal half of left humerus with damaged distal end, IB/P/B-0092; left hu-

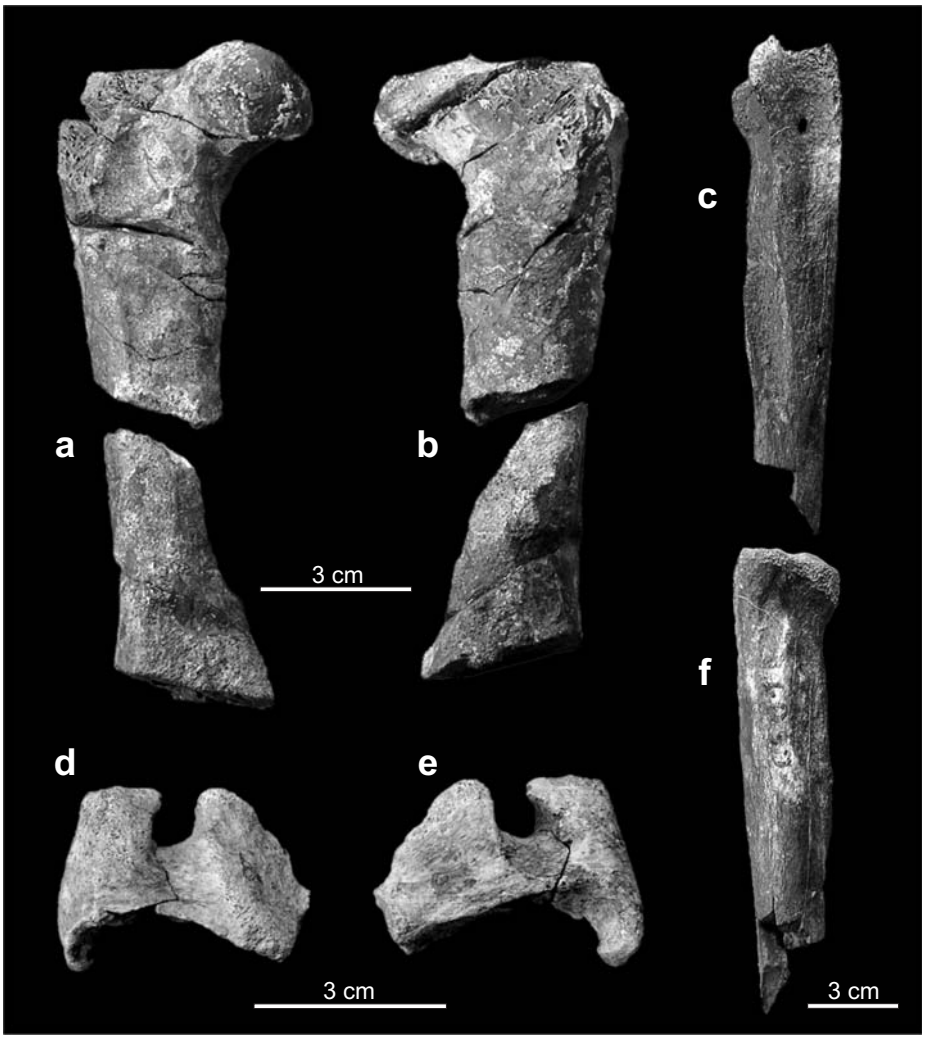

Fig. 5. Selected bones of *Anthropornis nordenskjoeldi* Wiman, 1905 from the Polish collection. Femur (specimen IB/P/B-0701; a – cranial view, b – caudal view), patella (specimen IB/P/B-0250b; d – medial view, e – lateral view) and tibiotarsus (specimen IB/P/B-0501; c – cranial view, f – caudal view).

merus, IB/P/B-0119 (Fig. 4e–g); right ulna, IB/P/B-0150 (Fig. 4c, d); incomplete left *os metacarpale majus* with damaged *phalanges dig. alulae*, IB/P/B-0613d; incomplete distal femur, IB/P/B-0476; incomplete distal left femur, IB/P/B-0480; incomplete distal right femur, IB/P/B-0660; distal right femur, IB/P/B-0675; right femur with damaged shaft, missing distal end, IB/P/B-0701 (Fig. 5a, b); incomplete distal tibiotarsus, IB/P/B-0360; distal right tibiotarsus, IB/P/B-0363; right tibiotarsus missing distal end, IB/P/B-0501 (Fig. 5c, f); damaged shaft of left tibiotarsus, IB/P/B-0512; incomplete proximal right tibiotarsus, IB/P/B-0536; incomplete distal

left tibiotarsus, IB/P/B-0636; right *digitus II phalanx 1* (*os dig. pedis*), IB/P/B-0575c; other referred specimens (see "Material and methods"): incomplete right *os quadratum*, IB/P/B-0094a (Fig. 4a, b); rear end of the right ramus of mandible, IB/P/B-0189; distal right humerus, IB/P/B-0307; proximal right humerus, IB/P/B-0478; distal left humerus, IB/P/B-0711; left *phalanx proximalis dig. majoris*, IB/P/B-0684; right patella, IB/P/B-0250b (Fig. 5d, e); incomplete left patella, IB/P/B-0823.

Description. — *Os quadratum* with a sharp lateral margin (*crista lateralis*). *Cotyla quadratojugalis* deep. Mandibular *facies articularis quadratica* deeply incised, *processus retroarticularis* probably reduced (the cause of uncertainty is the state of preservation). Shaft of humerus sigmoid, narrower distally than proximally. *Fossa pneumatica* undivided. Relative width of *condylus ventralis humeri* defined as (measurement no. 11/measurement no. 10) ×10: 4.4 – 4.8 (N = 2). Estimated (because of poor condition of most specimens) relative width of *condylus dorsalis humeri* defined as (width of condylus/measurement no. 10) ×10, does not exceed 7.0. *Olecranon* of ulna very proximal (located close to the proximal articular surface). *Phalanges dig. alulae* separated by a conspicuous notch. Both surfaces of *phalanx proximalis dig. majoris* convex. Femur and tibiotarsus large and very massive. Patella large and irregularly wedge-shaped, pierced by *canalis/sulcus m. ambientis*. Its *facies articularis femoralis* rough and concave. *Facies distalis* and the base of patella (assuming flatness of the latter) form an angle of 60–70°. Tibiotarsus with poorly developed *tuberositas poplitea* (erosion cannot be excluded in this case) and *fossa flexoria*. Shaft of tibiotarsus flattened. *Digitus II phalanx 1* (*os dig. pedis*) without a proximal pit on a plantar side; delimitation between *facies plantaris* and the trochlear surface very well marked.

Remarks. — This is the only species of fossil penguin known from the Antarctic also represented in the fauna from another continent – Australia (see Jenkins 1974, 1985).

Os quadratum and the partial mandible seem to be complementary in terms of the sculpture of respective surfaces, though the former could be from the skeleton of a somewhat smaller bird. Their sizes suggest attributing these bones to *A. nordenskjoeldi*. Two very fragmentary coracoids are much more massive than the specimen referred here to *A. grandis* and other fragments of large bones of this type from the Polish collection.

Simpson (1971a) included lack of a "definite preaxial angulation" (a feature of the humeral shaft) in generic diagnosis of *Anthropornis*. However, this appears unlikely as the feature is very exposed to erosion. For example, Jenkins' (1974) specimen belonging to *A. nordenskjoeldi* (Jenkins 1985) has, unlike Wiman's (1905b) bone assigned to the same species (Wiman 1905b, Simpson 1971a), a well pronounced preaxial angle. The best preserved humerus from the Polish collection described as *A. nordenskjoeldi*, specimen IB/P/B-0119 (Fig. 4e–g), has a considerably widened (towards *margo cranialis*) distal portion of *facies musculi coraco-*

brachialis caudalis. Incomplete humeri labeled as "other referred specimens" are all very massive. However, specimen IB/P/B-0478 has two striking features – its *fossa pneumatica* is quite large, and its *facies musculi supracoracoidei* is far less oblique in relation to the axis of the bone than in other bones described as *Anthropornis*.

Specimen IB/P/B-0150 (Fig. 4c, d) is the largest ulna within studied collection. Ulnae included by Wiman (1905b) in his Group 3 are obviously smaller (*e.g.*, see measurements in Marples 1953), so they probably belong to *A. grandis*. The largest carpometacarpus in the analyzed set, IB/P/B-0613d, is clearly bigger than Wiman's (1905b) specimens from his Group 3 and probably also than those studied by Marples (1953). Its estimated size is closer to that of the Australian specimen (see Jenkins 1974). The only phalanx from the wing skeleton assigned (with some doubt) to this species is larger than Marples' (1953) specimen from the British collection described as *A. nordenskjoeldi*, but smaller than the bone examined by Jenkins (1974). Its length is 53.4 mm.

Femora described by Marples (1953) as *A. nordenskjoeldi* as well as Wiman's (1905b) femur no. 3 probably belonged to a bird from the smaller species of *Anthropornis*. Both patellae labeled as "other referred specimens" resemble Marples' (1953) specimen assigned to *A. nordenskjoeldi* with respect to their size, shape of distal end and the size of *canalis/sulcus m. ambientis*. The length of facies *articularis femoralis* of the almost complete specimen is 35.9 mm, its width in the middle is 20.1 mm. The second bone belonged to a slightly larger bird. A diagnostic feature of the tibiotarsus (at generic level) is evident in only two proximal fragments. However, all tibiotarsi assigned to this species are partial bones of exceptionally large penguins. Specimen IB/P/B-0512 has the flattest shaft in the entire collection. It is interesting to note that Marples (1953) described the tibiotarsus as "an uncharacteristic bone". Wiman's (1905b: plate III, figs 5–5a) incomplete tibiotarsus no. 3 is probably too small to belong to *A. nordenskjoeldi*.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm7, and a single specimen (IB/P/B-0536) from Telm4–Telm6 (originally labeled as a bone from Unit II *sensu* Elliot and Trautman 1982).

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.

Diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002).

Material. — Nine specimens. Right coracoid with sternal half and medial margin damaged, IB/P/B-0454 (Fig. 6a, b); left humerus missing distal end, IB/P/B-0179 (Fig. 6c–e); left ulna, IB/P/B-0064; left ulna missing distal end, IB/P/B-0443; other referred specimens: incomplete proximal left humerus, IB/P/B-0590; proximal right ulna, IB/P/B-0109; proximal half of right carpometacarpus, IB/P/B-0438; left

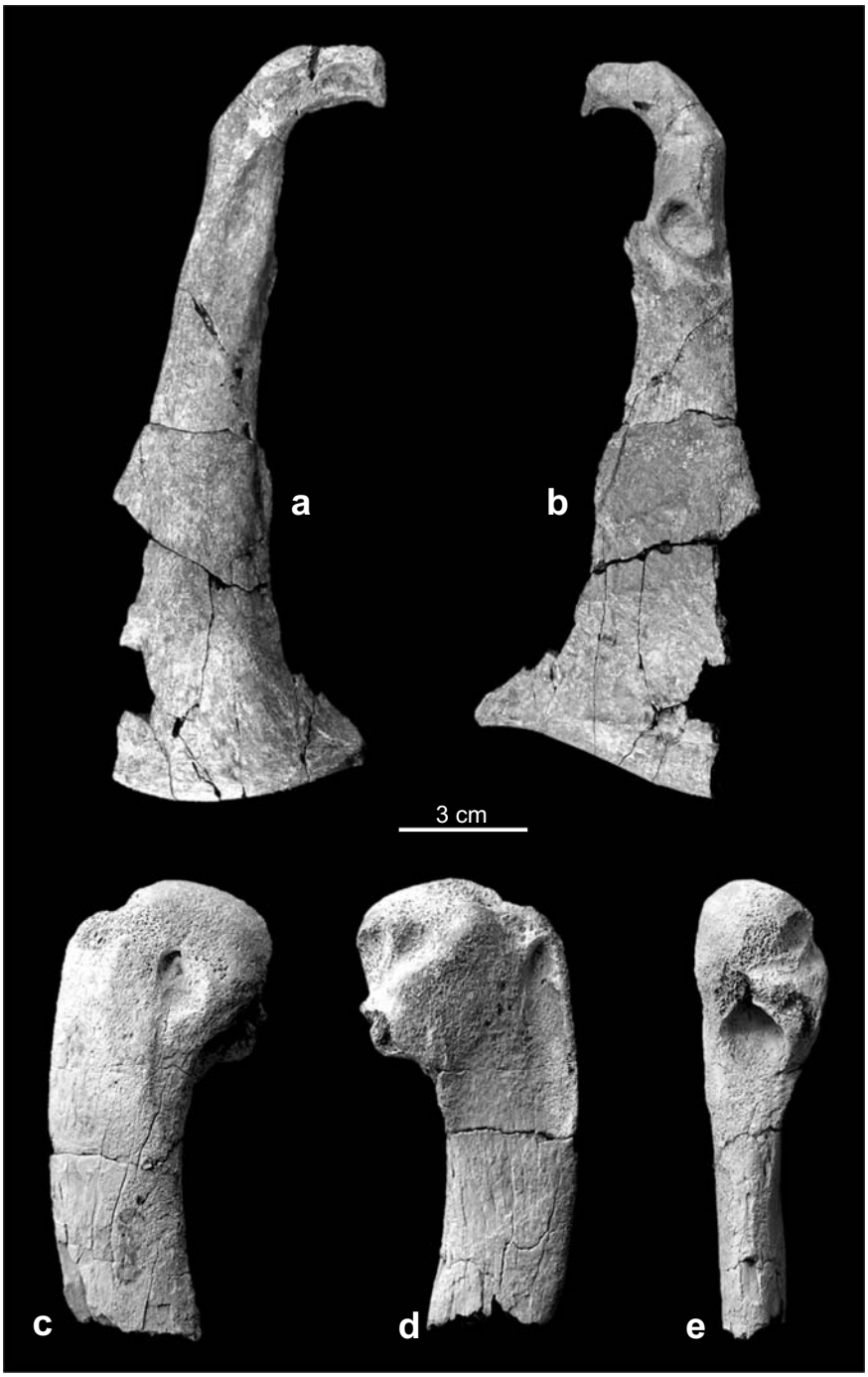

Fig. 6. Selected bones of *Anthropornis grandis* (Wiman, 1905) from the Polish collection. Coracoid (specimen IB/P/B-0454; a – ventral view, b – dorsal view) and humerus (specimen IB/P/B-0179; c – dorsal view, d – ventral view, e – caudal view).

tibiotarsus missing distal end, IB/P/B-0134; damaged shaft and proximal end of left tibiotarsus, IB/P/B-0336.

Description. — Stout coracoid with deep *facies articularis scapularis* and convex (when viewed from the ventral side) *facies articularis sternalis*. *Fossa pneumatica* of humerus undivided. *Olecranon* of ulna very proximal (located close to the proximal articular surface). *Tuberositas poplitea* and *fossa flexoria* (its distal part) of tibiotarsus probably better developed than in *A. nordenskjoeldi*. Shaft of tibiotarsus flattened.

Remarks. — I assigned the coracoid IB/P/B-0454 (Fig. 6a, b) to *A. grandis* because it is clearly smaller than the Australian bone identified as *A. nordenskjoeldi* (Jenkins 1974, 1985) and less robust than two other fragments from the Polish collection. Partial humerus IB/P/B-0179 (Fig. 6c–e) and IB/P/B-0119 (*A. nordenskjoeldi*) share, besides diagnostic features, a characteristic shape of *facies musculi coracobrachialis caudalis*. Its peculiar feature is a pit situated between *facies musculi coracobrachialis caudalis* and *f. m. supracoracoidei* which plunges proximally into the bone tissue. The second fragment of humerus assigned to *A. grandis* (with less confidence), specimen IB/P/B-0590, is too eroded to compare.

The size gradient within ulnae referred here to *Anthropornis* is evident – first two bones described as *A. grandis* are clearly smaller than the only specimen of *A. nordenskjoeldi*. However, the third fragment (IB/P/B-0109) is even smaller, and the fossa characteristic for the genus as well as *foramen nutricium* are only slightly pronounced. The only fragment of carpometacarpus considered here is smaller than specimen IB/P/B-0613d (*A. nordenskjoeldi*) and could have belonged to *A. grandis*.

Both tibiotarsi referred to this species, while having diagnostic feature of *Anthropornis*, are clearly smaller than bones assigned to *A. nordenskjoeldi*. Moreover, in respect to features listed in "Description", they approach the condition typical of *Palaeeudyptes* (see also description of *A. nordenskjoeldi*).

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm5 (single specimen, IB/P/B-0454) and Telm7.

Anthropornis sp.

Material. — Three specimens. Incomplete proximal left carpometacarpus, IB/P/B-0264c; distal right carpometacarpus, IB/P/B-0620a; incomplete right *os metacarpale majus*, IB/P/B-0716.

Remarks. — Estimated size and shape of these fragments are in accord with diagnostic features of *Anthropornis*; however, they are too poorly preserved to assign them to either species of this genus.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm5 (single specimen, IB/P/B-0716) and Telm7.

?*Anthropornis* sp.

Material. — One incomplete *os metacarpale majus*, IB/P/B-0462.

Remarks. — This specimen is very fragmentary; however, it is probably a part of the robust and relatively broad bone.

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

Palaeeudyptes Huxley, 1859

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

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

Type species: *Palaeeudyptes antarcticus* Huxley, 1859.

Revised diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002). Large or medium-sized coracoid (Fig. 2) lacking depression on its corpus just sternal to *facies articularis scapularis* and *facies a. humeralis*, and without an osseous crest sternal to both muscle insertions (both features are well developed in *Anthropornis*). Head of humerus quite massive with a relatively slender shaft (robust shaft in *Anthropornis*; Fig. 3), *margo caudalis* with a characteristic well pronounced narrowing in the middle of its length (unlike in *Anthropornis*). *Facies musculi latissimus dorsi* shifted distally from the head (located quite close to the head of a bone in *Anthropornis*), adjacent *foramen nutricium* situated, unlike in *Anthropornis*, on *facies ventralis*, close to *margo caudalis*. *Facies musculi supracoracoidei* parallel (or nearly so) to the axis of the bone (oblique in *Anthropornis* and *Archaeospheniscus*). Relative width of *condylus dorsalis humeri* (for a definition, see description of *A. nordenskjoeldi*) below 7 (over 8 in *Archaeospheniscus wimani*). Proximal part of *facies ventralis* of ulna without a hollow situated between main bone axis and *margo caudalis* (hollow present in *Anthropornis*). Carpometacarpus slender (unlike in *Anthropornis*). *Foramen interosseum proximale* (between tibiotarsus and fibula) well developed – the feature suggested by a concavity (poorly developed in *Anthropornis*) of the proximal part of tibiotarsal *margo lateralis* (fibula is not present in the collection).

Remarks. — Besides two Antarctic species of *Palaeeudyptes* presented below, there are two species known from New Zealand: *P. antarcticus* Huxley, 1859 (Oligocene; the first fossil penguin species formally described) and *P. marplesi* Brodkorb, 1963 (Late Eocene). Bones identified as *Palaeeudyptes* sp. are known from the Late Eocene of Australia (*e.g.*, Simpson 1975).

A considerable morphological diversity within humeri assigned here to *P. gunnari* (within limits set by a generic diagnosis) together with the mosaic character of distribution of diagnostic features, *i.e.*, features proposed by Simpson (1971a), across specimens do not support *Wimanornis* Simpson, 1971 as a distinct genus. *Wimanornis* was based exclusively on two humeri excluded by Simpson (1971a) from the hypodigm of *Eosphaeniscus gunnari* Wiman, 1905 (Simpson replaced *Eosphaeniscus* by *Palaeeudyptes*). Furthermore, specimens that Simpson (1971a) left in *Paleeudyptes* are poorly preserved (*e.g.*, Wiman 1905b: plate V, figs 6 and 8) making detailed comparisons extremely difficult if possible. The out-

put of my analysis agrees with that obtained by Myrcha *et al.* (2002) from the analysis of 126 tarsometatarsi from the Argentine and Polish collections.

Humeri of Antarctic penguins assigned to *Palaeeudyptes* differ somewhat from those from New Zealand. The relative volume of the *fossa pneumatica* is more variable and the shaft is more sigmoid in the former group as suggested by analyses of figures and descriptions in Marples (1952) and Simpson (1971b). Additionally, Simpson (1971b) supplemented his revised diagnosis of *Palaeeudyptes* in the section devoted to humeri with a note: "reference to genus probable but not certain".

Foramen nutricium located proximally at *margo caudalis* of ulna is present in only two specimens (a third bone is problematic), whereas this feature occurs in all specimens assigned to *Anthropornis*. Ulnae assigned here to this genus are characterized by a square-ended *olecranon* (the shape is best pronounced in small bones) – a feature typical, according to Marples (1952), of *Palaeeudyptes* (and *Anthropornis*). Marples (1952) stated that, in *Archaeospheniscus* (New Zealand specimens), the *olecranon* forms "a smooth curve". However, there is no ulna in the Polish collection that can be assigned (by its size) to that genus, so the diagnostic status of the feature remains unclear.

Tibiotarsi that possess distal ends and were assigned to *Palaeeudyptes* provide an excellent opportunity for comparisons with proximal articular surfaces of tarsometatarsi. Tarsometatarsi are holotype specimens of most fossil penguin species (*e.g.*, Simpson 1971a; Myrcha *et al*. 2002), and those which belong to birds from the Antarctic species of *Palaeeudyptes* (differing mainly in size) are quite numerous in the Polish collection (Myrcha *et al*. 2002). I have used this technique in my analyses.

Palaeeudyptes klekowskii Myrcha, Tatur *et* del Valle, 1990
(Figs 7–8)

1990. *Palaeeudyptes klekowskii* sp. nov.; Myrcha *et al.*: p. 197–199, figs 2–4.

Revised diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002). Large humerus with a spacious (small or moderate in volume in *P. gunnari*) *fossa pneumatica* (see "Remarks").

Material. — 27 specimens. Incomplete shaft and sternal end of right coracoid (probably from the same bone), IB/P/B-0854, 0857; left humerus, IB/P/B-0141; left humerus with damaged shaft, IB/P/B-0571; right humerus, IB/P/B-0578 (Fig. 7d–f); right ulna missing distal end, IB/P/B-0133; left ulna missing distal end, IB/P/B-0135; two right ulnae IB/P/B-0344, 0685; left ulna, IB/P/B-0503 (Fig. 7a, b); proximal left ulna IB/P/B-0506; left carpometacarpus, IB/P/B-0331 (Fig. 7c); proximal right tibiotarsus, IB/P/B-0248c; right tibiotarsus with ends and shaft damaged, IB/P/B-0357; proximal left tibiotarsus, IB/P/B-0369; left tibiotarsus IB/P/B-0626 (Fig. 8c, d); left *digitus II phalanx 1* (*os dig. pedis*), IB/P/B-0192a; other referred specimens: incomplete proximal right humerus, IB/P/B-0186; in-

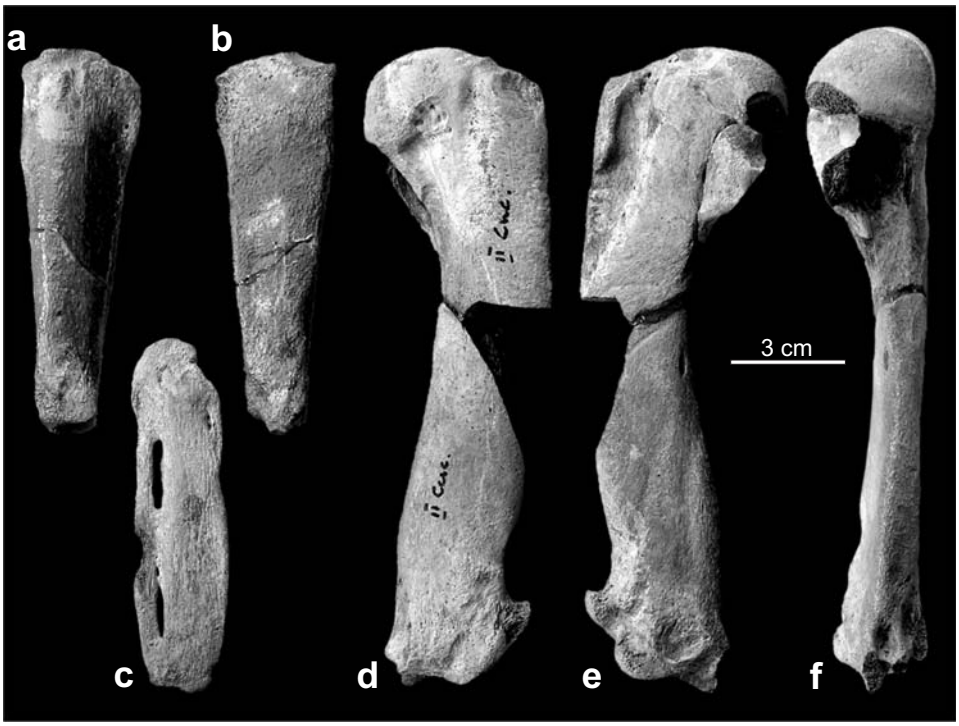

Fig. 7. Selected bones of *Palaeeudyptes klekowskii* Myrcha *et al.*, 1990 from the Polish collection. Ulna (specimen IB/P/B-0503; a – dorsal view, b – ventral view), carpometacarpus (specimen IB/P/B-0331; c – ventral view) and humerus (specimen IB/P/B-0578; d – dorsal view, e – ventral view, f – caudal view).

complete shaft of right humerus, IB/P/B-0372; two incomplete shafts of left humeri, IB/P/B-0375, 0726; two incomplete proximal left humeri, IB/P/B-0383, 0474; incomplete proximal right humerus, IB/P/B-0693; left *os metacarpale majus* and broken *os m. alulare*, IB/P/B-0499; right patella, IB/P/B-0250a (Fig. 8a, b); right *digitus II phalanx 2* (*os dig. pedis*), IB/P/B-0417.

Description. — Coracoid massive. Humerus with undivided *fossa pneumatica* and moderately sigmoid shaft. Relative width of *condylus ventralis humeri* (see description of *A. nordenskjoeldi*) is 4.4 (N = 1). *Olecranon* of ulna proximal and square-ended. Space between *os metacarpale minus* and *os m. majus* divided into two large gaps. Patella large and irregularly wedge-shaped, pierced by *canalis/sulcus m. ambientis*. Its *facies articularis femoralis* is rough and concave. *Facies distalis* and the base of patella (assuming flatness of the latter) form a right angle (or nearly so). *Tuberositas poplitea* and *fossa flexoria* of tibiotarsus well developed. Shaft of tibiotarsus flattened.

Remarks. — In my opinion, the coracoid from Group 3 of Wiman (1905b) should be assigned to this species. The volume of *fossa pneumatica* (for a definition see "Remarks" section for *Anthropornis*) in *P. klekowskii* is 7.1 (probably

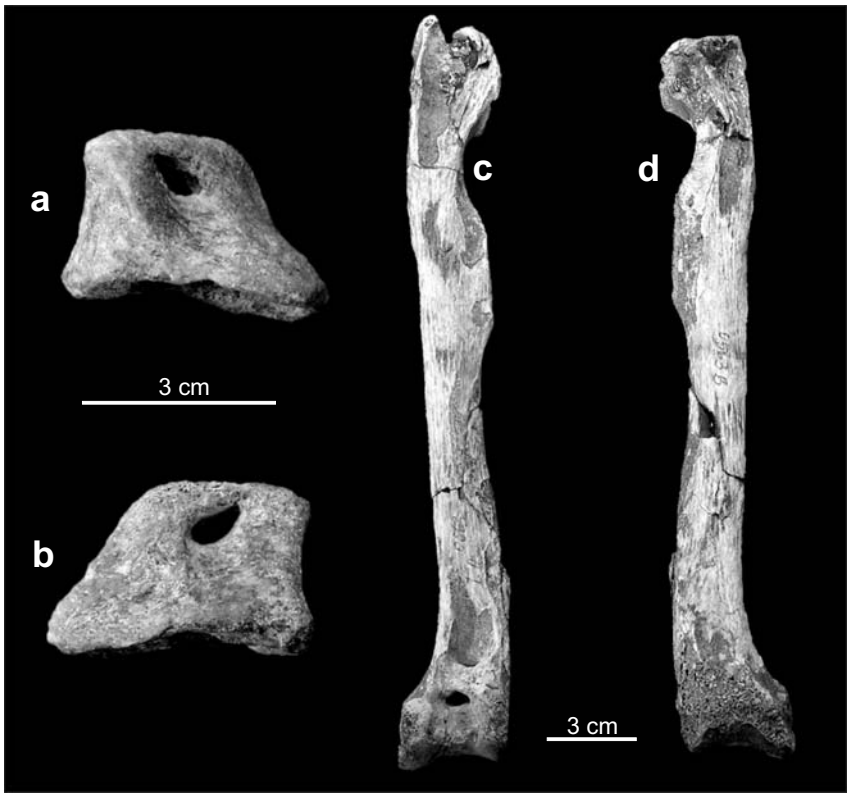

Fig. 8. Selected bones of *Palaeeudyptes klekowskii* Myrcha *et al.*, 1990 from the Polish collection. Patella (specimen IB/P/B-0250a; a – medial view, b – lateral view) and tibiotarsus (specimen IB/P/B-0626; c – cranial view, d – caudal view).

overestimated, based on a single specimen). The shaft of humerus IB/P/B-0578 (Fig. 7d–f) is slightly narrower proximally than distally, whereas the opposite is true for the specimen IB/P/B-0141.

Carpometacarpus IB/P/B-0331 (Fig. 7c) is the only nearly complete bone of this type in the studied collection. As this specimen is much larger than another slender (incomplete) bone of this type, IB/P/B-0145, I have assigned the former to this species. Partial carpometacarpus IB/P/B-0499 is somewhat smaller than IB/P/B-0331, and is referred to this species.

Patella IB/P/B-0250a (Fig. 8a, b) is a large bone though it is smaller than two such bones referred to *A. nordenskjoeldi*. The length of *facies articularis femoralis* is 40.3 mm; its width in the middle is 19.7 mm. The *canalis m. ambientis* is clearly more oval in shape than in those bones. Furthermore, a distal end of the *facies articularis femoralis* is not concave, while the rest of the surface is deeply excavated. In respect to the angle mentioned in the species' description, the studied specimen resembles patellae of *Palaeeudyptes* and *Archaeospheniscus* from New Zealand (see Marples 1952, 1953). A large fragment of tibiotarsus assigned by

Wiman (1905b: plate 3, fig. 4) to his Group 3 more closely resembles IB/P/B-0369 (*P. klekowskii*), than bones described here as *Anthropornis*.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), uppermost Telm5 or Telm6 (single specimen, IB/P/B-0578) and Telm7.

Palaeeudyptes gunnari (Wiman, 1905)
(Figs 9–10)

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. — Tarsometatarsal features as listed by Myrcha *et al.* (2002). Medium-sized humerus with a relatively small or moderate *fossa pneumatica* (cf. the spacious fossa in *P. klekowskii*; see also "Remarks").

Material. — 54 specimens. Two incomplete right coracoids, IB/P/B-0105, 0151 (Fig. 9d, e); incomplete shaft of right coracoid, IB/P/B-0613c; left coracoid, IB/P/B-0175; two incomplete left coracoids, IB/P/B-0136, 0345; incomplete shaft and damaged head of left humerus, IB/P/B-0060; right humerus missing portions of shaft, IB/P/B-0066; four proximal right humeri, IB/P/B-0075, 0187, 0371, 0389; proximal left humerus, IB/P/B-0126; right humerus, IB/P/B-0306 (Fig. 9a–c); incomplete proximal right humerus, IB/P/B-0373; incomplete right humerus, IB/P/B-0451; left humerus, IB/P/B-0472; left humerus missing portions of head and shaft, IB/P/B-0573; right ulna, IB/P/B-0083; right ulna missing fragment of shaft, IB/P/B-0455; proximal left ulna, IB/P/B-0692; right *os metacarpale majus* and broken *os m. alulare*, IB/P/B-0145; two right femora, IB/P/B-0103 (Fig. 10d, e), 0430; distal left femur (partly in matrix) with external bone tissue layer of adjacent tibiotarsus (bones joined by matrix), IB/P/B-0159 (Fig. 10c); two incomplete right femora, IB/P/B-0504, IB/P/B-0655; left femur with damaged proximal end, missing distal end, IB/P/B-0699; two distal right tibiotarsi, IB/P/B-0137b, 0248b; distal left tibiotarsus, IB/P/B-0161a; proximal left tibiotarsus, IB/P/B-0164a; two proximal right tibiotarsi, IB/P/B-0256, 0663; right tibiotarsus, IB/P/B-0654 (Fig. 10a, b); left *digitus III phalanx 1* (*os dig. pedis*), IB/P/B-0409; two right *dig. III phal. 1* (*ossa dig. pedis*), IB/P/B-0413, 0901; right *dig. III phal. 2* (*os dig. pedis*), IB/P/B-0589c; other referred specimens: three incomplete synsacra, IB/P/B-0102, 0319, 0589b (Fig. 9f); three incomplete humeral left scapulae, IB/P/B-0533, 0587a, 0869; two incomplete humeral right scapulae, IB/P/B-0606a, 0610; two incomplete proximal right humeri, IB/P/B-0058, 0168; two distal left humeri, IB/P/B-0144, 0377; incomplete distal right humerus, IB/P/B-0335; incomplete proximal left humerus, IB/P/B-0385; left *digitus IV phalanx 1* (*os dig. pedis*), IB/P/B-0236c.

Description. — *Crista spinosa synsacri* well developed. Coracoid is less robust than *P. klekowskii* but quite wide at its base (estimation only). *Facies articularis sternalis* convex (when viewed from the ventral side). Humerus with undivided *fossa pneumatica* and more or less sigmoid shaft (narrower distally than

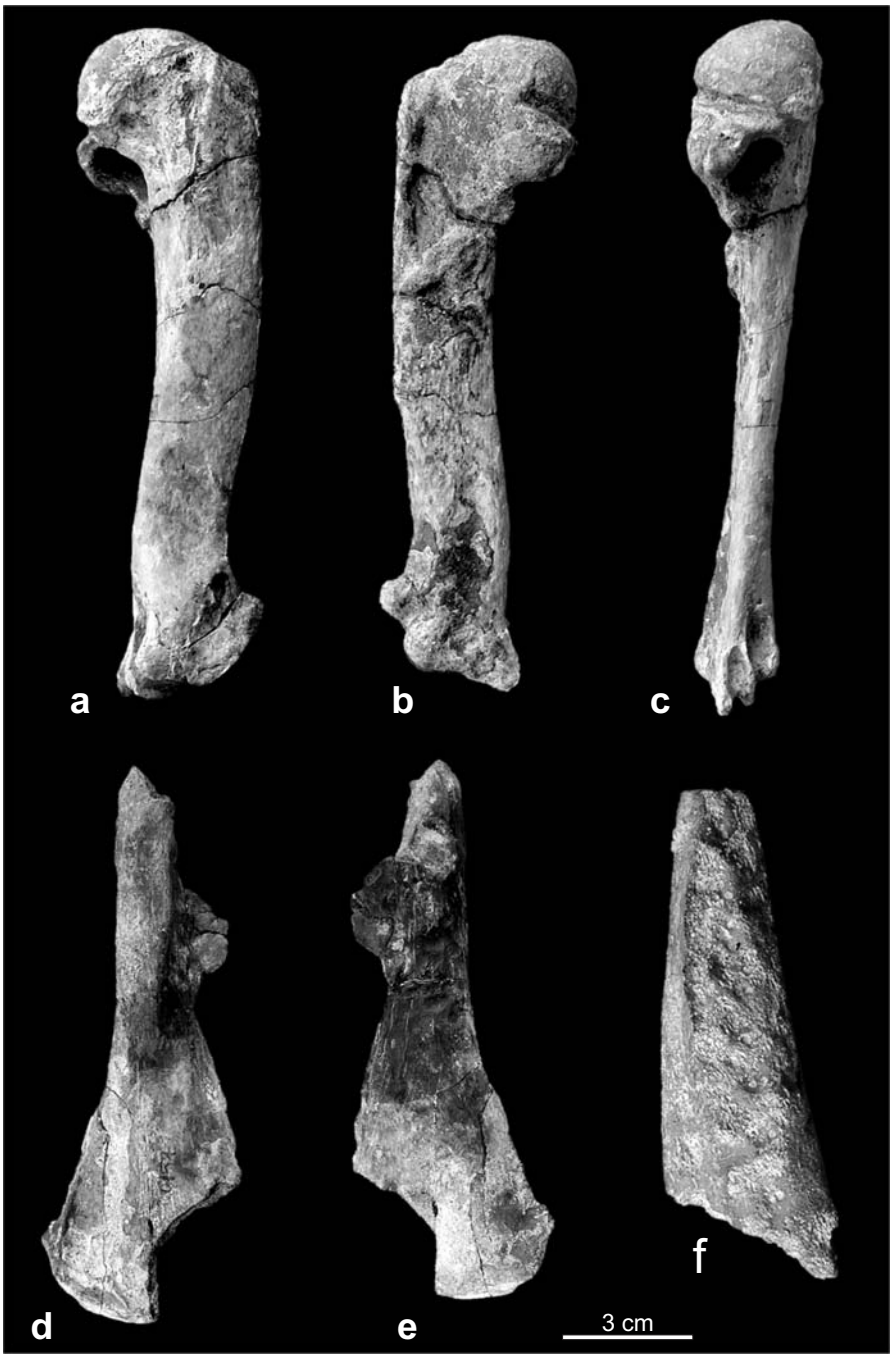

Fig. 9. Selected bones of *Palaeeudyptes gunnari* (Wiman, 1905) from the Polish collection. Humerus (specimen IB/P/B-0306; a – dorsal view, b – ventral view, c – caudal view), coracoid (specimen IB/P/B-0151; d – ventral view, e – dorsal view) and synsacrum (specimen IB/P/B-0589b; f – side view).

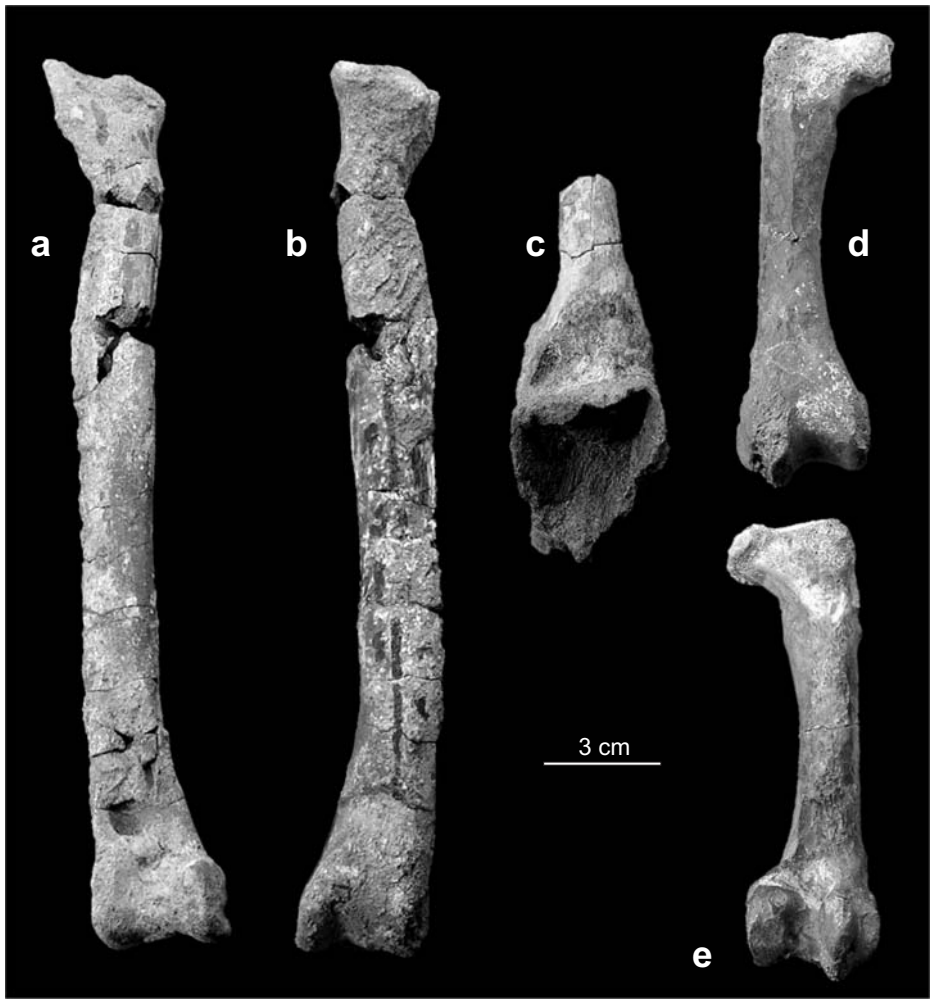

Fig. 10. Selected bones of *Palaeeudyptes gunnari* (Wiman, 1905) from the Polish collection. Tibiotarsus (specimen IB/P/B-0654; a – cranial view, b – caudal view), knee joint (specimen IB/P/B-0159; c – cranial view of femoral component and rotated fragment of adjacent tibiotarsus, represented by external layer of tissue) and femur (specimen IB/P/B-0103; d – cranial view, e – caudal view).

proximally). Relative width of *condylus ventralis humeri* (see description of *A. nordenskjoeldi*) ranges between 4.4 and 5.2 (N = 4, median = 4.5). *Olecranon* of ulna proximal (located close to the proximal articular surface) and square-ended. Femur quite massive (Fig. 11) with a relatively wide distal end, *crista trochanteris* moderately or not prominent. *Tuberositas poplitea* and *fossa flexoria* of tibiotarsus well developed. Shaft of tibiotarsus flattened.

Remarks. — Two partial synsacra, IB/P/B-0102 and IB/P/B-0589b (Fig. 9f), are similar in terms of size to Wiman's (1905b) specimen from his Group 5. This is

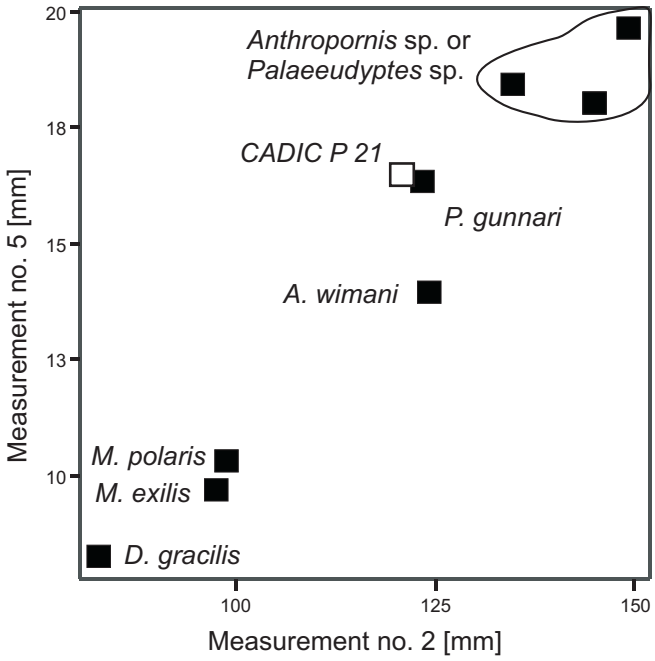

Fig. 11. Plot of femoral measurements no. 2 and 5 (see "Material and methods") for specimens from the Polish collection (see text; black squares) and the specimen from the Eocene of Tierra del Fuego (Clarke *et al*. 2003; white square).

probably also true for a tiny fragment of a caudal part of another synsacrum – IB/P/B-0319. In my opinion, they belonged to *P. gunnari*.

I included five incomplete scapulae in this species (as "other referred specimens"), based exclusively on their dimensions. The relative volume of humeral *fossa pneumatica* (for a definition see "Remarks" section for *Anthropornis*) in *P. gunnari* ranges from 3.2 to 4.6 (N = 7, median = 3.3). For notes on carpometacarpus IB/P/B-0145, see "Remarks" section for *P. klekowskii*.

Wiman's (1905b) femur from his Group 6, in my opinion, ought to be referred to *P. gunnari*. For femora from the Group 5 (Wiman 1905b), the label "*Palaeeudyptes* sp." is appropriate. Specimen IB/P/B-0159 (Fig. 10c) is a unique bone within the entire collection – it is a fragment of the knee joint. Considering its dimensions, the femoral component (see specimen's description) resembles most closely the specimen IB/P/B-0430 (a complete bone identified as *P. gunnari*). The tibiotarsal component is very poorly preserved (see specimen's description), however, it is smaller than a proximal end of IB/P/B-0626 (*P. klekowskii*).

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm7, and a single specimen (IB/B/P-0533) from Telm4–Telm6 (originally labeled as a bone from Unit II *sensu* Elliot and Trautman 1982).

Palaeeudyptes sp.

Material. — 69 specimens. 43 incomplete coracoids, IB/P/B-0104, 0171, 0224, 0237, 0452, 0460, 0461, 0464, 0465b, 0520, 0521, 0530, 0559, 0587e, 0608a, 0611b, 0611c, 0613b, 0616, 0827, 0828, 0830, 0831, 0834, 0842, 0844, 0846, 0850, 0851, 0855, 0856, 0858, 0859, 0860, 0861, 0862, 0873, 0875, 0876, 0880, 0881, 0882, 0884; ten incomplete humeri, IB/P/B-0098, 0379, 0388, 0390, 0453, 0700, 0703, 0719, 0720, 0737; three incomplete tibiotarsi, IB/P/B-0401, 0634, 0662; left tibiotarsus, IB/P/B-0537; two incomplete *ossa dig. pedis* (*digitus* II phalanx 1), IB/P/B-0249b, 0651d; two *ossa dig. pedis* (*digitus IV phalanx 1*), IB/P/B-0414, 0896; eight *ossa dig. pedis* (*digitus II phalanx 1*), IB/P/B-0420, 0424, 0589d, 0895, 0904, 0907, 0913, 0916.

Remarks. — Coracoid IB/P/B-0452, unlike others assigned to *Palaeeudyptes* sp., is quite well preserved. However, its measurements are intermediate in respect to values obtained from specimens described as *P. klekowskii* (N = 1) and *P. gunnari* (N = 6), and the small sample size precludes further analyses. In my opinion, the specimen placed by Wiman (1905b) in his Group 4 should be labeled as "*Palaeeudyptes* sp.". Humeri listed in this section possess either juvenile features or are poorly preserved.

An almost complete tibiotarsus IB/P/B-0537 is of intermediate length in respect to other well-preserved bones, IB/P/B-0626 (*P. klekowskii*) and IB/P/B-0654 (*P. gunnari*). Furthermore, its shaft is clearly narrower than these last two (maybe affected by erosion) as well as possessing a more massive distal end than IB/P/B-0654. Hence its assignment to *Palaeeudyptes* sp.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm4 or Telm5 (three specimens: IB/P/B-0520, 0521 and 0530), uppermost Telm5 or Telm6 (single specimen, IB/P/B-0388) and Telm7.

?*Palaeeudyptes* sp.

Material. — 14 specimens. Right ulna, IB/P/B-0441; left ulna, IB/P/B-0442; eight small fragments of carpometacarpi, IB/P/B-0208, 0264a, 0264d, 0439, 0516, 0629a, 0680, 0681; *os dig. pedis* (*digitus II phalanx 1*), IB/P/B-0163a; three *ossa dig. pedis* (*digitus ?IV phalanx ?1*), IB/P/B-0125b, 0192b, 0919.

Remarks. — Both ulnae are too worn and eroded for precise identification.

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. — Tarsometatarsal features as listed by Myrcha *et al.* (2002). *Facies musculi supracoracoidei* (in humerus) oblique in relation to the axis of the bone (parallel in *Palaeeudyptes*). Relative width of *condylus dorsalis*

humeri (see description of *A. nordenskjoeldi*) clearly larger than in *Anthropornis* and *Palaeeudyptes* (more in "Description" section for *A. wimani*) .

Remarks. — Marples (1952) indirectly stressed the smaller relative width of the sternal end of coracoids from New Zealand assigned to *Archaeospheniscus* compared with those described as *Palaeeudyptes*. This assessment seems to be true also in respect to coracoids from the Polish collection of Seymour Island material. However, their poor preservation precludes total certainty, and this feature is not included here in the generic diagnosis.

In a short listing of humeral features diagnostic at generic level, only those preserved in specimens from all species of *Archaeospheniscus* (see also "Remarks" section for *A. wimani*; Marples 1952 and Simpson 1971b, 1975) were considered here. There is, however, an exception – the humeral head morphology of *A. lopdelli* is not known (Simpson 1971b).

Archaeospheniscus wimani (Marples, 1953)
(Fig. 12)

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

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

Diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002).

Material. — 26 specimens. Incomplete right coracoid, IB/P/B-0466; two incomplete left coracoids, IB/P/B-0467, 0608b; incomplete left humerus, IB/P/B-0176 (Fig. 12a, b); right femur, IB/P/B-0641 (Fig. 12c, d); two shafts of right femora, IB/P/B-0658, 0687; left tibiotarsus, IB/P/B-0110 (Fig. 12e, f); ?left proximal tibiotarsus, IB/P/B-0137a; two incomplete shafts of tibiotarsi, IB/P/B-0218, 0802; incomplete shaft of left tibiotarsus, IB/P/B-0796; *digitus III phalanx 1* (*os dig. pedis*), IB/P/B-0908; other referred specimens: four incomplete right coracoids, IB/P/B-0234, 0832, 0871, 0878; four incomplete left coracoids, IB/P/B-0826, 0840, 0865, 0872; incomplete ?right *os metacarpale majus*, IB/P/B-0689; proximal right tibiotarsus, IB/P/B-0742; three *ossa dig. pedis* (*digitus II phalanx 1*), IB/P/B-0123b, 0534a, 0903.

Description. — Bones of an intermediate size between *Palaeeudypes gunnari* and *Delphinornis larseni* (the latter possessed the largest bones within entire set of small-sized species). Coracoid less massive and probably clearly narrower (estimation only) than in *P. gunnari*. Moderately massive head of humerus with undivided *fossa pneumatica*. The relative volume of *fossa pneumatica* (for a definition see "Remarks" section for *Anthropornis*) is 3.5 (probably overestimated, based on a single specimen). Relative width of *condylus ventralis humeri* (see description of *A. nordenskjoeldi*) is 5.3 (N = 1). Relative width of *condylus dorsalis humeri* (see description of *A. nordenskjoeldi*) is 8.2 (N = 1). Shaft of humerus probably slender. Femur and tibiotarsus slender (Fig. 11). The former bone with a relatively narrow distal end, *crista trochanteris* prominent (unlike in *P. gunnari*). Shaft of tibiotarsus flattened.

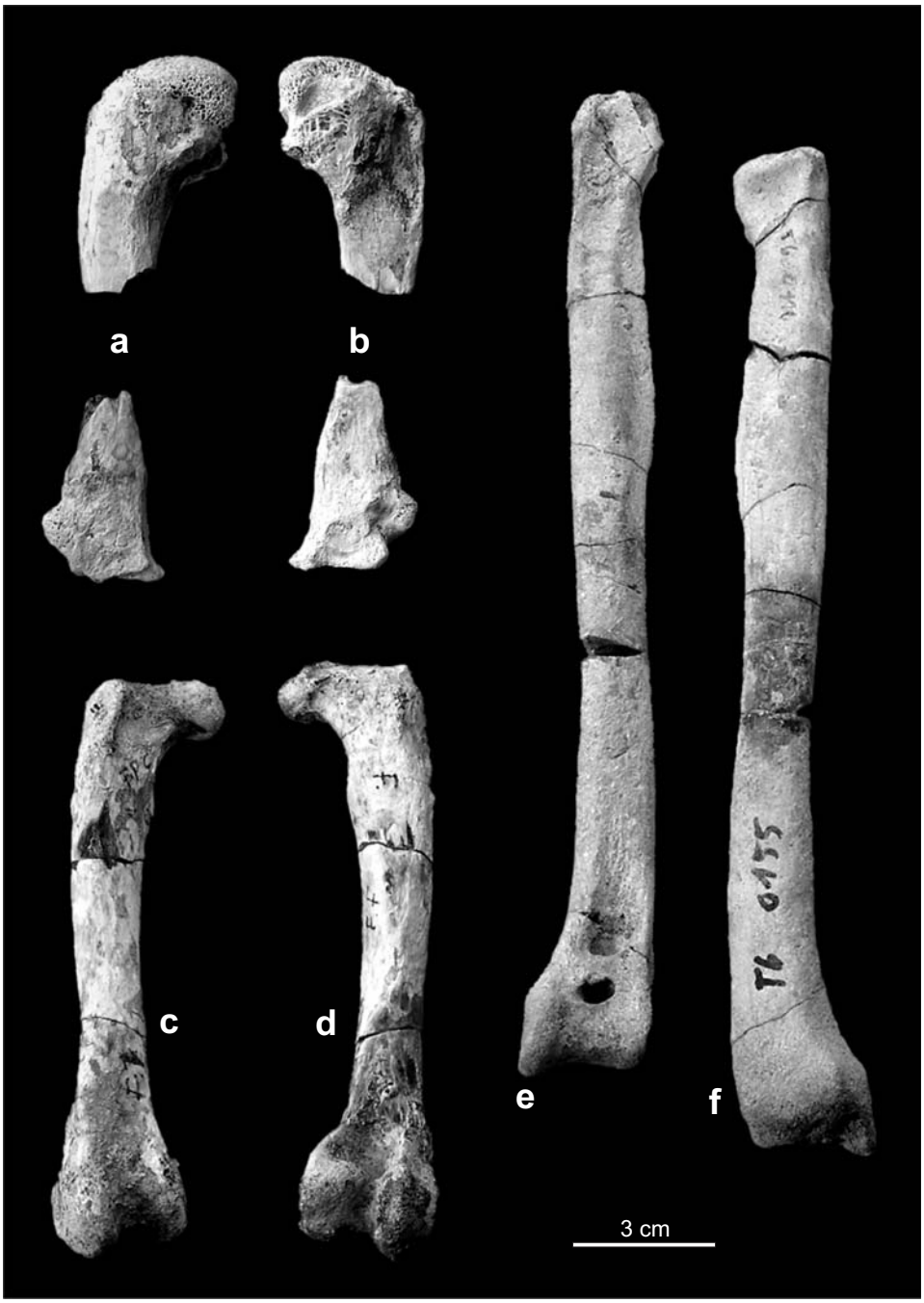

Fig. 12. Selected bones of *Archaeospheniscus wimani* (Marples, 1953) from the Polish collection. Humerus (specimen IB/P/B-0176; a – dorsal view, b – ventral view), femur (specimen IB/P/B-0641; c – cranial view, d – caudal view) and tibiotarsus (specimen IB/P/B-0110; e – cranial view, f – caudal view).

Remarks. — The smallest (in terms of bone dimensions; Fig. 2) and most ancient species within the genus, and the only one known from the Antarctic (*A. lopdelli* Marples, 1952 and *A. lowei* Marples, 1952 come from the Oligocene of New Zealand).

Eight coracoids labeled as "other referred specimens" are in a far worse condition than other such bones included in the "Material" section. Wiman (1905b) included two humeri in his Group 6, but they are too poorly preserved to compare with the only specimen from the Polish collection. A very incomplete fragment of carpometacarpus (IB/P/B-0689) was labeled as a "referred specimen" of *A. wimani* due to its estimated size only. I do not agree with Marples (1952) that "trochanter of the femur not projecting proximally beyond the articular head" is a valid diagnostic feature of the genus, because this feature is not unique to bones referred to *Archaeospheniscus* (*e.g.*, compare Figs 10d and 12c).

Occurrence. — Seymour Island, La Meseta Formation (Eocene), Telm5 (single specimen, IB/P/B-0865), Telm4–Telm6 (single specimen, IB/P/B-0534a, originally labeled as a bone from Unit II *sensu* Elliot and Trautman 1982), Telm7.

Delphinornis Wiman, 1905

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

Type species: *Delphinornis Larsenii* Wiman, 1905.

Revised diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002). *Condylus et epicondylus medialis* of small (see "Description" section for *A. wimani*) tibiotarsus clearly separated. Medial part of the ridge separating *sulcus extensorius* from the bone margin wide (or moderately so). The border between *facies caudalis* of tibiotarsus and its distal articular surface is aligned at right angle (or is slightly oblique) in relation to the bone axis (see "Remarks").

Remarks. — The correctness of assigning bones listed below to this genus is supported by their number. *Delphinornis* is probably the most numerous among the genera of small-sized Antarctic fossil penguins (see Myrcha *et al*. 2002). So far, diagnostic features of *Delphinornis* have been found exclusively in tarsometatarsi (Wiman 1905a, b; Simpson 1971a, Myrcha *et al.* 2002).

Features of femora assigned to this genus as "other referred specimens" (a bowl-like hollow just proximal to *sulcus patellaris* and wide *sulcus intercondylaris*) may be diagnostic at the generic level. However, unknown femur features of *D. arctowskii* and poor preservation of most bones, preclude using them in the diagnosis. Moreover, they are "other referred specimens" as two out of three recognized groups of small femora (*Delphinornis* and *Mesetaornis*) do not exhibit a clear pattern of a size-range distribution observed in tarsometatarsi – the most important diagnostic bones (see Myrcha *et al*. 2002). *Mesetaornis* and *Marambiornis* (formally single-species genera) are represented by both relatively large and small specimens, which suggests that each of them may consist of two species. Such a possibility is also suggested by humeri (see "Problematic specimens" section) and,

in case of *Mesetaornis*, by tarsometatarsi (Myrcha *et al*. 2002). These factors increase the uncertainty associated with the taxonomic position of the bones discussed.

The set of tibiotarsal features listed in the diagnosis does not occur in any bone assigned to other species of small-sized penguins. Specimen IB/P/B-0406 (a bone referred to *Marambiornis exilis*) most closely approximates that condition observed in *Delphinornis*.

Delphinornis larseni Wiman, 1905
(Fig. 13)

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

Diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002).

Material. — 18 specimens. Distal end and a large fragment of shaft of left tibiotarsus, IB/P/B-0337 (Fig. 13g, h); other referred specimens: humeral right coracoid, IB/P/B-0148; incomplete right coracoid, IB/P/B-0246; two humeral left coracoids, IB/P/B-0607, 0611a; incomplete shaft of right coracoid, IB/P/B-0833; incomplete shaft of left coracoid, IB/P/B-0874; right ulna, IB/P/B-0444 (Fig. 13a, b); right radius, IB/P/B-0446 (Fig. 13c, d); proximal right carpometacarpus, IB/P/B-0440; shaft and incomplete distal end of left femur, IB/P/B-0090 (Fig. 13e, f); two distal left tibiotarsi, IB/P/B-0154, 0405; two incomplete shafts of tibiotarsi, IB/P/B-0209, 0812; incomplete proximal tibiotarsus, IB/P/B-0261b; incomplete shaft and broken distal end of right tibiotarsus, IB/P/B-0741; *digitus IV phalanx 1* (*os dig. pedis*), IB/P/B-0428.

Description. — Shaft of ulna radically widening towards the proximal end. Both margins of radius parallel. Notch between *margo cranialis* and *caput radii* probably not developed. Shaft of tibiotarsus probably flattened. Femur with a bowl-like hollow just proximal to *sulcus patellaris*.

Remarks. — Six coracoids included in "other referred specimens" form a group of somewhat larger bones than those that may have belonged to "*Delphinornis*, *Mesetaornis* and/or *Marambiornis*" group (see "Problematic specimens" section), but they are clearly smaller than specimens assigned to *A. wimani*.

Three wing bones (ulna, radius and partial carpometacarpus; Fig. 13a–d) could have belonged to a single individual and their size suggests referral to *D. larseni* (*e.g.*, among ulnae and radii there are specimens of much smaller sizes).

Partial femur IB/P/B-0090 (Fig. 13e, f) is the largest bone of this kind within the set of specimens attributed to small-sized penguins. Tibiotarsus IB/P/B-0337 (Fig. 13g, h) is the largest example of this element within *Delphinornis* and its distal end (both *condyli* and *incisura intercondylaris*) fits the proximal articular surface of the best-preserved tarsometatarsus from the Polish collection assigned to *D. larseni* (Myrcha *et al*. 2002). The other two distal parts of tibiotarsi (IB/P/B-0154 and IB/P/B-0405) resemble the above-mentioned specimen in terms of the width of distal articular surfaces, but have clearly narrower distal parts of their

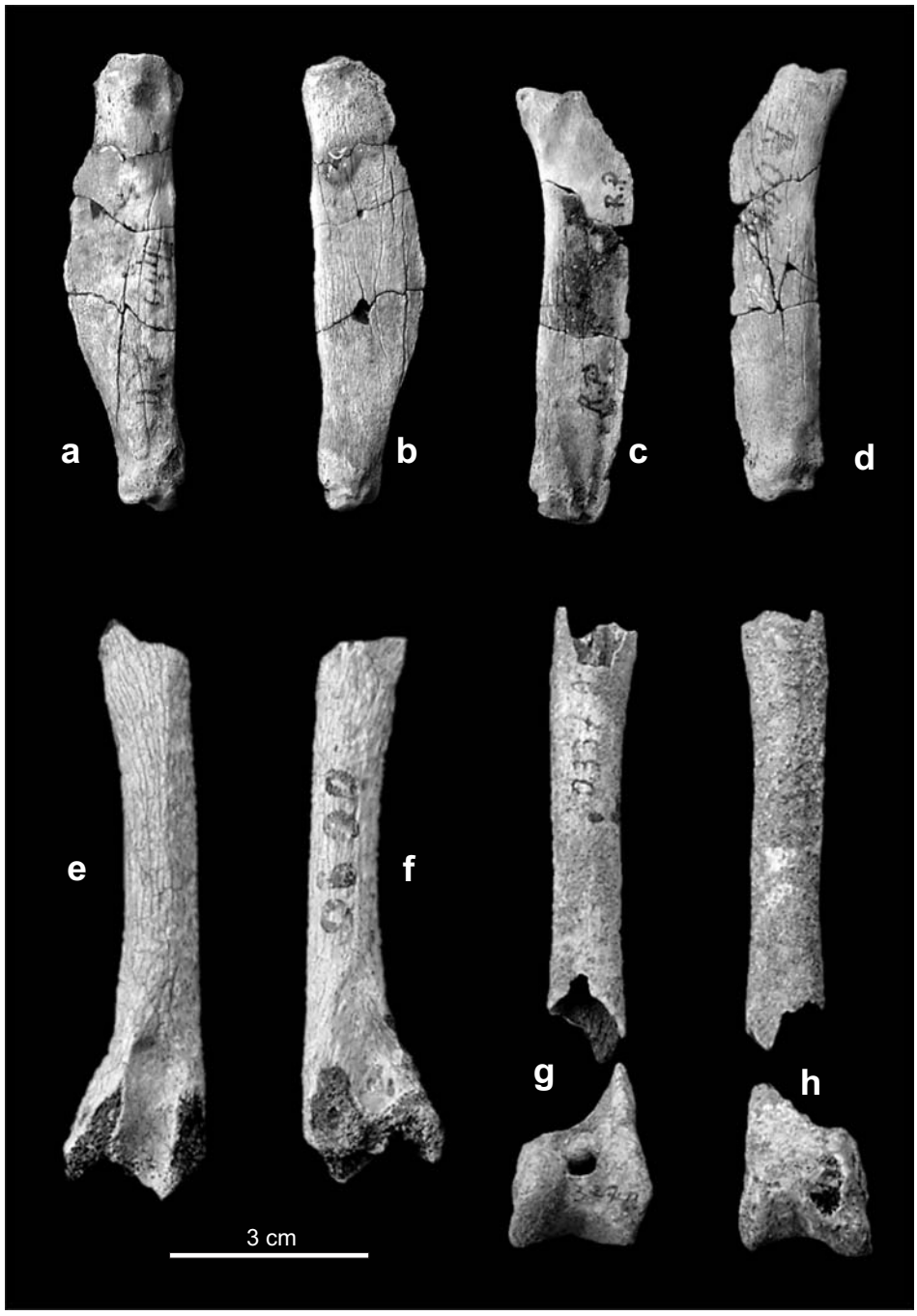

Fig. 13. Selected bones of *Delphinornis larseni* Wiman, 1905 from the Polish collection. Ulna (specimen IB/P/B-0444; a – dorsal view, b – ventral view), radius (specimen IB/P/B-0446; c – dorsal view, d – ventral view), femur (specimen IB/P/B-0090; e – cranial view, f – caudal view) and tibiotarsus (specimen IB/P/B-0337; g – cranial view, h – caudal view).

shafts. Hence assignment to "other referred specimens". Other tibiotarsi were placed in this section because of their size and poor preservation.

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

Delphinornis gracilis Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur *et* del Valle, 2002
(Fig. 14)

2002. *Delphinornis gracilis* sp. n.; Myrcha *et al.*: p. 30–31, fig. 11.

Diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002).

Material. — Two specimens. Distal end with a large portion of shaft of left tibiotarsus, IB/P/B-0408 (Fig.14c, d); other referred specimens: right femur, IB/P/B-0130 (Fig. 14a, b).

Description. — Femur with a bowl-like hollow just proximal to *sulcus patellaris*. *Sulcus intercondylaris* wide.

Remarks. — A distal end (both *condyli* and *incisura intercondylaris*) of tibiotarsus fits the proximal articular surface of the holotype tarsometatarsus from the Polish collection (Myrcha *et al*. 2002).

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

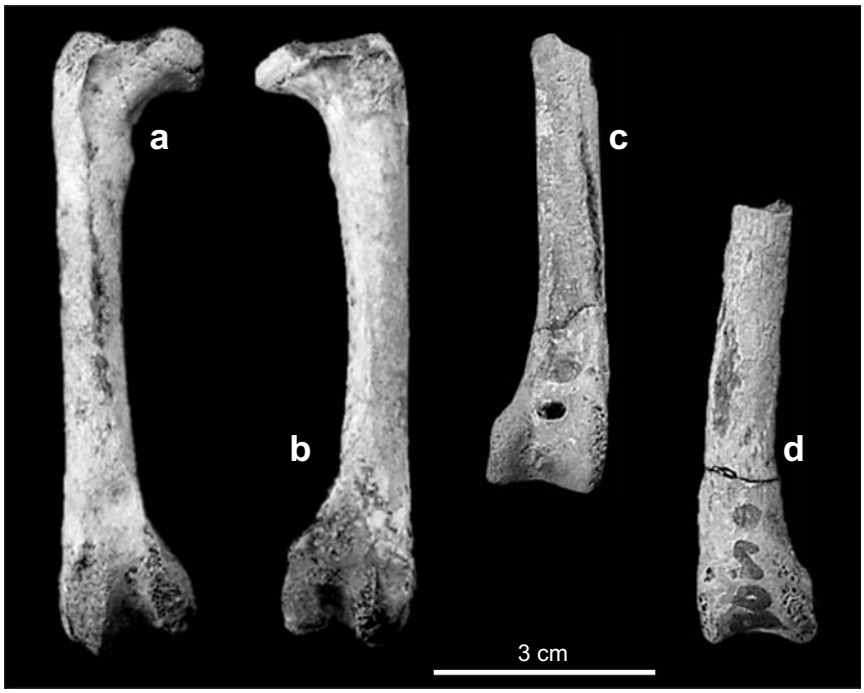

Fig. 14. Bones of *Delphinornis gracilis* Myrcha *et al.*, 2002 from the Polish collection. Femur (specimen IB/P/B-0130; a – cranial view, b – caudal view) and tibiotarsus (specimen IB/P/B-0408; c – cranial view, d – caudal view).

Delphinornis arctowskii Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur *et* del Valle, 2002
(Fig. 15)

2002. *Delphinornis arctowskii* sp. n.; Myrcha *et al.*: p. 31–32, fig. 12.

Diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002).

Material. — Three specimens. Strongly eroded right tibiotarsus, IB/P/B-0115 (Fig. 15a, b); left tibiotarsus missing proximal end, IB/P/B-0266; distal half of right tibiotarsus, IB/P/B-0500.

Description. — Shaft of tibiotarsus flattened. *Tuberositas poplitea* well developed.

Remarks. — Well preserved distal ends (both *condyli* and *incisura intercondylaris*) of tibiotarsi IB/P/B-0266 and IB/P/B-0500 fit the proximal articular surface of the holotype tarsometatarsus from the Polish collection (Myrcha *et al*. 2002).

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

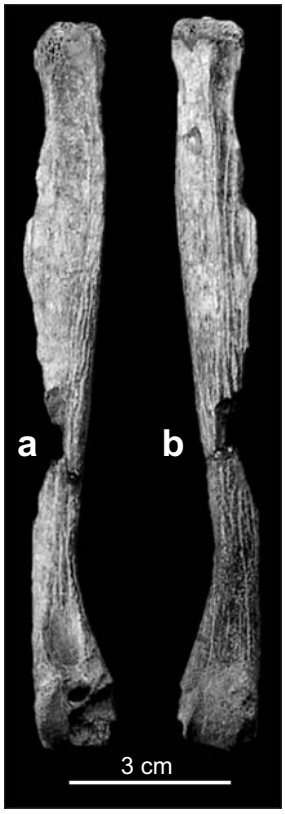

Fig. 15. Tibiotarsus of *Delphinornis arctowskii* Myrcha *et al.*, 2002 from the Polish collection. Specimen IB/P/B-0115; a – cranial view, b – caudal view.

Delphinornis sp.

Material. — One distal shaft of left tibiotarsus, IB/P/B-0744.

Remarks. — Poorly preserved bone with a wide medial part of the ridge separating *sulcus extensorius* from the bone margin.

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

?*Delphinornis* sp.

Material. — Two incomplete femora, IB/P/B-0073, 0437.

Remarks. — Bowl-like hollow just proximal to *sulcus patellaris* possible but not certain in both specimens. Femur IB/P/B-0437 with a wide *sulcus intercondylaris*. Both bones are intermediate in size compared to IB/P/B-0090 (*D. larseni*) and IB/P/B-0130 (*D. gracilis*).

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

Mesetaornis Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur *et* del Valle, 2002

2002. *Mesetaornis* gen. n.; Myrcha *et al.*: p. 32.

Type species: *Mesetaornis polaris* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur *et* del Valle, 2002.

Diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002).

Remarks. — See "Remarks" under *Delphinornis*.

Mesetaornis polaris Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur *et* del Valle, 2002
(Fig. 16)

2002. *Mesetaornis polaris* sp. n.; Myrcha *et al.*: p. 32–33, fig. 13.

Diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002).

Material. — Three bones with a "referred specimens" status (see "Material and methods"): nearly complete right femur, IB/P/B-0215 (Fig. 16a, b); two distal left tibiotarsi, IB/P/B-0207 (Fig. 16c–e), 0656.

Description. — Femur similar, in terms of size, to IB/P/B-0090 (*D. larseni*), but without hollow on *facies cranialis* which is typical of *Delphinornis*. *Sulcus intercondylaris* relatively narrow and deep. *Condylus et epicondylus medialis* of tibiotarsus connected by an osseus ridge. Medial part of the ridge separating *sulcus extensorius* from the bone margin narrow. The border between *facies caudalis* of tibiotarsus and its distal articular surface clearly oblique in relation to the bone axis.

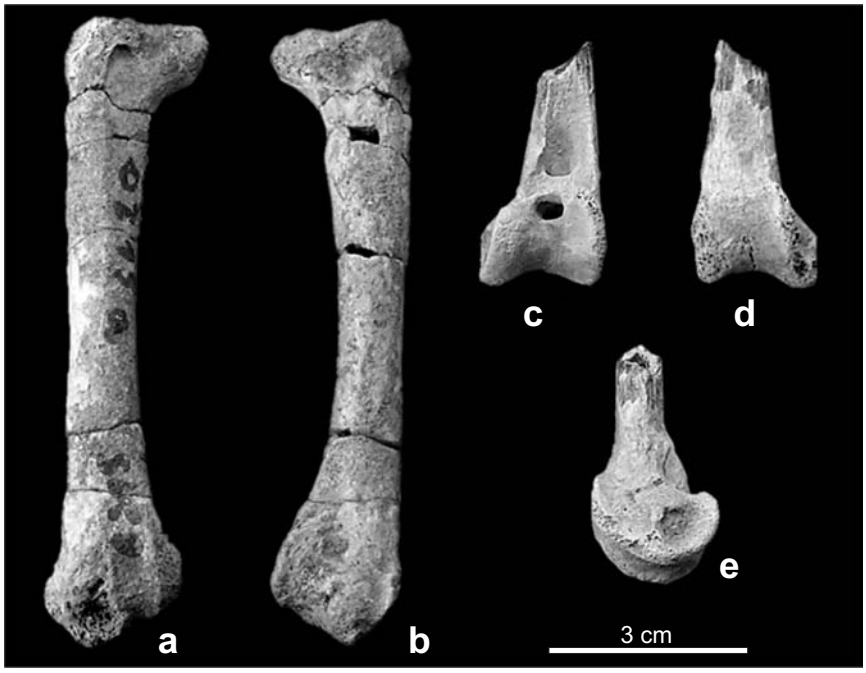

Fig. 16. Selected bones of *Mesetaornis polaris* Myrcha *et al.*, 2002 from the Polish collection. Femur (specimen IB/P/B-0215; a – cranial view, b – caudal view) and tibiotarsus (specimen IB/P/B-0207; c – cranial view, d – caudal view, e – medial view).

Remarks. — Distal ends (both *condyli* and *incisura intercondylaris*) of tibiotarsi articulate well with the proximal articular surface of the holotype tarsometatarsus from the Polish collection (Myrcha *et al*. 2002).

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

?*Mesetaornis* sp.

Material. — One incomplete right femur, IB/P/B-0436.

Remarks. — This specimen possesses both features of femur referred to *M. polaris*, but is a small bone (comparable with IB/P/B-0130 – *D. gracilis*). It has, however, a much more massive *condylus medialis* and narrower *sulcus intercondylaris* than specimen IB/P/B-0130.

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

Marambiornis Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur *et* del Valle, 2002

2002. *Marambiornis* gen. n.; Myrcha *et al.*: p. 34–35.

Type species: *Marambiornis exilis* Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur *et* del Valle, 2002.

Diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002).

Remarks. — See "Remarks" for *Delphinornis*.

Marambiornis exilis Myrcha, Jadwiszczak, Tambussi, Noriega, Gaździcki, Tatur *et* del Valle, 2002
(Fig. 17)

2002. *Marambiornis exilis* sp. n.; Myrcha *et al.*: p. 35–36, fig. 15.

Diagnosis. — Tarsometatarsal features as listed by Myrcha *et al.* (2002).

Material. — Two bones with a "referred specimens" status (see "Material and methods"): complete right femur, IB/P/B-0434 (Fig. 17a, b); distal left tibiotarsus, IB/P/B-0406 (Fig. 17c–e).

Description. — Femur of comparable length to a specimen IB/P/B-0090 (*D. larseni*) and IB/P/B-0215 (referred to *M. polaris*), but clearly less massive. It does not possess a characteristic hollow on *facies cranialis* (cf. *Delphinornis*). *Sulcus patellaris* considerably wider and probably shallower than in IB/P/B-0215 (specimen referred to *M. polaris*) and IB/P/B-0436 (?*Mesetaornis* sp.). *Crista supracondylaris medialis* thin (as in the smallest bones from two other species of small-sized penguins), *sulcus intercondylaris* relatively wide. *Condylus medialis* massive. Tibiotarsus smaller than both specimens referred to *M. polaris*. *Condylus et epicondylus medialis* not connected by an osseus ridge, *condylus medialis* massive. Medial part of the ridge separating *sulcus extensorius* from the bone margin narrow. The border between *facies caudalis* of tibiotarsus and its distal articular surface as in *Delphinornis*.

Remarks. — Distal end (both *condyli* and *incisura intercondylaris*) of tibiotarsus seems to fit the proximal articular surface of the holotype tarsometatarsus

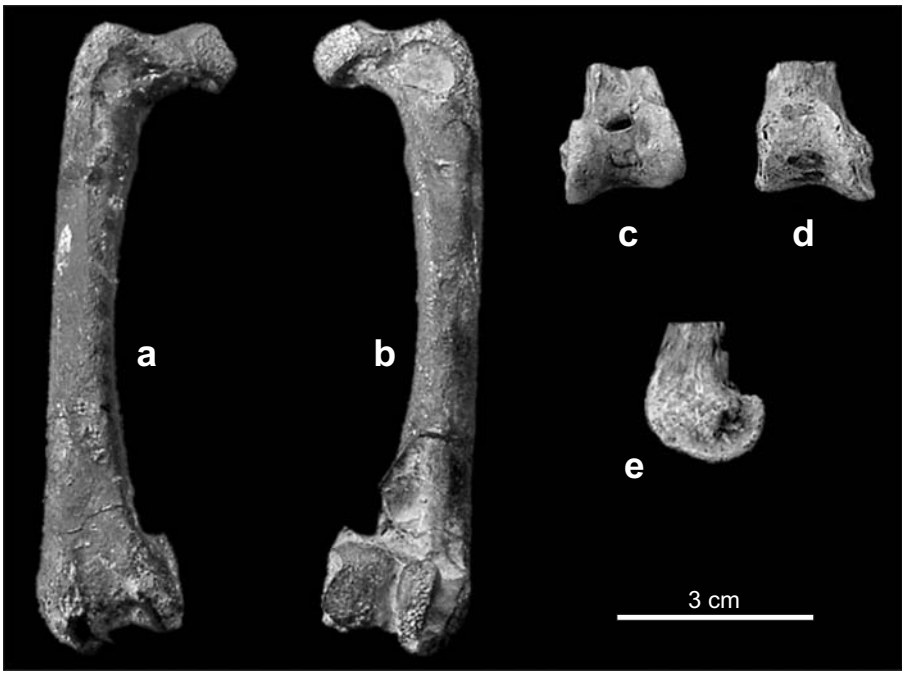

Fig. 17. Bones of *Marambiornis exilis* Myrcha *et al.*, 2002 from the Polish collection. Femur (specimen IB/P/B-0434; a – cranial view, b – caudal view) and tibiotarsus (specimen IB/P/B-0406; c – cranial view, d – caudal view, e – medial view).

from the Polish collection (Myrcha *et al*. 2002). However, I cannot exclude the possibility that this specimen belonged to an individual from a small *Delphinornis* species.

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

?*Marambiornis* sp.

Material. — One nearly complete left femur, IB/P/B-0458.

Remarks. — Femur of comparable length to smaller specimens from discussed taxa of small-sized penguins. Features as in specimen IB/P/B-0434, but *condylus medialis* not massive.

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

Problematic specimens

Skull and face (*cranium et facies*). — The Polish collection includes eight specimens from the cranial region that cannot be assigned to any known species. The most spectacular specimen (IB/P/B-0167) is a nearly complete, large and dagger-shaped upper jaw (see also Myrcha *et al*. 1990: fig. 5; Jadwiszczak 2003:

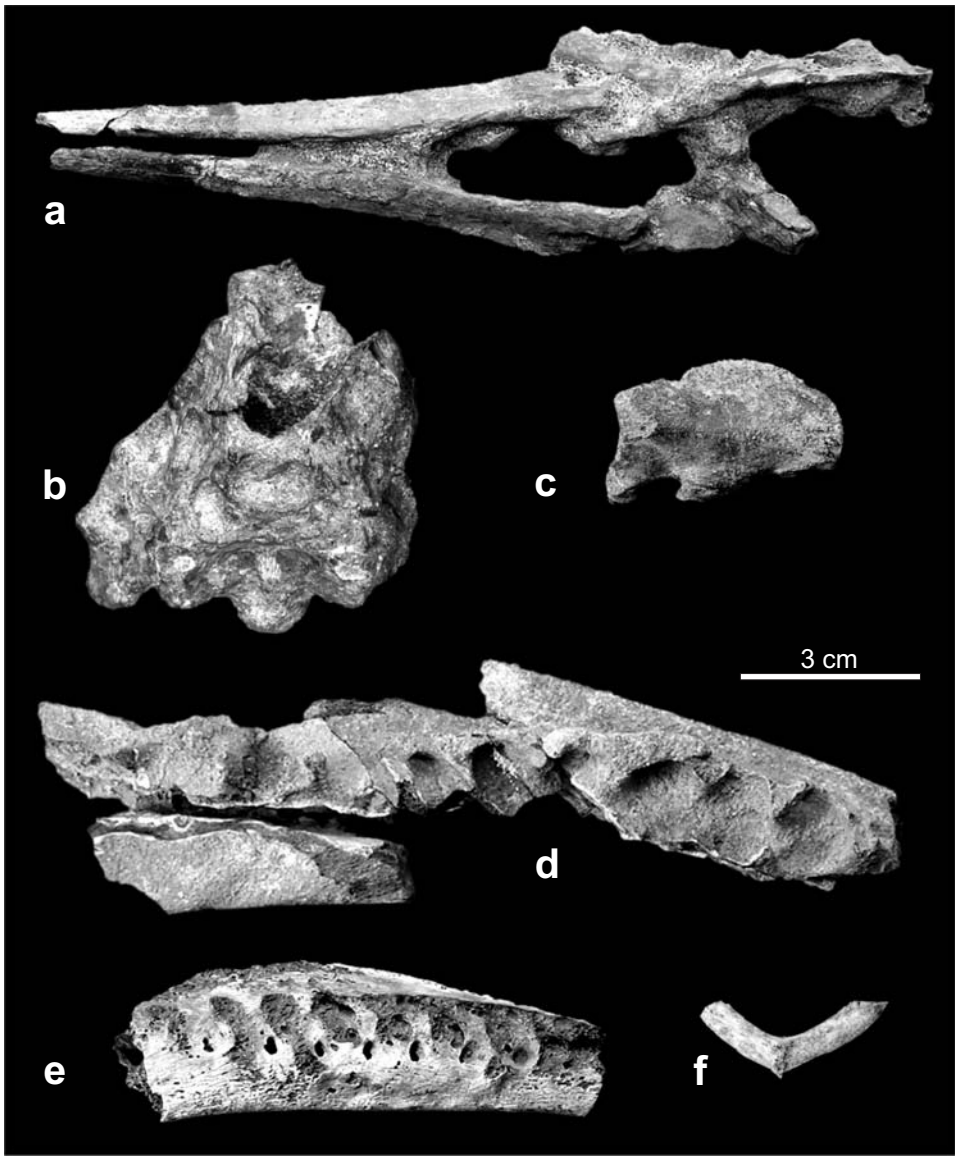

Fig. 18. Selected problematic bones from the Polish collection (see text for details). Mandible (specimen IB/P/B-0653; a – ventral view), neurocranium with a cranial base (specimen IB/P/B-0346; b – ventral view), pygostylus (specimen IB/P/B-0107; c – side view), synsacrum (specimen IB/P/B-0853; d – side view), synsacrum (specimen IB/P/B-0149; e – side view) and clavicle (specimen IB/P/B-0889; f – ventral view).

fig. 2) and the fragment of *os frontale* of the same individual. Myrcha *et al*. (1990) described it as ?*Palaeeudyptes* sp. (and suggested *P. klekowskii*), and I (in my previous papers: Jadwiszczak 2000, 2003) labeled this fossil as "*Anthropornis* sp. or *Palaeeudyptes* sp.". I believe the latter referral, after omitting *P. gunnari*, is more

accurate. The only formally presented remains of a fossil penguin bill from Seymour Island (excluding the Polish collection) are those described by Olson (1985: fig. 11) as ?*Palaeeudyptes* sp. Although, Olson's (1985) specimen has a much less complete region of an upper jaw than the specimen here, it also has considerable bill elongation. The partial *os frontale* is very narrow and, in respect to its size, closely resembles its counterpart from New Zealand labeled as "*Palaeeudyptes* sp." (Marples 1952, Simpson 1971b).

The incomplete mandible IB/P/B-0653 (Fig. 18a), by its estimated size, is larger and more stoutly constructed than its counterpart from the skeleton of a King Penguin (*Aptenodytes patagonicus*) – the species with the longest bill within recent Sphenisciformes. Moreover, the specimen comes from a skeleton of a clearly smaller bird than that discussed earlier. Hence, it seems likely that the partial mandible could have belonged to *Palaeeudyptes gunnari* or *Archaeospheniscus wimani*. Other cranial elements include three small fragments of a bill skeleton (IB/P/B-0955, 0956 and 0964) that are too fragmentary for identification.

Specimen IB/P/B-0346 (Fig. 18b) is an incomplete and deformed fragment of neurocranium (this and IB/P/B-0167 are the only fragments of a penguin brain case known from the Paleogene of Seymour Island; see also Marples 1952 and Simpson 1971b). It resembles the neurocranium of the King Penguin in size, but is more stoutly constructed and possesses a much larger *condylus occipitalis*. These features indicate that this bone belonged to a larger bird, most likely *A. wimani*, or to a small individual of *P. gunnari*. It has well developed temporal *fossae* which extend dorsally to the midline. The bifid paroccipital processes are produced both ventro-laterally and posteriorly. The *foramen magnum* is somewhat oval in shape. All specimens are from the unit Telm7 of the La Meseta Formation.

Vertebral column (*columna vertebralis*). — None of the 64 vertebrae from the Polish collection can be assigned to any recognized species or genus. A *pygostylus* IB/P/B-0107 (Fig. 18c) is the only bone of this kind known from the Seymour Island. The vertebrae that form the pygostyle can be easily recognized, suggesting a young age for the bird. Most of the other specimens can be divided into several categories: *vertebrae cervicales* (31 items), *vertebrae thoracicae* (13 items plus 5 so-called *v. cervicodorsales*) and *vertebrae caudales liberae* (3 items). Three additional vertebrae were labeled as "*vertebrae cervicales* or *v. cervicodorsales*" and eight other bones cannot be assigned to any category (because of their poor preservation). An intriguing feature of some cervical vertebrae (*e.g.*, IB/P/B-139 and IB/P/B-140) is their considerable elongation, *e.g.*, for IB/P/B-0139 the length-to-width ratio exceeds 5 (measurements 1 and 3 were used; see Table 9).

I sorted the examined set of vertebrae, basing solely on their dimensions, into two multigeneric taxonomic groups (Table 3). This method, which is the only approach possible in this case, was applied also to synsacra (all are incomplete). The largest bone within the collection, IB/P/B-0853 (Fig. 18d), appears to be compara-

Table 3

Taxonomical and anatomical identification of fossil penguin vertebrae (problematic specimens) from the Polish collection.

Taxonomic position	Specimens (IB/P/B)	Position within vertebral column
Anthropornis sp. and *Palaeeudyptes* sp. (maybe also *Archaeospheniscus wimani*)	0057, 0071, 0094b, 0111, 0122, 0128, 0139, 0140, 0143, 0198, 0205, 0219, 0308, 0315, 0316, 0320, 0629b, 0943	*vertebrae cervicales* 6-9
	0314, 0321, 0622	*vertebrae cervicales* 9
	0177, 0323, 0479	from left: *v. cervicalis* 10-13, 10-11, 12-13
	0166, 0311	*vertebrae cervicales*
	0188, 0220, 0310, 0527, 0922	*vertebrae cervicodorsales.*
	0528, 0926, 0928	*vertebrae cervicales* or *vertebrae cervicodorsales.*
	0063, 0086, 0160, 0235, 0239, 0309, 0312, 0313, 0925	*vertebrae thoracicae*
	0196	*vertebra caudalis*
	0107	*pygostylus*
genera of small-sized penguins: *Delphinornis, Mesetaornis, Marambiornis* (maybe also somewhat larger *Archaeospheniscus wimani*)	0181, 0317, 0570a, 0933	*vertebrae cervicales* 6-9
	0322	*vertebra cervicalis*
	0116	*vertebra thoracica*
	0934	*vertebra caudalis*
other specimens	0318, 0892, 0929	*vertebrae thoracicae*; too poorly preserved to consider their taxonomic position
	0240	*vertebra caudalis*; too poorly preserved to consider its taxonomic position
	0326, 0459c, 0468, 0651, 0930, 0938, 0940, 0942	too poorly preserved to consider both taxonomic and anatomical position

ble, in terms of size, with Wiman's (1905b) synsacrum no. 3 and presumably belonged to *Anthropornis* (both species of this genus ought to be taken into account) or *Palaeeudyptes klekowskii* (see also specimens referred to *P. gunnari*). Specimens IB/P/B-0328 and IB/P/B-0329, probably fragments of same bone, can be only labeled as "*Palaeeudyptes* sp. or *Archaeospheniscus wimani*". A clearly smaller specimen, IB/P/B-0149 (Fig. 18e), belonged to an individual from one out of three small-sized penguin genera: *Delphinornis*, *Mesetaornis* or *Marambiornis*. The very poorly preserved synsacrum IB/P/B-0330a cannot be confidently referred to any group. All specimens are from the unit Telm7 of the La Meseta Formation.

Sternum (*sternum*). — Three very fragmentary sterna represent two groups. Specimens IB/P/B-0327 and IB/P/B-0456 (fragments of a wide *margo costalis*) may be *Anthropornis* sp. and/or *Palaeeudyptes* sp. Width of *margo costalis* at the level of the second *processus costalis* (counting from *trabecula lateralis*) is 11.4 mm (specimen IB/P/B-0327). Size of the third specimen (IB/P/B-0353), represented by the region of contact of *carina sterni* and well developed even *sulcus*

articularis coracoideus, suggests a referral to *Palaeeudyptes gunnari* or *Archaeospheniscus wimani*. Width of the base of *carina sterni* near *margo cranialis* is 10.1 mm. So far, the only such fragment from Seymour Island was described by Marples (1953) and assigned to *Anthropornis nordenskjoeldi*. All specimens are from the unit Telm7 of the La Meseta Formation.

Scapula (*scapula*). — Most of the scapulae from the studied collection cannot be assigned to any recognized species or genus. I assigned these poorly preserved bones, based on their sizes, to two groups. The "*Anthropornis* sp. and/or *Palaeeudyptes* sp." group includes seven specimens: IB/P/B-0236, 0469, 0470, 0517, 0606b, 0835 and 0836. Furthermore, for the same reason, this referral seems appropriate to me for Wiman's (1905b) scapula no. 3. His scapula no. 6 (Wiman 1905b) is far too incomplete for taxonomic considerations. The second set consists of two bones (IB/P/B-0498 and IB/P/B-0887) belonging to individuals from probably two small-sized penguin species, as suggested by differences in width and degree of bending of *collum scapulae*. All specimens are from the unit Telm7 of the La Meseta Formation.

Coracoid (*coracoideum*). — Eight small fragmentary coracoids (IB/P/B-0080, 0210, 0465a, 0614, 0630, 0841, 0883 and 0886) could have belonged to birds from one or more species from the following genera: *Delphinornis*, *Marambiornis* and *Mesetaornis*. The fragmentary nature of coracoids (IB/P/B-0589e, 0829, 0838, 0839, 0845, 0849, 0863, 0866, 0877) excludes any taxonomic identification. All but one of the specimens are from the unit Telm7 of the La Meseta Formation. Coracoid IB/P/B-0863 was originally labeled from Unit II (*sensu* Elliot and Trautman 1982), which corresponds to the units Telm4–Telm6.

Clavicle (*clavicula*). — Clavicles of most birds form a *furcula* and the Polish collection of fossil penguin bones includes one specimen (IB/P/B-0889; Fig. 18f) from unit Telm7 of the formation, the only one known from Seymour Island. Width of the preserved *synostosis interclavicularis* is ca 7.1 mm or ca 8.3 mm (depending on the location of measurement points). The specimen has a poorly developed *apophysis furculae* – a feature observed in *Palaeeudyptes* from New Zealand (Marples 1952, Simpson 1971b). The taxonomic position of the specimen here remains, however, unknown.

Humerus (*humerus*). — Forty-nine fragmentary humeri from the Polish collection are devoid of characteristic features (due to poor preservation), but their sizes suggest that they represent large and medium-sized penguins (Table 4). Three genera can be considered: *Anthropornis*, *Palaeeudyptes* and *Archaeospheniscus*.

Seventeen humeri from the collection represent considerably smaller penguins (Table 4). Furthermore, those bones are morphologically variable. The distribution of features across specimens as well as their unsatisfactory preservation (with one exception) excludes any unequivocal taxonomic assignment. So far, six spe-

Table 4

Taxonomical identification of fossil penguin humeri (problematic specimens) from the Polish collection (see text for explanation of group IDs).

Taxonomic position	Specimens (IB/P/B)	
Anthropornis sp. and/or *Palaeeudyptes* sp. (maybe also *Archaeospheniscus wimani*)	0087, 0106, 0138, 0153, 0165, 0170, 0202, 0228, 0231, 0242, 0254, 0261a, 0374, 0376, 0378, 0382, 0384, 0387, 0391, 0393, 0394, 0396, 0449, 0475, 0482, 0514, 0538, 0539, 0691, 0695, 0704, 0705, 0706, 0707, 0708a, 0709, 0713, 0714, 0717, 0718, 0721, 0722, 0723, 0725, 0727, 0728, 0729, 0730, 0734	
Genera of small-sized penguins: *Delphinornis*, *Mesetaornis* and *Marambiornis*	group A1	0131, 0132, 0710
	group A2	0398, 0574a, 0712
	group B	0382, 0397, 0471
	other specimens	0199, 0447, 0574b, 0688, 0694, 0697, 0735, 0736

cies (grouped in four genera; Table 1) of small Antarctic fossil penguins have been erected (Wiman 1905a, b; Myrcha *et al*. 2002). One species (the only representative of its genus), *Ichtyopteryx gracilis* Wiman, 1905 is based on a tiny fragment of tarsometatarsus and Simpson (1971b, p. 383) called it "essentially indeterminate at present". However, the fossil material suggests a larger number of small-sized penguin species than those five already described (Myrcha *et al.* 2002).

I sorted specimens with well preserved heads into two groups (called "A" and "B"; Table 4). Six bones from group A possess a well developed (quite wide) groove between *margo caudalis* and the hollow limited by the articular surface of *caput humeri*, *facies m. supracoracoidei* and *f. m. coracobrachialis caudalis*. Three other humeri (group B) have a narrow groove.

Group A can be divided into two subgroups. Three specimens forming the subgroup A1 share three unique features:

1. Conspicuous, though narrow, groove parallel to *facies m. pectoralis*.
2. Narrow *facies m. coracobrachialis caudalis*.
3. A pocket formed by the hollow described in previous paragraph, which plunges proximally into the bone tissue.

The third feature is obvious in specimen IB/P/B-0132 (Fig. 19a, b) and is suggested by preserved parts of two other bones (Table 4).

Subgroup A2 is evidently heterogeneous. Bone IB/P/B-0712 resembles specimens from subgroup A1 in respect to the first and probably third feature. However, it possesses wide *facies m. coracobrachialis caudalis*. Specimen IB/P/B-0398 (Fig. 19e, f) also has wide *facies m. coracobrachialis caudalis*, but lacks the characteristic groove described above. Moreover, it possesses the third feature from above. Specimen IB/P/B-0574a has a very wide *facies m. coracobrachialis caudalis* and lacks the characteristic groove (a scar on the bone surface is most likely a juvenile character), but the hollow discussed above is developed similar to bones from group B. Furthermore, the *fossa pneumatica* is very small.

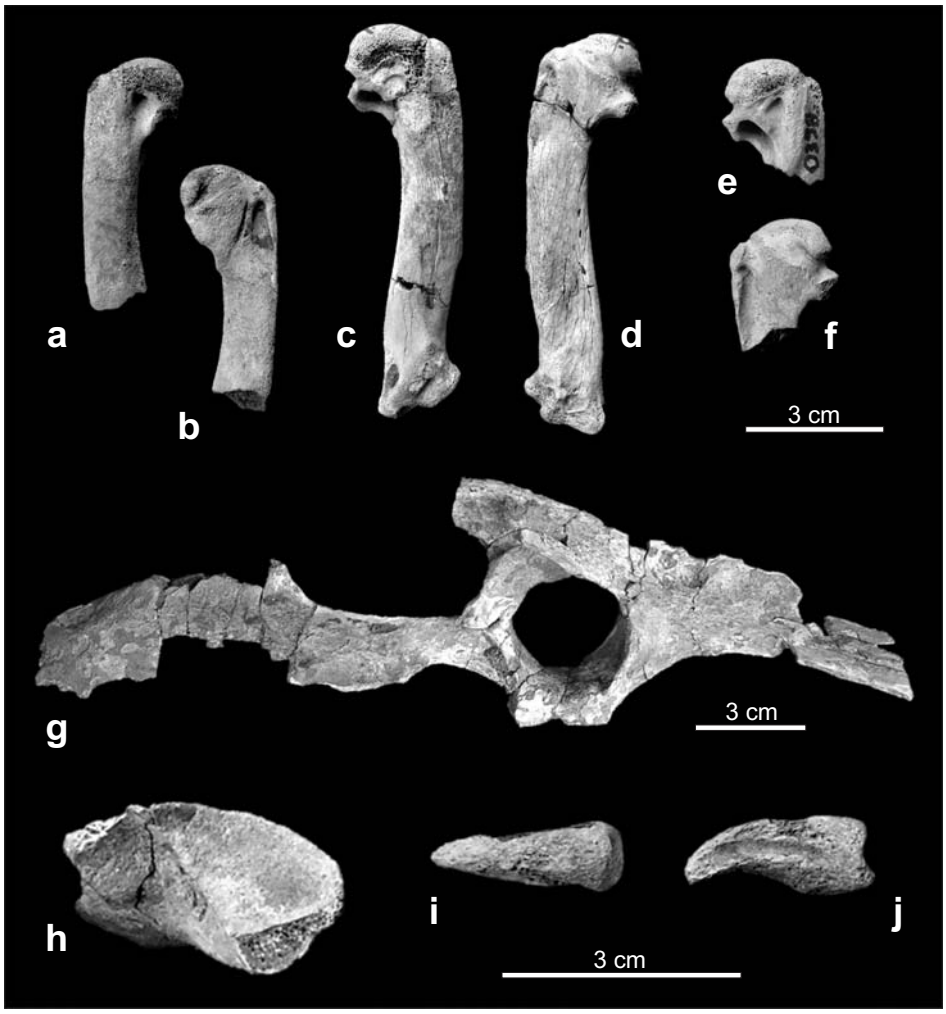

Fig. 19. Selected problematic bones from the Polish collection (see text for details). Humerus A1 (specimen IB/P/B-0132; a – dorsal view, b – ventral view), humerus B (specimen IB/P/B-0382; c – dorsal view, d – ventral view), humerus A2 (specimen IB/P/B-0398; e – dorsal view, f – ventral view), hip bone (specimen IB/P/B-0488; g – lateral view), another hip bone (specimen IB/P/B-0595; h – cranial fragment of acetabular surface) and ungual phalanx (specimen IB/P/B-0271a; i – dorsal view, j – side view).

Specimens IB/P/B-0382 (an almost complete humerus; Fig. 19c, d) and IB/P/B-0471 (two out of three humeri from group B) share, despite size differences, two additional features: *facies m. coracobrachialis caudalis* is narrow and the hollow between the articular surface of *caput humeri*, *facies m. supracoracoidei* and *f. m. coracobrachialis caudalis* is clearly bipartite. The former feature is also found in IB/P/B-0397, though the *facies* is much shorter. Because of the poor preservation of the bone, other features cannot be compared.

Two additional heads of humeri, IB/P/B-574b and IB/P/B-0694, lack (due to erosion) features that would assign them to either group above. The former specimen resembles IB/P/B-0382 in terms of the overall size and form of the hollow. Its *facies m. coracobrachialis caudalis* is, however, wide. Its *fossa pneumatica* is small (spacious in IB/P/B-0382). In all well preserved heads of small humeri (*e.g.*, IB/P/B-0382, 0398, 0132) *fossa pneumatica* is bipartite. Six specimens represent the more distal parts of humeri only.

All but five specimens discussed above are from the unit Telm7 of the La Meseta Formation. The exceptions are humeri IB/P/B-0538, 0539, 0713, 0714 originally labeled as bones from Unit II (*sensu* Elliot and Trautman 1982), which corresponds to the units Telm4–Telm6, and a single bone (IB/P/B-0717) from unit Telm5.

Ulna (*ulna*). — Fourteen large ulnae from the Polish collection, IB/P/B-0079, 0088, 0097, 0118, 0178, 0229, 0395, 0473, 0679, 0683, 0696, 0702, 0731 and 0732, because of their poor preservation, can only be referred to "*Anthropornis* sp. and/or *Palaeeudyptes* sp.". Nearly complete (though strongly eroded) specimen IB/P/B-0612 is clearly smaller than ulna IB/P/B-0444, which I included in a set of "other referred specimens" of *Delphinornis larseni*. All specimens are from the unit Telm7 of the La Meseta Formation.

Radius (*radius*). — Only one out of 16 analyzed radii can be (with some doubt) assigned to a species (IB/P/B-0446, see specimen listing at *Delphinornis larseni*). The rest of those bones, based on their sizes, may be divided into three groups. The first group contains the largest bones (IB/P/B-0152, 0172, 0448, 0715, 0738, 0824) belonging to individuals from one or two genera of large-sized penguins (*Anthropornis* and *Palaeeudyptes*). Specimen IB/P/B-0172 has a strikingly massive proximal end as well as relatively thin adjacent portion of shaft. This "swollen" fragment could be a result of a degenerative process rather than a diagnostic feature. The bone is, however, too incomplete to allow further considerations. Specimen IB/P/B-0738, probably the largest radius in the collection, is represented by a small and strongly eroded fragment of the proximal end.

A set of smaller remains can be labeled as "*Palaeeudyptes* sp. and/or *Archaeospheniscus wimani*". It is a heterogeneous group, though not in terms of bone sizes. Two specimens (IB/P/B-0156 and IB/P/B-0233) are clearly less stout proximally than another (IB/P/B-0445). Other bones from this group are either intermediate in respect to this feature (IB/P/B-0620b; eroded fragment) or represent more distal parts of radii (IB/P/B-0238, 0270 and 0682). Two of the smallest radii, IB/P/B-0690 and IB/P/B-0262b (both are incomplete and eroded), belonged to individuals from one or more genera of small-sized penguins: *Delphinornis*, *Mesetaornis* or *Marambiornis*.

All but two specimens are from the unit Telm7 of the La Meseta Formation. Specimen IB/P/B-0715 is from unit Telm5 and another one, IB/P/B-0690, was

originally labeled as a bone from Unit II (*sensu* Elliot and Trautman 1982), which corresponds to the units Telm4–Telm6.

Other wing bones. — Specimen IB/P/B-0204 (*phalanx proximalis digiti majoris*) is strongly eroded, but smaller (its length is 50.6 mm) than a well preserved bone assigned to *Anthropornis nordenskjoeldi* (IB/P/B-0684; its length is 53.4 mm). Nevertheless, it probably belonged to a large bird, either *Anthropornis* or *Palaeeudyptes*. It is larger than Marples' (1953) specimen from the British collection described as *A. nordenskjoeldi*, but smaller than the bone examined by Jenkins (1974). This bone comes from the unit Telm7 of the La Meseta Formation.

Hip/coxal bone (*os coxae*). — Ten very incomplete (except IB/P/B-0488, which is just incomplete) hip bones from the Polish collection are the only such specimens known from Seymour Island. This set is dominated by bones of large-sized penguins (*Anthropornis* and *Palaeeudyptes*) and is evidently heterogeneous. Specimens with a preserved cranial portion of *acetabulum* can be divided into two morphologically different groups. The first (specimens: IB/P/B-0488 [Fig. 19g], 0625 and 0627) is characterized by the non-interrupted, despite well marked narrowing, surface of *acetabulum*. In bones IB/P/B-0203 and IB/P/B-0595 (Fig. 19h), the continuity of the above-mentioned surface is broken by abrupt narrowing. In other massive remains, IB/P/B-0570b, 0927 and 0931, this portion is not preserved. Fragmentary *ilium* IB/P/B-0211 and *ischium* IB/P/B-0924 belonged to small-sized penguins (*Delphinornis*, *Mesetaornis* and/or *Marambiornis*). All specimens are from the unit Telm7 of the La Meseta Formation.

Femur (*femur*). — Sixty-three femora out of 92 analyzed specimens I referred to "*Anthropornis* sp. and/or *Palaeeudyptes* sp." (Table 5). This set contains both complete (*e.g.*, IB/P/B-0108, 0227, 0230, 0342, 0457 and 0643) and incomplete large bones (Fig. 11) lacking characteristic features and differing in their sizes. They are, however, smaller than specimens assigned to *A. nordenskjoeldi* and larger than those assigned to *P. gunnari*. Seven poorly preserved femora (Table 5)

Table 5

Taxonomical identification of fossil penguin femora (problematic specimens) from the Polish collection.

Taxonomic position	Specimens (IB/P/B)
Anthropornis sp. and/or *Palaeeudyptes* sp.	0059, 0082, 0108, 0129, 0158, 0161b, 0164b, 0164c, 0216, 0227, 0230, 0241, 0243, 0342, 0367, 0370, 0381, 0431, 0432, 0435, 0457, 0481, 0495, 0496, 0508, 0509, 0577, 0637, 0638, 0640, 0643, 0645, 0646, 0647, 0650, 0657, 0677, 0740, 0743, 0746, 0747, 0754, 0755, 0757, 0763, 0764, 0765, 0778, 0781, 0782, 0785, 0786, 0787, 0788, 0789, 0791, 0792, 0794, 0798, 0799, 0810, 0811, 0822
Genera of small-sized penguins: *Delphinornis*, *Mesetaornis* and *Marambiornis*	0507, 0518, 0758, 0801, 0816, 0817, 0885

belonged to individuals from one or more genera of small-sized penguins: *Delphinornis*, *Mesetaornis* and/or *Marambiornis*.

All but three specimens are from the unit Telm7 of the La Meseta Formation. Specimen IB/P/B-0577 comes from the unit Telm4 and other two bones, IB/P/B-

Table 6

Taxonomical identification of fossil penguin tibiotarsi (problematic specimens) from the Polish collection.

Taxonomic position	Specimens (IB/P/B)
Anthropornis sp. and/or *Palaeeudyptes* sp.	0069, 0074, 0096, 0173, 0225, 0232, 0248a, 0332, 0334, 0359, 0361, 0364, 0365, 0366, 0400, 0402, 0433, 0505a, 0505b, 0510, 0526, 0572, 0633, 0642, 0648, 0652, 0659, 0661, 0664, 0665, 0666, 0667, 0668, 0669, 0671, 0672, 0673, 0674, 0748, 0751, 0762, 0766, 0768, 0770, 0771, 0772, 0773, 0774, 0780, 0783, 0795, 0797, 0804, 0821
P. gunnari and/or *Archaeospheniscus wimani*	0535, 0745, 0749, 0750, 0752, 0753, 0759, 0760, 0775, 0776, 0777, 0793, 0800, 0803, 0805, 0806, 0807, 0808, 0814
Mesetaornis polaris or *Marambiornis exilis*	0333
Delphinornis sp. and/or *Mesetaornis polaris* and/or *Marambiornis exilis*	0260c, 0619a, 0644, 0649, 0756, 0769, 0809, 0815, 0820, 0918

Table 7

Taxonomical and anatomical identification of fossil penguin phalanges (problematic specimens) from the Polish collection.

Digit	Phalanx	Taxonomic position	Specimens (IB/P/B)
?II	?1		0902
II	2	*Palaeeudyptes gunnari* or *Archaeospheniscus wimani*	0185
III	1	*Palaeeudyptes klekowskii* and/or *Anthropornis nordenskjoeldi*	0410, 0411, 0893, 0894, 0897, 0911
		Palaeeudyptes sp. and/or *Anthropornis grandis*	0095a, 0095c, 0182, 0184, 0195, 0200, 0412, 0623, 0899, 0910, 0915
?III	?1		0123a
III	2	*Palaeeudyptes* sp. and/or *Anthropornis* sp.	0117a, 0418, 0419, 0427, 0582c, 0900, 0906, 0912
III	3	*Palaeeudyptes* sp. and/or *Anthropornis* sp.	0125c, 0429, 0493a, 0917
IV	1	*Palaeeudyptes klekowskii* and/or *Anthropornis* sp.	0117c, 0416, 0898
IV	2–4	*Palaeeudyptes* sp. and/or *Anthropornis* sp.	0191, 0236a, 0426
		?	0157b
?	*phalanx ungualis*	*Palaeeudyptes* sp. or *Anthropornis* sp.	0271a
?	?		0117b, 0125a, 0157a, 0157c, 0157d, 0163b, 0180, 0236b, 0245, 0249a, 0260a, 0260b, 0415, 0422, 0423, 0425, 0493b, 0511a, 0511b, 0511c, 0511d, 0511e, 0534b, 0905, 0914

0746 and IB/P/B-0747, were originally labeled as bones from Unit II (*sensu* Elliot and Trautman 1982), which corresponds to the units Telm4–Telm6.

Tibiotarsus (*tibiotarsus*). — Fifty-four different fragments of tibiotarsi (Table 6) characterized by moderately large size and poor preservation form a group labeled as "*Anthropornis* sp. and/or *Palaeeudyptes* sp.". Another 19 shafts or their fragments (Table 6) could have belonged to small individuals of *Palaeeudyptes gunnari* and/or larger representatives of *Archaeospheniscus wimani*.

A small and slender tibiotarsus IB/P/B-0333 (shaft and adjacent portions of both ends of a bone) possesses a relatively narrow medial portion of the ridge separating the *sulcus extensorius* from the bone margin. This feature is typical of *Mesetaornis* and *Marambiornis*. Ten small tibiotarsi (Table 6) are too poorly preserved for taxonomic consideration.

Most of specimens are from the unit Telm7 of the La Meseta Formation. Tibiotarsus IB/P/B-0526 is from the unit Telm4 or Telm5, another one (IB/P/B-0745) – from the unit Telm5. Eight additional bones (IB/P/B-0535, 0633, 0748, 0749, 0750, 0751, 0752 and 0753) are from Unit II (*sensu* Elliot and Trautman 1982), which corresponds to units Telm4–Telm6.

Phalanges (*ossa digitorum pedis*). — Table 7 contains a list of phalanges, which due to their poor preservation cannot be assigned to any genus at a reasonable level of confidence, or to species when two genera are represented. Two specimens, IB/P/B-0192a and IB/P/B-0271a (Fig. 19i, j), are of particular interest. The former possesses a conspicuous convex scar – an obvious mark of a healed trauma or a result of a degenerative process; the latter is the only penguin ungual phalanx known from Seymour Island. All specimens are from the unit Telm7 of the La Meseta Formation.

Measurements

Table 8

Measurements of head bones from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3	4	5	6	7	8	9
Anthropornis nordenskjoeldi	0094a								9.0	
	0189									24.4
Anthropornis sp. or *Palaeeudyptes klekowskii*	0167	232[1]	6.6							
Archaeospheniscus wimani or *P. gunnari*	0346			12.3[1]	16.0[1]	12.7	7.5	58.0[2]		

[1] approximate value owing to poor preservation of a specimen

[2] estimated value

Table 9

Measurements of vertebrae from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters. Abbreviations: C - *vertebrae cervicales*, C/T – *vertebrae cervicodorsales*, T – *vertebrae thoracicae*, Cd – *vertebrae caudales liberae*.

Specimens (IB/P/B)	Region of vertebral column	1	2	3	4
0139	C	48.7[1]	37.2	9.0	19.5[1]
0140	C	48.1[1]	43.1[1]	12.4	33.4
0943	C	47.1[1]		11.4	
0205	C	42.4[1]	22.1[1]	14.4	
0128	C	45.2	26.0	12.6	33.5
0111	C	41.8	20.3	21.4	36.6
0308	C	42.6[1]	19.4	16.9	34.2
0094b	C	41.4[1]	17.4		
0316	C		19.6	20.7	32.2
0320	C	38.8[1]		10.9	22.8
0322	C		22.3[1]	14.5	
0629b	C	38.8[1]	25.7[1]	14.6	
0122	C	34.0			
0166	C			18.5	
0317	C	26.9[1]	15.8	9.2[1]	17.9
0219	C		30.8[1]	12.4	
0181	C	34.2[1]		5.3[1]	
0570a	C	29.8[1]	8.9[1]	12.0	
0314	C	37.9[1]	20.1[1]	17.9[1]	
0143	C	37.0	15.0[1]		40.6
0315	C	39.1[1]	31.4[1]	13.7	
0198	C		29.3	21.4	44.1
0622	C	34.4	21.3	19.6	39.2
0321	C	27.7	18.8	16.9	32.7
0323	C	40.9		22.1	
0071	C			14.3	
0933	C	22.7[1]		14.1	
0311	C		21.7	19.4	
0479	C	28.7		23.0[1]	
0188	C/T		34.5[1]	25.1	33.0
0310	C/T	30.8[1]	28.9	12.4	
0220	C/T	32.4	33.5[1]		
0527	C/T	25.6[1]			
0116	T		23.6	12.4	13.7
0235	T		39.4	16.9	21.4
0239	T		25.9	14.1[1]	
0312	T	23.0[1]		12.8[1]	
0160	T	30.2[1]	29.9	13.2[1]	
0086	T		28.0[1]	10.1[1]	
0318	T		29.5[1]	13.8	18.4
0313	T		34.4[1]	14.4[1]	15.1[1]
0309	T	32.1[1]	29.4	14.5[1]	14.7
0892	T		34.6	14.5	18.2
0240	Cd		8.4		
0934	Cd	11.2	7.3		

[1] approximate value owing to poor preservation of a specimen

Table 10

Measurements of synsacra from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3	4
Anthropornis sp. or *Palaeeudyptes klekowskii*	0853	18.2			
Palaeeudyptes gunnari	0102		16.8		27.4
	0589b	18.5	14.7	34.1	24.8
Palaeeudyptes sp. or *Archaeospheniscus wimani*	0328		16.0[1]		
Delphinornis sp. or *Marambiornis exilis* or *Mesetaornis polaris*	0149	13.7	11.0	24.7[1]	19.4[1]

[1] approximate value owing to poor preservation of a specimen

Table 11

Measurements of scapulae from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3
Anthropornis sp. and/or *Palaeeudyptes* sp.	0263	21.1	7.5	
	0469		7.5	11.2
	0470	19.1[1]	8.4	
	0517	18.0	6.4	9.5
	0606b			10.4
	0835	17.9[1]	8.3	10.4
	0836	18.2	8.3	
Palaeeudyptes gunnari	0587a			8.4
	0606a	17.8[1]	6.1	
	0610		6.3	
	0869			8.0[1]
Delphinornis sp. and/or *Mesetaornis polaris* and/or *Marambiornis exilis*	0498	9.1	3.4	4.5
	0887	8.2[1]	3.9	

[1] approximate value owing to poor preservation of a specimen

Table 12

Measurements of coracoids from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3	4	5	6	7	8
Anthropornis nordenskjoeldi	0463			23.5				17.3	16.8
Anthropornis grandis	0454	197[1]	152.9	20.7	26.7	14.4	38.0	16.5	16.7
Palaeeudyptes klekowskii	0857				25.0	13.7			
Palaeeudyptes gunnari	0105			14.5	20.1	10.3		12.3	13.4
	0136		121.5	16.3	20.7	9.9	26.2	12.6	14.6
	0151		110.8		19.7	9.4	26.2	13.1	12.2
	0175	146.2[1]	113.9	16.4	19.1	10.7	31.5	13.6	13.6
	0345		116.0		19.4	10.6		12.9	13.4
	0613c			15.9[1]	18.6	9.6	27.9	12.0	12.1
Archaeospheniscus wimani	0466		113.6[1]	12.5[1]		9.3[1]	26.6	11.7	12.1
	0467			12.1	18.5	9.3	26.9	9.9[1]	
	0608b		108.7	11.8	18.7	9.3		9.8[1]	10.4
	0234			14.1	16.8[1]	9.2			
	0826				17.6	9.1			12.1[1]
	0840				19.8[1]	6.4[1]			
	0865				18.2	8.6			
	0871				17.2	8.8			
	0878							9.9	11.8
Delphinornis larseni	0246				15.2[1]	7.6[1]			10.7[1]
	0148				15.6	6.9	26.7	10.2	10.7
	0607				14.1	9.2		9.6[1]	10.2
	0611a			12.0	13.6	8.6		9.7[1]	10.6[1]
	0833				14.7	8.6			
	0874				16.2	7.9			
Delphinornis sp. and/or *Mesetaornis polaris* and/or *Marambiornis exilis*	0080			8.5	10.2	5.7	17.1	8.5[1]	8.1
	0210				9.9[1]	6.5[1]			7.5[1]
	0465a			9.3	11.0	6.2	8.9	9.9[1]	9.3
	0614				9.5	6.1		6.7[1]	8.0
	0630			7.9			9.0[1]		7.0[1]
	0841				12.4[1]	5.8[1]			
	0883							8.2[1]	7.0
	0886			8.2	10.1		15.4	8.2	8.0[1]

[1] approximate value owing to poor preservation of a specimen

Table 13

Measurements of humeri from the Polish collection (*A. nordenskjoeldi – P. gunnari*). Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3	4	5	6	7	8	9	10	11
Anthropornis nordenskjoeldi	0091			44.8[1]	28.9[1]							
	0092							32.9[1]	15.0[1]		19.1[1]	9.2[1]
	0119	152.2	99.2[1]	44.4[1]	27.7[1]	36.7[1]	18.5	33.3[1]	15.3[1]		18.8	8.3
	0307									44.1	18.8	7.6
	0478			45.6	31.2[1]	34.6	18.4[1]					
	0711									45.3[1]	19.2[1]	8.4[1]
Anthropornis grandis	0179		100.0[1]	36.7[1]	21.6[1]	32.1	17.9	30.8	14.0			
	0590					32.3						
Palaeeudyptes klekowskii	0141	150.4[1]	93.5[1]		24.1[1]	28.6	13.5	27.5	11.6	36.2[1]	16.0[1]	
	0571			39.4	28.1[1]		16.6	28.6	12.0		21.2[1]	
	0578	158[1]			27.6[1]	28.0	15.2	28.5	11.3		20.6	9.1
	0372						12.7[1]	28.9	12.2			
	0726							27.8	13.4			
	0186			36.4[1]		27.9	16.0					
	0375							30.9	13.1			
	0474			37.5[1]		26.0	12.9					
Palaeeudyptes gunnari	0060		84.6	32.9[1]			13.2	22.9	10.3			
	0066			31.9	20.9	25.3	14.2	22.4[1]	9.8[1]	35.8[1]	16.6	8.2
	0075			35.6								
	0126			35.6[1]	22.6	25.9	13.2					
	0187			33.2[1]	19.1[1]	24.5						
	0306	144.1	87.7	32.7	23.8[1]	24.4		23.1	9.9	38.0	16.5	7.2
	0371			36.1	21.7	26.7	13.1					
	0373						15.2					
	0389			35.8[1]								
	0451	142.2		33.1[1]		23.4[1]				39.1	16.4	8.5
	0472		90.2	37.0	22.3	26.6	15.1	25.8	12.8			
	0573			35.4[1]		24.7	13.5[1]		10.3[1]	30.4[1]	14.0[1]	6.5[1]
	0144							23.3[1]	10.4		12.5[1]	6.5[1]
	0335							24.3	10.9		15.5	6.9[1]
	0377							22.9	11.2	28.2[1]	13.7[1]	6.1[1]
	0058					28.4	13.7					
	0168			31.7[1]								
	0385			30.7[1]								

[1] approximate value owing to poor preservation of a specimen

Table 14

Measurements of humeri from the Polish collection (*Palaeeudyptes* sp., *A. wimani* and the smallest specimens). Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position		Specimens (IB/P/B)	1	2	3	4	5	6	7	8	9	10	11
Palaeeudyptes sp.		0098				17.8[1]	20.1[1]	10.0					
		0379			29.7[1]	18.4[1]	22.6	13.1					
		0388				20.6[1]	22.5	10.8[1]					
		0390					22.3[1]	11.4	21.0	8.4[1]			
		0453					19.9[1]	9.9					
		0700					18.1	7.8	18.7	7.2			
		0703				18.4	21.0	10.7					
		0719					22.1	10.8	21.7	9.4		11.6[1]	
		0720					21.5	10.0	21.5	8.3			
		0737							20.3	8.2			
Archaeospheniscus wimani		0176				18.0[1]	17.5[1]	9.0[1]			30.1[1]	12.1	6.4
Delphinornis sp. and/or *Mesetaornis polaris* and/or *Marambiornis exilis*	A1	0131			17.3[1]		11.1	6.2	11.5	5.3			
		0132		52.5	17.9[1]	11.8[1]	12.5	6.5	13.4	5.8			
		0710				13.2[1]	13.5[1]	7.3[1]					
	A2	0398			18.8[1]	12.8	13.0	7.7					
		0574a			16.8[1]	12.3	11.3	5.9					
		0712				13.1[1]	12.5						
	B	0382	91.3	58.4	21.7[1]	14.6	15.2	7.4	16.1	6.6	21.5[1]	10.4	6.6
	Other specimens	0199									15.3[1]	7.2[1]	3.9[1]
		0447					13.0[1]	5.7[1]	13.1	6.2[1]			
		0574b				14.6							
		0688					9.5	3.9	10.1	4.0			
		0694					12.8[1]	6.8[1]					
		0697					9.1	4.2	10.1	4.2			
		0735					9.7	5.1					
		0736					11.9	7.4	12.8	5.9			

[1] approximate value owing to poor preservation of a specimen

Table 15

Measurements of ulnae from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3	4	5	6	7	8	9
Anthropornis nordenskjoeldi	0150	114.7	18.4[1]	17.6[1]			25.0	9.5	19.8	11.9[1]
Anthropornis grandis	0064	103.2	18.8	18.9	35.4	12.3	21.1	8.2[1]	16.0	13.2
	0443		16.4	18.6	35.1[1]	12.7				
	0109		16.0	14.9[1]	31.4	12.7				
Palaeeudyptes klekowskii	0133		16.7[1]							
	0135		13.9[1]	16.4	31.0	11.8				
	0344	95.2	17.5	18.1	33.5	14.7	20.4	8.3	16.3[1]	13.4
	0503	101.7	15.5[1]	16.1[1]		13.0[1]	19.9	7.9	15.1[1]	13.5
	0506		18.8	17.6						
	0685	98.8	16.3[1]	16.8[1]	32.7[1]	14.7	20.5	7.8	16.7	10.5[1]
Palaeeudyptes gunnari	0083	82.4	15.2	14.3	30.0	11.5	18.5	6.9	13.9	10.6
	0455		13.3	14.2	25.5	10.3	15.9	6.5	11.8	10.8
	0692		15.0[1]	13.6[1]	29.3[1]	11.8				
?*Palaeeudyptes* sp.	0441	91.1	15.7	15.4[1]			18.0	8.0	12.0[1]	8.3[1]
	0442	89.2	14.4	14.4			20.7[1]	7.4	12.1[1]	9.9[1]
Anthropornis sp. and/or *Palaeeudyptes* sp.	0079									14.9
	0088									
	0097		13.6[1]	12.7[1]	23.0[1]	10.8[1]				
	0118								16.0[1]	13.2
	0178									10.4[1]
	0229		17.7	17.3						
	0395								16.8[1]	14.2
	0473								13.6	12.9
	0679								14.6[1]	11.5[1]
	0683								11.4[1]	8.8[1]
	0702								14.9	11.1
	0731								15.9[1]	12.0[1]
Delphinornis larseni	0444	68.9	7.2[1]	9.3			14.9[1]	4.5	9.3	8.6
Delphinornis sp. or *Mesetaornis polaris* or *Marambiornis exilis*	0612	60.6	6.4[1]	6.9			10.0[1]	4.1	6.4[1]	5.0[1]

[1] approximate value owing to poor preservation of a specimen

Table 16

Measurements of radii from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3	4	5	6	7	8	9
Anthropornis sp. and/or *Palaeeudyptes* sp.	0152		15.4[1]	12.0	21.9	6.8				
	0172		15.8[1]	12.8[1]	21.0[1]	10.2[1]				
	0448		14.7[1]	10.4[1]	21.3	7.9				
	0715		14.9	11.1	21.2	7.9				
	0738		16.8[1]							
	0824			12.7	19.1[1]	12.0				
Palaeeudyptes sp. and/or *Archaeospheniscus wimani*	0156	93.4	13.3	11.3	19.5	6.7	17.1	5.9	12.5[1]	8.5
	0233		14.9	10.9	17.7	6.5				
	0238								12.8[1]	9.4[1]
	0270								14.1	9.1[1]
	0445	90.2	12.3[1]	10.3[1]	18.7	8.3	17.9	6.5	10.8[1]	7.3
	0620b		13.6[1]	9.3[1]		7.8				
	0682								15.3	8.2[1]
Delphinornis larseni	0446	64.9[1]	8.9[1]		13.5	4.9	13.5	4.5	8.5	6.6
Delphinornis sp. and/or *Mesetaornis polaris* and/or *Marambiornis exilis*	0262b									6.2[1]
	0690					5.7[1]				

[1] approximate value owing to poor preservation of a specimen

Table 17

Measurements of carpometacarpi from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3
Anthropornis grandis	0438		20.3	
Anthropornis sp.	0264c		24.3	
Palaeeudyptes klekowskii	0331	94.1	23.3[1]	6.3
	0499	89.1		6.3
Palaeeudyptes gunnari	0145	76.6	15.0[1]	4.3
?*Palaeeudyptes* sp.	0264a		21.0[1]	
	0629a		16.5[1]	
	0680		22.1[1]	
	0681			6.2
Delphinornis larseni	0440		14.3	

[1] approximate value owing to poor preservation of a specimen

Table 18

Measurements of hip bones from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3	4	5
Anthropornis sp. and/or *Palaeeudyptes* sp.	0488	29.3	9.7	15.4		
	0570b					24.0[1]
	0595				28.0	
	0625	28.5	8.0			
	0627	25.8	10.8	12.7[1]		19.3
Delphinornis sp. and/or *Marambiornis exilis* and/or *Mesetaornis polaris*	0924		5.3[1]	9.4		

[1] approximate value owing to poor preservation of a specimen

Table 19

Measurements of femora from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3	4	5	6	7
Anthropornis nordenskjoeldi	0675						46.6	42.3
Anthropornis sp. and/or *Palaeeudyptes* sp.	0059			38.8				
	0108		133.7[1]					
	0216			39.2				
	0227					19.2		
	0230	137.6	145.5			18.0	40.6[1]	
	0243						37.3[1]	32.8
	0342	144.7[1]	149.4[1]			19.6	42.2[1]	
	0367						43.4	39.1
	0370						42.8[1]	35.3
	0435			41.6				
	0457	129.1[1]	135.1[1]			18.4	38.5	30.1[1]
	0496					17.8	41.4[1]	35.1
	0509					16.0		
	0643					17.4		
	0743					18.1[1]		
	0740					17.1[1]		
Palaeeudyptes gunnari	0103	119.8	123.6			16.3		30.1[1]
	0430					15.6		
	0504			36.1		15.7		
	0655					14.0		
	0699					16.0		
Archaeospheniscus wimani	0641	122.3	124.6	29.3	25.6[1]	13.9	27.7	26.9
	0658					13.3		
Delphinornis larseni	0090					10.6		
Delphinornis gracilis	0130		83.2[1]		12.2[1]	8.2		

Table 19 – continued

?*Delphinornis* sp.	0073					8.9		
	0437						21.5[1]	19.0[1]
Mesetaornis polaris	0215		99.3[1]	21.0		10.3		
?*Mesetaornis* sp.	0436					8.5	19.4	18.6
Marambiornis exilis	0434	94.6	98.0		13.2[1]	9.7	21.8	19.9[1]
?*Marambiornis* sp.	0458					8.2	18.5[1]	
Delphinornis sp. and/or *Mesetaornis* sp. and/or *Marambiornis* sp.	0518					8.1		
	0758					9.8		

[1] approximate value owing to poor preservation of a specimen

Table 20

Measurements of tibiotarsi from the Polish collection. Measurement categories were defined in "Material and methods", values are in millimeters.

Taxonomic position	Specimens (IB/P/B)	1	2	3	4	5	6	7
Anthropornis nordenskjoeldi	0360						41.4[1]	7.3
	0363					44.7	40.3[1]	8.0
	0512			24.2	13.8			
Anthropornis grandis	0134			18.2	12.4			
	0336			20.3	15.1[1]			
Palaeeudyptes klekowskii	0248c		32.0[1]					
	0357			18.2	14.7			
	0369		32.6					
	0626	235	27.5	18.9	13.2	34.7[1]		8.6
Palaeeudyptes gunnari	0137b						29.5[1]	
	0248b					30.0[1]	30.2	4.5
	0654	224[1]	26.5[1]	19.3	14.0	28.8	28.9[1]	
Palaeeudyptes sp.	0401		24.7					
	0537	226[1]	23.7[1]	16.7[1]				
Archaeospheniscus wimani	0110	211[1]	20.5	14.3	10.2			
	0796			15.0	10.6			
	0802			14.0	10.7			
Delphinornis larseni	0337			10.9	9.0	20.2		5.7
	0154					19.9	20.4	4.2
	0405					18.6	20.6	4.6
	0741			10.4				
Delphinornis arctowskii	0115	137[2]						4.3
	0266			9.4	7.3	16.4	17.8	3.9
	0500			9.9	7.3		19.0	4.4
Delphinornis gracilis	0408			8.5	7.2	15.0	14.7	3.3
Mesetaornis polaris	0207					18.3	19.3[1]	4.5
	0656					18.2	20.2	

Table 20 – continued

Marambiornis exilis	0406					17.7	16.6	4.6
Mesetaornis polaris or *Marambiornis exilis*	0333			8.6	7.0			
Delphinornis sp. and/or *Mesetaornis polaris* and/or *Marambiornis exilis*	0260c		17.1					
	0649			9.6	8.1			
	0756			8.3	6.9			
	0815			9.4[1]	7.9[1]			
	0918			8.9	6.7			

[1] approximate value owing to poor preservation of a specimen
[2] estimated value

Concluding remarks

Ten species grouped in six genera constitute a minimal reliable estimation of the Antarctic fossil penguin diversity. This estimate is consistent with the results obtained by Myrcha *et al*. (2002). *Wimanornis seymourensis* Simpson, 1971 is most likely not a distinct species, but the existence of unrecognized species of small-sized penguins is highly probable. Local fauna of Antarctic fossil penguins is clearly more taxonomically diverse than any such assemblage of present-day Sphenisciformes (see Case 1992), though it may be partially due to time-averaging (Fordyce and Jones 1990).

Two out of 54 specimens assigned to species of the largest penguins from the La Meseta Formation, *Anthropornis nordenskjoeldi* and *Palaeeudyptes klekowskii*, are from stratigraphic units older than Telm7, which testifies to a probable pre-Late Eocene origin of these taxa. Furthermore, Myrcha *et al*. (2002) reported such an age for several tarsometatarsi belonging to *Anthropornis grandis*, *Palaeeudyptes gunnari*, *Archaeospheniscus wimani* and *Delphinornis larseni* – a small subset of bones referred to these taxa. Thus *Delphinornis gracilis*, *D. arctowskii*, *Mesetaornis polaris* and *Marambiornis exilis* remain the only species known solely from the unit Telm7 (Late Eocene), and all ten recognized species may have co-existed in the Antarctic Peninsula region during that epoch. However, the picture is somewhat obscured, though not depreciated, by four specimens: single tarsometatarsus from the Argentine collection labeled as "?*Mesetaornis* sp.", two other tarsometatarsi from that set labeled as "*Delphinornis* sp." (see Myrcha *et al.* 2002) and a radius (IB/P/B-0690) of an unrecognized species of small-sized penguin from the Polish collection – these incomplete bones come from units older than Telm7. Some of the skeletal elements (neurocranium, pygostyle, clavicle, hip bone, and ungual phalanx) are reported for the first time from Antarctica.

The lack of complete or semi-complete skeletons of penguins from the La Meseta Formation may soon be, at least partially, compensated for by new findings from the Eocene Leticia Formation (Tierra del Fuego; see Clarke *et al*. 2003).

The combined analyses of these geographically and geologically close faunas would add a new dimension to studies of early Sphenisciformes.

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