# Partial limb skeleton of a "giant penguin" *Anthropornis* from the Eocene of Antarctic Peninsula

Piotr JADWISZCZAK

*Instytut Biologii, Uniwersytet w Białymstoku, ul. Świerkowa 20B, PL-15-950 Białystok, Poland*
*<piotrj@uwb.edu.pl>*

**Abstract**: The fossil record of the Antarctic penguins is dated to the late Paleocene of Seymour (Marambio) Island, but the largest spheisciforms, genera *Anthropornis* and *Palaeeudyptes*, originate from the Eocene La Meseta Formation. Here, the most complete large-scale reconstruction of a limb skeleton (a whole wing and a partial hind leg) of a Paleogene Antarctic penguin is reported. All bones are attributable to a single individual identified as *Anthropornis* sp. The comparative and functional analyses of the material indicate that this bird was most probably well-adapted to land and sea while having a number of intriguing features. The modern-grade carpometacarpal morphology is unique among known Eocene Antarctic species and all but one more northerly taxa.

Key words: Antarctica, Seymour Island, Eocene La Meseta Formation, Sphenisciformes, *Anthropornis*, wing, hind limb.

## Introduction

Penguins (Aves: Sphenisciformes), an order of flightless seabirds, most likely evolved in the Cretaceous and became highly specialized by the Eocene (*e.g.,* Jadwiszczak 2009). In recent years there has been considerable investigation of the penguin fossil record focusing mainly on the Paleogene period (Acosta Hospitaleche and Reguero 2010; Clarke *et al.* 2010; Sallabery *et al.* 2010; Acosta Hospitaleche and Jadwiszczak 2011; Fordyce and Thomas 2011; Jadwiszczak 2011; Jadwiszczak and Chapman 2011; Jadwiszczak and Mörs 2011; Ksepka *et al.* 2012; and others). Consequently, our knowledge of early spheisciforms has expanded with three regions (northern Antarctic Peninsula, New Zealand and western South America) as major sources of information on this record.

Paleogene Antarctic penguins originate solely from the late Paleocene and Eocene of Seymour Island (Antarctic Peninsula; Fig. 1) and are represented by several thousand specimens (Myrcha *et al.* 2002; Tambussi *et al.* 2005, 2006;

Jadwiszczak 2006a). Although all Paleocene and some Eocene non-Antarctic sphenisciform species were erected on the basis of partial skeletons (Jenkins 1974; Tambussi *et al.* 2005; Slack *et al.* 2006; Clarke *et al.* 2007, 2010), the record of Eocene penguins from Seymour Island almost exclusively comprises isolated bones (*e.g.,* Jadwiszczak 2006a). There are several exceptions, however. The most important of them appears to be an incomplete skeleton (announced as articulated) attributable to "giant" *Palaeeudyptes gunnari* (Wiman, 1905) from the Argentine collection (Acosta Hospitaleche and Reguero 2010; Figs 2B, D and 3F). It comprises bones from both the appendicular and axial skeleton. Other significant findings reported so far include a poorly preserved knee joint assigned to *P. gunnari* (Jadwiszczak 2006a), a partially articulated skeleton (coracoids, sternum, a segment of the vertebral column) from the Argentine collection (Acosta Hospitaleche and Di Carlo 2010) and a partial wing of an unidentified small-sized penguin from the Polish collection (Jadwiszczak 2010). Additional specimens are under investigation (Acosta Hospitaleche personal commun.; Jadwiszczak, *unpubl.*).

All of these associated fossils were identified relatively recently, yet there is a number of penguin bones from Seymour Island reported by Marples (1953; the British collection) that deserve special attention as some of these skeletal elements were claimed to probably belong to a single individual of *Anthropornis nordenkjoeldi* Wiman, 1905. *A. nordenskjoeldi* was one of the largest, if not the largest sphenisciform now known (Jadwiszczak 2001) and, like *Palaeeudyptes gunnari*, was most abundant during the late Eocene (Myrcha *et al.* 2002; Jadwiszczak 2006a, b; Tambussi *et al.* 2006). The lack of relevant comparative material resulted in a very conservative interpretation of the finding by Marples (1953), who illustrated elements of a distal left wing "assembled in natural position", but noted that "these bones may not belong to the same individual". Marples' (1953) work by no means exhausted the potential of the available material (37 bones and bone fragments).

Here, I describe and reinterpret the limb remains studied by Marples (1953), which in my estimation are assignable to a single individual of *Anthropornis*. The resulting reconstruction is contrasted with that based on material reported by Acosta Hospitaleche and Reguero (2010) and other specimens assigned to Paleogene penguins, with an analysis of their functional morphology.

## Geology, stratigraphy and age constraints

Seymour Island is an ice-free island located near the northern tip of the Antarctic Peninsula at 64°17'S, 56°45'W, in a backarc basin to the east of the Antarctic Peninsula magmatic arc (*e.g.,* Porębski 2000). The Eocene La Meseta Formation (Elliot and Trautman 1982) is exposed in the northeastern part of the island and constitutes the only source of information on Antarctic fossil penguins from that
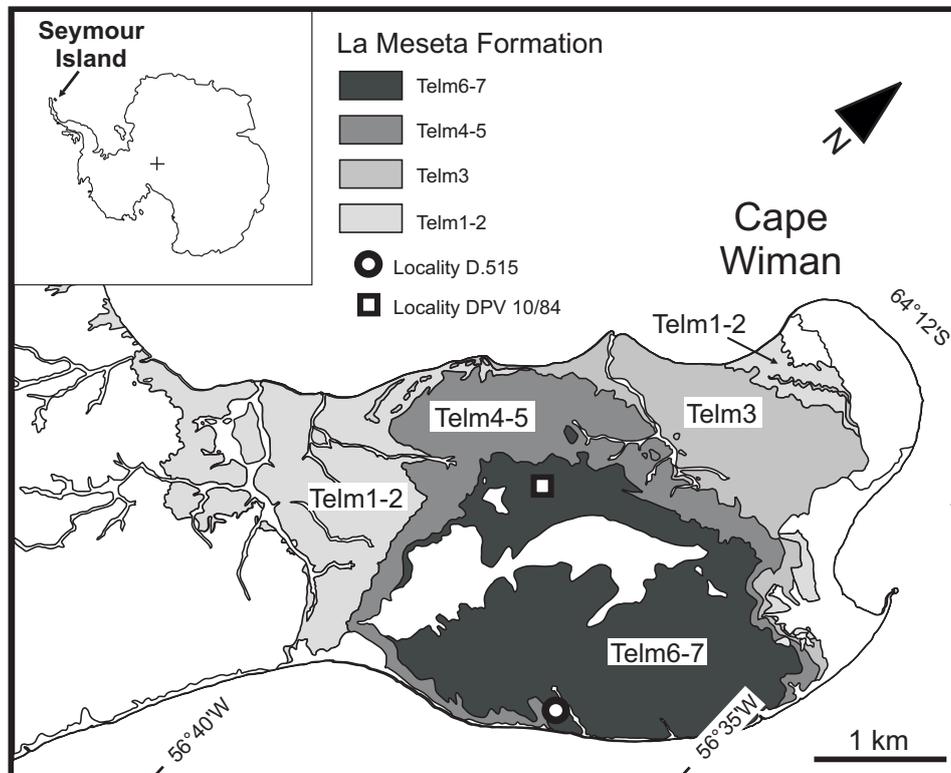
Fig. 1. Location map of units of the Eocene La Meseta Formation on Seymour Island (according to Sadler 1988) and collecting stations D.515 and DPV 10/84, where partial skeletons of *Anthropornis* sp. and *Palaeeudyptes gunnari* (NHMUK A3348/3355, A3357/3359, 3360[I], 3372 and MLP 96-I-6-13, respectively) were found.

epoch (Fig. 1). It is comprised of estuarine and shallow marine fossiliferous clastic deposits (720 m thick; Porębski 1995, 2000; Marenssi 2006; Tatur *et al.* 2011; Gaździcki and Majewski 2012). Sadler (1988) mapped the formation and recognized seven major lithofacies Telm1–Telm7 (Fig. 1) and this system is used here.

A vast majority of penguin bones, including material discussed here, originate from the uppermost unit of the La Meseta Formation, *i.e.* Telm7. Data ($^{87}$Sr/$^{86}$Sr ratios from mollusk shells) reported by Dutton *et al.* (2002) and Marenssi (2006) suggest a late Eocene (36.1 and 36.0 Ma, respectively) age for samples from this unit. Ivany *et al.* (2008) suggested that specimens from Telm7 and most of Telm6 were late middle to late Eocene in age. The age of the topmost few meters of the La Meseta Formation was estimated by Dingle and Lavelle (1998) to be 34.2 Ma (late late Eocene), but the youngest documented ages from the formation are those reported by Ivany *et al.* (2006): 33.6–34.8 Ma. The latter estimate may indicate the earliest Oligocene age for the very top of the formation (see also Montes *et al.* 2010).

## Material and methods

The presumptive partial skeleton of *Anthropornis* sp. discussed here (Figs 2, 3) was collected by W.N. Croft and T.P. O'Sullivan, members of the Falkland Islands Dependencies Survey, within the La Meseta Formation (Seymour Island) in 1946. The fossil were from the upper part of the original Swedish locality no. 11 (Wiman 1905; see Marples 1953) or the British locality D.515 (Marples 1953: figs 1, 2; Fig. 1). The skeleton consists of eight wing bones, a single coracoid, seven hind-limb bones and 21 poorly preserved fragments. All anatomically identifiable bones are from the left side of the body. Since they were assigned to a single lot D.515.17, they were presumably dispersed over an area not larger than "a few square yards" (due to solifluction; Marples 1953: p. 3 and 7). The skeleton is housed at the Natural History Museum, London (abbreviated NHMUK).

Comparative material from Antarctica is housed at the Institute of Biology, University of Białystok (Poland; abbreviated IB/P/B), the Naturhistoriska riksmuseet (Stockholm, Sweden; abbreviated NRM-PZ [fossil specimens], NRM-Z [recent specimens from the genus *Aptenodytes*]) and the Museo de La Plata (La Plata, Argentina; abbreviated MLP). Bones from the Argentine, British, Polish and Swedish collections of Antarctic fossil penguins were studied directly, whereas analyses of specimens from Australia, New Zealand and South America were based on published descriptions.

The reconstruction of the humerus (Fig. 2A) is based mainly on NRM-PZ A.43. Since no sesamoid bone accompanying an *Anthropornis*-like humerus is known, that outlined in Fig. 2 is a compromise based on its counterpart in *Icadyptes salasi* Clarke *et al.*, 2007 from the Eocene of Peru (Clarke *et al.* 2007) and *Kairuku grebneffi* Ksepka *et al.*, 2012 from the Oligocene of New Zealand (Ksepka *et al.* 2012). Modern penguins have one or two such bones at the level of the elbow (Louw 1992). The tarsometatarsus (Fig. 3A) was reconstructed mainly on the basis of three specimens: MLP 94-III-15-356b, MLP 96-I-6-19 and MLP 96-I-6-30. The tibiotarsus and tarsometatarsus of *Palaeeudyptes klekowskii* Myrcha *et al.*, 2002 (Fig. 3C) were fitted on the basis of sizes of their articular surfaces. *Palaeeudyptes*, a genus of very large-sized penguins known also from other regions and epochs, is paraphyletic according to some phylogenetic analyses (*e.g.,* Clarke *et al.* 2007), though Antarctic species are congeneric (see also Jadwiszczak and Mörs 2011).

Measurements were obtained using digital callipers and rounded to the nearest 0.1 mm. Anatomical nomenclature follows that of Baumel and Witmer (1993).

## Systematic paleontology

Class Aves
Order Sphenisciformes Sharpe, 1891 (also *sensu* Clarke *et al.* 2003)

Family Spheniscidae Bonaparte, 1831

*Anthropornis* Wiman, 1905

Type species: *Anthropornis nordenskjoeldi* Wiman, 1905.

Other included species: *Anthropornis grandis* (Wiman, 1905).

*Anthropornis* sp.
(Figs 2, 3)

**Material**. — 15 bones from the left limb skeleton of the same individual. Wing skeleton: damaged proximal and distal humerus, NHMUK A3355 and A3360(I); almost complete ulna (lacking most of its olecranon), NHMUK A3354; almost complete radius (lacking a small portion of its cranial margin), NHMUK A3353; complete radiale, NHMUK A3351; broken ulnare, NHMUK A3352; carpometacarpus lacking a large portion of the minor metacarpal bone, NHMUK A3350; complete proximal and distal phalanx of digitus majoris, NHMUK A3349 and A3348. Hind-limb skeleton: damaged proximal and distal tibiotarsus, NHMUK A3357; proximal fibula, NHMUK A3372; damaged tarsometatarsus (lacking two trochleae and proximal part), NHMUK A3358; complete first phalanx of third digit, complete first, second and third phalanx of fourth digit, NHMUK A3359.

**Description**. — All specimens described below are robust bones, obviously belonging to a very large-sized penguin, much larger than the recent Emperor Penguin (*Aptenodytes forsteri* Gray, 1844).

The proximal humerus has its articular surface clearly separated from the proximal end of the deltopectoral crest (*i.e.* dorsal tubercle). The border is also marked with a number of conspicuous nutritious foramina. The ligamental furrow (sulcus transversus) forms a wide shelf. The proximal part of the deltopectoral crest is broad in both proximal and ventral view. Its remaining portion is much thinner. An impression for insertion of m. coracobrachialis cranialis is quite narrow proximally and very wide distally. A surface for insertion of m. supracoracoidei appears to be oblique relative to the main axis of the bone. The distal humerus has a relatively wide (in distal view) dorsal (radial) condyle, and is clearly separated from the cranial margin of the bone by an indentation. The dorsalmost one of the trochlear processes strongly diverges caudally.

The ulna, relatively wide distally, gradually widens proximally and ultimately (about ¾ the distance from its distal end) forms a pronounced olecranon (as indicated by the concave shape of the preserved portion of the caudal margin). The olecranon is pierced by a conspicuous (in ventral view) foramen. The dorsoventral width of the main (ventral) cotyla is barely more than half the dorsoventral width of the proximal ulna. Both distal condyles are well developed. The radius is slightly shorter than ulna and quite uniformly wide along most of its length. The humeral cotyla is slightly oval. The radius was most probably devoid of a concave notch in the proximal part of its cranial margin (as indicated by the shape of the margin pre-
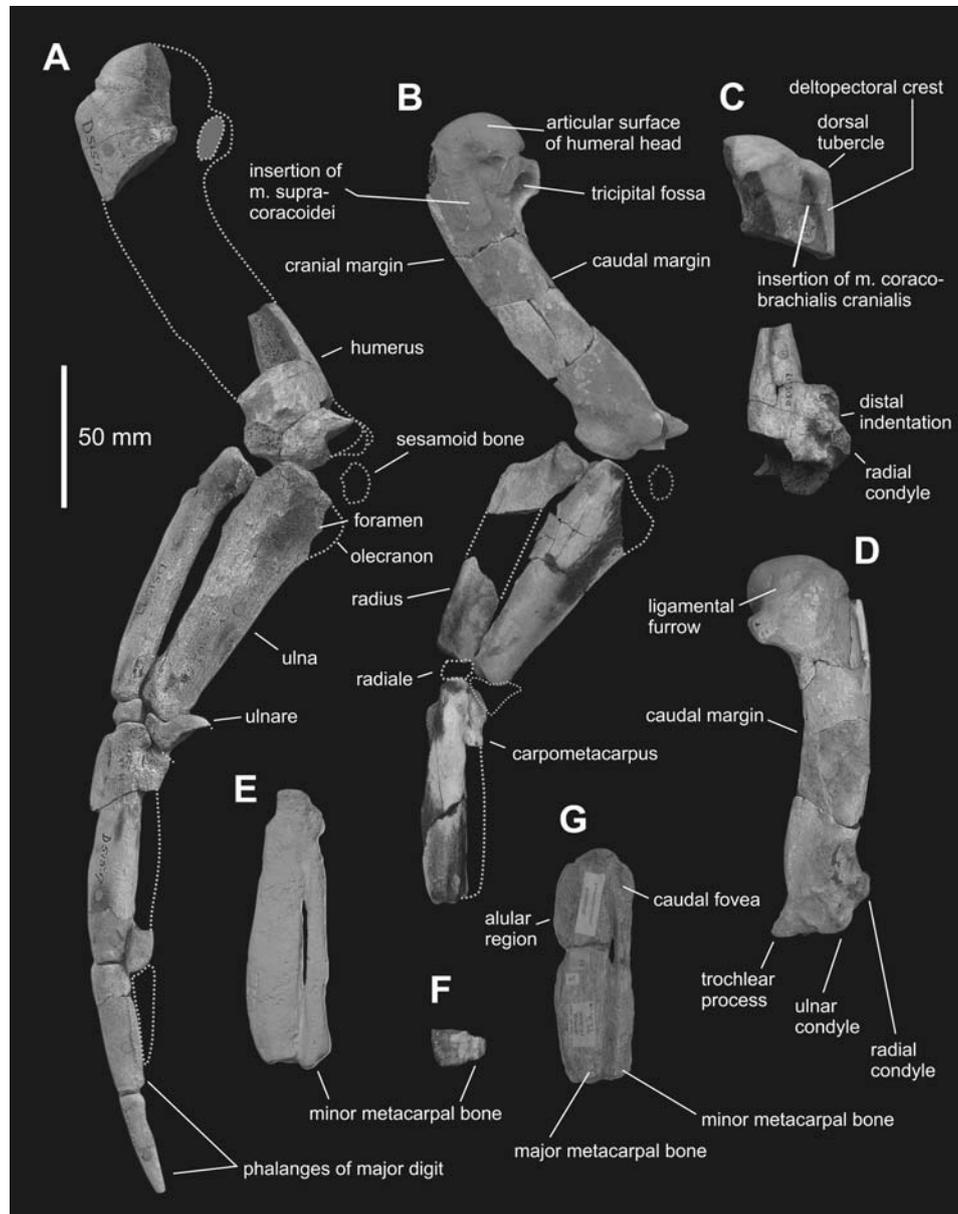
Fig. 2. Reconstruction of a wing skeleton of *Anthropornis* sp. (NHMUK A3348/3355, 3360[I]; **A** and **C**) and *Palaeeudyptes gunnari* (MLP 96-I-6-13; **B**, **D** and **F**) from the Eocene La Meseta Formation on Seymour Island. **E**. Cast of Jenkins' (1974) carpometacarpus from the Eocene of Australia (*Anthropornis*-like; NRM-PZ A.256e). **G**. Wiman's (1905) specimen from the Eocene of the La Meseta Formation (*Palaeeudyptes* sp.; NRM-PZ A.28). **B**, **D** and **G**. Specimens reversed to facilitate comparison. Dorsal (A, B, E, F, G) and ventral (C, D) views.
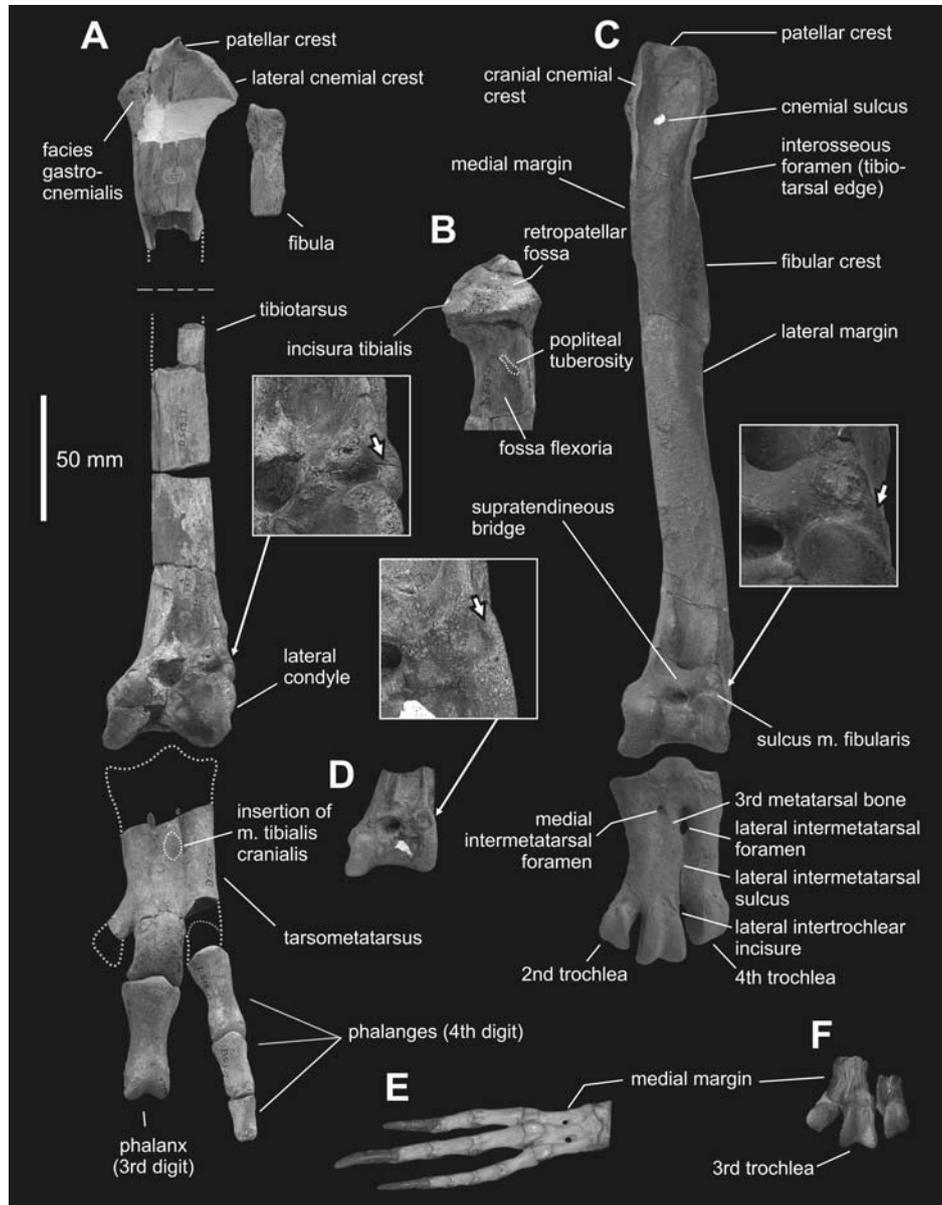
Fig. 3. Partial reconstruction of a hind-limb skeleton of *Anthropornis* sp. (NHMUK A3357/3359, 3372; **A** and **B** [proximal tibiotarsus]) and *Palaeeudyptes klekowskii* (IB/P/B-0369 [tibiotarsus], IB/P/B-0551 [tarsometatarsus]; **C**) from the Eocene La Meseta Formation on Seymour Island. **D**. Distal tibiotarsus (*Anthropornis*-like; IB/P/B-0366) from the La Meseta Formation. **E**. Foot of the recent King Penguin, *Aptenodytes patagonicus* Miller, 1778 (NRM-Z A.610473). **F**. Tarsometatarsus from a partial skeleton of *P. gunnari* (see Fig. 2; MLP 96-I-6-13) from the La Meseta Formation. **C** (tarsometatarsus only) and **D**. Specimens reversed to facilitate comparison. Cranial (tibiotarsi) and dorsal (tarsometatarsi and phalanges) views (A, C, D, E and F); proximocaudal view (B). E is not in scale.

served on both sides of the missing fragment). The distal radius has a well-marked contact surface for the ulna. The radiale is a compact bone, the ulnare is expanded caudally. The carpometacarpus is moderately long – *ca.* 13% shorter (along the major metacarpal bone) than the ulna (along the main axis). A conspicuous notch separates the alular part of the bone from the proximal articular surface. The caudal pit (fovea) that accommodates the distal edge of the ulnare is well developed. The distal end of the minor metacarpal bone projects clearly beyond its counterpart in the major metacarpal bone. The proximal and distal phalanges of the major digit are well developed and their lengths constitute (respectively) 48.5% and 37.2% of that for the ulna, and 55.6% and 42.6% of that for the carpometacarpus.

The patellar crest of the proximal tibiotarsus is short and oblique. The lateral cnemial crest deflects proximally so that the intercnemial sulcus is triangular in shape. The medial surface of the cranial cnemial crest (facies gastrocnemialis) is well developed and subdivided. The lateral border (proximal view) of the proximal tibiotarsus (incisura tibialis) is strongly concave. The retropatellar fossa is divided into the wide and rather shallow medial part, and the conspicuous pit located at the base of the lateral articular surface. The fossa flexoria is wide and relatively well developed. The popliteal tuberosity is conspicuous, though somewhat irregular in shape, constitutes the medial part of the proximal border of the above mentioned fossa. The proximal interosseous foramen is well developed. The supratendinal bridge of the distal tibiotarsus is wide. The sulcus m. fibularis is devoid of the lateral opening and forms a well pronounced small fossa or pit.

The lateral proximal intermetatarsal foramen is more proximal than its medial counterpart. The proximal third metatarsal bone is quite wide. The insertion for m. tibialis cranialis is wide though low. The medial margin of the bone is clearly not smoothly concave along its length. The lateral sulcus reaches the intertrochlear incisure and its medial counterpart is distinct though barely surpasses the midshaft.

**Measurements**. — See Table 1.

**Occurrence**. — The Eocene La Meseta Formation (Seymour Island, Antarctic Peninsula), Telm7, locality D.515 (Fig. 1).

**Taxonomic and taphonomic remarks**. — The above mentioned combination of tarsometatarsal features is typical of specimens assignable to *Anthropornis* and is listed in the revised generic diagnosis and specific descriptions by Myrcha *et al.* (2002). Other bones were assigned to *Anthropornis* by association with the aforementioned tarsometatarsus, and further observations support this assignment (see below and Discussion). The tarsometatarsus NHMUK A3358 resembles a holotype of *A. nordenskjoeldi* (NRM-PZ A.45) in size, but is slightly larger (Table 1). Acosta Hospitaleche and Jadwiszczak (2011) have recently reported the existence of an intriguing heterogeneity within the hypotarsal region of tarsometatarsi, taxonomically most important elements of the skeleton of fossil penguins that challenges the current intrageneric systematics of *Anthropornis*. Moreover, the

Table 1

Measurements (in mm) of fossil penguin bones from the La Meseta Formation and the recent Emperor Penguin (*Aptenodytes forsteri*). Abbreviations: L – length, LA – length along main axis, OTW – width (1/3 the distance from its distal end), TTW – width (2/3 the distance from its distal end), PW – proximal width, SW – the smallest width of the proximal shaft, DW – distal width, MW – midshaft width, WBT – width below medial tuberosity, WTT – width of the third trochlea, BTT – breadth of the third trochlea, DB – distal breadth.

| Skeletal elements and measurement IDs (equivalent measurement categories of Myrcha *et al.* [2002] and Jadwiszczak [2006a] in parentheses) | | *Anthropornis* sp. (NHMUK – partial skeleton; this study) | *Anthropornis nordenskjoeldi* (a type specimen NRM-PZ A.45) | *Palaeeudyptes gunnari* (MLP – partial skeleton) | *P. klekowski* (tibiotarsus, IB/P/B-0369; tarsometatarsus, IB/P/B-0551)[1] | *A. forsteri* (recent; NRM-Z A.611330) |
|---|---|---|---|---|---|---|
| Humerus | L (1) | ~151[2] | – | 135.1 | – | 131.1 |
| Ulna | L (1) | 99.5 | – | 87.3 | – | 94.6 |
| | OTW (6) | 21.1 | – | 19.7 | – | 17.4 |
| | TTW (4) | 26.9 | – | 27.0 | – | – |
| Radius | L (1) | 96.5 | – | – | – | 89.6 |
| | OTW (6) | 17.3 | – | – | – | 17.8 |
| | TTW (4) | 19.7 | – | – | – | – |
| Carpometacarpus | L (1) | 86.9 | – | 79.6 | – | 72.4 |
| | PW (2) | 24.7 | – | >19.4 | – | 21.2 |
| Major digit (prox. phalanx) | L (1) | 48.3 | – | – | – | – |
| Major digit (distal phalanx) | L (–) | 37.0 | – | – | – | – |
| Tibiotarsus | L (1) | – | – | – | ~253 | 213.0 |
| | PW (2) | 34.0 | – | – | 32.9 | – |
| | SW (–) | 22.9 | – | – | 22.0 | – |
| | DW (5) | 38.7 | – | – | 39.7 | – |
| | DB (6) | 45.8 | – | 25.4 | 40.3 | – |
| Tarsometatarsus | L (1) | ~90[3] | ~86.4 | – | 71.6 | 44.8 |
| | WBT (–) | 34.3 | 33.8 | – | – | – |
| | MW (4) | ~35.8 | – | – | 32.4 | 30.5 |
| | WTT (6) | 20.1 | – | 13.2 | 16.2 | – |
| | BTT (7) | 21.3 | ~19.8 | 15.8 | 20.8 | – |
| Phalanx (4th digit, proximalmost) | LA (–) | 36.0 | – | – | – | – |
| Phalanx (4th digit, middle) | LA (–) | 24.7 | – | – | – | – |
| Phalanx (4th digit, distalmost) | LA (–) | >17.0 | – | – | – | – |
| Phalanx (3rd digit) | LA (–) | 43.7 | – | – | – | – |

[1] Bones from a reconstructed skeleton presented in Fig. 3.

[2, 3] An estimate.

hypotarsus is missing in the analyzed tarsometatarsus. Hence I avoid any further species-level considerations.

All the specimens were collected near each other (for details, see Material and methods), and the entire set is homogeneous in terms of surface texture, color and relative dimensions of elements. Additionally, the fossils originate from the same side of the body (see above) and possess features rare in available fossils (see below). Some of these observations indicate a common taphonomic and geologic history and all of them collectively appear to belong to the same individual (see also Marples 1953: p. 7, and Simpson 1971: p. 363).

**Discussion**. — The discussion that follows is limited to Paleogene penguins with known partial skeletons. Humeri are traditionally regarded as important bones for penguin systematics and the specimen described above, though poorly preserved, resembles those formerly assigned to *Anthropornis* (Simpson 1971; Jadwiszczak 2006a; see also Jenkins 1974, 1985), and is clearly more robust than that of *P. gunnari* (Fig. 2). Unfortunately, due to poor preservation of humeral condyles its position relative to both the ulna and radius (*i.e.*, the angle formed by these bones) is only approximate (I am convinced it is close to the actual condition).

The shape of the ulna of *Anthropornis* differs slightly from that in *P. gunnari*. The distal shaft of the former bone is less slender than its counterpart in the latter specimen relative to the proximal shaft (see Fig. 2 and Table 1). The ulnare described above, even taking into account its incompleteness, differs in shape from its counterpart in *Inkayacu paracasensis* Clarke *et al.*, 2010 from the Eocene of Peru (Clarke *et al.* 2010), the latter being probably more expanded distally (*i.e.*, in parallel to the carpometacarpus).

The relative elongation of the minor metacarpal bone is one of the most characteristic features that separate *Anthropornis* from Antarctic *Palaeeudyptes*, all but one other Eocene penguin (see below) and *Waimanu* Jones *et al.*, 2006 from the Paleocene of New Zealand (Slack *et al.* 2006). The bone exceeds distally the major metacarpal and in this respect the former taxon resembles modern penguins as well as a specimen described by Jenkins (1974; see also Fig. 2A, E) from the Eocene of Australia and later claimed to belong to *Anthropornis nordenskjoeldi* (Jenkins 1985). Interestingly, a similar feature, though less developed, can be observed in *Kairuku* from the late Oligocene of New Zealand (Ksepka *et al.* 2012).

Marples (1953) noted, that the carpometacarpus from his reconstruction of the *Anthropornis* wing (he used the same specimens as me in this contribution) is probably too large to belong to the same individual. I do not agree with this statement. Actually, the carpometacarpus assigned to this genus is relatively shorter than that from a partial skeleton of *P. gunnari* (*ca.* 87% and 91% of the ulnar length, respectively; see Table 1 and Fig. 2), and slightly longer than that of *Icadyptes salasi* from the Eocene of Peru (85% of the ulnar length; Ksepka *et al.* 2008). In any case, its relative length falls within the limits for acceptable values.

Considering the hind-limb bones, two features of the tibiotarsus described above ought to be emphasized. Both, the shape of the lateral cnemial crest, and therefore also that of the intercnemial sulcus, and the form of the sulcus m. fibularis differ from its counterparts in *Palaeeudyptes*. The relative position of both cnemial crests also affect the length and orientation of the patellar crest (short and oblique vs. long and more horizontal in *Palaeudyptes*). A degree of proximal divergence of the lateral crest observed in NHMUK A3357 appears to be rare within known large-sized tibiotarsi, but on the other hand that part of the bone is broken in many specimens. Probably an incomplete (a damaged proximal part only) specimen NRM-PZ A.27 approaches NHMUK A3357 in this respect. Considering the form of the sulcus m. fibularis observed in the discussed bone, its counterpart in a much smaller IB/P/B-0366 is very similar in shape (Fig. 3D). However, the vast majority of analysed large-sized tibiotarsi resemble IB/P/B-0369 (Fig. 3C).

## Considerations on functional morphology of *Anthropornis*

The supposedly wide insertion surface for the supracoracoid muscle (Fig. 2A), though partly damaged, suggests the considerable size of the latter. As this muscle is responsible for elevating the humerus, drawing the wing caudally and raising the leading edge (Louw 1992), it was obviously large enough to serve this purpose well. The wide dorsal tubercle (Fig. 2C) indicates the well-developed minor deltoid muscle (see Schreiweis 1982), which assists in wing elevation and pronation. The insertion for the cranial coracobrachial muscle (which acts mainly as a humeral extensor) forms a proximally deeply etched triangular fossa (Fig. 2C), though it is a small muscle in all recent species (Schreiweis 1982). The wide distal portion of that fossa suggests well-developed pectoral muscles (or at least m. pectoralis thoracica; Bannasch, 1986: figs 29, 38), the most important component of the downward movement or power stroke of the penguin wing (Louw 1992). Clark and Bemis (1979) noted that, unlike most other birds, penguins generate thrust during both the downstroke and upstroke.

The elbow is a stiff joint in modern penguins and this limited mobility is even more pronounced in the distal part of the wing (*e.g.,* Louw 1992). The relative elongation of the minor metacarpal bone in *Anthropornis*, *i.e.,* its contiguity to the proximalmost portion of the major digit (Fig. 2A; unlike in [among others, see Discussion] *Palaeeudyptes gunnari*, Fig. 2F, G) must have resulted in an enhanced stiffness of the distalmost wing (metacarpal joint), similar to extant spheisciforms. In this respect, the discussed bird was more advanced than other Eocene (and Paleocene) penguins. On the other hand, the shape of the caudal expansion of the ulnare (indicated by the preserved fragment of its distal surface), together with the size of the caudal fovea of the carpometacarpus (Fig. 2A), testify to the pres-
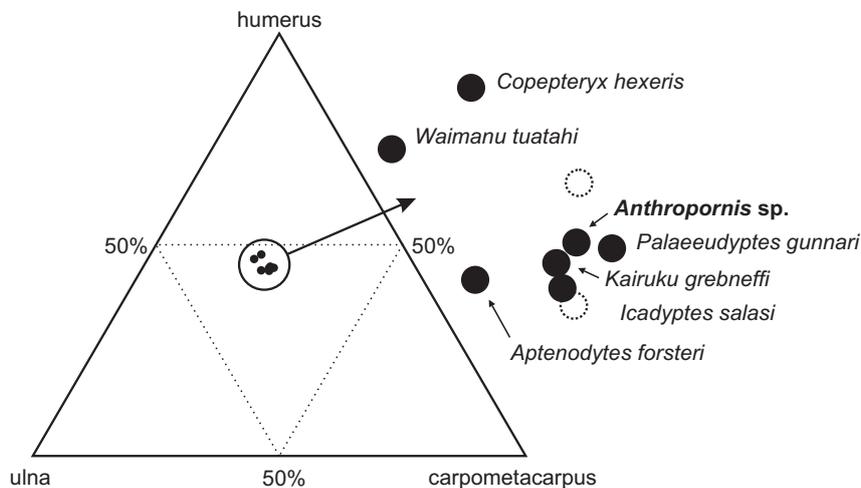
Fig. 4. Ternary diagram visualising proportions of the three main segments of the wing skeleton of Paleogene and recent (*Aptenodytes forsteri*) penguins. Data for *Anthropornis*, *Palaeeudyptes* and *Aptenodytes* are from Table 1, for *Icadyptes* and *Kairuku* – from Ksepka *et al.* 2012, for *Copepeteryx hexeris* Olson *et* Hasegawa, 1996 (a giant plotopterid - a wing-propelled diver from the late Oligocene of Japan) – from Olson and Hasegawa 1996, and in case of *Waimanu* proportions were estimated from Slack *et al.* 2006: fig. 1. Dotted circles show locations of *Anthropornis* sp. in case of the 5% over- and underestimation of its humeral length marked with a solid circle.

ence of some degree of mobility present within the carpal joint of *Anthropornis*, supposedly larger than in *Inkayacu paracasensis* (see Clarke *et al.* 2010: fig. 2A). This may have been related to the enhanced maneuverability useful during prey pursuits. Moreover, a clearly angled flipper of *Anthropornis* (Fig. 2A; a feature also present in much smaller early penguins, Jadwiszczak 2010: fig. 2) is not necessarily typical of poor divers (as postulated by Tambussi *et al.* [2006]), because there seems to be no correlation between such a morphological trait and diving ability (Ksepka and Ando 2011 and references therein).

The assessed proportions of three main long wing bones of the *Anthropornis*, *i.e.*, humerus, ulna and carpometacarpus, appear to resemble those in *Kairuku grebneffi* and *Palaeeudyptes gunnari* slightly more than their counterparts in other compared species (Fig. 4). Interestingly, this is not in line with the geological age of discussed species, *e.g., Kairuku* is late Oligocene in age, whereas *Icadyptes* comes from the Eocene (like *Anthropornis*).

The preserved bones of the partial hind-limb skeleton of *Anthropornis* are also interesting for their functional morphology. The enlarged (relative to that in *Palaeeudyptes*) surface of the cnemial sulcus (a feature of the proximal tibiotarsus, see above and Fig. 3A, C) may have supported the origin of a stout m. extensor digitorum longus (*e.g.,* Schreiweis 1982: fig. 12). This muscle had its antagonist in the most probably well-developed m. flexor digitorum longus, as indicated by the form of the origin of the latter, *i.e.* fossa flexoria (quite deep and wide; Fig. 3B).

The well pronounced incisura tibialis (Fig. 3B), a passage for the tendon of m. tibialis cranialis, the main flexor of the tarsometatarsus (Raikow 1985), suggests its considerable strength. Flexion is more important than extension in bipedal locomotion (Cracraft 1971; Gatesy and Biewener 1991), and birds with wider muscle insertions will develop more force, at the expense of velocity of muscular contraction (Bock 1974; Gans 1982). The unusual shape of the sulcus m. fibularis in *Anthropornis* (Fig. 3A, D) is hard to explain. It still separates the tuberculum retinaculi m. fibularis from the proximal part of the lateral condyle, but its lateral border may serve (among others) as some sort of a constructional reinforcement.

The wide tarsometatarsal insertion for the m. tibialis cranialis indicates, just like the incisura tibialis discussed above, a considerable strength of this flexor. The shape of the medial margin (different from a smoothly concave border in *P. gunnari*) appears to have a constructional importance as a body-mass-related supportive structure (see Acosta Hospitaleche and Jadwiszczak 2011, and Jadwiszczak and Mörs 2011). The well-pronounced medial divergence of the second trochlea testifies to the considerable spacing of the toes, a feature important for such large birds for maintaining the body balance during terrestrial locomotion and using them (the whole feet, in fact) as rudders when swimming. Whether Paleogene penguins used waddling as an effective strategy for ensuring stability in the frontal plane dynamics, as do recent sphenisciforms (Kurz *et al.* 2008), though probable, remains unknown.


## Conclusions

All penguin bones from the British collection acquired within the D.515 locality in 1946, and labelled as a lot no. 17, belong in a skeleton of a single individual assignable to the genus *Anthropornis*. According to the current systematics, it should be assigned to *A. nordenskjoeldi*, the largest Antarctic sphenisciform ever, but recent findings (see Taxonomic and taphonomic remarks) suggest caution in this respect.

The current work is the most bold attempt to reconstruct the limb skeleton of an Antarctic fossil penguin, and as such it will surely be a basis for further discussions. The comparative analysis of the material revealed a number of intriguing features, either with obvious interpretation (*e.g.,* the enlarged area of the cnemial sulcus) or not easily explicable on the basis of functional morphology, such as the unusual form of the tibiotarsal sulcus m. fibularis.

Some findings were possible due to the investigation of the assembled skeleton and/or reconstructed bones. For example, it seems that some degree of mobility exists within the carpal joint, whereas the metacarpal joint is stiff. The assessed proportions of three long wing bones of the *Anthropornis* approach the condition in *P. gunnari* and, intriguingly, also in considerably younger (in terms of geologi-

cal age) *K. grebneffi*. In any case, a number of features discussed in this work indicate that *Anthropornis* seems to be well-adapted to its environment. The reconstructed partial skeleton allows a better understanding of this fascinating "giant" bird while posing new questions.

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