C. R. Palevol 13 (2014) 555–560

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com

General palaeontology, systematics and evolution (Vertebrate palaeontology)

New giant penguin bones from Antarctica: Systematic and paleobiological significance

Nouveaux os de manchots géants de l'Antarctique : importance systématique et paléobiologique

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ARTICLE INFO

Article history:
Received 1st December 2013
Accepted after revision 26 March 2014
Available online 24 July 2014

Handled by Michel Laurin

Keywords:
Giant penguins
Palaeeudyptes klekowskii
Eocene
Antarctica
Submeseta Formation

ABSTRACT

A tarsometatarsus and a fragmented humerus of striking dimensions recently collected in the Late Eocene locality DPV 13/84 Submeseta Formation-level 38 Submeseta II-, Seymour (Marambio) Island, Antarctic Peninsula were both assigned to ***Palaeeudyptes klekowskii***. According to estimates, the tarsometatarsus would belong to the largest and most massive penguin described so far. This bird was probably a piscivorous penguin, with high diving ability for catching prey. Although the humerus is not an appropriate element for body mass or body length assessments, it also belonged to a huge penguin.

Mots clés :
Manchots géants
Palaeeudyptes klekowskii
Éocène
Antarctique
Formation Submeseta

RÉSUMÉ

Un tarsometatarsus et un humérus fragmenté d'énormes dimensions, récemment recueillis dans l'Éocène supérieur DPV 13/84 (niveau 38, Submeseta II) de la formation Submeseta de l'île Seymour (Marambio), péninsule Antarctique, ont été attribués à ***Palaeeudyptes klekowskii***. Selon les estimations, le tarsometatarsus appartiendrait au manchot le plus grand et le plus massif décrit jusqu'à présent. Cet oiseau a été un pingouin piscivore, avec une forte capacité de plongée sous-marine pour la capture des proies. Bien que l'humérus ne soit pas un élément approprié pour les évaluations de masse corporelle ou de longueur du corps, il appartenait aussi à un énorme manchot.

1. Introduction

The Sphenisciformes constitute a captivating group of birds due to several features. Even though all the living species are morphologically very similar, the range of size variation is notable. The group includes forms from as small

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http://dx.doi.org/10.1016/j.crpv.2014.03.008
1631-0683/

as 40 cm, such as the Little Blue Penguin *Eudyptula minor* Bonaparte, 1856, to those of up to 116 cm height, such as the Emperor Penguin *Aptenodytes forsteri* Gray, 1844 (Martínez, 1992).

The range of size increases considerably when fossil species are taken into account. Different ways to calculate body mass and length have already been proposed. Previous works have used different equations based on limb bone parameters. Some of the first estimates were based on tarsometatarsal, femoral and humeral lengths (Simpson, 1946, 1971, 1975, 1976) or on regressions of mean body masses using the living representatives as a *proxy* group (Livezey, 1989). Campbell and Marcus (1992) examined different families of birds and developed a series of equations to estimate body masses of extinct groups. They determined that best predictors in penguins are the tibiotarsus and femur. However, tarsometatarsal measurements were also considered reliable tools (Kirkwood et al., 1989; Rising and Somers, 1989; Senar and Pascual, 1997).

Given the estimates made by Jadwiszczak (2001) from living and fossil species, the more trustworthy measurements were selected for estimating body mass and height. Therefore, the width and the anteroposterior width of the tarsometatarsus were included in the equations obtained by linear regression model II. According to those equations and previous results, the largest known species is *Anthropornis nordenskjoeldi* with a length of 166.3 cm and 82.8 kg of body mass. The tiniest is the Patagonian species *Eretiscus tonni* with an estimate of 35 cm in length and 0.94 kg of body mass according to the same equations proposed by Jadwiszczak (2001).

Recently, an almost complete tarsometatarsus and a fragmented humerus of striking dimensions assigned to *Palaeeudyptes klekowskii* were collected. Both isolated remains come from the same levels assigned to the Late Eocene Submeseta Formation, Seymour (Marambio) Island, Antarctic Peninsula, West Antarctica. Body mass, body length and diving duration were calculated and discussed.

2. Material and methods

Abbreviations: MLP – Museo de La Plata, Argentina; NHM – Natural History Museum of London, United Kingdom.

Materials under study are permanently housed in the Museo de La Plata (MLP), La Plata, Argentina. The tarsometatarsus MLP12-I-20-116 and the humerus MLP-12-I-20-288 were collected during field work of the Instituto Antártico Argentino, in the Late Eocene–Earliest Oligocene Submeseta Formation in the DPV 13/84 (Isla Seymour-Marambio), Antarctica. Stratigraphy is according to Marenssi et al. (1998a), and Montes et al. (2010, 2013).

Osteological terminology follows Baumel and Witmer (1993), and measurements were taken with a vernier caliper with an accuracy of 0.1 mm. Body mass and body length were calculated through the equations obtained by Jadwiszczak (2001), and the most conservative values were used for paleobiological estimations. Details of the selected allometric equations are given in Table 1. It is worth noting that body length is a different value from the height of the living birds. Body length refers to the maximum measurements from the tip of the toes to the end of the bill, with the neck and legs outstretched.

Maximum and normal dive duration were calculated according to Watanuki and Burger (1999), whose hypothesis is based on the analysis made on nine species of extant penguins.

3. Provenance

The Middle Eocene–Earliest Oligocene Submeseta Formation (Montes et al., 2013) is the uppermost part of the former Early Eocene–?Earliest Oligocene La Meseta Formation (Unit III of Elliot and Trautman, 1982; Telm 7 of Ivany et al., 2006; Sadler, 1988), or La Meseta Alloformation (Marenssi et al., 1996, 1998a). This is the youngest unit exposed of the back-arc of the James Ross Basin, Antarctic Peninsula, cropping out in Seymour (=Marambio) Island (Fig. 1). This unit constitutes the top of the marine sedimentary sequence of the Basin, interpreted as the filling of an incised-valley system that is covered only by glaciomarine deposits of Miocene and post-Pliocene (Marenssi et al., 1998a).

The Submeseta Formation corresponds to the Facies Association III of Marenssi et al. (1998b), characterized by a uniform sandy lithology that represents a tidal shelf influenced by storms. Three different levels were recognized into this unit (Fig. 2) named from base to top: "Submeseta I", "Submeseta II", and "Submeseta III" (Montes et al., 2013).

The fossiliferous locality DPV 13/84 is among the most important for the study of Eocene penguins, where strata of level 38 (according to Montes et al., 2013) crops out. The first discovery at this site was made by the Nordenskjoeld expedition (Wiman, 1905) and many other remains were subsequently collected there (Acosta Hospitaleche, 2013a, b; Acosta Hospitaleche and Reguero, 2010, 2014).

Table 1
Equations of form $Y = aX^b$ obtained by Model II Regression method after transformation to logarithms (taken from Jadwiszczak, 2001), where BM and BL refer to body mass in kg and body length in mm respectively. Abbreviations: r, Pearson's product-moment correlation coefficient; CI, confidence interval; SEE, standard error of the estimate; PE, prediction error; Tmt W, tarsometatarsus width; Tmt ApW, tarsometatarsus antero-posterior width.

Tableau 1
Les équations de la forme $Y = aX^b$ obtenues par la méthode *Model II Regression* après transformation en logarithmes (données issues de Jadwiszczak, 2001), où BM et BL se réfèrent respectivement à la masse corporelle en kg et la longueur du corps en mm. Abréviations : r, coefficient de corrélation de produit-moment de Pearson ; CI, intervalle de confiance ; SEE, erreur standard sur l'estimation ; PE, erreur de prédiction.

X	Y	a	$b \pm 95\%$ CI	$r p < 0.01$	SEE	PE
BM	Tmt W	9.620	0.318 ± 0.084	0.96	0.043	0.017
BM	Tmt ApW	3.703	0.274 ± 0.071	0.96	0.036	0.012
BL	Tmt W	0.024	0.992 ± 0.378	0.92	0.060	0.046
BL	Tmt ApW	0.021	0.855 ± 0.319	0.92	0.050	0.029

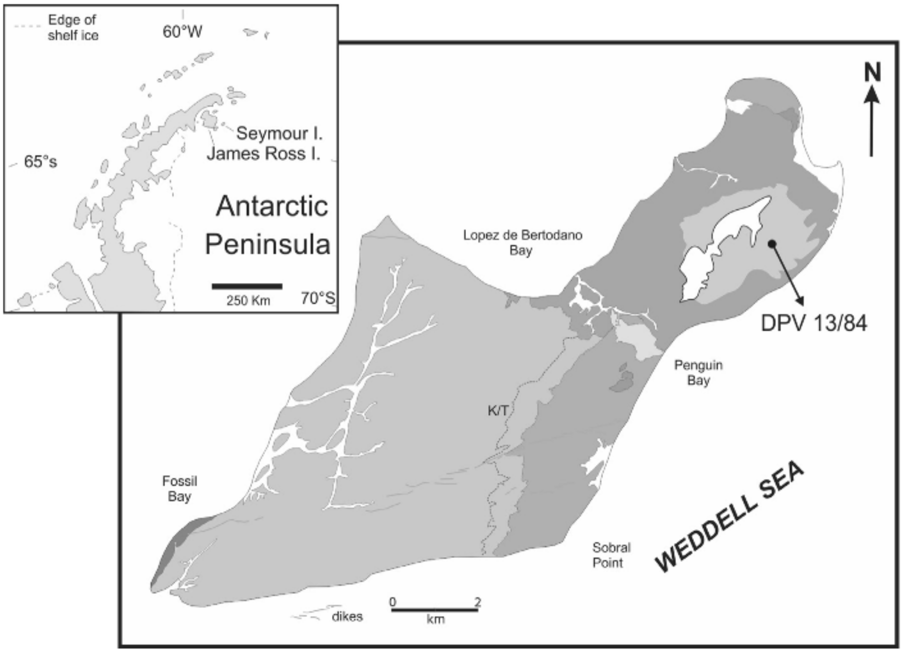

Fig. 1. Location map of the fossiliferous locality DPV 13/84 (Seymour-Marambio Island), Antarctic Peninsula, Antarctica.
Fig. 1. Carte de localisation de la localité fossilifère DPV 13/84 (île Seymour-Marambio), péninsule Antarctique, Antarctique.

4. Systematic paleontology

Order SPHENISCIFORMES Sharpe, 1891
Family SPHENISCIDAE Bonaparte, 1831
Palaeeudyptes Huxley, 1859
Palaeeudyptes klekowskii Myrcha et al., 1990
Fig. 3

Material: MLP12-I-20-116, right tarsometatarsus without trochlea IV.

Diagnostic features observed: The *margo medialis* is concave, with a V-shaped groove proximally developed. The *sulcus longitudinalis dorsalis medialis* is shallow and extends reaching half of the diaphysis, the foramen *vasculare proximale medialis* does not open plantarly.

Description: Large and robust (see measurements below), with a *margo medialis* clearly concave. The *sulcus longitudinalis dorsalis medialis* is shallow and only developed in its proximal end. The *foramen vasculare proximale medialis* does not pass through the tarsometatarsus, and only a vestigial opening appears in the *facies cranialis*. The *sulcus longitudinalis dorsalis lateralis* is wide and deep, weakening toward the *incisura intertrochlearis lateralis*. Large and oval foramen *vasculare proximale lateralis* opening in both *facies cranialis* and *lateralis*. In *Anthropornis*,

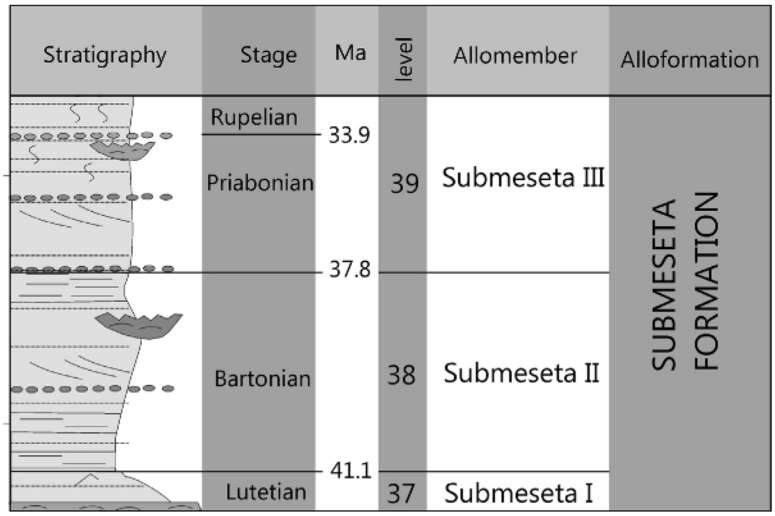

Fig. 2. Chronostratigraphic chart of the Submeseta and La Meseta Formations (Seymour Island Group). Modified from Montes et al. (2013)
Fig. 2. Tableau chronostratigraphique des formations Submeseta et La Meseta (groupe de l'île Seymour), modifié d'après Montes et al. (2013).

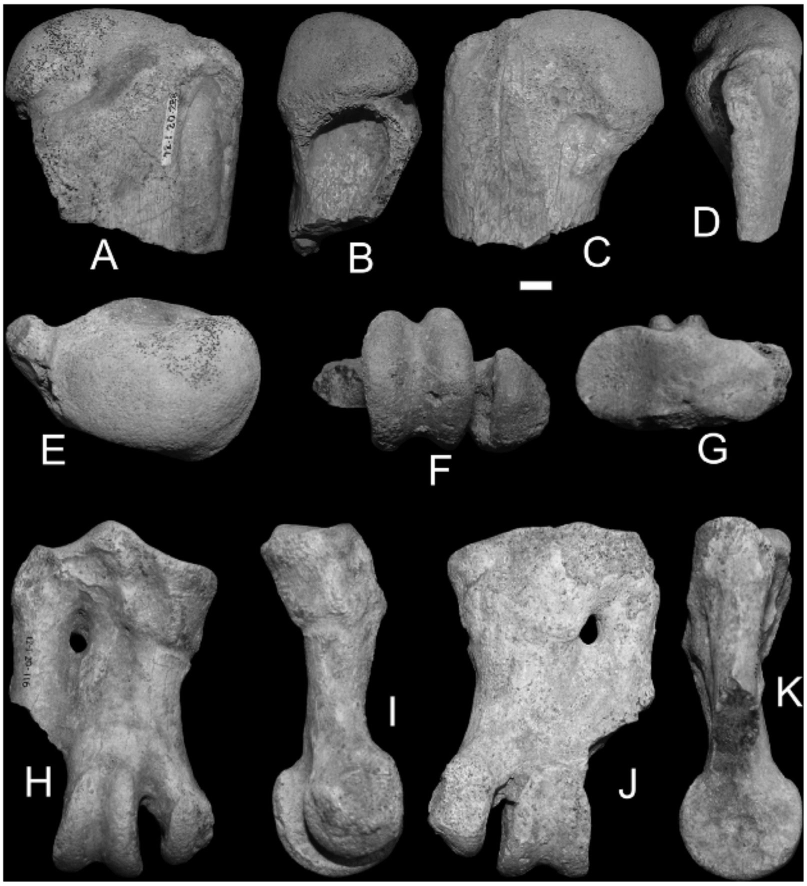

Fig. 3. *Palaeeudyptes klekowskii.* Humerus MLP 12-I-20-288. A. Anterior view. B. Ventral view. C. Posterior view. D. Dorsal view. E. Proximal view. Tarsometatarsus MLP 12-I-20-116 in F. Distal view. G. Proximal view. H. Dorsal view. I. Medial view. J. Plantar (ventral) view. K. Lateral view. Scale bar: 10 mm.

Fig. 3. *Palaeeudyptes klekowskii.* Humérus MLP 12-I-20-288. A. Vue antérieure. B. Vue ventrale. C. Vue postérieure. D. vue dorsale. E. vue proximale. Tarsometatarsus MLP 12-I-20-116. F. Vue distale. G. Vue proximale. H. Vue dorsale. I. Vue médiale. J. Vue plantaire (ventrale). K: Vue latérale. Barre d'échelle : 10 mm.

the *foramina vascularia proximalia* present the opposite condition (The *medialis* is more developed than the *lateralis*). *Tuberositas musculi tibialis cranialis* rounded and well marked. There is a V-shaped groove in the proximal part of the *margo medialis*. The *hypotarsus* is damaged by weathering but it seems that the *cristae hypotarsi* were poorly developed and did not extend beyond the opening of the *foramen vasculare proximale laterale*.

Measurements: Total length: 91.3 mm; width of trochlea II: 15.1 mm; width of trochlea III: 22.6 mm; anteroposterior width of trochlea II: 23.5 mm; anteroposterior width of trochlea III: 25.7 mm; anteroposterior width (at the *tuberositas tibialis cranialis* level): 14.1 mm; proximal lateromedial width: *ca.* 53.9 mm; lateromedial width at midpoint: 45.4 mm.

Material: MLP- 12-I-20-288 proximal end of left humerus.

Diagnostic features observed: the *fossa tricipitalis* is undivided, deep and rounded, the *tuberculum dorsale* is not well marked. The *incisura capitis* and the undivided *sulcus ligamentosus transversus* are connected to each other. The scar of the *musculi brachialis internus* is deep and the *facies musculi supracoracoideus* is shallow and straight.

Description: Large and massive epiphysis with an apparent slender shaft in comparison to that of *Anthropornis*. The cross section of the diaphysis is cuneiform. *Facies musculi supracoracoidei* parallel to the axis of the bone, whereas it is oblique in *Anthropornis* and *Archaeospheniscus*. The *latissimus dorsi* scar is shallow and rounded. The *fossa pneumatica* is small in comparison with that of *P. gunnari*. The *sulcus ligamentosus transversus* merges with the *incisura capitis*. The impression *coracobrachialis* is wide, weakening its boundaries toward the distal end. The *crista deltopectoralis* is constant in width and development along the sulcus of the *coracobrachialis* impression. The *tuberculum dorsale* is rounded and a notch separates it from the head.

Measurements: Proximal epiphysis width: 65.2 mm; anteroposterior epiphysis width: 41.6 mm; diaphysis width (proximal): 46.3 mm; diaphysis anteroposterior width (proximal): 23.2 mm; *sulcus m. supracoracoidei* width: 12.2 mm; *fossa tricipitalis* anteroposterior width: 20.8 mm.

5. Results and discussion

The MLP12-I-20-116, with 91.3-mm length, is the most massive tarsometatarsus known for *P. klekowskii* and therefore also for the genus. Hitherto, tarsometatarsi assigned to *Palaeeudyptes* were between 59–64.4 mm in length for *P. gunnari*, and 66.6–82.4 mm for *P. klekowskii* (Acosta Hospitaleche, 2013b; Acosta Hospitaleche and Reguero, 2014; Myrcha et al., 2002). In fact, the specimen MLP 12-I-20-116 is the largest tarsometatarsus ever described, exceeding also the known values for *Anthropornis nordenskjoeldi* (88.1 mm in length; Myrcha et al., 2002).

As expected, and according to the estimations, the MLP 12-I-20-116 belonged to a huge penguin. Subtle differences were obtained by using the two measurements selected for calculations. The tarsometatarsal width indicates a body mass of about 114.38 kg and 2.01 m in length, whereas the anteroposterior width implies a body mass of 116.21 kg and 2.02 m in total length. It is worth mentioning that the anteroposterior width was considered the most appropriate tarsometatarsal measurement for predicting the body mass of both fossil and extant species (Jadwiszczak, 2001). However, the most conservative values were used for further calculations in order to prevent overestimations.

It seems an extremely high value for both calculated parameters. Nevertheless, given that the living Emperor penguin reaches 46 kg and 136 cm in length – equivalent to nearly 116 cm in height (Martínez, 1992), and its tarsometatarsus is only about 50 mm in length (measurement taken in the NHM1197B), the estimated values based on an almost double sized tarsometatarsus are not beyond the expected assessment.

Assuming that the humerus proportions are not sensitive to significant intraspecific variation, it seems possible to calculate an approximate length of 259.2 mm for the MLP 12-I-20-288 on the basis of the measurements taken in the co-specific MLP 11-II-20-07, and scaling its size from the width of the proximal epiphysis (Acosta Hospitaleche, 2013b; Acosta Hospitaleche and Reguero, 2014). Dimensions of the humerus MLP 12-I-20-288 are also huge in comparison with the penguin bones described so far (Acosta Hospitaleche, 2013b; Acosta Hospitaleche and Reguero, 2014; Jadwiszczak, 2006; Tambussi et al., 2006). These values are only estimates and cannot be taken as absolute. The size range attributed to *P. klekowskii* becomes suspiciously broad, but it is important to remember that MLP 12-I-20-288 exhibits the diagnostic characters of the species, and their assignment is undeniable according to the current systematic paradigm. Something similar happens with *P. gunnari*, the other Antarctic species of the genus. This issue was rigorously addressed Jadwiszczak and Acosta Hospitaleche (2013) and Acosta Hospitaleche and Reguero (2014), recognizing a similar spectrum of variation for these taxa.

It was considered (Ksepka et al., 2012) that limb bones cannot be scaled to determine body size, because of the different proportions of skeletal elements between "stem" and living penguins. However, results obtained here are consequential when compared with other Paleogene penguins. *Kairuku grebneffi* would have approached 1.5 m in length (Ksepka et al., 2012). The tarsometatarsus described here is clearly larger than any species of *Kairuku* (*K. grebneffi* has a tarsometatarsus of 63.6 mm in length and MLP 12-I-20-116 is 91.3 mm), and consequently, estimations of size are higher. Something similar happens with MLP 12-I-20-288, none of the humeri ever known exhibits those measurements. The largest humerus assigned to an Antarctic penguin is 54 mm wide at the proximal epiphysis (Tambussi et al., 2006), whereas MLP 12-I-20-288 described here is 65.2 mm wide at the same point. Although data taken from different penguin species should not be used for extrapolations, they allow size comparisons, indicating also that tarsometatarsus MLP 12-I-20-116 and the humerus MLP 12-I-20-228 clearly belonged to large birds.

From the body mass estimation, and considering the extant species as a *proxy* group, some other paleobiological parameters could be calculated. The tarsometatarsus MLP 12-I-20-116 would belong to a penguin with high diving skills; capable of making longer breath-hold dives than other heavy animals (Kooyman, 1989). It was estimated that regular dives take 16.6 min (with potential and maximum dives of 40 min). These approximations, based on the equation of Watanuki and Burger (1999), are consistent with the generalized idea that Antarctic large penguins were piscivores. They probably used pursuit diving techniques for the capture of large fish. Gigantism would confer certain advantages for survival within the colony, a more effective defense against predators, and greater ability to catch prey.

Acknowledgements

The author acknowledges the Instituto Antártico Argentino and the Dirección Nacional del Antártico (Argentina), Consejo Nacional de Investigaciones Científicas y Técnicas and Agencia Nacional de Promoción Científica y Tecnológica and the Universidad Nacional de La Plata (Argentina) for constant support. She thanks Dr. Javier Gelfo (member of our Antarctic Heidi group) for helpful comments, and Dr. Cecilia Deschamps for improving the English grammar.

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