ISSN 0002-7014
AMEGHINIANA - 2016 - Volume 53 (3): 269 – 281

PALEOBIOLOGICAL REMARKS ON A NEW PARTIAL SKELETON OF THE EOCENE ANTARCTIC PENGUIN *PALAEEUDYPTES KLEKOWSKII*

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Abstract. A new incomplete penguin skeleton is described herein. It is assigned to *Palaeeudyptes klekowskii* Myrcha, Tatur and Del Valle, a giant sphenisciform from the Priabonian Submeseta Formation in Marambio/Seymour Island, Antarctic Peninsula. Also provided is a paleobiological discussion derived from the morphology of this skeleton. A thorough description of muscular origin and insertions, body mass, body length, and diving duration estimations support the hypothesis that the new specimen represents a marine bird with limited swimming skills wighing 40–44 kg and measuring 133.2–143.2 cm long.

Key words. *Palaeeudyptes klekowskii*. Eocene. Antarctica. Paleobiology.

Resumen. CONSIDERACIONES PALEOBIOLÓGICAS ACERCA DE UN NUEVO ESQUELETO DE PINGUINO EOCENO ANTÁRTICO DE *PALAEEUDYPTES KLEKOWSKII*. Un nuevo e incompleto esqueleto perteneciente a *Palaeeudyptes klekowskii* Myrcha, Tatur y del Valle, procedente de la Formación Submeseta (Priaboniano) de la Isla Marambio/Seymour, Península Antártica es aquí estudiado. Se brinda además una discusión acerca de sus atributos paleobiológicos a partir de la morfología del esqueleto. Una detallada descripción de los orígenes e inserciones musculares, sumado a las estimaciones de su masa, longitud corporal, y capacidades de buceo, soportan la idea de que el nuevo espécimen correspondió a un ave nadadora de unos 40–44 kg de peso y 133.2–143.2 cm de largo con limitadas capacidades locomotoras bajo el agua.

Palabras clave. *Palaeeudyptes klekowskii*. Eoceno. Antártida. Paleobiología.

It is believed that –like extant species– the oldest penguins were wing-propelled diving birds (*e.g.* Acosta Hospitaleche, 2014) but in fact little is known about the paleobiology of fossil penguins. The morphology of particular bones is one factor involved in the analysis of locomotor specialization, while other factors involve the proportions of limb elements (Nudds *et al*., 2004; Hinić-Frlog and Motani, 2010), bone section morphology (Habib and Ruff, 2008), and bone tissue modifications (Houssaye, 2009).

Very few studies have dealt with these issues, perhaps in part because the fossil record imposes important restrictions. The penguin fossil record in Antarctica is a clear example of this, as it consists of hundreds of isolated remains and scarce articulated or associated skeletons (Acosta Hospitaleche *et al*., 2013). The most complete fossil penguin specimens from Antarctica (Fig. 1) are the partial skeletons of *Palaeeudyptes gunnari* (Acosta Hospitaleche and Reguero, 2010), *P. klekowskii* (Acosta Hospitaleche and Reguero, 2014), and *Anthropornis* (Jadwiszczak, 2012). Most species were described based on a single element, too little for any reliable paleobiological study. Nevertheless, some approaches to the biomechanics of fossil penguins from Antarctica have been recently conducted (Acosta Hospitaleche, 2014 and references above).

The James Ross Basin is a unique place worldwide regarding the fossil record of penguins. This is so because it presents a continuous fossil-bearing sequence from the late Paleocene to the latest Eocene–early Oligocene?. A single species, *Crossvallia unienwillia* Tambussi, Reguero, Marenssi and Santillana, 2005, is known from the Antarctic Paleocene. The Eocene record from Seymour Island is remarkable as it suggests that penguins were significantly more diverse during the Paleogene than nowadays. Several recent studies record the abundant remains of fossil penguins from these levels (*e.g.*, Acosta Hospitaleche, 2014 and references therein) and a total of ten to fourteen species (Table 1) have been described from the Eocene of Antarctica (see Jadwiszczak, 2006, and Tambussi *et al.,* 2006 for details). Discrepancies in the number of species are fundamentally based on the presence in Antarctica of *Archaeospheniscus lopdelli*, *Palaeeudyptes antarctica*, and two species of the genus *Tonniornis* (Tambussi *et al.*, 2006; Tambussi and Acosta Hospitaleche, 2007), which as been disputed by Jadwiszczak (2006).

No other cases are known, in the fossil record or among extant species, in which so many different seabird species coexist in the same coastal region or in neighboring breeding colonies. The Antarctic penguin assemblage of the Submeseta Formation therefore represents an ecologically interesting case (Acosta Hospitaleche *et al.*, 2013). Time averaging is at a minimum and fossils are approximately contemporaneous with the entombing sediments (see Stilwell and Zinsmeister, 1992). Most if not all the remains recovered from these levels were transported for a short time before burial and therefore their accumulations represent parauthochtonous assemblages. Even considering the proposal of Jadwiszczak and Mörs (2011), which reduced the number of penguin species from fourteen to ten, it is clear that the Eocene penguins from Seymour Island constitute an assemblage that has no modern analogues.

This striking diversity would imply a number of advantages and drawbacks regarding the interactions with other species and the environment. While this association of species would have some advantages regarding potential predators, competition for nesting sites and prey would be greatly affected. Species foraging on the same prey could reduce competition and live sympatrically when their body sizes are different (Hutchinson, 1959; Spear and Ainley, 2007). This seems to be the case of Antarctic Eocene penguins, represented by a wide range of body-sizes usually grouped into four categories: small penguins about the same size of the extant little blue penguin, medium penguins (such as *Marambiornis*, *Mesetaornis* and *Delphinornis*) that reached the size of most modern penguins (*Spheniscus*,

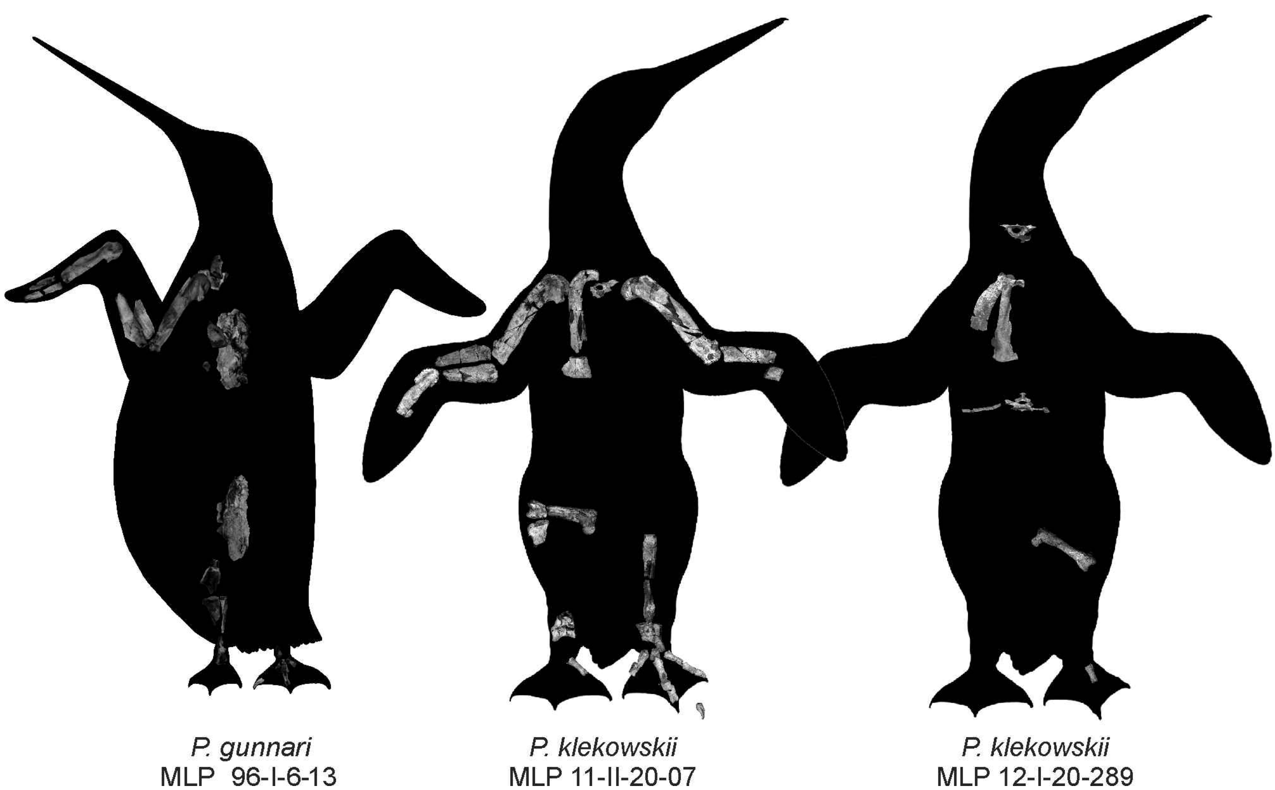

Figure 1. Schematic Antarctic skeletons of ***Palaeeudyptes*** (not to scale) reported so far, from left to right: ***P. gunnari*** **MLP** 96-I-6-13, ***P. klekowskii*** **MLP** 11-II-20-07, and ***P. klekowskii*** **MLP** 12-I-20-289 under study in the present contribution.

Pygoscelis, etc.), large penguins such as *Archaeospheniscus* and *Palaeeudyptes gunnari* (as tall as the Emperor penguin), and finally, the famous giant penguins represented by *Anthropornis* and *Palaeeudyptes klekowskii*, which were about 2 meters tall. The latter genus is widely distributed in the Eocene of Seymour Island (Acosta Hospitaleche *et al.*, 2013).

The incompleteness of the penguin fossil record in Antarctica has been a problem repeatedly noted in previous studies. In his pioneer work, Wiman (1905) grouped the remains of Antarctic fossil penguins according to their size and robustness. In a similar way –but using quantitative tools to support his hypotheses– Jadwiszczak (2006) assigned isolated and non-homologous elements to the different recognized species. Many of these associations were subsequently corroborated through the finding of new and more complete remains (*e.g.* Acosta Hospitaleche and Reguero, 2014), whereas others are still pending confirmation or rectification (Kandefer, 1994).

In this context, associated remains of Antarctic penguins identifiable at the species or genus level are significant given that they can provide new information on the anatomy, diversity, and paleobiology of fossil taxa. Here I report and analyze paleobiological aspects (body size, swimming capabilities) of an incomplete skeleton of *Palaeeudyptes klekowskii* recently found in Eocene deposits of Antarctica.

MATERIALS AND METHODS

The material under study was collected during the 2012 field-season of the Instituto Antártico Argentino (Dirección Nacional del Antártico, Argentina) in Marambio/Seymour Island. It is permanently housed in the collections of the División Paleontología de Vertebrados of the Museo de La Plata, La Plata, Argentina.

The comparative sample includes fossils from the collections of Museo de La Plata (**MLP**), Argentina; Museo Nacional de Historia Natural (**SGO-PV**), Chile; the Naturhistoriska Riksmuseet (**Nr**), Sweden; and the Natural History Museum (**NHM**), Great Britain, Institute of Biology, University of Białystok **(IB/P/B)**, Poland, and includes casts of Aus-

Table 1 – Summary of the Eocene penguin record of Antartica. Cucullaea II, Cucullaea I, Campamento, and Acantilados are allomembers included in La Meseta Formation. For each species: 0, absence; 1, presence (modified from Acosta Hospitaleche et al.*, 2013).*

Species	*Submeseta Formation*	*La Meseta Formation*			
		Cucullaea II	*Cucullaea I*	*Campamento*	*Acantilados*
Anthropornis nordenskjoeldii	1	1	1	1	0
Anthropornis grandis	1	1	1	1	0
Palaeeudyptes gunnarii	1	1	1	0	1
Palaeeudyptes klekowskii	1	1	1	0	0
Palaeeudyptes antarcticus	1	0	0	0	0
Delphinornis larsenii	1	1	1	0	0
Delphinornis arctowskii	1	0	0	0	0
Delphinornis gracilis	1	0	0	0	0
Mesetaornis polaris	1	0	1	0	0
Marambiornis exilis	1	0	1	0	0
Archaeospheniscus lopdelli	1	1	0	0	0
Archaeospheniscus wimani	1	0	1	0	0
Tonniornis mesetaensis	1	0	0	0	0
Tonniornis minimum	1	0	0	0	0

tralian specimens of *Anthropornis* and *Pachydyptes* housed in the last two institutions.

Anatomical terminology follows Baumel *et al.* (1993) for osteology and musculature. Measurements were taken with a Vernier Caliper of 0.01 increments and are given in millimeters. Paleobiological estimations follow Jadwiszczak (2001) for body mass and body length, and Watanuki and Burger (1999) for diving capabilities. Analysis of the coracoid joint follows Acosta Hospitaleche and Di Carlo (2010), and reconstruction of femur musculature has been made following the study of Schreiweis (1982). Sedimentology follows Marenssi *et al.* (1998a,b) and chronostratigraphy is according to Montes *et al.* (2013).

GEOLOGICAL SETTING

Specimen MLP 12-I-20-289 comes from Unit III (Priabonian) of the Submeseta Formation (Montes *et al.*, 2013), and was found at locality DPV 16/84 in Marambio/Seymour Island (Fig. 2), Antarctic Peninsula. The stratigraphy and sedimentology of these units have been studied in detail and an extensive description of the La Meseta Formation can be found in Marenssi *et al.* (1998a,b).

A chronostratigraphical update was recently provided by Montes *et al.* (2013), according to which the new Submeseta Formation was proposed for the upper part of the former Submeseta Allomember (La Meseta Alloformation).

The early Eocene to earliest Oligocene? La Meseta and Submeseta formations constitute a 720 meter-thick sequence filling up a 7 km wide valley cut down into the older sedimentary rocks of the island after the regional uplift and tilting of the Paleocene and Marambio Group beds (Marenssi *et al.*, 1998). These units comprise mostly poorly consolidated siliciclastic fine-grained sediments deposited in deltaic, estuarine and shallow marine environments as part of a tectonically-controlled incised valley system (Marenssi, 1995; Marenssi *et al.*, 1998b).

SYSTEMATIC PALEONTOLOGY

SPHENISCIFORMES Sharpe, 1891
SPHENISCIDAE Bonaparte, 1831

Palaeeudyptes Huxley, 1859

Type species. *Palaeeudyptes antarcticus* Huxley, 1859.

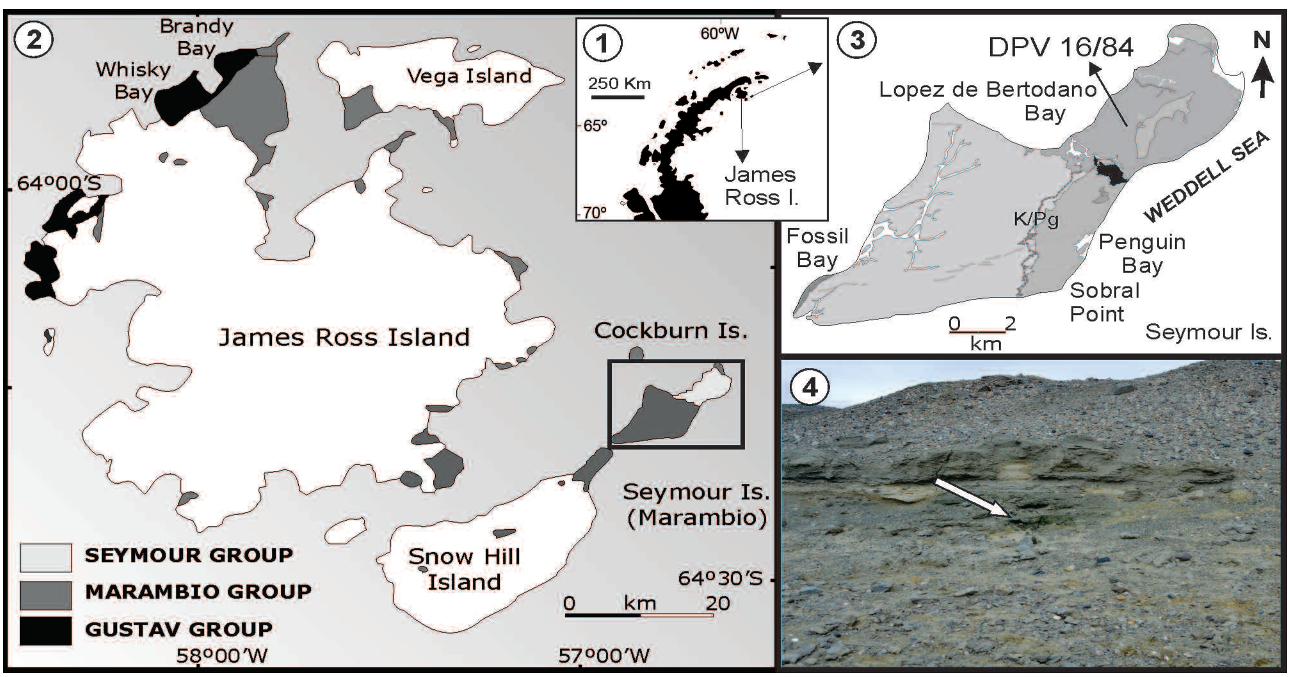

Figure 2. Location map: **1,** Antarctic Peninsula (West Antarctica) indicating location of Seymour (Marambio) Island; **2,** Detail of Seymour Island (the black square indicates the detail in **3**); **4,** Fossil locality DPV 16/84 where the uppermost levels of the Submeseta Formation crop out (the arrow indicates the site where the skeleton was found).

Palaeeudyptes klekowskii Myrcha, Tatur and
Del Valle, 1990
Figures 1, 3–5

Holotype. IB/P/B-0065 right tarsometatarsus, lacking trochlea IV, and most of the fourth metatarsal.

Referred specimen. MLP 12-I-20-289 (Fig. 1) incomplete associated skeleton (left femur, right coracoid, right scapula, two cervical vertebrae, thoracic vertebra, rib, pedal phalanx, and several bony fragments).

Measurements. Femur (maximum length 131.5 mm, latero-medial width of shaft 17.9 mm, cranio-caudal width of shaft 18.2 mm); scapula (dorso-ventral proximal width 41 mm, dorso-ventral width at the collar level 21 mm, latero-medial width at the collar level 8.4 mm); coracoid (maximum length 165 mm, latero-medial width at the foramen n. supracoracoidei level, dorso-ventral width at the foramen n. supracoracoidei level 12.4 mm); cervical vertebra (height of foramen 9.1 mm, width of foramen 10 mm, cranio-caudal extension of the body 38.7 mm, width of the body 14.1 mm); thoracic vertebra (height of foramen 9 mm, width of foramen 11.6 mm, cranio-caudal extension of the body 33.7 mm, width of the body 23.6 mm, cranial articular facet- height 13 mm, dorsal width 15 mm, ventral width 26.7 mm); rib (width 12 mm, dorso-ventral width 3.6 mm); pedal phalanx (length 37.4 mm, proximal latero-medial width 17.1, distal latero-medial width 8.7, minimum latero-medial width 12 mm, proximal height 15 mm, distal height 10.5 mm, minimum height 7.1 mm).

Locality and age. DPV 16/84 (S64° 14′ 27′′ S, 56° 38′ 43′′ W), Marambio Island (West Antarctica, Fig. 2). Eocene–?earliest Oligocene (Submeseta III- level 39-, Submeseta Formation, Seymour Island Group).

Description. The coracoid (Fig. 3.1, 3.4) is massive and flabelliform. The shaft is stout and the omal end is hook-like. The *facies articularis clavicularis* is oblique respect to the coracoid axis. *The processus acrocoracoideum* constitutes the proximal end. The *impressio lig. acrocoracohumeralis* is crested. The *facies artic. humeralis* is vertically expanded. The *cotyla scapularis* is rounded and deep. The *sulcus m. supracoracoidei* is wide and the *incisura n. supracoracoidei* is vertically enlarged. The *impressio m. sternocoracoidei* is shallow and barely delimited. The width of the *facies articularis sternalis* is constant along its entire length. The *angulus medialis* is moderate, and the *processus lateralis* is broken.

The *corpus scapula* (Fig. 3.5, 3.8) has parallel margins and the proximal end is massive. The acromion is medially expanded and dorsally curved; consequently the *facies articularis clavicularis* is dorsally located. The *tuberculum coracoideum* is wide and rounded, whereas the *facies articularis humeralis* is represented by a sub-rounded small facet. A depression on the *facies costalis* is located distal to the *tuberculum coraoideum*. The *collum scapula* is better defined on the *margo dorsalis*. The *extremitas distalis* are not preserved.

The *capitis* and *trochanter femoris* of the femur are proximally located at the same level (Fig. 4.1, 4.3, 4.5, 4.8). The *fovea ligamentaris capitis* is shallow and the *facies articularis acetabularis* is broadly expanded. The *crista trochanterica* is strong and continues with the robust *impression illiotrochantericae*. The *facies acetabularis antitrochanterica* is concave and well-marked, although the *fossa trochanteris* is absent. The *impression obturtoriae* is restricted to the most proximal end, and forms a sub-circular area. The *linea intermuscularis caudalis* is not visible, but the *linea lintermuscularis cranialis* is crest-like. The *sulcus patellaris* is broad and deepest proximally to the condyla. Consistently, the *sulcus intercondylaris* is also broad and a slightly medially displaced respect to the diaphysis. The *condylus lateralis* is more distally expanded than the *medialis*. The *fovea tendinus m. tibialis cranialis* is rounded and aligned with the diaphysis. The *epicondylus lateralis* is small.

The *fossa poplitea* is deep, broad and extended medially to the strong *crista supracondylaris medialis*. This crest runs proximally toward a central position on the diaphysis (respect to the lateral and medial facies). The *condylus medialis* is flat and wide, whereas the *condylus lateralis* is narrow, sharp, and separated from the proximally broader *trochlea fibularis* by a strong *crista tibiofibularis*. There is a slightly developed *tuberculum m. gastrocnemialis lateralis*.

Cervical vertebrae (Fig. 5.2) have a heterocoelous and cranio-caudally enlarged corpus. The *arcus* of the vertebra is preserved only in one of the cervicals, and the *processus spinosus* is low and developed at the caudalmost end part of the vertebra. The *zygapophysis cranialis* and *caudalis* are widely expanded, oval, and flat. The *foramen transversaria* is laterally compressed in the largest vertebra, but is circular in the other cervical. The *processus ventralis corporis* is incipiently developed.

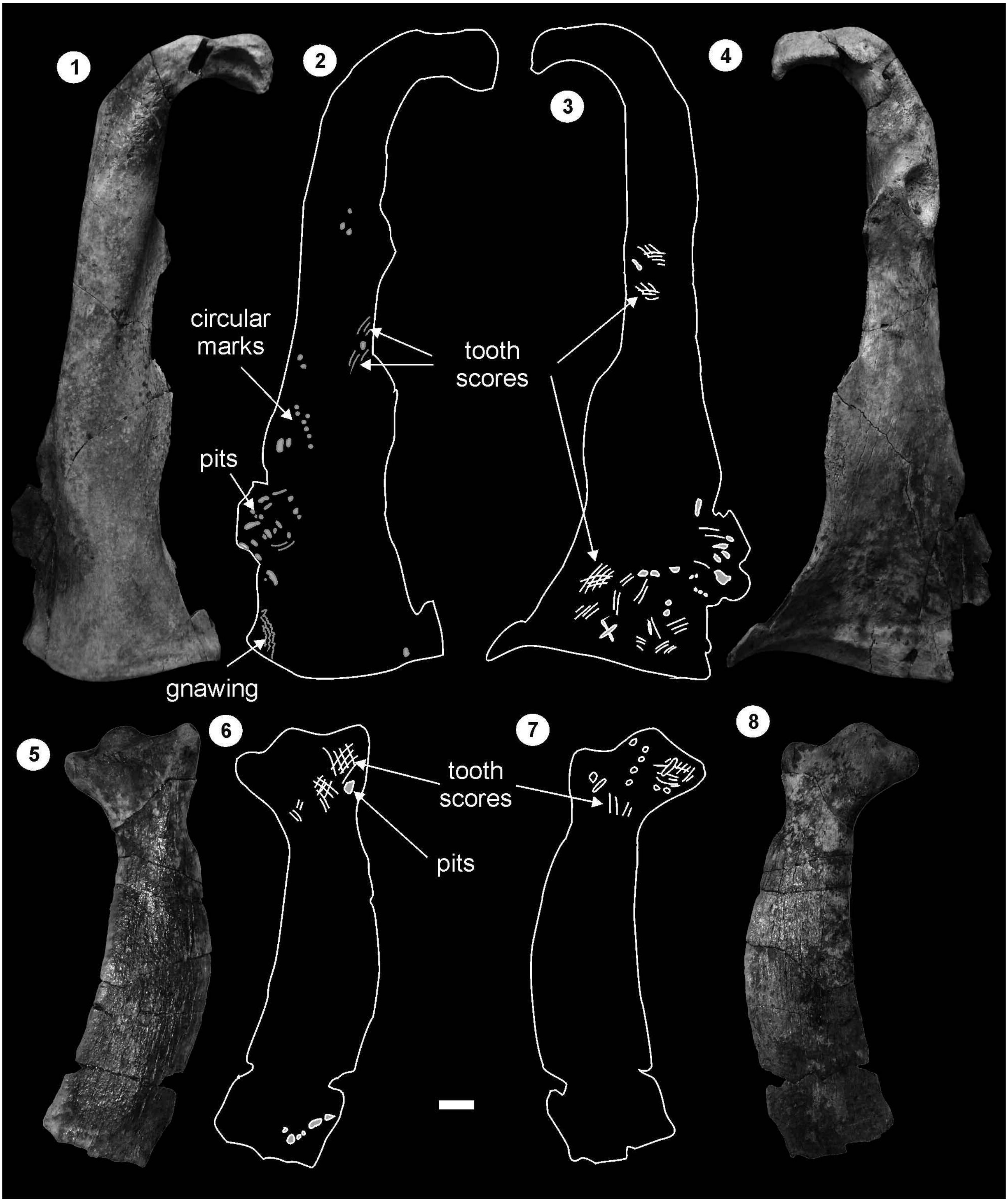

Figure 3. ***Palaeeudyptes klekowskii*** **MLP** 12-I-20-289: **1,** right coracoid in ventral view; **2,** Schematic drawing showing bite marks identified on the ventral surface; **3,** Schematic drawing showing counterparts of the bite marks on the dorsal surface; **4,** Right coracoid in dorsal view; **5,** Right scapula in ventral view; **6,** Schematic drawing indicating bite marks recognized in ventral view; **7,** Schematic drawing of corresponding marks in dorsal view; **8,** right scapula in dorsal view. Scale bar= 10 mm.

The thoracic vertebra (Fig. 5.1) has a heterocoelous corpus, being the lower part of the *facies articularis* wider than the upper one in both the *facies cranialis* and *caudalis*. The *processus transversalis* is horizontal and its end is expanded. The *processus spinosus* is robust and high, occupies the entire length of the vertebra, and its cranialmost tip forms a tubercle. The *processus ventralis corporis* is represented by a single, medially located projection.

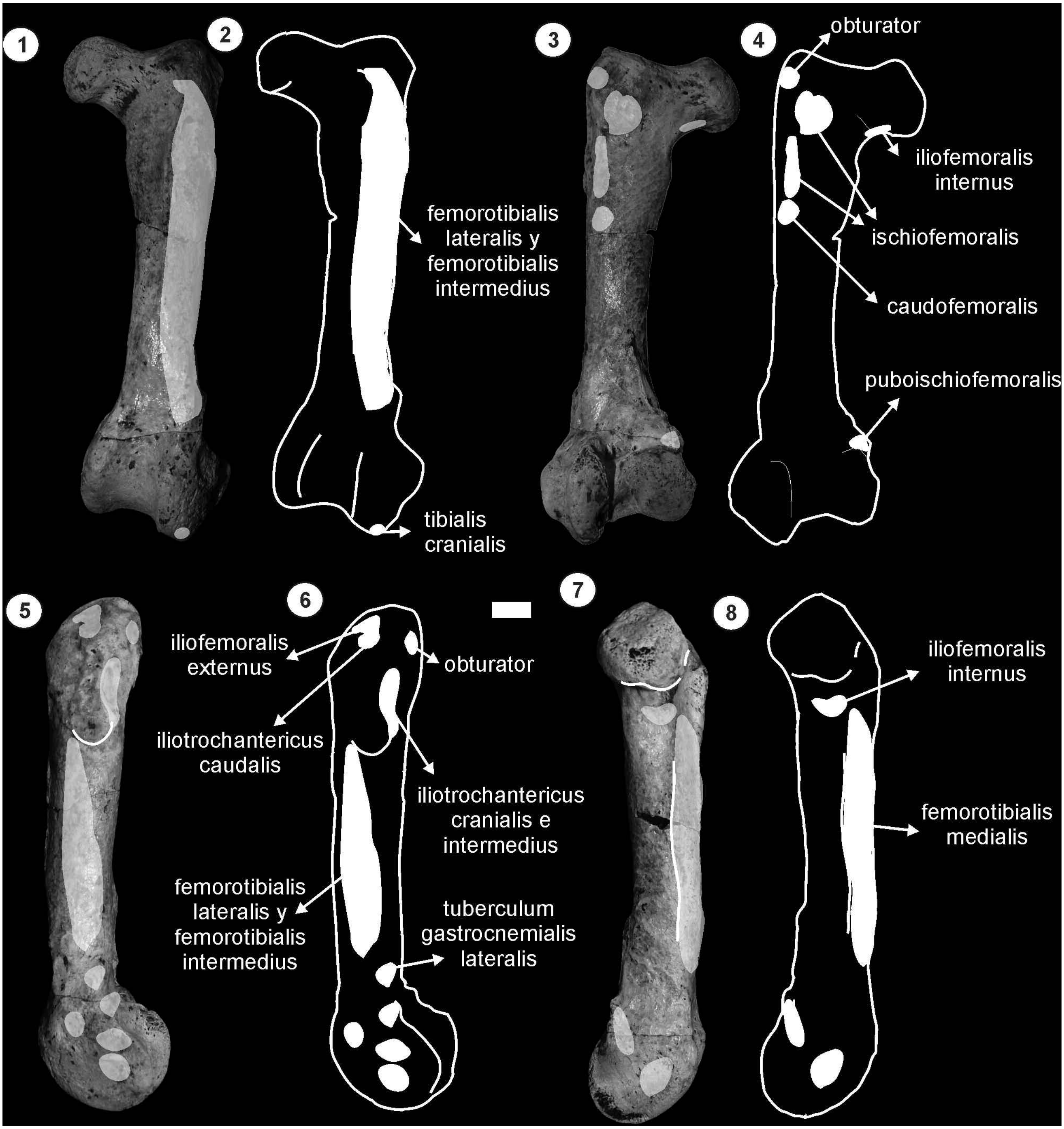

Figure 4. Femur of ***Palaeeudyptes klekowskii*** **MLP** 12-I-20-289: **1,** Cranial view; **2,** Schematic draw showing insertion and attachment of identified muscles in cranial view; **3,** caudal view; **4,** schematic draw showing muscular scars in caudal view; **5,** lateral view; **6,** schematic draw showing muscular attachments in lateral view; **7,** Medial view; **8,** Schematic draw showing the corresponding attachments in medial view. Scale bar= 10 mm.

The rib (Fig. 5.3) is curved and distally flat and proximally triangular in cross section. Although they are not preserved, the development of the *processus uncinatus* is evidenced through a mark on the *corpus costa*.

The pedal phalanx (Fig. 5.4) is large, massive, and dorso-plantarly compressed. The *cotyla articularis* is flat, high, and subtriangular, with rounded vertices. The *caput phalangis* is separated from the *corpus* by a slight constriction. The *trochlea articularis* and the *fovea subtrochlearis* are centrally positioned. The *fovea ligamentaris collateralis* are shallow. The *facies plantaris* is medio and distally concave, but proximally flat.

Taxonomic discussion. Some historical issues regarding the systematic assignment of fossil penguins worldwide are worth considering here. The size groups proposed by Wiman (1905) constituted the first attempt to classify isolated penguin remains, and were subsequently improved by other contributions (*e.g.* Jadwiszczak, 2006; Tambussi *et al.*, 2006).

Specimen MLP 12-I-20-289 is noticeably different in size and robustness from many of the known Antarctic species; thus, the assignation of this specimen to either small (*e.g.*, *Marambiornis*, *Mesetaornis*, *Delphinornis,* and *Tonniornis* species) or medium-sized (*Archeospheniscus*) penguins can be rejected. The size of its skeletal remains falls within the size range of the so-called "giant" Antarctic penguins *Anthropornis* and *Palaeeudyptes*, and possibly the Australian *Pachydyptes*.

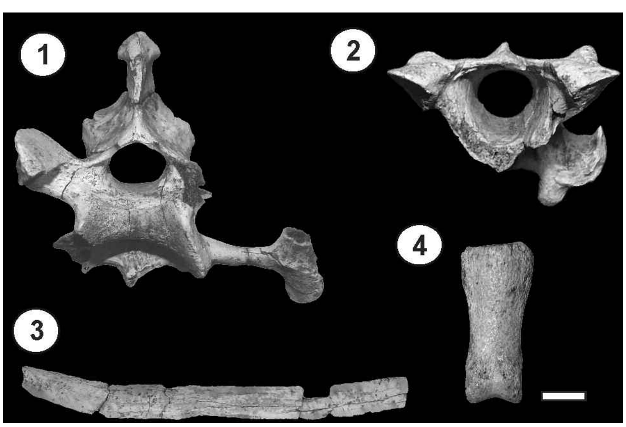

Figure 5. Other bones of ***Palaeeudyptes klekowskii*** **MLP** 12-I-20-289: **1,** Thoracic vertebra in cranial view; **2,** cervical vertebra in caudal view; **3,** rib; **4,** pedal phalanx in dorsal view. Each view was selected in order to show the best preserved side. Scale bar= 10 mm.

MLP 12-I-20-289 was compared with available material corresponding to these giant species. *Anthropornis* was originally known from tarsometatarsi (Wiman, 1905) and several remains were posteriorly referred to it, including a partial skeleton (Jadwiszczak, 2012) that is the most informative specimen known for this genus. Additionally, the elements originally described as *Pachydyptes simpsoni* by Jenkins (1974) were later referred to *A. nordenskjoeldi* by the same author (Jenkins, 1985). This referral, however, is not supported due the lack of comparable materials (homologous elements), even considering the humerus and the coracoid referred to *A. nordenskjoeldi* (see Jenkins, 1985). *A. nordenskjoeldi* was based on a single tarsometatarsus, whereas *Pachydyptes simpsoni* was described from a coracoid, humeri, radius, carpometacarpus, phalanx, and vertebrae. Moreover, the two paratypes of *Pachydyptes simpsoni* include the same skeletal elements but no tarsometatarsi (Jenkins, 1974). According to Ando (2007), *P. simpsoni* cannot be considered a junior synonym of *Anthropornis nordenskjoeldi*. Therefore, comparisons conducted here include *Pachydyptes simpsoni* (as a distinct species) and *Palaeeudyptes* (material of both Antarctic species is available for direct comparisons).

Pachydyptes simpsoni is a large species with short and robust bones. Its coracoid is an extremely massive element, with a more marked flabelliform shape, and a wider stercoracoracoideal base, compared to that of *Palaeeudyptes* and the specimen here described (MLP 12-I-20-289). Similarly, the coracoid of *Anthropornis* has been characterized by Jadwiszczak (2006) as large and robust. The shallow depression described, limited by the *facies articularis scapularis*, *facies a. humeralis*, *margo lateralis* and a crest sternal to both *facies* is not present in *Palaeeudyptes* or the coracoid here described. This structure is also found in the Australian coracoid (P 14157a) belonging to *P. simpsoni* (Jenkins, 1974).

MLP 12-I-20-289, although larger than the known specimens of *Palaeeudyptes*, fits the description of *Palaeeudyptes* by Jadwiszczak (2006). Most importantly, MLP 12-I-20-289 it is indistinguishable from another specimen previously referred to *Palaeudyptes* (MLP 11-II-20-07) regarding the morphology of the coracoid and femur (Acosta Hospitaleche and Reguero, 2014). Differences and similarities between the two Antarctic *Palaeeudyptes* species (*P.*

gunnari and *P. klekowskii*) have already been discussed in previous contributions (Acosta Hospitaleche and Reguero, 2010, 2014; Jadwiszczak and Acosta Hospitaleche, 2013; Acosta Hospitaleche, 2014) and following these criteria the assignment of MLP 12-I-20-289 to the smaller *Palaeeudyptes gunnari* can be rejected based on the difference in body size.

PALAEOBIOLOGICAL REMARKS

Femur function and involved musculature. The primary role of the femur is to provide support on land for the rest of the body, together with the tibiotarsus and tarsometatarsus. When penguins are standing, the femur is oriented nearly horizontally, which generates strong stress on this element. Consequently, the femur is subject to greater bending moments than compressive forces with respect to the tibiotarsus, which is the other element usually used for biomechanical studies (Campbell and Marcus, 1992). For that reason, the circumference of the femoral shaft must be large enough to support this stress. Unlike the tibiotarsus that plays an active role in locomotion, the femur provides static support (Campbell and Marcus, 1992).

Insertion and origin of most muscles can be easily identified in the femur of MLP 12-I-20-289 (Fig. 4.2, 4.4, 4.6, 4.8). The *m. iliofemoralis externus* is weakly developed in living penguins and its distal end inserts through a separate tendon next to the *iliotrochantericus caudalis* tendon on the *trochanteris femoris*. The *m. iliofemoralis internus* inserts on the caudomedial surface of the proximal end of the femur, just distal to the *capitis femoris*. The *iliotrochanterici* complex is constituted by three different muscles, one of them already mentioned above. The *iliotrochanterici cranialis* and *intermedius* insert together on the lateral surface of the *trochanter femoris*.

The *m. obturatorius lateralis* and *medialis* have a common insertion on the caudal border of the *trochanter femoris*. The *m. ischiofemoralis* is inserted distally, through a tendon that inserts on the *trochanter femoris* caudal to the insertion of the *m. iliotrochanterici cranialis* and *medius*. The *m. caudofemoralis* also inserts on the caudal surface of the femur.

The *m. puboischiofemoralis* is a powerful muscle that inserts proximally to the *condylus medialis* on the caudal surface. A related muscle is the *m. gastrocnemius*, divided into three distinct heads (*pars lateralis* and *pars intermedia* have their origin in the femur). The *pars lateralis* arises from a *tuberculum proximale* to the *condylus lateralis*, on the lateral surface of the femur. The *pars intermedia* has a tendinous origin located proximally to the *condylus medialis.*

The *m. femorotibialis lateralis* and *intermedius* arise on the cranio-lateral surface of the femoral shaft, extending along a wide area. The *m. femorotibialis medialis* originates on the medial facies.

The muscle attachments preserved indicate the development of a bulky and strong musculature, consistent with a sturdy skeleton. Furthermore, they also provide evidence for a pattern similar to that of living penguins regarding hindlimb muscle arrangement. This seems reasonable, since along the evolutionary history of penguins, major changes associated to diving specialization affected the structure of wings. The femur, however, seems to have been a much more conservative element.

Pectoral girdle and diving kinematics. The coracoid and scapula are key elements in the locomotor complex of penguins, which use their flippers to move under water. These structures not only articulate with the humerus but also provide attachment surfaces for "flight" muscles. The sternocoracoid articulation is the only mobile joint of the pectoral girdle. An outstanding characteristic of this region in penguins is the marked extension and curvature of the *facies articularis sternalis* that substantially limits wing abduction (Bannasch, 1986).

Although in MLP 12-I-20-289 the tips of the *angulus medialis* and *processus lateralis* are broken, the sternocoracoid joint seems moderately expanded (Fig. 1, 3.1, 3.4) in comparison with other Paleogene penguins (*e.g. Pachydyptes*, *Anthropornis*). This moderately expanded sternocoracoid joint would be unable to support the development of voluminous position muscles (*e.g.* m. *supracoracoideus*, m. *coracobrachialis caudalis*, m. *subcoracoideus*, m. *sternocoracoideus* and m. *subcoracoscapulares*) used for maintaining an appropriate plane of movement and transfer the propulsive forces generated by isotonic muscles (Bannasch, 1987). Consequently, if these muscles were poorly developed, movements during diving could not be as strong as in extant penguins, given that torque forces would tend to rotate the coracoid and detach it from the sternum.

Similarly, the outline of the scapula (Fig. 3.5–3.8) suggests that diving was not as efficient in this penguin as in its modern counterparts. Modern penguins developed a diving strategy based mainly on the refinement and adjustment of the angle of attack of the forces created by muscles involved in the diving movements of the forelimbs. A complex set of muscles maintains the stiffness of the pectoral girdle and is responsible for the movements of the humerus in the *cavitas glenoidalis*. Among those muscles, the *mm. rhomboidei superficialis*, *mm. rhomboidei profundus*, *mm. serrati superficialis*, and the *mm. serrati profundus* are not directly related to wing movements (Bannasch, 1986). However, they influence the relative lateral position of the scapula with respect to the pectoral girdle and the sternum, connecting also the ribs and the spine. Their attachment surface is enlarged in living Spheniscidae, whereas the *corpus scapula* of MLP 12-I-20-289 is comparatively narrower, which indicates the lack of functional optimization in terms of the resistance to forces transversal to the body axis during diving and swimming (see discussion in Acosta Hospitaleche and Di Carlo, 2012).

Body mass, body size and dive duration. Previous studies on penguins and other birds have concluded that the femur provides reliable body size estimations (Campbell and Marcus, 1992; Cubo and Casinos, 1997; Jadwiszczak, 2001). Moreover, among hind-limb bones, the femur is the element with less variation in the shape and size of its shaft. The well-preserved femur of MLP 12-I-20-289 (Fig. 3) allows estimating body size for this specimen.

For future comparative purposes, body size and body length values were calculated (following Jadwiszczak, 2001) using both Model I and Model II regression equations (see Table 2). However, because the X variable was not under the control of the researcher, Model II equations were preferred for further estimations such as diving capabilities. Inferences based on maximum femur length yield a body mass of 44.8 kg and a body length of 138.0 cm, whereas inferences based on femur diameter yield smaller values for body mass and length. The latero-medial and cranio-caudal widths resulted in estimates of 43.7 kg and 143.2 cm and in 40.6 kg and 133.2 cm, respectively. Estimation of diving skills was made using values obtained from the anteroposterior width of the shaft, a measurement directly related to the weight supported by the femur on land (Campbell and Marcus, 1992; Cubo and Casinos, 1997).

Analysis of the pectoral girdle of MLP 12-I-20-116 suggests that *Palaeeudyptes klekowskii* was a large penguin with some diving skills, and capable of relatively long dives. According to the allometric equation for dive duration as a function of body mass proposed by Watanuki and Burger

Table 2 – Equations of form Y= aXb obtained by Models I and II Regression after logarithmic transformation (taken from Jadwiszczak, 2001), where body mass and body length are expressed in kg and cm respectively. *Abbreviations: **L,** total femur length (131.5 mm); **LMW,** lateromedial width of diaphysis (17.9 mm), APW, anteroposterior width of diaphysis (18.2 mm); **r,** Pearson's product-moment correlation coefficient; **CI,** confidence interval. Most conservative values denoted in bold.*

X	Model	Y	a	b± 95% CI	r p<0.01	Kg/cm
Body mass	II	L	51.41	0.247±0.064	0.93	44.8
		LMW	4.99	0.338±0.095	0.93	43.7
		APW	5.26	0.335±0.067	0.96	**40.6**
	I	L	52.88	0.230±0.064	0.93	52.5
		LMW	5.192	0.313±0.095	0.93	52.2
		APW	5.364	0.323±0.067	0.96	44.0
Body length	II	L	0.393	0.804±0.218	0.92	138.0
		LMW	0.006	1.101±0.398	0.88	143.2
		APW	0.007	1.093±0.292	0.93	**133.2**
	I	L	0.592	0.742±0.218	0.92	145.4
		LMW	0.015	0.967±0.398	0.88	152.0
		APW	0.011	1.021±0.292	0.93	142.1

(1999), regular dives in *Palaeeudyptes klekowskii* could be estimated to have lasted about 7–8 minutes, and the potential maximum dive would have reached 19 minutes. These estimates are comparable with the values known for giant extant species such as the Emperor Penguin (*Aptenodytes forsteri*), which has a maximum dive duration of almost 16 minutes (see Table 3 for comparison with modern species).

Bite marks. The proximal end of the coracoid (Fig. 3.2, 3.3) and the scapula (Fig. 3.6, 3.7) bear lineal marks consistent with predation or scavenging evidence. These traces are thin lines located on the *facies dorsalis* and *costalis* of the scapula, and are interpreted as probable bite marks produced by small fishes. These could have occurred after the death of the animal, when bones were partially exposed and retaining soft tissues. Alternatively, these marks could have been produced if the remains were used as a substrate by sessile organisms.

CONCLUSIONS

For several reasons *Palaeeudyptes* is a key taxon for the understanding of penguin evolution. This genus seems to have been the most widespread geographically and most abundant Weddellian penguin in the Southern Hemisphere during the Eocene and probably the Oligocene (Acosta Hospitaleche and Reguero, 2010). *Palaeeudyptes* is also remarkable for its body size, with skeletons more than 2 meters long known from Antarctica.

Specimen MLP 12-I-20-289 described here is not the most complete specimen of *Palaeeudyptes klekowskii* (see Acosta Hospitaleche and Reguero, 2014), but it possesses some elements (*i.e.*, femur, scapula, coracoid) that are better preserved and allow inferring its body mass and making functional inferences regarding its swimming capabilities. The femoral measurements of MLP 12-I-20-289 indicate it was a large penguin, with body weight ranging between 40 and 44 kg and body length ranging between 133.2 and 143.2 cm.

Although the larger species of extant penguins are able to reach great depths during long dives, the morphology and extension of the sternocoracoid articulation and the narrow scapula of MLP 12-I-20-289 suggest limited swimming skills in comparison with its modern counterparts. In particular, MLP 12-I-20-289 is believed to have been a less specialized diver, at least regarding speed and/or depths, than giant extant species such as the Emperor Penguin *Aptetnodytes forsteri*. Based on the shape of the coracoid of MLP 12-I-20-289, the development of bulky muscle masses able to hold the sternocoracoid articulation in presence of strong forces is unlikely. The muscular masses, although moderately voluminous in this area, would probably not be large enough to maintain the elements in position during the strong movements imposed by the wing during diving.

Table 3 – Values of Body mass (in kg) and dive duration (in minutes) for some species of modern penguins obtained by direct observation. Data taken from Watanuki and Burger (1999).

Species	*Mass*	*Normal Dive Duration*	*Maximum Dive Duration*
Aptenodytes forsteri	*28*	*3.4-5-0*	*15.2-15.8*
Aptenodytes patagonicus	*13.4*	*4.5*	*7.7*
Pygoscelis papua	*6.1*	*2.4-2.8*	*4.5-6.2*
Pygoscelis adeliae	*4.6*	*1.2-1.7*	*2.7-4.5*
Pygoscelis antarctica	*4.1*	*1.2*	*3.0*
Eudyptes chrysolophus	*4.5*	*1.5*	*3.0*
Eudyptes chrysocome	*2.8*	*–*	*3.0*
Spheniscus magellanicus	*3.4*	*2.1*	*3.9*
Spheniscus demersus	*3.2*	*1.8-2.4*	*4.4*
Eudyptula minor	*1.2*	*0.4*	*1.5*

Adaptations for diving would have evolved very early in the history of the group. Improvement of the diving capacity would have been linked to the development of stronger bones and probably muscular structures enabling endurance of greater forces operating in a denser medium. In contrast, modern penguins would have optimized the force action of the flight apparatus by developing more precise movements, adjusting the angle of attack of each of the effective forces (see Acosta Hospitaleche and Di Carlo, 2010 for details).

Estimations in other *Palaeeudyptes* specimens concur with the results presented here, but only the finding of more complete remains will allow refinement of the paleobiological inferences advanced in this study.

ACKNOWLEDGMENTS

I thank the Instituto Antártico Argentino and the Dirección Nacional del Antártico, 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. J. N. Gelfo, M. Reguero, G. López, and S. Santillana, members of the Heidi field work team to which I belong. J. Posik for technical preparation, and C. Morgan for improving the English grammar.

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doi: 10.5710/AMGH.27.08.2015.2890

Submitted: March 7th, 2015

Accepted: September 3rd, 2015