Original article

Palaeeudyptes klekowskii, the best-preserved penguin skeleton from the Eocene–Oligocene of Antarctica: Taxonomic and evolutionary remarks☆

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ABSTRACT

A new fossil penguin skeleton from the La Meseta Formation collected at the locality DPV 13/84 (Seymour Island, Antarctic Peninsula) from the crinoid horizon located 40 m above the base of the 145 m-thick Submeseta Allomember (Late Eocene–Early Oligocene?) is described. The specimen is assigned to the species *Palaeeudyptes klekowskii* Myrcha, Tatur and del Valle, 1990; it is the most complete penguin skeleton ever recovered from Antarctica. Discoveries like this one are significant for the study of the anatomy and evolution of penguins, in particular regarding the Antarctic species included in the genus *Palaeeudyptes* Huxley, 1859. *P. klekowskii* closely resembles its smaller congeneric species *P. gunnari* (Wiman, 1905), with only the relative concavity of the *margo medialis* distinguishing the tarsometatarsi of both taxa. However, the results of a geometric morphometric analysis show some intra- and inter-specific variations, making possible the systematic assignment of the majority of the specimens. Size variation is congruent with the presence of two different species.

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1. Introduction

Even though La Meseta Formation (Eocene–Oligocene, Antarctic Peninsula) is one of the richest units in terms of diversity and abundance of fossil penguins, only a few articulated or associated skeletons from this unit have been described so far. Most of the remains are isolated and fragmented. This taphonomic characteristic of penguin record has compelled palaeontologists to propose a systematic scheme based entirely on isolated skeletal remains, making most species known only through a single element (the tarsometatarsus in most cases, or the humerus in a few others).

The systematics of Sphenisciformes presents substantial difficulties. Although a consensus has been reached regarding the classification scheme for all fossil species, based on tarsometatarsal features, the systematic usefulness of some characters need to be revised. Considering that size is not the best criterion for specific or generic level identification in living penguins, the use of size by itself in fossil taxonomy does not seem reasonable (see Jadwiszczak and Acosta Hospitaleche, 2013 for a discussion about size overlapping in *Palaeeudyptes*).

Only two associated skeletons have previously been collected and studied by the Argentinean research group within the Submeseta Allomember (Acosta Hospitaleche and Di Carlo, 2010; Acosta Hospitaleche and Reguero, 2010). The specimen MLP 96-I-6-13, assigned to *Palaeeudyptes gunnari* (Wiman, 1905), comes from the upper Submeseta Allomember in the southwestern slope of the plateau of the island (DPV 10/84; Fig. 1), stratigraphically 30–35 m below the top of the 145 m-thick *Anthropornis nordenskjoeldi* Biozone (Acosta Hospitaleche and Reguero, 2010). The second partially articulated skeleton, MLP 77-V-10-1, comes also from the Submeseta Allomember. The fossil locality was named DPV 20/84 in Acosta Hospitaleche and Di Carlo (2010), but recent field observations showed us that it actually corresponds to fossil locality IAA 5/12 (Fig. 1). This material would probably correspond to *Anthropornis*, *Palaeeudyptes*, or perhaps a new, undescribed taxon. The preservational state of this skeleton prevents a more specific systematic assignment, given that no diagnostic bones are preserved (Acosta Hospitaleche and Di Carlo, 2010). Additionally, elements of a probably associated wing of *?Delphinornis* were described by Jadwiszczak (2010), as well as a limb skeleton of *Anthropornis* (Jadwiszczak, 2012).

Palaeeudyptes is a key genus in the evolution of Paleogene Antarctic Sphenisciformes (Acosta Hospitaleche et al., 2013) and their spread along South American coasts (*Palaeeudyptes* is also
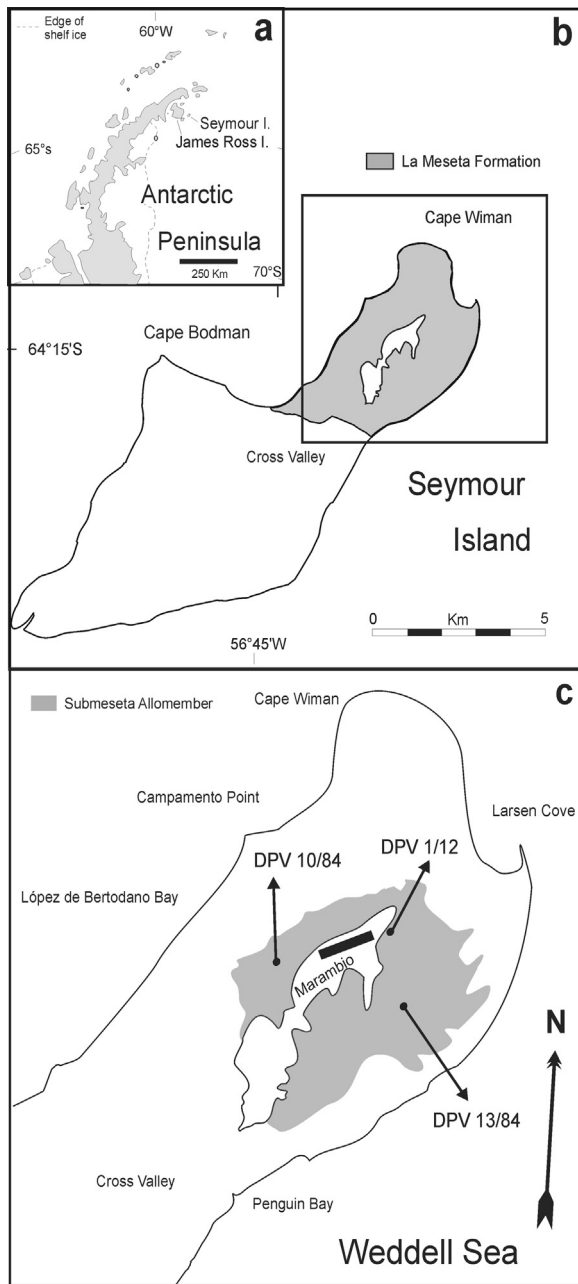
Fig. 1. a: map showing the location of Antarctic Peninsula, Antarctica; **b**: location of the La Meseta Formation in Seymour Island (= Marambio); **c**:sketch map of the northern part of Seymour Island showing the distribution of the Submeseta Allomember and the fossil penguin-bearing localities DPV 10/84, DPV 13/84 and IAA 1/12 in which the associated skeletons were found (modified from Marenssi et al., 1998a).

Upper Eocene) from Burnside, near Dunedin, was described by Marples (1952) and determined as *P. antarcticus* (Ksepka et al., 2012). Likewise, other articulated elements (Nb. C47-17) from Burnside Greensland (Waitakian, Middle Oligocene) were taxonomically assigned by Marples (1952) to *P. antarcticus*; they are morphologically comparable to the ones published by Hector (1872). These discoveries represented the first opportunities to jointly study the features and proportions of the tarsometatarsus and humerus in *Palaeeudyptes*.

P. marplesi was diagnosed after the re-study and the new interpretations of bones previously assigned to *P. antarcticus* (Marples, 1952) and subsequently to *Palaeeudyptes cf. antarcticus* (Simpson, 1957), and finally reallocated to this new species by Brodkorb (1963). An emended diagnosis was provided by Simpson (1971) when reviewing the New Zealand pre-Pliocene material. His results show only size differences with respect to the other species of the genus. No other remains were assigned to this taxon.

P. gunnari was based on an incomplete tarsometatarsus, which had originally been assigned to *Eospheniscus* Wiman, 1905 and then placed into *Palaeeudyptes* by Simpson (1971). It was not until recent times that the only articulated skeleton known was studied (Acosta Hospitaleche and Reguero, 2010). Based on the bones described in the above-mentioned work and the availability of new comparative elements, Sallaberry et al. (2010) were then able to assign new Chilean remains to *Palaeeudyptes*.

The last species erected was *P. klekowskii*, on the basis of a fragmented tarsometatarsus, larger than the other species of *Palaeeudyptes* (Myrcha et al., 1990).

At present, it is clear that *Palaeeudyptes* is widely represented in Antarctica and is the most frequent genus in Argentine and Polish collections (Myrcha et al., 2002; Reguero et al., 2013). For many years, this genus has been strongly questioned; discussions of this issue can be consulted in Ksepka et al. (2006) and Acosta Hospitaleche and Reguero (2010). Furthermore, Jadwiszczak and Mörs (2011) hypothesized that *P. gunnari* and *P. klekowskii* could belong to the same species, which would show sexual dimorphism in the tarsometatarsus (but see Jadwiszczak and Acosta Hospitaleche, 2013).

The successive findings of: isolated remains belonging to *Palaeeudyptes* in Chile (Sallaberry et al., 2010) and some others in Seymour Island; the first articulated skeleton belonging to *P. gunnari* in Antarctica (Acosta Hospitaleche and Reguero, 2010); the new skeleton studied here, assigned to *P. klekowskii*, provide an unique opportunity for the study of the genus *Palaeeudyptes*, and particularly its Antarctic species, a key taxon to understand the major evolutionary patterns of penguins.

The goal of the present contribution is to provide a descriptive and systematic study of the specimen MLP 11-II-20-07. In addition, we discuss the characters used for the discrimination of the different species of *Palaeeudyptes*.

2. Geological and depositional setting

The Submeseta Allomember, the uppermost unit of the La Meseta Formation (Marenssi et al., 1998a, 1998b), is composed of relatively resistant pebbly sandstone with shelly beds dominated by *Hiatella* and other veneroids. The abundance of veneroids and *Modiolus* in this allomember is characteristic, but these invertebrates are not clearly concentrated into shell beds as in the lower units – i.e., *Cucullaea* I and II allomembers. Individual shell beds could not be mapped readily in this unit.

Almost all fossil vertebrate specimens were found in a single horizon, easily distinguishable by occurrence of a high concentration of penguin bones and teleostean fishes (Fig. 2). In particular, the penguin skeleton was collected from the crinoid horizon that occurs in a fine-grained, greenish weathered glauconite (Fig. 3).

recorded in Chile; Sallaberry et al., 2010). Four fossil *Palaeeudyptes* species are known up to date: *P. antarcticus* (Huxley, 1859), *P. marplesi* Brodkorb, 1963, *P. gunnari* (Wiman, 1905), and *P. klekowskii* Myrcha, Tatur and Del Valle, 1990. In addition, it has been proposed that an elongated tarsometatarsus previously assigned to *Palaeeudyptes* could actually belong to a new species of this genus (Jadwiszczak, 2013).

P. antarcticus was the first fossil penguin ever described, based on an isolated tarsometatarsus (Huxley, 1859). Later on, the discovery of two specimens from New Zealand, showing associated skeletal elements, contributed to a better anatomical knowledge of the genus (Ksepka et al., 2006). A humerus associated with a tarsometatarsus (Nb. C43-80) from the Burnside marl (Kaiatan,

Fig. 2. Locality DPV 13/84, Seymour Island, Antarctic Peninsula, Antarctica.
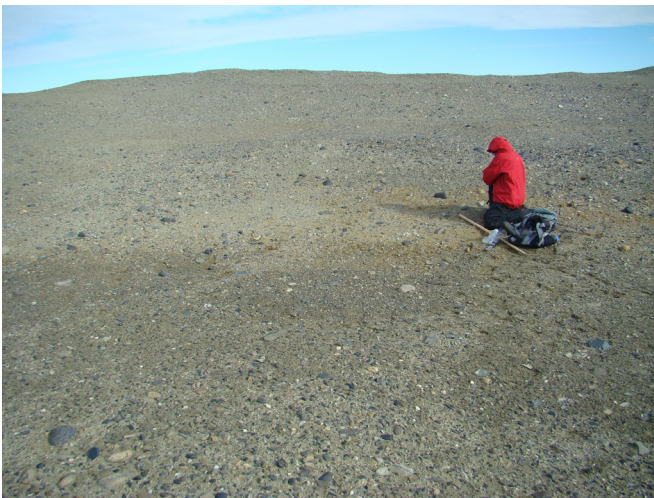

Fig. 3. Details of the locality DPV 13/84, where the skeleton MLP 11-II-20-07 was collected.

Stratigraphically, it is located 40 m above the base of the 145 m-thick Submeseta Allomember (Fig. 4).

The skeleton described here comes from the locality DPV 13/84 (GPS 64°14′45.4″S, 56°35′54.8″W; Fig. 1). In terms of sedimentological features, this locality is included in the facies association II of Marenssi et al. (1998b), which corresponds to a valley-confined estuary mouth to inner estuary complex (an invariable estuarine/shallow marine environment was also interpreted for these levels by Porebski, 2000). Tidal channels and mixed flats, tidal inlets and deltas, and washover and beach environments represent the interfingering of high and low energy environments. Most of the penguin bones recovered from this facies are disarticulated; although some are broken, most are complete, and with diverse degrees of abrasion. Most if not all were transported at least for a short time before burial and therefore their accumulations represent parautochthonous assemblages.

The age of these horizons has been established by Dingle and Lavelle (1998) by strontium dating as 34.2 Ma. Marine vertebrates, such as the gadiform "*Mesetaichthys*" (Jerzmanska and Swidnicki, 1992), a few benthopelagic lamniform sharks, a batoid and a chimeroid (Kriwet et al., 2012), and two skeletons of the primitive mysticete whale *Llanocetus denticrenatus* (Mitchell, 1989) were also recovered from this locality.
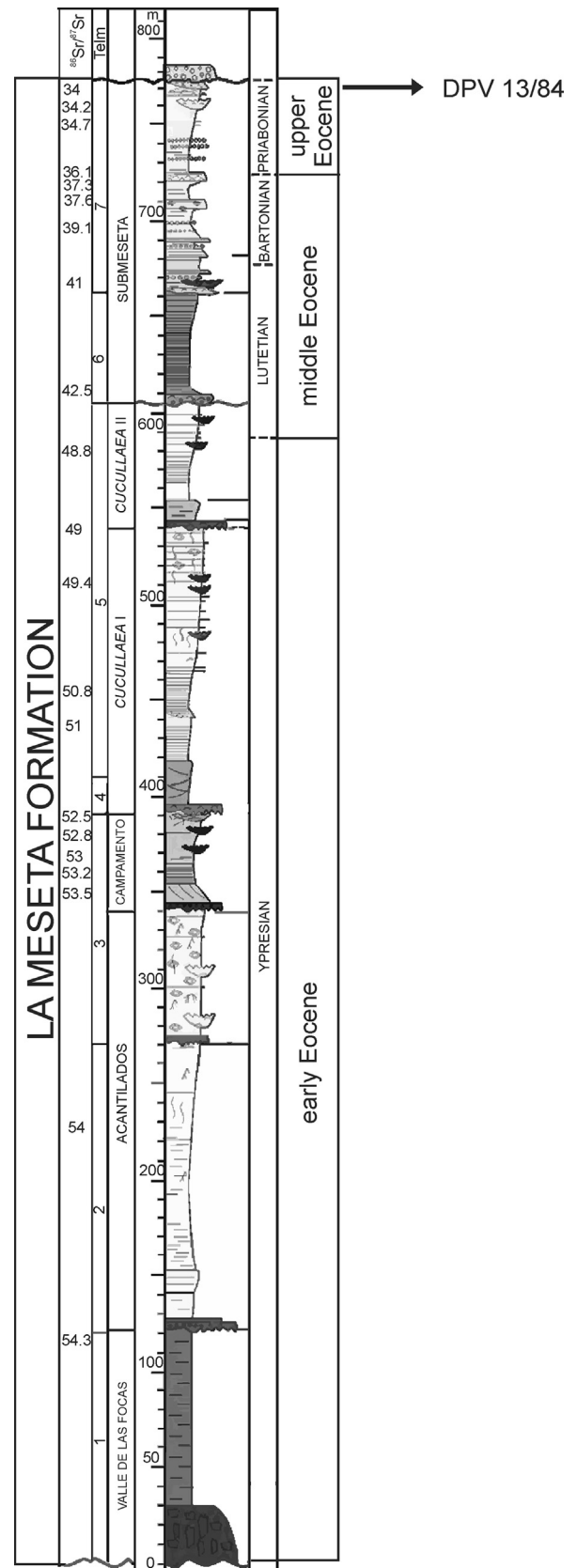

Fig. 4. Stratigraphic section of the La Meseta Formation, Seymour Island, Antarctic Peninsula, Antarctica (modified from Reguero et al., 2013). Fossil locality DPV 13/84 is indicated.

3. Material and methods

We follow the stratigraphic nomenclature presented in Marenssi et al. (1998a), and facies associations defined by Marenssi et al. (1998b). Geochronological and paleomagnetic data are taken from Montes et al. (2010).

The studied material (MLP 11-II-20-07) was collected on surface by staff belonging to the Instituto Antártico Argentino (IAA) during the 2012 field trip; it is housed at the Museo de La Plata (MLP), La Plata, Argentina. Tarsometatarsi used for comparison and discussion includes published material and new remains belonging to the Museo de La Plata. Anatomical terms used in descriptions follow Baumel and Witmer (1993). A discussion about the utility of the characters used in systematic assignment is given following proposals by Myrcha et al. (1990, 2002) and our own observations and measurements taken on both living and fossil species. Taking into account the original and emended diagnoses by Myrcha et al. (1990, 2002), published and new unpublished tarsometatarsi assigned to *Palaeeudyptes* were revised.

A geometric morphometric analysis was made on nineteen complete tarsometatarsi belonging to *Palaeeudytpes*, all coming from the La Meseta Formation in Seymour Island (= Marambio), in order to evaluate the shape variations of the only character (curvature of the *margo medialis*) that differentiates *P. klekowskii* from *P. gunnari*, both species co-occurring in Antarctica. Each tarsometatarsus was photographed in dorsal view, keeping the same focal distance. Dorsal view was preferred because the curvature of the *margo medialis* can be easily drawn in this way. The [x, y] coordinates of two extreme landmarks and eighteen semi-landmarks were digitized using TpsDig 2.17 (Rohlf, 2013). The two landmarks were located at the most proximal and most distal ends of the *margo medialis*, and the semi-landmarks were adjusted between them following Pérez et al. (2006). The nuisance parameters (size differences, orientation, and position) were removed through generalized Procrustes superimposition (Rohlf and Slice, 1990), so only the variation in shape of the landmark configurations was compared (Small, 1996). Procrustean superimposition scales all configurations so as to have centroid size (square root of the summed squared distances from all landmarks to the configuration centroid) equal to 1, translates all configurations so that all centroids are located at the origin, and rotates all configurations by an optimum angle in order to minimize the sum of squared distances between the corresponding landmarks. This technique also allows the calculation of mean shapes from samples (Rohlf and Slice, 1990). The computer graphics used here are the thin plate splines, whose function minimizes the energy required during the transformation. This energy is a function not only of the amount of transformation in shape, but also of the degree of closeness among the configuration points. Once these values were obtained, a relative warp analysis, a modification of principal component analysis for shape coordinate data, was made using the software tpsRelw (Rohlf, 2013). Deformation grids were obtained for each specimen.

4. Systematic paleontology

Class AVES Linnaeus, 1758
Order SPHENISCIFORMES Sharpe, 1891
Family SPHENISCIDAE Bonaparte, 1831
Genus *Palaeeudyptes* Huxley, 1859
Type species: *P. antarcticus* Huxley, 1859
Included species: *P. antarcticus* Huxley, 1859, *P. gunnari* (Wiman, 1905), *P. marplesi* Brodkorb, 1963, *P. klekowskii* Myrcha, Tatur and Del Valle, 1990.

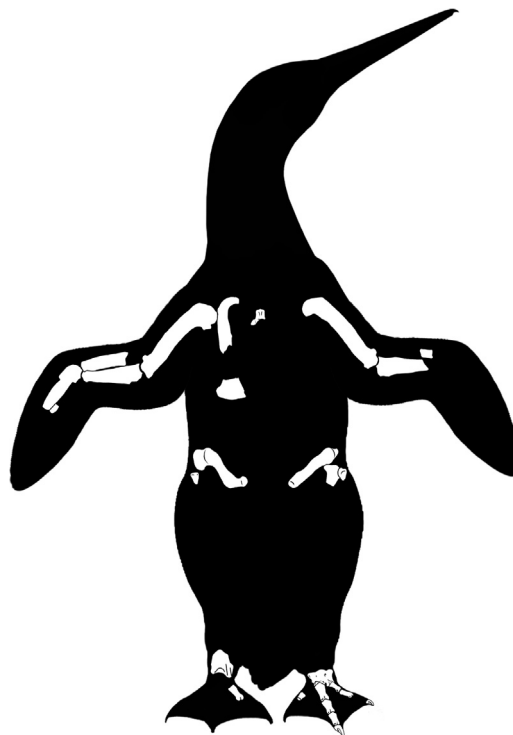*Palaeeudyptes klekowskii* Myrcha, Tatur and Del Valle, 1990
Figs. 5–7

Fig. 5. Associated skeleton MLP 11-II-20-07 assigned to *Palaeeudyptes klekowskii*, including: right and left humeri and ulnae, right radius and distal end of left radius, left carpometacarpus, right coracoid in two pieces, proximal and distal end of right femur, fragment of proximal end of left femur, proximal and distal end of right tibiotarsus, partial left tarsometatarsus, several pedal phalanges, two ungual phalanges, and several fragments of length bones and vertebrae.

Material: Associated skeleton MLP 11-II-20-07 (Fig. 5) including: left and right humeri, right and left ulnae, right radius and distal end of left radius, left carpometacarpus, right coracoid in two pieces, proximal and distal end of right femur, fragment of proximal end of left femur, proximal and distal end of right tibiotarsus, left tarsometatarsus (trochlea II is lacking, trochlea III is separated from the rest of the tarsometatarsus), several pedal phalanges, two ungual phalanges, several fragments of long bones and vertebrae.

Measurements (in mm):

- Humerus: total length: 143.3; proximal lateromedial width: 44.6; shaft lateromedial width at proximal level: 24.7; shaft lateromedial width at distal level: 23.2;
- Ulna: total length: 93.3; proximal lateromedial width: 31.2; distal lateromedial width: 16.4;
- Radius: distal lateromedial width: 16.1;
- Carpometacarpus: total length: 84.8; proximal lateromedial width: 25.6; distal lateromedial width: 23.4;
- Femur: proximal lateromedial width: 40.2; distal lateromedial width: 32.0;
- Tibiotarsus: distal lateromedial width: 35.1;
- Tarsometatarsus: lateromedial width at middle of the corpus: 28.4;
- Pedal phalanges: total lengths: 46.5, 42.0, 38.5, 25.9, and 19.7;
- Ungual phalanx: total length: 26.8.

Description:

Humerus (Fig. 6(a–d)). Shaft is slightly sigmoid with slightly marked *angulus preaxialis*. The diaphysis is narrower distally. The *tuberculum dorsale* is not well marked. The *fossa tricipitalis* is undivided, deep and rounded. The *tuberculum ventrale* is strong

Fig. 6. *Palaeeudyptes klekowskii*, MLP 11-II-20-07. **a, b**: right humerus; a, cranial view, b, caudal view; **c, d**: left humerus; c, cranial view, d, caudal view; **e, f**: left ulna; e, cranial view, f, caudal view; **g, h**: right ulna; g, caudal view, h, cranial view; **i, j**: right coracoid; l, cranial view, j, caudal view; **k, l**: left carpometacarpus; k, caudal view, l, cranial view; **m, n**: left radius; m, caudal view, n, cranial view. Scale bar: 30 mm.

and its fossa is oriented laterocaudally. The *incisura capitis* and the undivided *sulcus ligamentosus transversus* are connected to each other. The *crista pectoralis* is proximally wider and the *facies musculi pectoralis* is distally shallower. The scar of the *musculi brachialis internus* is very deep, whereas the *facies musculi supracoracoideus* is shallow and straight. The *condylus dorsalis* is strongly projected from the *margo cranialis*, the *incisura*

intercondylaris is wide and the *condylus ventralis* is more rounded that the former. The *trochlea humeri* are broken and only the most caudal one can be described; it is slender and projected almost perpendicular to the diaphysis. In addition, characters previously mentioned for *P. klekowskii* by Jadwiszczak (2006) and Tambussi et al. (2006) were observed in both humeri of this specimen. According to Jadwiszczak (2006), the humerus of *P. klekowskii* is
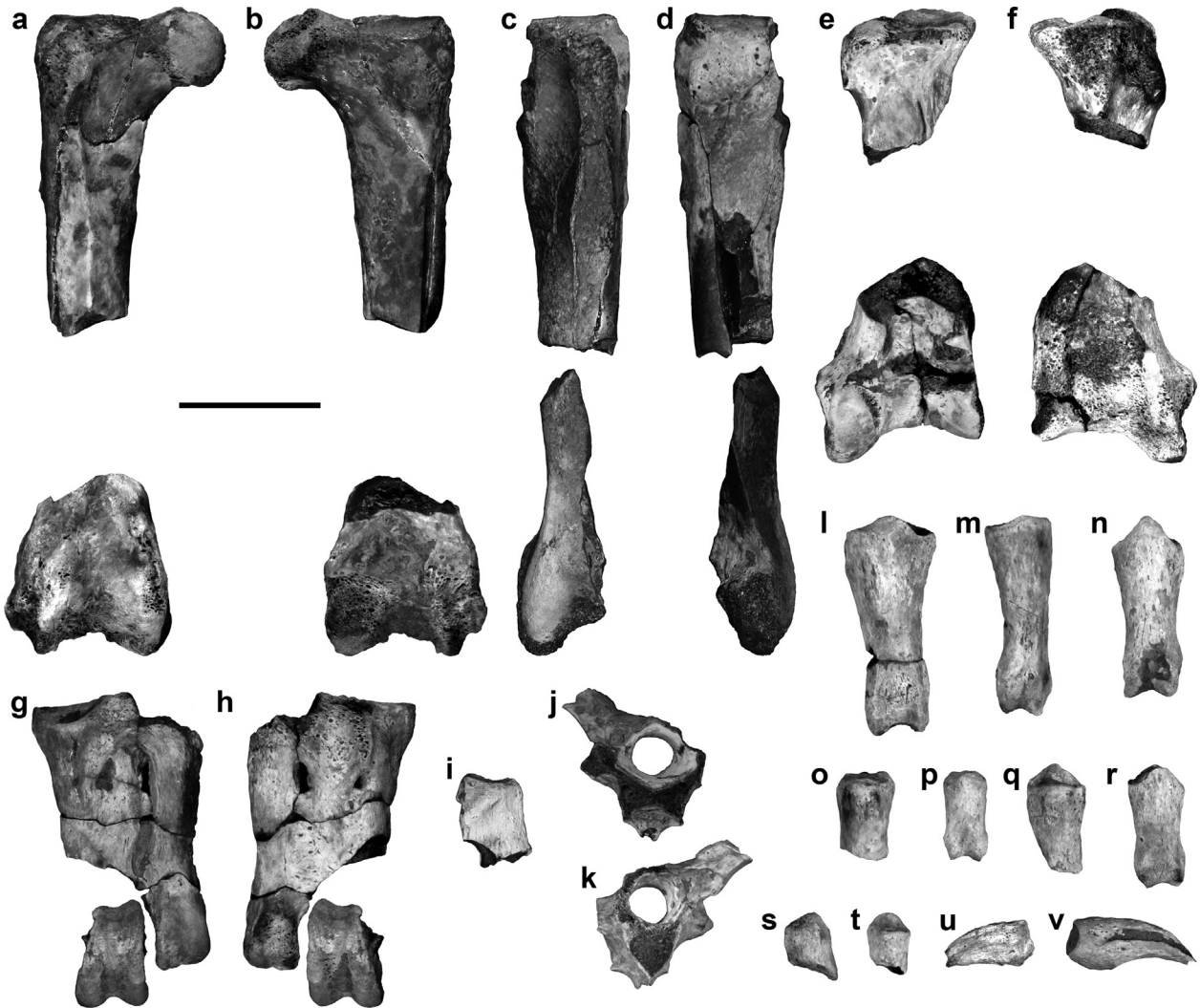
Fig. 7. *Palaeeudyptes klekowskii*, MLP 11-II-20-07. **a, b**: right femur; a, cranial view, b, caudal view; **c, d**: left femur; c, cranial view, d, caudal view; **e, f**: left tibiotarsus; e, cranial view, f, caudal view; **g, h**: left tarsometatarsus; g, cranial view, h, caudal view; **i**: left radius, cranial view; **j, k**: vertebra; j, cranial view, k, caudal view; **l–t**: pedal phalanges, cranial views; **u, v**: ungual phalanges, lateral views. Scale bar: 30 mm.

characterized by the undivided *fossa tricipitalis*, a moderately sigmoid diaphysis, and the shaft slightly narrower proximally than distally in some specimens. On the other hand, Tambussi et al. (2006) partially followed the systematic criterion of Kanfeder (1994) for the assignment of 21 humeri to *P. klekowskii*. Both approaches agree in the qualitative and metric characters employed.

Ulna (Fig. 6(e-h)). It is depressed and triangular as in all Sphenisciformes. The olecranon is expanded and quadrangular in shape. The *incisura radialis* is relatively wide. The *crista intercotylaris* is strong and elevated, and the *cotyla dorsalis* is deeply excavated. The *condylus ventralis* is rounded and the *condylus dorsalis* is more elongated. The *sulcus intercondylaris* between them is wide.

Radius (Fig. 6(m, n)). The *facies articularis radiocarpalis* is shallow and the sulcus tendinosus is slightly marked. The *tuberositas aponeurosis ventralis* is small and the sulcus tendinosus is shallow. The *depression ligamentosa* is well marked.

Carpometacarpus (Fig. 6(k, l)). It is a robust element, more than that of *P. gunnari*, which is more slender but almost equal in size. Although part of the bone is missing, it can be seen that the *sulcus tendinus* is shallow and wide and the *synostosis metacarpalis distalis* is well fused. The *trochlea carpalis* is rounded and the *fossa supratrochlearis* is expanded. The *facies articularis ulnocarpalis* is shallow. Relative distal extension of the *os metacarpale minus* is similar to that of the *os metacarpale major*, like in other *Palaeeudyptes* species. Otherwise, in *Anthropornis*, the *os metacarpale minus* is typically projected beyond the *os metacarpale major* (Jadwiszczak, 2012).

Coracoid (Fig. 6(i, j)). It is not very robust in comparison with the humerus. The *facies articularis clavicularis* is recurved, reaching an angle of almost 90° with respect to the shaft. The *facies articularis sternalis* is wide and c-shaped. The *angulus medialis* is slightly expanded, and not bent as in other Antarctic penguins.

Femur (Fig. 7(a–d)). The preserved portion of the shaft is straight and the *linea intermuscularis cranialis* is evident. The *caput femoris* is rounded. The *crista trochanteris* is strong and well differentiated from the *facies articularis antitrochanterica*. The *facies articularis acetabularis* is protruding. The *impressiones obturatoriae* are marked. At the distal end, the *sulcus intercondylaris* is expanded and wide. The *fossa poplitea* is larger and shallower than that of *P. gunnari*. The *condylus lateralis* and the *crista tibiofibularis* are eroded and consequently, it is not possible to assess if their margins were acute or rounded. The *crista supracondylaris medialis* is strongly developed.

Tibiotarsus (Fig. 7(e, f)). The *facies articularis medialis* is represented by a shallow depression that is divided from the rounded *caput fibulae* by a well-marked *area interarticularis*. The

condylus medialis is elongate, and the *epicondylus medialis* is rounded and very well developed. The edge of this condyle is a little eroded, but strongly developed. The *condylus lateralis* is aligned with the axis of the shaft; the *depresssio epicondylaris lateralis* is shallow.

Tarsometatarsus (Fig. 7(g, h)). This bone allows the systematic assignment of the skeleton. It is larger than in *P. gunnari.* In agreement with the original diagnosis, it is large and stout with a concave *margo medialis.* This concavity is clearly more strongly marked in the distal part due to the arc-shaped divergence of trochlea II. In *P. gunnari*, this concavity is more pronounced according to Myrcha et al. (2002), although this character seems also variable. The *margo lateralis* is straight. The lateral metatarsal groove is long and deep, running along the whole axis, and the lateral metatarsal foramen is well developed but small. The *sulcus extensorius medialis* is very shallow and short, visible in the proximal part only to about the middle of the shaft; the *foramen vasculare proximale mediale* is smaller than the *lateralis.* The second and third metatarsal are fused very strongly along their whole length, making the axis longer than in *P. gunnari.* Trochlea III is massive, clearly widening distally. The *eminentia intercotylaris* is wide and well developed. Three *cristae hypotarsalis* are present

proximally; the *crista medialis hypotarsi* is highest and longest, while the *cristae intermediae hypotarsi* is smallest. The *crista lateralis hypotarsi* runs obliquely to the proximal part of metatarsale IV in the direction of metatarsale III, ending at the internal margin of both *foramina vascularia proximalia.*

It differs from *Anthropornis* in having the *foramen vasculare proximale laterale* always present, larger and often more distal than its medial counterpart. The *sulcus longitudinalis dorsalis lateralis* is very deep proximally and markedly weakening towards the *incisura intertrochlearis,* a feature not observed in *Archaeospheniscus.* The surface of the *tuberositas musculi tibialis cranialis* is relatively smaller, though more pronounced than in *Anthropornis* and *Archaeospheniscus.* A V-shaped groove is present in the proximal part of the *margo medialis* (at least in bones from Seymour Island).

Both *fossae infracotylaris dorsale, medialis* and *lateralis* are present. The trochleae are relatively robust and strong. The *sulcus longitudinalis dorsalis medialis,* if present, is slight. The caudal opening of the *foramen vasculare proximale mediale* is situated slightly more medially than the *crista medialis hypotarsi* with respect to the major bone axis.

Phalanges (Fig. 7(l–v)). Nine pedal phalanges are preserved, some of which are very large and robust, probably belonging to the
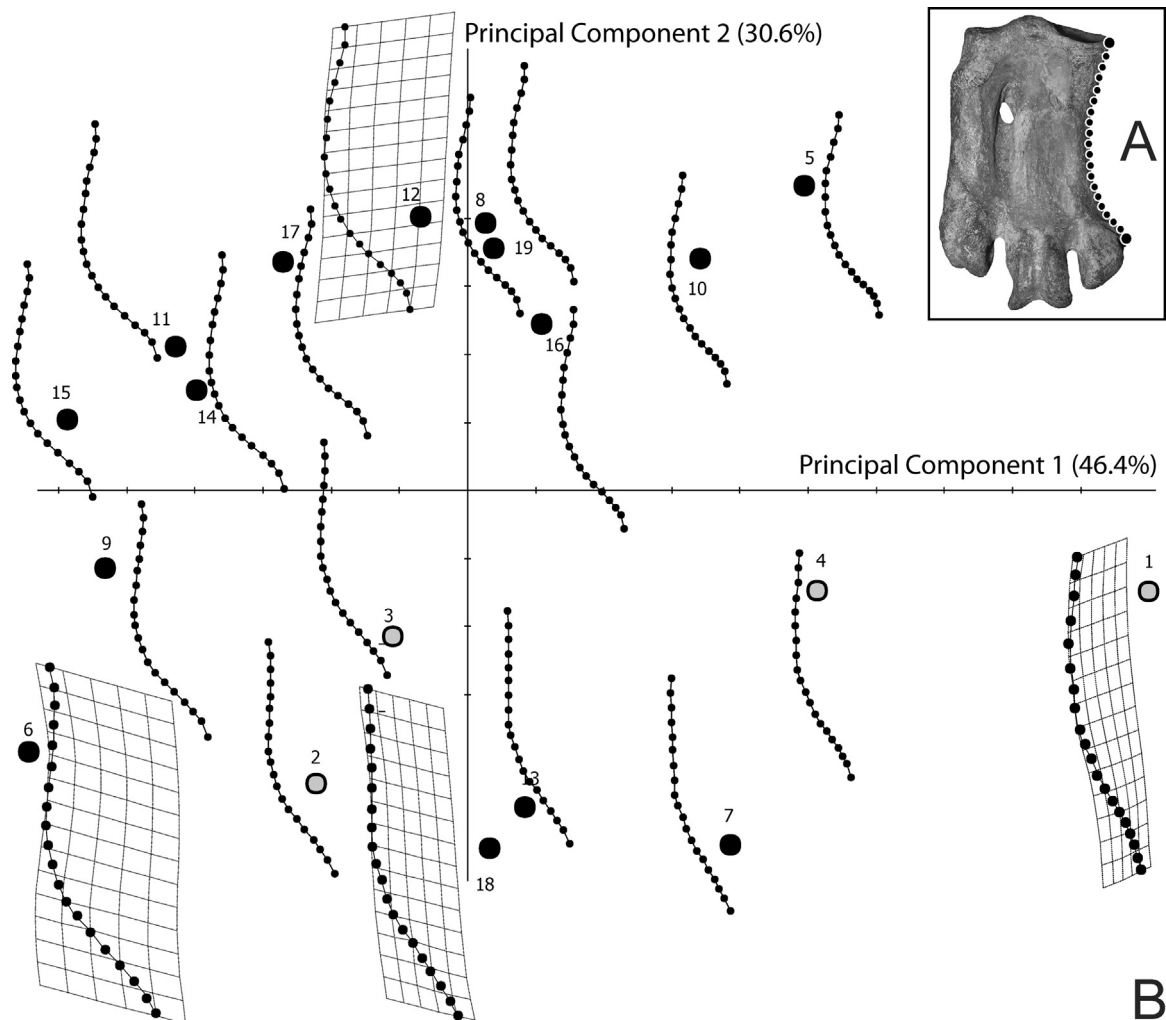

Fig. 8. Results of the morphometric geometric analysis. **A** (inset). Landmarks (large dots) and semi-landmarks (small dots) drawing the concavity of the *margo medialis.* **B.** Two first principal components (with associated percentages of explained variance) of the relative warps analysis; black circles correspond to *Palaeeudyptes klekowskii,* grey circles to *P. gunnari.* 1, MLP 84-II-1-47; 2, MLP 87-II-1-145; 3, MLP 93-X-1-15; 4, MLP 95-I-10-16; 5, 83-V-30-16; 6, MLP 83-X-1-108; 7, MLP 83-X-30-15; 8, MLP 84-II-1-126; 9, MLP 84-II-1-78; 10, MLP 93-X-1-6; 11, MLP 93-X-1-63; 12, MLP 94-II-2-222; 13, MLP 94-III-15-18; 14, MLP 94-III-15-20; 15, MLP 94-III-15-348; 16, MLP 94-III-15-395; 17, MLP 94-III-15-398; 18, MLP 94-III-15-4; 19, MLP 95-I-10-158. Grid lines kept only for the most extreme specimens (1 and 6 along the first principal component 1, 12 and 18 along the second principal component), whereas eliminated in other specimens to avoid nuisance in the graphic.

second and third digits. In contrast, others phalanges assignable to distal elements or to the fourth digit are smaller. In general, the proximal end is dorsally expanded and the distal end has strong edges. Two ungual phalanges are preserved. The ventral curvature is moderate and a deep sulcus runs along the lateral face toward the distal end. A weak tubercle is developed in the ventral surface at the proximal end.

5. Results and discussion

Considering that all the specimens included in our quantitative analysis are adults or at least sub-adults (no bone immaturity is evident in the compact bone texture, and fusion of elements is complete), the variation in size can only be attributed to intra-specific, maybe sexual, or to inter-specific differences, an issue beyond the analytical possibilities of the present fossil record. Only a few well-preserved partial skeletons are known and issues of variation cannot be quantitatively analyzed with the available sample.

Given the observed variations, it could be thought at first that tarsometatarsal characters are not appropriate for solving taxonomic issues. However, the systematic scheme of fossil penguins based almost entirely on tarsometatarsal features has proved its power for species discrimination. Moreover, in living taxa, the tarsometatarsus permits the recognition of every species (Acosta Hospitaleche and Gasparini, 2007; Walsh et al., 2007; Acosta Hospitaleche et al., 2011). A good example of that are the Patagonian Miocene species, for which the findings of more complete forms have confirmed the provisional assignment of other isolated elements (Acosta Hospitaleche, 2007; Acosta Hospitaleche et al., 2007, 2008). Something similar may happen here, where many skeletal elements were assigned taking into account their robustness, size, and the species known in the geological unit (e.g., Jadwiszczak, 2006).

Trusting in the power of the tarsometatarsus in systematic assignments, a second issue can be discussed in terms of inter-individual variability. Based on measurements taken from Göhlich (2007), we found 21% of variation in tarsometatarsal total length of *Spheniscus demersus*, 16% in *S. magellanicus*, and 10% in *S. humboldti*. Similar results were obtained in the present study based on our own observations in *Pygoscelis adeliae* (15%), *Pygoscelis papua* (13%), and *S. magellanicus* (16%). Results obtained in the giant species from the Eocene of Antarctica barely exceed these values. Size ranges are different in these species: 59–64.4 mm (11% of variation) and 66.6–82.4 mm (24%) for *P. gunnari* and *P. klekowskii*, respectively (data from Myrcha et al., 2002 and our own observations).

Only a qualitative feature discriminates *P. gunnari* from *P. klekowskii*: the concavity of the *margo medialis* (Fig. 8). We investigated the variation of this character through a geometric morphometric analysis. Results indicate that many of the specimens can be differentiated from the curvature of the *margo medialis*. However, three tarsometatarsi (MLP 83-X-30-15, MLP 94-III-XV-4, and MLP 94-III-15-398) previously assigned to *P. klekowskii* by Myrcha et al. (2002), actually fall into the morpho-space occupied by *P. gunnari*, whereas their sizes fit with *P. klekowskii* (length = 73.2 mm, 75.5 mm, and 82.4 mm, respectively). Consistently, results previously obtained show also the presence of some heterogeneity within the tarsometatasi of *Palaeeudyptes* (Jadwiszczak and Acosta Hospitaleche, 2013).

6. Conclusions

The finding of articulated skeletons is always worth considering for the study of any fossil group. Here, it contributes not only to the anatomical knowledge of the species, but also to better understanding the multiple issues that surround the evolutionary history of the genus *Palaeeudyptes*. The fossils described here belong to the most complete penguin skeleton ever recovered from Antarctic sediments. Discoveries such as this one are significant for the study of the anatomy and evolution of penguins. Until the present contribution, no associated or articulated fossil remains had been assigned to *P. klekowskii*. Although the only material known with certainty for *P. klekowskii* was a tarsometatarsus, several other remains, such as humeri and other elements, were also taxonomically assigned through the years. Previous assignments were based sometimes on the size and robustness of the elements, or on statistical grounds. It is now possible to state that the humeri assigned by Kanfeder (1994), Jadwiszczak (2006) and Tambussi et al. (2006) to this species perfectly fit in the description given here from this newly available skeleton.

P. klekowskii closely resembles its smaller congeneric species *P. gunnari*, although their size ranges differ. The relative concavity of the *margo medialis* differentiates their tarsometatarsi, although showing some intra-specific variability. Overall, the combination of both characters (size and concavity of *margo medialis*) is unique for each species. It could be congruent with sexual dimorphism as proposed by Jadwiszczak and Mörs (2011), although size differences between the two taxa appear definitely too large to be considered as a single species. *P. klekowskii* and *P. gunnari* are for sure closely related taxa. We believe that more exhaustive studies in the La Meseta Formation may lead to understand the phylogenetic relationship between them and with other Eocene penguin species.

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