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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.

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

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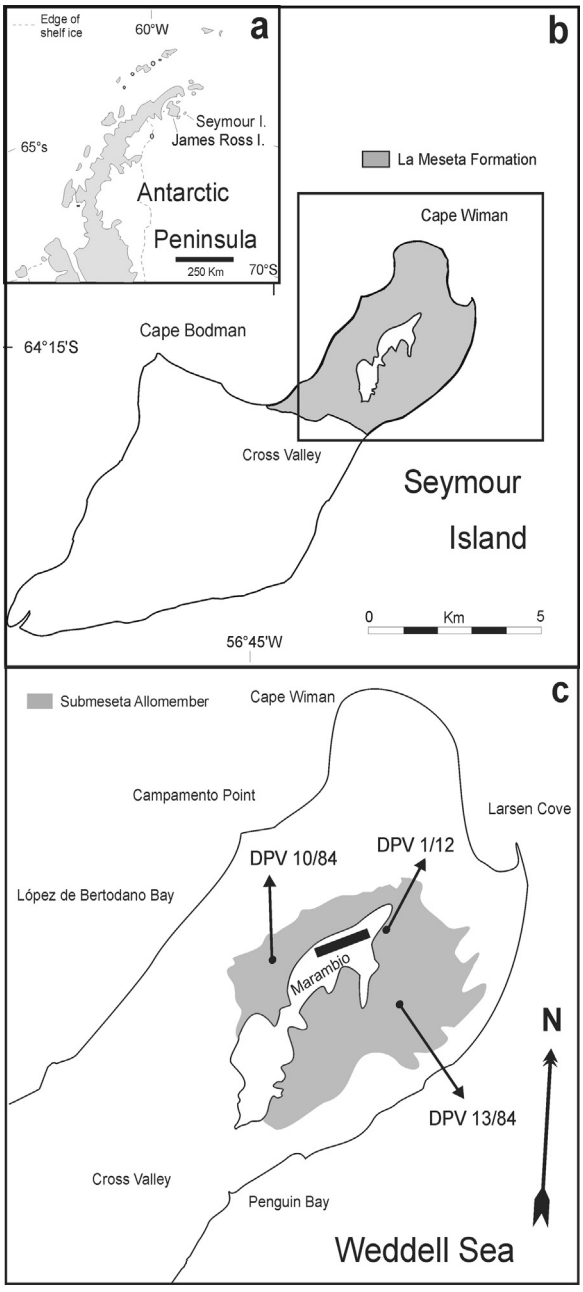

Fig. 1. a: map showing the location of Antarctic Peninsula, Antarctica; **b**: location of the La Meseta Formation in Seymour Island (= Marambio); **c**:sketch map of the northern part of Seymour Island showing the distribution of the Submeseta Allomember and the fossil penguin-bearing localities DPV 10/84, DPV 13/84 and IAA 1/12 in which the associated skeletons were found (modified from Marenssi et al., 1998a).

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, 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 *Paleeudyptes*, 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).