A new small-sized penguin from the late Eocene of Seymour Island with additional material of *Mesetaornis polaris*

Piotr Jadwiszczak, Marcelo Reguero & Thomas Mörs

To cite this article: Piotr Jadwiszczak, Marcelo Reguero & Thomas Mörs (2021): A new small-sized penguin from the late Eocene of Seymour Island with additional material of *Mesetaornis polaris*, GFF, DOI: 10.1080/11035897.2021.1900385

To link to this article: https://doi.org/10.1080/11035897.2021.1900385
A new small-sized penguin from the late Eocene of Seymour Island with additional material of *Mesetaornis polaris*

Piotr Jadwiszczak\(^a\), Marcelo Reguero\(^b\) and Thomas Mörs\(^c\)

\(^a\)Faculty of Biology, University of Białystok, Białystok, Poland; \(^b\)Instituto Antártico Argentino, Campus Miguelete, Buenos Aires, Argentina; \(^c\)Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden

**ABSTRACT**

Here, we report on two tarsometatarsi assignable to relatively small-sized Eocene Antarctic penguins, housed in the palaeozoological collections of Naturhistoriska riksmuseet, Stockholm. The Priabonian fossils were collected by museum staff during two joined Argentinean and Swedish expeditions from the Submeseta Formation on Seymour Island, Antarctic Peninsula. One specimen represents a new early sphenisciform, *Marambiornopsis sobrali* gen. et sp. nov., the sixth small-sized tarsometatarsus-based penguin species known from the Antarctic Eocene. Micro-CT scanning revealed the presence of quite large and essentially empty metatarsal medullary cavities. The second fossil can unequivocally be assigned to *Mesetaornis polaris*. The specimen represents only the second record of this species and supposedly a relatively young bird. Micro-CT scanning showed that in *M. polaris* the metatarsal medullary cavities are less developed than in *M. sobrali* – the cortical and trabecular bone tissues left rather little room for significant hollow spaces. Both specimens are also in different overall quality of their trabecular networks.

Genus name: LSID:urn:lsid:zoobank.org:act:604F02AA-DD0C-4789-B4D6-85EA68A39A68

Species name: LSID:urn:lsid:zoobank.org:act:477F0FCS-D07B-4A92-97FD-3C4B05BAF503

**Introduction**

Seabirds are and have always been associated mainly with depositional environments (e.g., Schreiber & Burger 2001). Such a connection, especially when accompanied by colonial breeding, increases the number of skeletal elements that can potentially be preserved as fossils. However, the old cliché, “there is strength in numbers”, cannot be uncritically applied in palaeontological context. The preservation of bones depends also on a number of other factors. For example, having larger-than-average structural thickness and density contribute heavily to their fossilization potential.

That is undoubtedly the case with penguins (Aves: Sphenisciformes) – the flightless, wing-propelled seabirds from the Southern Hemisphere. The pachyostotic (e.g., Meister 1962) or, more accurately, osteosclerotic (e.g., Cerda et al. 2015; Ksepka et al. 2015) long bones of penguins constitute a major part of their extensive fossil record (authors’ observation). In Antarctica, this record consists largely of disarticulated/isolated skeletal elements (Jadwiszczak et al. 2013; Acosta Hospitaleche et al. 2019; and references therein).

In such circumstances, two limb bones dominated the set of type specimens – the tarsometatarsi and humeri (Acosta Hospitaleche et al. 2019: figs. 7–8). Tarsometatarsi began to be used as holotypes much earlier than humeri, and respective species, except for a single case (secondary homonymy, see Jadwiszczak & Mörs 2011), remain widely accepted as distinct taxonomic entities (Myrcha et al. 2002; Jadwiszczak 2009; Acosta Hospitaleche et al. 2019). The bulk of the several thousand fossil penguin bones collected in the southern polar region (for a historical perspective, see Jadwiszczak 2009; Acosta Hospitaleche et al. 2017) derived from “giant” Eocene Sphenisciformes – *Anthropornis nordenskjoeldi* (supposedly the largest Antarctic penguin ever), *A. grandis*, *Palaeoodyptes klekowskii* and *P. gunnari*. Other tarsometatarsus-based species from this epoch are poorly represented or rare – a large-sized *Archaeospheniscus/Notodyptes wimani*, and five small-sized taxa: *Delphinornis larseni*, *D. gracilis*, *D. arctowskii*, *Marambiornis exilis* and *Mesetaornis polaris* (e.g., Myrcha et al. 2002; Jadwiszczak 2009; Acosta Hospitaleche et al. 2019). Here, we report on two tarsometatarsi assignable to relatively small-sized Eocene Antarctic penguins. On the basis of one of them, we describe a new early sphenisciform *Marambiornopsis sobrali* gen. et sp. nov., another specimen is a rare addition to the exceptionally modest hypodigm of *Mesetaornis polaris*.

Apart from two Miocene wing bones from the Prince Charles Mountains (Jadwiszczak et al. 2013), Antarctic fossil penguins are known exclusively from Seymour Island, Antarctic Peninsula (e.g., Acosta Hospitaleche et al. 2019). The overwhelming majority of them come from the late Eocene Submeseta Formation of Montes et al. (2013), or “Tertiary Eocene La Meseta” stratigraphic unit Telm 7 of Sadler (1988).
Materials and methods

The penguin bones described in this paper were collected by TM in February 2011 and February 2012 during joined Argentinean and Swedish expeditions. They were obtained from the richly fossiliferous Site NRM 2 (S 64°14.778’, W 056°37.169’; for map and chondrichthyan record see Kriwet et al. 2016) in the steep slope S of the Marambio Base. Here, the upper part of the Submeseta Formation (Submeseta II = level 38) according to Montes et al. (2013), equivalent to the upper part of the Telm 7 unit (see Sadler 1988), is exposed. Therefore, the penguin specimens are Priabonian (late Eocene) in age (Douglas et al. 2014).

Photographs of presented specimens were taken using a digital camera (Nikon D5100, equipped with a DX-format image sensor) paired with 40 mm macro lens (DX format-specific). Micro-CT scans were obtained at the Stockholm University Brain Imaging Centre (SUBIC) with the ZEISS Xradia 520 Versa 3D X-ray microscope, the X-ray source of 110 kV at 10 W and exposure time of 1 sec. The resulting pixel size was 46.96 μm. The individual slices were recorded as 16-bit TIFF image files (1004 × 1024 pixels). The 3D volumes were reconstructed and, together with slices, analysed using 3D Slicer (www.slicer.org; Fedorov et al. 2012) and InVesalius (invesalius.github.io) open source software. The additional digital preparation (matrix removal) and visualization were performed with the Pixologic ZBrush – advanced 3D sculpting software (pixologic.com; a licensed copy).

Both specimens are housed in the palaeozoological collections of the Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, under the inventory acronym NRM-PZ. The figured comparative material comes from the set permanently deposited in the Professor Andrzej Myrcha University Nature Centre, University of Białystok, Poland, under the inventory acronym IB/P/B.

Systematic palaeontology

CLASS AVES LINNAEUS, 1758

ORDER SPHENISCIFORMES SHARPE, 1891

FAMILY SPHENICIDAE BONAPARTE, 1831

Remarks

– Clarke et al. (2003: p. 3) postulated “that the name ‘Spheniscidae’ be formally applied to the clade comprised of the most recent common ancestor of all extant penguins and all of its descendants”. Here, we use the name in its traditional context.

Genus Marambiornopsis gen. nov.

Type species

– Marambiornopsis sobrali sp. nov. from the Submeseta Formation, Seymour Island (Antarctic Peninsula).

Differential diagnosis

– Marambiornopsis differs from other Eocene penguins in possessing a unique combination of features listed below.

Tarsometatarsus small (unlike in Anthropornis and Palaeoeudyptes) and strongly elongated (unlike in Archaeospheniscus/Notodytes). Both proximal vascular foramina small (like in Delphinornis and Marambiornis; both large in Archaeospheniscus/Notodytes, medial one especially large in Mesetaornis). Plantar opening of medial proximal vascular foramen situated close to the medial margin of second metatarsal, just distal to medial hypotarsal crest, and separated from the main hypotarsal sulcus (distal or mesiodistal relative to the medial hypotarsal crest, and separated from the main hypotarsal sulcus in Delphinornis; located within the main hypotarsal sulcus, and separated from the medial margin by the hypotarsal crest in Marambiornis and Mesetaornis). Tuberosity for insertion of m. tibialis cranialis wide (clearly wider than in Marambiornis, Mesetaornis and Delphinornis). Hypotarsal sulcus for tendon of m. flexor hallucis longus dist (unlike in Delphinornis), and only moderately wide (markedly narrower than in Marambiornis). Main hypotarsal sulcus (for tendon of m. flexor digitorum longus) located clearly abaxially relative to the main axis of the bone (like in Marambiornis and Mesetaornis, but said axis passes through the sulcus in Delphinornis). Medial hypotarsal crest clavate in proximal view (a variety of chisel-like shapes in Delphinornis, Marambiornis and Mesetaornis).

Etymology

– An existing name for a genus of Eocene fossil penguins (Marambiornis) combined with the Greek word ópsis for appearance, sight. Hence Marambiornopsis.

Marambiornopsis sobrali sp. nov.

Figs. 1 and 2A, E, I.

Material

– An isolated right tarsometatarsus; type specimen only.

Horizon and Locality

– Level 38 within the Submeseta Formation (Submeseta II Allomember), locality NRM 2, Slope S Marambio Base, S 64°14.778’, W 056°37.169’, Seymour Island, Antarctic Peninsula (Montes et al. 2013; Kriwet et al. 2016).

Age

– Upper TELM 7, Priabonian, late Eocene (Douglas et al. 2014).

Holotype

– NRM-PZ A542, Figs. 1 and 2A, E, I.

Etymology

– Named in honour of Navy Sub-Lieutenant José Maria Sobral, Argentinean geologist and member of the Swedish South Polar Expedition 1901–03 that discovered the first Antarctic penguin fossils.

Diagnosis

– As for genus.
Description

- NRM-PZ A542 is a well-preserved tarsometatarsus. The specimen is 43.8 mm long (maximally), 17.4 mm wide proximally and 19.7 mm wide distally, whereas its midwidth amounts to 15.1 mm. Two modest proximal vascular foramina are more widely spaced plantarly than dorsally, and the lateral

![Figure 1](image-url)

Figure 1. Type specimen (NRM-PZ A542) of *Marambionopsis sobralii* gen. et sp. nov. (Aves: Sphenisciformes) from the Submeseta Formation, Seymour Island; A–E: the tarsometatarsus in dorsal, medial, plantar, proximal and distal views, F–I: its micro-CT coronal-plane slices, J–K: its annotated 3D surface model (micro-CT based), L–N: its inner-structure visualization focused on air pockets and medullary cavities (cortical bone transparent; micro-CT based), O–P: its inner-structure visualization in a cross-sectional view (cortical bone transparent; micro-CT based), Q: a longitudinal section (oblique lateral view) through the metatarsal III (cortical and trabecular bone opaque; micro-CT based); scale bar is 1 cm.
one appears to be larger. The canal connecting matching openings for each foramen is (as revealed by micro-CT scanning; Fig. 1O) arcuate. Distally to the plantar opening of the medial foramen there is a distinct elongate elevation of the bone margin. The medial intermetatarsal sulcus is shallow and very short, its lateral counterpart is much better developed and can be traced up to the intertrocchlear incisure. The latter is also wide proximally. The distal vascular foramen is represented solely by its plantar opening. The wide tuberosity for the insertion of the *m. tibialis cranialis* appears to be tear drop-shaped. The hypotarsus is not simplified, and three crests are distinguishable. The well-preserved medial crest is most prominent, and the other two are in varying degrees of damage. The curvature of the cross section of the main hypotarsal sulcus creates an almost perfect circular arc, with two crests partially overhanging a resulting passage. The surface for the origin of the *m. abductor digitii IV* is laterally framed by a low marginal crest. The second metatarsal is gently curved, its medial margin seems to be downright straight over a long distance of its length. The fourth metatarsal is straight. The third trochlea is clearly more robust than the other two.

As revealed by micro-CT scanning (Fig. 1F–I, L–N, O–Q), the tarsal and proximalmost metatarsal as well as trochlear parts of the tarsometatarsus are rich in small, more or less interconnected, air pockets (hollow spaces within the 3D trabecular bony network; see Fig. 1Q), whereas the major parts of metatarsals are in this respect mostly dominated by large medullary cavities. The cavity inside the second metatarsal has the least variable diameter. The third metatarsal has the most spacious cavity, followed by the fourth and second metatarsals.

*Genus Mesetaornis* Myrcha et al., 2002

**Diagnosis**

According to Myrcha et al. (2002): “Strongly elongated tarsometatarsus with quite large foramen vasculare proximale mediale (smaller in *Delphinornis* and *Marambiornis*). Differs from *Delphinornis* in having the plantar opening of the foramen situated more medially (in relation to the main axis of the bone) than crista medialis hypotarsi. Tarsometatarsus differs from *Marambiornis* in having cristae intermediae hypotarsi separated by a relatively narrow groove”.

**Species included**

Monotypic, *M. polaris* from the Submeseta Formation, Seymour Island (Antarctic Peninsula).

**Remarks**

The genus is represented by two tarsometatarsi (IB/P/B-0278 and IB/P/B-0279b; Myrcha et al. 2002); however, only the former bone (Figs. 2C, G, K and Figs. 3D–F) has been originally assigned to a species (as a holotype). IB/P/B-0279b is very poorly preserved, but Myrcha et al. (2002) speculated that it could have represented another species. A few other specimens considered in this regard (Myrcha et al. 2002; Jadwiszczak 2006) are either isolated non-tarsometatarsal skeletal elements, devoid of “physical” ties to said tarsometatarsi, or are too incomplete for comparison. From this, it follows that the specimen described below is only the second specimen assignable to the sole named species of *Mesetaornis*.

*Mesetaornis polaris* Myrcha et al., 2002  
Fig. 3A–C, G–T.

**New material**

An isolated left tarsometatarsus NRM-PZ A824, partly in matrix.

**Horizon and Locality**

Level 38 within the Submeseta Formation (Submeseta II Allomember), locality NRM 2, Slope S Marambio Base, S 64°14.778′, W 056°37.169′, Seymour Island, Antarctic Peninsula (Montes et al. 2013; Kriwet et al. 2016).

**Age**

Upper TELM 7, Priabonian, late Eocene (Douglas et al. 2014).

**Description**

NRM-PZ A824 is a relatively well-preserved tarsometatarsus. Most of its dorsal side as well as trochleae with an adjacent area of the plantar surface are covered with the well-cemented matrix. The bone is 48.4 mm long (maximally), 18.1 mm wide proximally and 21.8 mm wide distally, whereas its midwidth amounts to 15.7 mm. After most of the matrix had been digitally removed from the specimen, it became possible to examine the most important aspects of its previously hidden outward appearance (Fig. 3G–L). The proximal vascular foramina are both quite large and elongate, especially in their dorsal openings, and only slightly more widely spaced plantarily. The proximal metatarsal III, that separates them, is deeply lowered in dorsal view. Taking into account the main axis of the bone, the medial foramen is clearly more adaxial than the medial hypotarsal crest. The medial intermetatarsal sulcus is shallow and short, its lateral counterpart is deep, quite wide, and can be traced up to the intertrocchlear incisure. Both plantar sulci are very shallow, albeit long and rather noticeable. Distally, close to said incisure, the lateral sulcus (on both sides) is replaced by a longitudinal series of perforations. There is no clear trace of the distal foramen or at least its distal bony framing. The tuberosity for the insertion of the *m. tibialis cranialis* is spindle-shaped and moderately wide. The hypotarsus is quite well developed, and three crests are distinguishable. The medial crest is partly broken, the main hypotarsal sulcus is relatively wide. The sulcus for a tendon of the *m. flexor hallucis longus* is shallow, because of the low lateral framing. The intermediate hypotarsal crest is prominent, slightly overhanging the main sulcus, its plantar edge rounded. The surface for the origin of the *m. abductor digitii IV* is very poorly marked and separated from the lateral margin. The second metatarsal is very gently curved, although its medial margin seems to be straight along the middle section. The fourth metatarsal is straight. The third trochlea is (expectedly) clearly more robust than the other two.
The micro-CT scanning revealed that the compact (cortical) and trabecular bone tissues left relatively little room for significant volumes of hollow spaces accounting for metatarsal medullary cavities (Fig. 3M–T). However, they can be observed along the distal second metatarsal, the distal two thirds of the fourth metatarsal, and, as several separate air spaces of highly diverse sizes, in the third metatarsal. The largest continuous empty volume appears to be inside the fourth metatarsal bone. The medullary cavity of the third tarsometatarsal, together with the associated trabecular bone, are characterized by a large content of some hyperdense material (Fig. 3M–P, R–T). This material has also spread into the troclea, penetrating much of its dense spongiosa-meshwork (Fig. 3O, P, T). Trabecular bone within the proximal tarsometatarsus (the tarsal part and adjacent fragments of metatarsals) is devoid of such an infill/coating (Fig. 3O, P, Q). The tarsal/metatarsal transition zone is clearly visible (Fig. 3M, O, P).

Discussion

The traits we used in our differential diagnosis of *Marambiornopsis sobrali* gen. et sp. nov. mainly reflect features found in generic diagnoses of Eocene penguins (Myrcha et al. 2002) that are regarded as rather stable. The latter claim is also based on our examination of available series of fossils (especially reasonable samples representing *Palaeoodytes* and *Delphinornis*) and present-day penguin tarsometatarsi, and the relevant published works. For example, the position of the medial proximal vascular foramen relative to the medial articular surface was used by Zusi (1975) in modern penguins as one of those traits that supported their separation into two phyletic lines. Moreover, the properties of the *m. tibialis cranialis* were considered useful for separating the tarsometatarsi attributable to *Aptenodytes* and *Pygoscelis* (see Zusi 1975).

The holotypic tarsometatarsus of *M. sobrali*, NRM-PZ A542, is shorter than both the holotype and paratype of *Marambiornis exilis* as well as the type specimen of *Mesetaornis polaris* (Fig. 2; Myrcha et al. 2002: table 1; Jadwiszczak & Mörs 2019: fig. 3). The differences amount to 4.8%, 7.2% and 11.7% respectively. Its elongation index (max. length/midwidth, 2.9) is below the value of 3.1 in said comparative bones, and is within the range for *Delphinornis larseni* (2.8–3.2; recalculated on data from Myrcha et al. 2002: table 1; Fig. 2).

The large area for the insertion of the *m. tibialis cranialis* (the flexor; Fig. 1A, J) is intriguing. The in-force moment arm represented by distance from the middle of the abovementioned insertion to the intertarsal joint resembles that in the holotype of *M. exilis* (authors’ observation). Given the similar out-force lever arm or length of both bones, the theoretical magnitude of the force output during joint flexion would be comparable (see also Zeffer & Norberg 2003; Jadwiszczak & Mörs 2019: p. 16). However, in NRM PZ A542, the flexor was supposedly stronger. The possible solution of this puzzle depends on the future availability of more complete material.

The dorsal opening of the distal vascular foramen was either broken or not ossified (Fig. 1A, J). It is rather unlikely that it would not have existed at all in the past. Considering small sphenisiforms from the Eocene, such a foramen was best developed and preserved in *D. larseni* (Fig. 2H; Jadwiszczak & Mörs 2019: fig. 2), other named species varied in this regard (Fig. 2F, G; Acosta Hospitaleche et al. 2019: fig. 8). The variability can also be easily observed at the intraspecific level, and an informative example comes from the above-mentioned genus. The holotype of *Delphinornis arctowski* is devoid of any traces of the plantar opening, but remnants of bony outgrowths are highly suggestive of the dorsal one. The paratype of the species, however, is characterized by the presence of both, although minute, openings (authors’ observation). Myrcha et al. (2002) in their description of *M. exilis* (two specimens involved) stated, that the foramen is “open and connected with incisura intertrocheal”, thus did not exist. Importantly, fossil penguin bones with both openings preserved, have also the third perforation there (perpendicular to those mentioned) – undoubtedly for a tendon of the *m. extensor brevis digiti IV* (Jadwiszczak 2015: fig. 7).

The presence of a large amount of small air pockets within the proximal and distal parts of the specimen NRM-PZ A542 results from the high content of spongious or trabecular bone compared with other regions (e.g., Fig. 1L–N, Q). Considering the proximal tarsometatarsus, the inner traces of fusion of the distal tarsal bone with metatarsals (a tarsal/metatarsal transition zone) have been apparently obliterated by bone remodeling processes (Fig. 1L). This suggests that the individual was a mature bird. If said traces were still present, such a zone would be manifested by the marked change of trabecular or small-air-pockets density (depending on the visualization settings), located proximal to both vascular foramina (e.g., see Fig. 3M, O, P).

The spongiosa bone tissue transfers mechanical loads from the articular surface to cortical bone. In terms of the mechanical competence of the resulting three-dimensional network, the number of trabeculae is more consequential than the size of individual elements (Metzger et al. 2020). In line with this, their distribution within the slice located close to proximal articular surfaces reflects a distribution of (especially compressive) forces acting on said surface. Unsurprisingly, the density of trabeculae is quite low in the middle of the bone (in proximal view), located below the area of the articular surface that has no contact with the tibiotarsal condyles (Fig. 1F).

In the metatarsals, distally to both proximal vascular foramina, the density of bone increases considerably (translucent spaces in Fig. 1L–N) due to compaction of the internal cortical tissues (Ksepka et al. 2015). Hence, the above-mentioned pockets are limited in their numbers there, although they are quite numerous along two intermetatarsal fusion zones. The relative-volume pattern for metatarsal cavities in *Marambiornopsis* is similar to that in *D. larseni* (Jadwiszczak & Mörs 2019: fig. 2.18; plain radiography). Moreover, the results from histological analyses reported by Cerda et al. (2015) revealed well-developed medullary cavities not only in *D. larseni* and *D. arctowski*, but also in *M. exilis* and even in the “giant” Palaeoodytes klekowski. The medullary cavities in other studied penguins (“giant” or large-sized *Anthropornis*
nordenskjöeldi, A. grandis, Archaeosphenicus wimani, and P. gunnari) were described as absent or strongly reduced (Cerda et al. 2015).

The new specimen NRM-PZ A824, attributable to *M. polaris* (Fig. 3A–C, G–T), is negligibly shorter (by 2.4%) than the holotype of this species (Fig. 2D–F; Myrcha et al. 2002: table 1). Its elongation index (max. length/midwidth) of 3.1 perfectly matches that in the above-mentioned bone (recalculated based on data from Myrcha et al. 2002: table 1). Considering other diagnostic features listed by Myrcha et al. (2002), also the large size of the medial proximal intermetatarsal foramen as well as the more adaxial location of its plantar opening as compared with that of the medial hypotarsal crest in NRM-PZ A824 fit the diagnosis.
Figure 3. Late Eocene penguin tarsometatarsi from the Submeseta Formation, Seymour Island; **A-C**: *Mesetaornis polaris*, NRM-P2 A824 (new specimen) in dorsal, plantar and proximal views, **D-F**: *Mesetaornis polaris*, IB/P/B-0278 (holotype) in proximal, dorsal and plantar views, **G**: semi-transparent visualisation of the outward appearance of NRM-P2 A824 (micro-CT based), **H-L**: its 3D surface model (micro-CT based), after digital removal of matrix, in dorsal, medial, plantar, proximal and distal views, **M-N**: its inner-structure visualization focused on air pockets, medullary cavities and radiologically-hyperdense coating material (cortical bone transparent; micro-CT based), **O-P**: its axial- and sagittal-plane slices (micro-CT based), **Q-T**: its coronal-plane slices (micro-CT based); scale bar is 1 cm.
The only minor incongruence is the width of a passage for the tendon of the *m. flexor hallucis longus* (between intermediate hypotarsal crests; see Jadwiszczak 2015). It appears to be somewhat wider than in the holotype (but still narrower than in *M. exilis*); however, the lateral hypotarsus is rather poorly preserved in the latter specimen. In our opinion, a strong lowering of the proximal metatarsal III in relation to the other metatarsals (in dorsal view; indicated by green arrows in Fig. 3), present in both the holotype of *M. polaris* and NRM-PZ A824, can be considered as another diagnostic feature separating this species from *M. exilis* where the lowering is poorly marked.

The most conspicuous non-diagnostic characteristic, that may serve as the starting point for our understanding of variability in this species, is the large size of the lateral proximal vascular foramen in NRM-PZ A824 (Fig. 3G, H, J, O). The lateral intermetatarsal sulcus seems to be better developed than in the holotype, except for the distalmost part, where the fusion between metatarsals is clearly yet to be completed. The latter observation, together with the quite traceable plantar intermetatarsal sulci (Fig. 3H, J), indicate a young age of the bird. The relevant intertrocchlear incisure in the holotype possesses small bony projections suggestive of some, more or less ossified, distal framing of the distal vascular foramen (not preserved). However, the new specimen is more obscure in this regard.

When analyzing the internal structure of NRM-PZ A824 (Fig. 3M–T), it is worth paying attention to the differences in the density of the trabecular network structure. Overall, it appears to be denser/more finely structured than in the type specimen of *Marambiornopsis sobrali* gen. et sp. nov., and this difference is traceable throughout the stacks of hundreds of micro-CT slices (authors’ observation). Moreover, the conspicuous tarsal/metatarsal transition trabecular zone (Fig. 3M, O, P), mentioned in the descriptive section, is another indication of a relatively young age of the studied individual.

The succedent previously-signalled aspect of the new specimen is the presence of some radiologically hyperdense material within the medullary cavity of the third metatarsal and inside its trochlea. It has mainly coating character, although within smaller inter trabecular pockets it effectively creates an infill. Supposedly, an unknown mineral dissolved in water (such as pyrite) penetrated the inner metatarsal space and crystallized. The possible entrance is quite obvious – the large nutrition foramen and its canal on the plantar side of the tarsometatarsus (Fig. 2J, M–N). The opening of this foramen is also visible in the holotype of *M. polaris* (Fig. 2F) and the canal is traceable also in the type specimen of *Marambiornopsis sobrali* gen. et sp. nov. (Fig. 1M, P).

The actual tarsometatarsus-based taxonomic diversity of small-sized penguins from the Eocene of Seymour Island has been claimed to be underestimated (Myrcha et al. 2002; Jadwiszczak 2008; Acosta Hospitalchele et al. 2019). Our findings contribute to a growing body of evidence in favour of this view, and also show that the chances to expand the knowledge of described, but poorly represented taxa, are not on the wane. Last but not least, we demonstrated a remarkable potential of the micro-CT imaging modality for non-destructive, yet versatile, studies of the limb bones of fossil penguins and other birds.

**Acknowledgments**

We thank the Argentinean Antarctic Institute (IAA-DNA), the Argentinean Air Force and the Swedish Polar Research Secretariat (SPES) for logistical support in Antarctica and Jonas Hagström (NRM) for assistance in the field. We thank Vivi Vajda (NRM) for making the CT scanning possible, Ashley Kruger (NRM) for the CT-scanning, the guest editors of GFF, Christian Skovsted and Vivi Vajda (both NRM), and two anonymous reviewers for their helpful comments. Financial support through SYNTHESYS funding made available by the European Community – Research Infrastructure Action under the FP6 Structuring the European Research Area Programme, project SE-TAF-4399 to P; from the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET) grant PIP 0462 and from the Argentinean National Agency for Promotion of Science and Technology (ANPCyT grant PICTO 0093/2010) to MR; from the Swedish Research Council (VR Grant 2009-4447) and from the Carl Trygggers Foundation (CTS grant 20:300) to TM is gratefully acknowledged.

**Disclosure statement**

No potential conflict of interest was reported by the authors.

**Funding**

This work was supported by the Agencia Nacional de Promoción Científica y Tecnológica [PICTO 0093/2010]; Carl Tryggers Stiftelse för Vetenskaplig Forskning [20:300]; Consejo Nacional de Investigaciones Científicas y Técnicas [PIP 0462]; Sixth Framework Programme [SYNTHESYS SE-TAF-4399]; Vetenskapsrådet [2009-4447].

**ORCID**

Piotr Jadwiszczak http://orcid.org/0000-0002-5263-1125
Marcelo Reguero http://orcid.org/0000-0003-0875-8484
Thomas Mörs http://orcid.org/0000-0003-2268-5824

**References**

Acosta Hospitalchele, C., Hagström, J., Reguero, M. & Mörs, T., 2017: Historical perspective of Otto Nordenskjöld’s Antarctic penguin fossil collection and Carl Wiman’s contribution. *Polar Record* 53 (271), 364–375. doi:10.1017/S0032247417000249.

Acosta Hospitalchele, C., Jadwiszczak, P., Clarke, J.A. & Cenizo, M., 2019: The fossil record of birds from the James Ross Basin, West Antarctica. *Advances in Polar Science* 30 (3), 251–273.

Cerda, I.A., Tambussi, C.P. & Degrange, F.J., 2015: Unexpected micro-anatomical variation among Eocene Antarctic stem penguins (*Aves*: sphenisciformes). *Historical Biology* 27 (5), 549–557. doi:10.1080/08912963.2014.896907.

Clarke, J.A., Olivero, E.B. & Puerta, P., 2003: Description of the earliest fossil penguin from South America and the first Paleogene vertebrate locality of Tierra del Fuego, Argentina. *American Museum Novitates* 3423 (1), 1–18. doi:10.1206/0003-0082(2003)3423<0001:DOTEFP>2.0.CO;2.

Douglas, P.M., Affek, H.P., Ivany, L.C., Houben, A.J., Sip, W.P., Slijis, A., Schouten, S. & Pagani, M., 2014: Pronounced zonal heterogeneity in Eocene southern high-latitude sea surface temperatures. *Proceedings of the National Academy of Sciences of the United States of America* 111 (18), 6582–6587. doi:10.1073/pnas.1321441111.

Fedorov, A., Beichel, R., Kalpathy-Cramer, J., Fine, J., Fillion-Robin, J.-C., Pujol, S., Bauer, C., Jennings, D., Fennessey, F.M., Sonka, M., Buatti, J., Aylward, S.R., Miller, J.V., Pieper, S. & Kikinis, R., 2012: 3D Slicer as an
image computing platform for the quantitative imaging network. *Magnetic Resonance Imaging* 30 (9), 1323–1341. doi:10.1016/j.mri.2012.05.001.

Jadwiszczak, P., 2006: Eocene penguins of Seymour Island, Antarctica: taxonomy. *Polish Polar Research* 27 (1), 3–62.

Jadwiszczak, P., 2008: An intriguing penguin bone from the Late Eocene of Seymour Island (Antarctic Peninsula). *Antarctic Science* 20 (6), 589–590. doi:10.1017/S0954102008001405.

Jadwiszczak, P., 2009: Penguin past: the current state of knowledge. *Polish Polar Research* 30 (1), 3–28.

Jadwiszczak, P., 2015: Another look at tarsometatarsi of early penguins. *Polish Polar Research* 36 (4), 343–354. doi:10.1515/popore-2015-0024.

Jadwiszczak, P., Krajewski, K.P., Pushina, Z., Tatur, A. & Zieliński, G., 2013: The first record of fossil penguins from East Antarctica. *Antarctic Science* 25 (3), 397–408. doi:10.1017/S0954102012000909.

Jadwiszczak, P. & Mörs, T., 2011: Aspects of diversity in early Antarctic penguins. *Acta Palaeontologica Polonica* 56 (2), 269–277. doi:10.4202/app.2009.1107.

Jadwiszczak, P. & Mörs, T., 2019: First partial skeleton of *Delphinornis larseni* Wiman, 1905, a slender-footed penguin from the Eocene of Antarctic Peninsula. *Palaeontologia Electronica* 22.2.34A, 1–31.

Krüver, J., Engelbrecht, A., Mörs, T., Reguero, M. & Pfaff, C., 2016: Ultimate Eocene (Priabonian) chondrichthysans (Holocephali, Elasmobranchii) of Antarctica. *Journal of Vertebrate Paleontology* 36 (4), e1160911. doi:10.1080/07380590.2016.1160911.

Ksepka, D.T., Werning, S., Scafani, M. & Boles, Z.M., 2015: Bone histology in extant and fossil penguins (Aves: sphenisciformes). *Journal of Anatomy* 227 (5), 611–630. doi:10.1111/joa.12367.

Meister, W., 1962: Histological structure of the long bones of penguins. *The Anatomical Record* 143 (4), 377–387. doi:10.1002/ar.1091430408.

Metzger, C.E., Burr, D.B. & Allen, M.R., 2020: Anatomy and structural considerations. In: M. Zaidi (ed.): *Encyclopedia of bone biology*, 218–232. Academic Press, San Diego, CA.

Montes, M., Nozal, F., Santillana, S., Marenssi, S. & Olivero, E., 2013: *Mapa Geológico de la Isla Marambio (Seymour)*; escala 1:20.000. Serie Cartográfica Geocientífica. Antártica. Contexto complementario. Instituto Geológico y Minero de España, Madrid y Instituto Antártico Argentino, Buenos Aires.

Myrcha, A., Jadwiszczak, P., Tambussi, C.P., Noriega, J.I., Gaździcki, A., Tatur, A. & Del Valle, R.A., 2002: Taxonomic revision of Eocene Antarctic penguins based on tarsometatarsal morphology. *Polish Polar Research* 23 (1), 5–46.

Sadler, P.M., 1988: Geometry and stratification of uppermost cretaceous and Paleogene units on Seymour Island, northern Antarctic Peninsula. In R.M. Feldmann & M.O. Woodburne (eds.): *Geology and paleontology of Seymour Island, Antarctic Peninsula*, 303–320. Geological Society of America Memoirs 169, Boulder, CO.

Schreiber, E.A. & Burger, J., 2001: *Biology of marine birds*. CRC Press, Boca Raton, FL. 740 pp.

Zeffer, A. & Norberg, U.M.L., 2003: Leg morphology and locomotion in birds: requirements for force and speed during ankle flexion. *Journal of Experimental Biology* 206 (6), 1085–1097. doi:10.1242/jeb.00208.

Zusi, R.L., 1975: An interpretation of skull structure in penguins. In B. Stonehouse (ed.): *The biology of penguins*, 59–84. Macmillan, London.