



Synsacra of the Eocene Antarctic penguins: new data on spinal maturation and an insight into their role in the control of walking

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Abstract: The synsacrum is an important element of the axial skeleton in birds, both volant and flightless. Little is known about the maturation of this complex bone in penguins. In this work, the supposedly ontogenetically youngest known synsacrum of early penguins was described. The analysis of this specimen, collected within the Eocene La Meseta Formation of Seymour (Marambio) Island, Antarctic Peninsula, revealed that this bird had attained at least the fledging stage of growth. Studies of three mature synsacra recovered from the same formation focused on the synsacral canals and, using indirect reasoning, their contents. These analyses revealed that the lumbosacral intumescence of the spinal cord and its extensions, the transverse canals, had been developed roughly like those in extant penguins (and also swifts and cormorants). The neural spine extensions (a non-nervous tissue) tracing the transverse grooves of the dorsal wall of the synsacral canal are currently considered as involved in the control of walking. The presented data suggest that such a sense organ gained its current penguin configuration by the late Eocene.

Key words: Antarctica, Seymour Island, La Meseta Formation, Paleogene, Sphenisciformes, synsacrum, spinal cord.

Introduction

The synsacrum (*os lumbosacrale*) is a component of the axial skeleton of some amniotes, nowadays present solely in birds. This is a complex structure made up of a number of ankylosed (in varying degree) vertebrae and synostosed on each side with the hip bone or *os coxae*. The avian synsacrum consists of the lumbar and sacral series, but also incorporates some caudalmost thoracic and cranialmost caudal vertebrae (Baumel and Raikow 1993; Baumel and Witmer 1993). Its length and shape are variable and depend on several factors, including the individual maturity and way the bird uses its legs (Baumel and Witmer 1993; Kaiser 2007).

In extant penguins (Aves: Sphenisciformes), the synsacrum comprises 13–14 vertebrae (Stephan 1979), although Pycraft (1898) reported a range of 12–14 bones. The earliest representative of this order, *Waimanu manneringi* Jones, Ando and Fordyce, 2006 from the Paleocene (66–56 Ma) of New Zealand, had 11 fused synsacral vertebrae and the entire segment was not longer than that in the living Emperor Penguin, *Aptenodytes forsteri* Gray, 1844 (Slack *et al.* 2006). On the other hand, the largest Paleogene (66–23 Ma) Antarctic penguin, the “giant” *Anthropornis nordenskjoeldi* Wiman, 1905 from the Eocene (56–34 Ma) of Seymour Island (*e.g.*, Jadwiszczak and Chapman 2011, fig. 1; see also Jadwiszczak 2012), possessed at least 14 synsacral elements (Jadwiszczak and Mörs 2011). Moreover, the differences between fossil synsacra are evidently not limited to their dimensions (Jadwiszczak 2006; Jadwiszczak and Mörs 2011).

Nonetheless, irrespective of its size (and shape), the most obvious primary function of the *os lumbosacrale* in birds, from the evolutionary point of view, appears to be shortening and stiffening the back in order to achieve a better performance during flight (Kaiser 2007). Although penguins are non-volant animals, the above-mentioned trait serves the same purpose during the so-called underwater flight. On hatching, however, such a structure is yet to be formed (*e.g.*, consult the scan of a one-day-old *Aptenodytes forsteri* available from the web page <http://www.digimorph.org>, accessed 4 February 2014). The most recent discovery regarding the importance of the synsacrum in modern birds, is its presumed role as a structure housing and, to some extent, shaping the sense organ of equilibrium involved in the control of walking (Necker 2006 and references therein).

In this paper I report on the probably ontogenetically youngest *os lumbosacrale* attributable to the Antarctic penguins from the Eocene La Meseta Formation of Seymour Island. Additionally, I reveal, based on penguin synsacra from the above-mentioned formation, the morphological intricacies of the lumbosacral spinal cord and surrounding tissue related to their postulated (Necker 2006) function as the sensory organ in birds. Thus, the purpose of the current contribution focused on fossil synsacra is twofold: to expand the knowledge on skeletal maturation in early penguins and to indirectly assess the condition and importance of the alleged posterior center for control of balance in these seabirds.

Geological setting

Seymour Island is located within the back-arc James Ross Basin, east of James Ross Island, northern Antarctic Peninsula (64°17'S, 56°45'W). The rocks making up the island are devoid of any permanent ice cover. The most fossiliferous strata (rich in penguin bones among others; *e.g.* Myrcha *et al.* 2002; Jadwiszczak 2006) are Eocene in age and are exposed in the north-eastern part of island, where they form the La Meseta Formation (Elliot and Trautman 1982).

The formation is characterized by a complex cut-and-fill stratigraphy with a recurrent motif of a transgressive-regressive cycle. It consists of mostly poorly consolidated siliciclastic sediments and represents deltaic, estuarine and shallow marine paleoenvironments (Porebski 2000; Marenssi 2006; Tatur *et al.* 2011).

Material and methods

The fossil synsacra of Antarctic penguins discussed in this paper were collected within the uppermost unit (Telm7 or Submeseta Allomember) of the Eocene La Meseta Formation (Seymour Island, Antarctic Peninsula). All these specimens, together with juvenile synsacra of extant penguins (a comparative material), are housed at the Institute of Biology, University of Białystok (Poland), in the collection of the Andrzej Myrcha University Centre of Nature (abbreviated IB/P/B). The bone IB/P/B-0319 (a juvenile synsacrum) had been already reported as a small fragment of a “problematic” *os lumbosacrale* (Jadwiszczak 2006), but owing to the recent enlargement of the above-mentioned collection (courtesy of Andrzej Gaździcki from the Polish Academy of Sciences), the specimen was partially reconstructed. Another synsacrum discussed in this work and previously reported as a “problematic specimen” (Jadwiszczak 2006) is IB/P/B-0853. Synsacra IB/P/B-0988 and IB/P/B-989 are new specimens.

The nomenclature of the segmentation system of synsacral vertebrae was based on that published by Stephan (1979). According to this scheme, the thoracic (*i.e.*, cranialmost) segment comprises a single vertebra with free ribs, which is directly followed by the thoracolumbar series (devoid of free ribs). The last thoracolumbar and first lumbar vertebrae can be differentiated by the lack of costal processes (rudiments of ribs) in the latter, a feature typical of all lumbar bones. The sacral series, unlike lumbar and caudal ones, is characterized by strong (“conspicuous” in Baumel and Witmer 1993, p. 91) costal processes. Anatomical nomenclature follows that of Baumel and Witmer (1993) and Breazile and Kuenzel (1993). Measurements were taken with digital calipers and rounded to the nearest 0.1 mm.

Results

Juvenile synsacrum

Material. — A partial penguin synsacrum (IB/P/B-0319) from the late Eocene of Seymour Island, Antarctic Peninsula (see Material and methods; Fig. 1).

Taxonomical position. — Indeterminate, but see Discussion.

Development stage. — A juvenile specimen (see below and Discussion).

Description. — The studied specimen (Fig. 1) is a large and relatively robust partial synsacrum comprising nine ankylosed vertebrae. The bone was recon-

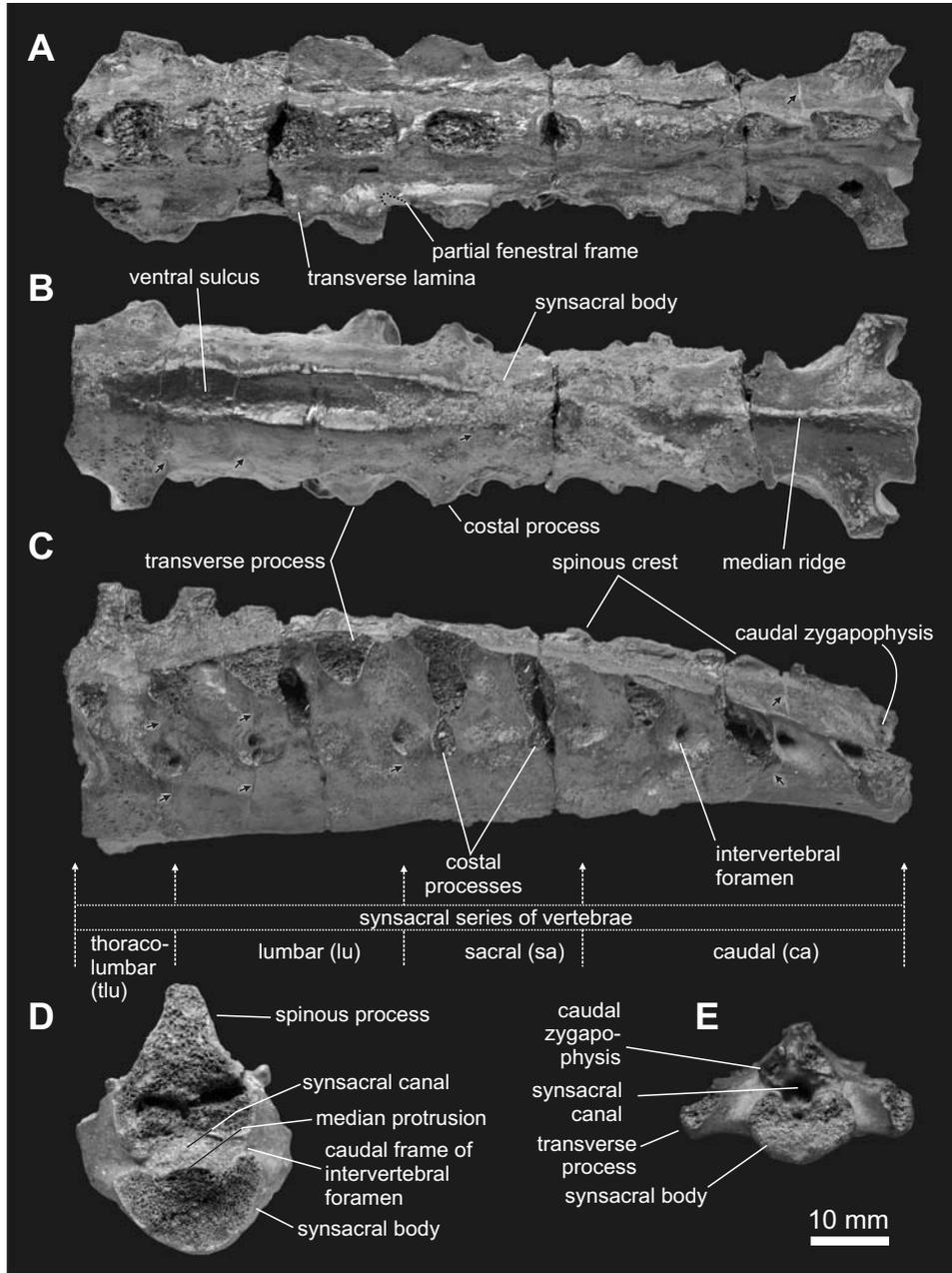


Fig. 1. Juvenile synsacrum (IB/P/B-0319) of a late Eocene penguin from the La Meseta Formation, Seymour Island. Dorsal (A), ventral (B), side (right, but mirrored here, C), cranial (D) and caudal (E) views. Black arrows point at intervertebral fissures.

structed from four fragments, but even within these several bony units, slight fissure markings, perpendicular to the main axis, are conspicuous. They are located

mainly within the cranial half of the specimen and roughly correspond to the boundaries between individual vertebrae during early ontogeny. The above-mentioned markings demarcate consecutive transversal swellings of the synsacral body (*corpus synsacri*).

The cranialmost vertebra, characterized by the costal and transverse processes apparently fused and forming a massive bony structure, represents the thoracolumbar segment. It is followed by three bones devoid of costal processes; hence they are assignable to the lumbar series. The sacral series is represented by two vertebrae with costal processes, the process in the cranial vertebra being clearly separated from its transverse counterpart. The last (*i.e.*, caudal) segment consists of three vertebrae. The transverse process is best developed (and preserved) in the caudalmost bone. The intervertebral foramina are rather small, although they are present along the entire fragment.

Extending along the ventral surface of the synsacrum (Fig. 1B), the ventral sulcus originates as a barely detectable depression within the cranialmost vertebra of the preserved series, widens and deepens in the anterior lumbar bone, forms another, substantially deeper, widening within the consecutive two lumbar elements, and gradually vanishes reaching the sacral series. The median ridge is best pronounced within the two caudalmost postacetabular vertebrae.

The spinous crest appears to be quite well-pronounced, but it is high to moderately high solely within the preacetabular segment formed by thoracolumbar and lumbar vertebrae. Actually, it is not a continuous ridge, but a series of separate spinous processes, with the probable exception of its cranialmost fragment. All the processes are coalesced at their bases, although in the case of two caudalmost structures, the coalescence is barely detectable. The transverse lamina does not form a uniform surface, and the presence of longitudinal ridges and sutures as well as intertransversal fenestrae is evident.

The cranial view (Fig. 1D) of the specimen reveals the cross section of the caudalmost thoracolumbar vertebra. The vertebral body is largely composed of dense cancellous bone, whereas the neural arch (including the spinous process), appears to exhibit a little bit more heterogeneous condition. Two lateral hollows dorsal to the canal presumably correspond to marrow cavities of the cranial zygapophyses. The opening of the canal is flattened dorsoventrally. Its ventral wall forms a wide, flat, and obviously longitudinal, median protrusion. The caudal view (Fig. 1E) exhibits the roughly circular opening of the synsacral canal, and well-developed transverse processes of the caudal vertebra. The synsacral body is broken exactly at the discontinuity defining the primary contact zone between two finally ankylosed caudal vertebrae. Moreover, the remnants of the caudal zygapophyses are conspicuous.

Measurements (in mm). — Length of preserved synsacral body, 110.1; length of lumbar segment (ventral view), 37.9; dorsoventral height of cranial end

(including spinous process), 37.6; width of synsacral body at level of 3rd lumbar vertebra, 17.9.

Adult synsacra

Material. — Three partial penguin synsacra, IB/P/B-0853, IB/P/B-0988 and IB/P/B-0989, from the late Eocene of Seymour Island, Antarctic Peninsula (see Material and methods; Fig. 2).

Taxonomical position. — Indeterminate, but see Discussion.

Development stage. — All specimens, judging from the lack of the intervertebral fissures and the adult-like condition of the spinous crest, are clearly more mature than IB/P/B-0319.

Description. — The specimen IB/P/B-0989 (Fig. 2A) comprises solely a dorsal, corresponding to fused neural arches, fragment of a relatively large synsacrum. All post-thoracic segments are represented: the thoracolumbar (five vertebrae), lumbar (three vertebrae), sacral (two vertebrae) and caudal (two vertebrae) series. The dorsal wall of the synsacral canal (“the lumbosacral vertebral canal” in Necker 2006) is well-preserved and characterized by the presence of the bilateral transverse grooves indicating the borders between successive vertebrae. The culmination of the canal enlargement (both deepening and widening) is located within two cranialmost lumbar (*sensu* Stephan 1979) vertebrae marking the probable position of the glycogen body within the lumbosacral intumescence of the spinal cord. This fragment encompasses the three deepest transverse grooves of the dorsal wall of the synsacral canal shaping the best-developed (anticipated) semi-circular lumbosacral canals of Necker (2006; not to be confused with the lumbosacral vertebral canal). These transverse grooves are connected by a smoothly running median longitudinal sulcus and the whole setup resembles a gear-shift-knob icon found in many cars (Fig. 2A). The sulcus becomes much shallower both cranially and caudally to that fragment.

The specimen IB/P/B-0853 (Fig. 2B) is more massive than the previous one. Three thoracolumbar elements are followed by three lumbar and two sacral ones as well as a single caudal vertebra. The dorsal wall of the synsacral canal is much worse preserved than that in IB/P/B-0989 (Fig. 2A) and can be most reliably analyzed within the caudalmost lumbar and both sacral vertebrae. The preserved bilateral transverse grooves weaken gradually towards the caudal end, although the one between the lumbar and sacral series is still well-developed. The overall shape of the specimen (in ventral view) allows estimating (quite confidently) the location of the culmination of the synsacral canal enlargement within two cranialmost lumbar vertebrae. As far as the above-mentioned features are considered, and taking into account the size difference, both discussed specimens generally resemble each other. The latter one possesses a large thoracolumbar portion of the synsacral body revealing the very flat, though wide, longitudinal median protrusion of the ventral wall of the synsacral canal, oriented towards the lumen of this duct.

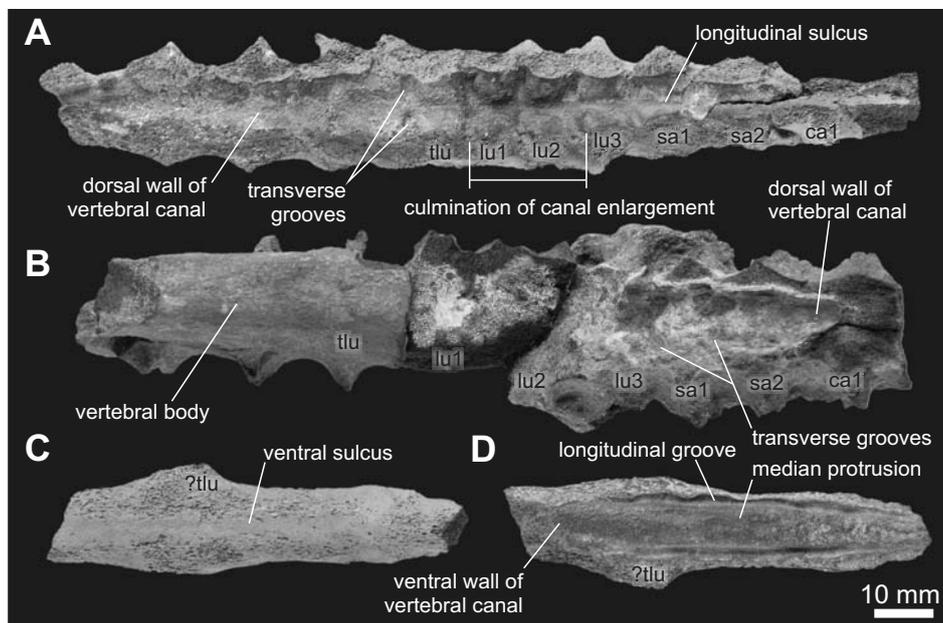


Fig. 2. Penguin synsacra from the Eocene La Meseta Formation, Seymour Island revealing details of the synsacral-canal morphology. **A.** IB/P/B-0989 (ventral view of the dorsal wall of the canal). **B.** IB/P/B-0853 (ventral view). **C, D.** IB/P/B-0988, ventral view (**C**) and dorsal view of the ventral wall of the canal (**D**). Three-character abbreviations mark vertebrae from different synsacral series and are explained in Fig. 1.

The least complete specimen, IB/P/B-0988 (Fig. 2C, D), is a fragmentary synsacral body comprising the partial thoracolumbar and complete lumbar as well as sacral series. The size of this bone appears to correspond to that of IB/P/B-0989. Two quite narrow, but deep, longitudinal grooves separate the rather flat ventral wall of the canal from both side (*i.e.*, left and right) walls of the synsacrum (Fig. 2D). Such a setting gives the impression of the presence of a median protrusion. This protrusion is widest at the level of the lumbar segment, which corresponds to the expected position of the intumescence of the spinal cord along the canal length. The ventral sulcus of the synsacrum appears to be poorly developed (Fig. 2C).

Measurements (in mm). — Total length of preserved part, 151.3 (IB/P/B-0853), 80.5 (IB/P/B-0988), 155.0 (IB/P/B-0989).

Discussion

Juvenile synsacrum

Judging from bone dimensions, the specimen IB/P/B-0319 belonged to a large seabird, in the size range of extant *Aptenodytes* penguins (Figs 1, 3) and three

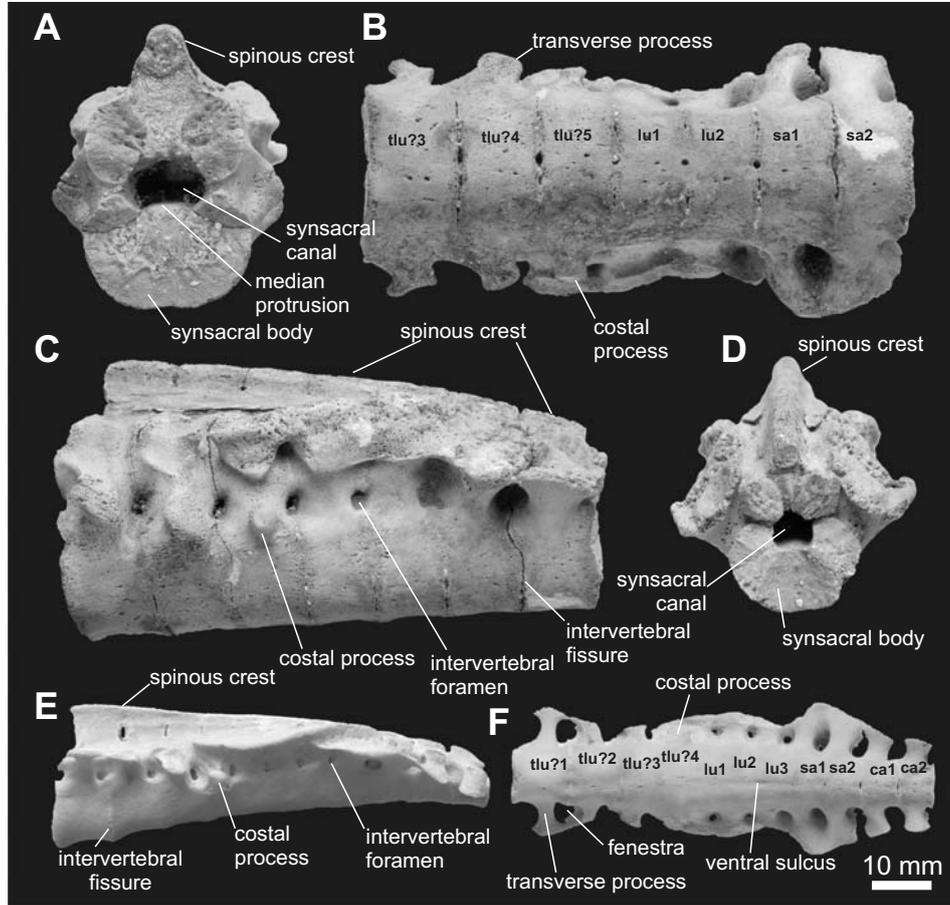


Fig. 3. Juvenile synsacra of extant penguins: *Aptenodytes* sp. (A–D) and *Pygoscelis* sp. (E, F). Cranial (A), ventral (B, F), side (C, E) and caudal (D) views. Three-character abbreviations mark vertebrae from different synsacral series and are explained in Fig. 1.

Eocene Antarctic species: *Archaeospheniscus wimani* (Marples, 1953), *Palaeudyptes gunnari* (Wiman, 1905) (a small individual¹; Jadwiszczak and Acosta Hospitaleche 2013) and *Anthropornis grandis* (Wiman, 1905) (small individual; see also Acosta Hospitaleche and Jadwiszczak 2011). The juvenile status of the specimen IB/P/B-0319 can be easily assessed based on a number of features. One of them is the presence of intervertebral fissures, which is typical of young extant penguins (Fig. 3). In the fossil bone they are slight and result from relatively weak fusion of the bony elements, which suggest juvenile age of the specimen. Still the maturation process has already slightly obliterated the fissures, probably corresponding to a

¹ However, some other, yet-to-be-described, species of *Palaeudyptes* ought to be taken into account as well – see Jadwiszczak 2013.

fledging stage of growth. Those fissures which do not match the boundaries between vertebrae (Fig. 1) probably result from some taphonomical factors.

Another feature of IB/P/B-0319 is the shape of the spinous crest, which is in fact represented by separate spinous processes fused at their bases (Fig. 1). The synsacra of juvenile extant penguins studied here (Fig. 3) display a more advanced but still incomplete fusion of the spinal processes, in contrast to those of the adult ones. The large size of gaps between processes, observed even within the lumbar series (*sensu* Stephan 1979; see Material and methods), appears to be unique when compared with that in both present-day and known Paleogene penguins (author's observation; Wiman 1905; Jadwiszczak 2006; Slack *et al.* 2006; Clarke *et al.* 2007; Ksepka *et al.* 2012). In my opinion, such a shape of the spinous crest, together with the presence of longitudinal furrows along its sides (Fig. 1), which tend to be reduced or absent in adult penguins (author's observation), strongly support the view of the juvenile age of the analyzed bone.

The ventral surface of the specimen IB/P/B-0319 is interesting as well. There is a very conspicuous ventral sulcus, located largely within three vertebrae of the lumbar segment (Fig. 1), a condition probably not prevailing in Eocene penguins (author's observation; Jadwiszczak and Mörs 2011). The condition of this feature in extant penguins varies between taxa, but is sometimes age-dependent. The sulcus is virtually non-existent or very poorly developed in both the juvenile and adult *Aptenodytes* penguins (Fig. 3; Jadwiszczak 2006; Jadwiszczak and Mörs, fig. 3), whereas in the genus *Pygoscelis* it seems to be slightly marked in very young individuals (Fig. 3F), but conspicuous in adults (author's observation). Intriguingly, in the fossil discussed here the state of this sulcus, which is typical of adult pygoscelids, is associated with a relatively young age.

I am convinced the specimen IB/P/B-0319 is apparently the least-mature Eocene *os lumbosacrale* among those either investigated by myself or reported so far. The individual was by no means a newly-hatched chick, a fledgling rather (or even slightly older), capable of surviving without the constant parental care. The fusion of the vertebrae in IB/P/B-0319 seems to be more complete than that in the modern specimen assignable to the genus *Aptenodytes* and displayed in Fig. 2A–D. Since the latter bone was collected on an island (Seymour or King George islands, Antarctic Peninsula) devoid of known breeding colonies of these penguins, the recent specimen and, correspondingly, the fossil bone, probably represent individuals that had been capable of making at least short treks to the sea.

Synsacral canal and its anticipated contents

The spinal cord in birds is characterized by two enlargements: the cervical and lumbosacral intumescences (Butler and Hodos 2005, fig. 8.6), the later enlargement²,

² To see its shape and size in the present-day Humboldt or Peruvian Penguin, *Spheniscus humboldti* Meyen, 1834, consult fig. 2 in Necker 2006.

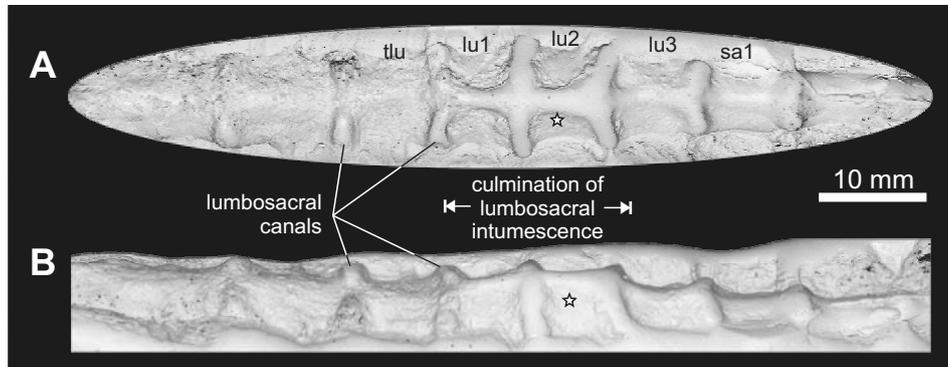


Fig. 4. Three-dimensional organization of lumbosacral canals in the penguin synsacrum (IB/P/B-0989) from the Eocene La Meseta Formation, Seymour Island. Photographs show a cast of the (dorsal) synsacral canal. **A.** Dorsal view. **B.** Side (right, but mirrored here) view. Stars mark a supposed position of the glycogen body. Three-character abbreviations mark vertebrae from different synsacral series and are explained in Fig. 1.

located at the level of the lumbosacral plexus (see Jelgersma 1951, fig. 1; Dubbeldam 1993, fig. 15.6), is usually larger than the former one in flightless birds (Brazile and Kuenzel 1993). An interesting feature of the lumbosacral intumescence of the spinal cord in birds is its dorsal split (“cleft” in Jelgersma 1951, “groove” in Necker 2005) leading to the formation of the so-called dorsal rhomboid (or lumbosacral) spinal fossa (or sinus). The fossa houses an enigmatic ovoid glial structure called the glycogen body (Jelgersma 1951; Brazile and Kuenzel 1993; Butler and Hodos 2005; Kaiser 2007; see also Giffin 1990). The position of the lumbosacral intumescence and glycogen body can be easily located, for the corresponding part of the synsacral canal is enlarged (Necker 2006). This enlargement is quite conspicuous in fossil penguins (Fig. 4) and is also manifested by the external swelling of the synsacral body (Figs 1–3; Baumel and Raikow 1993; author’s observation).

Butler and Hodos (2005) claimed that the anatomical details of the lumbosacral intumescence in birds were “one of the most dramatic examples of how locomotor patterns affect spinal cord morphology”. This statement is very pertinent, especially in light of results reported by Necker (2006, and references therein; see also Kaiser 2007). Almost fifteen years ago, Necker (1999) championed a hypothesis that some specializations within the lumbosacral region, encompassing both the spinal cord and synsacral canal, may have been involved in control of the balanced walking in birds. He noted that lumbosacral canals, which were actually evaginations made of meninges, filled with fluid and shaped by dorsal transverse grooves of the canal wall, looked similar to the semicircular canals in the inner ear. These canals open above the lateral accessory lobes of the spinal cord which are presumably stimulated mechanically by movement of the fluid (for a review, see Necker 2006). The system is also present in the extant penguins, although Necker (2006) noted that the transverse grooves of the dorsal

wall of the synsacral canal were shallow (like in cormorants and swifts; see Necker 2006, fig. 12).

The Eocene penguins obviously possessed both the swelling of the spinal cord and also had a system of lumbosacral canals (Fig. 2A, B). The system, in a form of the cast of the synsacral canal (specimen IB/P/B-0989), is presented on Fig. 4. It appears to be similarly (or slightly better) developed to that in present-day swifts (birds that rarely walk), although the culmination of the cord swelling is longer by one vertebra. It is much weaker than its counterpart in ostriches and even pigeons (see Necker 2006, fig. 12; for a great set of photographs, consult Jelgersma 1951). Apparently, at least some large-sized Eocene penguins, IB/P/B-0989 is probably *Aptenodytes*-like in size and IB/P/B-0853 – clearly larger, did not differ much from extant Sphenisciformes (see Necker 2006) in this regard. Such a resemblance is very informative, though. It can be interpreted in terms of the extreme specialization and adaptation to spend most of their life at sea.

The flat median protrusion of the ventral wall of the synsacral canal noted in the Eocene specimens is also present in modern penguins (Fig. 3A) and other birds as well (*e.g.*, Necker 2005, fig. 2B). Since the longitudinal grooves separating this protrusion from side walls deepen substantially within the lumbar segment (Fig. 2D), such a setting appears to be a useful feature when determining the location of the spinal cord intumescence and location of the glycogen body in some poorly preserved specimens.

Conclusions

The synsacrum IB/P/B-0319 from the Eocene La Meseta Formation provides an important insight into the process of maturation in the axial skeleton of early penguins. Its morphology represents an interesting mix of juvenile features (*e.g.*, intervertebral fissures) and traits for which the interpretation is more ambiguous (*e.g.*, the conspicuous ventral sulcus). Considering the individual age, the weight of evidence resulted from the former set appears to prevail. Moreover, judging from the degree of the vertebral fusion, the bird discussed above was not a very young chick (despite its seemingly very immature spinous crest), much more probably – at least a fledgling.

The analysis of the inner morphology of the more mature penguin synsacra from the same formation revealed that the lumbosacral intumescence of the medial cord and the shape of (transverse) canals were similar to those in some rarely walking birds (like swifts) and modern penguins. This finding suggests that the alleged lumbosacral sense organ for the control of walking gained its current penguin configuration by the late Eocene. Such a discovery testifies to the extreme specialization of these early seabirds. Analyses presented here are considered the preliminary step on the path to better understanding the intricacies of the form and function of the axial skeleton in Paleogene Sphenisciformes.

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