

## RESEARCH/REVIEW ARTICLE

# At the root of the early penguin neck: a study of the only two cervicodorsal spines recovered from the Eocene of Antarctica

Piotr Jadwiszczak

Institute of Biology, University of Białystok, Swierkowa 20B, PL-15-950, Białystok, Poland

**Keywords**

Antarctic Peninsula; La Meseta Formation; Palaeogene; early Sphenisciformes; cervicodorsal vertebrae.

**Correspondence**

Piotr Jadwiszczak, Institute of Biology, University of Białystok, Swierkowa 20B, PL-15-950 Białystok, Poland.  
E-mail: piotrj@uwb.edu.pl

**Abstract**

The spinal column of early Antarctic penguins is poorly known, mainly due to the scarcity of articulated vertebrae in the fossil record. One of the most interesting segments of this part of the skeleton is the transitional series located at the root of the neck. Here, two such cervicodorsal series, comprising reinterpreted known material and a new specimen from the Eocene of Seymour Island (Antarctic Peninsula), were investigated and contrasted with those of modern penguins and some fossil bones. The new specimen is smaller than the counterpart elements in recent king penguins, whereas the second series belonged to a large-bodied penguin from the genus *Palaeudyptes*. It had been assigned by earlier researchers to *P. gunnari* (a species of “giant” penguins) and a Bayesian analysis—a Bayes factor approach based on size of an associated tarsometatarsus—strongly supported such an assignment. Morphological and functional studies revealed that mobility within the aforementioned segment probably did not differ substantially between extant and studied fossil penguins. There were, however, intriguing morphological differences between the smaller fossil specimen and the comparative material related to the condition of the lateral excavation in the first cervicodorsal vertebra and the extremely small size of the intervertebral foramen located just prior to the first “true” thoracic vertebra. The former feature could have resulted from discrepancy in severity of external pneumatization. Both fossils provided valuable insights into the morphology and functioning of the axial skeleton in early penguins.

The spinal column, a hallmark feature of vertebrates, encloses the spinal cord, stiffens the body and provides attachment for girdles and muscles. In tetrapods, it is regionalized into presacral (cervical + thoracic), sacral and caudal series of vertebrae, which results from different *Hox* gene expressions along the anteroposterior body axis (Müller et al. 2010, references therein). In birds, the total number of vertebrae varies considerably, with most interspecific variation occurring in the cervical spine (Baumel & Witmer 1993).

Penguins (Aves: Sphenisciformes), highly specialized seabirds, have 47–48 vertebrae (Stephan 1979). According to Stephan (1979) and Guinard et al. (2010; but see Watson 1882), 13 of these bones are the neck (cervical) vertebrae and eight moveable-rib-bearing elements form

the dorsal (thoracic) series. However, two vertebrae at the root of the neck (i.e., the 14th and 15th ones, counting from the cranial end), that in most cases bear ribs not reaching the sternum (a feature not limited to penguins), have sometimes been counted among the cervical segment (e.g., Shufeldt 1901; see also Bertelli & Giannini 2005; Livezey & Zusi 2006). Importantly, these transitional spinal elements, termed “cervicodorsal vertebrae” (Baumel & Witmer 1993, references therein; figure 5.10 in Baumel & Raikow 1993; see also supporting information in Müller et al. 2010), form the caudalmost portion of the presacral spinal column within which some median-plane mobility is still possible (Stephan 1979). The neck folding into an S-shaped curve (and straightening if necessary) is important for penguins on both land and

sea for a number of reasons, for example, to improve hydrodynamics and body balance, and as an extendable “arm” for feeding and nest-building to name just two activities, and more (e.g., Guinard & Marchand 2010).

The spinal column of early penguins (i.e., those from the Palaeocene and Eocene epochs, 66.0–33.9 Mya) is poorly known. This is especially true for the Antarctic penguins, for their remains (found solely on Seymour Island, Antarctic Peninsula; Fig. 1) are, with few exceptions (Ksepka & Bertelli 2006; Acosta Hospitaleche & Di Carlo 2010; Acosta Hospitaleche & Reguero 2010; Jadwiszczak 2010, 2012; Jadwiszczak et al. 2013), isolated bones (Wiman 1905; Myrcha et al. 2002; Jadwiszczak 2006; Jadwiszczak & Chapman 2011; Jadwiszczak & Acosta Hospitaleche 2013, references therein). The oldest Antarctic penguin vertebra ever collected is a single poorly preserved thoracic element described by Jadwiszczak et al. (2013), a part of the incomplete skeleton of late Palaeocene *Crossvallia unienwillia* Tambussi, Reguero, Marensi & Santillana, 2005 from the Cross Valley Formation (Tambussi et al. 2005). So far, there have been only two reported series of articulated vertebrae of Palaeogene (66.0–23.0 Mya) Antarctic Sphenisciformes. These are a segment comprising three anterior thoracic skeletal elements assignable to *Palaeudyptes gunnari* (Wiman, 1905), a “giant” penguin from the Eocene–?early Oligocene La Meseta Formation (Fig. 1; Acosta Hospitaleche & Reguero 2010) and a very poorly preserved fragment of a supposedly caudal thoracic series of a very large sphenisciform from the same formation (Acosta Hospitaleche & Di Carlo 2010).

The purpose of this paper is to thoroughly describe, illustrate and eventually reinterpret the former of two

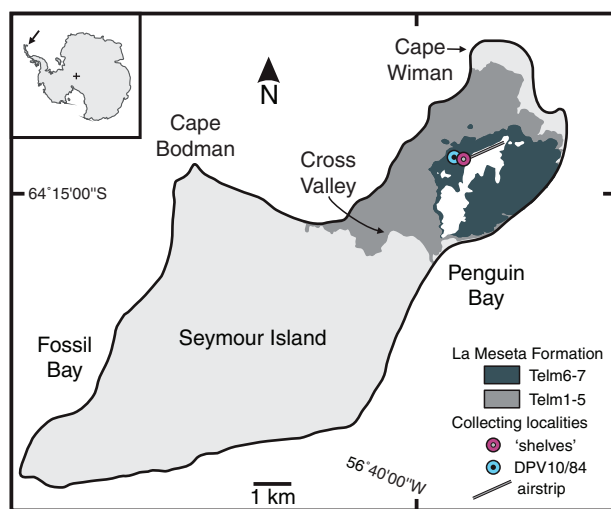
aforementioned fragments of the spinal column, heretofore documented only as an unannotated black-and-white photograph and a two-sentence description. Furthermore, I report on the new rare finding represented by three articulated vertebrae from the transitional cervicodorsal series belonging to a “non-giant” Eocene penguin from the La Meseta Formation (Seymour Island, Antarctica). Both specimens provide a unique opportunity to expand our knowledge of the axial skeleton in basal Sphenisciformes.

## Geological setting

Seymour (Marambio) Island is located in the Weddell Sea, within the James Ross Basin, a back-arc feature that developed east of a magmatic arc of the Antarctic Peninsula (Fig. 1; e.g., Porębski 2000). The siliciclastic sedimentary rocks of the Eocene–?early Oligocene La Meseta Formation crop out in the north-eastern part of the island (Fig. 1). These uplifted nearshore, estuarine and deltaic, mostly poorly consolidated, sediments are very fossiliferous, and have yielded a diverse marine and terrestrial fauna (including numerous penguins) and flora (Porębski 2000; Myrcha et al. 2002; Marensi 2006; Tatur et al. 2011; Reguero et al. 2013, references therein). A number of studies revealed that the sediments had come from the west–north-west, hence the source rocks must have been located within the nearby northern Antarctic Peninsula (Reguero et al. 2013, references therein). The recent micromorphological investigation of quartz sand grains (Kirshner & Anderson 2011) supports the dominant view that the La Meseta Formation is devoid of any evidence of glaciation. Hence, it represents the youngest preglacial succession on the Seymour Island (e.g., Marensi et al. 2002).

The base of the uppermost (or the youngest) unit of the La Meseta Formation, Telm7/Submeseta Allomember, was interpreted by Porębski (2000) as a basinward facies shift (supposedly bay-head delta deposits over those interpreted as the estuary mouth) followed by “transgressive reactivation” (alternately: flooding surfaces of transgressive marine origin and shorefaces). According to Marensi (2006), the lower part of Telm7 represents the inner estuary channels/shoals, its upper levels the shallow marine environment. For detailed stratigraphy of this unit, consult Myrcha et al. (2002, figure 2) and Reguero et al. (2013, figure 3.1).

Unit Telm7 of the La Meseta Formation has been traditionally regarded as late Eocene in age (Myrcha et al. 2002; Jadwiszczak 2006; Marensi 2006; Acosta Hospitaleche & Reguero 2010). Some recent works, however, have adopted the view that its lower levels can be dated



**Fig. 1** Map showing the location of Seymour (Marambio) Island, the La Meseta Formation and sampling sites.

to the middle Eocene (Reguero et al. 2013, references therein). The youngest documented ages (34.78–33.57 Mya) from the formation are based on strontium isotope stratigraphy and suggest that up to several of the uppermost metres overlaying the unit Telm7 may be as young as the earliest Oligocene (Ivany et al. 2006). Unfortunately, the GPS coordinates for the sampling locality reported by Ivany et al. (2006) are very inaccurate and do not allow locating the described section (see Marensi et al. 2010).

## Material and methods

The new material reported here is a short fragment of the spinal column of an early penguin from the Eocene–early Oligocene La Meseta Formation (Seymour Island, Antarctic Peninsula). It was found within the uppermost part of the formation, which corresponds to the upper level of the Telm7 unit or Submeseta Allomember (late Eocene), at the so-called “shelves” locality. The locality is situated 300 m west–south-west of the end of the airstrip, ca. 20 m below the top of the plateau in terms of altitude (Fig. 1). The specimen was collected by Andrzej Gaździcki and Andrzej Tatur (Polish Academy of Sciences) in 1992. The “shelves” site is known from numerous fossil penguin bones, *Cucullaea* and *Eurhomalea* bivalves, *Hiatella* gastropods and *Bourchardia* brachiopods as well as rare echinoderms (asteroids and echinoids) and whale remains (Tatur, pers. comm.). This specimen (IB/P/B-0981) is permanently deposited at the Institute of Biology, University of Białystok, Poland, in the collection of the Andrzej Myrcha University Centre of Nature (abbreviated IB/P/B).

Another short segment of the penguin spinal column discussed here was collected in 2008 by Marcelo Reguero (Museo de La Plata [MLP], Argentina) within the lower part of the Telm7 unit/Submeseta Allomember of the La Meseta Formation (Fig. 1). These “thoracic vertebrae still joined” come from the locality DPV 10/84, situated ca. 100 m below the top of the formation, and were accompanied by a number of other bones, including a partial tarsometatarsus and almost complete humerus, belonging in the same skeleton (for more details, including stratigraphy and depositional setting, see Acosta Hospitaleche & Reguero [2010]). The specimen is late Eocene (Acosta Hospitaleche & Reguero 2010) or late middle Eocene (figure 4.5 in Reguero et al. 2013) in age. A single catalogue number (MLP 96-I-6-13) was assigned to the entire partial skeleton, which was attributed by Acosta Hospitaleche & Reguero (2010) to *Palaeudyptes gunnari*. It is housed at the MLP, La Plata, Argentina.

The calculation of the Bayes factor (see Rouder et al. 2009 for a readable introduction), used to validate the taxonomic position of the latter specimen, was based on posterior probabilities obtained by Jadwiszczak & Acosta Hospitaleche (2013, appendix I) and the prior odds for the hypothesis  $H_0$ : *P. gunnari* to  $H_1$ : *P. klekowskii* Myrcha, Tatur & Del Valle, 1990 equal one (not favouring either hypothesis). The factor quantified the evidence of the data for  $H_0$  (not necessarily a “null hypothesis”) vs.  $H_1$ . The strength-of-evidence scale by Kass & Raftery (1995), categorizing the relative success of the hypotheses/models in predicting the data, was utilized. Bayes factors can be also, probably more correctly, interpreted as measures of change in support for  $H_0$  (relative to  $H_1$ ) (Lavine & Schervish 1999).

The comparative material studied directly is represented mainly by bones of both fossil and extant penguins from collection of the Andrzej Myrcha University Centre of Nature. Anatomical nomenclature follows that of Baumel & Witmer (1993). Measurements were taken with digital callipers and rounded to the nearest 0.1 mm.

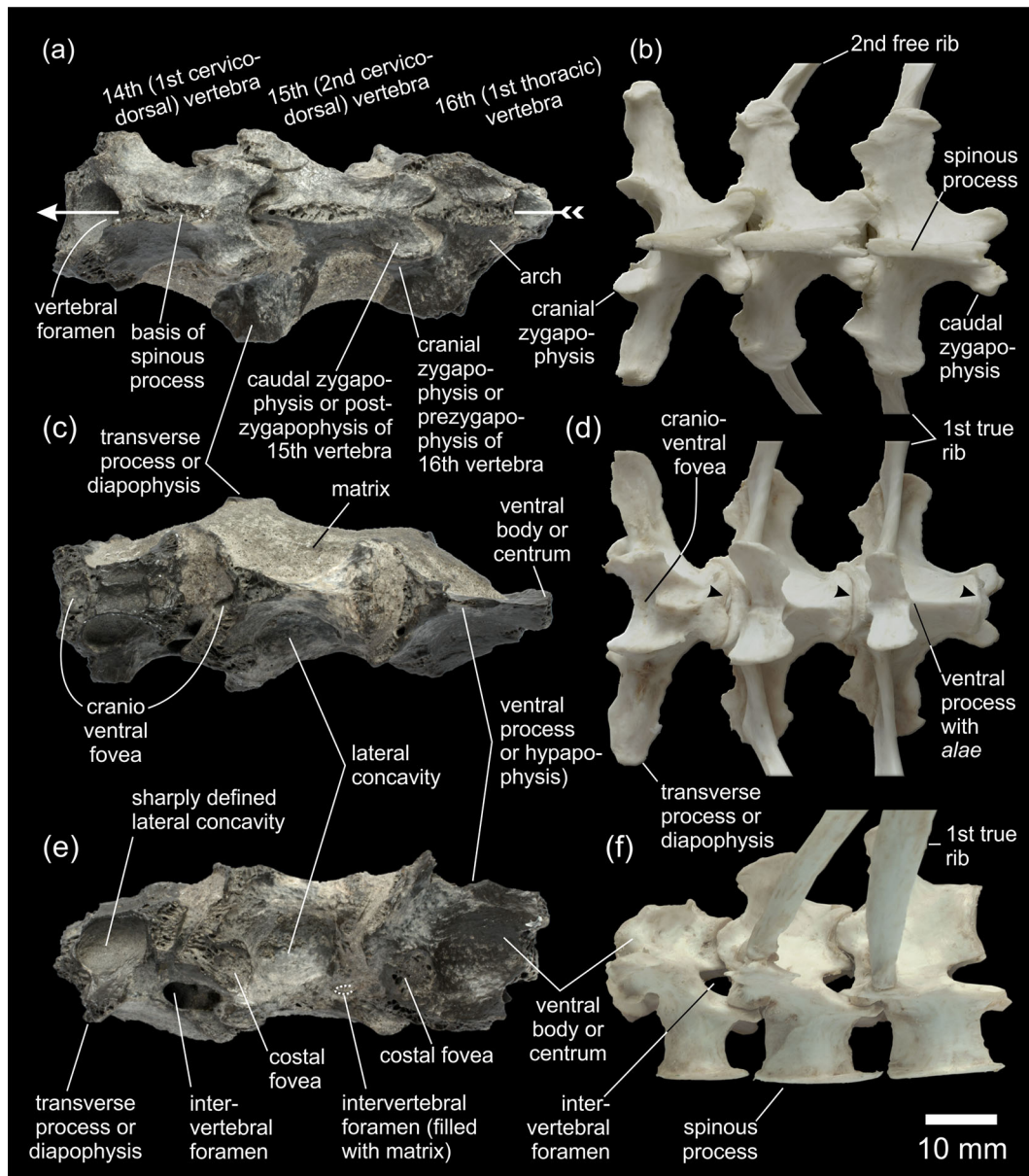
## Results

### New material (specimen IB/P/B-0981)

The segment of the spinal column presented here (Fig. 2a, c, e) is 67.3 mm long and comprises three incomplete vertebrae partly covered by the firmly solidified sedimentary rock (matrix). It probably represents an individual intermediate in size relative to the medium- and large-bodied recent penguins (Fig. 3). Its taxonomic position cannot be determined at present, but the four largest Eocene Antarctic penguins (“giant” sphenisciforms), from the genera *Anthropornis* and *Palaeudyptes*, can be quite safely excluded from considerations.

All articular surfaces preserved remain in immediate contact with matching elements of an adjacent bone (in the case of zygapophyses) or nearly so (the articular surfaces between the centra). In the latter case, there is only a thin layer of the matrix (1–3 mm) that separates both elements. The diameter of the vertebral canal is much larger cranially than caudally. The broken centra of two peripheral bones exhibit no signs of the internal pneumaticity.

The middle bone is clearly more slender (and less convex) than the cranialmost one in dorsal view. As a result, the margin of the vertebral arch between both caudal zygapophyses (*lacuna interzygapophysialis*) of the latter vertebra is wide and U-shaped, whereas its counterpart in the former bone is narrow and rather V-shaped. The interarcual gaps are lacking. The cranial zygapophyses



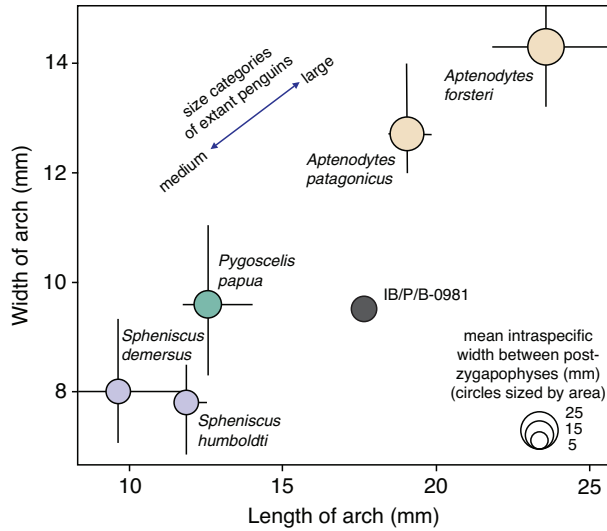
**Fig. 2** (a, c, e) Cervicodorsal region (specimen IB/P/B-0981) of the spinal column of an indeterminate late Eocene penguin from Seymour Island, Antarctic Peninsula and (b, d, f) the present-day gentoo penguin (*Pygoscelis papua*). Short free ribs that articulate with the cranialmost vertebra (in the latter specimen) have been removed. (a–b) Dorsal, (c–d) ventral and (e–f) side (right) view.

of the middle and caudalmost vertebrae are obliquely elevated above the surface of the transverse processes in such a way that articular surfaces are directed at an angle towards the median plane of the body. The respective caudal zygapophyses of the cranialmost and medial bones are quite conspicuously deflected to the sides. All vertebrae analysed here must have possessed the spinous processes as indicated by the elongated scars on dorsal surfaces that coincide with their main axes. In the two cranialmost bones, the scars do not reach the margin of

the vertebral arch. The third bone is lacking the relevant part. The transverse processes of the middle and caudalmost vertebrae are wide proximally.

The ventral surface of the cranialmost bone is wide. The slightly raised lateral margins and a very low quasi-medial crest divide the surface into two elongated and smooth-textured asymmetric parts (the area of the right one is much larger). Anteriorly to them, there is a conspicuous remnant of the presumably well-developed cranioventral fovea. Posteriorly, the aforementioned





**Fig. 3** Size comparison of the 14th (1st cervicodorsal) vertebrae of fossil (specimen IB/P/B-0981) and recent penguins (medians and ranges; Stephan 1979). The latter group is represented by the following species: emperor penguin (*Aptenodytes forsteri*;  $n=4$ ), king penguin (*A. patagonicus*;  $n=3$ ), gentoo penguin (*Pygoscelis papua*;  $n=7$ ), African penguin (*Spheniscus demersus*;  $n=6$ ) and Peruvian penguin (*S. humboldti*;  $n=3$ ).

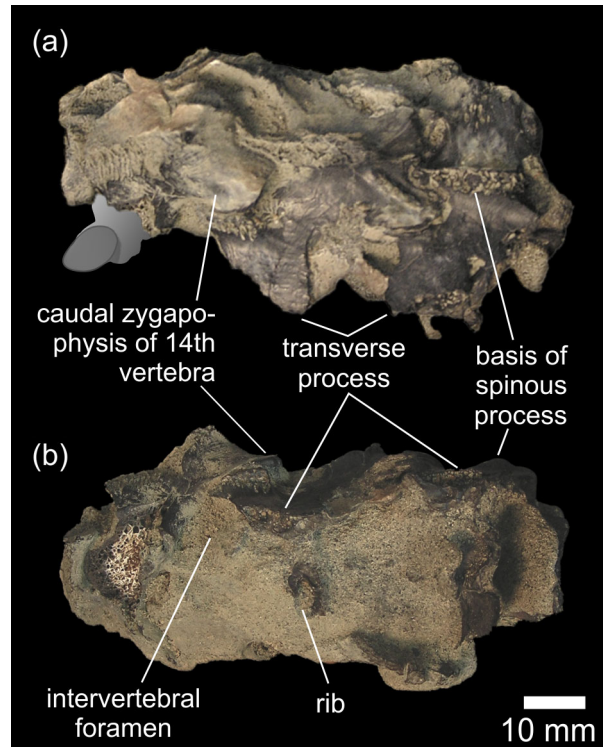
elongated structures adjoin the slightly elevated and rough-textured bony shelf. The ventral margin of the caudal articular surface is very wide and smoothly convex. Its medial part is somewhat depressed dorsally. The middle vertebra, like the cranialmost one, possesses the conspicuous cranioventral fovea and wide and smoothly concave margin of the cranial articular surface. However, its ventral aspect differs from that in the previous bone in being considerably concave laterally and having the ventral process. The process is best pronounced in its anterior half. The caudalmost vertebra is even thinner in ventral view, with the weak lateral concavity. The ventral process is longer cranio-caudally than its counterpart in the preceding bone, whereas the cranioventral fovea appears to be negligible. The ventral margin of the cranial articular surface is smoothly concave.

The side view of the studied segment of the spinal column reveals the probably most striking feature of this specimen, which is a deep and sharply delineated lateral excavation of the centrum of the cranialmost vertebra. The excavation is slightly ovoid in shape and bereft of any foramina. Its surface is unequivocally dull, but it is hard to determine whether this reflects the actual feature or is just an artefact. The surface is polished in both more caudal vertebrae. The lateral concavity of the middle vertebra is quite deep, but unlike in the preceding bone, its margins are not well-defined. The concavity in the caudalmost vertebra is much shallower. Both concavities

appear to be devoid of any foramina. There is a large intervertebral foramen between two cranialmost vertebrae, but that between the medial and caudalmost bones is barely recognizable (and filled by the matrix). In the case of the latter pair of bones, the remnants of the articular facets for the heads of the ribs (i.e., costal foveae) are very easy to notice, whereas the cranialmost vertebra is lacking the relevant part. The lateral margin of the caudal articular surface is clearly concave in both the cranialmost and middle bones and, correspondingly, the matching margins of the posteriorly located articular surfaces are convex. This condition together with that described for the ventral view indicates the presence of the saddle-shaped articular surfaces within two major joints preserved in the analysed specimen.

**Specimen MLP 96-I-6-13 (*Palaeudyptes gunnari*)**

This ca. 85-mm-long segment of the spinal column is made up of three vertebrae, clearly larger than those in IB/P/B-0981, and is mostly covered by the solidified matrix (Fig. 4). Its taxonomic position, determined by Acosta Hospitaleche & Reguero (2010), is plausible at



**Fig. 4** Cervicodorsal region (specimen MLP 96-I-6-13) of the spine column of *Palaeudyptes gunnari*: the large-bodied Eocene penguin from Seymour Island, Antarctic Peninsula. (a) Dorsal and (b) side (left) view. The transverse process in grey is reconstructed based on the original figure by Acosta Hospitaleche & Reguero (2010).

the generic level as indicated by the accompanied bones. The specific identification is very strongly supported by the value of the Bayes factor (0.9971/0.0029 or 343.8), clearly exceeding a threshold value of 150. The damaged fragments of the specimen show no evidence of internal pneumaticity. The cranialmost vertebra most probably lies at an angle to the main axis of the series (in dorsal view). The articular surfaces of the zygapophyses preserved in the cranialmost and middle bones are in contact with the matching surfaces of zygapophyses in the middle and caudalmost vertebrae.

The margin of the vertebral arch between both caudal zygapophyses of the cranialmost vertebra, and the zygapophysis itself, appear to be wider than their counterparts in the following bone. In both cases the margin is U-shaped, and the interarcual gaps are lacking. All cranial zygapophyses are obliquely elevated above the surface of the transverse processes in a way described for IB/P/B-0981. The caudal zygapophyses of the middle bone possess the characteristic elongated crests along their ventral surfaces. The basis of the spinous process is preserved in all three bones, but in the cranialmost one the condition is somewhat obscured due to poor preservation of the relevant fragment of the arch. In the two cranialmost bones, the remnants of the processes do not reach the margin of the vertebral arch. The third vertebra is missing the relevant part. The transverse processes of the middle and caudalmost vertebrae are wide proximally in dorsal view and relatively thin in side view. The relevant process in the cranialmost vertebra is probably clearly thinner in dorsal view, although much broader dorsoventrally, than that in both remaining bones. It is also markedly curved cranially. This condition can be assessed based on the original figure by Acosta Hospitaleche & Reguero (2010, figure 4) and, to some extent, can be also deduced from the fragment presented in Fig. 4a based on a photograph taken by the author in 2012. Moreover, the articular surface of the left cranial zygapophysis seems to be located more distantly from the spinous process than its counterparts in consecutive bones (see figure 4 in Acosta Hospitaleche & Reguero 2010).

The lateral side of the specimen is rather hard to interpret with the exception of the condition of the transverse processes mentioned earlier and the conspicuous proximal part of a broken rib. The rib is ovoid in its cross-section and unequivocally articulates with the middle vertebra. The protruding bony remnant located ventrally to the transverse process of the caudalmost bone presumably represents another vertebra. Moreover, there appears to be the well-developed intervertebral foramen between two cranialmost bones and a slight incomplete

outline of the lateral concavity of the anterior vertebra is recognizable.

## Discussion

The specimens described earlier represent two series made of three articulated vertebrae, hence each of them obviously represent a contiguous segment of the spinal column. According to Baumel & Witmer (1993) and Müller et al. (2010, supporting information), the cervical and thoracic vertebrae in birds can be separated by elements transitional in configuration (cervicodorsal vertebrae; Fig. 2b, d, f). Both penguin fossils discussed here possess such combination of features. These characters are discussed below and allow interpreting each set of bones in terms of two cervicodorsal vertebrae followed by a single thoracic element.

In specimen IB/P/B-0981 (new material), the presence of the heterocoelous (saddle-shaped) condition within two joints preserved is evident. The large and almost complete second cervicodorsal vertebra IB/P/B-0310 (*vertebra cervicodorsale* in Jadwiszczak 2006) is also conspicuously heterocoelous, and this is observed in a number of badly preserved cervicodorsal vertebrae of large stem penguins as well (e.g., IB/P/B-0220). However, the clearly narrow centrum of the broken caudalmost vertebra of IB/P/B-0981 strongly suggests the change in the character of the caudal articular surface and this condition is also evident in a quite well-preserved isolated vertebra IB/P/B-0982 (unpublished material, here identified by me as the first “true” thoracic element). According to Baumel & Witmer (1993), in penguins (also auks and some other birds), the elements of the thoracic series are characterized by the concave caudal articular surfaces (opisthocoelous condition). It is perfectly in line with the observation first made by Owen and confirmed by Watson (see Watson 1882) that the third thoracic bone (which corresponds to the 16th or first “truly” thoracic vertebra in Fig. 2) “shows the opisthocoelous character,” although its cranial surface is still saddle-shaped (Watson 1882; author’s observation). Stephan (1979) was incorrect in stating that the saddle-shaped joint is still present between the third and fourth thoracic vertebrae (i.e., the first and second “truly” thoracic element).

The condition of the ventral processes and adjacent portion of the bone in the analysed specimen provides further evidence of the transitory nature of this segment. The abrupt change in width (and morphological details) between the two cranialmost vertebrae from the wide (typical of the neck) ventral aspect into slender (typical of the thorax) one is conspicuous (see also Watson 1882; Stephan 1979). Such a change in width is also conspicuous

in dorsal view. Moreover, the presence of the cranioventral foveae in both aforementioned elements, and its absence in the caudalmost vertebra is consistent with Stephan's (1979) observation, that some movement of the spine in the median plane between the two cranialmost post-cervical vertebrae is still possible, but more caudally it becomes "virtually impossible." Baumel & Witmer (1993) noted that, during the ventral flexion of the neck, this fovea accommodates the ventral margin of the articular surface of the preceding vertebra. The large area for attachment of the elastic ligaments that prevent instability of the joint, located caudally to the base of the spinous process of the cranialmost vertebra, is indicative of the relative importance of these two vertebrae for the aforementioned mechanism. Obviously, both cranialmost elements of specimen IB/P/B-0981 were active during such a flexion, assisting the caudalmost cervical vertebrae in forming the curvature within the terminal fragment of the neck (see figure 5 in Guinard et al. 2010).

Stephan (1979) determined that vertebrae 14 and 15 in penguins (which correspond to the first and second transitional vertebrae; Fig. 2) are connected with articulated ribs that terminate free. According to the character matrix by Ksepka & Clarke (2010), this is decidedly the most common condition, but in some species transition to free cervicodorsal ribs begins at the 13th (two species) and, in a single taxon, even the 15th vertebra (Bertelli & Giannini 2005). The articular facets for rib attachment in specimen IB/P/B-0981 are preserved in the middle and caudalmost bones, the posterior one being noticeably larger. This presumably reflects the transition between the cervicodorsal and thoracic series (slender and short vs. more robust and much longer ribs).

Baumel & Raikow (1993) noted the presence of the exceptionally large intervertebral foramina in the cervicodorsal segment in birds, and the one between the two cranialmost bones of IB/P/B-0981 is huge indeed. Such a condition is also evident in extant penguins—e.g., king penguin (*Aptenodytes patagonicus* Miller, 1778), Magellanic penguin (*Spheniscus magellanicus* [Forster, 1781]), gentoo penguin (*Pygoscelis papua* [Forster, 1781]); (author's observation)—and is associated with the brachial plexus (see Baumel & Raikow 1993). This explains the relatively large diameter of the cranial portion of the vertebral canal in IB/P/B-0981 in terms of the room for the caudalmost portion of the so-called "cervical enlargement," a swelling of the spinal cord at the level of the wings. Interestingly, a decrease in size of the foramen between the middle and caudalmost vertebrae, relative to its predecessor, appears to be more well pronounced in the fossil specimen than in its recent counterparts.

The remnants of the transverse process in the anterior vertebra of IB/P/B-0981 appear to indicate that it was much broader dorsoventrally than its counterparts in consecutive bones, which is typical of the relevant region in extant penguins (author's observation). The abrupt change in depth and character of the lateral concavities among the two cranialmost elements is also, to a lesser degree, present in the transitional series of some extant penguins (e.g., from the genera *Eudyptes* and *Spheniscus*). Interestingly, the only fossil specimen identifiable as the first transitional vertebra of a "giant" penguin (IB/P/B-0922; *vertebra cervicodorsale* in Jadwiszczak 2006; here I clarify its location) and having the satisfactorily preserved lateral concavity is generally similar to the anterior bone. However, its concavity, though well-developed, is relatively shallower and not so sharply delineated.

In present-day birds, diverticula of the cervical air sacs can extend caudally as far as anterior thoracic series (e.g., Wedel 2005). The conspicuous lateral concavity in IB/P/B-0981 can represent a kind of "bony recess," a blind fossa, that may be occupied by part of such a structure. Some support for this hypothesis is provided by the matte surface of the excavation (assuming this is an actual feature), for this texture may be an external osteological imprint of a pneumatic diverticulum (see also Wedel 2005).

In modern Sphenisciformes, the vertebrae located at the base of the neck become clearly shorter than those from the thoracic region, which is especially well marked in dorsal view (author's observation; see also Shufeldt 1901). This trait together with the increasing oblique elevation of the cranial zygapophyses can be traced in specimen IB/P/B-0981.

Specimen MLP 96-I-6-13 (*Palaeudyptes gunnari*), although less well exposed from the matrix than IB/P/B-0981, also possesses a number of features typical of two craniodorsal and the first thoracic vertebrae in extant Sphenisciformes. The most obvious of such traits are those related to conspicuous differences in width of the arches, caudal zygapophyses and transverse processes, dorsoventral thickness of the last-mentioned structures, and the oblique elevation of the cranial zygapophyses. The presence of the outline of a large intervertebral foramen just caudal to the dorsoventrally thick transverse process together with the remnants of the moderately robust rib located posteriorly also strongly suggests, similarly to the condition in IB/P/B-0981, the actual location of the segment at the root of the neck. The morphology of the caudal fragments of the two cranialmost vertebrae in ventral view suggests probably similar joint mobility relative to that in the series discussed earlier.

## Conclusions

Two specimens discussed here undoubtedly represent the cervicodorsal region of the spinal column of Eocene penguins. In each case, two transitional vertebrae are followed by the first thoracic element, and they are the only such fossils reported from the Palaeogene of Antarctica. Although both of them resemble, in general terms, their counterparts in recent Sphenisciformes (as far as it can be assessed), some features appear to be unique, most notably the sharp delineation of the deep lateral concavity (maybe a pneumatization-related state) and the surprisingly small intervertebral foramen between the two caudalmost vertebrae in specimen IB/P/B-0981. The former feature distinguishes it from at least some fossil “giant” penguins. The condition of the articular surfaces, cranioventral fovea and attachment surfaces for the elastic ligaments located on the dorsal side, suggest that the joint mobility in the median plane appears to be roughly comparable to that in recent species. The early sphenisciform represented by specimen IB/P/B-0981 was probably larger than the extant gentoo penguin, but smaller than the present-day king penguin, and its taxonomic position remains unknown. Another specimen discussed earlier, MLP 96-I-6-13, is clearly larger than IB/P/B-0981, and its assignment to *Palaeudyptes gunnari* (see Acosta Hospitaleche & Reguero 2010) has been strongly supported here. Both fossils provided valuable insights into form and function in early penguins.

## Acknowledgements

I would like to thank Andrzej Gałdzicki, Warsaw, Poland, for transferring specimen IB/P/B-0981 to the collection at the University of Białystok and Andrzej Tatur, Warsaw, for his assistance in determining the position of the collecting site (so-called “shelves”). Marcelo Reguero, La Plata, Argentina, is thanked for inviting me to study the La Plata collection and his helpful suggestions on a submitted typescript of this paper. I am also greatly indebted to Daniel Ksepka, Raleigh, USA, the second reviewer, for his valuable comments and suggestions.

## References

Acosta Hospitaleche C. & Di Carlo U. 2010. The coracoids in functional and morphological studies of penguins (Aves, Spheniscidae) of the Eocene of Antarctica. *Rivista Italiana di Paleontologia e Stratigrafia* 116, 23–34.

Acosta Hospitaleche C. & Reguero M. 2010. First articulated skeleton of *Palaeudyptes gunnari* from the late Eocene of Isla Marambio (Seymour Island), Antarctica. *Antarctic Science* 22, 289–298.

Baumel J.J. & Raikow R.J. 1993. Arthrologia. In J.J. Baumel et al. (eds.): *Handbook of avian anatomy: nomina anatomica avium*. Pp. 133–218. Cambridge, MA: Nuttall Ornithological Club.

Baumel J.J. & Witmer L.M. 1993. Osteologia. In J.J. Baumel et al. (eds.): *Handbook of avian anatomy: nomina anatomica avium*. Pp. 45–132. Cambridge, MA: Nuttall Ornithological Club.

Bertelli S. & Giannini N.P. 2005. A phylogeny of extant penguins (Aves: Sphenisciformes) combining morphology and mitochondrial sequences. *Cladistics* 21, 209–239.

Guinard G. & Marchand D. 2010. Modularity and complete natural homeoses in cervical vertebrae of extant and extinct penguins (Aves: Sphenisciformes). *Evolutionary Biology* 37, 210–226.

Guinard G., Marchand D., Courant F., Gauthier-Clerck M. & Le Bohec C. 2010. Morphology, ontogenesis and mechanics of cervical vertebrae in four species of penguins (Aves: Sphenisciformes). *Polar Biology* 33, 807–822.

Ivany L.C., van Simaey S., Domack E.W. & Samson S.D. 2006. Evidence of an earliest Oligocene ice sheet on the Antarctic Peninsula. *Geology* 34, 377–380.

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

Jadwyszczak P. 2010. New data on the appendicular skeleton and diversity of Eocene Antarctic penguins. In D. Nowakowski (ed.): *Morphology and systematics of fossil vertebrates*. Pp. 44–50. Wrocław: DN Publisher.

Jadwyszczak P. 2012. Partial limb skeleton of a “giant penguin” *Anthropornis* from the Eocene of Antarctic Peninsula. *Polish Polar Research* 33, 259–274.

Jadwyszczak P. & Acosta Hospitaleche C. 2013. Distinguishing between two Antarctic species of Eocene *Palaeudyptes* penguins: a statistical approach using tarsometatarsi. *Polish Polar Research* 34, 237–252.

Jadwyszczak P., Acosta Hospitaleche C. & Reguero M. 2013. Redescription of *Crossvallia unienwillia*—the only Paleocene Antarctic penguin. *Ameghiniana* 50, 545–553.

Jadwyszczak P. & Chapman S.D. 2011. The earliest fossil record of a medium-sized penguin. *Polish Polar Research* 32, 269–277.

Kass R.E. & Raftery A.E. 1995. Bayes factors. *Journal of the American Statistical Association* 90, 773–795.

Kirshner A.E. & Anderson J.B. 2011. Cenozoic glacial history of the northern Antarctic Peninsula: a micromorphological investigation of quartz sand grains. In J.B. Anderson & J.S. Wellner (eds.): *Tectonic, climatic, and cryospheric evolution of the Antarctic Peninsula*. Pp. 153–165. Washington, DC: Geopress.

Ksepka D.T. & Bertelli S. 2006. Fossil penguin (Aves: Sphenisciformes) cranial material from the Eocene of Seymour Island (Antarctica). *Historical Biology* 18, 389–395.

Ksepka D.T. & Clarke J.A. 2010. *The basal penguin (Aves, Sphenisciformes) Perudyptes devriesi and a phylogenetic evaluation of the penguin fossil record*. *Bulletin of the American Museum of Natural History* 337. New York: American Museum of Natural History.



- Lavine M. & Schervish M.J. 1999. Bayes factors: what they are and what they are not. *The American Statistician* 53, 119–122.
- Livezey B.C. & Zusi R.L. 2006. *Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy: I. Methods and characters*. *Bulletin of Carnegie Museum of Natural History* 37. Pittsburgh, PA: Carnegie Museum of Natural History.
- Marensi S.A. 2006. Eustatically controlled sedimentation recorded by Eocene strata of the James Ross Basin, Antarctica. In J.E. Francis et al. (eds.): *Cretaceous–Tertiary high-latitude palaeoenvironments, James Ross Basin, Antarctica*. Pp. 125–133. London: Geological Society.
- Marensi S.A., Casadío S. & Santillana S.N. 2010. Record of late Miocene glacial deposits on Isla Marambio (Seymour Island), Antarctic Peninsula. *Antarctic Science* 22, 193–198.
- Marensi S.A., Net L.I. & Santillana S.N. 2002. Provenance, environmental and paleogeographic controls on sandstone composition in an incised-valley system: the Eocene La Meseta Formation, Seymour Island, Antarctica. *Sedimentary Geology* 150, 301–321.
- Müller J., Scheyer T.M., Head J.J., Barrett P.M., Werneburg I., Ericson P.G.P., Pol D. & Sánchez-Villagra M.R. 2010. The evolution of vertebral numbers in recent and fossil amniotes: the roles of homeotic effects and somitogenesis. *Proceedings of the National Academy of Sciences of the United States of America* 107, 2118–2123.
- Myrcha A., Jadwiszczak P., Tambussi C.P., Noriega J.I., Gaździcki A., Tatur A. & Del Valle R. 2002. Taxonomic revision of Eocene Antarctic penguins based on tarsometatarsal morphology. *Polish Polar Research* 23, 5–46.
- Myrcha A., Tatur A. & Del Valle R. 1990. A new species of fossil penguin from Seymour Island, West Antarctica. *Alcheringa* 14, 195–205.
- Porębski S.J. 2000. Shelf-valley compound fill produced by fault subsidence and eustatic sea-level changes, Eocene La Meseta Formation, Seymour Island, Antarctica. *Geology* 28, 147–150.
- Reguero M., Goin F., Acosta Hospitaleche C., Dutra T. & Marensi S. 2013. *Late Cretaceous/Paleogene West Antarctica terrestrial biota and its intercontinental affinities*. Dordrecht: Springer.
- Rouder J.N., Speckman P.L., Sun D., Morey R.D. & Iverson G. 2009. Bayesian t-tests for accepting and rejecting the null hypothesis. *Psychonomic Bulletin & Review* 16, 225–237.
- Shufeldt R.W. 1901. Osteology of penguins. *Journal of Anatomy and Physiology* 35, 390–404.
- Stephan B. 1979. Vergleichende Osteologie der Pinguine. (Comparative osteology of penguins.) *Mitteilungen aus dem Zoologischen Museum Berlin* 55 (Supplement *Annalen für Ornithologie* 3), 3–98.
- Tambussi C.P., Reguero M., Marensi S.A. & Santillana S.N. 2005. *Crossvallia unienwillia*, a new Spheniscidae (Sphenisciformes, Aves) from the Late Paleocene of Antarctica. *Geobios* 38, 667–675.
- Tatur A., Krajewski K.P. & Del Valle R.A. 2011. The facies and biota of the oldest exposed strata of the Eocene La Meseta Formation (Seymour Island, Antarctica). *Geological Quarterly* 55, 345–360.
- Watson M. 1882. *Report on the anatomy of the Spheniscidae collected during the voyage of HMS Challenger. On the scientific results of the Challenger Expedition during the years 1872–1876*. *Zoology* 7. Edinburgh: Neill & Co.
- Wedel M.J. 2005. Postcranial skeletal pneumaticity in sauropods and its implications for mass estimates. In K.A. Curry Rogers & J.A. Wilson (eds.): *The sauropods: evolution and biology*. Pp. 201–228. Berkeley, CA: University of California Press.
- Wiman C. 1905. Über die alttertiären Vertebraten der Seymourinsel. (On the lower Tertiary vertebrates of Seymour Island.) *Wissenschaftliche Ergebnisse der Schwedischen Südpolar Expedition 1901–1903* 3, 1–37.