

# A small whale reveals diversity of the Eocene cetacean fauna of Antarctica

SVITOZAR DAVYDENKO <sup>1</sup>, THOMAS MÖRS <sup>2,\*</sup> and PAVEL GOL'DIN <sup>1</sup>

<sup>1</sup>*Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, 15 Bogdan Khmelnytskyi Street, 01030, Kiev, Ukraine*

<sup>2</sup>*Department of Palaeobiology, Swedish Museum of Natural History, PO Box 50007, SE-104 05 Stockholm, Sweden*

\*corresponding author: [thomas.moers@nrm.se](mailto:thomas.moers@nrm.se)

**Abstract:** Cetacean fossils have been recorded from middle and late Eocene deposits on Seymour Island since the beginning of the twentieth century and include fully aquatic Basilosauridae and stem Neoceti. Here, we report a small cetacean vertebra tentatively referred to as Neoceti from the late Eocene of Seymour Island. It shows a mosaic of traits, some of which are characteristic of early Neoceti (anteroposteriorly long transverse processes; a ventral keel on the ventral side of the centrum; thin pedicles of the neural arch), whereas others are shared with Basilosauridae (low-placed bases of the transverse processes). However, some traits are unique and may be autapomorphic: presence of separate prezygapophyses on the vertebra at the thoracic/lumbar boundary and a proportionally short centrum. Both traits imply a fast swimming style, which is characteristic of modern dolphins rather than Eocene cetaceans. Thus, this specimen can be identified as Neoceti indet., with some hypothetical odontocete affinities. Along with a few other Eocene whale taxa, it seems to be among the earliest known members of Neoceti on Earth. The finding of small and fast-swimming Neoceti in Antarctica also demonstrates early diversification of cetaceans and ecological niche partitioning by them dating back as early as the late Eocene.

Received 17 June 2020, accepted 7 September 2020

**Key words:** divergence, evolution, morphology, Neoceti, Priabonian, Seymour Island

## Introduction

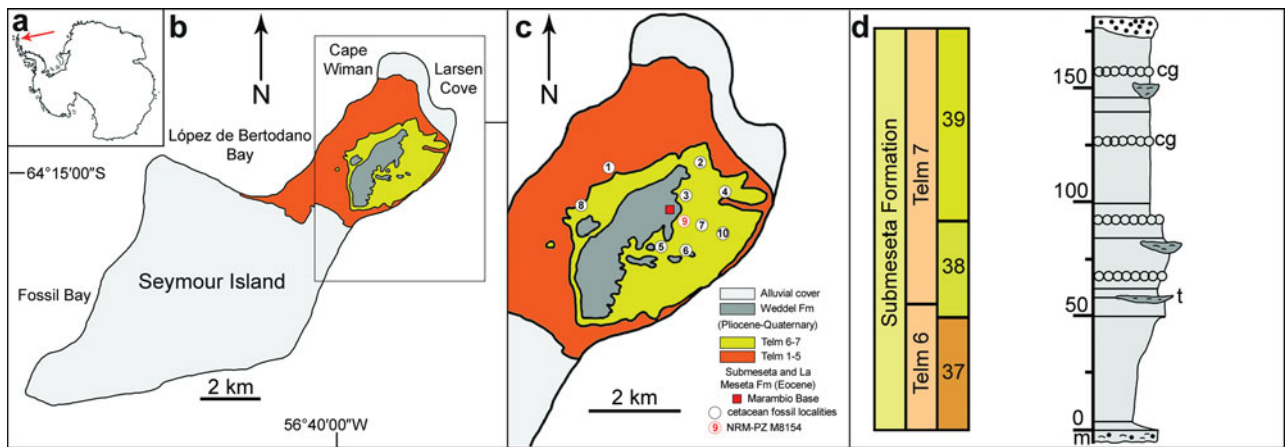
Seymour Island is rich in late Cretaceous and Palaeogene fossil records of terrestrial and aquatic tetrapods (Reguero 2019, Mörs *et al.* 2020). Palaeogene, secondarily aquatic tetrapods are represented by penguins (Jadwiszczak & Mörs 2017) and cetaceans, with all of the cetacean records coming from the La Meseta and Submeseta formations. Cetacean remains have been recorded from Seymour Island since the beginning of the twentieth century, when Wiman (1905) described two cetacean caudal vertebrae as *Zeuglodon* sp. (Fig. 1c). Eighty years later, vertebrae and sternum remains were described by Borsuk-Bialynicka (1988). Fordyce (1989) and Buono *et al.* (2016, 2019) reported isolated teeth, mandibles, vertebrae and ribs of Eocene whales and referred to them as Basilosauridae (the earliest fully aquatic cetaceans) or Cetacea indet. The toothed mysticete *Llanocetus denticrenatus* (Mitchell 1989, Fordyce & Marx 2018) has been found in the late Eocene Submeseta Formation of Seymour Island. It represents Neoceti, the crown group of cetaceans that includes baleen whales (Mysticeti) and toothed whales (Odontoceti). Another giant specimen of *Llanocetus* sp.

is known from its isolated teeth (Marx *et al.* 2019). In addition, a right innominate bone resembling that of another early mysticete, *Mystacodon selenensis* (Muizon *et al.* 2019), was found in the same formation (Buono *et al.* 2019). Therefore, all of the cetaceans known from Seymour Island are referred to as fully aquatic cetaceans (Pelagiceti, a group pooling together Basilosauridae and Neoceti).

Here, we report a small cetacean vertebra tentatively referred to as Neoceti from the late Eocene of Seymour Island and compare it with other early whale taxa.

## Geological setting and palaeoenvironmental context

The Submeseta Formation is located on Seymour Island, 100 km east of the Antarctic Peninsula, within the James Ross Basin (Fig. 1a & b). The formation and the underlying La Meseta Formation consist of a succession of sedimentary marine beds of sandstone, siltstone and shell, which are divided into seven lithofacies units referred to as 'Tertiary Eocene La Meseta' stratigraphic units (TELMs), representing the 720 m-thick fill of a 7 km-wide incised valley system (Sadler 1988, Marenssi *et al.* 2002). The two Eocene formations form together



**Fig. 1.** Location of Seymour Island (Antarctica) and the stratigraphy of its north-eastern part. **a.** Map of Antarctica showing the position of Seymour Island. **b.** Map of Seymour Island showing the location of the Eocene La Meseta and Submeseta formations. **c.** NRM-PZ M8154 and the main localities of cetacean fossils of the Submeseta and La Meseta formations. **d.** Simplified stratigraphic column of the Submeseta Formation based on data from Montes *et al.* (2013). 1) *Basilosauridae* indet., MLP 11-II-21-3 (Buono *et al.* 2019), 2) *Basilosauridae* indet., MLP 13-I-25-10, ?*Basilosauridae* indet., MLP 13-I-25-11 (Buono *et al.* 2019), 3) *Llanocetus* sp., IAA-PV-731 (Marx *et al.* 2019), 4) *Llanocetus* sp., MLP 12-XI-1-10 (Buono *et al.* 2019), 5) *Llanocetus denticrenatus*, USNM 183022 (Mitchell 1989, Fordyce & Marx 2018), 6) *Mysticeti* indet., MLP 84-II-1-568, *Cetacea* indet., MLP 82-IV-23-69 (Buono *et al.* 2019), 7) ?*Basilosauridae*, MLP 83-V-20-386, *Cetacea* indet., MLP 83-V-20-80 (Buono *et al.* 2019), 8) *Cetacea* indet., ZPAL M-VII/1 (Borsuk-Bialynicka 1988), 9) *Neoceti* indet., NRM-PZ M8154 (this study), 10) *Cetacea* indet., NRM-PZ M5655 (Wiman 1905). cg = conglomerates and sandstones, t = *Turritella* (a gastropod).

with the underlying middle-upper Palaeocene Cross Valley Formation of the Seymour Island Group, which rests on top of the upper Cretaceous-lower Palaeocene Marambio Group (Sadler 1988, Montes *et al.* 2013). Both formations have undergone minimal burial and diagenetic alterations (Marenssi *et al.* 2002). Ages based on  $^{87}\text{Sr}/^{86}\text{Sr}$  chemostratigraphy from bivalve carbonates indicate that the Submeseta Formation is bound with TELM 6, being *c.* 41 Ma or younger, and the top of TELM 7 lying at the Eocene/Oligocene boundary (Douglas *et al.* 2014).

The sedimentary facies of TELM 7 is shallow marine with inner estuary channels according to Marenssi *et al.* (2002). Mean sea-surface temperatures for TELM 7 range from  $\sim 11.3^\circ\text{C}$  to  $14.1^\circ\text{C}$  (Douglas *et al.* 2014). In strong contrast to the La Meseta Formation, chondrichthyan fishes are very rare in TELM 7, but gadiform bony fishes are quite abundant (e.g. Kriwet *et al.* 2016, Jadwiczak & Mörs 2017). Penguins are diverse and abundant in TELM 7 (e.g. Wiman 1905, Acosta Hospitaleche *et al.* 2017, Jadwiczak & Mörs 2017). Similarly to penguins, whales are also diverse and abundant in TELM 7 (e.g. Wiman 1905, Buono *et al.* 2016, 2019), and *Neoceti* are known exclusively from TELM 7 (Mitchell 1989, Buono *et al.* 2016, Fordyce & Marx 2018, Marx *et al.* 2019).

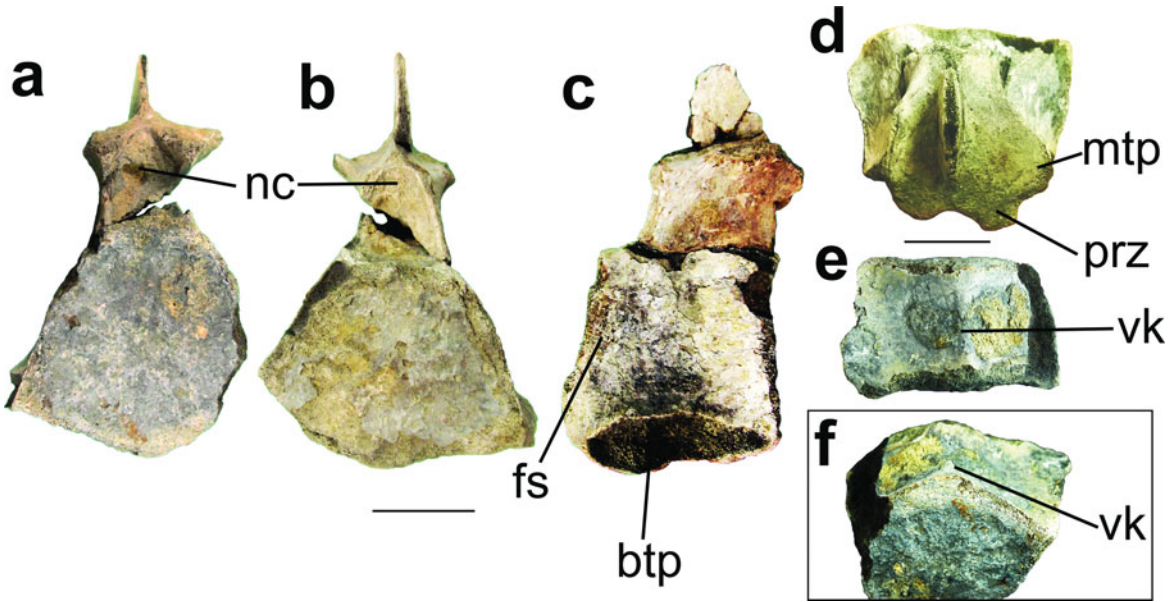
## Materials and methods

Specimen NRM-PZ M8154 is a single torso vertebra. The specimen described here was collected by TM in January

2012 at  $64^\circ 14' 39.42''\text{S}$ ,  $56^\circ 36' 52.62''\text{W}$  in a gully on the slope below and south-east of the Argentinian Marambio Base (Locality 9 in Fig. 1c). Here, marine sediments of the Submeseta Formation (Montes *et al.* 2013), or TELM 7 according to Sadler (1988), are exposed (Fig. 1c). Because the vertebra was not found *in situ*, it is unclear whether its provenance is level 38 or 39 of the Submeseta Formation (Fig. 1d). There is agreement on this part of the depositional succession on Seymour Island being late Eocene (Priabonian) in age (e.g. Douglas *et al.* 2014, Buono *et al.* 2016, Kriwet *et al.* 2016). The specimen is housed in the palaeozoological collections of the Swedish Museum of Natural History, Stockholm.

Measurements were taken point to point on the anterior side of the specimen if not specially mentioned. Anatomical terminology follows Uhen (2004). The anatomical abbreviations used in these measurements are as follows: H = centrum height and L = centrum length.

Analysis of the geometric morphometry of the anterior surface of the centra of the anterior lumbar vertebrae was conducted for the specimen under study and those of an additional 20 cetacean taxa, including 2 members of *Protocetidae*, 8 members of *Basilosauridae* and 10 members of *Neoceti* (4 mysticetes and 6 odontocetes). For *M. selenensis*, the only available posterior thoracic vertebra was used for the analysis. Ten landmarks were identified in all analysed specimens and digitized using *TpsDig* software (Supplemental Fig. S3). After the

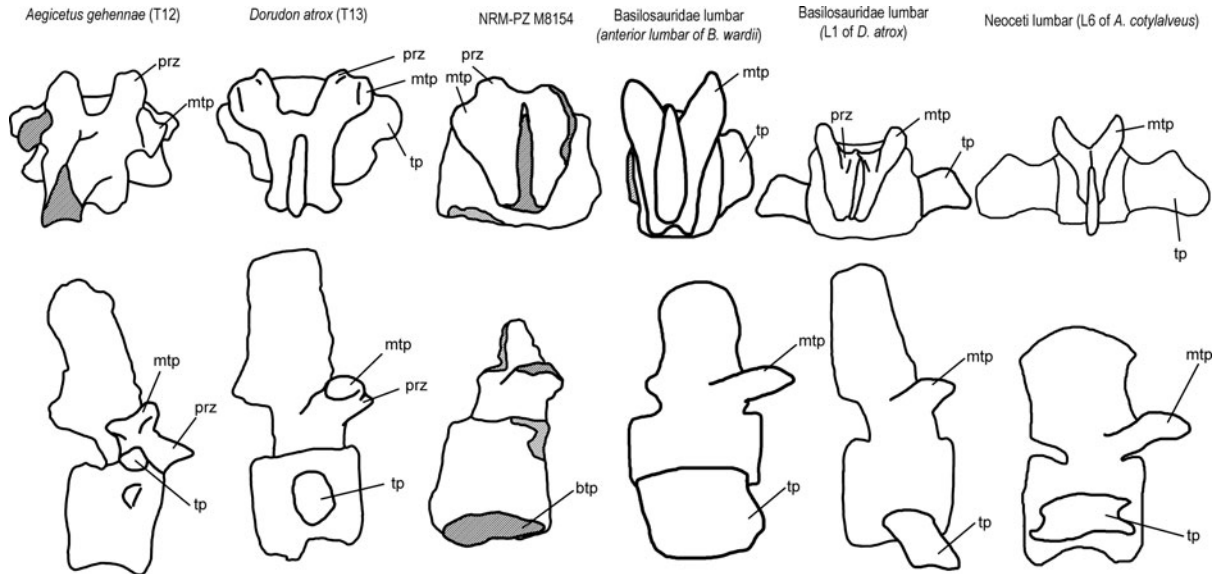


**Fig. 2.** Incomplete lumbar vertebra NRM-PZ M8154. **a.** Anterior, **b.** posterior, **c.** right lateral, **d.** dorsal, **e.** ventral and **f.** anteroventral views. btp = base of transverse process, fs = fusion suture, mtp = metapophysis, nc = neural channel, prz = prezygapophysis, vk = ventral keel. Scale: 50 mm.

Procrustes superimposition, principal component analysis of the symmetrical component of the shape was performed on the covariance matrix using *MorphoJ* v. 1.07a (Klingenberg 2011).

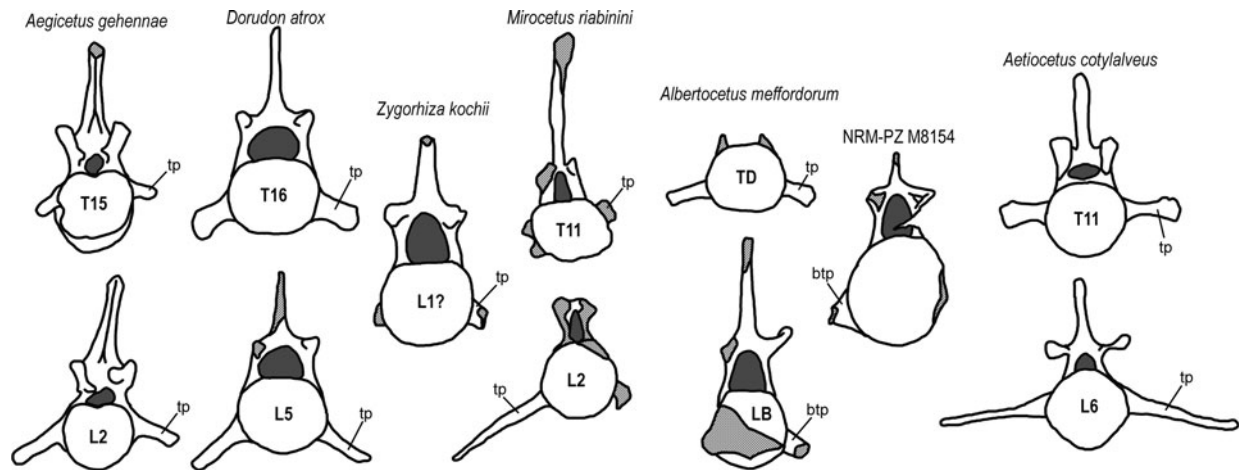
The institutional abbreviations used in these analyses are as follows: GMTSNUK = Geological Museum of Taras Shevchenko National University of Kiev, Ukraine;

MLP = Museo de La Plata, Argentina; MNHN = Muséum national d'Histoire naturelle, Paris, France; MUSM = Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; NRM = Swedish Museum of Natural History, Stockholm, Sweden; and ZPAL = Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.



**Fig. 3.** Comparison of the neural arch and transverse process anatomy of NRM-PZ M8154 and other cetaceans (schematic drawing) from the dorsal (top row) and right lateral (bottom row) views. btp = base of transverse process, mtp = metapophysis, prz = prezygapophysis, tp = transverse process. Not to scale.





**Fig. 4.** Comparison of the neural canal (grey shaded) and transverse process anatomy of NRM-PZ M8154 and other cetaceans (schematic drawing) from the anterior view. btp = base of transverse process, tp = transverse process. Not to scale.

## Results

Specimen NRM-PZ M8154 is shown in (Fig. 2). This new specimen represents a single vertebra of an adult cetacean close to physical maturation. It is tentatively identified as the posterior-most thoracic or anterior-most lumbar vertebra due to the large and triangular neural canal (Fig. 2a & b) and low, wide bases of transverse processes (Fig. 2c). The anterior and posterior articular surfaces of the centrum are roughly trapezoid and the lateral surfaces of the centrum are slightly transversely concave. In lateral view, the centrum is rectangular, and a ventral keel is seen on its ventral surface (Fig. 2e). The neural arch is best preserved near the anterior surface of the vertebra. The anteriorly directed prezygapophyses are short and robust. A laterally directed left metapophysis is preserved on the left lateral surface of the neural arch; it is slightly longer and thinner than the prezygapophysis (Fig. 2d). Transverse processes are attached to the ventral part of the centrum, with the bases situated approximately at the level of a quarter of the centrum height. The base of the right transverse process is relatively well preserved. It is anteroposteriorly elongated, being almost as long as the centrum. There is no significant cortical bone on the vertebral surface, and the whole centrum is composed of tight spongy bone, as is seen from natural fractures. Both epiphyses are completely fused to the centrum, and the fusion suture of the posterior epiphysis is only poorly visible on the right lateral surface of the centrum (Fig. 2c). The length of centrum is 62 mm and its width at its anterior end is 78 mm. The heights of centrum at its anterior and posterior ends are 78 and 76 mm, respectively. The total height of the vertebra (with the preserved part of the neural arch) is 161 mm.

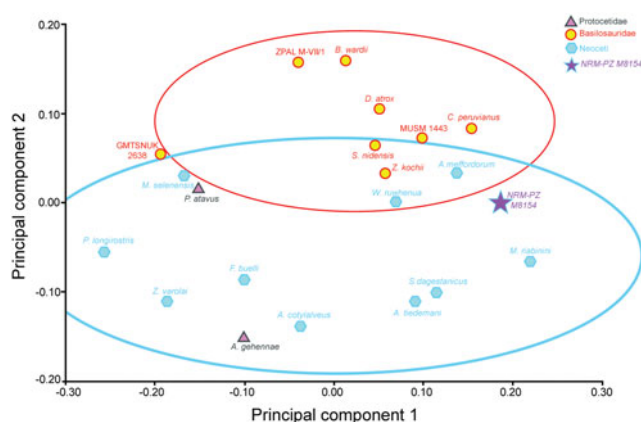
## Comparison

NRM-PZ M8154 is distinct among early extinct cetaceans with known posterior-most thoracic or anterior-most lumbar vertebrae (Supplemental Table SI) by the presence of relatively large, separate and anteriorly directed prezygapophyses (Fig. 3). Such an anatomy can be seen in the mid-posterior thoracic vertebrae of Protocetidae (anterior to T12 in *Aegicetus gehennae*, with the total count of thoracics as 15 (Gingerich *et al.* 2019)) and Basilosauridae (anterior to T13 of 17 thoracics in *Dorudon atrox* (Uhen 2004) and to T14 of 20 thoracics in *Cynthiacetus peruvianus* (Martínez-Cáceres *et al.* 2017)). However, all such vertebrae, unlike NRM-PZ M8154, also have anteroposteriorly and proximodistally short, highly placed bases of transverse processes. Unlike NRM-PZ M8154, protocetids have the centra constricted in the middle part and with highly placed bases of transverse processes in all posterior thoracic and anterior lumbar vertebra (Hulbert 1998, Gingerich *et al.* 2019). By contrast, the posterior-most thoracic vertebrae of basilosaurids bear relatively low-placed bases of transverse processes, as in NRM-PZ M8154 (Figs 3 & 4); however, their prezygapophyses are reduced as concave facets that are far smaller than metapophyses, and the neural canal is semi-circular (rather than triangular, as in NRM-PZ M8154). The triangular neural canal is typical of the lumbar vertebrae of many cetaceans (as well as the low-placed bases of the transverse processes) (Fig. 4), which, however, have only rudimentary prezygapophyses capped by metapophyses. Therefore, NRM-PZ M8154 may be identified either as the posterior-most thoracic vertebra with an unusually large neural canal or an anterior lumbar vertebra.

However, the presence of large prezygapophyses in the vertebral column is unique for both interpretations.

Furthermore, NRM-PZ M8154 differs in its anatomy and proportions from all known lumbar vertebrae of Eocene cetaceans. Its centrum is similar in proportions to protocetids (Hulbert 1998, Gingerich *et al.* 2019); however, it greatly differs from those in its derived, rectangular shape in lateral view, presence of the ventral keel and long transverse processes. Its centrum is slightly shorter and higher than the anterior lumbar vertebrae of *D. atrox* (Uhen 2004). The overall shape of the centrum resembles the lumbar vertebrae of *C. peruvianus* (Martínez-Cáceres *et al.* 2017) and *Stromerius nidensis* (Gingerich 2007), but these whales differ from NRM-PZ M8154 in body size (*C. peruvianus* is far larger and *S. nidensis* is slightly smaller). The centrum length/height ratio in NRM-PZ M8154 is 0.79, whereas in Basilosauridae it varies from 0.93 to 1.12 (*D. atrox*, 0.94 (L1), *Zygorhiza kochii*, 0.93 (L1) (Kellogg 1936), *C. peruvianus*, 1.02 (L1), *S. nidensis*, 1.12 (L2)). The neural canals of the lumbar vertebrae of *D. atrox* and *C. peruvianus* are oval, whereas those of *Z. kochii* and *S. nidensis* are triangular and similar to NRM-PZ M8154 (Fig. 4). The anteroposteriorly long transverse processes of NRM-PZ M8154 somewhat resemble those of *Basilotritus* spp. (Gol'din & Zvonok 2013) or *Pachycetus* spp. (Vliet *et al.* 2020) and MUSM 1443 (Uhen *et al.* 2011), a group of taxa that are similar in vertebral morphology. However, *Basilotritus*, *Pachycetus* and MUSM 1443, unlike NRM-PZ M8154, have elongated centra and pachyosteosclerotic cortex. Another Eocene cetacean from Ukraine, GMTSNUK 2638, shares long transverse processes (as well as bone histology) with NRM-PZ M8154, but it is larger and it has elongated centra (Gol'din & Zvonok 2013). The lumbar vertebrae of the Eocene mysticete *M. selenensis* (de Muizon *et al.* 2019) are unknown; however, its elongated posterior thoracic vertebrae (L/H ratio of ?T14 is 1.15) show that its posterior-lying vertebrae could be even longer than those of NRM-PZ M8154. Another fossil whale vertebra from Seymour Island, ZPAL M-VII/1, described by Borsuk-Bialynicka (1988), has similarly elongated transverse processes. However, it is larger than NRM-PZ M8154, and its centrum is proportionally longer. Finally, NRM-PZ M8154 lacks two vascular foramina separated by a bony septum, which are present on the ventral side of the lumbar vertebrae in all of the basilosaurids mentioned here.

A few derived traits are shared by NRM-PZ M8154 and Neoceti. First, anteroposteriorly long, transverse processes are common within Neoceti; they are particularly long in mysticetes (Fig. 3). Second, there is a distinct ventral keel on the centrum of NRM-PZ M8154 (Fig. 2): such a keel is observed in many extinct and extant Neoceti species (Emlong 1966, Buchholtz 2011)

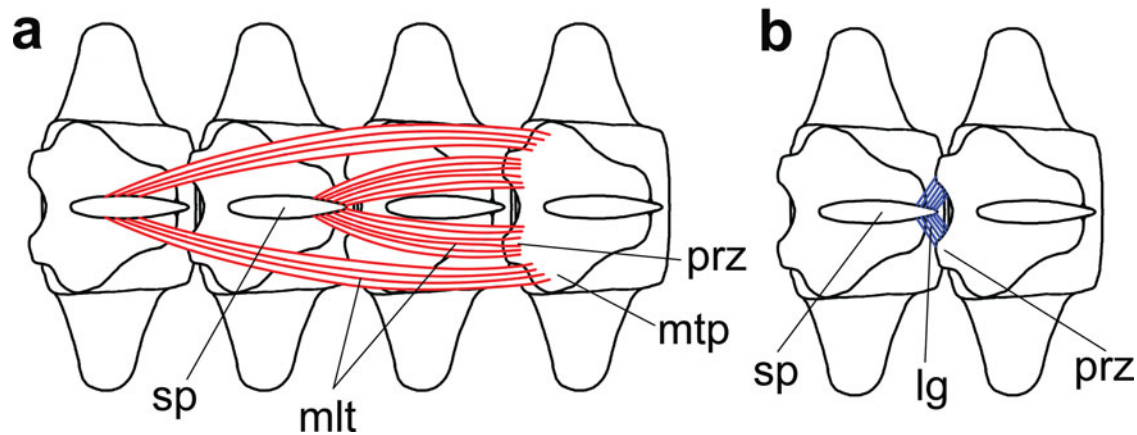


**Fig. 5.** Variation in vertebral centrum shape among cetaceans compared with NRM-PZ M8154, principal component 1 vs principal component 2; 90% confidence intervals for Basilosauridae and Neoceti are shown with ellipses.

and some protocetids (Gingerich *et al.* 2019), but not in basilosaurids (Uhen 2004, Martínez-Cáceres *et al.* 2017). Compared with Oligocene cetaceans, NRM-PZ M8154 is similar to the early odontocetes *Mirocetus riabinini*, *Albertocetus meffordorum* (Boessenecker *et al.* 2017) and *Ankylorhiza tiedemani* (Boessenecker *et al.* 2020) in the triangular shape of the neural canal (Fig. 4). However, all of these odontocetes have proportionally longer vertebrae than NRM-PZ M8154: their L/H ratios are 1.07 (L1) and 1.34 (LA), respectively. In addition, the bases of their transverse processes are higher placed than in NRM-PZ M8154. Furthermore, these odontocetes share relatively thin pedicles of the neural arch with NRM-PZ M8154. This state differs from the Oligocene mysticetes *Aetiocetus cotylalveus* (Emlong 1966) and *Fucaia buelli* (Marx *et al.* 2015), which have similar neural canals but more robust pedicles.

The similarity of NRM-PZ M8154 and Neoceti is supported by the principal component analysis of its geometric morphometry traits. In the shape of the vertebra, NRM-PZ M8154 is pooled together with Neoceti (rather than Basilosauridae) in the morphospace of the first two principal components. It is found to be the most similar to the Oligocene odontocetes *M. riabinini* and *A. meffordorum* (Fig. 5).

Finally, NRM-PZ M8154 has another unusual derived trait. Its L/H ratio is different from whales with Pattern 1 of cetacean vertebral anatomy, which is typical of Mysticeti and early Odontoceti (Buchholtz 2001, 2007). It is more similar to Pattern 3 of cetacean vertebral anatomy, which is usual for Neogene and modern Delphinida (e.g. the Miocene phocoenid *Piscolithax longirostris* (de Muizon 1984) has an L/H ratio of 0.68 (MNHN SAS 957, anterior lumbar vertebra) and many modern delphinids (Buchholtz 2001, Gillet *et al.* 2019).



**Fig. 6.** Functional interpretations of the morphology of the NRM-PZ M8154 neural arch, as seen from the dorsal view.

**a.** Prezygapophyses and metapophyses as reinforced places of insertion of multifidus muscles. **b.** Prezygapophyses as bases for interspinous ligaments. lg = ligament, mlt = multifidus muscle, mtp = metapophysis, prz = prezygapophysis, sp = spinal process.

In conclusion, NRM-PZ M8154 shows a mosaic of traits, some of which are derived and characteristic of early Neoceti (anteroposteriorly long transverse processes, a ventral keel on the ventral side of the centrum and thin pedicles of the neural arch), whereas others are shared with Basilosauridae (low-placed bases of the transverse processes) or Pelagiceti at most or in general (a rectangular centrum from the lateral view and a triangular neural canal), and some traits are unique and can be autapomorphic (presence of relatively large, separate, anteriorly directed prezygapophyses on the posterior-most thoracic or anterior-most lumbar vertebra and a proportionally short centrum, L/H ratio = 0.79). Thus, NRM-PZ M8154 can be identified as Neoceti indet., with some hypothetical odontocete affinities. Along with *Mystacodon*, *Llanocetus* and undescribed specimens (Buono *et al.* 2019), it seems to be one of the earliest known members of Neoceti on Earth.

## Discussion

### Body size

There is evidence of the existence of gigantic Neoceti in the late Eocene (Priabonian) in Antarctica: *L. denticrenatus* (9 m long) (Fordyce & Marx 2018) and *Llanocetus* sp. (12 m long) (Marx *et al.* 2019). The specimen described here is smaller: it is impossible to estimate the size of NRM-PZ M8154 due to its incompleteness and unusual vertebral proportions. However, as can be seen from the height and width of the centrum, it is comparable in size to *D. atrox* (~5 m) or *M. selenensis* (~4 m). Therefore, this is the evidence for coexisting small and large members of Neoceti in the late Eocene of Antarctica.

Importantly, among the undetermined late Eocene cetaceans reported from Seymour Island, there is a skull fragment of a small cetacean (MLP 83-V-20-386)

containing the skull vertex and the supraorbital process of the frontal bone (Buono *et al.* 2019: fig. 5a & b). Its anterolaterally directed supraorbital process with a rounded lateral margin and a distinct notch at the orbit resembles the anatomy of Eocene mysticetes (Fordyce & Marx 2018, de Muizon *et al.* 2019), whereas the trace on its dorsal surface can be hypothetically explained as a trace of the overlying maxilla (although this is somewhat speculative), making it similar to odontocetes. Therefore, its plausible interpretation is as Neoceti indet. The vertebra described here could belong to the same or a similar taxon as MLP 83-V-20-386. In addition, the innominate bone MLP 84-II-1-568 is notably small, and it could belong to a small mysticete similar to *M. selenensis* in size. Thus, the diversity of Neoceti from the late Eocene of Seymour Island could comprise at least three or even five taxa, including mysticetes and forms with some odontocete affinities.

### Functional morphology

The unusual anatomy of the prezygapophyses of NRM-PZ M8154 can be related to their functional morphology. They extend beyond the anterior margin of the centrum but are too short for articulation with the postzygapophyses of anterior-lying vertebra. Uhen (2004) suggests that large metapophyses of the thoracic, lumbar and anterior caudal vertebrae of the archaeocete *D. atrox* were insertion points for multifidus muscles. This suggestion is probably applicable to other early Pelagiceti that retain well-developed metapophyses. In this case, the long prezygapophyses of NRM-PZ M8154 could serve as reinforced places of insertion of multifidus muscles (Fig. 6a). In modern cetaceans, multifidus muscles provide a stiff platform for the longissimus muscle, which provides force to the caudal



spine (Berta *et al.* 2006). Another interpretation of such a morphology is for providing a base for interspinous ligaments (Fig. 6b) between the lateral surfaces of the neural spine of cranial vertebra and the medial surfaces of the articular processes of caudal vertebra (Long Jr *et al.* 1997).

Both functional interpretations of the prezygapophyses, as well as the short and high centrum, imply an increase of stiffness of the torso (Buchholtz 2001). This is evidence of a tail-driven lift-based high-speed locomotion style with a rigid torso and high-amplitude oscillations of the caudal region. Such a locomotion style is common for modern odontocetes but is unusual for early Pelagiceti (Fish 1996, Buchholtz 2001). However, any detailed and robust conclusions regarding NRM-PZ M8154 swimming mode, morphology and phylogenetic relations require more complete specimens.

#### *Initial divergence of Neoceti in Antarctica*

Fordyce (1989) suggested Antarctica as a region where Neoceti initially evolved into mysticetes and odontocetes in response to increasing isolation and cooling of Antarctica at the Eocene-Oligocene boundary. In fact, the discovery of late Eocene gigantic mysticetes *Llanocetus* spp. strongly supports the idea of Antarctic waters as an important region for the early evolution of Neoceti. The finding of small and fast-swimming Neoceti specimens different from *Llanocetus*, including NRM-PZ M8154, shows the early divergence and diversification of cetaceans and ecological niche partitioning by them dating back as early as the late Eocene in Antarctica.

#### Supplemental material

Three supplemental figures and two supplemental tables will be found at <https://doi.org/10.1017/S0954102020000516>.

#### Acknowledgements

TM is very thankful to the Argentine Antarctic Institute (IAA-DNA), especially M. Reguero and the Argentine Air Force for logistical support and for the hospitality at the Marambio Base, to the Swedish Polar Research Secretariat (SPFS) for logistical support and to J. Moly and J. O'Gorman for assistance in the field. The authors sincerely thank Mark D. Uhen for comments on an early draft of the paper and for providing photographs of the lumbar vertebrae of *Basilotritus wardii*, which were important for comparison. The authors also thank Yoshihiro Tanaka for additional comments on an early draft of the paper.

#### Author contributions

TM performed the fieldwork and photographed the specimen. SD and PG analysed the material. All authors

discussed the results, wrote the manuscript, provided illustrations and agreed upon the final version of the manuscript.

#### Financial support

Financial support from the Swedish Research Council (VR Grant 2009-4447) to TM is gratefully acknowledged.

#### References

- ACOSTA HOSPITALECHE, C., HAGSTRÖM, J., REGUERO, M. & MÖRS, T. 2017. Historical perspective of Otto Nordenskjöld's Antarctic fossil penguin collection and Carl Wiman's contribution. *Polar Record*, **53**, 10.1017/S0032247417000249.
- BERTA, A., SUMICH, J.L. & KOVACS, K.M. 2006. *Marine mammals: evolutionary biology*. Cambridge, MA: Academic Press, 738 pp.
- BOESSENECKER, R.W., AHMED, E. & GEISLER, J.H. 2017. New records of the dolphin *Albertocetus meffordorum* (Odontoceti: Xenorophidae) from the lower Oligocene of South Carolina: encephalization, sensory anatomy, postcranial morphology, and ontogeny of early odontocetes. *PLoS One*, **12**, 10.1371/journal.pone.0186476.
- BOESSENECKER, R.W., CHURCHILL, M., BUCHHOLTZ, E.A., BEATTY, B.L. & GEISLER, J.H. 2020. Convergent evolution of swimming adaptations in modern whales revealed by a large macrophagous dolphin from the Oligocene of South Carolina. *Current Biology*, **30**, 10.1016/j.cub.2020.06.012.
- BORSUK-BIALYNICKA, M. 1988. New remains of Archaeoceti from the Paleogene of Antarctica. *Polish Polar Research*, **9**, 437–445.
- BUCHHOLTZ, E. 2001. Vertebral osteology and swimming style in living and fossil whales (Order: Cetacea). *Journal of Zoology*, **253**, 10.1017/S0952836901000164.
- BUCHHOLTZ, E.A. 2007. Modular evolution of the Cetacean vertebral column. *Evolution and Development*, **9**, 10.1111/j.1525-142X.2007.00160.x.
- BUCHHOLTZ, E. 2011. Vertebral and rib anatomy in *Caperea marginata*: implications for evolutionary patterning of the mammalian vertebral column. *Marine Mammal Science*, **27**, 10.1111/j.1748-7692.2010.00411.x.
- BUONO, M.R., FORDYCE, R., MARX, F.G., FERNANDEZ, M. & REGUERO, M.A. 2019. Eocene Antarctica: a window into the earliest history of modern whales. *Advances in Polar Science*, **30**, 10.13679/j.advps.2019.0005.
- BUONO, M.R., FERNÁNDEZ, M.S., REGUERO, M.A., MARENSSI, S.A., SANTILLANA, S.N. & MÖRS, T. 2016. Eocene basilosaurid whales from the La Meseta Formation, Marambio (Seymour) Island, Antarctica. *Ameghiniana*, **53**, 10.5710/AMGH.02.02.2016.2922.
- DE MUIZON, C. 1984. *Les Vertébrés fossiles de la Formation Pisco (Pérou). Deuxième partie: Les Odontocètes (Cetacea, Mammalia) du Pliocène inférieur de Sud-Sacaco*. Paris: L'Institut Français d'Études Andines, 188 pp.
- DE MUIZON, C., BIANUCCI, G., MARTÍNEZ-CÁCERES, M. & LAMBERT, O. 2019. *Mystacodon selenensis*, the earliest known toothed mysticete (Cetacea, Mammalia) from the late Eocene of Peru: anatomy, phylogeny, and feeding adaptations. *Geodiversitas*, **41**, 10.5252/geodiversitas2019v41a11.
- DOUGLAS, P.M.J., AFFEK, H.P., IVANY, L.C., HOUBEN, A.J.P., SUP, W.P., SLUIJS, A. *et al.* 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**, 10.1073/pnas.1321441111.
- EMLONG, D. 1966. A new archaic cetacean from the Oligocene of northwest Oregon. *Bulletin of the Museum of Natural History, University of Oregon*, **3**, 1–51.

- FISH, F.E. 1996. Transitions from drag-based to lift-based propulsion in mammalian swimming. *American Zoology*, **36**, 628–641.
- FORDYCE, R. 1989. Origins and evolution of Antarctic marine mammals. *Special Publication of the Geological Society of London*, No. 47, 269–281.
- FORDYCE, R.E. & MARX, F.G. 2018. Gigantism precedes filter feeding in baleen whale evolution. *Current Biology*, **28**, 10.1016/j.cub.2018.04.027.
- GILLET, A., FRÉDÉRICH, B. & PARMÉNTIER, E. 2019. Divergent evolutionary morphology of the axial skeleton as a potential key innovation in modern cetaceans. *Proceedings of the Royal Society B: Biological Sciences*, **286**, 10.1098/rspb.2019.1771.
- GINGERICH, P. 2007. *Stromerius nidensis*, new archaeocete (Mammalia, Cetacea) from the upper Eocene Qasr El-Sagha Formation, Fayum, Egypt. *Contributions from the Museum of Paleontology*, **31**, 363–378.
- GINGERICH, P.D., ANTAR, M.S.M. & ZALMOUT, I.S. 2019. *Aegicetus gehennae*, a new late Eocene protocetid (Cetacea, Archaeoceti) from Wadi Al Hitan, Egypt, and the transition to tail-powered swimming in whales. *PLoS One*, **14**, 10.1371/journal.pone.0225391.
- GOL'DIN, P. & ZVONOK, E. 2013. *Basilotritus uheni*, a new cetacean (Cetacea, Basilosauridae) from the late middle Eocene of eastern Europe. *Journal of Paleontology*, **87**, 10.1666/12-080r.1.
- HULBERT, R.C. 1998. Postcranial osteology of the North American middle Eocene protocetid *Georgiacetus*. In THEWISSEN, J.G.M., ed. *The emergence of whales: evolutionary patterns in the origin of Cetacea*. New York: Springer, 235–267.
- JADWISZCZAK, P. & MÖRS, T. 2017. An enigmatic fossil penguin from the eocene of Antarctica. *Polar Research*, **36**, 10.1080/17518369.2017.1291086.
- KELLOGG, R. 1936. *A review of the Archaeoceti*. Washington, DC: Carnegie Institution of Washington, 357 pp.
- KLINGENBERG, C.P. 2011. *MorphoJ*: an integrated software package for geometric morphometrics. *Molecular Ecology Resources*, **11**, 10.1111/j.1755-0998.2010.02924.x.
- KRIWET, J., ENGELBRECHT, A., MÖRS, T., REGUERO, M. & PFAFF, C. 2016. Ultimate Eocene (Priabonian) chondrichthyans (Holocephali, Elasmobranchii) of Antarctica. *Journal of Vertebrate Paleontology*, **36**, 10.1080/02724634.2016.1160911.
- LONG JR, J.H., PABST, D.A., SHEPHERD, W.R. & McLELLAN, W.A. 1997. Locomotor design of dolphin vertebral columns: bending mechanics and morphology of *Delphinus delphis*. *Journal of Experimental Biology*, **81**, 65–81.
- MARENSSI, 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**, 341 10.1016/S0037-0738(01)00201-9.
- MARTÍNEZ-CÁCERES, M., LAMBERT, O. & DE MUIZON, C. 2017. The anatomy and phylogenetic affinities of *Cynthiacetus peruvianus*, a large *Dorudon*-like basilosaurid (Cetacea, Mammalia) from the late Eocene of Peru. *Geodiversitas*, **39**, 10.5252/g2017n1a1.
- MARX, F.G., TSAI, C.H. & FORDYCE, R.E. 2015. A new Early Oligocene toothed 'baleen' whale (Mysticeti: Aetiocetidae) from western North America: one of the oldest and the smallest. *Royal Society Open Science*, **2**, 10.1098/rsos.150476.
- MARX, F.G., BUONO, M.R., EVANS, A.R., FORDYCE, R.E., REGUERO, M. & HOCKING, D.P. 2019. Gigantic mysticete predators roamed the Eocene Southern Ocean. *Antarctic Science*, **31**, 10.1017/S095410201800055X.
- MITCHELL, E.D. 1989. A new cetacean from the late Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 10.1139/f89-273.
- MONTES, M., NOZAL, F., SANTILLANA, S., MARENSSI, S. & OLIVERO, E. 2013. *Mapa Geológico de Isla Marambio (Seymour), Antártida, escala 1:20,000*. Serie Cartográfica. Madrid: Instituto Geológico y Minero de España.
- MÖRS, T., REGUERO, M. & VASILYAN, D. 2020. First fossil frog from Antarctica: implications for Eocene high latitude climate conditions and Gondwanan cosmopolitanism of Australobatrachia. *Scientific Reports*, **10**, 10.1038/s41598-020-61973-5.
- REGUERO, M.A. 2019. Antarctic paleontological heritage: late Cretaceous Paleogene vertebrates from Seymour (Marambio) Island, Antarctic Peninsula. *Advances in Polar Science*, **30**, 10.13679/j.advps.2019.0015.
- SADLER, P.M. 1988. Geometry and stratification of uppermost Cretaceous and Paleogene units on Seymour Island, northern Antarctic Peninsula. In FELDMANN, R.M. & WOODBURN, M.O., eds. *Geology and Paleontology of Seymour Island, Antarctic Peninsula*. *Geological Society of America Memoir*, No. 169, 303–320.
- UHEN, M.D. 2004. Form, function, and anatomy of *Dorudon atrox* (Mammalia, Cetacea): an archaeocete from the middle to late Eocene of Egypt. *Papers on Paleontology*, **34**, 1–238.
- UHEN, M.D., PYENSON, N.D., DEVRIES, T.J., URBINA, M. & RENNE, P.R. 2011. New middle Eocene whales from the Pisco Basin of Peru. *Journal of Paleontology*, **85**, 10.1666/10-162.1.
- VLIET, H.J. VAN, BOSSELAERS, M., VAHLDIEK, B., PAYMANS, T. & VERHEIJEN, I. 2020. Eocene cetaceans from the Helmstedt region, Germany, with some remarks on *Platyosphys*, *Basilotritus* and *Pachycetus*. *Cainozoic Research*, **20**, 121–148.
- WIMAN, C. 1905. Über die alttertiären Vertebraten der Seymourinsel. In NORDENSKJÖLD, O., ed. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901–1903*. Stockholm: Lithographisches Institut des Generalstabs, 1–37.