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Eocene cetaceans from the Belgian-Dutch coastal waters

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ABSTRACT

Thirteen cetacean vertebrae and a vertebral neural arch fragment are described and figured. All have been dredged from the southern part of the North Sea, in the tidal channels Het Scheur, Belgium, and Wielingen in the estuary of the Westerschelde, near the Belgian-Dutch border. Here, strata of the Middle Eocene Maldegem Formation and of the Late Eocene parts of the Zelzate Formation crop out at the seafloor. The vertebral centra are mostly large and show basilosaurid characteristics. Based upon morphology, three different main types are recognised. The first morphotype apparently represents a new taxon, the second one closely resembles a vertebra of a cetacean from the Priabonian of Maastricht, the Netherlands and the third is assigned to the genus *Pachycetus* which taxon is, amongst others, also known from the Bartonian and maybe Priabonian of Ukraine and Germany in Europe. In the vertebrae of the latter morphotype, maybe two subtypes, a large and a smaller one can be discerned. With at least three different large taxa, the seafloor at Wielingen and Het Scheur appears to be a surprisingly important site of Eocene cetacean remains in Europe.

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INTRODUCTION

Basilosaurids were the first fully aquatic cetaceans, which are known from the Middle and Late Eocene. Adaptations to a swimming lifestyle are, amongst others, detachment of the pelvis from the vertebral column and strongly reduced hind limbs, indicating that the animals could not support their weight on land. The dentition is characterised by denticulated premolars and molars and the loss of the upper molar M3. Basilosaurids are known from almost all continents (Marx *et al.* 2016). Although basilosaurid remains are not common in Europe (Van Vliet *et al.* 2019), over the last decades a substantial number of finds from this continent has been described (e.g. Uhen & Berndt 2008, Post 2007, Schouten 2011, Gol'din & Zvonok 2013, Gol'din *et al.* 2014a, Van Vliet *et al.* 2019, Mychko & Tarasenko 2020, Van Vliet *et al.* 2020 & Tarasenko 2022). Recently, vertebrae with basilosaurid features have been reported from the tidal channels Het Scheur and Wielingen in the southern margin of the North Sea. The first vertebra was noticed by one of the authors (KP) in 1996, amidst remains of Neogene cetaceans. The latter are being harvested in massive numbers by fishermen in this region for more than a century (Post & Reumer 2016). After 1996, more vertebrae with comparable features were discovered, resulting in a collection of the here described thirteen vertebral centra and one part of a vertebral neural arch (Post

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2007, Schouten 2011, Post *et al.* 2017). Being dredged out of the sea, all vertebrae are isolated *ex situ* finds. The vertebrae, apparently belonging to three morphotypes, here called 'Morphotype A, B and C', the last one (Morphotype C) possibly consisting of two subtypes are compared with vertebral centra of known archaeocete taxa. Since postcrania of archaeocetes bear more diagnostic features, than postcrania of extant cetaceans (Gingerich & Zouhri 2015), the diversity in vertebral characteristics regarding size, elongation and the presence of a compact, circumferential, multi-layered cortex (CCMC) can sometimes be used for identification at family or even genus level.

Material and methods

All described vertebrae are housed in the collections of the Natural History Museum Rotterdam (Rotterdam, the Netherlands). All (except vertebra NMR-13472) have been dredged by commercial fishing between 1996 and 2017 from the North Sea floor in the region of the tidal channels of Wielingen at the Belgian-Dutch border and in the estuary of the Westerschelde, and the nearby Het Scheur in the Belgian part of the North Sea (Fig. 1a-b) (Post 2007, Schouten 2011, Post *et al.* 2017). With the help of a fisherman, the most probable locality of origin of some specimens (NMR-12331, NMR-12332, NMR-12333; see section Morphotype C) was traced at Het Scheur, Belgium, near Buoy 10. Here an expedition of the Natural History Museum Rotterdam in September 2016 dredged a new archaeocete vertebra (NMR-13472, see section Morphotype C) within the area 51°24'8493''N-03°16'4424''E and 51°24'7208''N – 03°13'7370''E (Post *et al.* 2017).

The relative length (L/Wa) of a vertebral centrum is calculated by its anteroposterior length (preferably the dorsal length if known) divided by its anterior width. Because the epiphyses are lacking in almost all vertebral centra, the given relative length will be mostly underestimated. The relative width (Wa/Ha) of a vertebral centrum is calculated by its anterior width divided by its anterior height.

The genus names *Platyosphys* Kellogg, 1936 and *Basilotritus* Gol'din & Zvonok, 2013, are replaced by *Pachycetus* Van Beneden, 1883 (following Van Vliet *et al.* 2020). We follow Houssaye *et al.* (2015) and Martínez-Cáceres *et al.* (2017) for anatomical and osteological terms. The mostly rather small, nutrient vascular openings, which seem to be more or less randomly scattered on the vertebral surface, are here called 'punctae' (following Uhen 1999), to avoid confusion with the mostly large dorsal and ventral vascular foramina, which, being part of the vertebral central sinus, can occur on a more or less fixed place along the midline of vertebral centra.

Anatomical abbreviations — ant, anterior; CCMC, compact circumferential multi-layered cortex; Cd, caudal vertebral centrum; dors, dorsal; epi, epiphyses; f, foramen; H, height; Ha, anterior height; L, length; Ld, dorsal length; Lu, lumbar vertebral centrum; Lv, ventral length; NA, neural arch; p, punctae; post, posterior; Rel, relative; Sa, sacral vertebral centrum; Th, thoracic vertebral centrum; vent, ventral; W, width; Wa, anterior width

Institutional abbreviations —FV, Canadian Geological Survey, now Canadian Museum of Nature; GMTSNUK, Geological Museum of Taras Shevchenko National University of Kiev, Ukraine; KOM,

Kirovograd Oblast Museum, Ukraine; FSAC Bouj, Faculty of Sciences Aïn Chock, Boujdour collection; MMNS, Mississippi Museum of Natural Science, Jackson, USA; MNHN, Muséum national d'histoire naturelle, Paris, France; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; NHMM Natuurhistorisch Museum Maastricht (Museum of Natural History, Maastricht), the Netherlands; NMNH-P Paleontological Museum, National Natural History Museum of the Academy of Sciences of Ukraine, Kiev, Ukraine; NMR, Natural History Museum Rotterdam, Rotterdam, the Netherlands; NWMNH, Northwest Museum of Natural History, Portland, Oregon; St, Naturkundemuseum Stuttgart, Germany; USMN, United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA

The generic part of the specimen numbers of the material kept in NMR (NMR999100 to NMR99910000) is replaced by a hyphen below, after the specimen number is cited once in full (e.g. NMR999100003882 is cited as NMR-3882).

Geologic setting

Where the Westerschelde Estuary enters the North Sea from the southwestern part of the Netherlands, tidal channels are part of a dynamic system of sea currents and migrating sands. At the end of the nineteenth century, a new tidal channel, nowadays called Het Scheur, was created by natural processes, to the west of Wielingen (Kornman *et al.* 2000) (Fig. 1). Quaternary strata, covering Palaeogene strata in this area, are less than 10 m thick and, at some locations like Het Scheur, even less than 2.5 m (Du Four *et al.* 2006). From the early sixties of the twentieth century until now, Wielingen and Het Scheur are artificially deepened, to create a large route for navigation (Kornman *et al.* 2000). By these dredging activities, the overlying Quaternary strata have been removed and Palaeogene strata now subaqueously crop out at the seafloor. At Wielingen, layers from the Priabonian (Late Eocene) parts of the Zelzate Formation are encountered. The Priabonian strata consist of clay with some sands, reaching a thickness of about 40-90 m (Du Four *et al.* 2006). The Ruisbroek Member, the Oligocene upper part of the Zelzate Formation does not crop out in this region (Kornman *et al.* 2000, Du Four *et al.* 2006) and is only present beneath the strata from the Boom Clay Formation more to the northeast (Du Four *et al.* 2006, TNO-GDN 2020). At Het Scheur, the Maldegem Formation crops out (Du Four *et al.* 2006). This Formation, Lutetian to Bartonian in age (Middle Eocene), consists of grey and bluish-grey layers of fine sands and clay, reaching a thickness of about 45 to 60 m (Du Four *et al.* 2006). For an overview of the Palaeogene and Neogene strata underneath the Pleistocene and Holocene sediments in the North Sea at the Belgian and Dutch border see Fig. 2a. The Palaeogene strata are tilted, dipping to the northeast and are covered in this direction with increasingly thicker layers from the Neogene and Quaternary (Fig. 2b). A section with the members of the Maldegem and Zelzate Formations is given in Fig. 2c.

Systematic Paleontology
Order CETACEA Brisson, 1762
Unranked clade PELAGICETI Uhen, 2008
?Family BASILOSAURIDAE Cope, 1868
?Basilosauridae indet.

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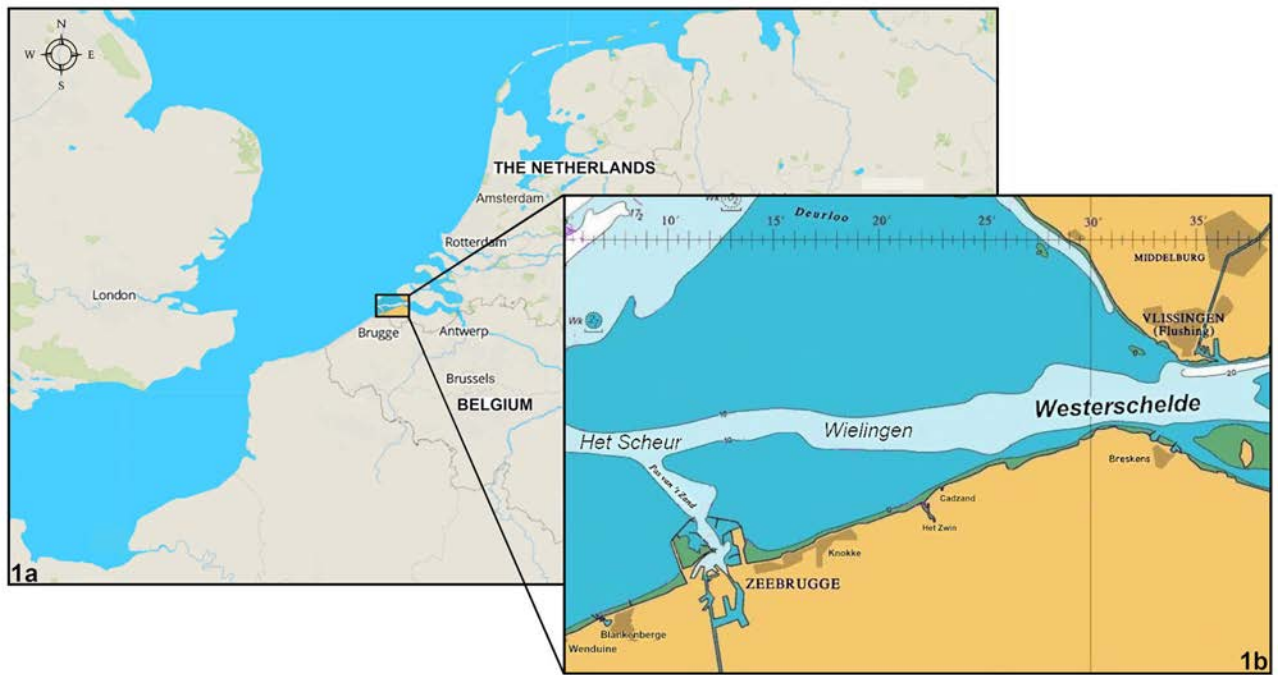
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Figure 1. Study site. a: Map of the southern North Sea, showing the position of the fossil locations Wielingen and Het Scheur, Southern Bight North Sea; b: the locations of Wielingen at the Belgian-Dutch border, and Het Scheur, Belgium.
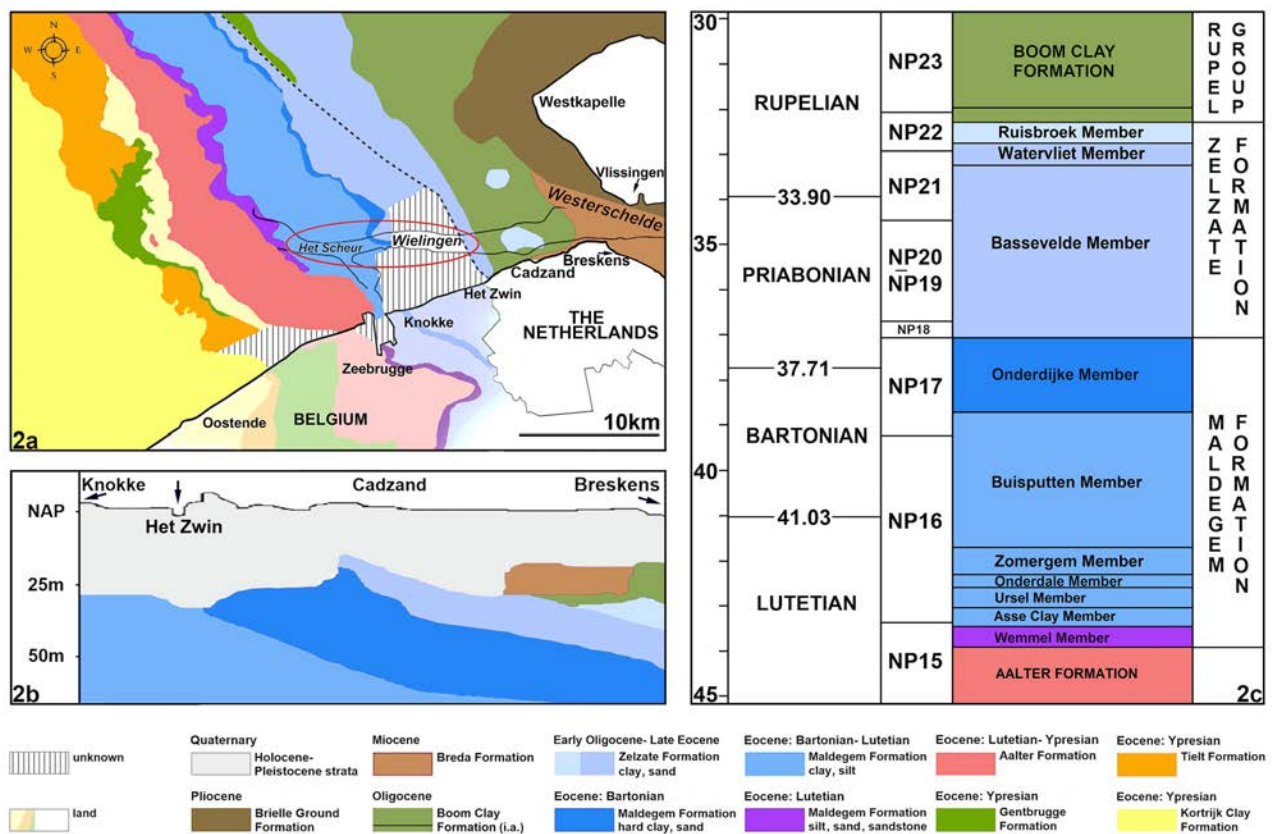

Figure 2. Stratigraphy of the Palaeogene and Neogene sediments in the region of Wielingen and Het Scheur, Southern Bight North Sea. a: Palaeogene and Neogene strata directly beneath the Pleistocene and Holocene sediments at the seafloor; red ellipse indicates locations of Wielingen and Het Scheur; dotted line indicates the border of Belgium with the Netherlands at sea; coloured strata at sea (modified after Du Four *et al.* 2006: fig. 3) are explained in the captions below the figures; transparent coloured strata (modified after Le Bot *et al.* 2003: fig. 7) - not further explained in the captions- indicate the continuation of these strata on land (Belgium). b: the tilting of the Palaeogene strata towards the north-northeast in the study area (modified after Du Four *et al.* 2006: fig. 4). NAP (Normaal Amsterdams Peil or Amsterdam Ordnance Datum) = mean sea level of the North Sea. Note that the Oligocene Ruisbroek Member of the Zelzate Formation is only present beneath the Boom Clay Formation to the north in this area (and also that the Miocene deposits are at this location more prominently present than in Fig. 2a). c: section of the Zelzate and Maldegem formations (based on De Smet *et al.* 1997: tabel 2.1, Steurbaut *et al.* 2015: figs 3-4, Gradstein *et al.* 2020).

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Morphotype A

Figs 3-8; Table 1a, b

Material — One anteriormost and one posterior thoracic vertebral centrum (NMR999100160635; NMR999100003402); two lumbar vertebral centra (NMR999100003403; NMR999100003882); one caudal vertebral centrum (NMR999100010283).

Comments — NMR-3402 and NMR-3403 have been briefly described by Post (2007) and Schouten (2011); NMR-3882 has been described by Schouten (2011).

Description— Large vertebral centra, with only the basis of the transverse processes and the pedicles of the neural arch preserved. Most vertebrae are heavy in weight; the vertebra is then called 'permineralised', as the original bone is apparently replaced by minerals. They are not-elongated, with a relative length between 0.48 and 0.60 (Table 1a). The width to height ratio ranges from about 1.10 (NMR-160635, anteriormost thoracic vertebra without epiphyses) to 1.37 (NMR-10283, caudal vertebra with epiphyses). The dorsal, lateral and ventral surfaces of the centra have multiple (up to several tens of), rather large punctae. There is a CCMC, which consists of a thin compact outer part, about 2 to 3 mm thick and a more trabecular, inner part, that is about 15 to 17 mm thick. This part of the cortex is hardly distinguishable from the spongiose and trabecular bone underneath. The epiphyses are lacking in almost all vertebrae, except vertebra NMR-10283. The epiphyseal surfaces show a more or less regular radiating pattern of ridges at the periphery, with a more chaotic pattern at the central area (see also Fig. 3c). The anterior and posterior sides are more or less flat. All vertebral centra have one or more conspicuous vascular foramina on both the dorsal and ventral sides. When present, the transverse processes or the bases of the transverse processes of the vertebrae are located in a dorsoventrally low position on the vertebral centrum and directed anteroventrally. Vertebral dimensions are given in Table 1a.

NMR-160635 is an anteriormost thoracic vertebral centrum, which is heart-shaped in anterior view and small compared to the other vertebrae of this morphotype. The vertebral centrum is permineralised. It is brownish-red to grey in colour and abraded. Multiple punctae are present, especially near the epiphyseal surfaces (Fig. 4d). The pedicles of the neural arch are almost completely lost by abrasion. Two dorsal foramina are present. The right one consists of two adjacent foramina
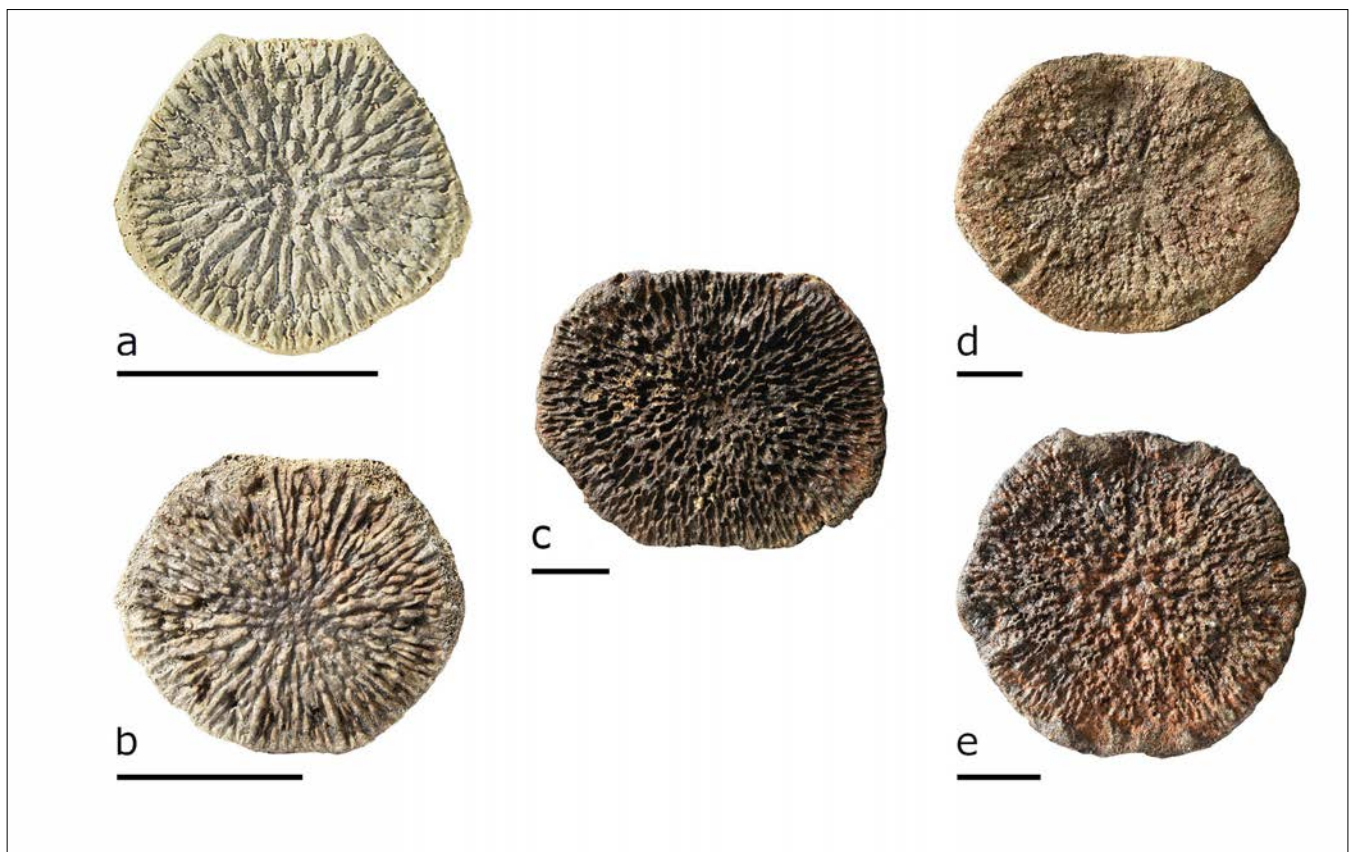

Figure 3. Comparison of the vertebral epiphyseal surface of an Eocene cetacean (c) with the epiphyseal surfaces of two odontocetes (a, b) and of two mysticetes (d, e). The vertebral epiphyseal surfaces in odontocetes show a clearly radiating pattern, whereas this pattern in mysticetes can be called chaotic. The epiphyseal surface of vertebra NMR999100003403 (c), ascribed to an Eocene cetacean shows an intermediate pattern, radiating at the periphery, but chaotic at the more central region. a: lumbar vertebral centrum of a ziphiid, *Mesoplodon bidens* Sowerby, 1804 (Recent, Southern Bight North Sea), NMR999000002216; b: lumbar vertebral centrum of a delphiniid, *Globicephala melas* Traill, 1809 (Recent, Southern Bight North Sea), NMR999000002797; c: lumbar vertebral centrum of Morphotype A, NMR999100003403 (Eocene, North Sea, region Wielingen-Het Scheur); d: thoracic vertebral centrum of an eschrichtiid, *Eschrichtius robustus* Lilljeborg, 1861 (Recent, Southern Bight North Sea), NMR999100001938; e: caudal vertebral centrum of an indeterminable mysticete (Neogene, Southern Bight North Sea), NMR999100008172. All epiphyseal surfaces are in anterior view. Scale bar 5 cm.

Table 1a: vertebral dimensions Morphotype A, presumed indeterminable basilosaurid (in mm) from Wielingen or Het Scheur.

No. & Figs, in Figs 18 & 19: dark-red spheres	Vertebra	Length	Width NA	Width	Height	Rel L= Ld/Wa	Rel W = Wa/Ha	References
NMR999100160635 Fig. 4, Fig. 18: A1	?Th1**)	56 (dors) 57 (vent)	?	103 (ant) 126 (post)	75 (ant) 82 (post)	0.54	1.37	This article
NMR999100003402 Fig. 5, Fig. 18: A2	Th**)	123 (dors) 118 (vent)	116	237 (ant) 231 (post)	179 (ant) 180 (post)	0.52	1.32	Post 2007, Schouten 2011, this article
NMR999100003403 Fig. 6, Figs 18 & 19: A3	Lu**)	110 (dors) 112 (vent)	118	229 (ant) 228 (post)	183 (ant) 190 (post)	0.48	1.25	Post 2007, Schouten 2011, this article
NMR999100003882 Fig. 7, Figs 18 & 19: A4	Lu**)	94 (dors) 92 (vent)	98	178 (ant) 180 (post)	145 (ant) 145 (post)	0.53	1.23	Schouten 2011, this article
NMR999100010283 Fig. 8, Figs 18 & 19: A5	Cd	127 (dors) 135 (vent)	67	210 (ant) 212 (post)	191 (ant) 185 (post)	0.60	1.10	This article

Table 1b: vertebral dimensions of some other basilosaurids (in mm).

No. & taxon	Age, formation & country	Vertebra	Length	Width NA	Width	Height	Rel L= Ld/Wa	Rel W = Wa/Ha	References
USMN 11401a: 1	Priabonian, Jackson Group, Georgia	Lu *)	104	?	147 (ant) ? (post)	143 (ant) ? (post)	0.71	1.03	Kellogg 1936: table 67
USMN 11401a: 3	Priabonian, Jackson Group, Georgia	Lu **)	108	?	166 (ant) 103 (post)	142 (ant) 146 (post)	0.65	1.17	Kellogg 1936: table 67
MMNS VP 445 *Cynthiacetus maxwelli* Uhen, 2005	(Bartonian-) Priabonian, Yazoo Clay Formation, Mississippi	LuA**)	87 (dors) 82 (vent)	?	118 (ant) 116 (post)	?	0.74	?	Uhen 2005: table 3
MNHN.F.PRU 10 *Cynthiacetus peruvianus* Martínez-Cáceres & de Muizon, 2011,	Priabonian, Otuma Clay Formation, Peru	Lu1	134 (dors) 130 (vent)	?	145 (ant) 152 (post)	130 (ant) 141 (post)	0.92	1.12	Martínez-Cáceres *et al.* 2017: table 9
MNHN.F.PRU 10 *Cynthiacetus peruvianus*	Priabonian, Otuma Clay Formation, Peru	Lu12	142 (dors) 143 (vent)	?	161 (ant) 166 (post)	160 (ant) 164 (post)	0.88	1.01	Martínez-Cáceres *et al.* 2017: table 9

*) with one epiphysis; **) without epiphyses Abbreviations ?, unknown; /, fraction

separated by a septum. Ventrally, two adjacent foramina, separated by a septum are present on the left side and one large foramen on the right side (Fig. 4d). These ventral foramina are located quite laterally, instead of lying along the midline. Therefore, the dorsoventral vascular canals connecting the dorsal and ventral foramina, appear to draw an angle of 45°, with a (virtual) vertical, dorsoventral line. The ventral foramina are joined by multiple, randomly scattered, large punctae, resembling foramina because of their large size (Fig. 4).

NMR-3402 is a posterior thoracic vertebral centrum. The break surfaces of the apophyses are fresh, but partly overgrown with encrustations of bryozoan colonies and barnacles. The vertebral centrum is permineralised. It is brownish in colour and not abraded. Multiple punctae are especially abundant near the epiphyseal surfaces, making the surface pock-marked. Two dorsal foramina are present, one on each side of a median ridge. The transverse processes are located on the lateral sides, just below mid-centrum height. They are short and
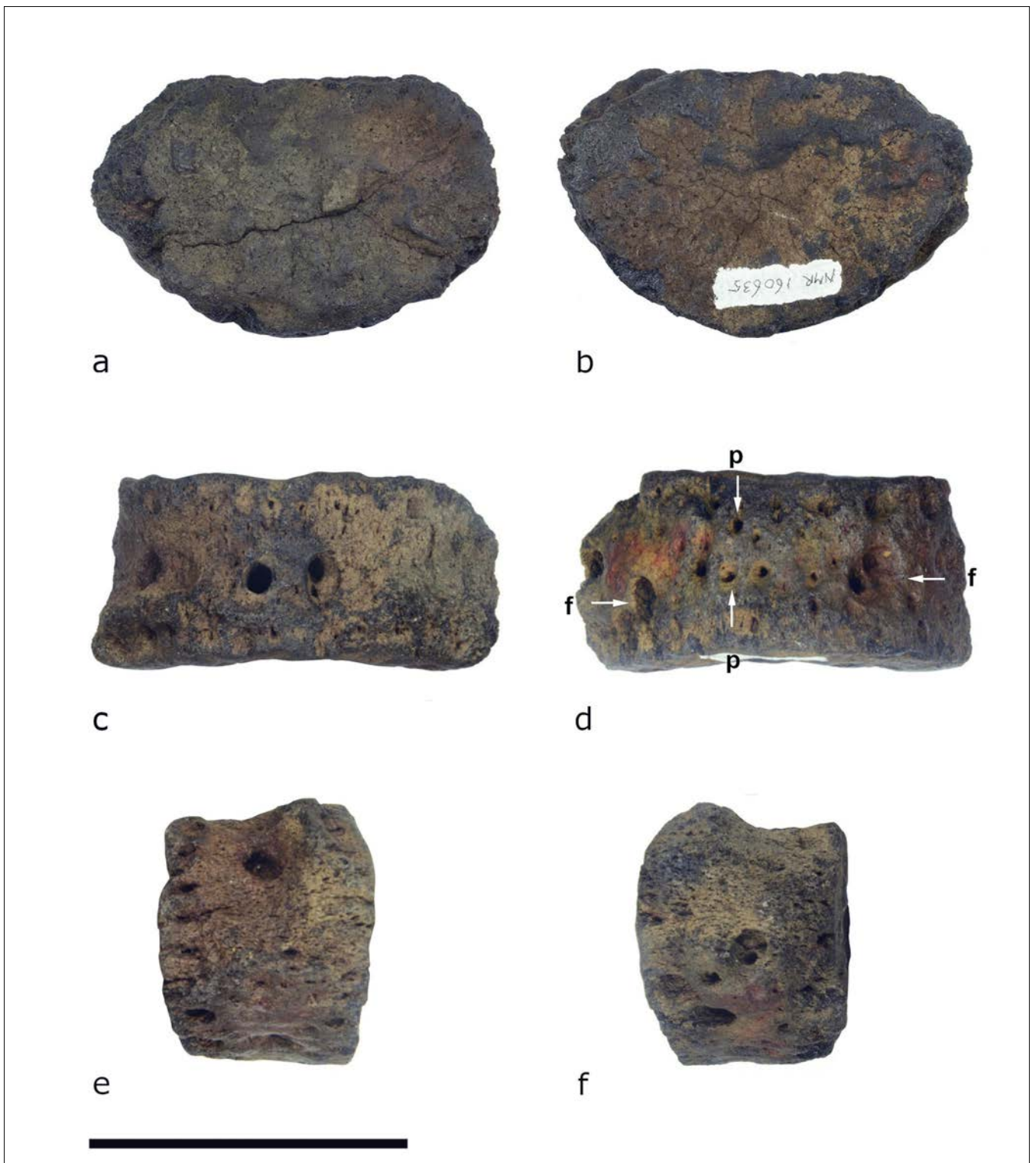
Figure 4. Anteriormost thoracic vertebral centrum, NMR999100160635, Morphotype A, from the region of Wielingen (Belgian-Dutch border), or Het Scheur (Belgium) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Horizontal arrows with 'f' in 4d indicate the ventral foramina, lying quite laterally; vertical arrows with 'p' in 4d indicate some examples of the multiple, large punctae. Scale bar 10 cm.

bear a large fovea for the articulation of the corresponding rib. Some damage did occur at the posterior side of the dorsal and ventral median ridges. The ventral median ridge is broad. Ventral foramina seem to be lacking; some punctae are present (Fig. 5).

NMR-3403 is a lumbar vertebral centrum. The break surfaces of the pedicles of the neural arch and the transverse processes are fresh, but partly overgrown with encrustations. The vertebral centrum is permineralised. It is brownish in colour and not abraded. Two rather large dorsal foramina are present on the dorsal side, one on each side of a low median ridge. The right foramen is accompanied by a smaller foramen. The basis of the left transverse process is preserved, while the basis of the right process is nearly completely lost. The transverse processes are located low on the lateral sides, near the ventral side. Four vascular foramina are located on the ventral side of the centrum. Two of these are located on the left side. A large foramen is located approximately on the midline or slightly to the right; a small foramen is located on the right side. There is no median ventral ridge (Fig. 6).

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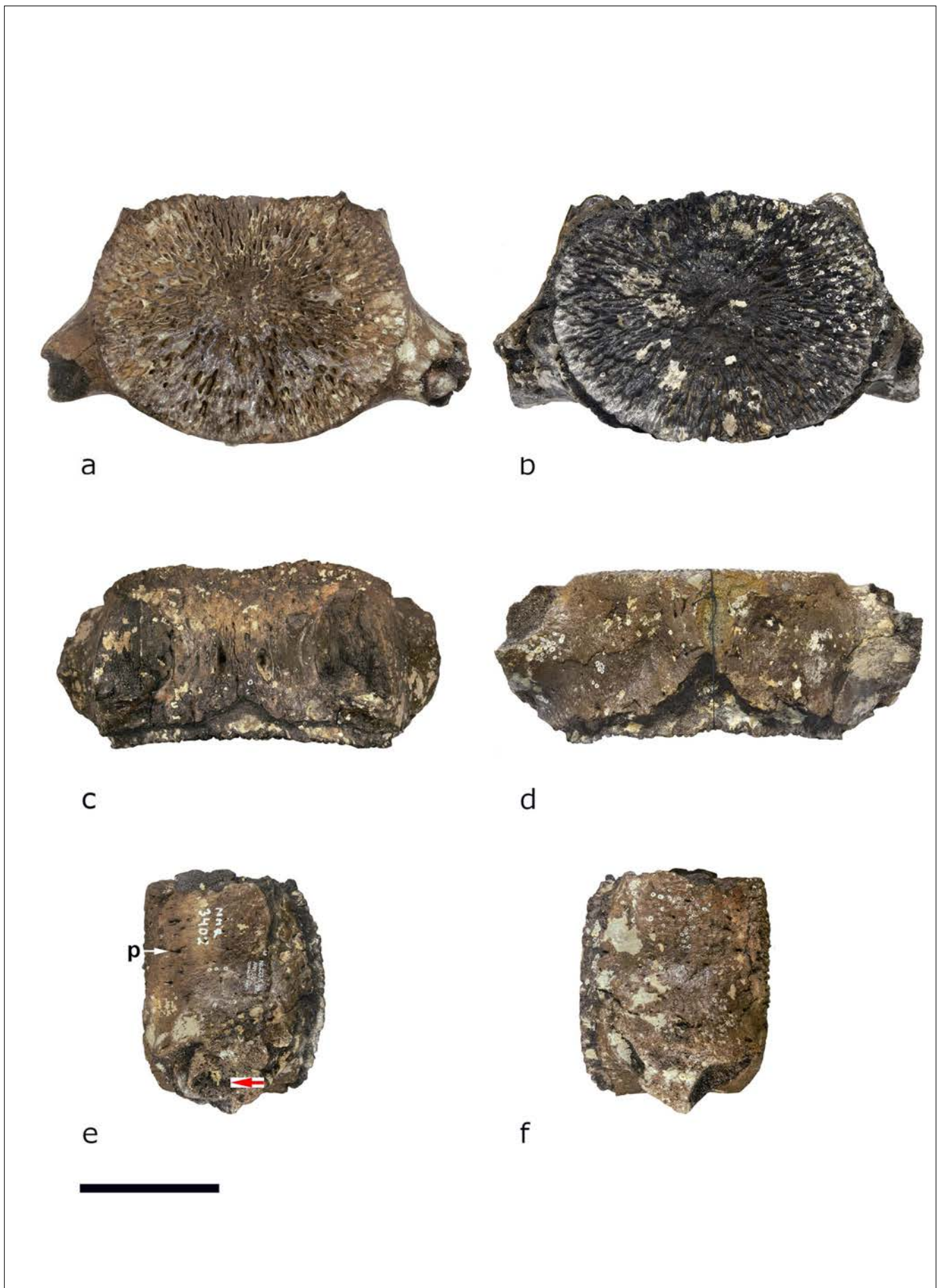
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Figure 5. Posterior thoracic vertebral centrum, NMR999100003402, Morphotype A, from the region of Wielingen (Belgian-Dutch border), or Het Scheur (Belgium), in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Arrow with 'p' in 5e indicates some examples of the multiple punctae near the anterior epiphyseal surface. Red arrow in 5e indicates the fovea for the rib. Scale bar 10 cm.

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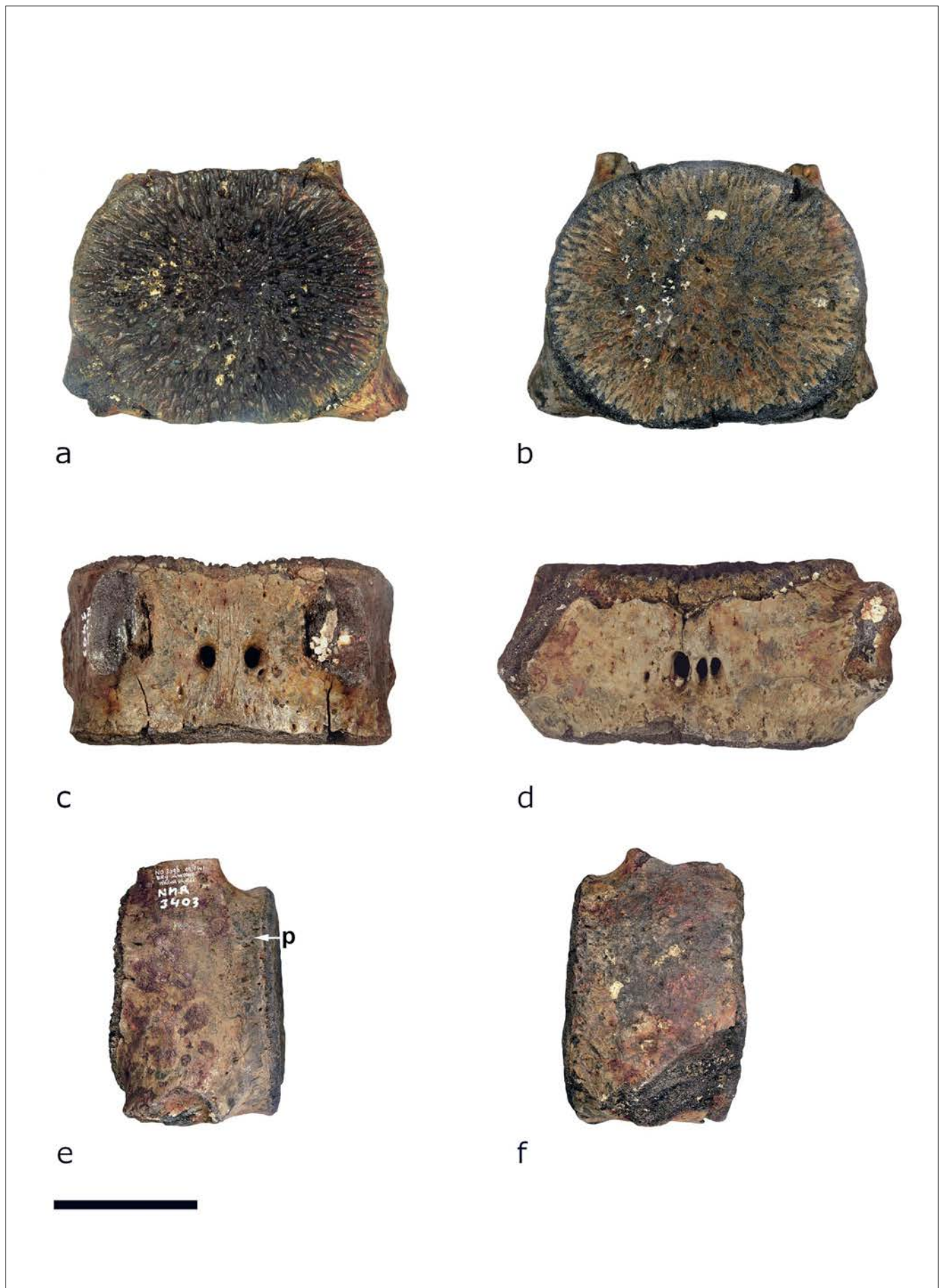
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Figure 6. Lumbar vertebral centrum, NMR999100003403, Morphotype A, from the region of Wielingen (Belgian-Dutch border), or Het Scheur (Belgium), in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Arrow with 'p' in 6e indicates some examples of the multiple punctae near the posterior epiphyseal surface. Scale bar 10 cm.

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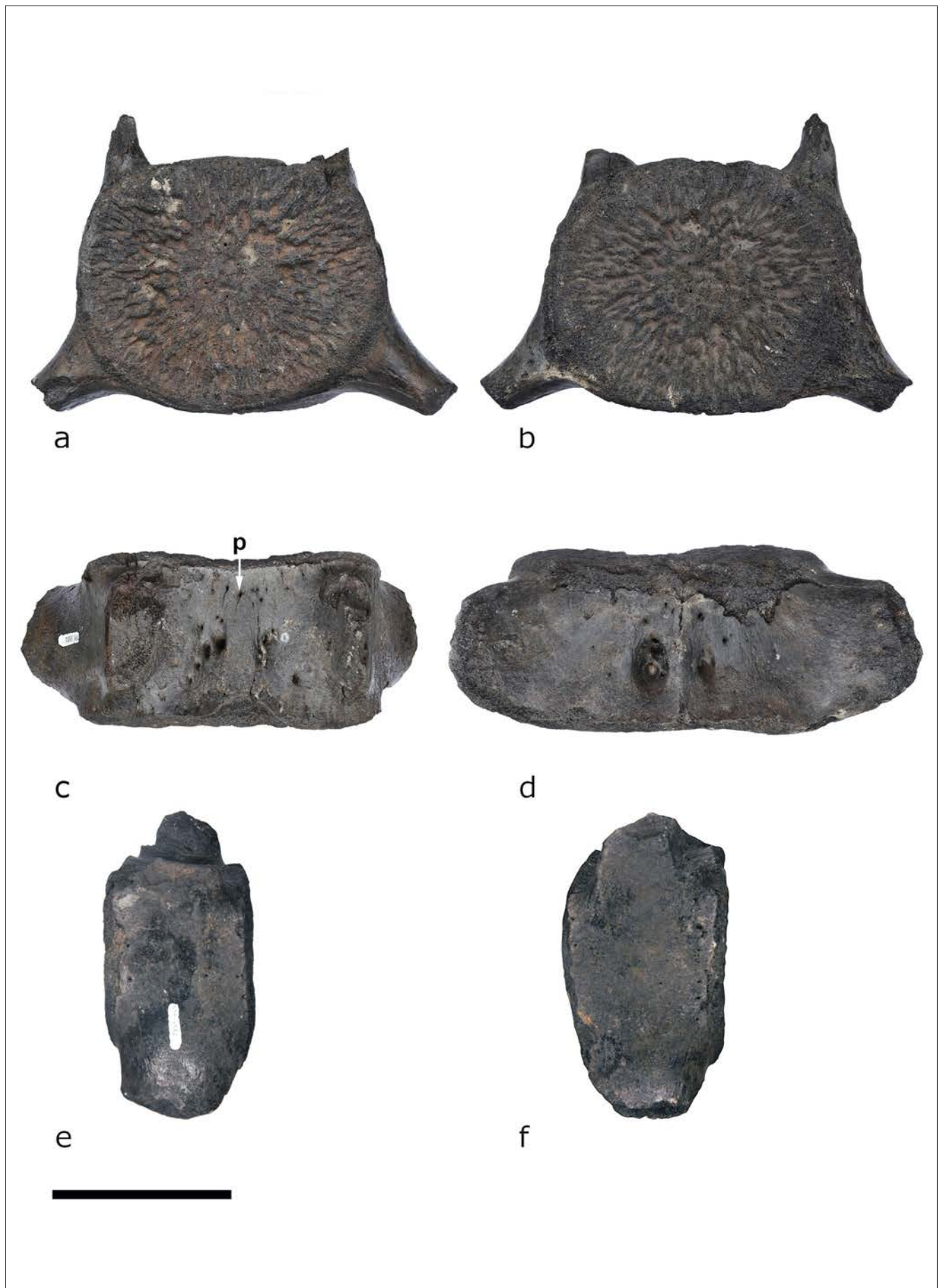
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Figure 7. Lumbar vertebral centrum, NMR999100003882, Morphotype A, from the region of Wielingen (Belgian-Dutch border), or Het Scheur (Belgium), in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Arrow with 'p' in 7c indicates some examples of the multiple punctae near the anterior epiphyseal surface. Scale bar 10 cm.

NMR-3882 is a lumbar vertebral centrum. The break surfaces of the transverse processes and the pedicles of the neural arch are fresh. The vertebral centrum is permineralised. It is grey in colour and slightly abraded. Punctae are especially abundant on the right lateral side near the anterior epiphyseal surface. The dorsal side has a few, large punctae. Six vascular foramina are located on the dorsal side: two on the left and four on the right side of a broad and low median ridge. The left pair of two foramina is accompanied by several large, foramen-like punctae. The transverse processes are partly preserved and are located low along the lateral sides, but slightly more dorsally than in centrum NMR-3403. Two large concavities with vascular foramina are located on the ventral side, on each side of a sharp, but low median ridge. The left concavity is smaller and consists of two to three confluent foramina, separated by thin bony septa. The right concavity consists of at least seven foramina, all of them separated by thin bony septa (Fig. 7).

NMR-10283 is an anterior caudal vertebral centrum. The break surfaces of the apophyses are fresh. Because of its low weight, the vertebral centrum appears to be less permineralised than the other centra. It is brown in colour and not abraded. There are only a few punctae on the lateral and ventral sides of the vertebral centrum. The anterior epiphysis is incompletely fused, and partly broken. The posterior epiphysis is fused with the vertebral centrum and has a shallow central concavity. The epiphyses are about 15 mm thick, consisting mainly of trabecular bone. The neural canal is smaller than that of the other vertebral centra. A vascular foramen is located on each side of a low dorsal median ridge, the left foramen smaller than the right. Each foramen consists of confluent smaller foramina. The CCMC is more compact than in the other vertebrae of this morphotype. The outermost layers have flaked off at some places. The basis of the left transverse process is more or less completely lost, the basis of the right transverse process is preserved. They are located on the lateral sides, lower than in centrum NMR-3402, but more dorsally than in centrum NMR-3403 and NMR-3882. Ventrally, one large and one small foramen are located on the left side of a low median ridge, with the small foramen more to the left, and the large foramen located near this ridge. The haemal processes are nearly completely lost (Fig. 8).

Discussion — The vertebral centra of Morphotype A differ from vertebral centra of Morphotype B and C in their short length compared to the width and height, in having a more variable number of foramina on the dorsal and ventral sides and in having a far thinner CCMC. The presence of the transversely wide neural arches, the ventral foramina and the anteroventrally directed transverse processes are vertebral characteristics of basilosaurids and some archaic mysticetes, such as *Llanocetus denticrenatus* Mitchell, 1989 and *Diorocetus hiatus* Kellogg, 1968 (Kellogg 1936: 42, 47-48, Van Vliet *et al.* 2019). Like in basilosaurids (such as *Basilosaurus cetoides* Owen, 1839 (Kellogg 1936: 47), '*Pontogeneus brachyspondylus*' Müller, 1849 (*sensu* Kellogg 1936) and *Cynthiacetus peruvianus* Martínez-Cáceres & de Muizon, 2011 (Martínez-Cáceres *et al.* 2017: figs 55-56, 68-73, 76-77)), the transverse processes of especially the posterior thoracic NMR-3402, but also of the two lumbar vertebrae NMR-3403 and NMR-3882 are placed low at the ventral base of the lateral sides. This is not seen in protocetids (Hulbert 1998, Gingerich *et al.* 2019, Davydenko *et al.* 2020), nor Neogene Pelagiceti (compare e.g. with

Eurhinodelphis cocheteuxi du Bus, 1872 - see Abel 1931, *Pelocetus calvertensis* Kellogg, 1965 or in extant cetaceans). The transverse processes in the caudal vertebra NMR-10283 are positioned more dorsally on the lateral sides, than in the posterior thoracic vertebral centrum and the two lumbar vertebrae of this morphotype, which is also seen in the basilosaurids *Cynthiacetus peruvianus* (see Martínez-Cáceres *et al.* 2017: 103-104), *Dorudon atrox* Andrews, 1906 (see Uhen 2004: figs 81-87, 89-91) or *Zygorhiza kochii* Reichenbach in Carus, 1847 (see Kellogg 1936: figs 54-62).

A CCMC is noted in vertebrae and ribs of basilosaurids (Müller 1849, Gol'din & Zvonok 2013) and some Palaeogene and Neogene (Miocene) mysticetes (Fordyce & Watson 1998, Gol'din *et al.* 2014b, Van Vliet *et al.* 2019). The pattern of the epiphyseal surfaces (chaotic in the central region and radiating at the periphery) differs from extant cetaceans, among which odontocetes show a clearly radiating and mysticetes a chaotic pattern (KP, *pers. observation*; see Fig. 3 for a comparison of the anterior epiphyseal surface of NMR-3403 with that of two Recent odontocetes and one Recent mysticete and a mysticete from the Neogene).

Width and height of the vertebral centra of Morphotype A, are comparable to those of the not-elongated vertebrae of the 'dorudontine' basilosaurid '*Pontogeneus brachyspondylus*' (*sensu* Kellogg 1936) (Kellogg 1936: tables 64-65), but their length is far shorter and their relative length much lower. The relative length is lower, than that of the lumbar vertebrae in *Cynthiacetus maxwelli* Uhen, 2005, *C. peruvianus*, and that of six unnamed basilosaurid lumbar vertebrae, USNM 11401, from Georgia, USA, which are unusually short (Kellogg 1936: 256) (Table 1b). Moreover, while being shorter, some vertebrae are larger in width and height, than those of *C. maxwelli*, *C. peruvianus* or the aforementioned six basilosaurid lumbar vertebrae USNM 11401 (Table 1b). The extremely short length of the vertebrae of Morphotype A cannot be explained by differences in ontogenetic age and maturity of the specimens involved, as the caudal vertebral centrum NMR-10283 of Morphotype A represents a nearly fully-grown individual. Besides, if the length was solely attributable to a juvenile or even prenatal age, then the vertebrae would have acquired enormous proportions, larger than in all other basilosaurids known, when being fully-grown.

NMR-160635 is small compared to the more posterior thoracic and lumbar vertebrae. It is here tentatively, not with complete certainty, assigned to Morphotype A, because of its remarkably small length and multiple dorsal and ventral foramina, not seen in the vertebral centra of Morphotype B and C.

NMR-3402 and NMR-3403 are remarkably similar in size, preservation and colour, contrary to the other three vertebrae of this type. Both vertebral centra seem comparable in ontogenetic age. The fractures of the apophyses seem to be recent, but are overgrown with encrustations. NMR-3402 has been trawled in 1996; NMR-3403 has been found five years later in the garden of a fisherman. Nevertheless, it seems possible, that they have belonged to the same individual (Post 2007). The many punctae near the anterior epiphyseal surface in vertebral centrum NMR-3403 (Fig 6e) and especially vertebral centrum NMR-3402 (Fig 5e), are indicative of enhanced metabolic activity,
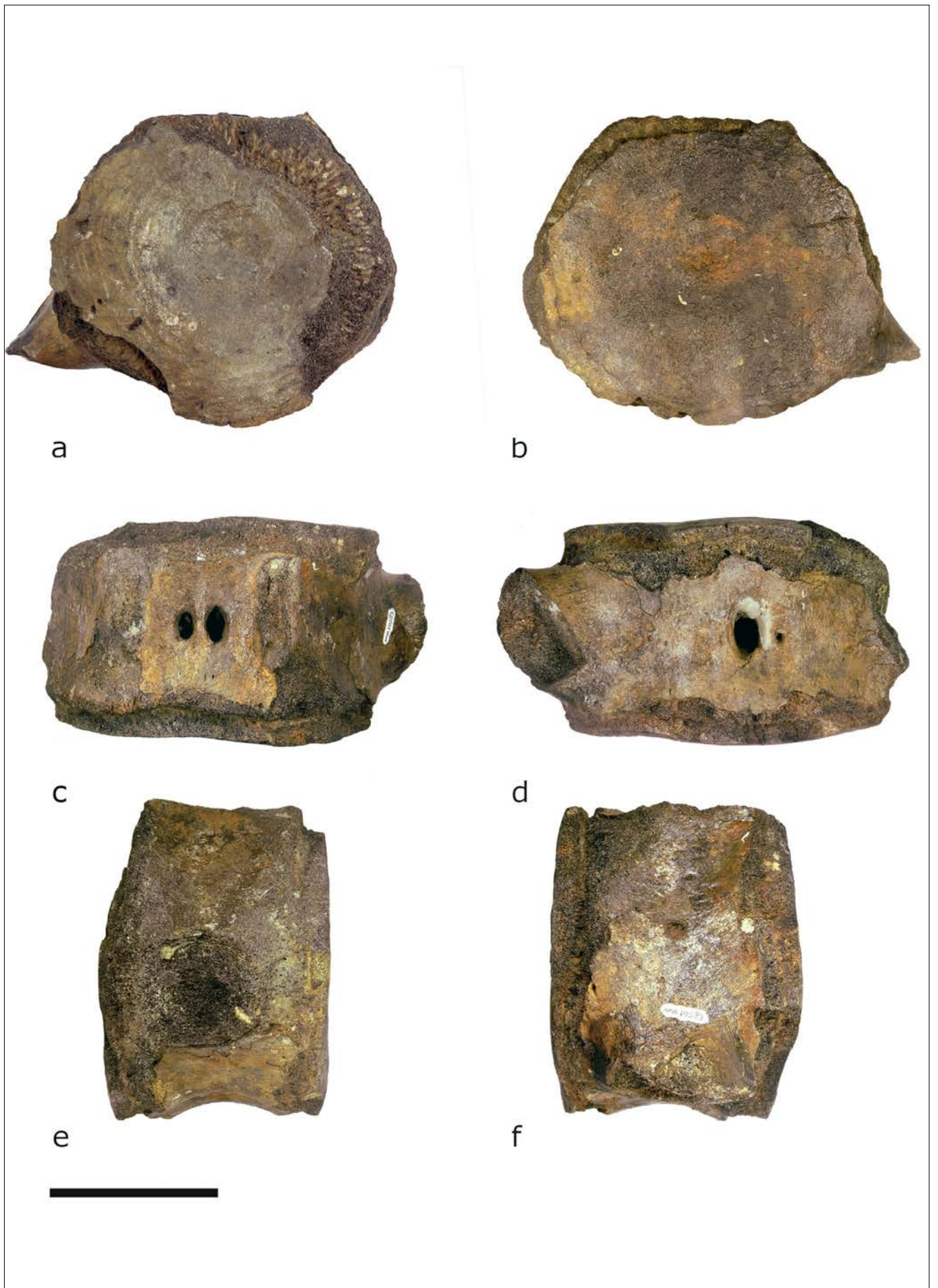
DEINSEA

Figure 8. Anterior caudal vertebral centrum, NMR999100010283, Morphotype A, from the region of Wielingen (Belgian-Dutch border), or Het Scheur (Belgium), in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Scale bar 10 cm.

due to growth in this area. The same pattern is noted in NMR-3882.

The two lumbar vertebral centra of Morphotype A have a variable number of dorsal and ventral foramina. Lumbar vertebrae in other basilosaurids mostly have a constant number of two dorsal and two ventral foramina (e.g. *Dorudon atrox* Andrews, 1906 (Uhen 2004) and *Basilosaurus cetoides* Owen, 1839 (Kellogg 1936)). The presence of multiple ventral foramina is also seen in some lumbar vertebrae of *Cynthiacetus peruvianus* (Martínez-Cáceres *et al.* 2017: 96-98). Maybe this variability is age-related, as the caudal vertebra NMR-10283 corresponding to an almost fully-grown individual shows a 'normal' count of two dorsal and two ventral foramina. But three of these foramina are unusually large, compared to known basilosaurids.

The vertebrae of Morphotype A show derived features, like a thin CCMC and a short vertebral length, not seen in the basilosaurid taxon *Pachycetus* with basal features. As the epiphyseal surfaces are flat, not rounded, the vertebrae have a low curvature. This, in combination with the very short vertebral length, must have given the torso a high elastic stability (Buchholtz & Schur 2004). Movement would have been in waves with a low amplitude and a long wavelength; therefore the swimming mode was efficient, resulting in a greater speed (Buchholtz 2001). No doubt, the increase of velocity was enhanced by the relatively low weight of the vertebral centra, because of the thin CCMC. This movement was very different from that of *Basilosaurus* spp. with very long torso vertebrae, suggestive of a high flexibility, large undulations with a high amplitude, and a short wavelength, resulting in low speed, but a high manoeuvrability. A short relative vertebral length can be seen as an advanced adaptation to an aquatic environment (Buchholtz 2001).

It is not possible to determine from which strata the vertebrae of Morphotype A originated; their geologic age could range from the Middle to Late Eocene. The derived features seem to be suggestive for an origin from the Priabonian Zelzate Formation. The six short basilosaurid lumbar vertebrae USNM 11401 (mentioned above) originated from the Priabonian of Georgia (Kellogg 1936: 256).

The first mysticetes are known from the Priabonian and ribs and vertebrae of some archaic mysticetes show basilosaurid characteristics like osteosclerosis (Van Vliet *et al.* 2019). For example, the geologically oldest mysticete, *Mystacodon selenensis* Lambert *et al.*, 2017 from the Priabonian of Peru has pachyosteosclerotic ribs and, according to the figures, also vertebrae with a CCMC (de Muizon *et al.* 2019: figs 32-37). The thoracic vertebrae with fused epiphyses, having a relative length of about 0.85 (estimated from the aforesaid figures),

are however by far not as short as the vertebrae of Morphotype A. Although till date Eocene mysticetes are only known from the Southern Hemisphere (Mitchell 1989, Lambert *et al.* 2017, Fordyce & Marx 2018), the hypothesis that the vertebrae of Morphotype A might have belonged to an archaic mysticete taxon instead of an archaeocete, cannot be completely ruled out.

We tentatively consider the vertebral centra of Morphotype A to represent the same taxon. This is apparently a new taxon (as was earlier suggested by Schouten 2011), having vertebrae with a shorter length of the centrum, than seen in all other known basilosaurid species, as well as a low degree of osteosclerosis. The vertebral centra however lack sufficient diagnostic features to erect a new taxon.

?Family BASILOSAURIDAE Cope, 1868
?Basilosauridae indet.

Morphotype B

Fig. 9; Table 2a, b
Material — One presumably posterior thoracic (or anterior lumbar) vertebral centrum (NMR999100010284).

Description — NMR-10284 is interpreted as a posterior thoracic (or maybe an anterior lumbar) vertebral centrum. The break surfaces of the apophyses are fresh. The vertebral centrum is permineralised. It is brownish to gray in colour and slightly abraded. For dimensions, see Table 2a. It is not-elongated, with a relative length <0.93; and a relative width of about 1.06 (Table 2a). A CCMC is only present along the midpart of the centrum and is most prominent at the basis of the transverse processes; it is here about 9 to 20 mm thick. The cortex bears many punctae. It has suffered superficial damage and has flaked off near the epiphyseal sides. For this reason, the anterior and posterior width and height would originally have been larger. On the anterior side, traces of the epiphyseal disc have been preserved; the epiphysis lacks completely on the posterior side. Both epiphyseal surfaces show a more or less radiating pattern of deep grooves and high ridges. These parts of grooves and ridges are remarkably thick and measure anteriorly about 33 mm (including remnants of the epiphyseal disc) and posteriorly 17mm in anteroposterior length. Between the pedicles of the neural arch is a weak median dorsal ridge. One foramen is located on the left side of a very low dorsal ridge, one smaller foramen accompanied by two punctae on the right side. The centrum is narrower at mid-length, than at the epiphyseal sides. The basis of the left transverse process is broken. The basis of the right transverse process is about 99 mm in length. It is located on the ventral

Table 2a: vertebral dimensions Morphotype B, presumed indeterminable basilosaurid (in mm) from Wielingen or Het Scheur.

No. & Figs, in Figs 18 & 19: dark-green sphere	Vertebra	Length	Width NA	Width	Height	Rel L= Ld/Wa	Rel W = Wa/Ha	References
NMR999100010284 Fig. 9, Fig. 18 & 19: B	Th (post) or Lu (ant) *)	177 (dors) 170 (vent)	88	>190 (ant) e>187 (post)	> 180 (ant) > 183 (post)	< 0.93	?1.06	This article

Table 2b: vertebral dimensions of some other basilosaurids (in mm)

No. & taxon, in Fig. 19: green spheres	Age, formation & country	Vertebra	Length	Width NA	Width	Height	Rel L= Ld/Wa	Rel W = Wa/Ha	References
NHMM197955 no.1 'Maastricht whale'	Priabonian, Klimmen Member, the Netherlands	Th (post) or Lu (ant) *)	?	?	e225	e180	?	e1.25	Van Vliet *et al.* 2019: table 1
NHMM197955 no.4 'Maastricht whale' Fig. 19: 1	Priabonian, Klimmen Member, the Netherlands	?Lu *)	e>172	?	e187	e>127	e>0.92	e<1.47	Van Vliet *et al.* 2019: table 1
PIN5821/1 Fig. 19: 2	Late Eocene, Beloglinskaya Formation, Russia	Lu 2 or 3	164	?	163 (ant) 192 (post)	135 (ant) 143 (post)	1.01	1.21	Tarasenko 2022: table 1
PIN5821/4 Fig. 19: 3	Late Eocene, Beloglinskaya Formation, Russia	Lu 5	167	?	172 (ant) 195 (post)	124 (ant) 126 (post)	0.97	1.39	Tarasenko 2022: table 1
NWMNH 2151 Fig.19:4	Priabonian, Middle Member, Keasy Formation, Oregon	Post ThA	138 (dors) 139 (vent)	?	176 (ant) 169 (post)	142 (ant) 146 (post)	0.78	1.24	Uhen & Taylor 2020: table 1
NWMNH 2151 Fig. 19:5	Priabonian, Middle Member, Keasy Formation, Oregon	Post ThB	144 (dors) 136 (vent)	?	171 (ant) 181 (post)	145 (ant) 150 (post)	0.84	1.18	Uhen & Taylor 2020: table 1
NWMNH 2151 Fig.19:6	Priabonian, Middle Member, Keasy Formation, Oregon	Post ThC	148 (dors) e140 (vent)	?	178 (ant) 185 (post)	e149 (ant) 156 (post)	0.83	e1.19	Uhen & Taylor 2020: table 1
No. M.68 Berlin 'Pontogeneus brachyspondylus' Müller, 1849 (sensu Kellogg 1936)	Priabonian, Yazoo Formation, Jackson Group, Alabama	Th 11	>163	98	~175 (ant) 172 (post)	~115 (ant) 134 (post)	?	~1.52	Kellogg 1936: table 64
No. Berlin 'Pontogeneus brachyspondylus' sensu Kellogg 1936	Priabonian, Yazoo Formation, Jackson Group, Alabama	Th 15	~204	?	? (ant) ? (post)	? (ant) ? (post)	?	?	Kellogg 1936: table 64
USNM No. 776 'Pontogeneus brachyspondylus' (sensu Kellogg 1936) Fig. 19: 7	Priabonian, Yazoo Formation, Jackson Group, Alabama	Lu3	223	?	220 (ant) 220 (post)	182 (ant) 187 (post)	1.01	1.21	Kellogg 1936: table 65
USNM No. 2211 'Pontogeneus brachyspondylus' (sensu Kellogg 1936) Fig. 19: 8	Priabonian, Yazoo Formation, Jackson Group, Alabama	Lu 11	240	?	212 (ant) 214 (post)	192 (ant) 200 (post)	1.13	1.10	Kellogg 1936: table 65
USNM No. 2211 'Pontogeneus brachyspondylus' (sensu Kellogg 1936) Fig. 19: 9	Priabonian, Yazoo Formation, Jackson Group, Alabama	Lu 12	241	?	213 (ant) 224 (post)	>187 (ant) ? (post)	1.13	<1.14	Kellogg 1936: table 65

*) with one epiphysis; **) without epiphyses

Table 2b: vertebral dimensions of some other basilosaurids (in mm) [continued].

No. & taxon in Fig. 19: green spheres	Age, formation & country	Vertebra	Length	Width NA	Width	Height	Rel L= Ld/Wa	Rel W = Wa/Ha	References
USNM No. 2211 'Pontogeneus brachyspondylus' (sensu Kellogg 1936) Fig. 19: 10	Priabonian, Yazoo Formation, Jackson Group, Alabama	Lu 13	237	?	208 (ant) 224 (post)	~186 (ant) 196 (post)	1.14	~1.12	Kellogg 1936: table 65
USNM No. 2211 'Pontogeneus brachyspondylus' (sensu Kellogg 1936) Fig. 19: 11	Priabonian, Yazoo Formation, Jackson Group, Alabama	Lu 14	234	?	205 (ant) 213 (post)	184 (ant) >173 (post)	1.14	1.11	Kellogg 1936: table 65
FV 8748	Priabonian, Escalante Formation, British Columbia	Lu	111	92	166 (ant) 183 (post)	>131 (ant) 120 (post)	0.67	<1.27	Kellogg 1936, Uhen & Taylor 2020
MNHN.F.PRU 10 Cynthiacetus peruvianus Martínez-Cáceres & de Muizon, 2011	Priabonian, Otuma Formation, Peru	Th 10	101 (dors) 100 (vent)	80	107 (ant) 122 (post)	88 (ant) 98 (post)	0.94	1.22	Martínez-Cáceres et al.: 2017: table 7
MNHN.F.PRU 10 Cynthiacetus peruvianus	Priabonian, Otuma Formation, Peru	Lu 11	142 (dors) 142 (vent)	?	162 (ant) 164 (post)	160 (ant) 164 (post)	0.88	1.01	Martínez-Cáceres et al. 2017: table 7
MMNS VP 445 Cynthiacetus maxwelli Uhen, 2005	(Bartonian-) Priabonian, Yazoo Clay Formation, Mississippi	ThE*)	83 (dors) 76 (vent)	?	116 (ant) 117 (post)	91 (ant) 102 (post)	0.72	1.27	Uhen 2005: table 3
MMNS VP 445 Cynthiacetus maxwelli	(Bartonian-) Priabonian, Yazoo Clay Formation, Mississippi	LuA*)	87 (dors) 82 (vent)	?	118 (ant) 116 (post)	? (ant) ? (post)	0.74	?	Uhen 2005: table 3
St11414 Masracetus markgrafi Gingerich, 2007	Priabonian, Birket quarun Formation, Egypt	Posterior-most Th	134	?	174	136	0.77	1.28	Slijper 1936: table 23, Gingerich 2007
St11414 Masracetus markgrafi	Priabonian, Birket quarun Formation, Egypt	Lu 11	143	?	175	144	0.82	1.22	Slijper 1936: table 23, Gingerich 2007

*) without epiphyses

part of the lateral side and was probably directed anteroventrally. On the left part of the ventral side, some layers of the multi-layered cortex have been erased; the remaining multi-layered cortex has a smooth surface. The right part of the ventral side is rough, without characteristic structures. Except for several round punctae, there are no ventral foramina (Fig. 9).

Discussion — The vertebral centrum of Morphotype B differs from the vertebral centra of Morphotype A and C in having a significantly larger relative length than those of Morphotype A, and a smaller relative length than those of Morphotype C, in having small dorsal foramina, in having probably small or maybe no ventral foramina, and in the absence of elongated transverse processes, contrary to the vertebrae of Morphotype C. The CCMC is only present at the midpart of the centrum, probably because of abrasion at the epiphyseal sides. The

anterior and posterior parts consist of what originally seems to have been spongy bone. The vertebral centrum shows the earlier mentioned characteristics: the transverse processes were most probably directed anteroventrally instead of horizontally and are located low on the lateral side, the neural arch is wide and there is a (partial) CCMC. The epiphyseal surfaces of the centrum show a pattern that can be described as both irregular and radiating, resembling that of the vertebrae of Morphotype A (see section 'discussion Morphotype A'). NMR-10284 is interpreted as a thoracic vertebra because of the broad neural arch and the absence of ventral foramina, but an anterior lumbar position cannot be not excluded. In the large basilosaurid taxa *Basilosaurus cetoides*, '*Pontogeneus brachyspondylus*' (*sensu* Kellogg 1936), *Pachycetus* spp. from Europe and *Cynthiacetus peruvianus*, ventral foramina are invariably present in lumbar vertebrae (Kellogg 1936, Martínez-Cáceres *et al.* 2017: 89-100, Van Vliet
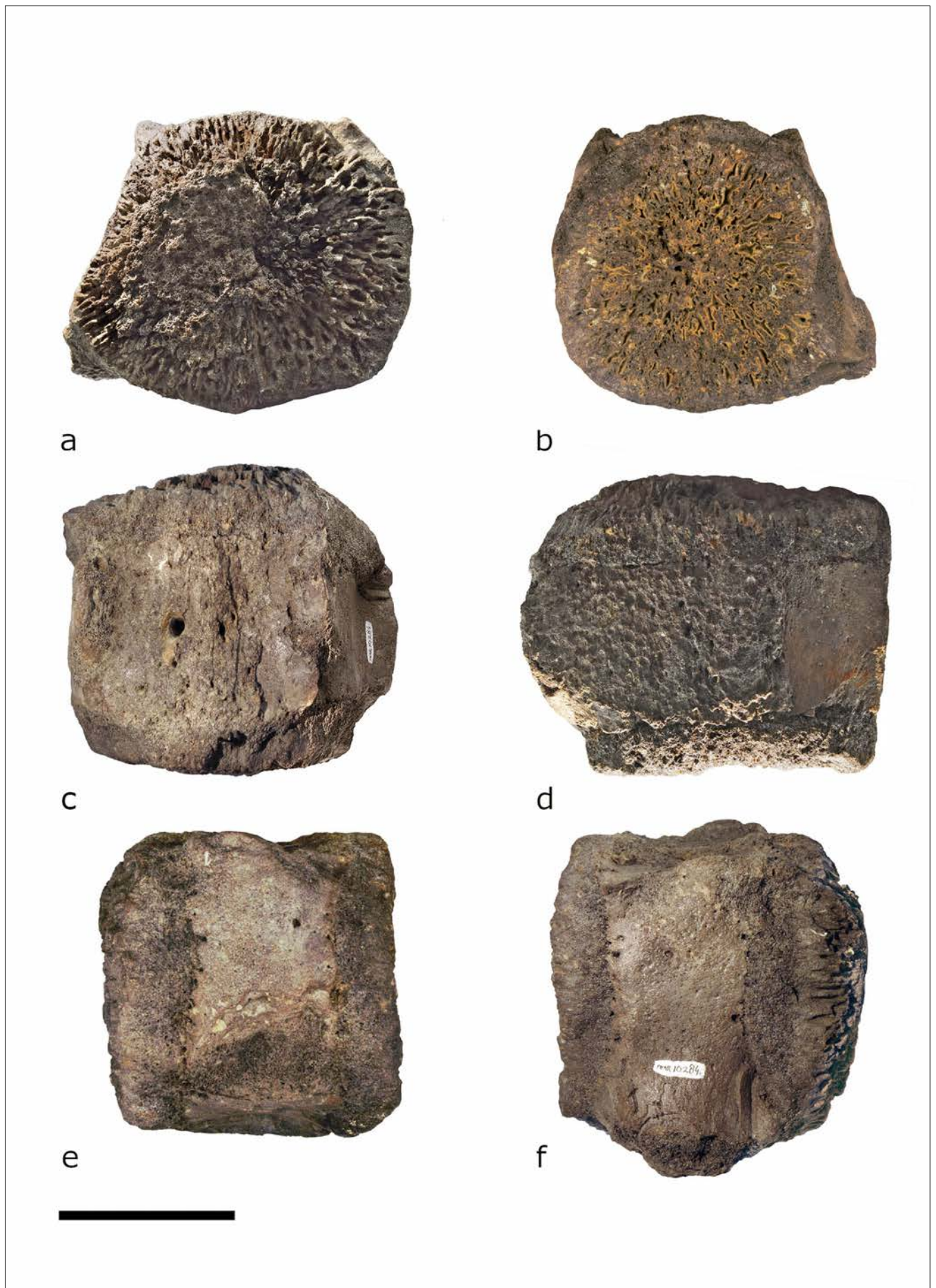
Figure 9. Presumably central-posterior thoracic (or anterior lumbar) vertebral centrum, NMR999100010284, Morphotype B, from the region of Wielingen (Dutch-Belgian border), or Het Scheur (Belgium), in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Scale bar 10 cm.

et al. 2020). However, ventral foramina are not or only sometimes present in thoracic vertebrae. In *B. cetoides*, thoracic vertebrae lack ventral foramina altogether (Kellogg 1936) and they have not been described (or figured) in thoracic vertebrae of '*Pontogeneus brachyspondylus*' (*sensu* Kellogg 1936). In thoracic vertebrae assigned to *Pachycetus* from Europe, ventral foramina are variably present (Van Vliet et al. 2020) and in *C. peruvianus* ventral foramina are not present in Th1-9, but do occur in Th10 and more posterior thoracic vertebrae (see Martínez-Cáceres et al. 2017: 74).

The relative dimensions of vertebra NMR-10284 resemble those of the not-elongated vertebrae of *Cynthiacetus maxwelli, C. peruvianus, Masracetus markgrafi* Gingerich, 2007, an indeterminable basilosaurid NWMNH2151 (Uhen & Taylor 2020) and '*Pontogeneus brachyspondylus*' (*sensu* Kellogg 1936). The dimensions are larger than those of *C. peruvianus, C. maxwelli,* or *M. markgrafi* (Slijper 1936: table 23), and slightly larger than the three posterior thoracic vertebrae NWMNH2151. Width and height of the centrum are also larger than those of a Th11 of '*P. brachyspondylus*' (*sensu* Kellogg 1936). Kellogg (1936: table 64) gives dimensions of Th10-12 and Th15, and Th11 is the largest of these. However, all these thoracic vertebrae are broken and their original length is in fact unknown. Also the dimensions are larger than those of two anterior lumbar vertebral centra PIN5821/1 and PIN5821/4 from an indeterminable basilosaurid from Gorny Luch, Russia (Tarasenko 2022: table 1) (Table 2b). The length is only comparable to that of this Th11 of '*P. brachyspondylus*' (*sensu* Kellogg 1936). All these vertebrae retain their epiphyses, in contrast to NMR-10284. The dimensions are almost similar to those of a reconstructed, probably lumbar vertebra of a partial cetacean skeleton (NHMM197955 no.4) from the Priabonian parts of the Tongeren

Formation of Maastricht, the Netherlands (Van Vliet et al. 2019: table 1). This skeleton was attributed to a probable basilosaurid with vertebral centra that are of comparable size to those of '*P. brachyspondylus*' (*sensu* Kellogg 1936), but an early mysticete could not be ruled out completely for this specimen for the same reasons as given above (Van Vliet et al. 2019; see discussion Morphotype A).

All cetaceans mentioned in the latter section are known from Priabonian strata (Table 3b), except *C. maxwelli* that is possibly also known from the Bartonian (Uhen 2013). For these reasons, it seems not improbable that the vertebral centrum NMR-10284 originated from the Priabonian parts of the Zelzate Formation. If so, both cetaceans (the here described NMR-10284 and NHMM197955 from Maastricht) could belong to the same taxon, as the distance between Maastricht and Wielingen is less than 200 km. Also in the case of NMR-10284, an early mysticete taxon instead of an archaeocete taxon cannot be completely excluded (see also discussion Morphotype A). Nevertheless, Uhen & Taylor (2020) stated about the three rather similar vertebrae (NWMNH2151) that they belonged to a basilosaurid, because of the combined presence of punctae, the anteroposteriorly broad neural arches, neural spines and transverse processes, and the anteroventrally directed transverse processes.

Family BASILOSAURIDAE Cope, 1868
Genus *PACHYCETUS* Van Beneden, 1883
Species indet.

Morphotype C

Figs 10-17; Table 3a, b, c, d, e

Table 3a: vertebral dimensions Morphotype C, *Pachycetus* sp. probably from Het Scheur.

No. & Figs, in Figs 18 & 19: dark-blue spheres	Vertebra	Length	Width NA	Width	Height	Rel L= Ld/Wa	Rel W = Wa/Ha	References
NMR999100012331 Fig. 10, Fig. 18: C1	Th**)	163 (dors) 158 (vent)	85	127 (ant) 147 (post)	107 (ant) 102 (post)	1.28	1.19	This article
NMR999100012332 Fig. 11, Fig. 18: C2	Th**)	162 (dors) 155 (vent)	83	132 (ant) 152 (post)	109 (ant) 114 (post)	1.23	1.21	This article
NMR999100003404 Fig. 13, Figs. 18 &19: C3	Lu**)	>208 (dors) >165 (vent)	78	>150 (ant) e175 (post)	e125 (ant) 124 (post)	?	?	Post 2007, Schouten 2011, Post et al. 2017, this article
NMR999100016645 Fig. 14 Figs. 18 &19: C4	Lu**)	204 (dors) 195 (vent)	e76	e148 (ant) 156 (post)	e120 (ant) 124 (post)	e1.38	e1.23	This article
NMR999100150840 Fig. 15	Lu orTh**	>99 (dors) > 85 (vent)	55	122 (ant?) ? (post?)	94 (ant?) ? (post?)	?	1.30	This article
NMR999100013472 Fig. 16	Lu**)	>107 (dors) >99 (vent)	?	?(ant) ?(post)	95? (ant) 121 (post)	?	?	Post 2007, this article
NMR999100150839 Fig. 17, Figs. 18 &19: C5	Lu**)	121 (dors) 118 (vent)	e55	102 (ant?) 105 (post?)	89 (ant?) 82 (post?)	1.19	1.15	This article

DEINSEA

Table 3b: dimensions neural arch Morphotype C, *Pachycetus* sp. (in mm) probably from Het Scheur.

No. & Fig	Vertebra	Length	Width NA	Width	Height	References
NMR999100012333 Fig. 12	?Th	1 76	?	132	121	This article

Table 3c: lumbar vertebral dimensions in *Pachycetus* spp. and *Pachycetus*-like cetaceans (in mm).

No. & taxon, in Fig. 19: blue spheres	Age, formation & country	Vertebra	Length	Width NA	Width	Height	Rel L= Ld/Wa	Rel W = Wa/Ha	References
Pachycetus (Platyosphys) paulsonii Brandt, 1873 Fig. 19: 1	Bartonian-Priabonian, Kharkiv Formation (Kyiv Formation or Obukhiv Formation?), Ukraine	Lu1 *)	269 (vent)	126	~173 (ant)	~162 (ant)	~155 (Lv/Wa)	~1.07	Kellogg 1936: table 24
Pachycetus (Platyosphys) paulsonii Fig. 19: 2	Bartonian-Priabonian, Kharkiv Formation, Ukraine	Lu'2'	283 (vent)	128	161 (ant)	151 (ant)	1.76 (Lv/Wa)	1.07	Kellogg 1936: table 24
Pachycetus (Platyosphys) paulsonii Fig. 19: 3	Bartonian-Priabonian, Kharkiv Formation, Ukraine	Lu'3'	282 (vent)	109	165 (ant)	157 (ant)	1.71 (Lv/Wa)	1.05	Kellogg 1936: table 24
Pachycetus (Platyosphys) paulsonii Fig. 19: 4	Bartonian-Priabonian, Kharkiv Formation, Ukraine	Lu'5'	274 (vent)	107	164 (ant)	157 (ant)	1.67 (Lv/Wa)	1.04	Kellogg 1936: table 24
Pachycetus (Platyosphys) paulsonii Fig. 19: 5	Bartonian-Priabonian, Kharkiv Formation, Ukraine	Lu'7'	231 (vent)	~56	157 (ant)	147 (ant)	1.47 (Lv/Wa)	1.07	Kellogg 1936: table 24
Pachycetus (Platyosphys) paulsonii Fig. 19: 6	Bartonian-Priabonian, Kharkiv Formation, Ukraine	Sa'8' (Lu'8')	233 (vent)	55	~154 (ant)	~141 (ant)	~1.51 (Lv/Wa)	~1.09	Kellogg 1936: table 24
Pachycetus (Platyosphys) paulsonii Fig. 19: 7	Bartonian-Priabonian, Kharkiv Formation Ukraine	Lu'1'	260 (vent)	70	155	140	1.68 (L/W)	1.11	Kellogg 1936: table 25
Pachycetus (Platyosphys) paulsonii Fig. 19: 8	Bartonian-Priabonian, Kharkiv Formation Ukrainer	Lu'3 '	228 (vent)	55	150	145	1.52 (L/W)	1.03	Kellogg 1936: table 25
NMR999100151795 *Pachycetus* sp. Fig. 19: 9	Bartonian-Priabonian, Gehlberg Formation Germany	Lu **)	>223 (dors) >223 (vent)	?	e140 (ant) e178 (post)	>117 (ant) 130 (post)	e>1.59	e<1.20	Van Vliet et al. 2020: appendix table 2b
ID20-2/ID20-4 *Pachycetus* sp. Fig. 19: 10	Bartonian-Priabonian, Gehlberg Formation, Germany	Lu **)	235 (dors) 239 (vent)	e70	e130 (ant) e140 (post)	131 (ant) 124 (post)	>1.81	e0.99	Van Vliet et al. 2020: appendix table 2b
USMN534001 *Pachycetus* sp. Fig. 19: 11	Bartonian-Priabonian, Stockletten Formation, Germany	Lu (epi?)	210	?	161	?	1.30	?	Uhen & Berndt 2008

Table 3c: lumbar vertebral dimensions in *Pachycetus* spp. and *Pachycetus*-like cetaceans (in mm) [continued].

No. & taxon, in Fig. 19: blue spheres	Age, formation & country	Vertebra	Length	Width NA	Width	Height	Rel L= Ld/Wa	Rel W = Wa/Ha	References
KOM44693 P 195 *Pachycetus* (*Basilotritus*) sp. Fig. 19: 12	Bartonian-Priabonian, Kyiv Formation or Obukhiv Formation, Ukraine	Lu**)	202	95	136 (ant) 157 (post)	126 (ant) 125 (post)	1.49	1.08	Gol'din & Zvonok 2013: appendix 3
GMTSNUK 2638D '*Platyosphys einori*' Gritsenko 2001 or basilosaurid *incertae sedis* Fig. 19: 13	Priabonian, Obukhiv Formation, Ukraine	Lu**)	188	63	152 (ant) 144 (post)	>105 (ant) >76 (post)	1.24	<1.45	Gritsenko 2001, Gol'din & Zvonok 2013: appendix 4 Davydenko et al 2021
GMTSNUK 2638E '*Platyosphys einori*' or basilosaurid *incertae sedis* Fig. 19: 14	Priabonian, Obukhiv Formation, Ukraine	Lu or Cd**)	199	41	136 (ant) 134 (post)	>70 (ant) >79 (post)	1.46	<1.94	Gritsenko 2001, Gol'din & Zvonok 2013: appendix 4, Davydenko et al 2021
GMTSNUK 2638C '*Platyosphys einori*' or basilosaurid *incertae sedis* Fig. 19: 15	Priabonian, Obukhiv Formation, Ukraine	Lu or Cd**)	212	60	153 (ant) 140 (post)	>78 (ant) >82 (post)	1.39	<1.96	Gritsenko 2001, Gol'din & Zvonok 2013: appendix 4, Davydenko et al 2021
GMTSNUK 2638A '*Platyosphys einori*' or basilosaurid *incertae sedis* Fig. 19: 16	Priabonian, Obukhiv Formation, Ukraine	Lu or Cd**)	234	76	157 (ant) 136 (post)	>97 (ant) >98 (post)	1.49	<1.62	Gritsenko 2001, Gol'din & Zvonok 2013: appendix 4, Davydenko et al 2021
GMTSNUK 2638B '*Platyosphys einori*' or basilosaurid *incertae sedis* Fig. 19: 17	Priabonian, Obukhiv Formation, Ukraine	Lu or Cd**)	225	67	155 (ant) 156 (post)	>80 (ant) >75 (post)	1.45	<1.94	Gritsenko 2001, Gol'din & Zvonok 2013: appendix 4, Davydenko et al 2021

*) with one epiphysis; **) without epiphyses

Abbreviations ~, about; /, fraction

Material — Two thoracic vertebral centra (NMR999100012331, NMR999100012332), a partial vertebral neural arch, probably of a thoracic vertebra (NMR999100012333), a posterior thoracic or anterior lumbar vertebral centrum (NMR999100150840) and four lumbar vertebral centra (NMR999100003404, NMR999100013472, NMR999100016645 and NMR999100150839).

Comments — NMR-3404 has been described by Post (2007), Schouten (2011) and Post *et al.* (2017), and NMR-13472 by Post *et al.* (2017).

Description — Large vertebral centra with only the pedicles of the neural arch and the basis of the transverse processes preserved. The centra are elongated, with a relative length between 1.19 and e1.38. The height is smaller than the width, with a relative width ranging between 1.15 to 1.30 (Table 3a). The epiphyses are mostly lacking, although sometimes some traces of the disc are preserved. The epiphyseal sur-faces show a more or less radiating pattern of grooves and ridges. The pedicles of the neural arch and (the basis) of the transverse processes are elongated and massive. The transverse processes were directed anteroventrally. They all have a thick CCMC, about 5 to 23 mm thick. The surface is often pock-marked by elongated punctae. Vertebral dimensions are given in Table 3a; dimensions of the neural arch are given in Table 3b.

NMR-12331 is a central-posterior thoracic vertebral centrum. On the break surfaces of the pedicles of the neural arch, a thick CCMC is visible. The centrum is grey to black in colour and abraded. The surface of the vertebral centrum has large punctae that are sometimes hard to distinguish from the multiple drilling holes made by organisms. The anterior epiphyseal surface is saddle-shaped, the posterior epiphyseal surface flat. On the lateral sides of the anterior epiphyseal surface, a large fovea for the capitulum of the rib is present. Just posterior to this fovea, an excavation is present on the transverse process, which is

Table 3d: vertebral dimensions in *Pachycetus wardii* & *P. aithai* (in mm).

Taxon, in Fig. 19: grey spheres	Age, formation & country	Vertebra	Length	Width NA	Width	Height	Rel L= Ld/Wa	Rel W = Wa/Ha	References
USNM 310633 *Pachycetus wardii* Uhen, 1999 Fig. 19: 1	(Lutetian-)Bartonian, Comfort Member, Castle Hayne Formation, North Carolina	LuB	164 (dors) 165 (vent)	?	110 (ant) 120 (post)	93 (ant) 96 (post)	1.49	1.18	Uhen 1999: appendix 1
USNM 449549 *Pachycetus wardii* Fig. 19: 2	(Lutetian-)Bartonian, Comfort Member, Castle Hayne Formation, North Carolina	LuC	~164 (dors) ~163 (vent)	?	119 (ant) ~137 (post)	~109 (ant) ~112 (post)	~1.38	~1.09	Uhen 1999: appendix 1, Uhen 2013
FSAC Bouj *Pachycetus aithai* Gingerich & Zouhri, 2015 Fig. 19: 3	Bartonian, Aridal Formation, Morocco	Lu1?	151	44	100 (ant) 109 (post)	88 (ant) 89 (post)	1.51	1.14	Gingerich & Zouhri 2015: table 2
FSAC Bouj *Pachycetus aithai* Fig. 19: 4	Bartonian, Aridal Formation, Morocco	Lu2?	158	44	104 (ant) 111 (post)	87 (ant) 94 (post)	1.52	1.20	Gingerich & Zouhri 2015 table 2
FSAC Bouj *Pachycetus aithai* Fig. 19: 5	Bartonian, Aridal Formation, Morocco	Lu3?	175	42	111 (ant) 108 (post)	101 (ant) 102 (post)	1.58	1.10	Gingerich & Zouhri 2015 table 2

Abbreviations ~, about; /, fraction

interpreted as the fovea for the tuberculum of the rib. Both foveae are confluent (Fig. 10e). A posterior fovea on the lateral sides of the posterior epiphyseal surface is maybe also present. Between the pedicles of the neural arch a median ridge is present. The ridge has suffered some damage at the midpart. Signs of possibly two inconspicuous foramina are located on the left side, while two foramina are clearly visible on the right side of this ridge. The lateral projection of the elongated transverse processes is only short. They are located at mid-height of the lateral sides. The ventral side of the centrum lacks a median ridge or foramina (Fig. 10).

NMR-12332 is a central-posterior thoracic vertebral centrum. A thick CCMC is visible, e.g. on the anterior break surface of the left transverse process. The centrum is grey to black in colour and is more abraded than NMR-12331. There are many, rather large punctae and drilling holes made by organisms over the entire surface. The anterior epiphyseal surface is saddle-shaped, the posterior epiphyseal surface more or less flat. A large fovea for the capitulum of the rib is present on the anterior end of the transverse process. Just posterior to this fovea, an excavation is present on the transverse process, which is interpreted as the fovea for the tuberculum of the rib (Fig. 11f). Both foveae are confluent. A posterior fovea seems to be absent. A median ridge is located between the pedicles of the neural arch. Some confluent small oval foramina (two on the left, three on the right) are located in an elongated fossa on each side of this ridge. The lateral projection of the elongated transverse processes is only short, slightly larger than those of NMR-12331. They are located at mid-height of the lateral sides. The ventral side is

smooth, with two shallow lateral ridges, but without a ventral median ridge. A small foramen is present on both the left and right sides of the midline, the left foramen being larger than the right one (Fig. 11).

NMR-12333 is the dorsal part of a vertebral neural arch. It probably belonged to an anterior-central thoracic vertebra. The partial neural arch is thoroughly permineralised and yellowish to grey in colour. The broken pedicles are pachyosteosclerotic (Fig. 12d). The neural spine is partly preserved and is broken anteriorly. The left metapophysis is lost, the right metapophysis has suffered some damage. The postzygapophyses are well preserved and have the shape of a half cone, with a flattened ventral surface, and with a rounded posterior end (Fig. 12c). Their anteroposterior length is about 5 cm. The prezygapophyses are broken (Fig. 12).

NMR-3404 is a moderately elongated, lumbar vertebral centrum. Some break surfaces are abraded, but the fractures at the posterior epiphyseal surface are fresh, although the surface is overgrown with encrustations. There are multiple drilling holes made by marine organisms. A large cavity on the basis of the left transverse process in the lumbar vertebral centrum NMR-3404 (Fig. 13e), is probably due to the disappearance of the spongy bone by scavenging organisms. The osteosclerotic cortex around the cavity is still present. As especially the originally soft bone marrow has been removed, most probably the damage has occurred in the past, when the vertebral centrum was not yet hardened by permineralisation - indeed maybe immediately *post mortem*. The centrum is permineralised,

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Table 3e: vertebral features in *Pachycetus* spp., shared by vertebral centra, Morphotype C, Het Scheur, Belgium

Features	NMR-12331 (Th)	NMR-12332 (Th)	NMR-12333 (NA ?Th)	NMR-3404 (Lu)	NMR-16645 (Lu)	NMR-150840 (?Th/Lu)	NMR-13472 (Lu)	NMR-15039 (Lu)	References
Tapering vertebrae	+	+	?	?	~	?	?	?	Brandt 1873, Gingerich & Zouhri 2015
Width > height	+	+	+	?	?	?	?	+	Brandt 1873, Gol'din & Zvonok 2013, Gingerich & Zouhri 2015
Pachyostotic pedicles neural arch	+	+	+	?	+	?	+	+	Brandt 1873, Gol'din & Zvonok 2013
Elongated pedicles neural neural arch	+	+	+	+	+	?	+	+	Uhen 1999, Gol'din & Zvonok 2013
Elongated torso vertebrae	+	+	?	+	+	?	?	+	Brandt 1873, Kellogg 1936, Uhen 1999, Gol'din & Zvonok 2013
Elongated transverse processes	+	+	?	+	+	?	+	+	Brandt 1873, Kellogg 1936, Uhen 1999, Gol'din & Zvonok 2013
Compact circumferential multi-layered cortex	+	+	+	+	+	+	+	+	Brandt 1873, Uhen 1999, Gol'din & Zvonok 2013
Pock-marked surface; punctae	~	~	~	+	+	+	+	+	Uhen 1999, Gol'din & Zvonok 2013
Inner structure consists of two coni[b)	?	?	?	+	+	+	?	?	Brandt 1873, Van Vliet et al. 2020
Ventral ridge, on both sides elongated fossae	-	-	?	+	?	+	-	+	Van Vliet et al. 2020
Elongated ventral foramina directed antro-posteriorly	-	-	?	~	?	+	?	-	Kellogg 1936, Van Vliet et al. 2020
Presence anterior notch transverse process[c)	-	-	?	+	?	?	-	-	Uhen 1999, Van Vliet et al. 2020

a) Not present in *Pachycetus wardii* Uhen, 1999 (Uhen 2013)

b) Described in *Pachycetus aithai* Gingerich & Zouhri, 2015 (Gingerich & Zouhri 2015) and in *Pachycetus* sp. from the Helmstedt region, Germany (Van Vliet et al. 2020)

c) Described in *Pachycetus wardii* (Uhen 2001) and in *Pachycetus* sp. from the Helmstedt region, Germany (Van Vliet et al. 2020)

Abbreviations

e ?, unknown; +, present; -, absent

yellowish - brownish in colour and abraded. Contrary to the other parts of the centrum, the posterior epiphyseal surface does not show signs of abrasion. It is however partially damaged, showing a fresh break surface on the left part. Because of this damage, the round outline of the posterior conus is visible (Fig. 13b). The inner structure of torso vertebrae in this genus consists of two coni, an anterior and a posterior one; see also Gingerich & Zouhri (2015) and Van Vliet et al. (2020). The CCMC is remarkably thick, most prominently at the transverse processes. On the vertebral surface large punctae are present. The surface of the anterior side is rough and uneven, due to traces of the epiphyseal disc. The posterior epiphyseal disc is lacking. Between the pedicles of the neural arch is a prominent median ridge. A small dorsal foramen is located on each side of this ridge. On the left side, a part of the centrum is broken. The basis of the right transverse process is anteroposteriorly nearly as long as the centrum and is located on the ventral part of the lateral side. Although some damage did occur, a notch is still visible on the anterior side (Fig. 13d: arrow). The ventral side is rough with some damage. On each side of a low ventral ridge, an elongated ventral foramen is located in an elongated groove; because of abrasion, these grooves are difficult to see. The left foramen is much larger than the right one.

NMR-16645 is a moderately elongated, lumbar vertebral centrum, missing a part of the right side. The fracture sides are fresh. The CCMC is thick, especially on the preserved part of the transverse process. About one third of the anterior epiphyseal surface is lacking, the posterior epiphyseal surface is complete. The centrum is completely permineralised, black in colour and abraded. The surface shows narrow, elongated punctae. Only the left pedicle of the neural arch is preserved. The dorsal vertebral surface between the pedicles is preserved on the posterior part. There is one dorsal foramen on the left side of a narrow median ridge; on the right side two small foramina are present. A large part of the left transverse process is preserved, but anteriorly a part has been broken. It is located on the ventral part of the lateral side. The right transverse process is missing. Ventrally, the left side of the centrum is preserved, including a prominent median ridge and a deep, narrow and elongated fossa on both sides of this ridge. In each fossa, an elongated, transversely compressed foramen is present, the left one being larger than the right one. Lateral to the right fossa, a large part of the vertebra is missing; the right foramen is lying along the break surface. It appears to be fan-shaped in a very characteristic way, because of its elongation and being transversely compressed. It is in the shape of a 'V' turned upside down, and is directed posteroventrally, with the posterior side of the 'V' oblique at an angle of about 45°, and the anterior side of the 'V' at an angle of 90° with respect to the ventral surface of the vertebra (Fig. 14f: arrows). Due to damage, the inner structure of the centrum is revealed. The left half of the anterior conus is seen along the break surfaces. It is about 70 mm in height, from the anterior epiphyseal surface to mid-length of the centrum. On the posterior side, the CCMC is broken along an inner conus which originally consisted of spongy bone. The posterior conus is broad at the epiphyseal surface and tapers toward mid-length of the centrum. It is anterior-posteriorly about 90 mm in length. The surface of the conus has multiple, longitudinal imprints of small blood vessels (sulci), running from the midpart of the centrum to the epiphyseal surface (Fig. 14f).

NMR-150840 is a probably thoracic or lumbar vertebral centrum; only the presumably anterior half has been preserved, consisting of the main part of a conus. The centrum was originally elongated. The centrum is permineralised, black in colour and slightly abraded. The presumably anterior epiphysis seems to have been near fusion with the centrum, but has broken off. The remaining epiphyseal surface is therefore concave. The pedicles of the neural arch are damaged. There is a dorsal median ridge with a round foramen on the (presumably) left side and an inconspicuous foramen on the other side. The transverse processes are missing. The ventral side has suffered much damage, missing the complete surface. The hardly visible conus was about 60 mm in height and dorsally flattened. The centrum is broken at the midpart; this part of the vertebra consists completely of compact bone. At this location, the top of the two original coni have approximated each other. There is no sign of ventral foramina, maybe because of damage (Fig. 15).

NMR-13472 is a partial lumbar vertebral centrum, lacking both anteriorly and posteriorly a considerable part. Its original length cannot be estimated. The centrum appears to be only slightly permineralised, judged by its low weight. It is black in colour and not abraded. A CCMC is present at e.g. the ventral side of the vertebral centrum. The

inner part of the centrum consists of spongy bone. The width of the neural arch is rather small compared to the other described vertebral centra of this morphotype. On the dorsal side of the centrum a large cavity is present, probably caused by damage of the bone surrounding the original dorsal foramina. Remnants of a prominent dorsal median ridge are visible near the posterior epiphyseal surface. The left transverse process is partly preserved on the posterior side and shows a thick CCMC. The right transverse process is partly preserved on the anterior side. Both transverse processes were originally anteroposteriorly as long as the vertebral centrum. They are placed low on the ventral part of the lateral sides. Elongated punctae are scattered along the ventral surface of the centrum (see Fig. 16d). Ventrally, a rather broad fossa is present, having a small foramen on the left side and two adjacent, small foramina on the right side (Fig. 16).

NMR-150839 is a lumbar vertebral centrum, slightly distorted by pressure. The vertebra shows damage on the presumably left side. Along break surfaces a CCMC is visible. The centrum is permineralised, black in colour and slightly abraded. Elongated punctae are scattered along the surface and multiple small punctae occur near the posterior epiphyseal side. The epiphysial surfaces are flat. The width of the neural arch is only about 55 mm. On the presumably anterior side, some remnants of a dorsal median ridge are present. Some small dorsal foramina are present near the median ridge. The (presumably) left transverse process is missing. The (presumably) right transverse process shows damage on the lateral side. It is located low on the ventral part of the lateral side. The ventral side has a low median ridge and two elongated, shallow fossae. The (presumably) left fossa has two or three small foramina (Fig. 17).

Discussion — The vertebral centra of Morphotype C differ from vertebral centra of Morphotype A and B in being elongated, having (if present) elongated ventral foramina, having anterior-posteriorly elongated transverse processes, and in the presence of a thick CCMC. The vertebrae have the aforementioned characteristics, that are not present in Recent cetaceans: anteroventrally directed transverse processes (except for NMR-12331 and NMR-12332), which are in lumbar vertebrae placed low on the lateral sides, wide neural arches, and a CCMC, with five vertebral centra (NMR-12332; NMR-3404; NMR-16645; NMR-150839; NMR-13472) having one or two small to large foramina on the ventral side (see discussion for Morphotype A). The epiphyseal surfaces show a more or less regular radiating pattern of bony ridges at the periphery, with a more chaotic pattern in the central area, resembling that of the vertebrae of Morphotype A and B.

The pachyosteosclerotic pedicles of the neural arch (NMR-12332, NMR-12333, NMR-3404), and the apparently anteroposteriorly elongation of the pedicles of the neural arch and the transverse processes (NMR-3404, NMR-16645), are considered diagnostic for the basilosaurid genus *Pachycetus* (Gol'din & Zvonok 2013, there called *Basilotritus*, see also section 'terminology' and Table 3d). These and other features (height of the centrum less than the width; elongation torso vertebrae; presence of a CCMC; pock-marked surface of the centrum; inner part of torso vertebrae consisting of two coni; elongated ventral foramina; anterior notch on transverse processes of lumbar centra) of the vertebral centra of Morphotype C, shared with those of *Pachycetus* are given in Table 3c. Notwithstanding these vertebral
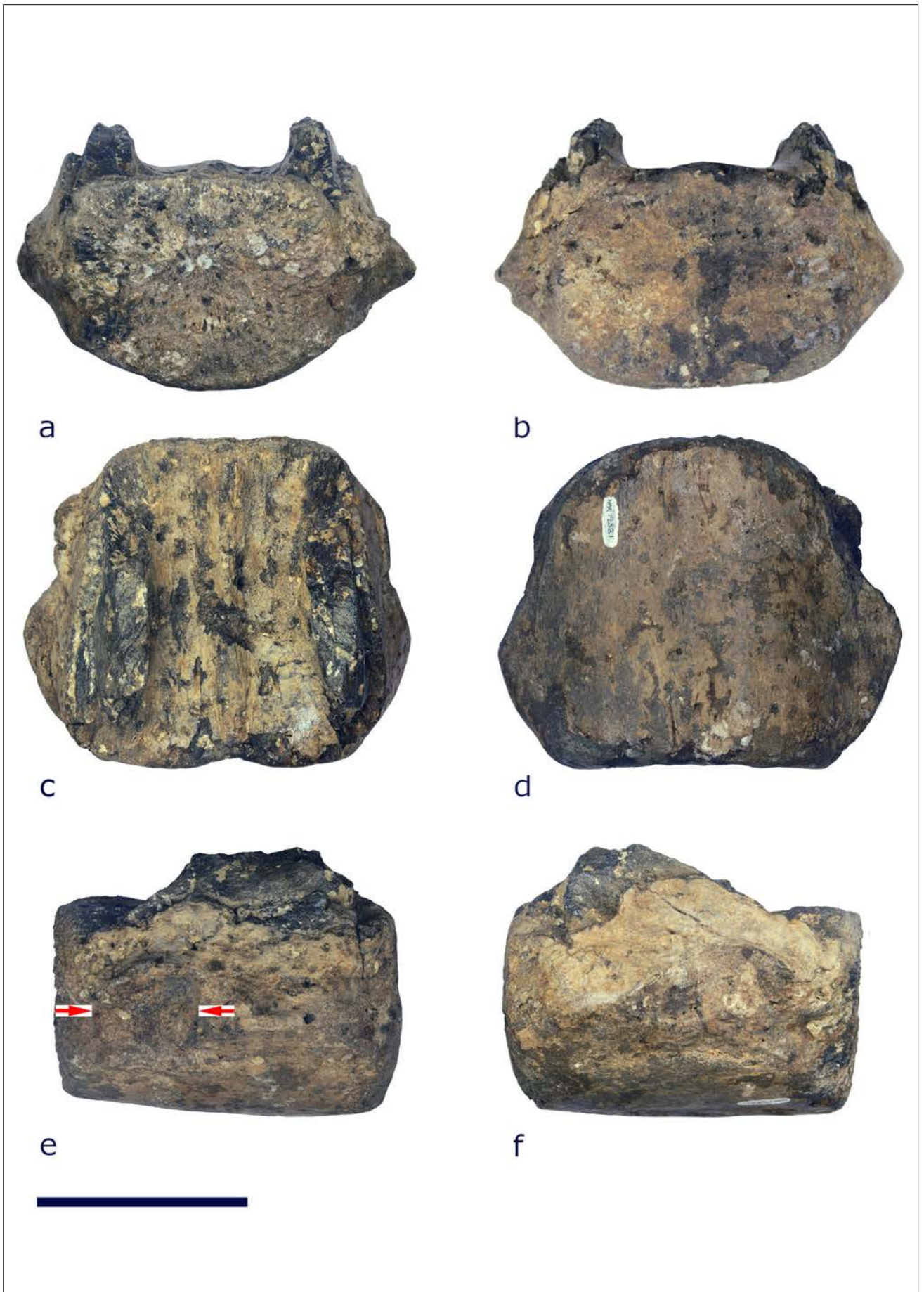
Figure 10. Central-posterior thoracic vertebral centrum, NMR999100012331, Morphotype C, *Pachycetus* sp., from Het Scheur, Belgium, in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Left arrow in 10e indicates the anterior fovea for the capitulum of the rib; right arrow indicates the probable fovea for the tuberculum of the rib on the transverse process. Scale bar 10 cm.
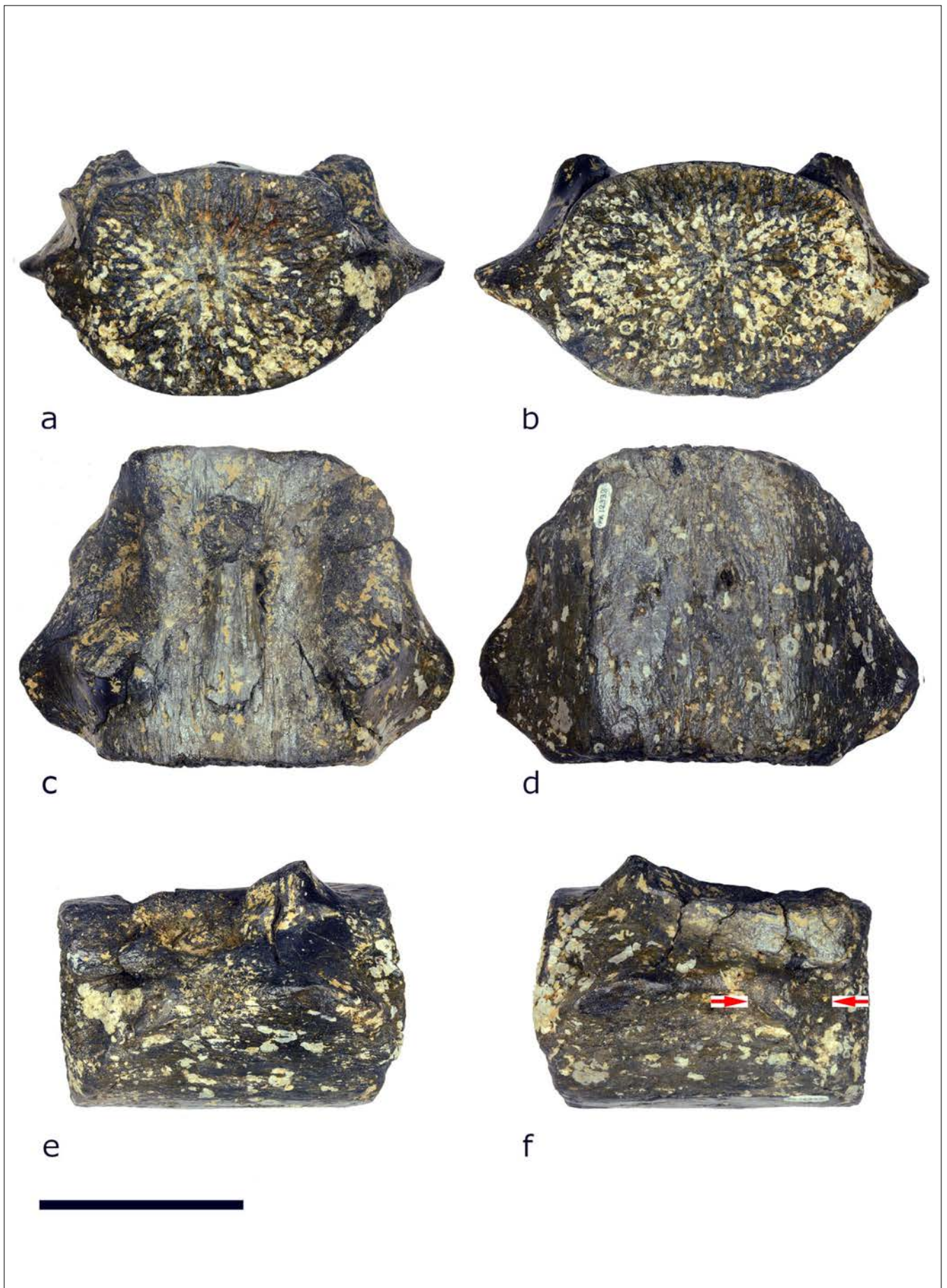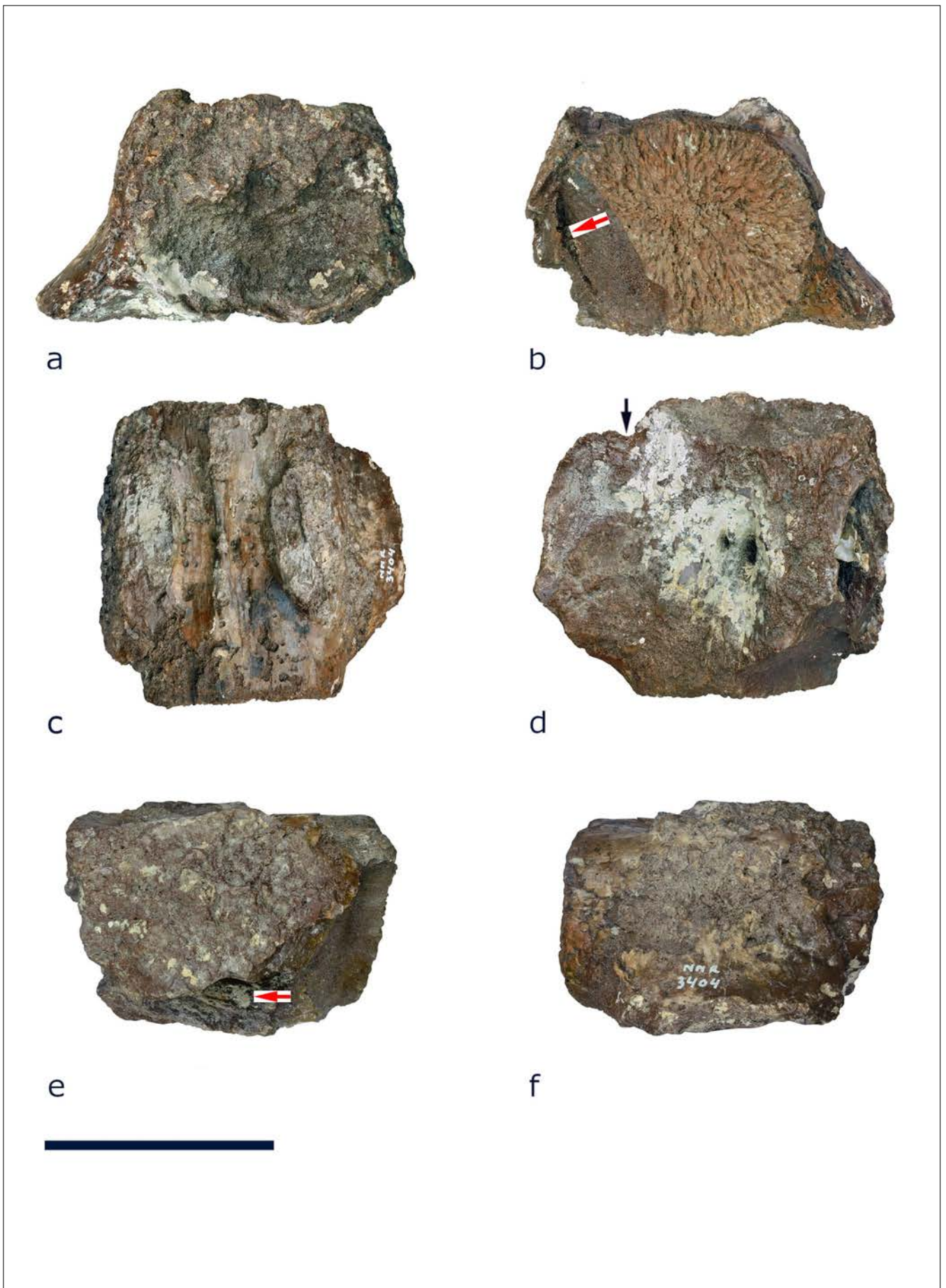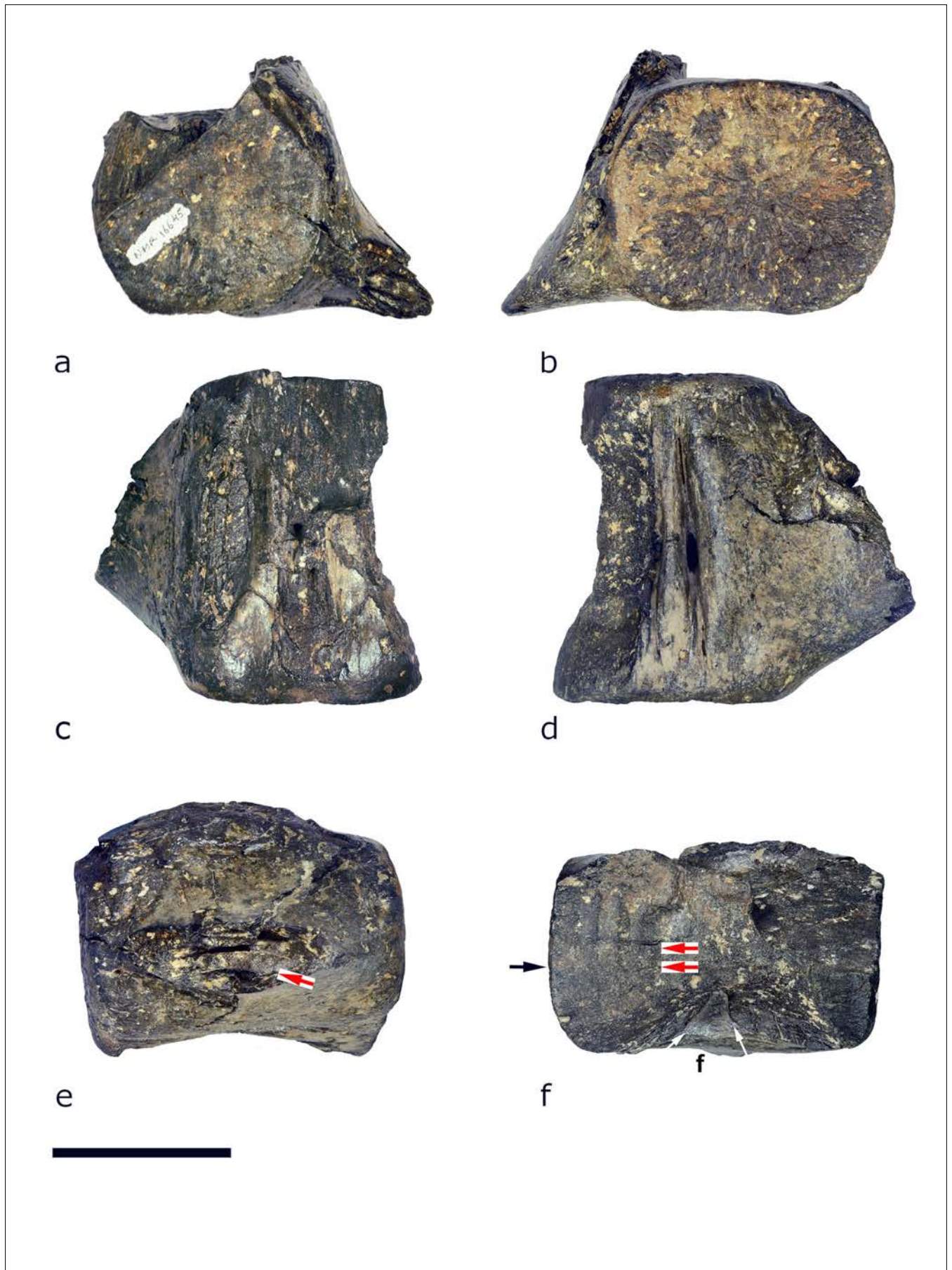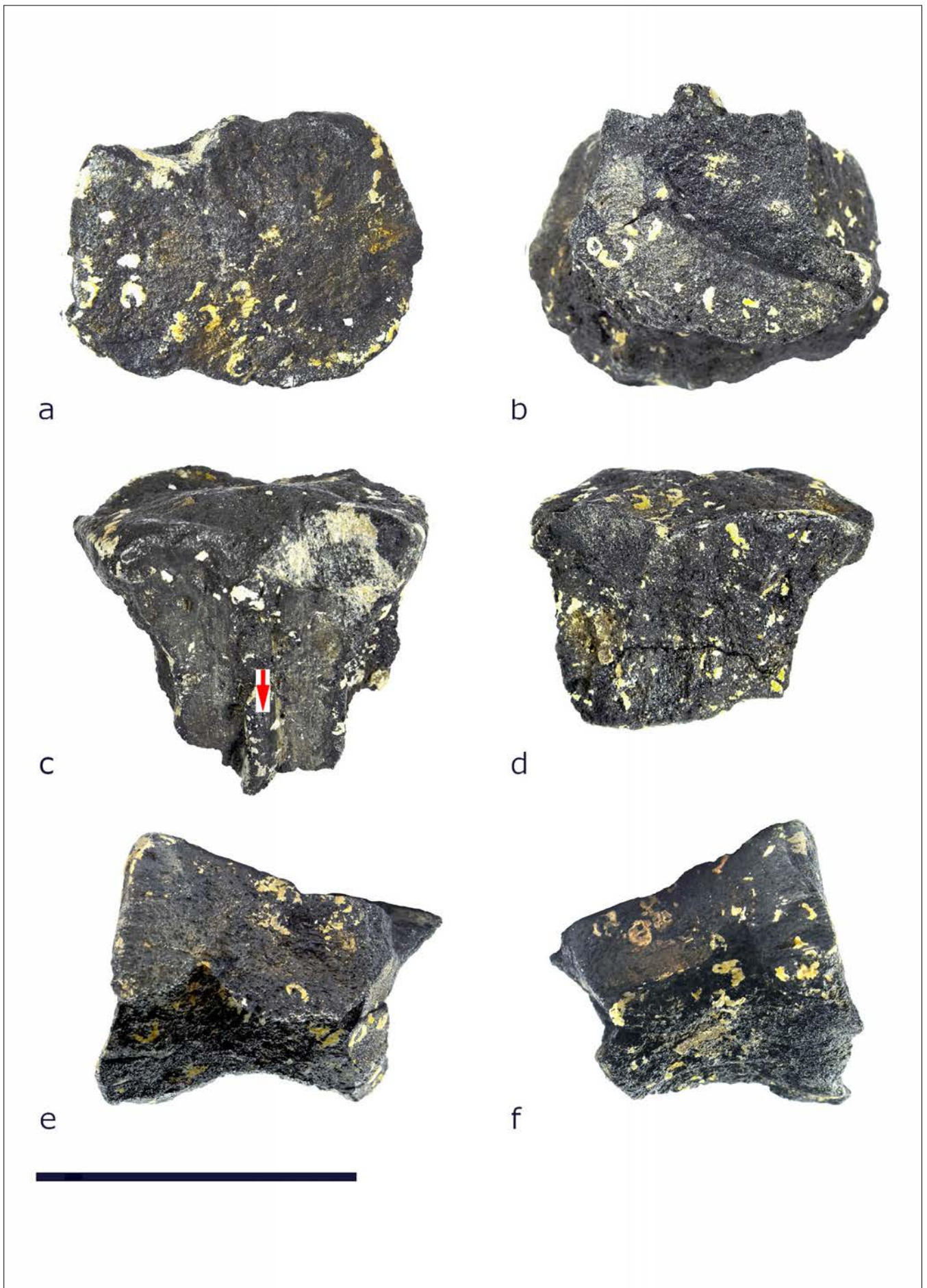
Figure 11. Central-posterior thoracic vertebral centrum, NMR999100012332, Morphotype C, *Pachycetus* sp., from Het Scheur, Belgium, in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Left arrow in 11f indicates the probable fovea for the tuberculum of the rib on the transverse process; right arrow in 11f indicates the anterior fovea for the capitulum of the rib. Scale bar 10 cm.
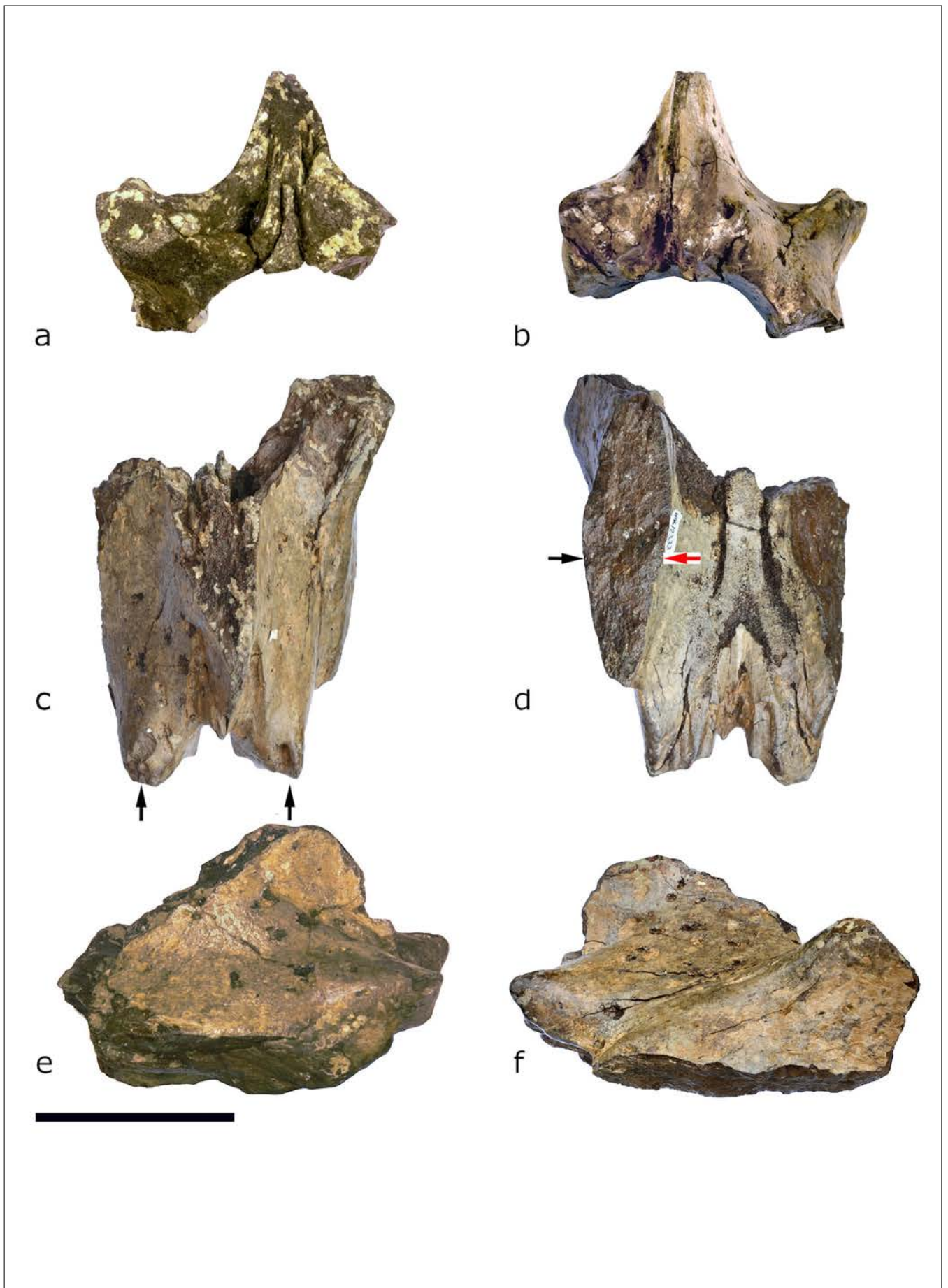
Figure 12. Partial neural arch of a presumably central thoracic vertebra, NMR999100012333, Morphotype C, *Pachycetus* sp., from Het Scheur, Belgium, in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Arrows in 12c indicate the postzygapophyses; arrows in 11d indicate the pachyosteosclerotic right pedicle of the neural arch. Scale bar 10 cm.
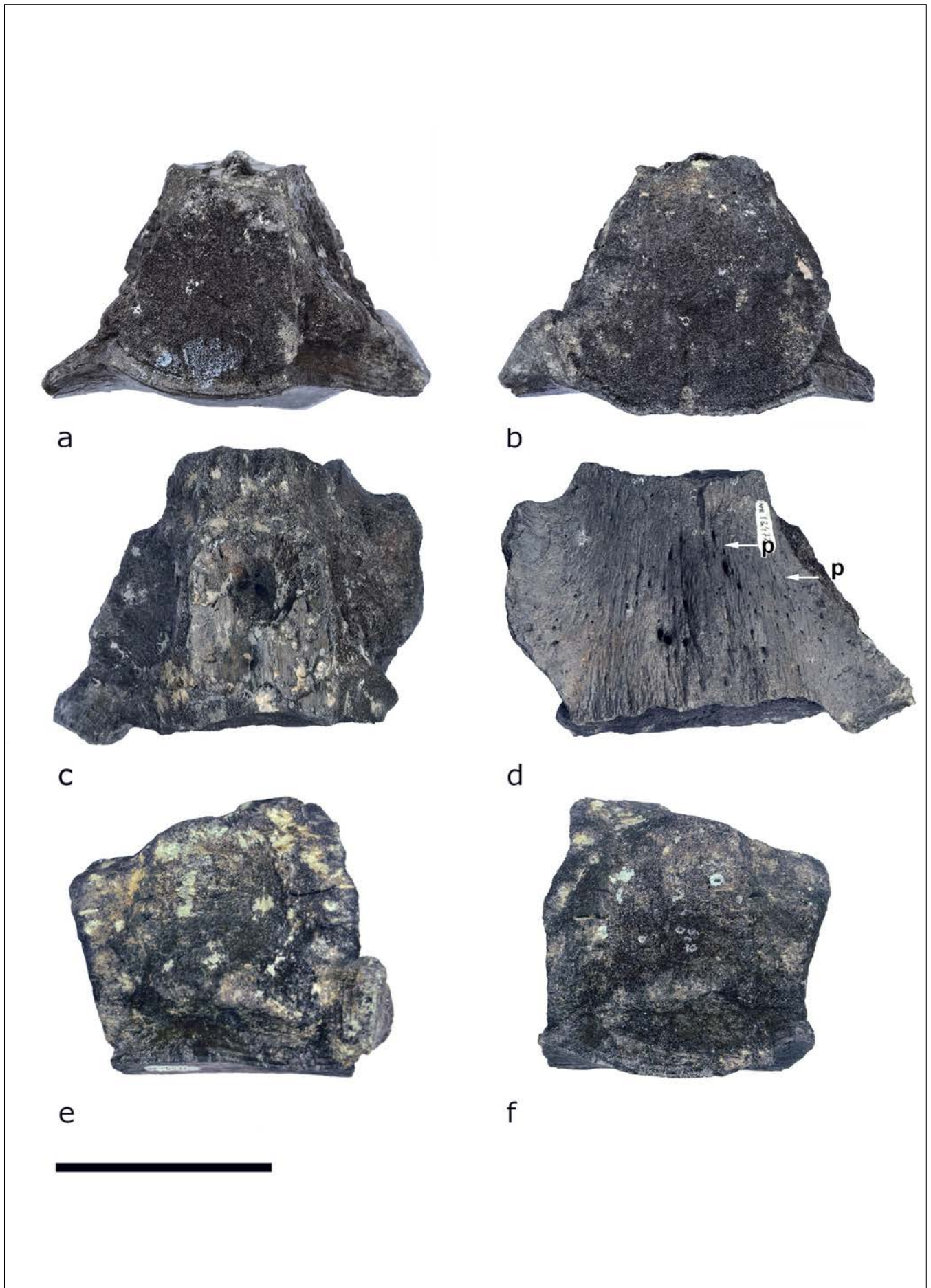
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Figure 13. Lumbar vertebral centrum, NMR999100003404, Morphotype C, *Pachycetus* sp., from Het Scheur, Belgium, in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Arrow in 16b indicates a part of the outline of the posterior conus. Arrow in 13d indicates the partial preserved anterior notch. Arrow in 13e indicates a large burrow made by an organism before permineralisation. Scale bar 10 cm.
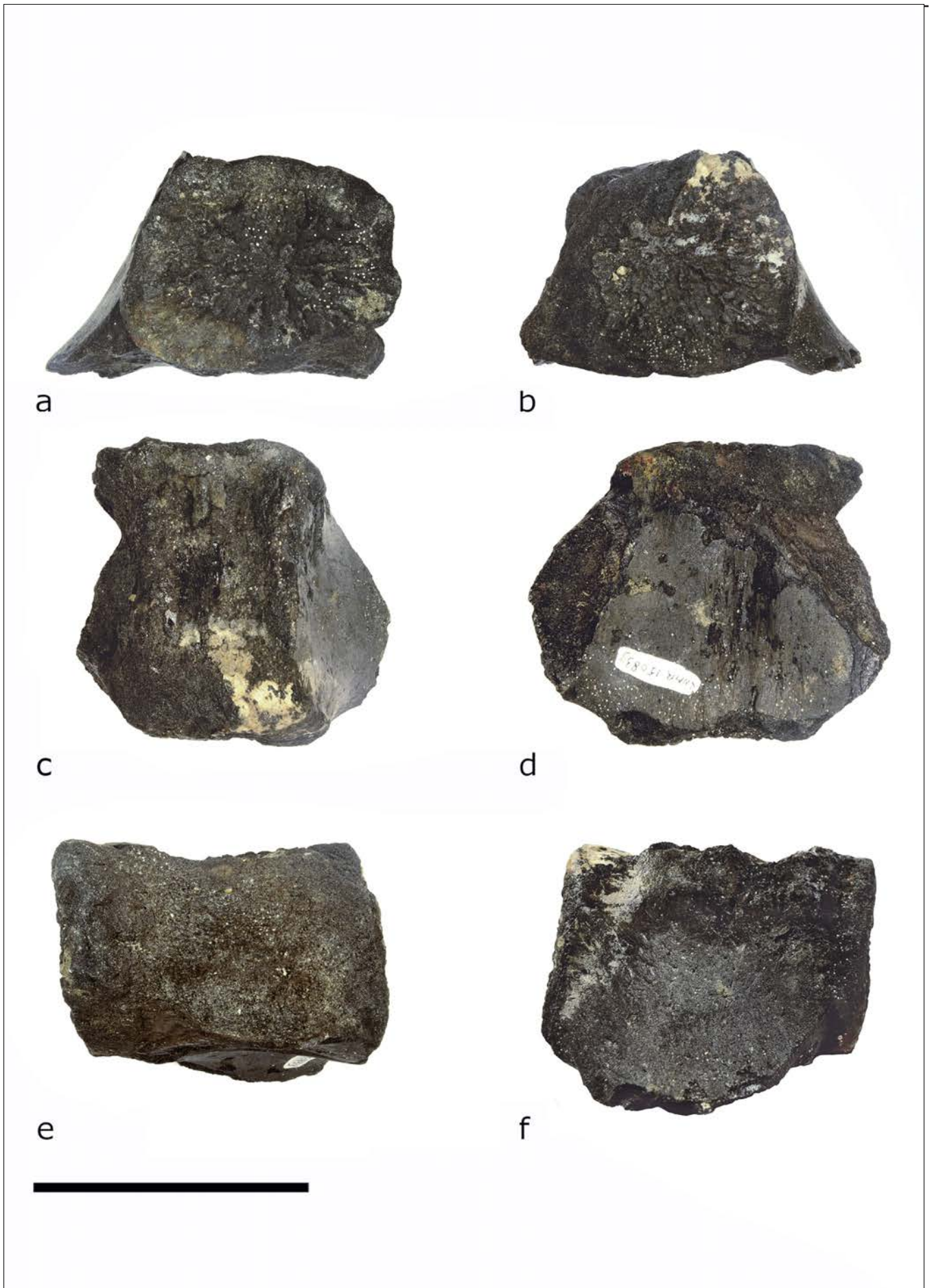
Figure 14. Lumbar vertebral centrum, NMR999100016645, Morphotype C, *Pachycetus* sp., from Het Scheur, Belgium, in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Arrow in 14e indicates the compact, multi-layered cortex on the onset of the transverse process. Left horizontal arrow in 17f indicates the base of the posterior conus; the two horizontal arrows to the right indicate two longitudinal blood vessels along the surface of the conus; the white arrows with 'f' on the ventral side of the centrum indicate the shape of the right ventral foramen in longitudinal section. Scale bar 10 cm.

Figure 15. Posterior thoracic or lumbar vertebral centrum, NMR999100150840, Morphotype C, *Pachycetus* sp., from Het Scheur, Belgium, in presumably the anterior (a), posterior (b), dorsal (c), ventral (d), left ventrolateral (e) and right ventrolateral (f) view. Arrow in 15c indicates the median dorsal ridge. Scale bar 10 cm.

Figure 16. Partial lumbar vertebral centrum, NMR999100013472, Morphotype C, *Pachycetus* sp., from Het Scheur, Belgium, in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Arrows with 'p' in 17d indicate the multiple, elongated punctae. Scale bar 10 cm.

Figure 17. Lumbar vertebral centrum, NMR999100150839, Morphotype C, *Pachycetus* sp., from Het Scheur, Belgium, in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) view. Scale bar 10 cm.
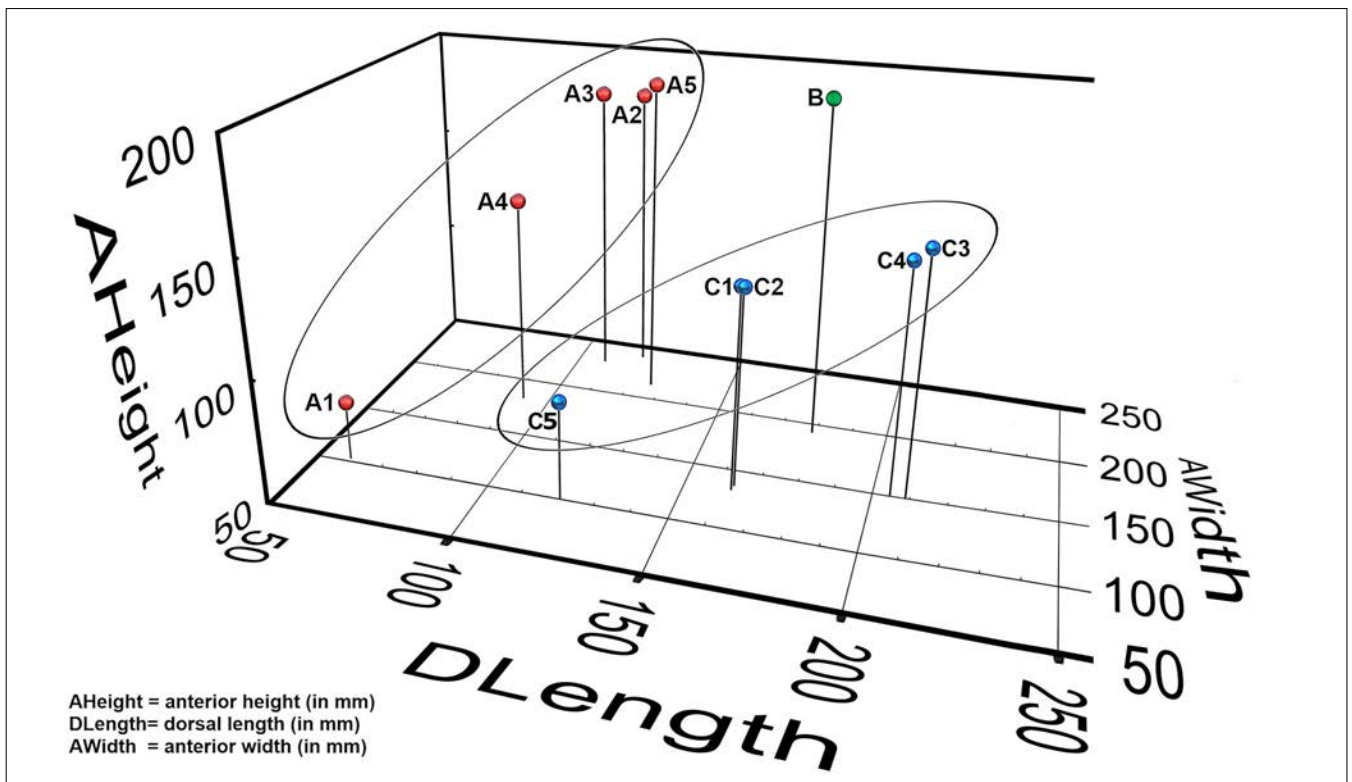
Figure 18. Plot of the three Morphotypes A, B and C, discerned in the vertebral centra, from the region of Wielingen (Belgian-Dutch border), and Het Scheur (Belgium). The dorsal length, anterior width and anterior height of the vertebral centra are indicated in a three-dimensional diagram. Vertebrae of Morphotype A are indicated by the red spheres A1-5 (A1: NMR999100160635; A2: NMR999100003402; A3: NMR999100003403; A4: NMR999100003882; A5: NMR999100010283). Vertebra of Morphotype B is indicated by the green sphere B (B: NMR999100010284). Vertebrae of Morphotype C are indicated by the blue spheres C1-5 (C1: NMR999100012331; C2: NMR999100012332; C3: NMR999100003404; C4: NMR999100016645; C5: NMR999100150839).

characteristics of *Pachycetus* spp., the genus is otherwise still poorly known and a complete skull has for example not been described until now (Gingerich & Zouhri 2015).

NMR-12331 and NMR-12332 are rather similar; the former has a relative length of 1.28, the latter a relative length of 1.23 (both without epiphyses). They probably had the same position in the vertebral column, or were positioned adjacent to each other. They are interpreted as central-posterior thoracic vertebrae, because the transverse processes are positioned at mid-height of the lateral sides of the vertebral centrum. More anterior thoracic vertebrae of *Pachycetus* are less elongated (Van Vliet *et al.* 2020), and more posterior thoracic vertebrae lack foveae along the epiphyseal surfaces. The central-posterior thoracic vertebra NMR-12331 with maybe posterior foveae on the lateral sides, seems to differ from those in *Pachycetus aithai* Gingerich & Zouhri, 2015 in which the posterior foveae are absent from Th4 onwards (Gingerich & Zouhri 2015). The two ventral foramina in the thoracic centrum NMR-12332 are not present in the thoracic centrum NMR-12331. The neural arch, NMR-12333 is clearly anterior-posteriorly elongated and has pachyosteosclerotic pedicles; it is therefore assigned to Morphotype C.

The lumbar vertebral centra NMR-3404 and NMR-16645 have both dorsal and ventral foramina, as well as median ridges. These are present in other lumbar vertebrae assigned to the genus *Pachycetus* from Europe (Ukraine, Germany) as well (Van Vliet *et al.* 2020). The ventral

foramina in the lumbar vertebrae of *Pachycetus* species are elongated and located in elongated grooves (Kellogg 1936, Uhen & Berndt 2008: fig. 2, Weems *et al.* 2011: fig. 3, Gol'din & Zvonok 2013, Van Vliet *et al.* 2020), as in the vertebral centrum NMR-16645. The original shape of the ventral grooves in the vertebral centrum NMR-3404 is difficult to notice, due to abrasion. The shape of the right ventral foramen in NMR-16445 (a 'V' turned upside down), is similar to a ventral foramen in a partial lumbar vertebral centrum from Germany (ID20-2), assigned to *Pachycetus* sp. (Van Vliet *et al.* 2020). The posterior conus of NMR-16445 is 20 mm longer than the anterior one. An anterior notch as seen in the transverse process of NMR-3404 has been described and figured for the second, but not for the first lumbar vertebra in *Pachycetus wardii* Uhen, 1999 (Uhen 2001: fig. 5), and also in a lumbar vertebra (NMR999100151795) from the Helmstedt region (Van Vliet *et al.* 2020: plate 3).

The dimensions of the vertebrae of Morphotype C (except for some (one to three) vertebral centra - see below) are generally larger than those of *P. aithai* (Gingerich & Zouhri 2015: table 2) and *P. wardii* (Uhen 1999: appendix 1, Uhen 2001: table1). In comparison with the *Pachycetus* species from Ukraine, the dimensions of the thoracic vertebrae NMR-12331 and NMR-12332 of Morphotype C, are larger than those of thoracic vertebrae NMNH-P OF-2096 of *P. uheni* Gol'din & Zvonok, 2013 (Gol'din & Zvonok 2013: appendix 2), but are comparable to two thoracic vertebrae KOM 44760 P202, and -61 P203 of *Pachycetus* sp. (Gol'din & Zvonok 2013: appendix ta-
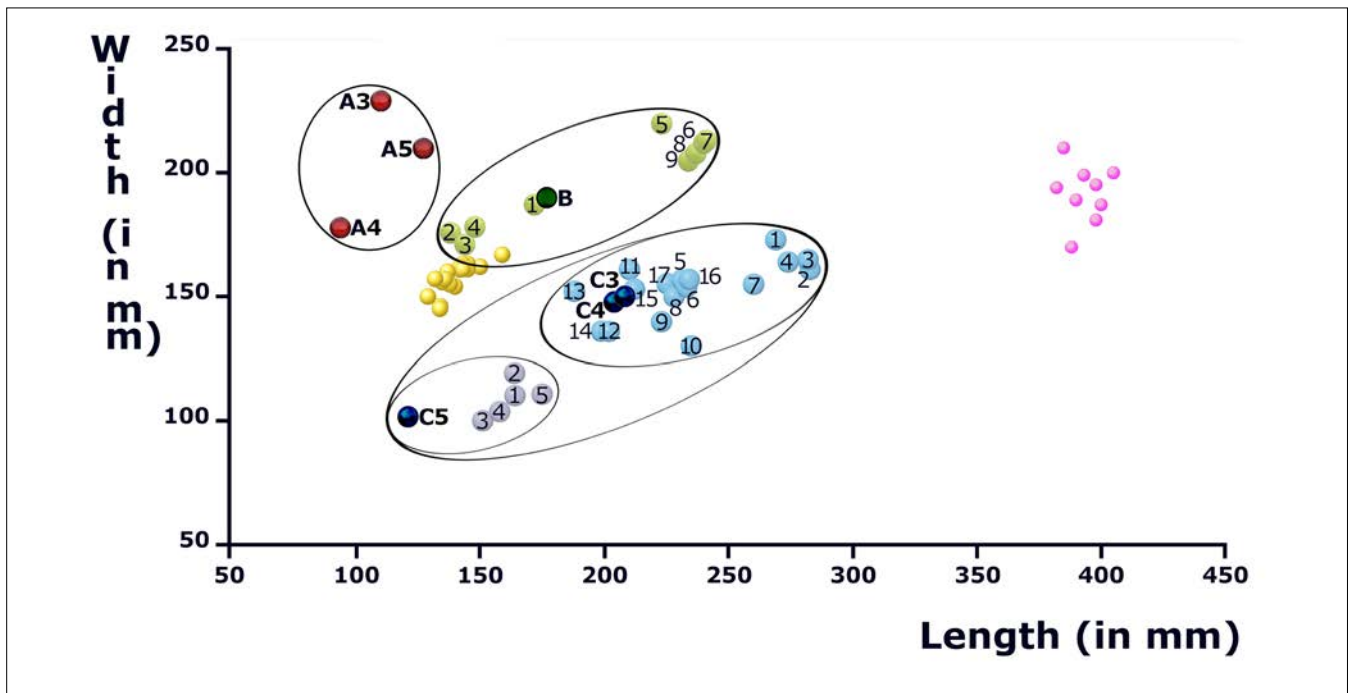
Figure 19. Plot of the three Morphotypes A, B and C, discerned in the vertebral centra from the region of Wielingen (Dutch-Belgian border), and Het Scheur (Belgium), compared with (mostly lumbar) vertebrae of several taxa of Eocene cetaceans.

Cluster A, the length of the vertebral centra is much shorter than the width. Red spheres A3-4: lumbar vertebral centra and red sphere A5: caudal vertebral centrum of Morphotype A, assigned to a presumed indeterminable basilosaurid (Table 1a).

Cluster B, the length of the vertebrae in this cluster is more or less similar to the width. Dark-green sphere: thoracic (or anterior lumbar) vertebral centrum of Morphotype B, assigned to a presumed indeterminable basilosaurid (Table 2a); green spheres 1-11: thoracic and lumbar vertebral centra of basilosaurids from other countries (Table 2b).

Cluster C, the length of the vertebrae in this cluster is much larger than the width. Dark-blue spheres 3-5: lumbar vertebral centra of Morphotype C, assigned to *Pachycetus* spp. (Table 3a); blue spheres 1-17: large lumbar vertebral centra with *Pachycetus*-like characteristics (Table 3c); grey spheres 1-5: small lumbar vertebral centra of *Pachycetus* spp. from other countries (Table 3d).

Yellow spheres: lumbar vertebral centra Lu1-17 of *Cynthiacetus peruvianus* Martínez-Cáceres & de Muizon, 2011 from Peru (Martínez-Cáceres *et al.* 2017: table 9). Purple spheres: lumbar vertebral centra Lu1-13 (except Lu2, 3, 4, 7) of *Basilosaurus cetoides* Owen, 1839 from Alabama (Kellogg 1936: table 10). The yellow and purple spheres fall mostly outside the range of the three clusters.

ble 3) and a thoracic centrum of *P. paulsonii* Brandt, 1873 (Kellogg 1936: table 25). Moreover, the dimensions are only slightly larger than those of a presumably posterior thoracic vertebra, NsT90, of *P. robustus* Van Beneden, 1883 and a posterior thoracic vertebra, ID20-B, of *Pachycetus* sp. from Helmstedt, Germany (Van Vliet et al. 2020: appendix table 2a, 2b). The lumbar centra of Morphotype C seem however smaller than lumbar vertebrae (with epiphyses) of *P. paulsonii* from Ukraine (Kellogg 1936: table 24-25) and *Pachycetus* sp. from Helmstedt, Germany (Van Vliet *et al.* 2020: appendix table 2b), but their length could have been larger in fully-grown individuals.

NMR-150840 is too fragmentary to determine its position in the vertebral column. NMR-13472 and NMR-150839 are identified as lumbar vertebral centra, as the transverse processes are located near the ventral base of the lateral sides of the vertebrae, and the fairly small width of the neural canal (in both ~55 mm). Nevertheless, the ventral foramina are small compared with the large ventral foramina in the lumbar vertebral centrum NMR-16645 and also those of NMR-151795 and ID20-2 from the Helmstedt region, Germany (Van Vliet *et al.* 2020). The vertebral centrum NMR-150839 and possibly originally NMR-13472 and NMR-150840 too, are smaller than the other vertebral centra of Morphotype C. NMR-13472 and NMR-150840

are however too fragmentary to determine with certainty their original dimensions. The vertebral centrum NMR-150839 (Fig. 19: C5) is even smaller than the lumbar vertebrae of the small species *P. wardii* and *P. aithai* (Fig. 19: grey spheres 1-5). This could be explained by the fact that the vertebrae of the latter two species are fully-grown with fused epiphyses. It is however not yet possible to determine, whether these vertebrae from the North Sea actually represent a fourth morphotype, being a small species of *Pachycetus,* or that their small size can be attributed to the ontogenetic age of the indivuals involved.

Of the vertebral remains, assigned to Morphotype C, *Pachycetus* sp., with certainty three vertebrae (NMR-12331, NMR-12332, NMR-13472) and the partial neural arch (NMR-12333) have been dredged from Het Scheur (Post *et al.* 2017); at this site the Middle Eocene Maldegem Formation crops out at the seafloor. The genus *Pachycetus* is known from the Bartonian and maybe also Priabonian of Ukraine and Southern Russia (Gol'din & Zvonok 2013), the Bartonian to Priabonian of Germany (Uhen & Berndt 2008, Van Vliet *et al.* 2020), the Bartonian Aridal Formation at Gueran, Morocco (Gingerich & Zouhri 2015), and the Bartonian and maybe the late Lutetian of North Carolina and Virginia, USA (Uhen 2005, Uhen 2001, Weems *et al.* 2011). Vertebrae of a partial skeleton, MUSM1443, from the

Bartonian of Peru (Uhen *et al.* 2011), and also a caudal vertebral centrum, MUSM3594 from the Ypresian to latest Bartonian of Amazonia, Peru (Davydenko *et al.* 2018) share features with *Pachycetus*. *Pachycetus* is an early diverging basilosaurid with basal features and considered by Gol'din *et al.* (2014a; there called *Basilotritus*) as maybe confined to the Bartonian; indeed a younger age cannot be proven with certainty. For these reasons, also the other, here described vertebrae of Morphotype C (NMR-3404, NMR-150839, NMR-150840 and NMR-16645) could have originated from the Maldegem Formation at Het Scheur.

Conclusion

The here described thirteen vertebral centra and the neural arch have been dredged from the artificially deepened tidal channels Het Scheur in the Belgian part of the North Sea, and Wielingen at the Belgian-Dutch border in the Westerschelde Estuary, between 1996 and 2017. All vertebrae belong to large cetacean taxa and maybe a smaller taxon too. These large taxa were probably comparable in size to or even larger than *Cynthiacetus peruvianus*, that because of its large, but not-elongated vertebrae is thought to have reached a length of 9 m (Martínez-Cáceres *et al.* 2017). Almost certainly their length did not succeed that of *Basilosaurus cetoides*, that because of its large and very elongated vertebrae, could pobably reach a length of 20 m (Voss *et al.* 2019). The lack of small ('dorudontine') species in this collection cannot be the result of the sampling methods; dredging from the seafloor with commercial fishing nets will also collect fossils of a few centimetres (KP, *pers. observation*). Nearly all vertebrae seem to represent young, not fully-grown individuals. The same phenomenon was seen in *Pachycetus* vertebrae from the Helmstedt region, Germany. The epiphyses are more often fused in *Pachycetus* vertebrae from Ukraine, but also here in quite a few vertebrae the epiphyses are lacking (Van Vliet *et al.* 2020). Gol'din *et al.* (2014a) however attributed the relatively high frequency of vertebrae from Ukraine with unfused epiphyses to neoteny, in which case those vertebrae could have been from adult specimens retaining juvenile features.

Three different morphotypes, A, B and C are recognised, differing in proportions and size, the thickness of the CCMC, and number and size of foramina (if present), which are assigned to three different taxa (Fig. 18). The vertebral centra of Morphotype A and Morphotype B could have originated from either the Middle Eocene Maldegem Formation at Het Scheur or, more probable, from the Late Eocene parts of the Zelzate formation at Wielingen. The vertebral centra of Morphotype A, being wide and high, but anteroposteriorly very short (Fig. 19), presumably represent a new taxon with characteristics pointing to a basilosaurid with derived features. The dimensions of the vertebral centrum of Morphotype B are comparable in size with vertebra of the cetacean NHMM197955 from the Priabonian of Maastricht, the Netherlands. These two vertebral centra are slightly larger than thoracic vertebral centra (NWMNH2151) from the Priabonian of Oregon, USA (Uhen & Taylor 2020), or lumbar vertebral centra (PIN5821/1 & 4) from the Late Eocene of Gorny Luch, Russia (Tarasenko 2022), both assigned to indeterminable basilosaurids. They are more or less comparable in size with thoracic vertebral centra of an indeterminable basilosaurid, NWMNH2151 from the Priabonian of Oregon, USA (Uhen & Taylor 2020) and comparable in size with vertebral centra of '*Pontogeneus*

brachyspondylus' (*sensu* Kellogg 1936) from the Priabonian of Alabama, North America (Fig. 19). The vertebrae of Morphotype A (including the vertebral centrum NMR-160635) and Morphotype B are tentatively assigned to basilosaurid taxa. Nevertheless, as these vertebrae might have originated from Priabonian sediments, a hypothetical assignment to early mysticetes cannot be excluded. All vertebrae of Morphotype C probably originated from the Middle Eocene Maldegem Formation, which subaqueously crops out in Het Scheur, Belgium. Having all characteristics in common with vertebrae of *Pachycetus* spp., they are ascribed to *Pachycetus* sp., and most probably represent a basilosaurid taxon with basal features known from the Bartonian (and maybe also Priabonian) of Ukraine, Southern Russia and Germany (Fig. 19). Maybe in the vertebrae of Morphotype C, two subtypes, a large and a small one can be discerned. Comparison of the small vertebral centra of Morphotype C with the two small species of *Pachycetus* known (*P. aithai*, *P. wardii*) is however hampered by the fact that in the vertebra NMR-150839, apparently from an immature individual, the epiphyses are lacking, and that the other two vertebrae (NMR-13472, NMR-150840) are very fragmentary. The taxa of the discerned morphotypes are not necessarily of the same geological age. Nevertheless, the tidal channels Wielingen and Het Scheur yield a relatively rich assemblage of large Eocene cetaceans with at least three clearly different large taxa and possibly a smaller taxon too, which is as yet unparalleled by other European sites.

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