

# A Palaeogene cetacean from Maastricht, southern Limburg (The Netherlands)

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We report on the find of a partial cetacean skeleton from Palaeogene strata exposed in the former ENCI-HeidelbergCement Group quarry at Sint-Pietersberg, south of Maastricht (southern Limburg, The Netherlands). The material available, collected in 1979, comprises a series of fragmentary vertebrae and ribs from the basal portion of the so-called ‘Laagpakket van Klimmen’ (Klimmen Member, Tongeren Formation; Middle North Sea Group), a shallow-marine unit of Late Priabonian (Late Eocene) to Early Rupelian (Early Oligocene) age that rests unconformably on biocalcarenes of latest Cretaceous (Late Maastrichtian) age. These associated skeletal remains, assumed to be from a single individual, constitute the first *in-situ* record of a Palaeogene (presumably Late Priabonian) cetacean from the Netherlands. The material is tentatively interpreted as a large-sized basilosaurid archaeocete, although the possibility that it represents an archaic mysticete cannot be ruled out entirely.

KEY WORDS: Whales, Basilosauridae, Klimmen Member, Upper Eocene, Europe

## Introduction

The family Basilosauridae (Cetacea, Pelagici) comprises extinct, fully marine whales that are known with certainty from upper Middle Eocene to Eocene-Oligocene boundary strata (Marx *et al.*, 2014). Basilosaurids had a global distribution, with records from Europe, Africa, Asia, North and South America, and Antarctica (Marx *et al.*, 2016). Formerly, this archaeocete family was divided into two subfamilies, i.e., the Dorudontinae, with relatively short vertebrae and the Basilosaurinae with markedly elongated posterior thoracic, lumbar and anterior caudal (torso) vertebrae (Uhen, 1998). However, recent phylogenetic analyses have not provided evidence of a monophyletic subfamily Dorudontinae (Martínez-Cáceres *et al.*, 2017) and it is more than likely that vertebral elongation is too poor a characteristic to make a subfamily well supported (Uhen, 2013). Osteosclerosis and the presence of a circumferential, compact and multi-layered cortex (CCMC) in torso vertebrae were first not-

ed amongst basilosaurid taxa by Müller (1849). In spite of the fact that these features have received much attention in recent years (see Uhen, 1999, 2001, 2013; Gol'din & Zvonok, 2013), their diagnostic significance remains uncertain. This issue will be elaborated upon in the section ‘Discussion’. Vertebrae of various species of basilosaurid display a wide range of variation as far as size, elongation and presence or absence of a CCMC are concerned (Appendix Table 1). Differences in bone structure, as well as in size and length of torso vertebrae, amongst basilosaurid species are held to be indicative of different swimming modes and occupation of different ecological niches (Gingerich & Zouhri, 2015).

To date, localities across Europe have yielded only chance and mostly fragmentary finds of basilosaurids. Some specimens recovered in the nineteenth and twentieth centuries, such as *Platyosphys paulsonii* (compare Gol'din & Zvonok, 2013) and ‘*Zeuglodon* (*Zygorhiza*) *wanklyni*’ (see Kellogg, 1936) are presumed lost. Others,

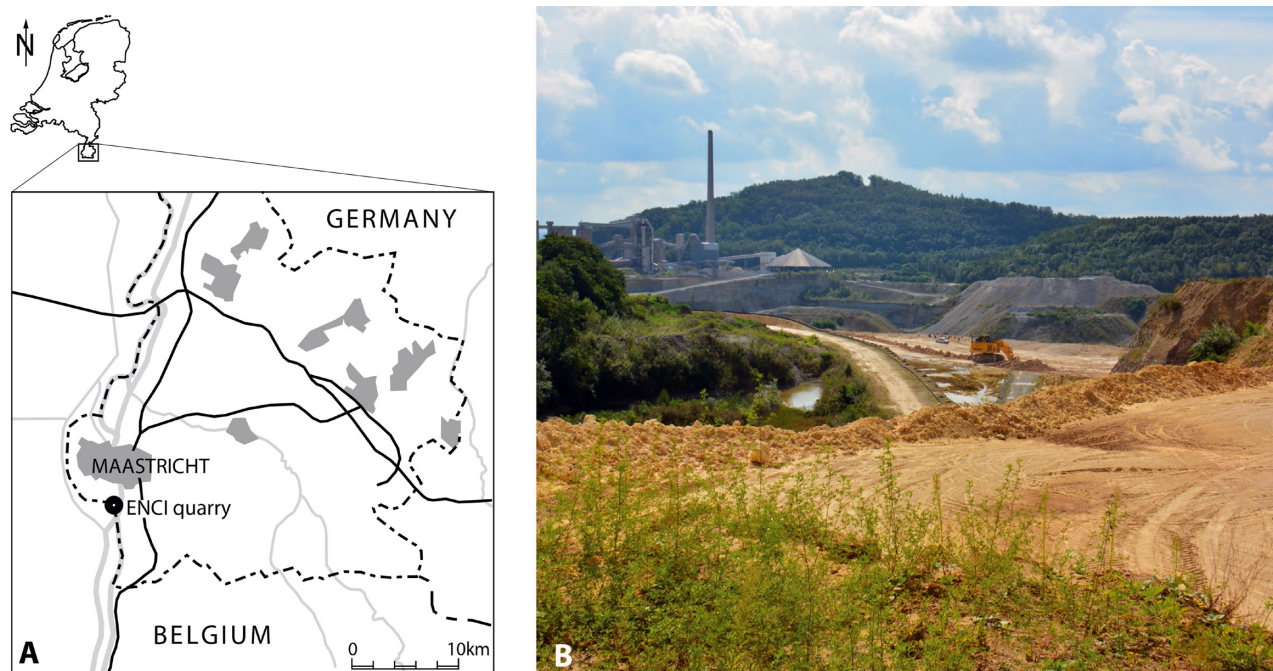
such as '*Zeuglodon puschii*' Brandt, 1873 and '*Zeuglodon vredense*' Landois, 1884 have subsequently been re-diagnosed as Neoceti (Kellogg, 1936). At the moment, we are aware of at least seven partial basilosaurid skeletons from Europe, including five from Ukraine (Gol'din & Zvonok, 2013), one from Russia (Kalmykov, 2012) and another one from Italy (Pilleri & Fulgosi, 1989). An eighth find, from Austria (Uhen & Tichy, 2000), comprises a set of at least ten associated teeth. For an overview of European Eocene cetaceans, reference is made to Appendix Table 2.

Until now, from the Dutch-Belgian border area (southern North Sea) five isolated vertebrae with basilosaurid characteristics have been described. These had been trawled from the sea floor at localities situated within the same tidal channel of the estuary of the river the Scheldt ('de Schelde'), namely, 'Het Scheur' (Belgium) or possibly between 'Het Scheur' and the nearby site of 'De Wielingen' (The Netherlands), to where they could have been transported by currents. Three of these vertebrae, housed in the collections of the 'Natuurhistorisch Museum Rotterdam' (or 'Het Natuurhistorisch'), The Netherlands, i.e., NMR9991-3402, NMR9991-3403 and NMR9991-3404, were described and illustrated by Post (2007). Schouten (2011) recorded another recent find (NMR9991-3882) and NMR 9991-13472 has recently been mentioned by Post *et al.* (2017). A few others have not yet been described (see 'Discussion'). At the locality 'De Wielingen', Lower Oligocene (Rupelian, Boom Clay Formation) strata crop out on the sea floor, but a few kilometres to the West, at the locality 'Het Scheur', there is a subaqueous outcrop of Middle Eocene strata that have been assigned to the Maldegem Formation (Du Four *et al.*, 2006). All current-

ly available vertebrae probably originate from the latter lithostratigraphical unit at 'Het Scheur' (Post *et al.*, 2017).

## Material and methods

The present skeletal elements were recovered from greenish grey, fine to medium-grained sands ('Laagpakket van Klimmen') in the northwestern corner of the ENCI-HeidelbergCement Group quarry (Sint-Pietersberg, south of Maastricht; Fig. 1) in April 1979 by the late Werner M. Felder (engineer and field geologist at the former Geologisch Bureau, Heerlen) and subsequently recovered by himself, together with his brother, the late Peter J. Felder (then staff member at the Natuurhistorisch Museum Maastricht) and Alexis W.F. Meijer (then curator of palaeontological collections at the same museum). At the time, the sandy overburden at the locality with the whale bones had been removed almost completely by bulldozers to access the underlying biocalcarenes for production of Portland cement. The sandy level containing the whale bones was still in place in a broad, shallow depression (palaeorelief) in the underlying biocalcarenes. The sands in the depression could be assigned with certainty to the base or lowermost portion of the Klimmen Member. The bones were collected after a considerable area (some tens of square metres) had been screened for additional material. Strontium isotope analyses in 2016 of some bone samples, by Hubert Vonhof and Renée Janssen (Vrije Universiteit, Amsterdam) were unsuccessful, owing to diagenetic alteration of the material. Matrix samples taken from the bones and the lower portion of the Klimmen Member, as exposed several years ago at the quarry, have not yielded



**Figure 1.** A: Map with the location of the ENCI-HeidelbergCement Group quarry in the southeastern part of the Netherlands, south of the city of Maastricht; B: View on the ENCI-HeidelbergCement Group quarry in 2016. Foreground: yellowish- brownish sands of the Klimmen Member, background: the outline of the Sint-Pietersberg.

any age-diagnostic microfossils either (Stephen Louwye, pers. comm., 2015 and 2017).

Geological setting

The Tongeren Formation, as currently understood (De Mulder *et al.*, 2003), comprises the Klimmen and Goudsberg members in the southern part of the Netherlands (Kuyl, 1975). The former has been dated as Late Priabonian (Late Eocene) to Early Rupelian (Early Oligocene) and could be the equivalent of transgressive and early highstand deposits of Haq’s TA 4.3 sequence (Haq *et al.*, 1988). The fine- to medium-grained, greenish grey to brownish yellow, glauconitic sands of the Klimmen Member reflect a shallow-marine environmental setting (Van Adrichem Boogaert & Kouwe, 1993-1997; De Mulder *et al.*, 2003). The ‘Laagpakket van Klimmen’ is still accessible (thickness *c.* 5 m) in the northwestern corner of the grounds of the former ENCI-HeidelbergCement Group quarry, resting unconformably on biocalcarenites of the uppermost Maastrichtian (Meerssen Member of the Maastricht Formation; Schiøler *et al.*, 1997; Rademakers, 1998; Felder & Bosch, 1998, 2000; Jagt & Jagt-Yazykova, 2012). In places, there is a thin level of small, black and rounded flint pebbles and occasional shark teeth, at the base of the Klimmen Member. The overlying, thoroughly decalcified sands contain dispersed small mica particles and are yellowish to brownish in colour, the lower portion being more finely grained, with a coarsening-upward trend. Calcitic fossils appear to be extremely rare, but there are scattered records of benthic foraminifera (nummulitids) and limonitic ‘ghosts’ of venerid and other bivalves. At the top, an orange purple soil horizon, the Hoogbut-

sel Horizon, is often found; this has been interpreted to be the result of temporary emergence (Kuyl, 1975; Van Adrichem Boogaert & Kouwe, 1993-1997; De Mulder *et al.*, 2003). The Klimmen Member is conformably overlain by the Goudsberg Member (Fig. 2).

Abbreviations:

- NHMM Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands
- NMR Natuurhistorisch Museum Rotterdam (or ‘Het Natuurhistorisch’), The Netherlands
- OU Geology Museum, University of Otago, Dunedin, New Zealand

Terminology:

We follow Houssaye *et al.* (2015) for anatomical and histological terms.

Systematic palaeontology

- Order Cetacea Brisson, 1762
- Suborder Pelagiceti Uhen, 2008
- ?Family Basilosauridae Cope, 1868
- ?Basilosauridae indet.

*Material* – An association of 43 bones, registered as a single lot (NHMM 197955), and recently catalogued by the authors: 1-7, partial vertebral centra; 8-12, fragments of vertebral transverse processes; 13-35, rib fragments and 36-43, unidentifiable bone fragments. Vertebral dimensions are listed in Table 1; those of rib fragments can be found in Table 2.

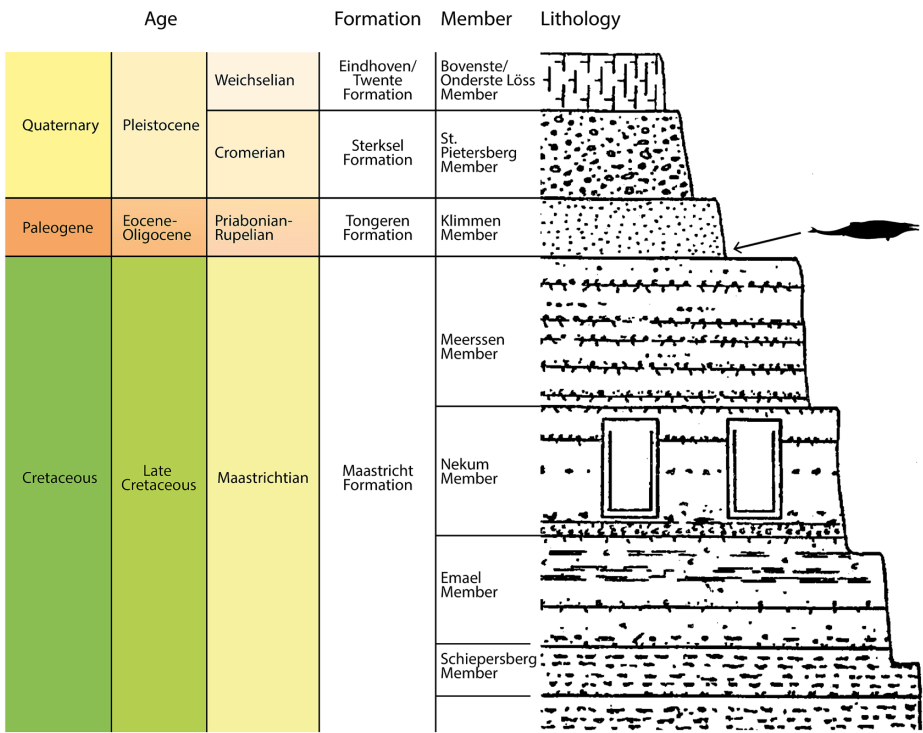
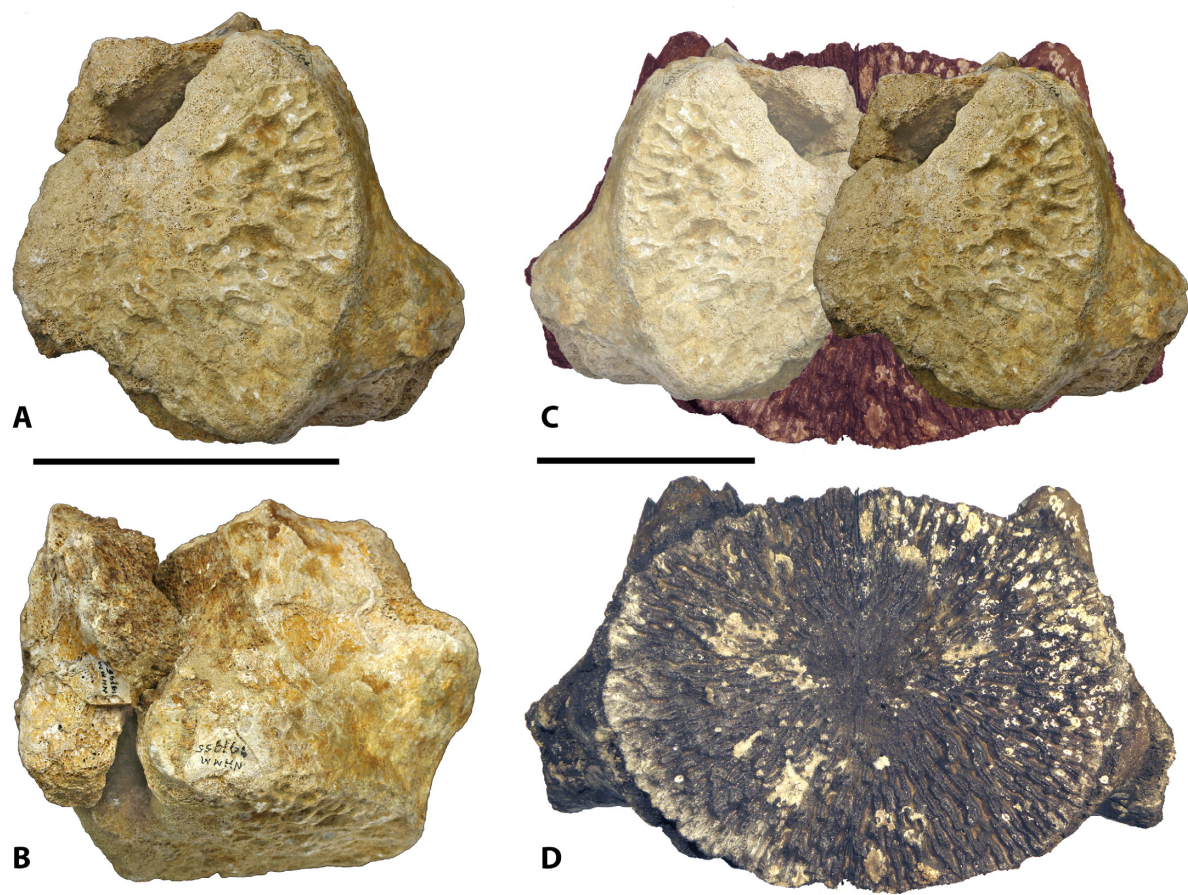


Figure 2. Stratigraphy of the Neogene, Palaeogene and uppermost Cretaceous sediments at the ENCI-HeidelbergCement Group quarry. Modified from Jagt *et al.* 1998. *Grondboor en Hamer*, 52: 94.





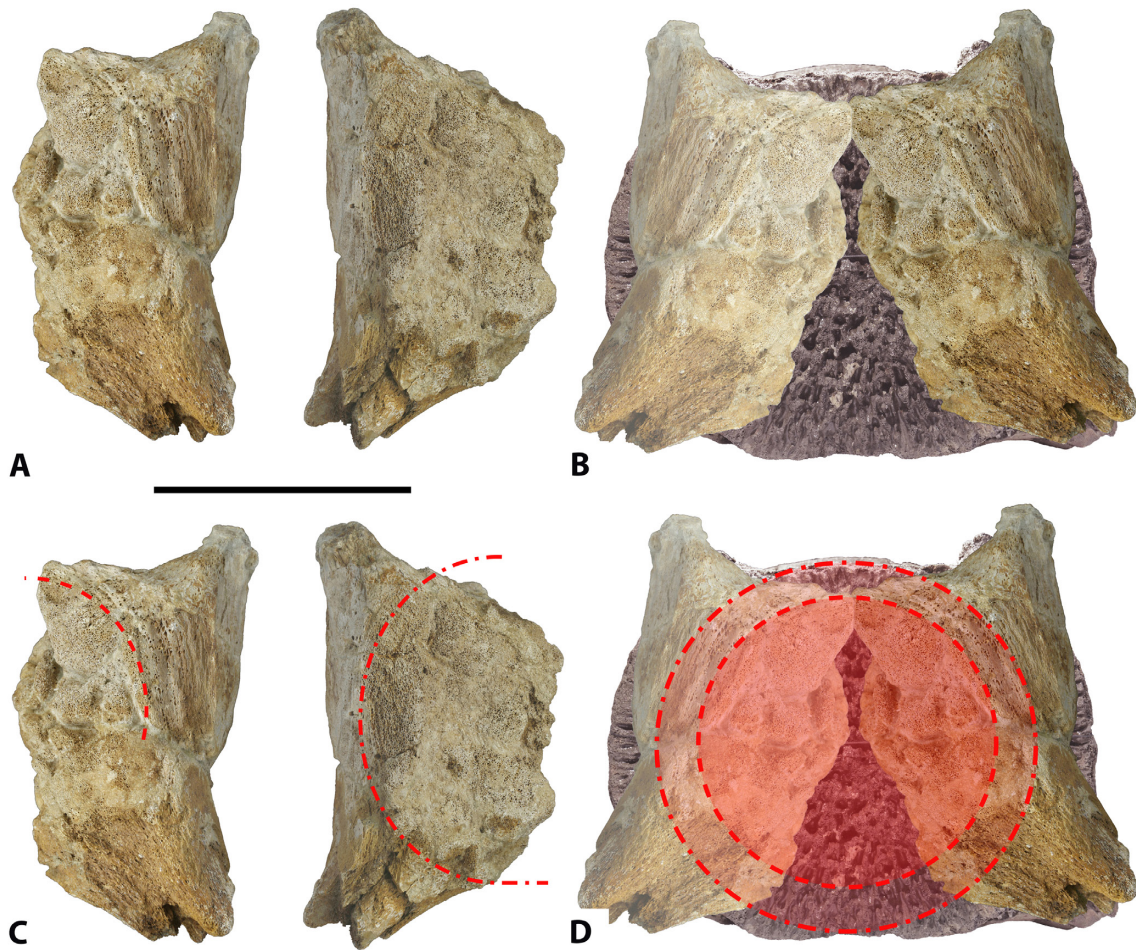
**Figure 3.** NHMM 197955, nr. 1 indet. cetacean, thoracic vertebra. A: axial view; B: dorsal view; C: reconstruction projected upon vertebra NMR9991-3402, indet. basilosaurid, dredged from probably ‘Het Scheur’, Westerschelde Estuary, North Sea, Belgium; D: vertebra NMR9991-3402, posterior view. Scale bars 10 cm.

| Fragment No. | L        | Width neural arch | H *)       | W *)          | Rel width neural arch |                       |
|--------------|----------|-------------------|------------|---------------|-----------------------|-----------------------|
| No. 1        | +92 dors |                   | +108       | 98            |                       | Th (post) or Lu (ant) |
|              | +99 vent |                   | +108       | 100           |                       |                       |
| e No. 1      | ?        | e130              | e180       | e225          | e0.6                  |                       |
| No. 2        | 73       |                   | ?          | +60 x 75 x 66 |                       | Vertebral epi. surf.  |
| No. 3        | ?        |                   | 86         | 60            |                       | Th or Lu              |
|              | ?        |                   | 96         | 65            |                       |                       |
| No. 4        | +76 dors |                   | +123       | 92            |                       | Probably Lu           |
|              | +86 vent |                   | +127       | 83            |                       |                       |
| e No. 4      | e+172    | e110              | e+127 ant? | e187 ant?     | e0.6                  |                       |
| No. 5        | 76 dors  | e90               | 92 ant     | +108 ant      | e0.8                  | Th (ant)              |
|              | 83 vent  |                   | 75 post    | +101 post     |                       |                       |
| No. 6        | 67       |                   | ?          | 41            |                       | Fragment              |
| No. 7        | 11       |                   | ?          | +22 x 27      |                       | Epi. disc fragment    |

**Table 1.** Dimensions of partial vertebral centra. Measurements (in mm) of the vertebral centra of the Palaeogene cetacean, NHMM 197955, from the ENCI Cement Quarry in Maastricht, The Netherlands.

Abbreviations: **ant**, anterior; **dors**, dorsal; **H**, height of vertebral centrum; **e**, estimate; **L**, length of vertebral centrum; **epi**, epi-physal; **Lu**, lumbar vertebra; **post**, posterior; **surf**, surface; **Th**, thoracic vertebra; **vent**, ventral; **W**, width of vertebral centrum. +, indicates original dimensions of the vertebral centrum were greater; ?, missing data.

\*) Except for vertebra 5, and maybe vertebra 4, it is impossible to determine which side is anterior or posterior, due to the fragmentary state of the centra.



**Figure 4.** NHMM 197955, nr. 4 indet. cetacean, probably lumbar vertebra. A left: axial view, midpart of the centrum with imprints of the vascularisation system; A right: axial view, probably anterior side of the centrum; B: reconstruction, showing the midpart of the vertebral centrum, projected upon vertebra NMR9991-3403, indet. basilosaurid, dredged from probably ‘Het Scheur’, Westerschelde Estuary, North Sea, Belgium; C left: dashed line showing the contact of the cone, near the top, with the compact, multi-layered cortex; C right: dashed line showing the contact of the base of the cone with the compact, multi-layered cortex; D: cone in the reconstruction: small circle is near the top of the cone, large circle is at the base of the cone. Scale bar 10 cm.

*Description* – The partial vertebral centra and transverse processes display multi-layered, cortical bone, probably reflecting cyclical differences in bone growth. Cortex thickness varies between 5 and 25 mm. Layers of compact cortex are separated from each other by one or several layers of trabecular bone. Each set of compact and trabecular bone is about 1 mm thick. At the surface of the cortex of compact multi-layered bone, small ‘pockmarks’ are visible, corresponding to openings of small vascular canals. Underlying the cortex is trabecular bone.

NHMM 197955-1 is a thoracic vertebra preserving half of the centrum and the base of one of the transverse processes. On one side, probably the posterior, the epiphyseal surface is well preserved. It has a rather rough and more or less irregular pattern of small canals and ridges, with a shallow, near-oval central concavity. The epiphyseal disc is missing (Fig. 3A-D).

NHMM 197955-2 is a fragmentary centrum of a thoracic or lumbar vertebra, preserved merely as a triangular piece of bone with traces of epiphyseal structures.

NHMM 197955-3 is a fragmentary centrum of a thoracic or lumbar vertebra, broken into two pieces.

NHMM 197955-4 probably represents a lumbar vertebra and preserves the right, presumably anterior part of the centrum, the base of the right transverse process and the base of the right pedicle of the neural arch. The transverse process is deflected ventrally and is located towards the ?anterior epiphyseal surface of the centrum. The vertebral surface between the transverse process and the pedicle is smooth and slightly concave. A small foramen is located between the remaining part and its (now lost) left counterpart. Traces of the epiphyseal surface are preserved on the ?anterior side. Fractures within the vertebral centrum reveal imprints of extensive vascularisation. Here, in the median portion of the centrum, it is seen that the compact, multi-layered cortex is structured around a cone of trabecular bone within the vertebra (see ‘Discussion’). We estimate that the original neural arch would have been approximately 11 cm in width (Fig. 4A-D).



**Figure 5** (top next page). NHMM 197955, nr. 5 indet. cetacean, anterior or central thoracic thoracic vertebra. A: ventral view; B: dorsal view; C: anterior view; D: posterior view with a reconstruction of the pedicle of the neural canal at the left side. Scale bar 10 cm.

| Fragment No. | L   | H  | W    |                              |
|--------------|-----|----|------|------------------------------|
| No. 13a-b    | 175 | 47 | 27   | Angle; Figs 6B, 7F-G         |
| No. 14a-b    | 168 | 50 | 25   | ?Angle; Figs 6E,, 7C-E       |
| No. 15a-d    | 331 | 36 | 25   | Distal angle; Fig. 6C        |
|              | 315 |    |      | Straight, end to end         |
| No. 16a-b    | 123 | 45 | 23   | Fig. 6A                      |
| No. 17a-c    | 191 | 43 | 25   | Figs 6D, 7H-J.               |
| No. 18       | 98  | 53 | 27   |                              |
| No. 19       | 123 | 45 | 28   |                              |
| No. 20       | 55  | 48 | [21] |                              |
| No. 21       | 87  | 42 | 27   |                              |
| No. 22       | 83  | 44 | 23   |                              |
| No. 23       | 62  | 40 | 25   | Fig. 7A                      |
| No. 24       | 72  | 38 | 26   |                              |
| No. 25       | 106 | 35 | 26   | Angle                        |
| No. 26       | 78  | 34 | 20   |                              |
| No. 27       | 37  | 32 | 25   |                              |
| No. 28       | 38  | 42 | [23] |                              |
| No. 29       | 93  | 29 | 25   |                              |
| No. 30       | 62  | 32 | [15] |                              |
| No. 31       | 79  | 26 | 21   |                              |
| Nos. 32, 33  |     |    |      | Small fragments              |
| No. 34       | 62  | 24 | 20   |                              |
| No. 35       | 87  | 27 | [18] |                              |
|              |     |    |      | ?Distal end of rib:          |
| No. 36       |     | 53 | 28   | Anterior broken end; Fig. 7B |
| Nos 36 + 37  | 112 | 61 | 32   | Measured at midpoint         |
| No. 37       |     | 56 | 44   | ?Distal intact end           |

**Table 2.** Dimensions of rib fragments. Measurements (in mm) of rib fragments of the Palaeogene cetacean, NHMM 197955, from the former ENCI-HeidelbergCement Group quarry, Maastricht, The Netherlands.  
Abbreviations: **W**, width of rib fragment; **H**, height of rib fragment; **L**, length of rib fragment.

On account of the dorsal position of the base of the transverse process, NHMM 197955-5 is a near-complete centrum of an anterior or central thoracic vertebra. The anterior epiphyseal disc is fully fused with the centrum; on the other side only remnants of the epiphyseal surface are preserved. Dorsally, some imprints of possible vascular structures are visible at fractured surfaces along the median line. The dorsal surface of the centre between the two pedicles is partially broken. We estimate the neural arch to have been about 9 cm in width (Fig. 5A-C).

**Figure 6** (bottom next page). NHMM 197955, indet. cetacean, rib fragments, A: nr.16a, b; B: nr.13a, b; C: nr.15a, b, c, d; D: nr.17a, b, c; E: nr.14a, b. Scale bar 10 cm.

NHMM 197955-6 is a small piece of of a vertebral centrum, with traces of the epiphyseal surface preserved on one side. NHMM 197955-7 is a small piece of the epiphyseal disc.  
NHMM 197955-8 to 12 are fragmentary vertebral transverse processes. At least one of these is from a thoracic vertebra, as it retains the articular surface for the corresponding rib. The shape of this articular surface indicates that the corresponding rib was still tightly articulated to the transverse process.  
In total 23, or maybe 24, rib fragments are available, with maximum widths and heights of about 25-28 and 45-53 mm, respectively. Five pieces of rib, consisting of several fragments, are longer than 120 mm; the longest measures 331 mm in length. The fragments belong to at least three separate ribs, as three (possibly four) angles are preserved. Each rib fragment displays a compact cortex of multi-layered bone. The ribs are osteosclerotic and, because of the thickened osteosclerotic cortex, probably also pachyostotic (Houssaye *et al.*, 2015, p. 19). The thickest part of the cortex is roughly 15-18 mm thick and is apparently situated on the anterolateral side of many rib fragments. However, the cortex has been flaked off in some fragments, making it impossible to determine the location of the thickest part. A medullary area of trabecular bone is seen beneath the cortex. There is no open medullary cavity (Fig. 6A-E, Fig. 7). NHMM 197955-36 and -37 belong together and possibly represent a pachyostotic distal rib fragment.

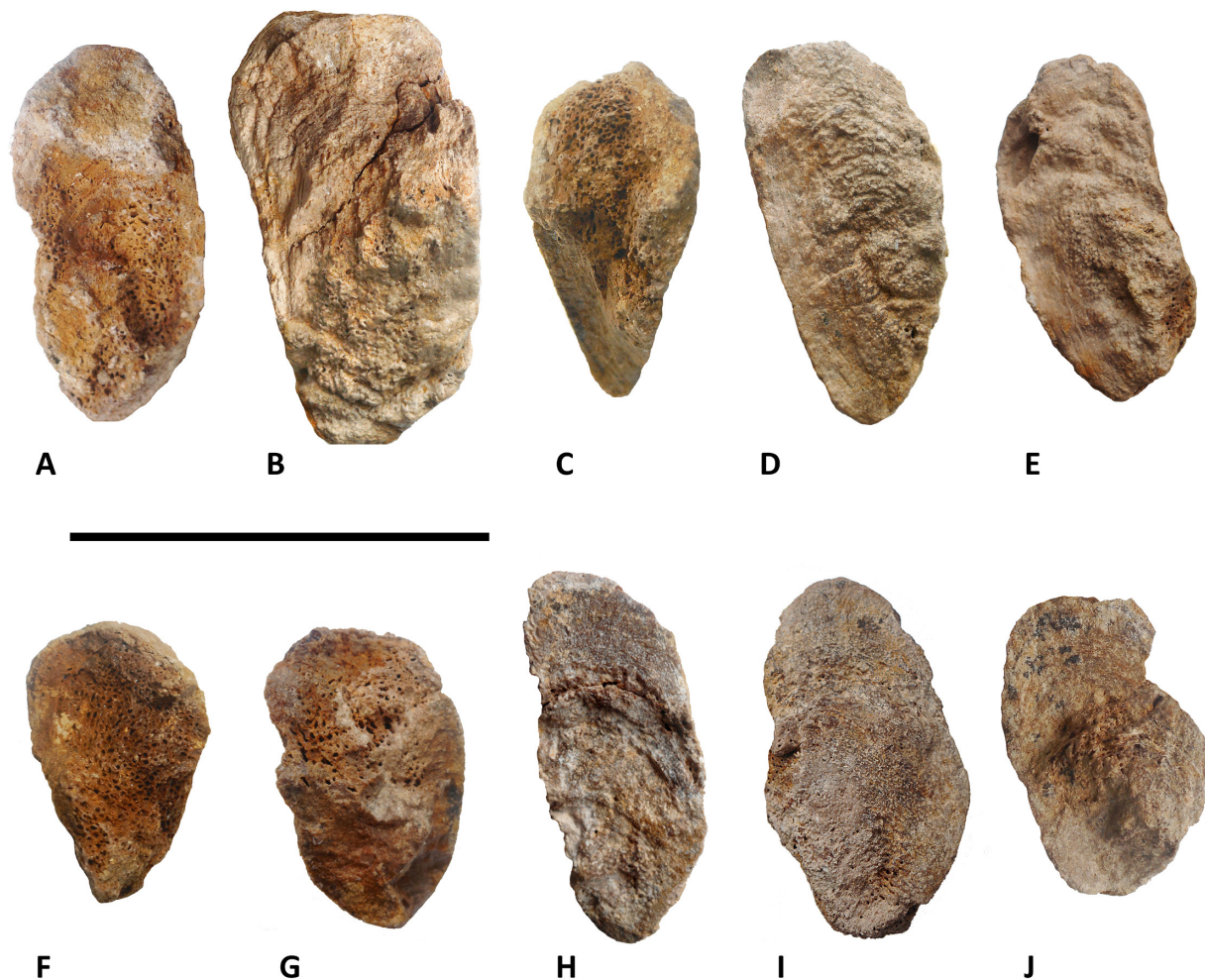
*Remarks* – This is the sole find of a cetacean from the Klimmen Member in southern Limburg (The Netherlands) to date. Given that all bones were recovered in close proximity (see above), they probably belonged to a single individual. They do not differ in colour or preservation and lack any signs of abrasion or transport. The same holds true for the fractured surfaces. Although, at first sight, the bone does not seem to have been much changed by the fossilisation process, it is in fact remarkably solid and probably silicified. The fragmentary state and dispersal of the material were undoubtedly caused by large-scale excavations at the site.

**Discussion**

As mentioned above, we interpret all the bones contained in lot NHMM 197955 to represent a single individual, which was still young or subadult, as indicated by partially fused vertebral epiphyses (Moran *et al.*, 2015). The vertebral centra and rib fragments have the following characteristics that will be discussed below: i) the pres-







**Figure 7.** NHMM 197955, indet. cetacean, rib fragments. Anterior is to the left, medial is downwards. The thickest part of the cortex is situated at the anterolateral side of the ribs. A: rib fragment 23, proximal view; B: rib fragment 36, proximal view; C: ribfragment 14a, proximal view; D: ribfragment 14a, distal view, mirrored; E: ribfragment 14b, distal view, mirrored; F: ribfragment 13a, proximal view, mirrored; G: ribfragment 13b, distal view; H: ribfragment 17c, distal view, mirrored; I: ribfragment 17b, proximal view; J: ribfragment 17b, distal view, mirrored. Scale bar 5 cm.

ence of a circumferential compact, multi-layered cortex (CCMC) in both centra and ribs; ii) the ventrally projecting transverse process of the lumbar vertebral centrum NHMM 197955-4; iii) the large width of the neural canal in the lumbar and thoracic vertebral centra NHMM 197955-4 and -5; iv) the probable presence of an extensive vascular system in the vertebral centrum NHMM 197955-4.

i) – Osteosclerosis, as observed in the vertebrae and ribs of lot NHMM 197955, is not seen in the extant *Delphinus delphis* Linnaeus, 1758 and other modern cetacean taxa (de Buffrénil *et al.*, 1990; Gray *et al.*, 2007), but is widespread in archaeocetes. Ribs of the basalmost whales (*Pakicetus attockii* West, 1980) and their closest relatives, including the raoellid *Indohyus* Rao, 1971, show osteosclerosis (Gray *et al.*, 2007; Cooper *et al.*, 2012), while ribs of *Ambulocetus natans* Thewissen, Madar & Hussain, 1996 are pachyosteosclerotic (Gray *et al.*, 2007). Vertebrae and ribs of the remingtonocetid *Remingtonocetus do-*

*mandaensis* Gingerich, Haq, Khan & Zalmout, 2001 and protocetids (*Rodhocetus kasranii* Gingerich, Raza, Arif, Anwar & Zhou, 1994, *Maiacetus inuus* Gingerich, Haq, von Koenigswald, Sanders, Smith & Zalmout, 2009 and *Qaisracetus arifi* Gingerich, Haq, Khan & Zalmout, 2001) are osteosclerotic with a circumferential, compact and multi-layered cortex (CCMC) (Houssaye *et al.*, 2015). In basilosaurids, a CCMC is seen in torso vertebrae and ribs of *Platyosphys* (*Basilotritus*) *uheni* Gol'din & Zvonok, 2013, *Pl. paulsonii* (Gol'din & Zvonok, 2013) and '*Pontogeneus brachyspondylus*' (*sensu* Kellogg, 1936) [see illustrations in Müller, 1849]. *Basilosaurus isis* Andrews, 1904 has osteosclerotic, probably also pachyostotic ribs and vertebrae with a partial CCMC ('a yoke of compact bone surrounding the mid-centrum, neural arches and transverse processes') (Houssaye *et al.*, 2015, p. 23). However, osteosclerosis is not restricted to archaeocetes; some archaic mysticetes display postcranial osteosclerosis as well. Ribs of the Late Eocene, tooth-bearing mysticete *Llanocetus denticrenatus* Mitchell, 1989 are osteo-



sclerotic and a vertebra (R. Ewan Fordyce field number, REF 10-23.12.86.1) found nearby and possibly belonging to this specimen, is osteosclerotic at the transverse processes (Fordyce & Watson, 1998; a collection number or institution has not been provided). A probable archaic mysticete (OU 21813), from the Lower Oligocene of New Zealand has osteosclerotic vertebrae and ribs with multi-layered, compact bone and probably pachyostosis (Fordyce & Watson, 1998). Some mysticetes from the Upper Oligocene of New Zealand (OU 21939 and OU 22028) have ribs with a CCMC and only a small core of spongy bone (Fordyce & Watson, 1998). Ribs of the Oligocene *Aetiocetus cotylalveus* Emlong, 1966 from Oregon, USA, are osteosclerotic too (Beatty & Dooley, 2009). Osteosclerosis, without pachyostosis, is seen in the Middle Miocene baleen-bearing mysticete *Diorocetus hiatus* Kellogg, 1968 and, to a lesser extent, also in other contemporaneous chaemysticetes such as *Metopocetus* Cope, 1896 and *Parietobalaena* Kellogg, 1924 (see Beatty & Dooley, 2009). The Late Miocene *Cetotherium riabinini* Hofstein, 1943, and other chaemysticetes from the eastern Paratethys have pachyosteosclerotic ribs, as well as lumbar and caudal vertebrae (Gol'din *et al.*, 2014). Postcranial osteosclerosis in certain Miocene Chaemysticeti is either a plesiomorphic feature or may have redeveloped for buoyancy control or specialised feeding strategies (Beatty & Dooley, 2009; Gol'din *et al.*, 2014).

The compact, multi-layered cortex of vertebra NHMM 197955-4 (Fig. 4D) is possibly structured around a cone of spongy bone. Gingerich & Zouhri (2015) described the inner structure of vertebrae of the basilosaurid *Platyosphys aithai* Gingerich & Zouhri, 2015 and the protocetid *Eocetus schweinfurthi* Fraas, 1904 as formed by an anterior and a posterior cone. The broadest part of each cone is on the epiphyseal side, tapering towards the mid-point of the centrum. At this mid-point, the circumferential cortex reaches its greatest thickness.

The thickest part of the cortex in the numerous rib fragments of NHMM 197955 is probably located on the anterolateral side, with the medullary area of trabecular bone on the posteromedial side. Data on basilosaurid ribs, as taken from the literature, vary as far as the position of the core of trabecular bone and the position of the thickest part of the cortex are concerned. According to Gol'din & Zvonok (2013), the core of trabecular bone is situated at the centre of the rib in *Platyosphys (Basilotritus) uheni*. Houssaye *et al.* (2015) noted that the core of trabecular bone was strongly off-centered in *Basilosaurus isis*, with the thickest part of the cortex being lateral (or posterolateral, according to their figure 13). De Buffrénil *et al.* (1990) mentioned that the thickest part of the cortex was found on the medial side of the studied rib in *Basilosaurus cetoides* Owen, 1839.

The bone of the pieces NHMM 197955-36 and -37) presumably is a distal rib fragment; it is thicker than the other rib fragments and clearly pachyostotic. Indeed, the distal part of ribs of *Basilosaurus cetoides* and *B. isis* is remarkably thicker, giving the rib a 'club-like' appearance (Kellogg, 1936; de Buffrénil *et al.*, 1990; Houssaye

*et al.*, 2015); the same is true for *Platyosphys* Kellogg, 1936 (Zvonok, 2012, fig. 2) and *Cynthiacetus peruvianus* Martínez-Cáceres & de Muizon, 2017 (see Martínez-Cáceres *et al.*, 2017). Also the distal part of the ribs of the Early Oligocene mysticete OU 21813 is 'somewhat swollen' (Fordyce & Watson, 1998, p. 164).

ii) – The transverse process of the lumbar vertebral centrum NHMM 197955-4 is directed ventrally. This is also seen in basilosaurids such as *Basilosaurus cetoides* (Kellogg, 1936, p. 47), '*Pontogeneus brachyspondylus*' (*sensu* Kellogg, 1936) and *Cynthiacetus peruvianus* (see Martínez-Cáceres *et al.*, 2017, p. 88). In more derived mysticetes the transverse processes are directed horizontally (Sanders & Barnes, 2002). However, the above-mentioned vertebra REF 10-23.12.86.1, possibly of the Late Eocene mysticete *L. denticrenatus* also has more or less ventrally deflected transverse processes (Fordyce & Watson, 1998). The transverse processes of lumbar and caudal vertebrae of the archaic mysticete *Eomysticetus whitmorei* Sanders & Barnes, 2002 from the Upper Oligocene (Chandler Bridge Formation) of South Carolina, USA (Sanders & Barnes, 2002) are also directed ventrally. However, the transverse processes of the more archaic tooth-bearing aetiocetids *Aetiocetus cotylalveus* and *Fucaia buelli* Marx, Tsai & Fordyce, 2015 are directed horizontally.

iii) – The distance between the pedicles of the neural arches of the thoracic and lumbar vertebral centra NHMM 197955-1, -4 and -5 appears to be rather large. The neural arch of thoracic vertebrae of *B. isis* is 'queroval' (Stromer von Reichenbach, 1908, p. 27) and widened in *B. isis* and *B. cetoides* (Stromer von Reichenbach, 1908, p. 60). Kellogg (1936, p. 42) remarked that all thoracic vertebrae of *Basilosaurus cetoides*, '... have an unusually low and broad neural canal, progressively larger toward the hinder end of this series'. The same is true for *Cynthiacetus peruvianus* in which the neural arch of Th4-19 is horizontally rectangular, with only the neural arch of Th20 being taller than wide (Martínez-Cáceres *et al.*, 2017, pp. 72-80). Vertebrae of the Late Oligocene mysticete *Eomysticetus whitmorei* have 'features, intermediate between archaeocetes and mysticetes' (Sanders & Barnes, 2002, pp. 333- 334). The vertebral column is not completely known, but thoracic vertebrae of this species also have broad and low neural arches. Although it is beyond the scope of the present paper to give a full record of the relative width of the neural arches in cetacean species, a comparison is made between several basilosaurids and neocetes in Appendix Table 3. The relative width of the neural arches in anterior and central thoracic vertebrae does not differ much between the mentioned basilosaurids and neocetes and the estimated value of vertebra NHMM 197955-5 (e0,8) is comparable with that of both. However, the relative width in posterior thoracic and lumbar vertebrae of basilosaurids is, in agreement with Kellogg (1936), proportionally large. The values for the posterior thoracic or anterior lumbar vertebra NHMM 197955-1 and the lumbar vertebra NHMM

197955-4 (both e0,6) are comparable with those of basilosaurids, and not with those of the neocetes listed (see Appendix Table 3).

*iv*) – Lumbar vertebrae of basilosaurids such as *Zygorhiza kochii* Kellogg, 1936 (pp. 144-150), *Dorudon atrox* Andrews, 1906 (see Uhen, 2004, p. 88), *Basilosaurus cetoides* (Kellogg, 1936, p. 47), *Platyosphys paulsonii* (Kellogg, 1936, p. 99) and '*Pontogeneus brachyspondylus*' (*sensu* Kellogg, 1936, p. 253), have two, sometimes even more, vascular foramina on both ventral and dorsal sides. Dorsal and ventral foramina are often lacking in anterior thoracic and posterior caudal vertebrae of basilosaurids. Vertebral ventral foramina in Neoceti have not been described except in the vertebra REF 10-23.12.86.1, which possibly belongs to *Llanocetus denticrenatus*. Dorsal and ventral vertebral foramina in archaocetes are indicative of an extensive vascular system. Such a vascular system is probably visible in NHMM 197955-4: a small dorsal foramen is seen, as are traces of vascular structures in the centrum as revealed by fractures, but if there have been ventral foramina, they are not present anymore, due to damage. The anterior thoracic vertebra NHMM 197955-5 has no dorsal or ventral foramina.

In view of the fact that these features i-iv are plesiomorphic, they do not have enough diagnostic value to make a positive identification at family level. Both geochronological age and morphological features point to either a basilosaurid, or an archaic mysticete. If NHMM 197955 indeed represents a basilosaurid, the non-elongated vertebral centra contrast markedly with those of *Basilosaurus* Harlan, 1834 and *Platyosphys* (Appendix, Table 1), rather indicating a 'dorudontine' species. Considering size of ribs and vertebral centra, this must have been a large animal. The original size of the vertebrae will undoubtedly have exceeded that of the large 'dorudontines' *Cynthiacetus peruvianus* (see Martínez-Cáceres *et al.*, 2017), *C. maxwelli* Uhen, 2005 (see also Uhen, 2013) and *Masracetius markgrafi* Gingerich, 2007 (see Slijper, 1936, table 23), but is comparable to '*Pontogeneus brachyspondylus*' (*sensu* Kellogg, 1936) from the Bartonian-Priabonian Upper Jackson Group of Alabama. Like NHMM 197955, '*P. brachyspondylus*' has lumbar vertebrae with transverse processes that are directed anteriorly and ventrolaterally, and with dorsal and ventral foramina (Kellogg, 1936, p. 253) and torso vertebrae with a CCMC as seen in illustrations provided by Müller (1849). A lumbar vertebral centrum (still undescribed), dredged from the tidal channel 'Het Scheur' in the southern North Sea, seems to be morphologically similar to the vertebral centrum NHMM 197955-4. This vertebra is probably older than NHMM 197955 (see above; Post *et al.*, 2017).

Regarding a possible archaic mysticete, to date, only two Late Eocene mysticetes are on record, namely *Mystacodon selenensis* Lambert, Martínez-Cáceres, Bianucci, Di Celma, Salas-Gismondi, Steurbaut, Urbina & de Muizon, 2017, from the lower Upper Eocene of Peru, and the large *Llanocetus denticrenatus* from the uppermost Eocene of Antarctica. Vertebral remains of *M. selenensis* have not

yet been described. As noted above, ribs of *L. denticrenatus* and the large lumbar vertebra (REF10-23.12.86.1), possibly belonging to this specimen, display plesiomorphic features (Fordyce & Watson, 1998). Thus, an interpretation of NHMM 197955 as an early mysticete cannot be excluded even if the two Priabonian mysticetes referred to above were based on material collected in the Southern Hemisphere.

## Conclusions

Having been recovered from shallow-marine strata of the lowermost portion of the Klimmen Member, the partial ENCI whale skeleton, is considered to be of Late Eocene age and to constitute the first *in-situ* record of a Palaeogene cetacean from the Netherlands. The geochronological age and the plesiomorphic morphological features, observed in vertebrae and ribs suggest basilosaurid affinities for this specimen, with the size of the centra being comparable to '*P. brachyspondylus*' (*sensu* Kellogg, 1936). However, because mysticetes first appeared during the Late Eocene and likewise display plesiomorphic features, an interpretation of NHMM 197955 as an early mysticete cannot be ruled out entirely.

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## References

- Andrews, C.W. 1904. Further notes on the mammals of the Eocene of Egypt. Part III. *Geological Magazine* 5: 211-215.
- Andrews, C.W. 1906. *A descriptive catalogue of the Tertiary vertebrata of the Fayûm, Egypt*. London: British Museum (Natural History): 324 pp.
- Beatty, B.L., & Dooley, A.C. 2009. Injuries in a mysticete skeleton from the Miocene of Virginia, with a discussion of buoyancy and the primitive feeding mode in the Chaeomysticeti. *Jeffersoniana, Contributions from the Virginia Museum of Natural History* 20: 1-28.
- Bogachev, V.V. 1959. Remains of a cetacean from the Oligocene of Tsimlyanskaya. *Trudy Instytuta Mineral'nykh Resursiv*



- Akademii Nauk USSR, Kiev* 1: 40-42.
- Brandt, J.F. 1873a. Untersuchungen über die fossilen und sub-fossilen Cetaceen Europas. *Mémoires de L'Académie Impériale des Sciences de Saint-Petersbourg* 7: 1-372.
- Brandt, J.F. 1873b. Über bisher in Russland gefundene Reste von Zeuglodonten. *Mélanges biologiques tirés du Bulletin de L'Académie Impériale des Sciences de Saint-Petersbourg* 9: 111-112.
- Brisson, M.J. 1762. *Regnum animale in classes IX. distributum, sive synopsis methodica sistens generalem animalium distributionem in classes IX, & duarum primarum classium, quadrupedum scilicet & cetaceorum, particularem divisionem in ordines, sectiones, genera & species. Cum brevi cuiusque speciei descriptione, citationibus auctorum de iis tractantium, nominibus eis ab ipsis & nationibus impositis, nominibusque vulgaribus. Editio altera auctior.* Lugduni Batavorum (Leiden): 296 pp.
- Buffrénil, V. de, Ricqlès, A. de, Ray, C.E. & Domning, D.P. 1990. Bone histology of the ribs of the archaeocetes (Mammalia: Cetacea). *Journal of Vertebrate Paleontology* 10: 455-466.
- Cooper L.N., Thewissen J.G.M., Bajpai S., and Tiwari B.N. 2012. Postcranial morphology and locomotion of the Eocene raoellid *Indohyus* (Artiodactyla: Mammalia). *Historical Biology* 24: 279-310.
- Cope, E.D. 1868. An addition to the vertebrate fauna of the Miocene period, with a synopsis of the extinct Cetacea of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia* 19: 138-157.
- Cope, E.D. 1896. Sixth contribution to the knowledge of the marine Miocene fauna of North America. *Proceedings of the American Philosophical Society* 35: 139-146.
- De Mulder, E.F.J., Geluk, M.C., Ritsema, I., Westerhoff, W.E. & Wong, T.E. 2003. *Geologie van Nederland, deel 7. De ondergrond van Nederland.* Nederlands Instituut voor Toegepaste Geowetenschappen TNO, Utrecht: 379 pp.
- Diedrich, C.G. 2013. The most northerly record of the sirenian *Protosiren* and the possible polyphyletic evolution of manatees and dugongs. *Natural Science* 5: 1154-1164.
- Du Four, I., Schelfaut, K., Vanheteren, S., Van Dijk, T. & Van Lancker, V.R.M. 2006. Geologie en sedimentologie van het Westerscheldemondingsgebied. In: Coosen, J. et al. (eds.) *Studiedag: de Vlakte van de Raan van onder het stof gehaald*, Oostende. *VLIZ Special Publication* 35: 16-29.
- 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.
- Fedorovsky, A. 1912. A record of a fossil cetacean in Zmiev uyezd of Kharkov Government. *Trudy Obshchestva Ispytateley Prirody Kharkovskogo Universiteta* 14: 253-287.
- Felder, W.M. & Bosch, P.W. 1998. Geologie van de St. Pietersberg bij Maastricht. *Grondboor & Hamer* 52(3) [Limburg-nummer 9A: Geologie van de St. Pietersberg]: 53-63.
- Felder, W.M. & Bosch, P.W. 2000. *Geologie van Nederland, deel 5. Krijt van Zuid-Limburg.* Nederlands Instituut voor Toegepaste Geowetenschappen TNO, Delft/Utrecht: 192 pp.
- Flower, W.H. 1883. On the arrangement of the orders and families of existing Mammalia. *Proceedings of the Zoological Society of London* 1883: 178-186.
- Fordyce, R.E. & Watson, A.G. 1998. Vertebral pathology in an Early Oligocene whale (Cetacea, ?Mysticeti) from Wharekuri, North Otago, New Zealand. *Mainzer naturwissenschaftliches Archiv, Beiheft* 21: 161-176.
- Fraas, E. 1904. Neue Zeuglodonten aus dem Unteren Mittel-eocän vom Mokattam bei Cairo. *Geologische und palaeontologische Abhandlungen* 6: 199-220.
- Gingerich, P.D. 2007. *Stromerius nidenensis*, new archaeocete (Mammalia, Cetacea) from the Upper Eocene Qasr El-Sagha Formation, Fayum, Egypt. *Contributions from the Museum of Paleontology, the University of Michigan* 31: 363-378.
- Gingerich, P.D., Raza, S.M., Arif, M. Anwar, M. & Zhou, X. 1994. New whale from the Eocene of Pakistan and the origin of cetacean swimming. *Nature* 368: 844-847.
- Gingerich, P.D., ul-Haq, M., Khan, I.H. & Zalmout, I.S. 2001. Eocene stratigraphy and archaeocete whales (Mammalia, Cetacea) of Drug Lahar in the eastern Sulaiman range, Balochistan (Pakistan). *Contributions from the Museum of Paleontology, the University of Michigan* 30: 269-319.
- Gingerich, P.D., ul-Haq, M., von Koenigswald, W., Sanders, W.J., Smith, B.H. & Zalmout, I.S. 2009. New protocetid whale from the Middle Eocene of Pakistan: birth on land, precocial development and sexual dimorphism. *PLoS ONE* 4: e4366.
- Gingerich, P.D. & Zouhri, S. 2015. New fauna of archaeocete whales (Mammalia, Cetacea) from the Bartonian Middle Eocene of southern Morocco. *Journal of African Earth Sciences* 111: 273-286.
- Gol'din, P.E., Zvonok, E.A. & Krakhmalnaya, T.V. 2012. New records of "Eocetus" sp. (Mammalia: Cetacea) from the Eocene of Ukraine. *Geolog Ukrainy* 39: 104-113.
- 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: 254-268.
- Gol'din, P., Startsev, D. & Krakhmalnaya, T. 2014. The anatomy of the Late Miocene baleen whale *Cetotherium riabinini* from Ukraine. *Acta Palaeontologica Polonica* 59: 795-814.
- Gol'din, P.E., Zvonok, E.A., Rekovets, L., Kovalchuk, A. & Krakhmalnaya, T.V. 2014. *Basilotritus* (Cetacea: Pelagiaceti) from the Eocene of Nagornoye (Ukraine): New data on anatomy, ontogeny and feeding of early basilosaurids. *Comptes Rendus Palevol* 13: 267-276.
- Gray, N.-M., Kainec, K., Madar, S., Tomko, L. and Wolfe, S. 2007. Sink or Swim? Bone Density as a Mechanism for Buoyancy Control in Early Cetaceans. *The Anatomical Record* 290: 638-653.
- Gritsenko, V. 2001. New species *Platiosphys einori*, Archaeoceti from Oligocenic deposits of Kiev. *Visnyk Kyivskogo Natsionalnogo Universyteta Imeni Tarasa Shevchenka, Seriya Geologiya* 206: 17-20.
- Halstead, L.B. & Middleton, J. 1902. Notes on fossil whales from the upper Eocene of Barton, Hampshire. *Proceedings of the Geologists' Association* 83: 185-190.
- Haq, B.U., Hardenbol, J. & Vail, P.R. 1988. Mesozoic and Cenozoic chronostratigraphy and cycles of sea-level change. In: C.K. Wilgus, B.S. Hastings, C.G.St.C. Kendall, H.W. Posamentier, C.A. Ross & J.C. van Wagoner (eds.), *Sea-level changes: an integrated approach. Society of Economic Paleontologists and Mineralogists, Special Publication* 42: 71-108.

- Harlan, R. 1834. Notice of fossil bones in the Tertiary formation of the State of Louisiana. *Transactions of the American Philosophical Society* 4: 397-403.
- Hofstein, I.D. 1948. Pachyostosis in fossil whales. *Zbirnyk Prats z Paleontologii i Stratygrafii, Instytut Geologichnyh Nauk URSR* 1: 65-75.
- Houssaye, A., Tafforeau, P., de Muizon, C. & Gingerich, P.D. 2015. Transition of Eocene whales from land to sea: evidence from bone microstructure. *PLoS One* 10: e0118409.
- Hudleston, W.H. 1902. Creechbarrow: An Essay in Purbeck Geology. *Proceedings of the Dorsal Natural History Museum and Antiquarian Field Club* 23: 146-190.
- Jagt, J.W.M., Leloux, J. & Dhondt, A.V. 1998. Fossielen van de St. Pietersberg. *Grondboor en Hamer*, 52: 94.
- Jagt, J.W.M. & Jagt-Yazykova, E.A. 2012. Stratigraphy of the type Maastrichtian – a synthesis. In: Jagt, J.W.M., Donovan, S.K. & Jagt-Yazykova, E.A. (eds.), Fossils of the type Maastrichtian (Part 1). *Scripta Geologica Special Issue* 8: 5-32.
- Kalmykov, N.P. 2012. New finding of the ancient whale *Basilosaurus* (Cetacea, Archaeoceti: Basilosauridae) in the Lower Don area. *Doklady Earth Sciences* 442: 178-180.
- Kellogg, R. 1924. Description of a new genus and species of whalebone whale from the Calvert Cliffs, Maryland. *Proceedings of the United States National Museum* 63: 1-14.
- Kellogg, R. 1936. *A review of the Archaeoceti*. Carnegie Institution of Washington, Washington DC: 366 pp.
- Kellogg, R. 1968. A hitherto unrecognized Calvert cetothere. *Bulletin of the United States National Museum* 247: 133-161.
- Kellogg, R. 1968. Fossil Marine Mammals from the Miocene Calvert Formation of Maryland and Virginia, part 1: a new whalebone whale from the Miocene Calvert Formation. *United States National Museum Bulletin* 247: 1-45.
- Kellogg, R. 1968. Fossil Marine Mammals from the Miocene Calvert Formation of Maryland and Virginia, part 8: supplement to description of *Parietobalaena palmeri*. *United States National Museum Bulletin* 247: 175-197.
- Koch, A. 1899. Schwanzwirbelreste eines ausgestorbenen Cetaceen von Kolzsvár. *Földtani Közlöny* 19: 204-209.
- Kuyl, O.S. 1975. Lithostratigrafie van de Mio-Oligocene afzettingen in Zuid-Limburg. In: Zagwijn, W.H. & Van Staalduinen, C.J. (eds.), *Toelichting bij geologische overzichtskaarten van Nederland*. Rijks Geologische Dienst, Haarlem: 56-63.
- Lambert, O., Martínez-Cacères, M., Bianucci, G., di Celma, C., Salas-Gismondi, R., Steurbaut, E., Urbina, M. & de Muizon, C. 2017. Earliest mysticete from the Late Eocene of Peru sheds new light on the origin of baleen whales. *Current Biology* 27: 1-7.
- Landois, H. 1884. Mitteilung von dem Funde von Zeuglodonresten bei Münster. *Verhandlungen des naturhistorischen Vereins der Preussischen Rheinlande und Westfalens, Correspondenzblatt* 41: 49-50.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis*. Editio decima, reformata. Stockholm (Laurentius Salvius): 1384 pp.
- 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: 172 pp.
- Marx, F.G., Lambert, O. & Uhen, M.D. 2014. *Cetacean paleobiology*. John Wiley & Sons Ltd., Chichester: 1-319.
- Marx FG, Tsai C-H, and Fordyce RE. 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* 2:150476.
- 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: 2219-2235.
- Moran, M.M., Bajpai S., George J.C., Suydam, R., Usip, S. & Thewissen, J.G.M. 2015. Intervertebral and epiphyseal fusion in the postnatal ontogeny of cetaceans and terrestrial mammals. *Journal of Mammalian Evolution* 22: 93-109.
- Müller, J. 1849. *Über die fossilen Reste der Zeuglodonten von Nordamerika, mit Rücksicht auf die europäischen Reste aus dieser Familie*, 1-38. G. Reimer, Berlin.
- Omura H., Nishiwaki, M., Ichihara, T., Kasuya, T. 1962. Osteological note on a sperm whale. *The scientific reports of the Whales Research Institute* 16: 35-45.
- Owen, R. 1839. Observations on the *Basilosaurus* of Dr. Harlan (*Zeuglodon cetoides*, Owen). *Transactions of the Geological Society of London* 6: 69-79.
- Pilleri, G. 1989. An archeocete vertebra from the Upper Eocene of Taradell, Catalonia, Spain. *Contributions to the Paleontology of some Tethyan Cetacea and Sirenia (Mammalia)* 2: 7-12.
- Pilleri, G. & Fulgosi, F.C. 1989. First Archaeoceti record from the Eocene of Italy (Varano, Northern Apennines). *Contributions to the Paleontology of some Tethyan Cetacea and Sirenia (Mammalia)* 2:87-101.
- Post, K. 2007. Raadsels uit de Noordzee. *Cranium* 24: 31-38.
- Post, K., Hoekman, A. & De Wilde, B. 2017. Oerwalvissen op de bodem van de Noordzee. *Cranium* 34: 46-49. [In Dutch]
- Rademakers, P.C.M. 1998. Geologische orgelpijpen. *Grondboor & Hamer* 52(3) [Limburgnummer 9A: Geologie van de St. Pietersberg]: 71-77.
- Rao, A.R. 1971. New mammals from Murree (Kalakot Zone) of the Himalayan foot hills near Kalakot, Jammu and Kashmir state, India. *Journal of the Geological Society of India* 12: 124-134.
- Sanders, A.E. & Barnes, L.G. 2002. Paleontology of the Late Oligocene Ashley and Chandler Bridge Formations of South Carolina, 3: Eomysticetidae, a new family of primitive mysticetes (Mammalia: Cetacea). *Smithsonian Contributions to Paleobiology* 93: 313-356.
- Schiöler, P., Brinkhuis, H., Roncaglia, L. & Wilson, G.J. 1997. Dinoflagellate biostratigraphy and sequence stratigraphy of the Type Maastrichtian (Upper Cretaceous), ENCI Quarry, The Netherlands. *Marine Micropaleontology* 31: 65-95.
- Schouten, S. 2011. De wervels van Basilosauridae: een overzicht van en een vergelijking met raadselachtige vondsten uit de Noordzee. *Cranium* 28: 17-25.
- Seeley, H.G. 1876. Notice of the occurrence of remains of a British *Zeuglodon* (*Z. wanklyni*, Seeley) in the Barton Clay of the Hampshire Coast. *The Quarterly Journal of the Geological Society of London* 32: 428-432.
- Seeley, H.G. 1881. Note on the caudal vertebra of a cetacean discovered by Prof. Judd in the Brockenhurst Beds, indica-



- tive of a new type allied to *Balaenoptera* (*Balaenoptera juddi*). *The Quarterly Journal of the Geological Society of London* 37: 709-712.
- Slijper, E.J. 1936. *Die Cetaceen, vergleichend- anatomisch und systematisch. Ein Beitrag zur vergleichenden Anatomie des Blutgefäß-, Nerven- und Muskelsystems, sowie des Rumpfskelettes der Säugetiere, mit Studien über die Theorie des Aussterbens und der Foetalisation.* 's-Gravenhage, Martinus Nijhoff: 590 pp.
- Stromer von Reichenbach, E. 1908. Die Archaeoceti des ägyptischen Eozäns. *Beiträge zur Paläontologie und Geologie Österreich- Ungarns und des Orients Wien* 21: 106-178.
- Thewissen, J.G.M., Madar S.I. & Hussain S.T. 1996. *Ambulocetus natans*, an Eocene cetacean (Mammalia) from Pakistan. *Courier Forschungsinstitut Senckenberg* 191: 1-86.
- Uhen, M.D. 1998. Middle to Late Eocene basilosaurines and dorudontines. In: J.G.M. Thewissen (ed.), *The emergence of whales. Evolutionary patterns in the origin of Cetacea*. Plenum Press, New York/London: 29-61.
- Uhen, M.D. 1999. New species of protocetid archaeocete whale, *Eocetus wardii* (Mammalia: Cetacea) from the Middle Eocene of North Carolina. *Journal of Paleontology* 73: 512-528.
- Uhen, M.D. 2001. New material of *Eocetus wardii* (Mammalia, Cetacea) from the Middle Eocene of North Carolina. *Southeastern Geology* 40: 135-148.
- Uhen, M.D. 2004. Form, function and anatomy of *Dorudon atrox* (Mammalia, Cetacea): an archaeocete from the Middle to Late Eocene of Egypt. *The University of Michigan, Papers on Paleontology* 34: 1-222.
- Uhen, M.D. 2005. A new genus and species of archaeocete whale from Mississippi. *Southeastern Geology* 43: 157-172.
- Uhen, M.D. 2008. New protocetid whales from Alabama and Mississippi, and a new cetacean clade, Pelagiceti. *Journal of Vertebrate Paleontology* 28: 589-593.
- Uhen, M.D. 2013. A review of North American Basilosauridae. *Bulletin and Contributions to Alabama Paleontology, Alabama Museum of Natural History* 31: 1-45.
- Uhen, M.D. & Berndt, H.-J. 2008. First record of the archaeocete whale family Protocetidae from Europe. *The Fossil Record, Museum für Naturkunde der Humboldt Universität zu Berlin* 11: 57-60.
- 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: 955-969.
- Uhen, M.D. & Tichy, G. 2000. A new basilosaurid from Austria. *Journal of Vertebrate Paleontology* 20 [Supplement to no. 3]: 74A-75A.
- Van Adrichem Boogaert, H.A. & Kouwe, W.F.P. 1993-1997. Stratigraphic Nomenclature of the Netherlands. Revision and update by RGD and NOGPA.TNO- NITG. Geological Survey of the Netherlands. *Mededelingen Rijks Geologische Dienst* 50.
- West, R.M. 1980. Middle Eocene large mammal assemblage with Tethyan affinities, Ganda Kas region, Pakistan. *Journal of Palaeontology* 54: 508-533.
- Zouhri, S., Gingerich, P.D., Elboudali, N., Sebti, S., Noubhani, A., Rahali, M. & Meslouh, S. 2014. New marine mammal faunas (Cetacea and Sirenia) and sea level change in the Samlat Formation, Upper Eocene, near Ad-Dakhla in southwestern Morocco. *Comptes Rendus Palevol* 13: 599-610.
- Zvonok, E.A. 2012. On the problematic Eocene cetacean from Nagirne site (Kirovograd province, Ukraine) and the significance of archaeocetes for stratigraphic research. *Geolog Ukrainy* 1-2: 87-93.

**Appendix table 1.** Diversity in lumbar vertebrae amongst Basilosaurids

|                           |   | <b>Elongation</b> | <b>CCMC</b> | <b>Vertebra</b>       | <b>Rel L<br/>(L:W)</b> | <b>References</b>  |
|---------------------------|---|-------------------|-------------|-----------------------|------------------------|--|
| <b>LARGE</b>              |   |                   |             |                       |                        |  |
| <b>SHORT</b>              |   |                   |             |                       |                        |  |
| A1                        | USNM 11401a, 1  | –                 | ?           | Lu *)                 | 0.71                   | Kellogg, 1936, table 67  |
|                           | USNM 11401a, 3  |                   |             | Lu **)                | 0.65                   |  |
| A2                        | <i>Cynthiacetus maxwelli</i><br>MMNS VP 445   | –                 | ?           | LuA **)               | 0.73                   | Uhen, 2005   |
| <b>NOT ELONGATED</b>      |   |                   |             |                       |                        |  |
| B1                        | <i>Cynthiacetus peruvianus</i><br>MNHN.F.PRU 10   | –                 | ?           | Lu1<br>Lu11           | 0.92<br>0.87           | Houssaye <i>et al.</i> , 2015<br>Martínez-Cáceres <i>et al.</i> , 2017 |
| B2                        | ' <i>Pontogeneus brachyspondylus</i> '<br>(sensu Kellogg, 1936)<br>USNM 2211, 1<br>USNM 2211, 2 | –                 | +           | Lu3<br>Lu13           | 1.01<br>1.14           | Kellogg, 1936, table 65  |
| <b>ELONGATED</b>          |   |                   |             |                       |                        |  |
| C1                        | <i>Platyosphys (Basilotritus)</i> sp.<br>KOM44693<br>P 195 L                                    | +                 | +           | Lu **)                | 1.49                   | Gol'din & Zvonok, 2013, Appendix 3                                     |
| C2                        | <i>Platyosphys paulsonii</i>  | +                 | +           | Lu2<br>Lu7            | 1.76<br>1.47           | Kellogg, 1936, table 24  |
| <b>VERY ELONGATED</b>     |   |                   |             |                       |                        |  |
| D                         | <i>Basilosaurus cetoides</i><br>USNM 4675, 12261  | +                 | partial     | Lu1<br>Lu6<br>Lu13    | 1.94<br>1.9<br>1.79    | Kellogg, 1936, table 10  |
| <b>MEDIUM</b>             |   |                   |             |                       |                        |  |
| E                         | MUSM 1443   | +/-               | +           | ?                     | ?                      | Uhen <i>et al.</i> , 2011, table 1                                     |
| <b>SMALL</b>              |   |                   |             |                       |                        |  |
| <b>NOT ELONGATED</b>      |   |                   |             |                       |                        |  |
| F1                        | <i>Dorudon atrox</i><br>UM 101215   | –                 | –           | Lu1<br>Lu11           | 0.79<br>0.77           | Uhen, 2004, Appendix V   |
| F2                        | <i>Zygorhiza kochii</i><br>USNM 4678  | –                 | ?           | Lu2<br>Lu9            | 0.90<br>0.95           | Kellogg, 1936, table 36  |
| <b>SLIGHTLY ELONGATED</b> |   |                   |             |                       |                        |  |
| G                         | <i>Stromerius</i> sp.<br>UHC DAK140 35  | +                 | ?           | post Lu<br>or ant Ca? | 1.19                   | Zouhri <i>et al.</i> , 2014, table 2                                   |

Relative length (Rel L) = L(dors)/W(ant):

... - 0,80: short      0,85-1,15: not elongated      1,15-1,45: slightly elongated      1,45-1,75: elongated      1,75-...: very elongated

Abbreviations:

**ant**, anterior; **Ca**, caudal vertebra; **CCMC**, compact, circumferential multi-layered cortex; **dors**, dorsal; **L**, length; **Lu**, lumbar vertebra; **MNHN** Muséum national d'Histoire naturelle, Paris, France; **MMNS** Mississippi Museum of Natural Science, Jackson, Mississippi; **MUSM** Departamento de Paleontologica de Vertebrados, Museo de Historia Natural de San Marcos collections, Lima, Peru; **post**, posterior; **Rel L**, Relative length; **UHC DAK**: Faculté des Sciences, Université Hassan-II, Dakhla collection, Casablanca, Morocco; **UM** University of Michigan Museum of Paleontology, Ann Arbor, Michigan; **USNM** United States National Museum of Natural History, Smithsonian Institution, Washington DC; **W**, width.

-, without; +, with; ?, unknown; \*) without posterior epiphysis; \*\*) without both epiphysis



Appendix table 2. European Eocene Cetaceans

| Locality  | Identification   | Material                                  | CCMC | Age  | References                 |
|---|--|---|------|--|----------------------------|
| Austria: St Pankras   | Basilosauridae indet.                                      | Cat.no. unknown: teeth                    | -    | Sandstone of St.Pankras, Lutetian or Bartonian         | Uhen & Tichy, 2000         |
| Belgium (Dutch- Belgian border): dredged from probably 'Het Scheur', Westerschelde Estuary, North Sea | Cetacea indet.   | NMR9991-3402: thoracic or lumbar vertebra | -/+  | Probably Maldegem Formation, Probably Bartonian        | Post, 2007                 |
| Belgium (Dutch- Belgian border): dredged from probably 'Het Scheur', Westerschelde Estuary, North Sea | Cetacea indet.   | NMR9991-3403: lumbar vertebra             | -/+  | Probably Maldegem Formation, Probably Bartonian        | Post, 2007                 |
| Belgium (Dutch- Belgian border): dredged from probably 'Het Scheur', Westerschelde Estuary, North Sea | Cetacea indet.   | NMR9991-3882: lumbar vertebra             | -/+  | Probably Maldegem Formation, Probably Bartonian        | Schouten, 2011             |
| Belgium (Dutch-Belgian border): dredged from probably 'Het Scheur', North Sea                         | Cetacea indet.   | NMR9991-3404: lumbar vertebra             | +    | Probably Maldegem Formation, Probably Bartonian        | Post, 2007                 |
| England: Barton Cliff, Hampshire  | <i>'Zeuglodon (Zygorhiza) wanklyni' Nomen nudum</i>        | No cat.no.: skull (lost)                  | -    | Naish Member?, Barton Beds Formation, Bartonian        | Seeley, 1876               |
| England: Barton Cliff, Hampshire  | <i>'Zeuglodon (Zygorhiza) wanklyni' Nomen nudum</i>        | NHMUK M. 11090: cervical vertebra         | -    | Barton Beds Formation, Bartonian                       | Andrews, 1907              |
| England: Barton Cliff, Hampshire  | <i>'Zeuglodon (Zygorhiza) wanklyni' Nomen nudum</i>        | NHMUK M 12346: thoracic vertebra          | -    | Barton Beds Formation, Bartonian                       | Halstead & Middleton, 1972 |
| England: Barton Cliff, Hampshire  | <i>'Zeuglodon (Zygorhiza) wanklyni' Nomen nudum</i>        | Cat.no. unknown: isolated epiphysis       |      | Barton Beds Formation, Bartonian                       | Halstead & Middleton, 1972 |
| England: Chewton Bunny, Hampshire   | Basilosauridae indet. ( <i>'Eocetus drazindai'?</i> )      | NHMUK M 26552: thoracic vertebra          | ?    | Naish Member, Barton Beds Formation, Bartonian         | Halstead & Middleton, 1972 |
| England: Cliffend, Hampshire  | Basilosauridae indet. ( <i>Basiloterus</i> sp.? )          | NHMUK M 26553: caudal vertebra            | ?    | Naish Member, Barton Beds Formation, Bartonian         | Halstead & Middleton, 1972 |
| England: Creechbarrow Hill  | <i>'Dorudontinae'</i> indet                                | ?   | ?    | Creechbarrow Limestone Formation, Bartonian            | Hudleston, 1902            |
| England: Roydon, Hampshire  | Basilosauridae indet. <i>'Zygorhiza juddi' Nomen nudum</i> | No. M. 133: caudal vertebra               | ?    | Brockenhurst series, Headon Hill Formation, Priabonian | Seeley, 1881               |
| Germany: Fürstenau  | Cetacea indet.?  | Cat.no. unknown: vertebral remains        |      | Lutetian   | Diedrich, 2013             |

Appendix 2, continued next page

## Appendix 2, continued

| Locality   | Identification   | Material   | CCMC | Age   | References   |
|--|--|--|------|---|--|
| Germany: Rohrdorf  | <i>Platyosphys (Basilotritus)</i> sp.  | USNM 534001: vertebra  | +    | Stockletten Formation, Bartonian                              | Uhen & Berndt, 2008                                    |
| Germany: Rohrdorf  | Basilosauridae indet. probably dorudontine   | Cat.no. unknown: premolar  | -    | Stockletten Formation, Bartonian                              | Uhen & Berndt, 2008                                    |
| Italy: Varano, Parma Apennines                                     | <i>Dorudon</i> sp.?  | Cat.no. unknown: 12 teeth, radius, rib fragments, skull fragments  | ?    | Priabonian  | Pilleri & Fulgosi, 1989                                |
| Netherlands: Maastricht  | Cetacea indet. features comparable to ' <i>Pontogeneus brachyspondylus</i> ' ( <i>sensu</i> Kellogg, 1936) | NHMM197955, ENCI 1 lumbar vertebra, 1 post thoracic - ant lumbar, 1 ant-central thoracic vertebra, 4 vertebral fragments, 5 transverse processes, 23 (24?) rib fragments | +    | Klimmen Member, probably Priabonian                           | This paper   |
| Romania: Cluj Napoca   | <i>Berardiopsis miocae-nus Nomen dubium</i>  | Cat.no. unknown: caudal vertebra   | ?    | Upper Eocene strata   | Koch, 1899   |
| Russia: Khoroshevskaya Cossack Village, Tsymlyansk water reservoir | Cetacea indet. basal basilosaurid  | Cat.no. unknown: pectoral girdle bones, 3 vertebrae (two caudal), rib fragments teeth  |      | Kharkov Formation, late Bartonian or Priabonian               | Kalmykov, 2012; Gol'din & Zvonok, 2013                 |
| Russia: Tsymlyansk Cossack Village                                 | <i>Platyosphys paulsonii</i>   | Cat.no. unknown: 3 vertebrae; teeth  | +    | Bartonian or Priabonian                                       | Bogachev, 1959   |
| Spain: Taradell, Catalonia   | Basilosauridae indet.  | MGSB No. 25.191: vertebra  | +    | Bartonian   | Pilleri, 1989  |
| Ukraine: Beloskelevatoye Village, Luhansk Province                 | <i>Platyosphys (Basilotritus) uheni</i>  | NMNH-P OF-2096: tympanic bulla, 3 posterior thoracic vertebrae, 1 rib fragment   | +    | Kiev Formation: Kiev horizon, late Bartonian                  | Zvonok, 2012; Gol'din & Zvonok, 2013                   |
| Ukraine: Kurenevka, Kiev   | <i>Platyosphys (Basilotritus) uheni</i>  | NMNH-P OF 1694: posterior thoracic vertebra<br>NMNH-P OF 1695: anterior lumbar vertebra rib fragments  | +    | Kiev horizon?, late Bartonian                                 | Gol'din et al., 2012; Gol'din & Zvonok, 2013           |
| Ukraine: Bugajewka, Izjum district                                 | <i>Platyosphys paulsonii</i>   | Cat.no. unknown: 5 vertebrae (lost)  | +    | Kharkov Formation, late Bartonian or Priabonian               | Kellogg, 1936  |
| Ukraine: Chigirin  | <i>Platyosphys paulsonii</i>   | Cat.no. unknown: vertebra + neural arch (lost)   | +    | Kharkov Formation: Obukov horizon, late Bartonian- Priabonian | Brandt, 1873a,b; Kellogg, 1936; Gol'din & Zvonok, 2013 |
| Ukraine: Chigirin, Stone Mountain, Tyasma River                    | <i>Platyosphys paulsonii</i>   | Cat.no. unknown: 2 vertebrae (lost)  | +    | Kharkov Formation: Obukov horizon, late Bartonian- Priabonian | Brandt, 1873a,b; Kellogg, 1936; Gol'din & Zvonok, 2013 |

Appendix 2, continued next page

## Appendix 2, continued

| Locality  | Identification                               | Material   | CCMC | Age   | References                                     |
|---|--|--|------|---|--|
| Ukraine: Koropovo, Kharkov Government             | <i>Platyosphys paulsonii</i>                 | Cat.no. unknown:<br>7 lumbar, 1 sacral, 2 caudal vertebrae, a chevron bone, a few rib fragments and bone fragments (lost)  | +    | Kharkov Formation, late Bartonian or Priabonian                               | Brandt, 1873a; Fedorovsky, 1912; Kellogg, 1936 |
| Ukraine: Nagirne (Nagornoye), Kirovograd Province | <i>Platyosphys (Basilotritus)</i> sp         | Nb.: a single individual!<br>NMHH-P NGr- 2, 3, 4, 7, 8, 12, 14, 15, 17, 18:<br>3 teeth, 3 vertebrae, sternal element, rib, scapula, phalange;<br>GMSTNUK 15/1-9 and NMNH-P NGr-13:<br>7 teeth, sternal element, rib, phalange;<br>NMNH-P NGr- 1, 5, 6, 9, 10, 11, 16, 17:<br>Tooth, mandible fragments, 4 vertebrae, 3 sternal elements, fragments ribs, scapular fragments, indet fragments | +    | Obukov horizon (lowermost part), Bartonian                                    | Zvonok, 2012; Gol'din et al., 2014             |
| Ukraine: Velyka(ya) Andrusovka                    | <i>Platyosphys (Basilotritus)</i> sp         | KOM 44693 P 195: lumbar vertebra   | +    | Kiev or Obukhov Horizon, Bartonian?   | Gol'din & Zvonok, 2013                         |
| Ukraine: Vlavoska                                 | <i>Platyosphys (Basilotritus)</i> sp         | KOM 44760 P 202, KOM 44761 P 203, KOM 44762 P 204:<br>3 thoracic vertebrae;<br>KOM 44759 P 201:<br>1 lumbar vertebrae  | +    | Obukov Horizon, late Bartonian to Priabonian                                  | Gol'din & Zvonok, 2013                         |
| Ukraine: Pirogovo, Kiev                           | <i>Platyosphys einori</i> basal basilosaurid | GMTSNUK 2638:<br>8 vertebrae, scapula fragment, rib fragments  | +    | Between Obukov horizon - Mezhygorsk horizon, Bartonian, Priabonian - Rupelian | Gritsenko, 2001                                |

## Abbreviations:

**CCMC**, compact, circumferential multi-layered cortex; **ENCI**, ENCI-HeidelbergCement Group quarry, Maastricht, The Netherlands; **GMTSNUK**, Geological Museum of Taras Shevchenko National University of Kiev, Ukraine; **KOM**, Kirovograd Oblast' Museum, Ukraine; **MGSB**, Museu Geològic del Seminari de Barcelona; **NHMM**, Natuurhistorisch Museum Maastricht, The Netherlands; **NHMUK**, Natural History Museum, London, England; **NMNH-P**, Paleontological Museum, National Natural History Museum of the Academy of Sciences of Ukraine, Kiev, Ukraine; post, posterior; **NMR** – Natuurhistorisch Museum Rotterdam (or 'Het Natuurhistorisch'), The Netherlands; **USNM**, United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

-, without; +, with; ?, unknown.



**Appendix table 3.** Relative width neural arch in thoracic and lumbar vertebrae, in several cetaceans.

| Cetacea indet. | NHMM197955-05,<br>Th(ant/centr) |                | NHMM197955-1.<br>Th(post) / Lu(ant) |                 | NHMM197955-4,<br>Lu |                 | References     |                 |                 |                 |
|----------------|---------------------------------|----------------|-------------------------------------|-----------------|---------------------|-----------------|----------------|-----------------|-----------------|-----------------|
|                | e0.8                            |                | e0.6                                |                 | e0.6                |                 | This article   |                 |                 |                 |
|                | <i>B.cetoid</i>                 | <i>C.peruv</i> | <i>Z.kochii</i>                     | <i>Z.kochii</i> | <i>E.whitm</i>      | <i>D.hiatus</i> | <i>Pa.palm</i> | <i>Pe.calve</i> | <i>Pe.calve</i> | <i>Ph.macro</i> |
| Th1            | 0.5                             | 0.6            | ?                                   | 0.7             | ?                   | 0.8             | ?              | 0.7             | ?               | 0.6             |
| Th2            | 0.6                             | 0.8            | ?                                   | 0.8             | 0.7                 | ?               | 0.6            | 0.7             | ?               | 0.7             |
| Th3            | 0.8                             | 0.8            | ?                                   | 0.8             | 0.8                 | ?               | 0.5            | 0.6             | ?               | 0.7             |
| Th4            | 0.8                             | 0.8            | ?                                   | 0.9             | ?                   | ?               | 0.6            | 0.6             | ?               | 0.7             |
| Th5            | 0.9                             | ?              | 0.7                                 | 0.8             | e0.7                | ?               | 0.6            | ?               | ?               | 0.8             |
| Th6            | 0.9                             | 1.0            | 0.6*                                | 0.8             | ?                   | ?               | 0.5            | 0.5             | ?               | 0.6             |
| Th7            | 0.9                             | ?              | ?                                   | 0.8             | 0.7                 | 0.6             | 0.5            | 0.5             | ?               | 0.6             |
| Th8            | 0.8                             | 0.9            | 0.6*                                | 0.8             | e0.6                | ?               | 0.5            | 0.5             | ?               | 0.5             |
| Th9            | ?                               | 0.8            | 0.6                                 | ?               | ?                   | 0.6             | 0.4            | ?               | 0.5             | 0.4             |
| Th10           | 0.7                             | 0.7            | 0.6                                 | ?               | ?                   | 0.5             | 0.4            | 0.4             | 0.4             | 0.4             |
| Th11           | 0.6                             | 0.7            | ?                                   | ?               | ?                   | 0.5             | 0.4            | 0.3             | 0.4             | 0.3             |
| Th12           | 0.6                             | 0.7            | 0.5*                                | ?               | ?                   | 0.4             | 0.4            | ?               | 0.3             |                 |
| Th13           | ?                               | 0.6            | 0.5*                                | ?               |                     |                 |                |                 |                 |                 |
| Th14           | ?                               | 0.6            | 0.5                                 | ?               |                     |                 |                |                 |                 |                 |
| Th15           | 0.5                             | 0.6            | 0.5                                 | ?               |                     |                 |                |                 |                 |                 |
| Th16           |                                 | 0.6            |                                     |                 |                     |                 |                |                 |                 |                 |
| Th17           |                                 | 0.6            |                                     |                 |                     |                 |                |                 |                 |                 |
| Th18           |                                 | 0.5            |                                     |                 |                     |                 |                |                 |                 |                 |
| Th19           |                                 | 0.5            |                                     |                 |                     |                 |                |                 |                 |                 |
| Th20           |                                 | 0.5            |                                     |                 |                     |                 |                |                 |                 |                 |
| Ref            | 1)                              | 2)             | 3)                                  | 4)              | 5)                  | 6)              | 7)             | 8)              | 9)              | 10)             |
|                | <i>B.cetoid</i>                 | <i>C.peruv</i> | <i>Z.kochii</i>                     | <i>Z.kochii</i> | <i>E.whitm</i>      | <i>D.hiatus</i> | <i>Pa.palm</i> | <i>Pe.calve</i> | <i>Ph.macro</i> |                 |
| Lu1            | ?                               | ?              | ?                                   | ?               |                     | 0.4             | 0.4            | ?               | 0.3             |                 |
| Lu2            | ?                               | ?              | 0.5                                 | ?               |                     | 0.5             | ?              | ?               | 0.2             |                 |
| Lu3            | ?                               | ?              | 0.5                                 | 0.6             |                     | 0.4             | ?              | 0.3             | 0.2             |                 |
| Lu4            | ?                               | ?              | ?                                   | ?               |                     | 0.4             | ?              | ?               | 0.2             |                 |
| Lu5            | ?                               | ?              | 0.4                                 | ?               |                     | 0.4             | ?              | 0.3             | 0.2             |                 |
| Lu6            | 0.5                             | ?              | 0.4                                 | 0.5             |                     | 0.4             | 0.3            | 0.3             | 0.2             |                 |
| Lu7            | 0.5                             | ?              | 0.4                                 | ?               |                     | 0.4             | 0.3            | 0.3             | 0.2             |                 |
| Lu8            | 0.5                             | ?              | ?                                   | ?               |                     | 0.4             | 0.2            |                 | 0.2             |                 |
| Lu9            | 0.6                             | ?              | 0.4                                 | ?               |                     | 0.3             | 0.2            |                 |                 |                 |
| Lu10           | 0.5                             | ?              | ?                                   | ?               |                     | 0.3             | 0.2            |                 |                 |                 |
| Lu11           | 0.5                             | ?              | ?                                   | ?               |                     | 0.2             |                |                 |                 |                 |
| Lu12           | 0.5                             | ?              | ?                                   | ?               |                     |                 |                |                 |                 |                 |
| Lu13           | 0.5                             | ?              | ?                                   | 0.3             |                     |                 |                |                 |                 |                 |
| Lu14           | 0.4                             | ?              | ?                                   | ?               |                     |                 |                |                 |                 |                 |
| Lu15           | 0.4                             | ?              | 0.2                                 | 0.3             |                     |                 |                |                 |                 |                 |
| LuA            |                                 |                |                                     |                 | 0.3                 |                 |                |                 |                 |                 |
| LuB            |                                 |                |                                     |                 | e0.2                |                 |                |                 |                 |                 |
| Ca?            |                                 |                |                                     |                 | e0.2                |                 |                |                 |                 |                 |
| Ref            | 11)                             | 12)            | 13)                                 | 14)             | 15)                 | 16)             | 17)            | 18)             | 19)             |                 |

Relative width is anterior width of neural arch (or pedicles) / anterior width of vertebral centrum.

Values with \*: Relative width is anterior width of neural arch (or pedicles) / posterior width of vertebral centrum.

Explanation appendix 3, continued next page

## Abbreviations:

**ant**, anterior; **B.cetoid**, *Basilosaurus cetoides*; **centr**, central; **Ca**, caudal vertebra; **ChM**, The Charleston Museum, Charleston, South Carolina; **C.peruv**, *Cynthiacetus peruvianus*; **D.hiatus**, *Diorocetus hiatus*; **e**, estimated dimension; **E.whitm**, *Eomysticetus whitmorei*; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **Lu**, lumbar vertebra; **post**, posterior; **Pa.palm**, *Parietobalaena palmeri*; **Pe.calve**, *Pelocetus calvertensis*; **Ph.macro**, *Physeter macrocephalus*; **Ref**, references; **Th**, thoracic vertebra; **USNM**, United States National Museum of Natural History, Smithsonian Institution, Washington DC, USA; **Z.kochii**, *Zygorhiza kochii*.

?, unknown.

## References:

- 1) USNM 4675, table 9, in: Kellogg, 1936.
- 2) MNHN.F.PRU10. table 7, in: Martínez-Cáceres et al., 2017.
- 3) USNM 4679, table 34, in: Kellogg, 1936.
- 4) USNM 11962, table 35, in: Kellogg, 1936.
- 5) ChM P V4253, table 4, in: Sanders et al., 2002.
- 6) USNM 23494, table 'dorsal vertebrae', p. 149, in: Kellogg, 1968.
- 7) USNM-23208, 'dorsal vertebrae', p. 194 in: Kellogg, 1968.
- 8) USNM 11976, table 'dorsal vertebrae', p. 27 in: Kellogg, 1968.
- 9) USNM 23058, table 'dorsal vertebrae', p. 27, in: Kellogg, 1968.
- 10) Table 6, in: Omura et al., 1962.
- 11) USNM 4675 & 12361. table 10. in: Kellogg, 1936.
- 12) MNHN.F.PRU10. table 9, in: Martínez-Cáceres, et al., 2017.
- 13) USNM 4678, table 36, in: Kellogg, 1936.
- 14) USNM 12063, table 38, in: Kellogg, 1936.
- 15) ChM PV4253, table 5, in: Sanders et al., 2002.
- 16) USNM 23494, table 'lumbar vertebrae', p. 149, in: Kellogg, 1968.
- 17) USNM-23203, 'lumbar vertebrae', p. 195, in: Kellogg, 1968.
- 18) USNM 11976, table 'lumbar vertebrae', p. 34, in: Kellogg, 1968.
- 19) Table 6, in: Omura et al., 1962.