

Eocene cetaceans from the Helmstedt region, Germany, with some remarks on *Platyosphys*, *Basilotritus* and *Pachycetus*

Henk Jan van Vliet^{1,6}, Mark Bosselaers^{2,3}, Bernd-W. Vahldiek⁴, Theo Paymans¹ & Ivo Verheijen⁵

¹ Abel Tasmanstraat 41, 3531 GS Utrecht, the Netherlands; email: henkjanvanvliet@yahoo.com

² Koninklijk Belgisch Instituut voor Natuurwetenschappen, Vautierstraat 29, 1000 Brussel; e-mail: mark.bosselaers@telenet.be

³ Koninklijk Zeeuwsch Genootschap der Wetenschappen, Kousteensedijk 7, 4331 JE Middelburg, the Netherlands; email: mark.bosselaers@telenet.be

⁴ Altenwahlungen 20, 29693 Böhme, Germany; email: Bernd.Vahldiek@t-online.de

⁵ University of Tübingen/Senckenberg HEP, Paläon 1, 38364, Schöningen; email: i.k.a.verheijen@gmail.com

⁶ Corresponding author

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New archaeocete remains from the Helmstedt region, Germany, are reported. The first series of bones is from the open cast mine at Alversdorf, 2 km to the northwest of Offleben, consisting of isolated vertebral centra, rib fragments and two teeth. The second series of bones, a skull fragment, an unidentifiable, triangular bone, vertebrae and rib fragments, as well as a distal tibia fragment, has been found in the open cast mine Treue, about 5 km to the northeast of Schöningen. Historically, from the same Helmstedt region, cetacean vertebrae and rib fragments have been described by Van Beneden in 1883 (and also published by Geinitz, 1883b). He regarded the remains as belonging to mysticetes from the Oligocene, for which he erected the genus *Pachycetus*. Here, *Pachycetus robustus* Van Beneden, 1883 is assigned as type species. Vertebra NsT90 is herein assigned as *lectotype* for that species. Kuhn (1935) ascribed these fossils to archaeocetes and added some newly found vertebrae in his description. Lienau (1984) figured additional cetacean remains from the same region. Presumably all these finds (the older as well as the new material here reported for the first time) have been derived from marine beds of the Gehlberg Formation, which is Bartonian to Priabonian in age. At least two taxa are recognised: a large one (consistent with *Pachycetus* Van Beneden, 1883), and a smaller one (consistent with a small ‘dorudontine’). A comparison is made between the new material and the earlier described finds, as well as with archaeocete fossils from eastern Europe (Ukraine and southwestern Russia). Some notes are added on the validity of the genus names *Platyosphys* Kellogg, 1936 and *Basilotritus* Gol’din & Zvonok, 2013, which are here referred to as *Pachycetus*.

KEY WORDS: Basilosauridae, whales, Eocene, Helmstedt, Germany

Introduction

In 1883, Van Beneden published a description of four vertebral centra and two rib fragments, sent to him by Geinitz, director of the *Musée Royal de Mineralogie* of Dresden (see also Geinitz, 1883a; Geinitz, 1883b). This material was, as Van Beneden thought, derived from the Oligocene *couches phosphates* (strata rich in phosphorite concretions) of Helmstedt, in the Braunschweig region, Germany. Based on the width of the neural canal Van Beneden supposed that the vertebrae belonged to two new species of mysticetes. Aware of the Palaeogene age of this cetacean material, he noted some peculiarities not encountered in extant mysticetes, such as the presence of foveae, articulation surfaces for the rib at the vertebral centrum. Indeed, over time the fossil record of mysticetes shows a tendency towards a reduction in the number of two-headed ribs. In many extant mysticetes articulation sites of the

ribs are lacking at the vertebral centra that enhances the mobility of the thorax (Slijper, 1936, pp. 209-214). One ‘lumbar’ vertebra (*vertèbre* 1, NsT90 according to the labels in the Senckenberg Naturhistorische Sammlungen, Dresden) and a large distal rib fragment (NsT92-A) were assigned to *Pachycetus robustus* Van Beneden, 1883, “an animal with the length of *Balaenoptera rostrata*” (Van Beneden, 1883, p. 2). Three vertebrae (*vertèbre* 2, 3 & 4, NsT93, NsT91, resp. NsT94) and a smaller rib fragment (NsT37) were assigned to *Pachycetus humilis* Van Beneden, 1883, “an animal with a length not larger than *Globicephala*” (Van Beneden, 1883, p. 2).

Kuhn (1935) redescribed the four vertebral centra of Van Beneden and described three additional vertebrae from the Trendelbusch pit near Runstedt in the region of Helmstedt. He added illustrations of two of Van Beneden’s vertebrae (*vertèbre* 1 & 2, NsT90 & NsT94), and also of

two of the new vertebrae (*Wirbel A & C*; here: Kuhn-A & Kuhn-C) to his descriptions. Although all these vertebrae had been found in the 'Phosphoritlagerstätten' (strata rich in phosphorite concretions), then considered to be early Oligocene in age, Kuhn (1935) postulated that they originated from the late Eocene. He remarked, that the first vertebra (Kuhn-A) could be Oligocene in age, as it was only very slightly abraded. He considered the name *Pachycetus* as 'not fitting' (*uneinheitlich*) and he also ascribed the large and smaller remains from this region to two different species of archaeocetes. He gave the two species the old name '*Zeuglodon*', "*following a communication by letter from Slijper*". However, Kuhn (1935) actually discerned three taxa. Firstly, according to him, the vertebral centrum NsT90 belongs to a large archaeocete with elongated vertebrae, which he assigned to '*Zeuglodon*' (now *Basilosaurus* Harlan, 1834) cf. *isis* Andrews, 1904, but he mentioned also differences with vertebrae of *B. isis* (see section Terminology). Secondly, Kuhn (1935) remarked, that NsT91 and NsT93 could belong to one species, maybe also a large archaeocete, but with non-elongated vertebrae. He added, that the vertebral centrum NsT91 is too short to belong to the same taxon as vertebral centrum NsT90. Finally, he assigned vertebral centrum NsT94, as well as the newly described vertebral centra Kuhn-A, Kuhn-B and Kuhn-C to probably one taxon, a smaller species, which he assigned to '*Zeuglodon*' (HJvV: now *Saghacetus* Gingerich, 1992) cf. *osiris* Dames, 1894. Kellogg (1936) did not include the archaeocetes of Helmstedt in his detailed 'Review of the Archaeocetes'. Having been published just one year before, Kuhn's work probably had not yet reached Kellogg.

In 1984 Lienau figured a 'premolar' (as he supposed), a rib fragment and two vertebral centra from the Helmstedt region remarking those were archaeocete remains. He noted that these fossils and a not-figured tooth fragment had been derived from the middle to late Eocene Gehlberg Formation at the open cast mine Treue. Furthermore, he doubted the validity of the genus name *Pachycetus* and remarked that the remains could belong to *Basilosaurus* sp. Harlan, 1834 (= *Zeuglodon* Owen, 1839). He added however, that according to the opinion of Rothausen, the name *Pachycetus* was probably still valid, as the remains had not been reviewed in later years, and could not be ascribed to one of the known genera. The 'premolar' and the not-figured tooth were ascribed by him to 'Dorudontidae' Miller, 1923 *gen. et sp. indet.*

The newly reported archaeocete material from the nearby village of Alversdorf and from the open cast mine Treue originates from the same region as the historical material; the new material and the nomenclatory assignment deserve study and comparison with the historical material.

Material and methods

In Table 1a-e, an overview is given of all Eocene cetacean and possible cetacean remains here described from the

Helmstedt region with the locality of each find and, if known, by whom it has been found, the present location, as well as stratigraphic details.

All measurements were taken with a digital caliper. All values were rounded to a millimetre. The relative length (RL) of a vertebral centrum is calculated by dividing the dorsal length by the anterior transverse width: $RL = Ld/Wa$ = Length dorsal/Width anterior.

Key data are presented in Tables 1 and 2. Supplementary data are presented in the Appendix which is available online at www.wtkg.org/tijdschriften/cainozoic-research.

Abbreviations

BKB	Braunschweigischen Kohlen-Bergwerke
CCMC	compact, circumferential multi-layered cortex
GPIM	Geologisch-Paläontologisches Institut Mainz, Paläontologie (Institut für Geowissenschaften der Johannes Gutenberg-Universität Mainz)
NMR	Natuurhistorisch Museum Rotterdam

The numbers NMR999100151793 to NMR999100151805 are abbreviated in the main text (but not in tables and captions) to NMRx1793 to NMRx1805;

NsT	(= MMG: NsT), Museum für Mineralogie und Geologie: Niedersachsen Tertiär, Senckenberg Naturhistorischen Sammlungen, Dresden.
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Terminology

In his monograph on the fossil and subfossil cetaceans from Europe, Brandt (1873) published a description, provided by Paulson, with several figures of the vertebrae of the new species *Zeuglodon rossicus* from Ukraine. The main vertebral characteristics were mentioned by Paulson (see discussion in the section Morphotype A). As he expected that this species would not be restricted to Russia, Brandt changed the name *Zeuglodon rossicus* proposed by Paulson to *Zeuglodon paulsonii*. Apparently, Paulson did not object to this change in nomenclature. Nevertheless Abel (1914), and Kuhn (1935) still referred to *Zeuglodon rossicum* (*sic!*) Paulson, 1873, instead of *Zeuglodon paulsonii* Brandt, 1873. In 1936, Kellogg proposed the new combination *Platyosphys paulsonii* (Brandt, 1873). This seems a correct decision, because the combination *Platyosphys paulsonii* Brandt & Paulson, 1873 is not considered appropriate.

Gol'din & Zvonok (2013) published new material from Ukraine, which was ascribed to a basal basilosaurid with many features in common with the earlier finds from Ukraine. Because the holotype of *P. paulsonii* has been lost, Gol'din & Zvonok (2013) proposed a new genus name, *Basilotritus* and a new species, *B. uheni*, for recently discovered remains that have many vertebral features in common with *P. paulsonii*. Because the disappearance of a holotype is no reason for considering a

taxon name a *nomen dubium*, as long as a scientific description and illustrations are still existing, Gingerich & Zouhri (2015) disputed the validity of this new genus.

Van Beneden (1883) described vertebrae and ribs from the Helmstedt region, now in the Senckenberg Naturhistorischen Sammlungen Dresden. Later Kuhn (1935) provided a new description of the same vertebrae with some illustrations, amongst others vertebrae NsT90 and NsT94. Features of these vertebrae and ribs are similar to those of *Platyosphys* spp. from Ukraine (for the vertebrae, see Table 2). Although neither Van Beneden (1883) nor Kuhn (1935) were aware of their resemblance, both authors mentioned important specific features. Van Beneden (1883) noticed the elongation of the pedicles of the neural arch in vertebral centrum NsT90 and the tapering of the centrum itself, the thickness of the pedicles in vertebral centrum NsT94, the large width compared to the height in vertebral centrum NsT93, and the resemblance of the large distal rib fragment NsT92 with a sirenian rib. Kuhn (1935), but not Van Beneden (1883), described the elongation of the transverse processes of the vertebral centrum NsT90. He added that the vertebral centra were not cylindrical, but larger in width than in height, and as such, they could not be assigned to *B. isis*.

Van Beneden (1883) assigned the large vertebral centrum NsT90 and a large rib fragment NsT92-A in the Senckenberg Naturhistorischen Sammlungen Dresden to the taxon *Pachycetus robustus*. Based on the thickness of rib fragment NsT92-A, Van Beneden (1883) chose the genus name *Pachycetus* (meaning ‘thick whale’) for these cetacean remains. This was long before Kellogg (1936) proposed the genus name *Platyosphys* for the Ukrainian material. Therefore, by the rules of the ICZN Article 23, the name *Pachycetus* has priority. Following ICZN Article 69 *Pachycetus robustus* is assigned as type species. As Van Beneden (1883) started his description of *P. robustus* with NsT90, and that fossil has most of the vertebral characteristics of the genus (Table 2), it is here assigned as *lectotype* of the species (ICZN Article 74). Van Beneden (1883) assigned the smaller vertebrae and rib fragments to *Pachycetus humilis*. We however assign most other vertebrae and rib fragments in the Dresden collection studied by Van Beneden (1883), except rib fragment NsT37, to the same large cetacean Morphotype A, *Pachycetus* sp., maintaining the name *Pachycetus robustus* Van Beneden, 1883 only for NsT90 and NsT92-A. Also, many cetacean remains in the newly described series are assigned to Morphotype A, *Pachycetus* sp, because the remains do not allow for an identification at species level. *Pachycetus robustus* could possibly be a junior synonym of *Pachycetus paulsonii*, but due to the fragmentary status of the remains from the Helmstedt region this is uncertain. The rib fragment NsT37, described by Van Beneden (1883) as *Pachycetus humilis*, is tentatively referred to the smaller Morphotype B, an unidentifiable basilosaurid and this name is hence considered a *nomen nudum*.

Geological setting

Palaeogene sediments, ranging in age from the early Palaeocene to locally late Oligocene are present in an area of about 350 km² in the surroundings of Helmstedt, Germany (Lotsch, 1998; Volkmann, 2003; Hamann *et al.*, 2015). The sediments were deposited in a 70-75 km long and about four to seven km wide NNW-SSE elongated basin with a sedimentary history heavily influenced by salt tectonics. This basin, the Helmstedt-Oschersleber Depression, is divided by a longitudinal ridge or diapir, the Late Permian Helmstedt-Stassfurt salt wall, that was formed by the upward flow of subterranean salt (Hamann *et al.*, 2015). It consists of salt (Zechstein) and sandstone (Buntsandstein or Bunter), both from the Triassic. The movement of these salt layers to the salt wall (halokinesis) caused depressions on both sides of this saddle (Bachmayer & Mundlos, 1968).

Estuarine sediments with lignites, deposited in this basin, belong to the upper Palaeocene to lower Eocene Schöningen Formation and to the middle Eocene Helmstedt Formation (Riegel *et al.*, 2015). This region was the southern bight of the Palaeogene North Sea, in fact a large estuary filled by fluvial deposits originating from the continent (Hamann *et al.* 2015). The strata show an alternating sequence of marine and terrestrial conditions, reflecting various transgressions and regressions. The Helmstedt Formation was once thought to be Oligocene in age, but a middle Eocene age has been proven by its microfloras (spores and pollen) and by the middle Eocene vertebrate fauna from the lowest parts of the overlying sediments (Riegel *et al.*, 2012). Since the eighteenth century the lignite strata in the Helmstedt region have been exploited, from the second half of the nineteenth century even in open cast mines (Bachmayer & Mundlos, 1968; Volkmann, 2003). This lasted until 2016, when the open cast mine of Schöningen was shut down (IV, pers. obs.). An overview of the open cast mines in the Helmstedt region is given in Fig. 1.

The Helmstedt Formation is capped by marine sediments of the Annenberg, Gehlberg und Silberberg Formations (Lienau, 1984). For a schematic stratigraphic section through these strata, see Fig. 2. The formations are assumed to be Eocene in age, based on dinocysts and nanoplankton biostratigraphy (Erbacher, 2008). The basal part of the Annenberg Formation, which unconformably overlies the Helmstedt Formation, is assigned to the Lutetian (Erbacher, 2008; Riegel *et al.*, 2012). However, most of the Annenberg Formation was deposited in the Bartonian, pertaining to the NP15 and 16 zones (Gramann *et al.*, 1986). The depth of the sea was about 150 m (Lienau, 1984, p. 90). Only at the lowermost parts, some strata occur with basal gravel and phosphorite. The sediments feature a rich autochthonous fauna with molluscs (Anderson & Raabe, 1990), shark teeth, and vertebrae and otoliths of teleosts (Lienau, 1984). In open cast mine Treue the overlying Gehlberg Formation is divided into three parts, each containing strata with phosphorite

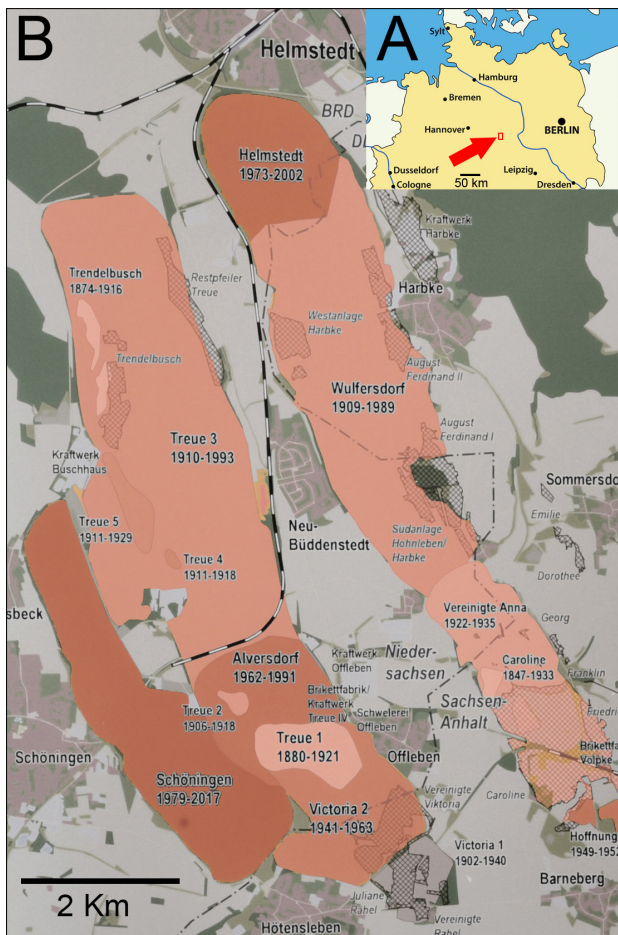


Figure 1. A: Map of Germany with the location of Helmstedt and its surroundings; B: the location of the open cast mines in the Helmstedt region. In each separate mine, numbers indicate in which years the excavation of lignite has been conducted. Modified after a map in the Heimatmuseum of Schöningen.

concretions or with clay ironstone (*Toneisenstein*) (Bachmayer & Mundlos, 1968; Schleich *et al.*, 1994). The lower green unit is considered to be middle Eocene in age (Erbacher, 2008) and is relatively poor in phosphorite concretions (Lienau, 1984). There is a phosphorite stratum, G5 (*Phosphoritgeröll-Lage*), containing a few concretions (Lienau, 1984), and below this another stratum with phosphorite concretions containing crab fossils (K IV, *Phosphoritlage mit Krebsen*, see Vahldiek in Schleich *et al.*, 1994). The overlying two units are placed within the Priabonian: the upper brown unit and maybe also the lowest part of the upper green unit in NP19-20, and the upper part of the upper green unit in NP21 (Lotsch, 1998). Four phosphorite strata have been recognised, namely G1 to G4 in descending stratigraphic order (Lienau, 1984). These are generally considered to be storm deposits (*e.g.* Hillmer & Mundlos, 1981), but Vahldiek (in: Schleich *et al.*, 1994) reported on the possibility of erosional horizons formed during periods of lower sea level. The whole stratal package, with crossbeddings, layers with a high diversity of colours and limonite concretions, was probably deposited

in rapidly moving water. The sea was relatively shallow with a depth of less than 100 m (Vahldiek in: Schleich *et al.*, 1994), or even 50-70 m (Lienau, 1984, p. 94). Archaeocete remains have been reported in four of the five phosphorite bearing strata of the Gehlberg Formation (Priabonian: G1, large vertebrae, as well as rib fragments of unidentifiable dorudontids; G3/ K III, *Pachycetus* sp.; G4, bones of dorudontids; Bartonian: G5, bones of dorudontids (Schleich *et al.*, 1994), and a thoracic vertebral centrum, NMRx1793, as well as a possible cetacean distal tibia fragment, NMRx1799 (this article) from K4. The strata have also yielded a rich chondrichthyan fauna; molluscs have only rarely been preserved, due to decalcification (BV, pers. obs.). In the past, this phosphorite was exploited, being used as fertiliser (Schmid, 2006). Outcrops of greensands with layers of phosphorite concretions, were present in clay pits at Helmstedt, Büddenstedt and Alversdorf among other localities (Schmid, 2006). The location of the former pits with outcrops of phosphorite bearing strata at Büddenstedt is not known anymore, probably due to the massive expansion of the open cast mine Treue (Bachmayer & Mundlos, 1968). The stratigraphically higher Silberberg Formation, formerly regarded as of early Oligocene age (Lienau 1984, 1985), is now placed in the late Eocene, Priabonian, zone NP21 (Gramann *et al.*, 1986; Lotsch, 1998; Erbacher, 2008). The sea was more than 100 m deep, but probably sometimes groundswells could reach the seafloor (Bachmayer & Mundlos, 1968, p. 686). A rich mollusc fauna has been described, with gastropods, bivalves, large cephalopods, corals and sponges (Lienau, 1984). Förster & Mundlos (1982) were the first to recognise that the marls of the Silberberg Formation contain the most diverse crab fauna known from Northern Germany. However, vertebrate fossils have not been found (Lienau, 1984). Oligocene strata from the Rupelian and Chattian overlie the Silberberg Formation (Lotsch, 1998).

Systematic palaeontology

Order Cetacea Brisson, 1762
Suborder Pelagiceti Uhen, 2008
Family Basilosauridae Cope, 1868

Genus *Pachycetus* Van Beneden, 1883 Species *Pachycetus robustus* Van Beneden, 1883

Table 1a
Plate 2, figs C1-C4 & D1-D2
Appendix table 2a. Dimensions of a vertebral centrum
Appendix table 3a. Dimensions of a rib fragment

• *Senckenberg Naturhistorischen Sammlungen, Dresden*

Material – One vertebral centrum, NsT90, and one rib fragment NsT92, here indicated as NsT92-A.

Comments – According to Van Beneden (1883) all the

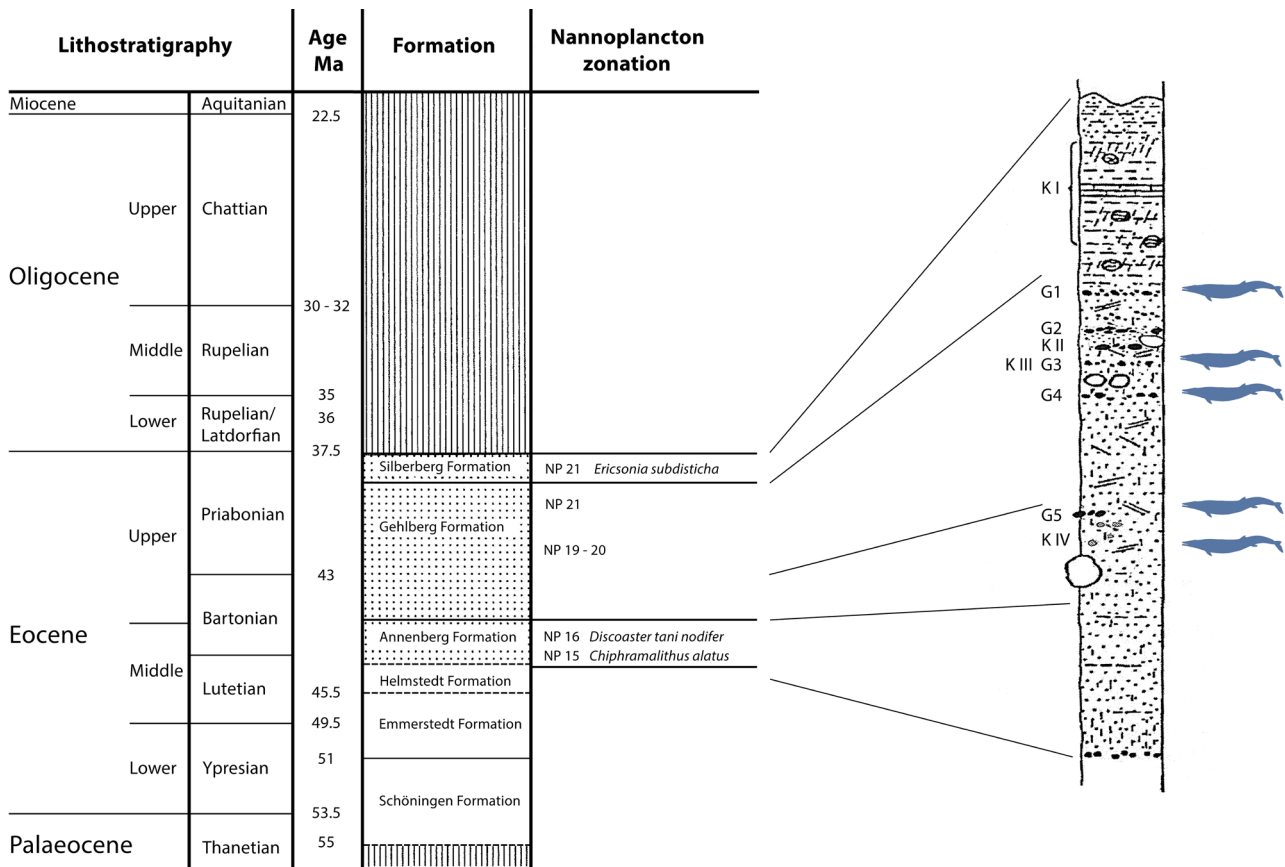


Figure 2. Stratigraphy of the Palaeogene sediments in the Helmstedt region. Modified after the combined figures of Lienau, 1984, Abbildung 9 (left) and Mundlos, 1975, Abbildung 1 (right).

cetacean remains described by him have been found in Helmstedt. Kuhn remarked, that NsT90 has been found in Büddenstedt, near Helmstedt. According to the labels, NsT90 and NsT92 have been found in Helmstedt. NsT92 consists of a lot of two large distal rib fragments, namely NsT92-A and NsT92-B. NsT92-A is, with respect to its dimensions, the one that was originally assigned by Van Beneden (1883) to *Pachycetus robustus*. The rib fragment was not described by Kuhn (1935). Both Van Beneden (1883) and Kuhn (1935) mentioned that the cetacean remains originated from the *Phosphoritlagerstätten* near Helmstedt. These *Phosphoritlagerstätten* most certainly belong to the Gehlberg Formation, the only formation that is rich in phosphorhite concretions (Lienau, 1984).

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Description – NsT90, is a centrum of a posteriormost thoracic, or maybe an anteriormost lumbar vertebra. The epiphyseal surfaces are flat. The anterior side is more or less pentagonal, the posterior side more rectangular, being ventrally flat. The pedicles of the neural arch have a maximum thickness of 31 mm; they are elongated, but due to damage their original length cannot be measured. At the broken surfaces, a compact and thick cortex is visible. Due to damage, the cortex is absent at the anterior and ventral posterior sides. The transverse processes are missing; the onsets are elongated and 123 mm in length.

There is a prominent ventral keel, with a fossa at each side. A ridge is present lateral to each of these fossae. There are no large ventral foramina. Some small vascular foramina are scattered at the ventral side. The centrum is slightly abraded, mineralised and brown to grey in colour (Plate 2, figs C1-4).

NsT92-A is a fragment of a right rib. The distal part is thick, with a rounded and blunt end, whereas proximally it is slenderer. The cortex is broken at the distalmost part of the rib. The distal part of the rib has a shallow, broad longitudinal fossa at the antero-medial side. The surface of the rib fragment has multiple little holes, probably made by scavengers (Plate 2, figs D1-2).

Discussion – The dimensions of the posterior epiphyseal surface of the vertebral centrum NsT90 are larger than the original dimensions of the anterior surface. This anterior tapering cannot be solely ascribed to damage of the cortex at the anterior side, but is also seen in the arrangement of the conspicuous ventral fossae and the onset of the transverse processes. The ventral side of NsT90 closely resembles the ventral side of a caudal vertebra of *P. wardii*, figured by Uhen (2001, fig. 6A), but here several large ventral foramina are present. Moreover, the width of the neural canal in NsT90 precludes its identification as a caudal vertebra. Van Beneden (1883) de-

scribed this vertebral centrum as a lumbar vertebra and based on the low position of the transverse processes at the vertebral centrum, Kuhn (1935, p. 225) considered it a probably posterior lumbar vertebra. Kellogg (1936, p. 98) remarked however, that in *Pachycetus paulsonii* from Ukraine, the transverse processes of the posterior lumbar vertebrae “are placed somewhat higher” than those of the anterior lumbar, where they “arise near the base of the centrum”. Indeed, the ventral fossae and ridges could indicate a lumbar vertebral centrum. Judging from the original description, there is a resemblance with a vertebra from Ukraine of *Pachycetus* sp. (NMNH-P OF-2096) tentatively identified by Gol’din & Zvonok (2013, p. 260) as an anterior lumbar vertebra (Lu1). However, a longitudinal ridge at the ventral side has also been described in the two posteriormost thoracic vertebrae of *B. isis* (Kellogg, 1936, p. 92). The vertebral centrum NsT90, without epiphyses, has a moderate elongation with a relative length between 1.46 and 1.28; see Appendix table 2b. Damage of the cortex at the anterior side precludes an accurate comparison with the relative length of vertebral centra of *Pachycetus paulsonii* from Ukraine. A posterior thoracic vertebra of *P. paulsonii* (numbered ‘Th1’ in Kellogg, 1936, table 25) has a relative length of 1.18; the two shortest lumbar vertebrae, (numbered ‘Lu1’ & ‘Lu7’ in Kellogg, 1936, table 24), have a relative length of 1.55 resp. 1.47. ‘Lu1’ has one, ‘Th1’ and ‘Lu7’ two fused epiphyses; numbers in Kellogg, 1936, are provisional, as exact positions in the vertebral column are unknown. Based upon its relative length, identification of NsT90 as an anteriormost lumbar vertebra cannot be excluded. But elongated, large ventral foramina are absent in NsT90. The three lumbar vertebrae of *Pachycetus* sp. here described (see section Morphotype A) and those of *Pachycetus paulsonii*, described by Kellogg, (1936, p. 98) have elongated ventral foramina. Moreover, ventral foramina are present in all, also the anteriormost, lumbar vertebrae of the large basilosaurids *Basilosaurus cetoides* (Kellogg, 1936, pp. 47-54) and *Cynthiacetus peruvianus* (Martínez-Cáceres *et al.*, 2017, pp. 89-100). Because of the absence of elongated ventral foramina, NsT90 is here tentatively identified as one of the posteriormost thoracic vertebrae.

The rib fragment NsT92-A resembles a rib of *Pachycetus* sp., GMTSNUK 15/9 from Nagornoye, Ukraine, figured by Zvonok (2012, fig. 2), especially regarding the very thick, pachyosteosclerotic distal part, but the same is seen in basilosaurids like *Cynthiacetus peruvianus* (Martínez-Cáceres *et al.*, 2017) and even the earliest mysticete *Mystacodon selenensis* Lambert *et al.*, 2017 (Muizon *et al.*, 2019). It is probably an anterior rib, as in *P. wardii* only the anterior ribs are thickened, not the posterior ones (Uhen, 1999). This is also true for the ribs of *C. peruvianus* (rib 3 to rib 5; see figs 57-60 in Martínez-Cáceres *et al.*, 2017). In cross-section, the thickened distal part is antero-posteriorly flattened, with a height that is about 0.6 of its width at the thickest point (NsT92-A: H(distal)/W(distal) = 47/81; see Appendix table 3a). In both *C. peruvianus* and *Mystacodon*, this thickened distal part of

the anterior ribs is oval in cross-section; in *Basilosaurus* however, the ribs are more circular (Muizon *et al.*, 2019, p. 442).

Genus *Pachycetus* Van Beneden, 1883

Sp. indet.

Morphotype A

Table 1b

Plate 1; Plate 2, figs A1-3, B1-3, E1-2 & F1; Plate 3
Appendix table 1a. Dimensions of (pre-)molars
Appendix table 2b. Dimensions of vertebral centra
Appendix table 3b. Dimensions of rib fragments

• *Heimatmuseum Schöningen*

Material – A presumed premolar, ID21, four vertebral centra, ID20-A, ID20-B, ID20-3, ID20-2, and one rib fragment, ID20-6.

Comments – The original numbers written on vertebrae ID20-A and ID20-B are unreadable due to bleaching and the vertebrae have been given a provisional number.

Although no stratigraphic details have been provided, we assume that the cetacean remains from the open cast mine Aufschluss BKB Alversdorf-Büddenstedt at Alversdorf were collected from the phosphorite bearing greensands of the Gehlberg Formation.

• *Natuurhistorisch Museum Rotterdam*

Material – Four vertebral centra, NMRx1793, NMRx1794, NMRx1795 and NMRx1796, and one rib fragment, NMRx1797.

Comments – This material has been collected by Mr. B. Vahldiek in the years 1975-1992.

• *Senckenberg Naturhistorischen Sammlungen, Dresden*

Material – Three vertebral centra, NsT91, NsT93, and NsT94, and three rib fragments, NsT92, here indicated as NsT92-B, NsT41 and NsT-A.

Comments – Kuhn remarked that NsT94 had been found in Büddenstedt, near Helmstedt. According to the labels, NsT91 has been found in Helmstedt, NsT94 in Büddenstedt and NsT93 in Runstedt near Helmstedt. Rib fragment NsT92-B has not been described by Van Beneden (1883). NsT41 could be the rib fragment mentioned by Van Beneden as “having no peculiarities” (Van Beneden, 1883, p. 6), but it is also possible he pointed to a rib fragment from Runstedt. This latter does not have a catalogue number and is here indicated with NsT-A. The rib fragments were not described by Kuhn (1935).

• *Institut für Geowissenschaften, University of Mainz*

Material – A presumed molar, GPIM P 4010.

Comments —The presumed molar GPIM P 4010 was briefly described and figured by Lienau (1984, p. 72, table IX and fig. 15) as “*Dorudontidae gen. et sp. indet.*”. It originates from the phosphorite bearing stratum G1 of the Gehlberg Formation at the open cast mine Treue.

• *Present location unknown - publication Lienau (1984)*

Material – A vertebral centrum without catalogue number, here indicated as Lienau-A, a rib fragment without catalogue number, here indicated as Lienau-B.

Comments – The vertebral centrum Lienau-A was briefly described and figured as *Pachycetus robustus*, albeit with some hesitation (“*because a review [of these cetacean remains] has not been made, the genus [Pachycetus] is still valid*” (Rothausen, pers. comm.) see Lienau 1984, p. 72-73 and table IX, fig. 13. The rib fragment Lienau-B was figured as “*rib of an archaeocete*” (Lienau, 1984, table IX, fig. 16). The catalogue numbers of the vertebra and rib fragment are unknown; herein the vertebra is given the provisional number Lienau-A and the rib fragment Lienau-B. The present locations of Lienau-A (in 1984 legacy Lierl), and Lienau-B (in 1984 in the private collection of Wulf) could not be traced.

All the cetacean remains mentioned and figured by Lienau (1984) come from the Gehlberg Formation at the open cast mine Treue.

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Description – ID21 is a distal half of a presumably left upper premolar with only the distal root preserved. The principle cusp and the mesial part of the crown are lacking. It has four accessory denticles. The largest accessory denticle shows some apical wear. At the distal side it has five little second order denticles. A carina is running along the distal side of the denticles. The enamel has rather coarse striations at the lingual side and somewhat less coarse striations at the labial one. A crenulated cingulum is well developed on the distal edge of the crown and has multiple tubercles, forming a ring around the most basal accessory denticle. At the midpart of this ring, the cingulum is rather high, looking like a broad extra denticle. The crenulated cingulum continues both at the labial and lingual sides, but is here much narrower. The distal root has a clear longitudinal groove at the mesial side. It consists of two fused roots with two partly fused pulp cavities, apparently filled with sediment. The tooth is not abraded (Plate 1, figs A1-6).

GPIM P 4010 is a distal half of a presumably left upper molar, with only the distal root preserved. The mesial part of the crown as well as a large part of the probably principle cusp are lacking. The molar has three accessory

denticles; the enamel of the most distal one is broken at the base of the crown. The other two are preserved completely, but show some apical wear. At the distal side both display two little second order denticles. At the labial side they have some slender, longitudinal ridges with tiny denticle-like spines; the largest accessory denticle even three (Plate 1, fig. B2 with magnification). Moreover, at its lingual side this denticle has a longitudinal ridge with about five, tiny denticle-like spines that are larger than the spines at the labial side. Probably also the principle cusp had a longitudinal ridge with spines at its labial side, but the enamel is broken from the mesial part of the cusp. The crenulated cingulum originally formed a ring around the most basal denticle, probably similar to that of ID21, but the enamel is missing at this particular part of the cingulum. The cingulum continues at both the labial and lingual sides, but there it is much narrower and it is nearly absent at the midpart of the crown. On the labial cingulum the enamel is partly broken. There is one, open pulp cavity. At its mesial side the preserved root is broken along the whole length. The tooth is not abraded (Plate 1, figs B1-5).

For general vertebral features in Morphotype A, see Table 2. In all vertebral centra described in this section the epiphyses are lacking. In addition, none of the neural arches is preserved and only the pedicles of the neural arch are still present, except for the caudal centrum NMRx1796 in which the neural arch is preserved.

NsT94 is a more or less heart-shaped centrum of one of the anteriormost thoracic vertebrae. Due to abrasion, the original radiating pattern is only faintly visible at the epiphyseal sides. The pedicles of the neural arch are partly preserved and are 22 mm thick. There is a slightly damaged dorsal median keel, with one foramen on both the left and right sides. No foveae are visible. There is no ventral keel; two small ventral foramina are present. The centrum is abraded, strongly mineralised and grey to brown in colour with yellow striations (Plate 1, figs C1-4).

NsT93 is a more or less heart-shaped centrum of an anterior thoracic vertebra. The epiphyseal surfaces are flat, with a radiating pattern. A piece at the left part of the centrum with the pedicle of the left neural arch is missing. The right pedicle has a maximum thickness of 25 mm; it is 51 mm in length. There is a dorsal median keel with a foramen on the right side. A fovea is present at both the anterior and posterior right sides of the vertebral centrum. There is no ventral keel and there are no ventral foramina. The centrum is slightly abraded, mineralised and yellow to brown in colour (Plate 1, figs D1-3).

ID20-A is the centrum of an anterior thoracic vertebra. A radiating pattern is visible at both the epiphyseal sides. The anterior surface is saddle-shaped, whereas the posterior surface is slightly concave. The posterior epiphyseal surface is larger in width and height than the anterior one. The pedicles are about 28 mm thick and show a compact

cortex, about 3 mm thick, of multi-layered bone. The left pedicle has an anterior-posterior length of 55 mm. There is a strong, but shallow median dorsal keel with a groove on both sides; a vascular foramen is present in both grooves. There are two rather large foveae anteriorly and two small foveae posteriorly. Between the anterior and posterior foveae a weak crest runs along the whole length of the centrum. There is no ventral keel and there are no ventral medial foramina, but there are ventrally some small, vascular foramina near the epiphyseal sides. The centrum is not abraded, light grey in colour and seems to be less mineralised than nearly all other vertebrae and rib fragments (Plate 1, figs E1-3).

NsT91 is a centrum of an anterior-central thoracic vertebra. Due to abrasion, the radiating pattern at the anterior and posterior epiphyseal sides is hardly visible. The anterior side is flat, whereas the posterior side is rounded by abrasion. The pedicles of the neural arch are 20 mm thick and 61 mm in length. There is a dorsal median keel with a foramen at both sides. The onset of the transverse processes is nearly as long as the vertebral centrum. The transverse processes are lacking. There is no ventral keel and there are no ventral foramina. The centrum is abraded, mineralised and brown in colour (Plate 1, figs F1-3).

NMRx1793 is a partial centrum of an anterior-central thoracic vertebra, with only the right anterior upper part of the epiphyseal surface preserved. The epiphyseal side is flat. Only a part of the right pedicle of the neural arch is preserved and shows multi-layered bone. It is 22 mm thick. There is a flat median dorsal keel, with several small foramina at both sides. The centrum is mineralised and black in colour (Plate 1, figs G1-2).

NMRx1794 is the presumably right half of a central-posterior thoracic vertebral centrum, with only half of the epiphyseal surface preserved (probably the anterior). Only the right pedicle of the neural arch is preserved; it is about 25 mm thick and has a cortex of multi-layered bone. The small transverse process at the lateral side of the centrum has a large, rugose cavity that represents the articulation surface for the rib. The midpart of the centrum is pierced by imprints of a ventrodorsal vascular system, with several vascular canals. Dorsally, two canals are visible, lying closely together. Ventrally two canals are found, one at the anterior, one at the posterior. Apparently, there have been two dorsal and two ventral foramina that are not preserved due to damage. The centrum is mineralised and black in colour (Plate 2, figs A1-3).

ID20-B is a centrum of a posterior thoracic vertebra. The height is less than the width. Dorsally there is some damage at both epiphyseal sides. The anterior epiphyseal surface is saddle-shaped; the posterior side is flat. The left pedicle of the neural arch is damaged, the right one is partly preserved and 38 mm thick. There is an elongated, very shallow median dorsal keel. The transverse processes are elongated. They are short and located halfway

the height of the centrum. Both processes are damaged. At the broken surfaces, a compact cortex is visible, but its thickness cannot be measured due to mineralization. There are no dorsal or ventral foramina. The vertebra is abraded, thoroughly mineralized and bluish to dark grey in colour; the original colour has been altered by the application of a protecting varnish (Plate 2, figs B1-3).

ID20-3 is a part of a posterior thoracic or, perhaps more probably, lumbar vertebral centrum. It consists of the abraded midpart of a vertebral centrum, solely formed by compact bone. There are neither epiphyseal sides, nor transverse processes. The anterior side is hollow, the posterior side is shallower; these are the imprints of the conical cancellous bone, that are now lost. A remnant of one pedicle of the neural arch is preserved. There is a rather large dorsal fissure, running antero-posteriorly, probably through the central vascularisation canals (which are not visible anymore). Ventrally, a foramen is present, which seems to consist of three confluent canals: a larger central one and a smaller one on both the left and the right sides. It is mineralised and grey to black in colour.

NMRx1795 is the left half of a large lumbar vertebral centrum. The anterior epiphyseal surface is missing, as the anterior conus is not present anymore. The posterior epiphyseal side is slightly concave. The left pedicle of the neural arch is preserved with a maximum thickness of 30 mm and a length of 154 mm. The surface of the vertebral centrum has multiple pockmarks. The transverse process is elongated, with an antero-posterior length of about 196 mm, beginning at least 23 mm from the original anterior epiphyseal surface and ending about 25 mm from the posterior epiphyseal surface. The left transverse process is completely preserved and has an anterior notch (Plate 3, fig. C2). It has a thick, compact, multi-layered cortex and at its thickest point (i.e. about the midpart of the vertebra) it is more than 22 mm thick. The vertebral centrum was originally composed of two conical parts of bone, tapering towards the midpart of the centrum in the shape of a skewed hourglass (see the description of ID20-2/ID20-4), but only the posterior conus is preserved. It is made of cancellous bone and is 120 mm in length. The originally two conical parts were surrounded by a cortex of compact, multi-layered bone with multiple, longitudinal vascular channels (Plate 3, fig. C3). At its thickest point, (i.e. in the midpart of the centrum), the cortex is 36 mm thick at the dorsal side and more than 50 mm thick at the partly damaged ventral side. The original ventrodorsal vascular system at the midpart of the centrum is hardly visible due to abrasion and damage. Only the posterior ridge of the ventral vascular foramen is visible. The cortex displays some damage anteriorly. The vertebra is abraded, thoroughly mineralised and yellowish-brown in colour (Plate 3, figs C1-4).

ID20-2/ID20-4 is the right half of a large lumbar vertebral centrum. The anterior epiphyseal surface is somewhat convex, whereas the posterior one is concave. The right pedicle of the neural arch is preserved, with a maxi-

imum thickness of 34 mm and a length of 133 mm. Anteriorly, the cortex has been flaked off from the conus. The surface of the vertebral centrum has multiple pockmarks, which represent the orifices of small vascular canals. Only the onset of the right transverse process is preserved. It is elongated, with an posterior-anterior length of around 180 mm, beginning about 25 mm from the anterior epiphyseal surface and ending about 35 mm from the posterior epiphyseal surface. The transverse process has a maximum thickness of 53 mm at about the midpart of the vertebra, and has a thick multi-layered cortex of about 11 mm thick. The freshly fractured side enables the observation of the inner structure of the centrum. It is composed of two coni of cancellous bone, tapering towards the midpart of the centrum in the shape of an hourglass. As the coni are flattened dorsally (forming the posterior and anterior floor of the neural arch; see Plate 3, fig. B2), and the tops of the coni are positioned more to the dorsal sides, the hourglass-like shape is skewed. The bases of the coni are nearly as broad as the epiphyseal surface. The posterior conus is larger than the anterior one (126 mm versus 116 mm in length). The anterior conus (with a separate catalogue number ID20-4) is detached from the centrum. It has several longitudinal vascular imprints, running from the top of the conus to its base, at regular distances from each other. The coni are surrounded by a cortex of compact, multi-layered bone, showing many longitudinal, postero-anteriorly oriented, vascular channels. This cortex is thickest at the midpart, being 36 mm thick dorsally and 66 mm thick ventrally, and thin at the epiphyseal sides and at the posterior and anterior floor of the neural arch. Here, the centrum is pierced by imprints of a dorso-ventral vascular system. Dorsally, two branches run towards two separate and round, adjacent foramina, both of which are apparently situated at the left side of the midline. At the ventral side, a vascular canal at the ventral side broadens at the surface, turning itself into a large, elongated, medio-laterally compressed and fan-shaped foramen. It has the shape of a skewed 'V', turned 'upside-down', with the point of the 'V' going into the vertebral centrum. The opening of the 'V' is directed ventrally and posteriorly, with the anterior line running more or less straight from the (dorsal) centre of the vertebra to what was the opening of the ventral foramen before the vertebra was fractured. The posterior line is running oblique, at an angle of about 45° with the ventral surface of the vertebral centrum. The vertebra is abraded, mineralised and is bluish-dark grey in colour; the original colour has been altered by the application of a protecting varnish (Plate 3, figs A1-2, B1-3).

Lienau-A is the presumably right half of a lumbar vertebral centrum, with the onset of one transverse process preserved. The centrum looks very similar to ID20-2 and NMRx1795, with two coni and the imprint of a fan-shaped, ventral vascular foramen in the midpart of the centrum. Dimensions have not been provided in the description.

NMRx1796 is the centrum of an anterior-central cau-

dal vertebra. The centrum is waisted: it is narrower and thinner at the midpart of the centrum than at the epiphyseal sides. The posterior epiphyseal surface is smaller in width and height than the anterior side and is slightly convex, the anterior epiphyseal surface being slightly saddle-shaped. The neural arch is about 45 mm in length; it is placed 22 mm anterior to the posterior epiphyseal surface. Both metapophyses have been damaged. There is no neural spine, but the bone surface on the medial line has some rugosities and could be interpreted as a vestigial ridge. Each of the pedicles of the neural arch is about 10 mm thick. Between the pedicles, there is a median dorsal fossa with three dorsal foramina in a straight line, which are about 4-6 mm in length. Three small foramina are positioned close to the anterior epiphyseal side. The transverse processes are directed laterally and have a vertebral arterial foramen, each about 10 mm long. The ventral side has a deep medial fossa with one foramen, about 8 mm in length. The centrum is only slightly abraded, mineralised and light grey in colour (Plate 3, figs D1-4).

NsT92-B, a right rib, is a slightly smaller fragment than NsT92-A. It is from the same rib region as rib NsT92-A, showing the bulging distal end, the slenderer proximal part and a shallow fossa at the antero-medial side. Both the distal and proximal ends are broken. The distal end is corroded probably by disintegration of pyrite. The surface of the rib fragment has multiple little holes, probably made by scavengers (Plate 2, figs E1-2).

ID20-6 is a fragment of a large rib, probably from the midpart of the rib. The distal part is thicker than the proximal part.

NsT41 is a broad, rectangular rib fragment.

NsT-A is a fragmentary and abraded rib fragment.

Lienau-B is a rib fragment, probably from the midpart of the rib. Dimensions have not been provided in the description.

NMRx1797 is a slender rib fragment (Plate 2, fig. F1).

Discussion – The absence of the principle cusp in ID21 is due to a fresh fracture, not to dental wear. Several characteristics of this cheek tooth are shared with two premolars (maybe P2, GMTSNUK 15/2; P3 or P4?, GMTSNUK 15/4) of *Pachycetus* sp. as described by Gol'din *et al.* (2014), namely: the presence of "denticles of the second order" on the accessory denticles of the premolars, a cingulum and a similar size. Gol'din *et al.* (2014, p. 273) consider the presence of small, second order denticles on the premolars an advanced derived character of *Pachycetus*. The presence of multiple small tubercles, seen on the mesial and distal parts of the cingulum of ID21, has been described in a premolar (GMTSNUK 15/2) of *Pachycetus* species from Ukraine (Gol'din *et al.*, 2014). Accessory tubercles on the cingulum of premolars are also seen in *Eocetus schweinfurthi* Fraas, 1904, but not on the acces-

sory denticles of the crown (Gingerich & Zouhri, 2015, p. 283), as seen in ID21. The striae of the presumed premolar from Schöningen are deeper than in the premolars figured by Gol'din *et al.* (2014, fig. 2). The lingual side of the premolar is more striated than the labial side. A cingulum like that of *Pachycetus* is not or only partly present in premolars of *Basilosaurus cetoides* Harlan, 1834 and *B. isis* (Kellogg, 1936, pp. 24-35, 83-84), whereas it is well developed in *e.g.* the protocetid *Aegicetus gehennae* (Gingerich *et al.*, 2019). The cingula on P2, 3 and 4 have a small denticle-like prominence in *Pachycetus* (Gol'din *et al.*, 2014), as is seen in this Schöningen tooth. The distal root in ID21 was originally clearly separated from the mesial one, which excludes an assignment to an upper molar (see below in this section). The transverse diameter of 35 mm is significantly larger than that of GPIM P 4010 (and also larger than the transverse diameter in cheek teeth of *Pachycetus* sp. from Ukraine, see Appendix table 1b). In *B. cetoides* and *Cynthiacetus peruvianus* Martínez-Cáceres & Muizon, 2011 the transverse width of the upper premolars P2 and P3 is larger than in the other upper and lower premolars and molars, most probably because of the two fused distal roots (Appendix table 1c). ID21 is therefore tentatively identified as a left upper posterior premolar, P2, P3, maybe P4.

Like in ID21, second order denticles are seen on the denticles of GPIM P 4010, as well as enamel striae and a cingulum. The presence of tiny denticle-like spines upon ridges on the accessory denticles has not been mentioned in literature. The root of GPIM P 4010 appears to be broken along the whole mesial side, which seems to indicate that this root was originally fused with the mesial root. An upper molar, M1 (GMUTSNUK 15/3) in *Pachycetus* sp. from Ukraine, described and figured by Gol'din *et al.* (2014), has two closely approximated roots, which are not fused. An M2 (GMUTSNUK 15/1), described and figured by Gol'din *et al.* (2014) has two fused roots. However, this molar has two accessory denticles at the distal side, whereas GPIM P 4010 has three. Both the upper M1 and M2 in *B. cetoides* have “ankylosed roots”, the only cheek teeth with a fused mesial and distal root in the whole dentition of this taxon (Kellogg, 1936, pp. 30-36). For this reason, GPIM P 4010 could be a left upper M2, maybe an M1, but due to the fragmentary state, assignment to another position (except an upper P2 to P4, because of their thickness) cannot be excluded. This molar seems to have been somewhat larger than M1 and M2 (GMUTSNUK 15/3 resp. GMUTSNUK 15/1), described by Gol'din *et al.* (2014); see Appendix tables 1a & b. The latter, M2, shows signs of a lifetime injury (Gol'din *et al.*, 2014), which may have hampered its growth. As the pulp cavities are open and as there is only little apical wear, both teeth, ID21 and GPIM P 4010 have belonged to a relatively young individual.

The vertebral centra referred to Morphotype A share almost all features with the vertebrae of *Pachycetus* (*Platyosphys* and *Basilotritus*) species from Ukraine, described by Paulson (in: Brandt, 1873), Kellogg (1936),

Gol'din & Zvonok (2013) and Gingerich & Zouhri (2015). These features can be listed as follows. The thoracic and also the first anterior lumbar vertebrae taper towards the anterior side (Paulson, in Brandt, 1873; Uhen, 1999; Gingerich & Zouhri, 2015). The height of the vertebral centra is smaller than the width, in contrast to *Basilosaurus* Harlan, 1834 and *Eocetus schweinfurthi* (Gingerich & Zouhri, 2015). The torso vertebrae are elongated, although to a smaller extent than in *Basilosaurus* (Gol'din & Zvonok, 2013). The transverse processes are elongated too (Paulson, in Brandt, 1873; Kellogg, 1936; Gol'din & Zvonok, 2013), as well as the pedicles of the neural arch (Gol'din & Zvonok, 2013). The elongations of the vertebral centra, transverse processes and the neural arch are smaller in *P. wardii* (Uhen, 2013) and absent in the torso vertebrae of *E. schweinfurthi* (Gingerich & Zouhri, 2015) or *Basilosaurus* (Kellogg, 1936). The centra of torso vertebrae in *Pachycetus* have a compact, circumferential, multi-layered cortex, here abbreviated to CCMC (Paulson, in Brandt, 1873; Uhen, 1999). Pachyostosis is less developed in vertebrae of *E. schweinfurthi* (Gingerich & Zouhri, 2015). The surface of the CCMC has multiple pock marks, which represent the openings of little vascular canals (Gol'din & Zvonok, 2013), similar to the vertebrae of *E. schweinfurthi* (Uhen, 1999). The transverse processes and the pedicles of the neural arch also display a CCMC (Gol'din & Zvonok, 2013). The pedicles of the neural arch of the thoracic, lumbar and caudal vertebrae of *Pachycetus* are pachyostotic (Paulson in Brandt, 1873, fig. 3b; Gol'din & Zvonok, 2013), but not in *P. wardii* (Uhen, 2013). Vertebrae in *P. aithai* (Gingerich & Zouhri, 2015) and *E. schweinfurthi* consist of two conical cancellous bone, surrounded by a thick, multi-layered cortex (Gingerich & Zouhri, 2015). These conical parts have not yet been described either in European *Pachycetus* species, or in *P. wardii*. Lumbar vertebrae have two, sometimes four, elongated ventral foramina (Kellogg, 1936). The presence of these characteristics in the vertebral centra of Morphotype A is shown in Table 2.

In Appendix table 2b the thoracic and lumbar vertebral centra are arranged according their increasing length and (in most cases) relative length. The assignment of the anteriormost thoracic vertebrae to Morphotype A is complicated by three factors. Like the anterior thoracic vertebrae in *P. wardii* and *P. aithai*, the anterior thoracic vertebrae of Morphotype A are supposedly small and especially the anteriormost ones could be easily misidentified as vertebrae of smaller basilosaurids. They lack some characteristics such as the elongation of the centrum, the transverse processes and the pedicles of the neural arch. Finally, the anteriormost thoracic vertebral centra (Th1-3) of Morphotype A cannot be compared directly with the anteriormost vertebrae of *Pachycetus* species from Ukraine, because these have not been described. The anteriormost thoracic vertebrae are however known for the smaller species *P. aithai* and *P. wardii*. The vertebral centrum NsT94 shares pachyostosis of the pedicles of the neural arch with the other vertebrae of *Pachycetus* (Table 2). The vertebral centrum is far smaller, than the

other anterior thoracic vertebral centra referred to Morphotype A. There is not much difference in size between NsT94 and the thoracic vertebrae of small, 'dorudontine' basilosaurids, like *Dorudon* Gibbes, 1845, or *Zygorhiza* True, 1908. The anteriormost vertebrae are also small in *P. aithai* and *P. wardii*. The small size of NsT94 could be partly due to the young age of the specimen involved. The centrum is more or less heart-shaped, resembling the vertebral centrum NsT93. Based on the pachyostotic pedicles of the neural arch, NsT94 is assigned to Morphotype A, although an assignment to a smaller cetacean cannot be excluded. NsT94 is presumably one of the anteriormost thoracic vertebrae.

The anterior to anterior-central thoracic vertebrae NsT93, ID20-A and NsT91 are significantly larger, than the comparable vertebrae of the small 'dorudontine' basilosaurids *Dorudon* or *Zygorhiza*. Apart from their size, these three vertebral centra are here referred to Morphotype A, because of their characteristics, shown in Table 2. Due to the fragmentary preservation state, not much can be said about the original length or the relative length of the vertebral centra NMRx1793 and NMRx1794. The small transverse process, with a large cavity for the articulation of the rib, at the lateral side of the vertebral centrum NMRx1794 indicates, that this vertebra had a central-posterior position.

The presence of dorsal or ventral foramina in the thoracic vertebrae referred herein to Morphotype A, *Pachycetus* sp., seems variable: dorsal foramina are present in some centra (NsT94, NsT93, NsT91, ID20-A, NMRx1794 and NMRx1793), whereas they are lacking in the posterior thoracic vertebrae ID20-B and NsT90. Ventral foramina are present in NsT94, NMRx1794 and maybe NsT90, whereas they are lacking in NsT93, NsT91, ID20-A and ID20-B. A thoracic vertebra of *P. paulsonii* from Ukraine has two dorsal foramina and one foramen located anteriorly at the ventral side (Paulson *in* Brandt, 1873, p. 338). This was also observed by Gol'din & Zvonok (2013), who added that dorsal foramina were lacking in the three thoracic vertebrae of *P. uheni* (NMNH-P OF-2096) or *Pachycetus* sp. (three or four thoracic vertebrae, KOM44762 P204 to ?KOM44759 P201).

The transverse process, preserved in NMRx1795 and ID20-2, is directed both outward and in a ventral direction, as in *Pachycetus* (Kellogg, 1936) and other basilosaurids (Kellogg, 1936), but also in some primitive mysticetes (Fordyce & Watson, 1998; Van Vliet *et al.*, 2019). The transverse process of NMRx1795 has a distinct anterior notch (Plate 3, fig. C2) similar to Lu2, (but not Lu1) in *P. wardii* (Uhen, 2001). Both lumbar centra here described, are elongated. NMRx1795 has a relative length of (probably slightly) more than 1.59 and the vertebral centrum ID20-2 has an estimated relative length of 1.81 (without epiphyses), see Appendix table 2b. This is larger than that of lumbar vertebrae in *Pachycetus wardii* (relative length ~1.5, see Uhen, 1999), but about the same as the relative length of the longest lumbar vertebrae in

P. paulsonii. According to Kellogg (1936), 'Lu2', 'Lu3' and 'Lu5' (table 24) have a relative length of 1.67-1.76; 'Lu1' and 'Lu5' (table 25) have a relative length of 1.67-1.68 (numbers vertebrae in Kellogg are provisional, as exact positions in the vertebral column are unknown). The estimated length of the figured lumbar vertebral centrum Lienau-A seems larger than the lumbar vertebral centrum 20-2 from Alversdorf in the Heimatmuseum of Schöningen (260 versus 235 mm).

The caudal vertebra NMRx1796 is not elongated with a relative length of 0.69 (Appendix table 2b). The cortex is thin, with apparently only a few layers of compact bone. The transverse processes are pierced by a vertebral foramen. Instead of a neural spine, only a vestigial ridge seems to be present on the midline of the neural arch. The last two features suggest that this vertebra had an anterior-central position, maybe in the series Ca4 to Ca9 (see Appendix table 2c). The transverse processes are as long as the vertebral centrum. Compared with the transverse processes of the caudal vertebrae of *e.g.* *C. peruvianus*, these are elongated (see fig. 76 in Martínez-Cáceres *et al.*, 2017) and NMRx1796 is therefore assigned to Morphotype A, *Pachycetus* sp.

The rib fragment NsT92-B has a great resemblance to NsT92-A. Also here, the distal part is very thick and pachyosteosclerotic distal part, that is antero-posteriorly flattened. Like NsT92-A, the height is about 0.6 of its width at the thickest point (NsT92-B: H(distal)/W(distal) = 48/77; see Appendix table 3b). Based upon their dimensions the rib fragments NMRx1797 and Lienau-C (which dimensions had to be estimated) are both referred to Morphotype A, but a similar broadening of the distal side is not present.

The epiphyses of all the vertebrae from the Helmstedt region belonging to Morphotype A are lacking. The same disproportionality between the numbers of juvenile and fully grown vertebrae is noted in a collection of comparable archaeocete vertebrae in NMR (K. Post, pers. comm.). The epiphyses of quite a few vertebrae in *Pachycetus* sp. from Ukraine are lacking too, for example in four associated vertebrae KOM 44759 P 201 to 204 (Gol'din & Zvonok, 2013), and in the vertebrae of a partial skeleton, NMNH-P Ngr-6 to 12 (Gol'din *et al.*, 2014). On the other hand, some individuals of *Pachycetus* spp. from Ukraine do have partly or completely fused epiphyses: three thoracic vertebrae of a partial skeleton, NMNH-P OF-2096, assigned to *P. uheni*, (Gol'din & Zvonok, 2013), and seven out of ten vertebrae, assigned to *P. paulsonii* (Kellogg (1936, table 24). Judged by the vertebrae, the number of immature individuals of *Pachycetus* sp. from the Helmstedt region seems to be much higher than in Ukraine.

In cetaceans a tendency is observed toward evolving "a vertebral column which consists of a large number of uniform vertebrae" (Slijper, 1936, pp. 325, 335). This often makes identification of isolated postcrania of whales

from the Neogene difficult, if not impossible. However, in various (Palaeogene) species of Basilosauridae the vertebrae show much more variation (Van Vliet *et al.*, 1999, table 1). Features of *Pachycetus* were called very characteristic by Gingerich & Zouhri (2015, p. 284), who added: “*Platyosphys* (here *Pachycetus*) has been little discussed in the archaeocete literature because the morphology of the vertebrae is so distinctive”. All cetacean remains of Morphotype A, recognised both in the earlier finds and in the newly described finds from the Helmstedt region, can most confidently be referred to the genus *Pachycetus*. In size and in vertebral features the torso vertebrae are comparable to *Pachycetus* species from Ukraine (Brandt, 1873; Kellogg, 1936; Gol'din & Zvonok, 2013; Gol'din *et al.*, 2014). The material from the Helmstedt region, consisting of isolated and fragmentary bones, does not exhibit enough diagnostic features to make a identification on species level possible. It cannot be not excluded that more than one species of *Pachycetus* is present in this material.

Vertebrae of *P. aithai* (Gingerich & Zouhri, 2015) and *P. wardii* (Uhen, 1999) share characteristics with the finds from Europe, but are significantly smaller in size. *Pachycetus* is considered a basal basilosaurid with some protocetid characteristics. Compared with more derived basilosaurids, in *P. wardii* the innominate is less reduced (Uhen, 2013), and there is a lower number of thoracic (probably 12) and lumbar (probably 6) vertebrae (Uhen, 2001). The likely related, relatively small MUSM1443 from Peru has 11 or 12 thoracic, and an unknown number of lumbar vertebrae (Uhen *et al.*, 2011).

B. cetoides and *Dorudon atrox* Andrews, 1906 have 15 or 16 thoracic and 20 lumbar vertebrae (Kellogg, 1936), and *C. peruvianus* even 20 thoracic and 17 lumbar vertebrae (Martínez-Cáceres *et al.*, 2017). As *Pachycetus* species from Europe are only known by isolated finds or at best partial skeletons, specific details like the number of vertebrae and the size of the innominate are still uncertain.

According to Gol'din *et al.* (2014), the occurrence of *Pachycetus* maybe restricted to the Bartonian, but possibly also present in the Priabonian (Uhen, 2013). The finds from the Helmstedt region are Bartonian and Priabonian in age. It is possible that the cetacean finds in Priabonian strata have been derived from older strata. For example, the uplifting due to halokinesis could soon after deposition have caused erosion of Bartonian sediments deposited within the reach of the salt diapir. However, the presumed molar GPIM P 4010 according to Lienau (1984) from the Priabonian stratum G1 (see Table 1), is fresh and does not show abrasion by currents and transport. The same seems to be true for the caudal vertebra ID730, also from the Priabonian stratum G1 (see Table 1), which is only slightly abraded.

Distribution – Large species of *Pachycetus*, such as *P. paulsonii* and *P. uheni* are known from the Bartonian of Ukraine and southwestern Russia (Paulson in Brandt, 1873; Kellogg, 1936; Gol'din & Zvonok, 2013; Gol'din *et al.*, 2014). In addition, an isolated vertebra from the

Bartonian to Priabonian Stockletten Formation of Rohrdorf, Germany (Uhen & Berndt, 2008) has been referred to *Pachycetus* sp. (Gol'din & Zvonok, 2013). *P. wardii* Uhen, 1999 is known from the Bartonian Castle Hayne and Piney Point Formations of Virginia and North Carolina, USA (Uhen, 2005, 2013; Weems *et al.*, 2011). *P. aithai* is known from the Bartonian Aridal Formation at Guéran, Morocco, Africa. MUSM1443, a yet unnamed taxon from the Bartonian Paracas Formation of Peru can be probably included in the same group as *Pachycetus* (Uhen *et al.*, 2011; Gol'din & Zvonok, 2013).

Basilosauridae indet.

Morphotype B

(small ‘dorudontine’)

Table 1c

Plate 4

Appendix table 4a. Dimensions of a rostrum

Appendix table 5a. Dimensions of a deciduous incisor

Appendix table 6a. Dimensions of a cervical vertebral centrum (Ce2)

Appendix table 6c. Dimensions of a cervical vertebral centrum (Ce6)

Appendix table 7a. Dimensions of thoracic-caudal vertebral centra

Appendix table 7b. Dimensions of a rib fragment

• Heimatmuseum Schöningen

Material – One partial rostrum, ID20-7, one presumed deciduous incisor, ID24, two vertebral centra, ID75, here indicated as ID75-A & B, a fragment of a neural arch, ID20-C.

Comments – The original registration number on the neural spine is not present anymore and this fragment has been given the provisional number ID20-C by the authors.

• Senckenberg Naturhistorischen Sammlungen, Dresden

Material – One rib fragment, NsT37.

Comments – Van Beneden (1883) mentioned that NsT37 originated from the *Phosphoritlagerstätten* near Helmstedt. According to the label it was found in Runstedt near Helmstedt. NsT37 was described by Van Beneden (1883) as a rib fragment with an articulation facet at one end and measuring 70 or 80 mm in length. He assigned it to *Pachycetus humilis* (see Table 1).

• Present location unknown - publication Lienau (1984)

Material – One vertebral centrum without catalogue number, here indicated als Lienau-C.

Comments – This centrum was briefly described and figured by Lienau (1984, p. 72-73, table IX, fig. 14), who assigned it to *Pachycetus humilis* (with some hesitation - see above, section Morphotype A). A catalogue number is unknown and the vertebra has been given the provisional numbers Lienau-C by the authors. We could not trace the location of Lienau-C (in 1984 in the private collection of Wulf).

• **Formerly in the Bayerische Staatssammlung für Paläontologie und Geologie in Munich**

Material – Three vertebral centra, here indicated as Kuhn-A, B & C.

Comments – The vertebral centra Kuhn-A, B & C have been described by Kuhn (1935), but not by Van Beneden (1883). The catalogue numbers are unknown and the vertebrae have been given the provisional numbers Kuhn-A, B & C by the authors. The vertebrae probably got lost during World War II.

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Description – ID20-7 is a partial rostrum, apparently with two alveoli. Because of adhering matrix, the alveoli are obscured. At its ventral side, as well at the proximal and distal parts, the bone is broken. It is more or less abraded and brownish in colour (Plate 4, figs A1-2).

ID24 is an isolated incisor, which is labio-lingually compressed and has a fine carina on both the mesial and distal sides. The distal carina has small serrations. The root is curved distally. Damage is evident at the base of the root. The tooth is not or only slightly abraded and brownish in colour. It has been glued with its labial side upon a small glass plate (Plate 4, figs B1-2).

ID75-A is the second cervical vertebra. The odontoid process (dens) of the axis is about 23 mm high. The posterior epiphyseal surface is concave. The neural arch is broken. Both the transverse processes have been preserved, with on each side a rather large vertebroarterial canal of about 10 mm in length and 6 mm wide. The vertebra is abraded, mineralised and brownish to dark grey in colour (Plate 4, figs C1-3).

ID75-B is a sixth cervical vertebral centrum with fused epiphyses. The anterior and posterior epiphyseal surfaces are concave. The neural arch is not preserved. The vertebral surface between the pedicles of the neural canal is slightly damaged. The anterior side is slightly damaged at the dorsal side. The two large transverse processes have been preserved, antero-posteriorly about 30 mm in length and 32 mm in width at the onset near the centrum. They are directed ventrally, protruding 50 mm from the centrum. A vertebroarterial canal is located at both lateral sides of the centrum, each about 17 mm in length and 15 mm in width. The vertebra is abraded, mineralised and bluish-grey in colour; the original colour has been

changed by the application of a protecting varnish (Plate 4, figs D1-2).

Lienau-C is a thoracic vertebral centrum with only the two pedicles of the neural arch preserved. There are no epiphyses. The thoracic centrum resembles NsT94 from Dresden, although the pedicles of the neural arch are here less thick. Dimensions have not been given in the description.

ID20-C is a fragment of the neural arch with the onset of a neural spine, apparently a part of a small vertebra. It is abraded and brownish-grey in colour.

Kuhn-A is a vertebral centrum without epiphyses. The width between the pedicles of the neural arch is 36 mm. The short transverse processes are located laterally, with a fovea for the rib, and right above it, separated by a small groove, a triangular diapophysis is present. For this reason, it is described by Kuhn (1935) as a transitional thoracic centrum. At the ventral side, several vascular foramina, unequal in size, are separated by a median keel. It is only slightly abraded.

Kuhn-B is a small vertebral centrum without epiphyses. The transverse processes are as long as the vertebral centrum, placed at a low dorsoventral position and projecting ventrally. It has been described by Kuhn (1935) as an anterior caudal vertebra. It is abraded and severely damaged.

Kuhn-C is a vertebral centrum without epiphyses. The centrum is waisted. The anterior width between the pedicles of the neural arch is 18 mm. At the ventral side a vascular foramen of about 4 mm in width is present. It has been described by Kuhn as a central-posterior caudal vertebra. The vertebra is abraded. We refer to the article of Kuhn (1935) for a more detailed description of Kuhn-A, B & C.

NsT37 is a rectangular rib fragment with a broken proximal end. The distal part is swollen and has an abraded articulation surface, probably for the articulation with the sternum (Plate 4, figs E1-2).

Discussion – The size of the rostrum fragment ID20-7 points to a small cetacean, Morphotype B. Dimensions fit rather well with those of *D. atrox* (Appendix table 4b). Nevertheless an assignment to a young, physically immature individual, belonging to Morphotype A, *Platyospys* sp. cannot be completely excluded.

The length of the incisor from Schöningen is indicative of a small species, not of a large species like Morphotype A, *Pachycetus* sp. (see Appendix table 5b). Although *Zygorhiza* and *Dorudon* can be distinguished by some dental characteristics, *i.e.* the presence or absence of a cingulum on premolars 2, 3 and 4, the incisor has no characteristics to assign it to a particular genus. The dimensions of ID24 are rather close to those of the first deciduous lower inci-

sor, dI1 of *Zygorhiza kochii* Reichenbach in Carus, 1847, but also to those of a first, dI1, or third, dI3, deciduous upper incisor (however, not to those of a dI1, which is far smaller) of *D. atrox* (see Appendix table 5c). ID24 has a mesial and distal carina; these carinae are more developed in dI3, than in dI1 or dI2 of *D. atrox*. Moreover, the distal carina has small serrations (see Plate 4, fig. B2), as was described in dI3 of *D. atrox* (Uhen, 2004, p. 17). An identification as a right upper dI3 remains uncertain and one has to bear in mind that it is difficult to tell apart even upper from lower incisors in the case of *D. atrox* (Uhen, 2004, p. 23).

The vertebral centra referred to Morphotype B can be distinguished from those of Morphotype A, based upon the absence of the features shown in Table 2 (features of vertebrae in *Pachycetus* sp.) and their generally significantly smaller size.

ID75-B, the vertebral centrum Ce6 from Alversdorf, now in the Heimatmuseum of Schöningen, is short. This rules out the possibility of its referral to a protocetid, as cervical vertebrae in protocetids were longer, namely intermediate between those of more primitive whales and the more derived basilosaurids (Uhen, 1998, p. 47; Hulbert *et al.*, 1998; Gingerich *et al.*, 2001; Gingerich & Capetta, 2014). In Appendix table 6d, the relative lengths of some protocetid and basilosaurid cervical vertebrae are listed. The cervical vertebra Ce6 from Schöningen is narrower and lower than the cervical vertebrae (C4, 5, 7) of *Pachycetus* sp. from Ukraine described by Gol'din *et al.* (2014), see Appendix table 6d. Dimensions of the vertebral centra Ce2 and Ce6 are comparable to those of small 'dorudontines', such as *Dorudon atrox* and *Zygorhiza kochii* (see Appendix tables 6B & D). The vertebral arterial foramina have been preserved in both Ce2 and Ce6. Both cervical vertebrae have fused epiphyses, in contrast with the other vertebrae, except a caudal one, which is described below. This does not mean that these vertebrae undoubtedly have belonged to mature individuals, as in whales the vertebrae in the cervical and caudal regions fuse at an early age (Moran *et al.*, 2015).

Although the anterior thoracic vertebral centrum Lienau-C has similar outlines as NsT94, its estimated dimensions are far smaller. Width and height seem to be about 30% less than in NsT94 (see Appendix tables 2b & 7a). Based upon the pedicles of the neural arch lacking pachyostosis and its small size it is assigned to Morphotype B.

According to Kuhn, four small vertebrae, the earlier described NsT94, and the three vertebrae described by him (i.e. Kuhn-A, Kuhn-B and Kuhn-C) could represent the same species with non-elongated and small vertebrae, which he compared with '*Zeuglodon*' (= *Saghacetus*) cf. *osiris* Dames, 1894. The vertebral centra, Kuhn-A, B & C are indeed comparable with small 'dorudontine' basilosaurids. But the vertebral centra are larger than those of the late Priabonian *Saghacetus* ('*Zeuglodon*') *osiris* (see Kellogg, 1936, pp. 201-202) or those of *Stromerius ni-*

densis Gingerich, 2007 (see Gingerich, 2007, table 1) and have about the same size as the vertebrae of *Dorudon* and *Zygorhiza* (see Kellogg, 1936, table 33 and Uhen, 2004, table 11).

The presence of vascular foramina at the ventral side of the thoracic vertebrae, as described in the vertebra Kuhn-A (Kuhn, 1935), was not mentioned by Kellogg (1936) in his detailed description of the vertebral column of *Zygorhiza kochii*, nor by Gingerich (2015). In *Z. kochii*, ventral vascular foramina seem to be present only in the lumbar and caudal vertebrae (Kellogg, 1936). However, ventral foramina, varying in size, in thoracic vertebral series have been described in *Dorudon atrox* (Uhen, 2004, p. 79) and *Ancalacetus simonsi* Gingerich & Uhen, 1996 (Gingerich & Uhen, 1996, p. 385). The presence or absence of ventral vascular foramina in thoracic vertebrae of small 'dorudontine' basilosaurids has not been described as a diagnostic feature and could reflect an intraspecific variability like in the thoracic vertebrae of *Pachycetus* sp. (see discussion above on Morphotype A). Gingerich (2015) reported that in *Zygorhiza*, in contrast with *Dorudon*, the width of the neural canals in thoracic vertebrae equals their height. In the vertebral centrum Kuhn-A, only the pedicles of the neural arch are preserved and therefore width and height of the neural canal cannot be used for a positive identification. According to Kuhn (1935), Kuhn-A is a Th8 or Th9, because it is a transitional thoracic vertebra. In *Z. kochii* the transitional thoracic vertebra is indeed a Th9 (Kellogg, 1936, p. 140).

The slightly swollen distal end of rib fragment NsT37 is slender, by far not as thick as the rib fragments NsT92-A & B. Both in large and small basilosaurids the rib dimensions are quite variable as they depend on their location in the rib cage, and in the case of fragments, also on the part of the rib involved. Therefore, the assignment to Morphotype B (instead of the large taxon Morphotype A) is not completely certain.

The co-existence of more than one species of small archaeocetes in this area cannot be excluded. Given the rarity of archaeocetes in Europe, we tentatively assign the here described remains of small cetaceans, all being derived from the same region, and probably all from the same formation, to one taxon, here referred to as Morphotype B. Morphotype B was presumably a 'dorudontine' basilosaurid, comparable in size to *Dorudon* or *Zygorhiza*. There are not enough characteristics to assign these vertebrae to a specific genus.

Distribution in Europe – Several small, 'dorudontine' basilosaurids have been described from the Bartonian and Priabonian of Europe. Uhen & Berndt (2008) described a small premolar, probably of a 'dorudontine' basilosaurid, from the Bartonian to Priabonian Stockletten Formation of Rorhendorf, Germany. Vertebrae of small 'dorudontine' basilosaurids, ascribed to *Zygorhiza* (Seeley, 1881; Andrews, 1907; Hudleston, 1902; Halstead & Middleton, 1972), and a skull, now long lost (Seeley, 1876) are known

from the Bartonian of England. An incomplete skeleton of *Dorudon* sp. from the Priabonian of Varano, Italy, has been described by Pilleri & Cigala Fulgosi (1989).

Basilosauridae indet.

Table 1d

Plate 5, figs A1-3

Appendix table 8. Dimensions of a possible supraorbital process

• Senckenberg Naturhistorischen Sammlungen, Dresden

Material – A bone fragment, most probably part of a small rib, Dresden-A.

Comments – This bone fragment was mentioned neither by Van Beneden (1883), nor by Kuhn (1935). It has no catalogue number and is indicated here under the provisional number Dresden-A.

• Natuurhistorisch Museum Rotterdam

Material – A skull fragment, NMRx1798.

Comments – This material has been collected by Mr. B. Vahldiek in the years 1975-1992.

• Present location unknown - publication Lienau (1984)

Material – A tooth fragment, here indicated as Lienau-D.

Comments – This tooth fragment was mentioned together with the presumed molar GPIM P 4010 under the heading “*Dorudontidae* gen. et sp. indet.” (Lienau, 1984, p. 72). Illustrations nor dimensions have been provided. It has been found in the open cast mine Tagebau Treue, near Büddenstedt, an *ex situ* find and therefore it is not certain from which formation it has been derived. The catalogue number is unknown and the tooth fragment herein has been given the provisional number Lienau-D. We could not trace the location of Lienau-D (in 1984 in the private collection of Hintzen).

• Poster exposition Göttingen (2008)

Material – One caudal vertebra, here indicated as Göttingen-A.

Comments – This vertebral centrum was figured on a poster for a whale exposition in 2008, and indicated as “*Pachycetus*-vertebra, late Eocene of Helmstedt”. Its dimensions have not been given. The catalogue number is unknown and herein the vertebra has been given the provisional number Gottingen-A. We could not trace the

location of Gottingen-A and the description is based on the picture on the poster.

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Description – Dresden-A is probably a fragment of a small rib, with broken ends and evidence of damage at one side. It is rather badly abraded.

NMRx1798 is a rectangular, more or less flat piece of bone, slightly arched. A crest is visible at one side, possibly the lateral side. It represents a part of the skull, possibly the supraorbital process of the os frontale. At the concave side a triangular surface is present, that is broadest towards the possible supraorbital crest, narrowest at the opposite end (Plate 5, figs A1-3).

The picture on the poster for an exposition in Göttingen shows the posterior and left lateral side of a cetacean vertebra Göttingen-A, an anterior caudal vertebra. The centrum is waisted. The posterior epiphysis is fused with the centrum. It has a rounded to hexagonal shape. At the right ventral side, a part is missing. The neural arch has two metaphyses and a neural spine which is maybe partly broken. The left transverse process is directed laterally; it is unclear, whether there is a vertebroarterial foramen. The centrum does not seem to be abraded and is yellowish in colour.

Discussion – All remains discussed in this section, apparently are cetacean bones, but an assignment to a large or small morphotype cannot be given. Assignment of the tooth fragment Lienau-D, or of the caudal vertebra Göttingen-A to Morphotype A, or Morphotype B cannot be given because of lack of information on diagnostic characters. The caudal vertebra has a neural spine. Appendix table 2c demonstrates that a neural spine is present in the caudal series Ca1-3 in two species of basilosaurids and in the series Ca1-5 in *Zygorhiza kochii*. Göttingen-A is here interpreted as one of the anteriormost caudal vertebrae. Notwithstanding the fused posterior epiphysis, this vertebra may also have belonged to a juvenile specimen, because of early epiphyseal fusion in caudal and cervical cetacean vertebrae (Moran *et al.*, 2015).

Incertae sedis

Table 1e

Plate 5, figs B1-5 & C1-6

Appendix table 9a. Dimensions of a possible sternal element

Appendix table 9b. Dimensions of a possible distal tibia fragment

Appendix table 9c. Dimensions of unidentifiable bone fragments

• Senckenberg Naturhistorischen Sammlungen, Dresden

Material – A possible sternal element, NsT89 from Runstedt and an unidentifiable bone fragment, NsT49.

Comments – NsT89 was described by Van Beneden (1883, p. 7) as a “perfectly symmetric bone, at first sight a phalange of a large cetacean, but on a better look a sternebra of a terrestrial mammal”. He added that, as Geinitz had ascribed a tooth to *Lophiodon rhinoceros* Rütimeyer 1862 this might be a “second sternebral element of this ungulated mammal”. Geinitz (1883b), apparently partly disagreeing with him, described it as a metatarsal (and not a sternebra) of, possibly, *Lophiodon rhinoceros*, most probably because some molars and a mandible of this species had been found at these sites. The bone fragment NsT49, was mentioned neither by Van Beneden (1883), nor by Kuhn (1935).

• *Natuurhistorisch Museum Rotterdam*

Material – A collection of a possible distal tibia fragment, NMRx1799, and six bone fragments, NMRx1800, NMRx1801, NMRx1802, NMRx1803, NMRx1804 and NMRx1805.

Comments – This material has been collected by Mr. B. Vahldiek in the years 1975-1992.

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Description – NsT89 is a rather large, long bone, damaged at the anterior side. At one side it has a broad, bilateral articulation site that is rather spongy and rugose, and possibly the posterior. Also the (possibly) anterior side is spongy and rugose, which indicates the presence of cartilaginous tissue in life. At the probably ventral side, it has an anteroposterior, broad ridge along the midline. It is slightly abraded and yellow to brown in colour (Plate 5, figs C1-6).

NMRx1799 is possibly a distal fragment of a right tibia. Distally the epiphysis of this bone of a probably juvenile individual is lacking and there seems to be a slightly developed medial malleolus. In distal view the epiphyseal side is pentagonal in shape. In proximal view the shaft is triangular. The proximal side is broken; the fracture is fresh and a thick cortex, about 3 to 10 mm thick, is visible. There is no open medullary cavity. At the right, medio-ventral (‘anterior’) side the fragment shows multiple bite marks of predators, probably sharks. The bone is not abraded and grey in colour (Plate 5, figs B1-5).

NsT49 could be part of a vertebra, a rib or a partial chevron. It has broken ends, showing concentric, multi-layered, but rather spongy bone. It is abraded.

NMRx1800, NMRx1802, NMRx1803, NMRx1804 and NMRx1805 are small pieces of bone.

NMRx1801 is a triangular bone fragment.

Discussion – The remains discussed in this section cannot be assigned with certainty to a marine or terrestrial taxon.

According to Holbrook (pers. comm.) NsT89 is not the metatarsal of a species of *Lophiodon* Cuvier, 1822 (contra Geinitz, 1883b) or even a perissodactyl. NsT89 superficially resembles metacarpal 5 in *Cynthiacetus peruvianus* (Martínez-Cacéres *et al.*, 2017, fig. 87) and the protocete *Aegicetus gehennae* Gingerich *et al.*, 2019 (fig. 14), but these are about two to three times shorter. There is no resemblance with other metacarpal bones. NsT89 also resembles the mid or posterior part of a manubrium sterni in *Pachycetus wardii*, figured by Uhen (2001, figs 7A & B). However, NsT89 is not ‘T’-shaped, missing the broad anterior end, but maybe this part has broken off. Two anterior mesosternal elements and a xiphisternum of *Pachycetus* sp. from Ukraine were described by Gol’din *et al.* (2014). The two anterior elements are broad, whereas NsT89 is slender. More probably NsT89 could be a distal sternal element, as was suggested by Uhen (pers. comm.). It indeed resembles the distal sternal elements of e.g. *Aegicetus gehennae* (Gingerich *et al.*, 2019, fig. 12). However, the slender xiphisternum of *Pachycetus* sp. from Ukraine was described by Gol’din *et al.* (2014) as a bifurcated bone, contrary to NsT89. Assignment of NsT89 to a sternal element would be in agreement with Van Beneden’s suggestion (1883), but because of its slenderness certainly not the second one, but either part of the manubrium or a posterior mesosternal element. Moreover, as it was found in marine sediments, if NsT89 is a sternal element, it more probably belongs to an archaeocete, rather than a terrestrial mammal. Because of its relatively large size, NsT89 would have belonged to Morphotype A, *Pachycetus* sp., rather than to the smaller Morphotype B. The identification of NsT89 as a sternal element remains uncertain.

NMRx1799 is here interpreted as a right distal tibia fragment. It bears some resemblance to the distal part of a tibia in *Lophiodon* (Holbrook, 2009, fig. 13), but as it is a bone from a juvenile individual, without distal epiphysis, assignment to a possible terrestrial taxon is uncertain (Holbrook, pers. comm.). Although the bone is not fully grown it has a thick, compact cortex, without open medullary cavity, as the tibia of the protocete *Maiacetus inuus* Gingerich *et al.*, 2009 (Houssaye *et al.*, 2015). This might be regarded as an adaptation to a marine environment (Houssaye *et al.* 2015; see also Madar, 1998). In addition, the traces of shark teeth corroborate the assignment to a marine mammal. NMRx1799 shares similarities with the tibia in *A. gehennae* (Gingerich *et al.*, 2019, fig. 16). The shaft is not rounded, but triangular in cross section, more outspoken in NMRx1799. Both tibiae are more or less pentagonal in distal view. The medial malleolus is small in both tibiae. As the epiphysis of the distal side is lacking, no comparisons (a.o. regarding the astragalar facet) can be made with that in *A. gehennae*. If correct, this tibia was most probably larger than the tibiae in *Cynthiacetus peruvianus* (see Martínez-Cacéres *et al.*, 2017, fig. 91) or *Basilosaurus isis* (see Uhen, 1998, fig. 9). NMRx1799 has been found in marine sediments and its osteological characteristics point to a marine mammal; if assigned to a cetacean, it would be the first find of an archaeocete tibia

from Europe. Because NMRx1799 is an isolated find and the tibia in *Pachycetus* is unknown, the identification to a particular taxon, marine or even terrestrial, is uncertain.

The triangular bone NMRx1801 has a rather loose bone structure; it is not certain, whether this is a cetacean bone.

Conclusions

At least two archaeocete taxa, a large Morphotype A and a smaller Morphotype B are recognised in the cetacean fossil material from the Bartonian-Priabonian Gohlberg Formation, Helmstedt region, Germany. The vertebrae of Morphotype A are generally considerably larger than those of Morphotype B and further differ from these by means of the characteristics listed in Table 2. The presence of two taxa is in accordance with the description by Kuhn (1935) of the finds from the same region. Earlier, Van Beneden (1883) described two cetacean taxa from this region, belonging to two ‘Oligocene mysticetes’, namely *Pachycetus robustus* and *Pachycetus humilis*. The name *Pachycetus robustus* is maintained for vertebra NsT90 and rib fragment NsT92-A. All other cetacean remains described by Van Beneden, with the exception of rib fragment NsT37, can probably be referred to Morphotype A, *Pachycetus* sp. NsT90 and NsT92-A, as well as vertebrae and ribs in Morphotype A share all observed diagnostic characteristics with those of *Pachycetus (Platyosphys)* species from Ukraine. Therefore *Platyosphys* Kellogg, 1936 is considered a junior synonym of *Pachycetus* Van Beneden, 1883. Assignment at species level is not possible for the isolated, mostly fragmentary remains from the Helmstedt region. Maybe *Pachycetus* sp. did not solely occur in the Bartonian, as a few hardly or not abraded remains have been found in Priabonian strata as well. It is noteworthy that the epiphyses are lacking in nearly all the vertebrae of both Morphotypes A and B; therefore these vertebrae have belonged to juvenile and immature individuals.

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Table 1a. *Pachycetus robustus*

Location & collection number	Bone	Site	Stratum	Age	Collector	References
<i>Senckenberg Naturhistorischen Sammlungen, Dresden</i>						
NsT90	Posterior thoracic (?anterior lumbar) vertebra	<i>Phosphoritlagerstätten</i> Helmstedt	?	Middle-Late Eocene	Funk	Geinitz, 1883a, 1883b Van Beneden, 1883 Kuhn, 1935
NsT92-A	Distal rib fragment	<i>Phosphoritlagerstätten</i> Helmstedt	?	Middle-Late Eocene	Funk	Geinitz, 1883a, 1883b Van Beneden, 1883

Table 1b. Ascribed to morphotype A, *Pachycetus* sp.

Location & collection number	Bone	Site	Stratum	Age	Collector	References
<i>Heimatmuseum Schöningen</i>						
ID21	?Upper premolar (?P2,3, or 4)	Open cast mine BKB Alversdorf (with the remark: 'near Büddenstedt')	?	Middle-Late Eocene	Putzmann	This article
ID20-A	Anterior thoracic vertebra	Open cast mine BKB Alversdorf	?	Middle-Late Eocene	Putzmann	This article
ID20-B	Posterior thoracic vertebra	Open cast mine BKB Alversdorf	?	Middle-Late Eocene	Putzmann	This article
ID20-3	Posterior thoracic or lumbar vertebra	Open cast mine BKB Alversdorf	?	Middle-Late Eocene	Putzmann	This article
ID20-2 + ID20-4	Lumbar vertebra + detached anterior conus	Open cast mine BKB Alversdorf	?	Middle-Late Eocene	Putzmann	This article
ID20-6	Rib fragment	Open cast mine BKB Alversdorf	?	Middle-Late Eocene	Putzmann	This article
<i>Natuurhistorisch Museum Rotterdam</i>						
NMR999100151793	Anterior-central thoracic vertebra	Open cast mine Treue 3, 'Nordwand'	K4	Bartonian	Vahldiek	This article
NMR999100151794	Central-posterior ('transitional') thoracic vertebra	Open cast mine Treue 3, 'Nordwand'	G1	Priabonian	Vahldiek	This article
NMR999100151795	Lumbar vertebra	Open cast mine Treue3, 'Nordwand'	G4	Priabonian	Vahldiek	This article
NMR999100151796	Anterior-central caudal vertebra	Open cast mine Treue 3, 'Nordwand'	G1	Priabonian	Vahldiek	This article
NMR999100151797	Rib fragment	Open cast mine Treue 3, 'Nordwand'	G4	Priabonian	Vahldiek	This article
<i>Senckenberg Naturhistorischen Sammlungen, Dresden</i>						
NsT94	Anterior thoracic vertebra (?Th1)	<i>Phosphoritlagerstätten</i> Büddenstedt	?	Middle-Late Eocene	?	Van Beneden, 1883 Geinitz, 1883b Kuhn, 1935
NsT93	Anterior thoracic vertebra	<i>Phosphoritlagerstätten</i> Runstedt	?	Middle-Late Eocene	?	Geinitz, 1883a, 1883b Van Beneden, 1883 Kuhn, 1935
NsT91	Anterior-central thoracic vertebra	<i>Phosphoritlagerstätten</i> Helmstedt	?	Middle-Late Eocene	?	Geinitz, 1883a, 1883b Van Beneden, 1883 Kuhn, 1935

*continued on next page***Table 1.** Overview of all finds described in this paper, mostly remains from archaeocetes, from the Helmstedt region.

Abbreviations: **BKB**, Braunschweigischen Kohlen-Bergwerke; **Ce**, cervical vertebral centrum; **G**, stratum with phosphorite concretions; **GPIM**, Institut für Geowissenschaften, Paläontologie, Universität Mainz; **ID**, identification; **K**, stratum with crab fossils; **NMR**, Natuurhistorisch Museum Rotterdam; **NsT**, Staatlichen Naturhistorische Sammlungen, Museum für Geologie und Mineralogie, Dresden; **post**, posterior; **Th**, thoracic vertebral centrum; **?**, unknown

Table 1b. continued

Location & collection number	Bone	Site	Stratum	Age	Collector	References
NsT41	Rib fragment	<i>Phosphoritlagerstätten</i> Helmstedt	?	Middle-Late Eocene	?	Van Beneden, 1883
NsT92-B	Distal rib fragment	<i>Phosphoritlagerstätten</i> Helmstedt	?	Middle-Late Eocene	?	This article
NsT-A	Rib fragment	<i>Phosphoritlagerstätten</i> Runstedt	?	Middle-Late Eocene	?	This article
Institut für Geowissenschaften, University of Mainz						
GPIM P 4010	? Upper molar (?M1, or 2)	Open cast mine Helmstedt	G1	Priabonian	Raabe	Lienau, 1984
Publication Lienau (1984); present location unknown						
Lienau-A	Lumbar vertebra	Open cast mine Treue 3 'Nordwand'	?	Middle-Late Eocene	'Legacy Lierl'	Lienau, 1984
Lienau-B	Rib fragment	Open cast mine Treue 3 'Nordwand'		Middle-Late Eocene	'Collection Wulf'	Lienau, 1984

Table 1c. Ascribed to morphotype B, Basilosauridae indet. (small 'dorudontine')

Location & collection number	Bone	Site	Stratum	Age	Collector	References
Heimatmuseum Schöningen						
ID20-7	Partial rostrum	Open cast mine BKB Alversdorf	?	Middle-Late Eocene	Putzmann	This article
ID24	Deciduous incisor (?dI3, dI1, or di1)	Open cast mine BKB Alversdorf	?	Middle-Late Eocene	Putzmann	This article
ID75-A	Cervical vertebrae (Ce2)	Open cast mine BKB Alversdorf	?	Middle-Late Eocene	Putzmann	This article
ID75-B	Cervical vertebrae (Ce6)	Open cast mine BKB Alversdorf	?	Middle-Late Eocene	Putzmann	This article
ID20-C	Neural spine	Open cast mine BKB Alversdorf	?	Middle-Late Eocene	Putzmann	This article
Senckenberg Naturhistorischen Sammlungen, Dresden						
NsT37	Distal rib fragment	<i>Phosphoritlagerstätten</i> Runstedt	?	Middle-Late Eocene	?	Van Beneden, 1883
Publication Lienau (1984); present location unknown						
Lienau-C	Anterior thoracic vertebra	Open cast mine Treue 'Nordwand'	?	Middle-Late Eocene	'Collection Wulf'	Lienau, 1984
Bayerische Staatssammlung für Paläontologie und Geologie in Munich; present location unknown						
Kuhn-A	Central ('transitional') thoracic vertebra	Open cast mine Trendel- busch	?	Middle-Late Eocene	?	Kuhn, 1935
Kuhn-B	Anterior caudal vertebra	Open cast mine Trendel- busch	?	Middle-Late Eocene	?	Kuhn, 1935
Kuhn-C	Central-posterior caudal vertebra	Open cast mine Trendel- busch	?	Middle-Late Eocene	?	Kuhn, 1935

continued on next page (table 1d)

Table 1 continued

Table 1d. Ascribed to Basilosauridae indet.

Location & collection number	Bone	Site	Stratum	Age	Collector	References
<i>Natuurhistorisch Museum Rotterdam</i>						
NMR999100151798	Skull fragment ?supra-orbital process	Open cast mine Treue 3, 'Nordwand'	G4	Priabonian	Vahldiek	This article
<i>Senckenberg Naturhistorischen Sammlungen, Dresden</i>						
Dresden-A	Rib fragment	<i>Phosphoritlagerstätten</i> Runstedt	?	Middle-Late Eocene	?	This article
<i>Poster exposition Göttingen (2008); present location unknown</i>						
Göttingen-A	Anterior caudal vertebra	'Helmstedt'	?	Late Eocene	?	Poster for an exhibition, 2008
<i>Publication Lienau (1984); present location unknown</i>						
Lienau-D	Tooth	Open cast mine Treue 'Nordwand'	?	Middle-Late Eocene	'Collection Hintzen'	Lienau, 1984

Table 1e. Ossa incertae sedis

Location & collection number	Bone	Site	Stratum	Age	Collector	References
<i>Natuurhistorisch Museum Rotterdam</i>						
NMR999100151799	Distal tibia fragment	Open cast mine Helmstedt	K4	Bartonian	Vahldiek	This article
NMR999100151800	Unidentifiable bone	'Helmstedt'	?	?	Vahldiek	This article
NMR999100151801	Unidentifiable bone	'Helmstedt'	?	?	Vahldiek	This article
NMR999100151802	Unidentifiable bone	'Helmstedt'	?	?	Vahldiek	This article
NMR999100151803	Unidentifiable bone	Open cast mine Treue	G5	Bartonian	Vahldiek	This article
NMR999100151804	Unidentifiable bone	Open cast mine Treue	G5	Bartonian	Vahldiek	This article
NMR999100151805	Unidentifiable bone	Open cast mine Treue	G5	Bartonian	Vahldiek	This article
<i>Senckenberg Naturhistorischen Sammlungen, Dresden</i>						
NsT49	Unidentifiable bone	<i>Phosphoritlagerstätten</i> Helmstedt	?	Middle-Late Eocene	?	This article
NsT89	?Sternal element	Runstedt	?	?	?	Van Beneden, 1883 Geinitz, 1883b

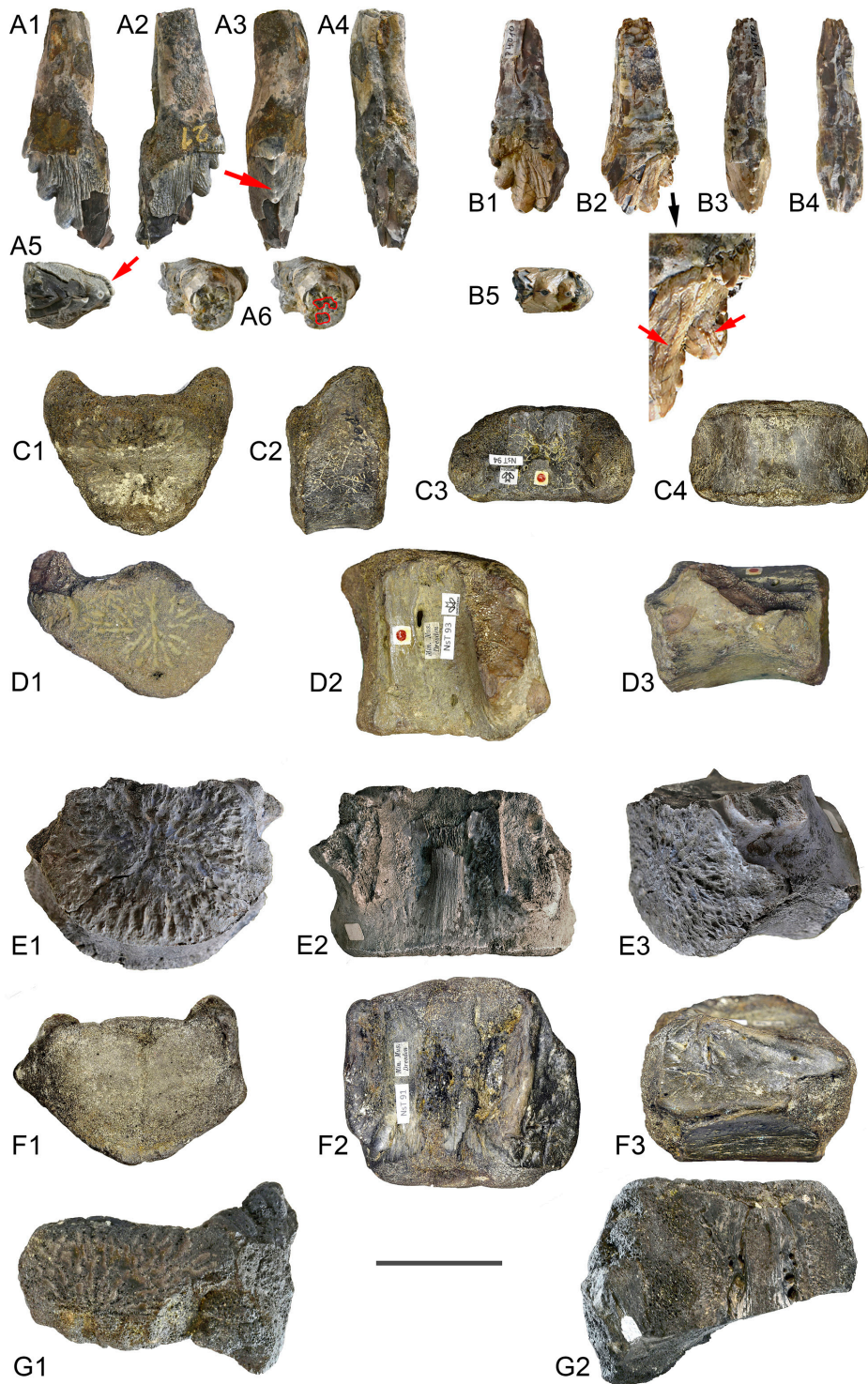


Plate 1. Dental elements and thoracic vertebral centra, Morphotype A, *Pachycetus* sp., from the Helmstedt region. A: ?upper pre-molar, (left ?P2,3, or 4), ID21 (Alversdorf) in lingual (A1), labial (A2), distal (A3), mesial (A4), occlusal (A5) and dorsal (A6) view. Arrow in A3 indicates the denticles of the ‘second order’; arrow in A5 indicates the cingulum with the ring of the protuberances; red lines in A6 indicate the pulp cavities; B: ?upper molar (left ?M1, or 2), GPIM P 4010 (Helmstedt) in lingual (B1), labial (B2), distal (B3), mesial (B4) and occlusal (B5) view. Vertical arrow at B2 points to a magnification of the distal crown base, with horizontal arrows indicating the longitudinal ridges with spines; C: anteriormost thoracic vertebral centrum, NsT94 (Büddenstedt), in anterior (C1), left lateral (C2), dorsal (C3) and ventral (C4) view; D: anterior thoracic vertebral centrum, NsT93 (Runstedt), in anterior (D1), dorsal (D2) and right lateral (D3) view; E: anterior thoracic vertebral centrum, ID20-A (Alversdorf), in anterior (E1), dorsal (E2) and left antero-lateral (E3) view; F: anterior-central thoracic vertebral centrum, NsT91 (Helmstedt), in anterior (F1), dorsal (F2) and right lateral (F3) view; G: anterior-central thoracic vertebral centrum, NMR999100151793 (open cast mine Treue 3), in anterior (G1) and dorsal (G2) view. Scale bar 5 cm.

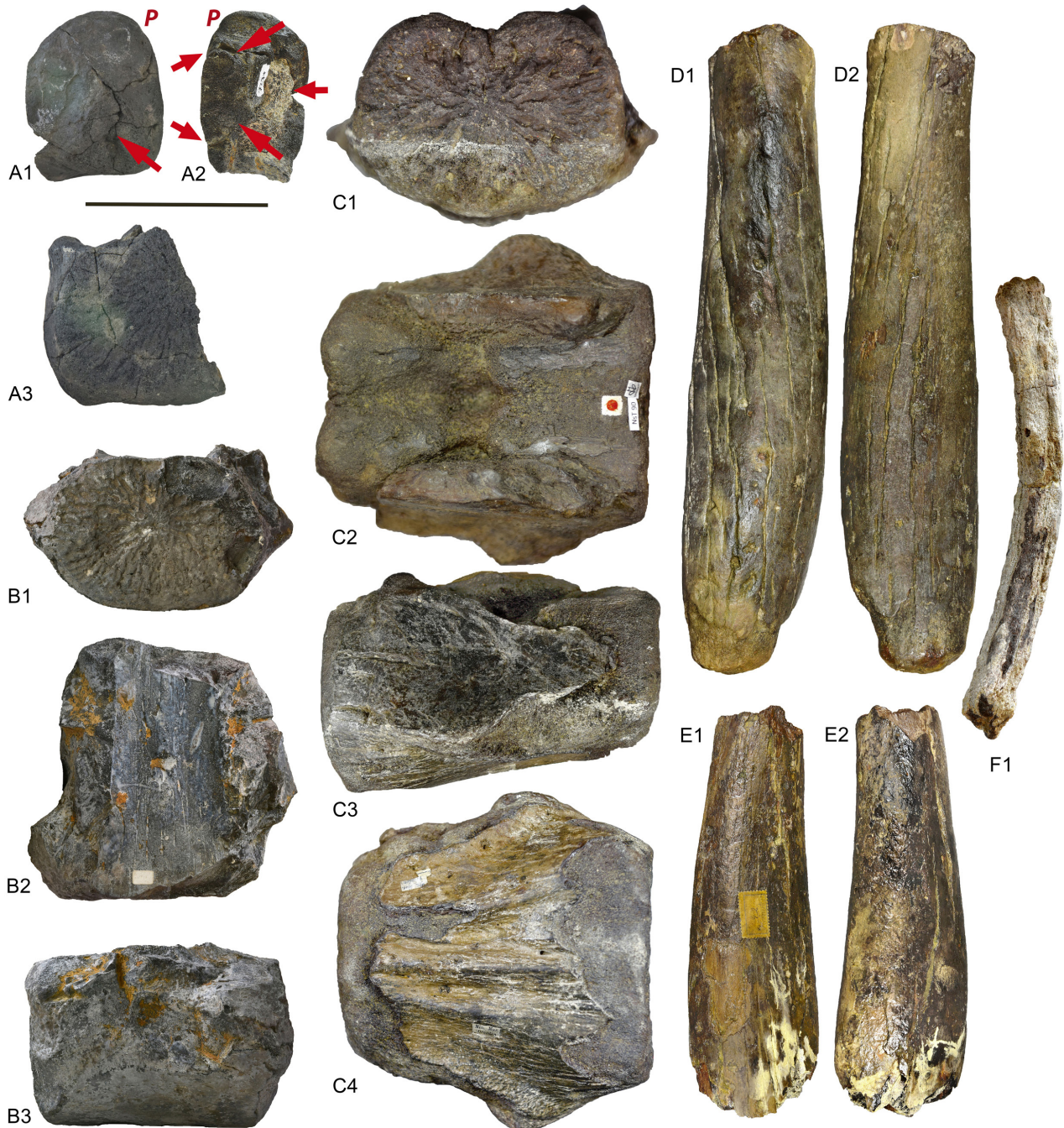


Plate 2. Posterior thoracic vertebral centra and rib fragments, *Pachycetus robustus* and Morphotype A, *Pachycetus* sp., from the Helmstedt region. A: central-posterior thoracic vertebral centrum, NMR999100151794, *Pachycetus* sp. (open cast mine Treue 3), in right lateral (A1), midsagittal (A2) and anterior (A3) view. Arrow in A1 indicates the cavity for the articulation of the rib; arrows in A2 indicate the dorso-ventral vascular system; 'p' in A1 and A2 indicates the right pedicle of the neural arch; B: posterior thoracic vertebral centrum, ID20-B, *Pachycetus* sp. (Alversdorf), in posterior (B1), dorsal (B2) and left lateral (B3) view; C: posterior thoracic, or anterior lumbar vertebral centrum, NsT90, *Pachycetus robustus* (Helmstedt), in anterior (C1), dorsal (C2), right lateral (C3) and ventral (C4) view; D: distal part of a right anterior rib, NsT92-A, *Pachycetus robustus* (Helmstedt), in postero-lateral (D1) and antero-medial (D2) view; E: distal part of a right anterior rib, NsT92-B, *Pachycetus* sp. (Helmstedt), in postero-lateral (E1) and antero-medial (E2) view; F1: rib fragment, NMR999100151797, *Pachycetus* sp. (open cast mine Treue 3). Scale bar 10 cm.

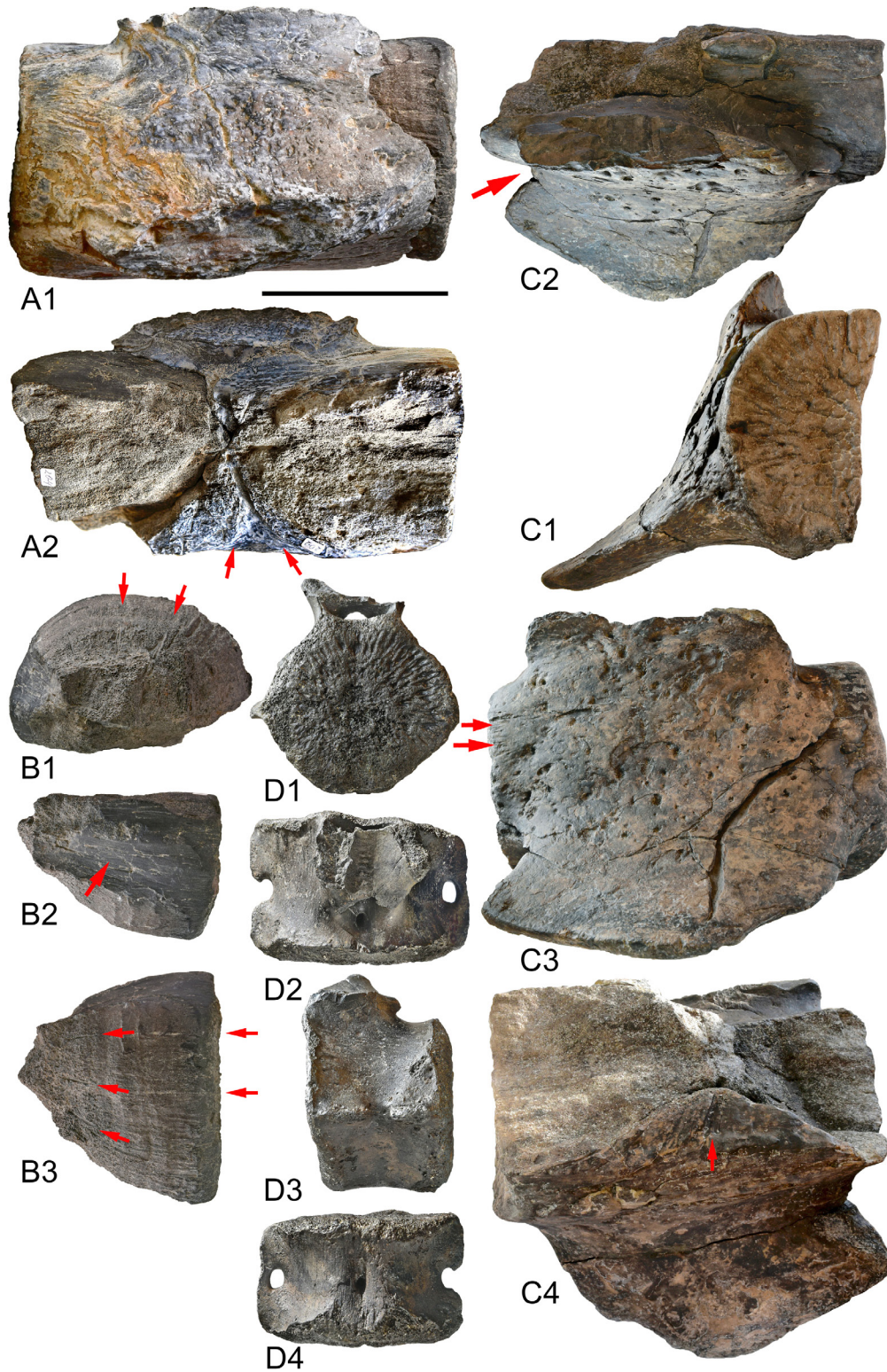


Plate 3. Lumbar vertebral centra and caudal vertebra, Morphotype A, *Pachycetus* sp., from the Helmstedt region. A: lumbar vertebral centrum, ID20-2 & ID20-4 (Alversdorf), in right lateral (A1) and midsagittal (A2) view. Arrow in A2 indicates the imprint of the ventral, fan-shaped, vascular canal; B: conus of lumbar vertebral centrum, ID 20-4, in anterior (B1), dorsal (B2) and right lateral (B3) view. Arrow in B2 indicates the flattened dorsal surface of the conus; arrows in B1 and B3 indicate the longitudinal vascular canals along the conus; C: lumbar vertebral centrum, NMR999100151795 (open cast mine Treue 3), in posterior (C1), dorsal (C2), left lateral (C3) and ventral-midsagittal (C4) view. Arrow in C2 indicates the anterior notch of the transverse process; arrows in C3 indicate the multiple longitudinal vascular canals in the compact cortex around the conus; arrow in C4 indicates the abraded imprint of the fan-shaped vascular canal; D: posterior caudal vertebra, NMR999100151796 (open cast mine Treue 3), in anterior (D1), dorsal (D2), left lateral (D3) and ventral (D4) view. Scale bar 10 cm.



Plate 4. Rostrum, probably Morphotype B, dental element, two cervical vertebrae and a rib fragment Morphotype B, indet. basilosaurid, from the Helmstedt region. Rostrum fragment, ID20-7 (Alversdorf), in dorsal (A1) and ventral (A2) view; B: Deciduous incisor (right ?dI3, dI1, or left ?dI1) ID24 (Alversdorf), A: in lingual (B1) and distal (B2) view. In B2, the labial (right) side of the root, but not the crown, has been retouched with Photoshop; C: cervical vertebra, Ce2, ID75-A (Alversdorf), in anterior (C1), posterior (C2) and dorsal (C3) view; D: cervical vertebra, Ce6, ID75-B (Alversdorf), in anterior (D1) and dorso-posterior (D2) view. Scale bar 5 cm; E: distal part of a rib, NsT37 (Runstedt), in ?antero-medial (E1) and ?posterior (E2) view, the latter showing the slightly thickened most distal part. Scale bar 5 cm.

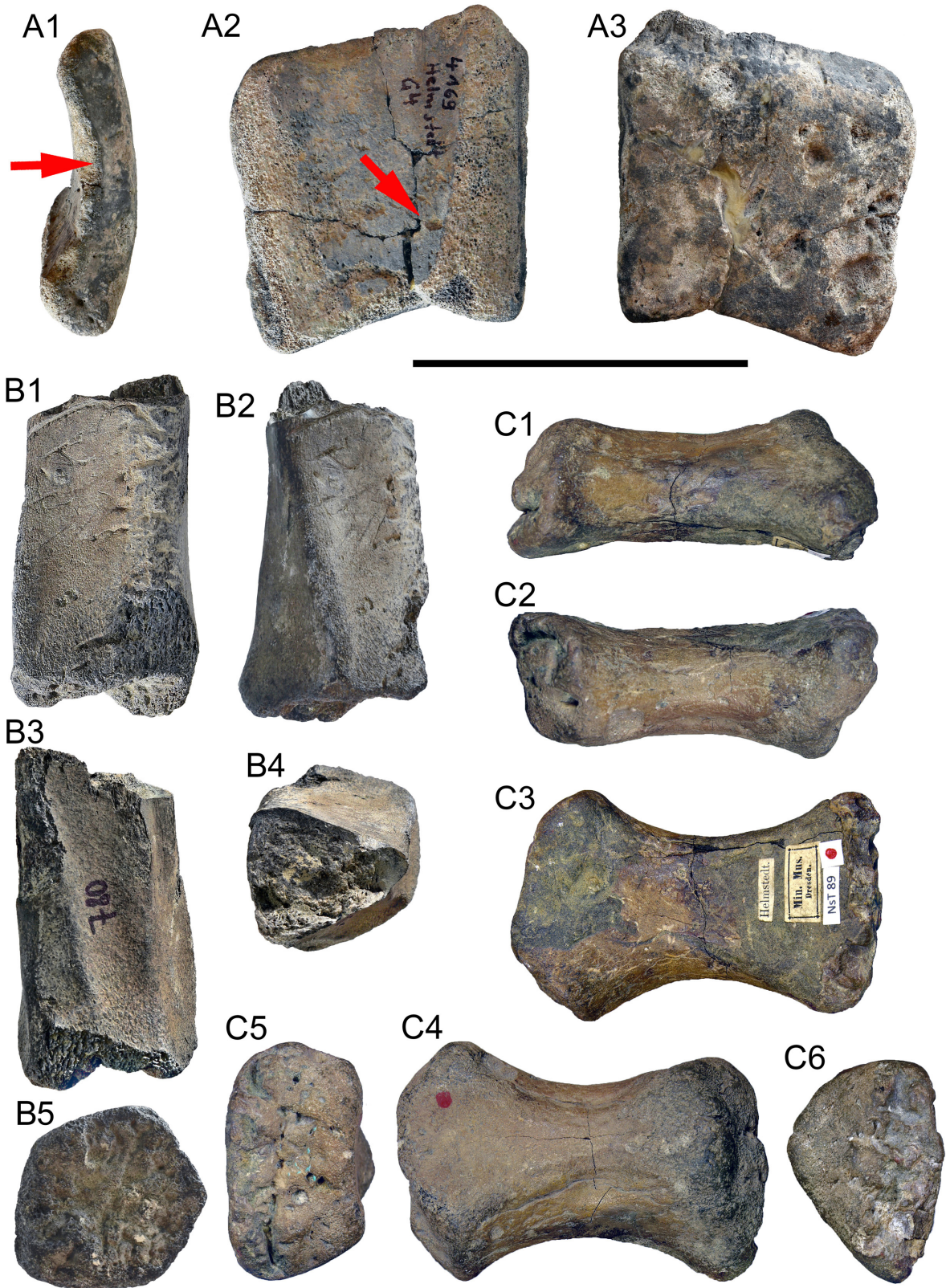


Plate 5. Cetacean skull fragment, a possible cetacean distal tibia fragment and a possible cetacean sternal element from the Helmstedt region. A: ?supraorbital process of the frontal, NMR999100151798 (open cast mine Treue 3), in lateral (A1), ventral (A2) and dorsal (A3) view. Arrow in A1 indicates the possible orbital crest; arrow in A2 indicates the possible fossa to the optic groove; B: distal tibia fragment (?Morphotype A, *Pachycetus* sp.), NMR999100151799 (Helmstedt), in medio-ventral (B1), medial (B2), dorsal (B3), proximal (B4) and distal (B5) view. C: possible distal sternal element (?Morphotype A, *Pachycetus* sp.), NsT89 (Runstedt), in ?right lateral (C1), ?left lateral (C2), ?dorsal (C3), ?ventral (C4), ?anterior (C5) and ?posterior (C6) view. Scale bar 10 cm.