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Bartoncetus wanklyni, new genus of a small dorudontine whale from the Bartonian of England; a lost skull and a forgotten postcranial skeleton

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ABSTRACT

Since 1913, the Bournemouth Natural Science Society has housed a partial postcranial skeleton, regarded as a small archaeocete whale from the Barton Clay Formation at Highcliffe and Barton-on-Sea, England. Despite being mentioned at least once in literature, it has never been thoroughly described. In 1876, Seeley described a small basilosaurid skull from the same location and formation, naming it *Zeuglodon wanklyni*; illustrations were not provided by him. Later, Kellogg (1936) reclassified it as *Zygorhiza wanklyni* Seeley, 1876. Unfortunately, the skull was lost soon after its discovery. Traditionally, small basilosaurid remains from Barton-on-Sea cliffs have been assigned to '*Zygorhiza*' *wanklyni*, but this name is now generally regarded a *nomen dubium*. The skeleton, newly described here, provides an opportunity for re-evaluation of this taxon. Both the skeleton and skull can be attributed to a juvenile, small dorudontine basilosaurid, apparently representing the same taxon, comparable in size to a juvenile *Dorudon atrox* Andrews, 1906. Based on several unique features, we establish a new genus, *Bartoncetus*. Similar remains have been discovered in the Helmstedt region of Germany, part of the same Eocene North Sea Basin, and possibly also in Varano, Italy. Based on dinocysts in the adhering sediments, the partial skeleton has been dated to 39.5 to 40.5 Ma, *i.e.*, during the middle Bartonian, the middle Eocene. This makes it one of the oldest, well-dated remains of a small dorudontine basilosaurid currently known.
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1. Introduction

Archaeocetes are early cetaceans, evolving from a terrestrial life to a life in water. Of the archaeocetes, the Basilosauridae represents the first family of whales that were fully adapted to an aquatic environment (Marx et al., 2014). They are known from maybe as early as the Lutetian until the late Priabonian, Eocene (Van Vliet et al., 2019, 2025). Members of this family show a large diversity, ranging from small (some Pachycetinae, some Dorudontinae) to large (Pachycetinae, Basilosaurinae and other Dorudontinae). Small dorudontine basilosaurids, having not-elongated vertebrae, are listed in Table 1. Remains of basilosaurids have been found around the whole world (Marx et al., 2014). In Europe, remains are rare and the fossils often are fragmentary (Van Vliet et al., 2019). Yet, basilosaurid fossils from Europe have been described as early as the second half of the nineteenth century; *Pachycetus paulsonii* was *e.g.,* described by Paulson (in Brandt, 1873) (Van Vliet et al., 2019). Another early described archaeocete is known from England: a skull that was first described by Seeley in 1876. It is one of the topics of this article. In 1872, this nearly complete, small basilosaurid skull was discovered by Mr Arthur Wanklyn in the Barton cliffs of southern England, near Barton-on-Sea. Unfortunately, during collection, the skull fell and broke when it tumbled from the cliffs. Wanklyn assembled the fragments and transported them to his residence. However, the skull was subsequently lost upon Wanklyn's death. The description of the fragments by Seeley (1876)

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Table 1
List of small dorudontine basilosaurids, presently known.

Small Dorudontinae
Ancalecetus simonsi Gingerich and Uhen, 1996
Chrysocetus fouadassii Gingerich and Zouhri, 2015
Chrysocetus healyorum Uhen and Gingerich, 2001
Dorudon atrox Andrews, 1906
Dorudon serratus Gibbes, 1845
Ocucajea picklingi Uhen et al., 2011
Saghacetus osiris Dames, 1894
Stromerius nidensis Gingerich, 2007
Supayacetus muizoni Uhen et al., 2011
Tutcetus rayanensis Antar et al., 2023
Zygorhiza kochii Reichenbach in Carus, 1847
'*Zygorhiza*' *juddi* Seeley, 1876
'*Zygorhiza*' *wanklyni* Seeley, 1881

was preliminary and without illustrations, yet detailed and based on his notes taken four years prior. Seeley (1876) assigned the skull to a new taxon, *Zeuglodon wanklyni*. Andrews (1907) commented on the skull's discovery in his description of a cervical vertebra, Ce6, NHMUK11090 from the same locality and horizon, attributing it 'without much doubt' to *Ze. wanklyni*. Kellogg (1936) later assigned the lost skull to the genus *Zygorhiza* (*Zy. wanklyni*) and referred Ce6, NHMUK11090 previously described by Andrews (1907), to the same taxon. Other rare and isolated remains of small basilosaurids from Barton-on-Sea have also traditionally been attributed to *Zy. wanklyni*, *e.g.,* the cervical vertebra Ce6, NHMUK11090 by Andrews (1907), the thoracic vertebra, NHMUK12346 by Halstead and Middleton (1972), and the here described postcranial skeleton, BNSS0777 by Hooker (1986), not to mention several finds posted on fossil forums. Uhen (1996a, 1996b, 1998) declared *Zy. wanklyni* a *nomen dubium*, although McLeod and Barnes (2008) still considered the taxon to be valid. Gingerich et al. (2022) suggested that the lost skull might be assignable to a species of *Pachycetus*.

The partial postcranial skeleton of a small dorudontine basilosaurid, BNSS0777, according to the labels assigned to *Zeuglodon wanklyni* Seeley, 1876 is housed in the Bournemouth Natural Science Society (BNSS). This skeleton is part of a fossil collection from the cliffs at Barton-on-Sea, amassed by Mrs Susan Juliana Maria Hamilton Dent (1838–1913). Her nephew, Mr Henry Montague Hamilton Dent (1875–1958), inherited and expanded the collection. The Bournemouth Natural Science Society acquired the entire collection in 1913 for the sum of £118 (accession number 1913/3). Andrews (1907) noted that a local collector had sold 'some associated vertebrae to casual visitors to Barton', hoping this find would emerge for further scientific investigation. This might be the first official mention of BNSS0777. As seen above, Hooker (1986) briefly mentioned the partial skeleton, noting that '*about two dozen associated vertebrae*' are held by the Bournemouth Natural Science Society. This significant find has not been described previously and is critical in order to clarify the validity of the taxon '*Zy.*' *wanklyni* (Fig. 1).

The thoracic vertebra and an epiphyseal disc fragment, NHMUK 12346, mentioned above, could originally have been part of BNSS0777, as will be discussed. According to the label, they were donated by Mr R. Egerton-Godwin to the Natural History Museum in London in 1923, 10 years after BNSS0777 was sold to the Bournemouth Museum. Without doubt this is Robert Egerton Godwin (1884–1961), whose sister and later also his mother lived in Barton-on-Sea. He was a collector of prehistoric artefacts and discoverer of a hoard of Roman coins (Hobbs, 2021). Jeremy Hooker (pers. comm., October 24, 2024) pointed out, that also the postcranial skeleton BNSS0777 could have been discovered by Godwin, the 'local collector' mentioned by Andrews (1907) who, after selling most of it to Mrs Hamilton Dent, kept the vertebra and epiphyseal disc (NHMUK12346) for himself until donating it to the NHM in London.

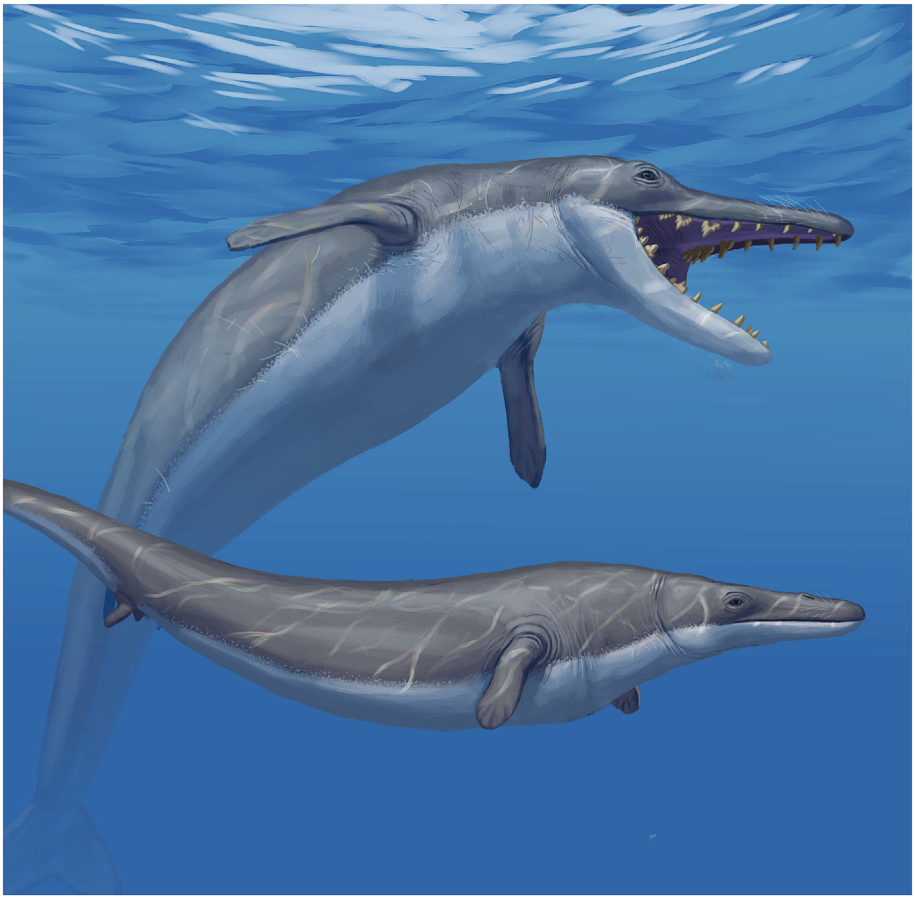


Fig. 1. Palaeoart reconstruction of the living *Bartoncetus wanklyni* (Seeley, 1876), gen. et comb. nov. by Jonas Hakkens.

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2. Material and methods

2.1. Aims

Aims of this study are to describe the partial, postcranial skeleton BNSS0777, to investigate possible connections with the lost skull of *'Zy.' wanklyni* and in addition to evaluate the finds of small dorudontine remains from England and other parts of western Europe.

We made the following two working assumptions:

a) We argue that the lost skull, found by Mr Wanklyn and described by Seeley (1876) and the partial, postcranial skeleton, BNSS0777 from the collection of Mrs Dent and described in this paper belong to the same taxon.
b) We hypothesise that the lost skull and the partial, postcranial skeleton, BNSS0777 probably belong to the same individual, a juvenile dorudontine archaeocete.

For testing these working assumptions both the partial, postcranial skeleton, BNSS0777 and the lost skull are analysed. With the first assumption, if proven, we can establish the validity of the old name *'Zygorhiza' wanklyni* Seeley, 1876 again, here to be named *Bartoncetus wanklyni* (Seeley, 1876) gen. et comb. nov., for which we chose a neotype. With the second assumption, if proven, we can declare BNSS077 the syntype of *Bartoncetus wanklyni* (Seeley, 1876) gen. et comb. nov.

2.2. Methods

After inventorying, fragments of vertebrae that fitted together were glued with acrylic glue dissolved in acetone. We measured all specimens, using a digital calliper. Images were taken with a Nikon D810 camera and an iPhone 14 Pro Max.

2.2.1. Calculations

The relative length of a vertebral centrum is calculated by the dorsal anteroposterior length to anterior width ratio: relative length = L / dWa; in Ce2, the posterior width is used: relative length = Ld / Wp. Because the epiphyses are lacking in nearly all vertebral centra, the given relative length will be an underestimation. The relative width of a vertebral centrum is calculated by the width to height ratio: relative width = W / H and, when known, by the anterior width to anterior height ratio: relative width = Wa / Ha.

2.2.2. Palynological analysis

The investigation of the geological age of the studied specimen relies on the analysis of organic-walled dinoflagellate cysts (dinocysts) which are retrieved from the attached sedimentary material of the currently examined skeleton. Dinocysts are resistant capsules (cysts), which are, as part of a complex life-cycle, produced by dinoflagellates, a group of unicellular eukaryotic algae, belonging to the clade Alveolata within the domain Eukaryota according to most investigators (Fensome and Munsterman, 2026). The present sample was processed for palynology by Nico Janssen (TNO) using the facilities of Utrecht University and Geological Survey of the Netherlands. During a standard chemical process, 35% hydrochloric acid and 30% hydrofluoric acid were used for carbonate and silicate digestion respectively (Janssen and Dammers, 2008). The resultant kerogens were sieved over a 10 μm mesh. The microscopic slides were mounted in glycerine-jelly and sealed with a cover slip.

The microscopy analysis was carried out according to standard procedures. The palynomorph association on the slides is counted, using a Leica microscope magnification of 500×, until a total of *ca.,* 200 sporomorphs (spores and pollen) and dinoflagellate cysts is reached. The miscellaneous categories (*Botryococcus*, inner chambers of foraminifers, *Tasmanaceae*, *etc.*) were also calculated but kept outside the total sum of palynomorphs. The remainder of the slide is thereafter scanned for any (rare) dinocyst species which are simply noted as 'present' (+ symbol on the distribution chart). Diagnostic species are discussed in the text, and a complete distribution chart including all species found is given in Appendix Figure A.

The so-called 'Lentin and Williams' index was followed for the dinoflagellate cyst taxonomy (Fensome et al., 2019). The age interpretation is based on the 'Last Occurrence Datum' (LOD: extinction) and 'First Occurrence Datum' (FOD: origination) of dinoflagellate cysts, which are calibrated to the geological time. Palynological interpretation is based on key-references concerning the palynostratigraphy of the Paleogene from the North Sea region such as: Bujak et al. (1980), Heilmann-Clausen (1985), Powell (1992), Bujak and Mudge (1994), Köthe (2003), Eldrett et al. (2004), Van Simaeys et al. (2005) and Iakovleva (2024). The standard dinocyst zonation used for the Eocene is from Bujak and Mudge (1994).

2.3. Terminology

We follow Uhen (2004) and Martínez-Cáceres et al. (2017) for anatomical terms.

2.4. Institutional abbreviations

BNSS, Bournemouth Natural Science Society; **BGS**, British Geological Survey; **CGM**, Cairo Geological Museum, Cairo, Egypt; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **FSAC Bouj**, Faculté des Sciences Ain Chock, Boujdour collection, Université Hassan-II de Casablanca, Morocco; **GMTSNUK**, Geological Museum of Taras Shevchenko National University of Kiev, Ukraine; **GPIM**, Geologisch-Paläontologisches Institut Mainz, Paläontologie (Institut für Geowissenschaften der Johannes Gutenberg-Universität Mainz, Germany); **GSM**, Georgia Southern Museum, Statesboro, Georgia; **GSP-UM**, Geological Survey of Pakistan–University of Michigan collection, Quetta, Balochistan; **HNS**, Haus der Natur Salzburg, Austria; **KPG-M**, Laboratoire de Paléontologie, Institut des Sciences de l'Evolution, Université de Montpellier II—Sciences et Techniques du Languedoc, (France); **MMGD NsT**, Museum für Mineralogie und Geologie Dresden, Niedersachsen Tertiär, Senckenberg Naturhistorische Sammlungen, Dresden, Germany; **NMNH-P**, Paleontological Museum, National Natural History Museum of the Academy of Sciences of Ukraine, Kiev, Ukraine; **NHMUK**, Natural History Museum, London, England; **RGM**, Naturalis Biodiversity Center, Leiden, the Netherlands; **SCSM**, South Carolina State Museum, Columbia, South Carolina; **SMNS**, Staatliches Museum für Naturkunde in Stuttgart (State Museum of Natural History in Stuttgart), Germany; **TM**, Teyler's Museum, Haarlem, the Netherlands; **UMMP**, University of Michigan Museum of Paleontology, Ann Arbor, Michigan; **USNM**, United States National Museum of Natural History, Washington DC.

2.4.1. Anatomical abbreviations

afa, articulation facet with the atlas; **alv**, alveolus; **ant**, anterior; **C**, upper canine; **CBL**, condylobasal length; **Cd**, caudal vertebra; **Ce**, cervical vertebra; **Cr**, crown; **DD**, deciduous dentition; **di**, deciduous lower incisor; **dI**, deciduous upper incisor; **dia**, diapophysis; **dors**, dorsal; **dPm**, deciduous upper premolar; **fragm**, fragment; **fragms**, fragments; **H**, height; **Ha**, anterior height; **I**, upper incisor; **ID**, identification number; **Le**, left; **L**, length; **Ld**, dorsal length; **Lu**, lumbar vertebra; **Lv**, ventral length; **m**, lower molar; **M**, upper molar; **max**, maximum; **me**, mean; **mesio-dist**, mesiodistal; **NA**, neural arch; **par**, parapophysis; **PD**, permanent dentition; **pm**, lower premolar; **Pm**, upper premolar; **prz**, prezygapophsis; **post**, posterior; **poz**, postzygapophysis; **RBC**, rostrum breadth at the canines; **Ri**, right; **rel L**, relative length; **rel W**, relative width; **Th**, thoracic vertebra; **trp**, transverse process; **vef**, vertebrarterial foramen; **ventr**, ventral; **vert.**, vertebra; **verts.**, vertebrae; **W**, width; **Wa**, anterior width; **Wp**, posterior width; **?**, unknown; /, fraction; >, more than; >>, far more than; <, less than.

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3. Geological setting

Eocene strata are present in a large area of Hampshire and the Isle of Wight in southern England, known as the Hampshire Basin (Fig. 2). In fact, this basin is part of a much larger Tertiary syncline, the Hampshire–Dieppe Basin in the eastern part of the Channel between present-day England and France. To the southwest it is bordered by a line from Bembridge on the Isle of Wight, England to St Valéry-en-Caux in the Normandy region, France, to the northeast by the Weald–Artois Anticline (Curry and Smith, 1975; Smith and Curry, 1975). Sediments of the Eocene Barton Group are exposed in the cliffs between Highcliffe and Barton-on-Sea, Hampshire, England in a rather small area: nowadays 850 m in length, but in the past, before sea-defences had been made, maximum less than 3.0 km in length (West, 2020, figure 'Barton, Highcliffe and Hordle - Cliff Section'). It is the type section of the Bartonian Stage (BGS, British Geological Survey, Barton Clay Formation). The Barton Group consists of three formations, the Barton Clay Formation, overlain by the Chama Sand Formation and the Becton Sand Formation. The Barton Clay Formation is about 38 to 83 m thick and uppermost Lutetian to Bartonian in age, ranging from 38.4 to 41.5 Ma (King, 2016, fig. 72). A bed of flint pebbles marks the base of the Barton Clay Formation. Burton (1933) recognised 14 units in the Barton Group, each named by a letter (A–L). Much attention has been given to a layer with nummulites, the *Nummulites prestwichianus* bed about 14 m above the bed with flint pebbles (Prestwich, 1857; Keeping, 1887). Fluegeman (2014) proposed the base of the Bartonian Stage to begin at the *N. prestwichianus* bed, which is in C18r. Nowadays the base of the Bartonian Stage is considered somewhat lower, at the top of C19n, 41.3 Ma, ending within C17n.2n, 37.71 Ma (Fig. 3). For a detailed historical review of attempts to define the Barton Group, see Hooker (1986). The stratigraphy of most archaeocete finds was not provided by their collectors, but it is supposed that they were derived from Beds B–D in the Bartonian part of the Barton Clay Formation (Fig. 3A), because of the presence of abundant grains of glauconite in the adhering matrix (Hooker, 1986). Lenses of granular glauconite are present in the lower part of Bed E too (Hooker, *pers. comm.*, October 17, 2024). Also, the grey clay adhering to some of the bones of BNSS0777 contains abundant glauconite.

4. Results

4.1. Systematic palaeontology

Cetacea Brisson, 1762
Pelagiceti Uhen, 2008
Basilosauridae Cope, 1868
Bartoncetus gen. nov.

Type and only included species: *Bartoncetus wanklyni* (Seeley, 1876) gen. et comb. nov.

Etymology. Barton from the locality Barton-on-Sea where the material, presently described, has been found. 'Barton' in Barton-on-Sea, meaning Beorma's Farm from 'Beorma', personal name and 'ton' from 'tun' (Old English), enclosure. 'Cetus' from 'ketos' (Greek), latinised to 'cetus', meaning large sea animal or whale.

***Bartoncetus wanklyni* (Seeley, 1876) new combination**

Nomenclatural act. This published work and the nomenclatural act it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix https://zoobank.org/. The LSID for this publication is: C1C46C72-9186-4EA6-8AA8-576166043B76.

Synonymy.
Zeuglodon wanklyni (Seeley, 1876, 428–432)
Zygorhiza wanklyni (Kellogg, 1936, 174–176)
'*Zygorhiza*' *wanklyni* (see Uhen, 1996a, 1996b, 403; Uhen, 1998, 38)

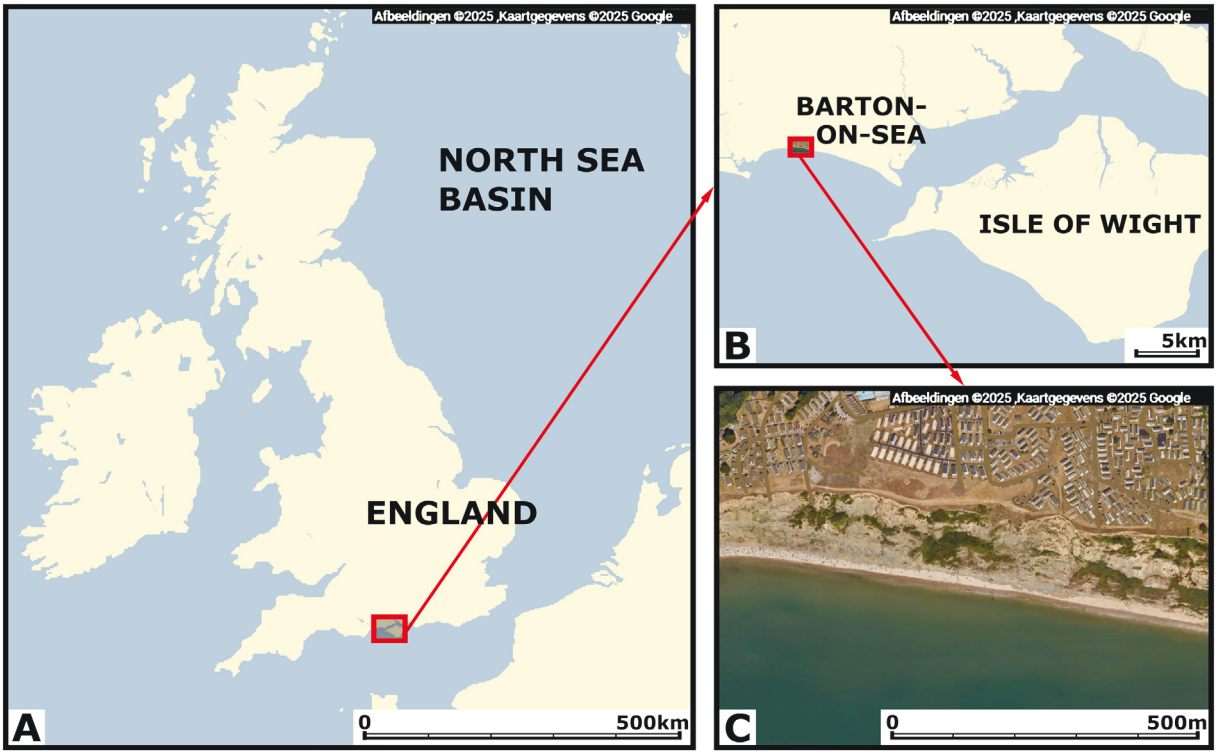


Fig. 2. Barton-on-Sea, England, the place where BNSS0777 has been found. A. Map of England. B. Map, showing the location of Barton-on-Sea, England. C. Cliffs between Highcliffe and Barton-on-Sea, showing the outcropping of the Barton Clay Formation in aerial view.
A–C: Modified after Google Maps.

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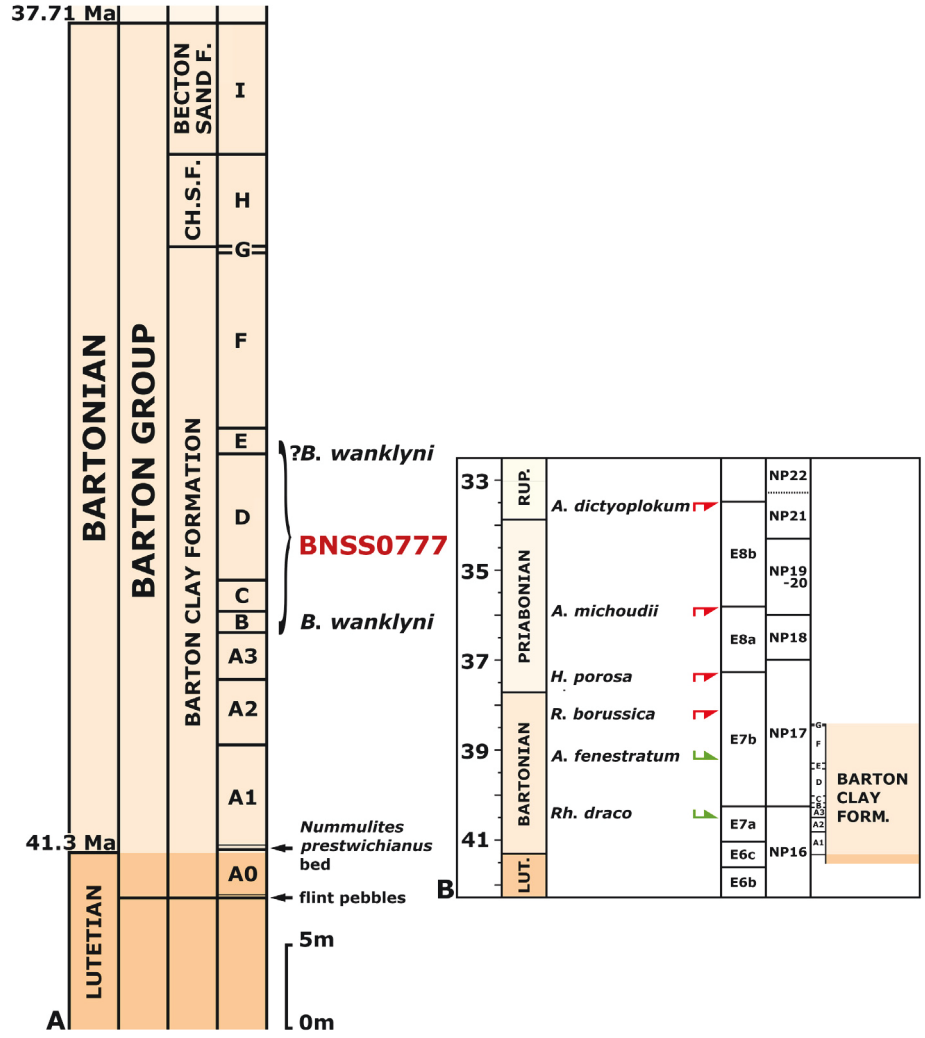


Fig. 3. Section of the early Eocene strata in Christchurch Bay, England and the distribution of dinocysts, as encountered in BNSS0777. A. Section of the Barton Clay Formation: stratigraphy of the Lutetian and Bartonian sediments in Christchurch Bay, England. Strata with finds of small dorudontine archaeocetes are indicated with braces. Modified after Hooker (1986, text-figure 2) and information from the British Geological Survey, Barton Clay Formation (https://webapps.bgs.ac.uk/lexicon/lexicon.cfm?pub=BAC). B. Section of the Barton Clay Formation correlated with age-diagnostic dinoflagellates in the sediments adhering to BNSS0777. Based on Bujak and Mudge (1994) (dinoflagellate cysts), Eldrett et al. (2004) (polarity zones), adjusted to the Geologic Time Scale 2020, Gradstein et al. (2020). Age of the Barton Clay Formation ranging from approximately midway Chron19r (41.4 Ma) to the earliest part of Chron17r (38.4 Ma) (King, 2016, fig. 72). Lut., Lutetian; Rup., Rupelian; *A. dictyoplokum*, *Areosphaeridium dictyoplokum*; *A. fenestratum*, *Areosphaeridium fenestratum*; *A. michoudii*, *Areosphaeridium michoudii*; *H. porosa*, *Heteraulacacysta porosa*; *R. borussica*, *Rottnestia borussica*; *Rh. draco*, *Rhombodinium draco*. Down-left elbow arrows indicate the last occurrence datum (LOD), and up-left elbow arrows indicate the first occurrence datum (FOD) of the dinocyst taxa.

Holotype. Skull (lost); without ID (Seeley, 1876).

Neotype. A series of associated vertebrae, BNSS0777.

Type locality. Barton-on-Sea, cliffs between Highcliffe and Barton-on-Sea. Stratigraphy: Barton Clay Formation, type stratum from Bed B to the lower part of E. According to R. Chapman (pers. comm.) the skeleton has been derived from Bed D, just above a horizon with septaria.

Stratigraphical age and distribution. Bartonian, Middle Eocene of England, as well as possibly the Bartonian and Priabonian, Middle–Late Eocene of Germany and Italy.

Referred specimens. A cervical vertebra 6 (Ce6), (NHMUK11090); thoracic vertebra (Th7 or 8, NHMUK12346); presumably posterior thoracic vertebra (NHMUK60000), all from the same locality and formation.

Diagnosis. *Bartoncetus wanklyni* (Seeley, 1876) gen. et comb. nov. is characterised by the following unique combination of features. Small basilosaurid with premolars that are larger than permanent premolars of *Tutcetus rayanensis* Antar et al., 2023 and *Antaecetus aithai* Gingerich and Zouhri, 2015 and have more and also crenulated denticles. The widths and mesiodistal lengths of the alveoli of the upper dC1 and dPm1, and of the cheek teeth of dPm2–3 (and probably dPm4) of *B. wanklyni* are similar to the mesiodistal lengths of the upper dC1 respectively the dPm1–4 in the small dorudontines *Dorudon atrox* and *Dorudon serratus* (specimen USMN16638). A presumed upper dI has wrinkled enamel, with about 12 short, vertical irregular folds at both sides near the base of the crown, with fine striae on the root, and with faint ridges, not seen in deciduous upper incisors of *D. atrox*. The upper dPm2–3 have a cingulum and longitudinal striae at the lingual sides. The upper dPm2 has four mesial and distal denticles, different from *D. atrox* in which dPm2 has two mesial and three distal denticles and different from *D. serratus* in which dPm2 has two mesial and two distal denticles. Most probably also the upper dPm3 has four mesial and distal denticles, different from *D. serratus* in which dPm3 has three mesial and two distal denticles, but similar to *D. atrox* in which dPm3 has three to four mesial and four distal denticles. Denticles of upper dPm2–3 are faintly crenulated, not seen in other small dorudontine basilosaurids.

Cervical vertebrae Ce3–7 are smaller in length than those of Protocetidae and Pachycetinae; the torso vertebrae are not-elongated, contrary to those of Protocetidae and small Pachycetinae. The cervical vertebrae Ce2, BNSS0777 (with fused epiphyses) and Ce6, NHMUK11090 (with fused posterior epiphysis) and the posterior

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thoracic or lumbar vertebra, NHMUk60000 (without epiphyses) have nearly fully grown or subadult dimensions which are larger than dimensions of comparable vertebrae of a fully grown *Saghacetus osiris* Dames, 1894, *Chrysocetus fouadassii* Gingerich and Zouhri, 2015 and *Stromerius nidensis* Gingerich, 2007 and are comparable to those of a juvenile to subadult *Chr. haelyorum* Uhen and Gingerich, 2001, or a small fully grown *Dorudon atrox* and *Zy. kochii*, and most probably smaller than those of a juvenile '*Zy.*' *juddi* Seeley, 1881. Ce2 has dorsoventrally long articulation facets for the atlas, that are larger than in *D. atrox* or *Chr. haelyorum* and a neural spine that is shorter than in Ce2 of *Chr. healyorum*. The transverse processes are dorsoventrally small, with a distance between diapophysis and parapophysis of 11.5 mm, smaller than seen in *D. atrox*; the parapophyses are positioned more dorsally and the diapophyses are smaller than the parapophyses. Ce6 has an oval-shaped centrum, not seen in other small dorudontine basilosaurids, except *D. serratus* and has vertebrarterial foramina smaller than those of *Zygorhiza kochii*. The prezygapophyses are directed slightly more dorsally, than seen in Ce6 of *D. atrox*. The parapophyses are comparable to those of *D. atrox*. The thoracic vertebrae have thick onsets of the pedicles of the neural arch, indicative of pachyostosis, not seen in other small dorudontine basilosaurids. The thoracic vertebrae have ventral foramina from Th5 onwards.

Material. A skull (lost). A cervical vertebra 6 (Ce6), NHMUK11090. A partial, postcranial skeleton, comprising a collection of 78 bones, registered as a single lot (BNSS0777), mostly vertebrae and vertebral fragments: 7 cervical vertebral centra and fragments; 5 thoracic vertebral centra and 14 fragmentary vertebral centra; 18 epiphyses and epiphyseal fragments; 6 neural arches and fragments; 26 fragments of vertebral processes; one post-cervical vertebral fragment with a fused epiphysis; and one rib fragment. The total number of bones and bone fragments presently differs from that on the labels (118), because 40 fragments could be reassembled (Fig. 4). Vertebral dimensions are listed in Appendix Table A.1 (Fig. 3).

Curation information. Attached to the postcranial skeleton BNSS0777: four labels with the following texts: *Zeuglodon wanklyni*. An axis (0777/a1); four vertebral centra (0777/b4); 50 pieces of vertebral centra (0777/c50); 26 neural arches, spines, or dorsal processes (0777/d26); and 37 epiphyses (0777/e37). Middle Barton Beds. Barton, Hants. Dent Collection. One label with the text: 'NB Upper Barton Beds, not Middle'. See Figure 4.

Comments. Although the holotype of *Zeuglodon wanklyni* Seeley, 1876 is lost and no illustrations have been provided, the species name is considered valid for the following reasons: (a) It was published before 1931; (b) the original description by Seeley (1876) was made from direct observations of the skull in 1872; (c) since then the name has been in use for the remains of small basilosaurids from the Barton Clay Formation of Barton-on-Sea, England until now; (d) it proved to be sufficient for determining diagnostic features; and (e) a vertebra, Ce6 (NHMUK11090) with diagnostic features was published by Andrews (1907) and referred to this taxon. Kellogg (1936) referred the skull and the vertebra Ce6 (NHMUK11090) to the genus *Zygorhiza* True, 1908 as *Zygorhiza wanklyni*. The here described partial skeleton BNS0777 and the skull are assigned to the same, small dorudontine taxon as will be discussed; Ce6, BNSS0777 indicates that Ce6, NHMUK11090 indeed also belongs to this taxon. We here follow Godfrey and Lambert (2023), who retained the names of some Miocene odontocete taxa (*Phocageneus venustus* Leidy, 1869 and *Zarhachis flagellator* Cope, 1868) in comparable cases, and retain the species name *wanklyni*, but shall change the genus *Zygorhiza*, given by Kellogg (1936) for reasons described in this paper. Both the lost skull and BNSS0777 have diagnostic characteristics, which differ from other small dorudontine taxa known. We believe that it is necessary to designate a neotype for this taxon and to declare BNSS0777 this neotype, in order to clarify the validity of this taxon.

Description. For the description of the skull, see Seeley (1876) and for Ce6, NHMUK11090, see Andrews (1907); for the latter, some remarks are added in the section '*other finds from England*'.

The partial skeleton BNSS0777 comprises the anterior region of the vertebral column: the cervical region, minus Ce1, probably most of the entire thoracic, a part of the lumbar region, and at least one caudal vertebra. The anterior part of the vertebral column (the cervical and anterior thoracic region) is better preserved than the posterior part.

Cervical region. Five cervical vertebral centra, numbered vertebrae A–F (Ce2–'3', Ce'5', Ce6–7); four fragments, one attributed to Ce'4'. The pedicles of the neural arches are fused with the centra, contrary to what is seen in the post-cervical vertebral centra. Ce'3'–'5' have quotation marks, because the position is not completely certain.

Vertebra A, the axis, is exquisitely preserved. The neural canal is heart-shaped. The dens is fused with the centrum and the posterior epiphysis is partly fused. The vertebra has posteriorly two rather large postzygapophyses. The articulation surfaces for the atlas are half-moon shaped and protrude laterally. The posterior surface of the centrum is more or less octagonal and concave. A vertebrarterial foramen, about 14 mm in (dorsoventral) length and 6 mm in width, is present on both lateral sides at the base of the transverse process. The foramina pierce the small transverse processes beneath the protruding articulation surfaces with the atlas. The transverse processes are short; anteriorly they are hidden by the articulation surfaces for the atlas. There is a thin ventral median keel (Fig. 4, vert. A; Fig. 5A1–3).

Vertebra B is broken into two parts. The centrum is oval-shaped. Due to damage, the transverse processes and the neural arch are lacking. The epiphyseal ridges are rather shallow. The length and relative length are larger than that of Ce'4' and Ce'5' and, because this is also the case in cervical vertebrae of *D. atrox* (Uhen, 2004, appendix V), it is tentatively assigned to Ce'3' (Fig. 4, vert. B; Fig. 5B).

Vertebra C is a single, small fragment of a vertebral centrum. Due to damage, the transverse processes and the neural arch are lacking. In the preserved part, the epiphyses are fused with the centrum. The length is smaller than that of Ce'3' and larger than that of Ce'5', and because this is also the case in cervical vertebrae of *D. atrox* (Uhen, 2004, appendix V), it is tentatively assigned to Ce'4' (Fig. 4, vert. C; Fig. 5C).

Vertebra D is broken into four parts. The centrum is oval-shaped. Due to damage, the transverse processes and the neural arch are lacking.



Fig. 4. Assembled vertebrae of the partial, postcranial skeleton of '*Zygorhiza*' *wanklyni* Seeley, 1876, BNSS0777, from the Bartonian of Barton-on-Sea, England. Cervical vertebrae: vertebrae A–F. Thoracic, lumbar and caudal vertebrae: vertebrae G–W, positioned according their length (increasing from left to right). Vertebra X, Th'8', NHMUK12346 is figured beneath the vertebral column, BNSS0777 and the arrow indicates the probable position in the column. Scale bar is 50 mm.

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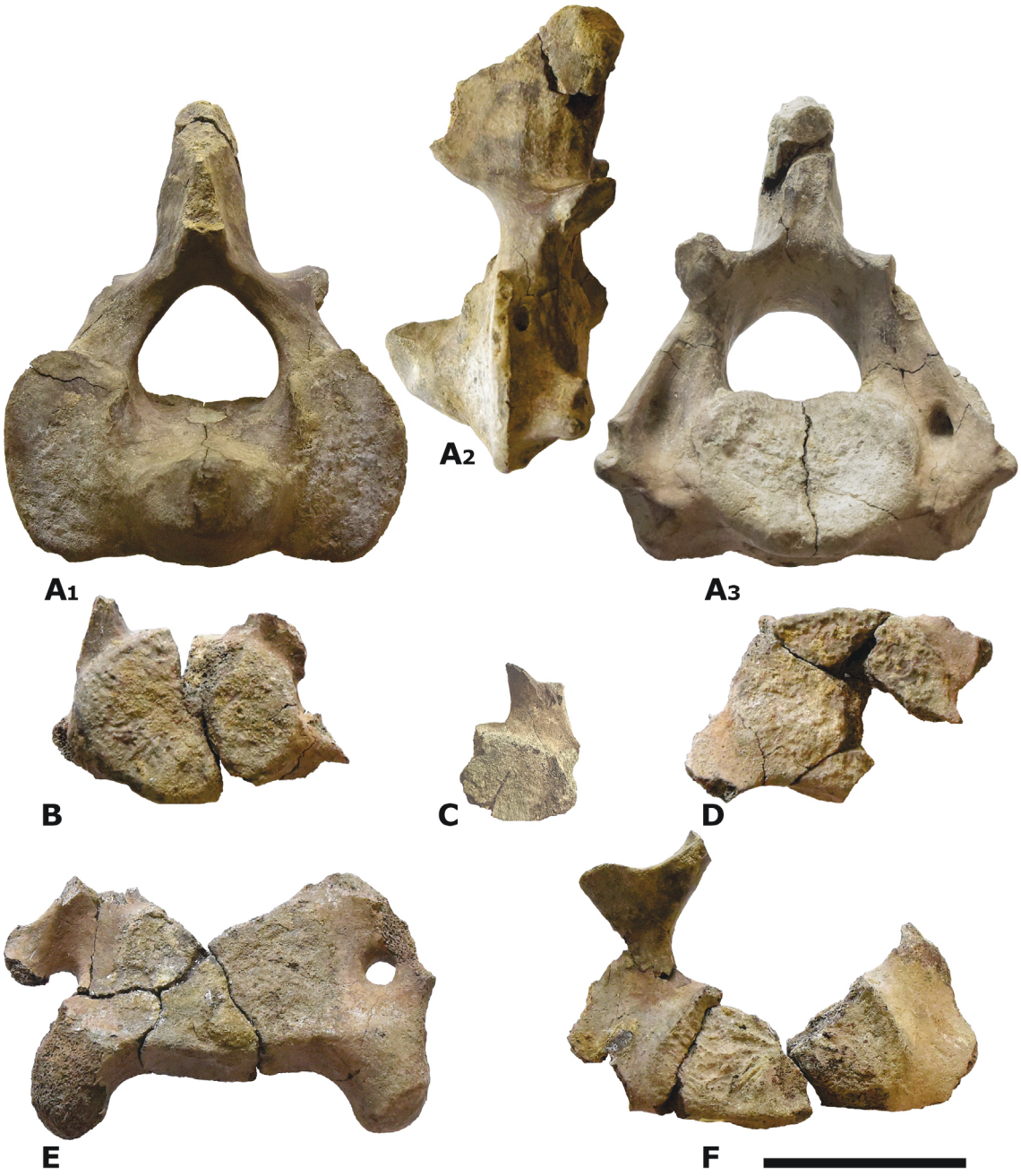


Fig. 5. Cervical vertebrae, vertebrae A–F (Ce2, Ce'3'–'5', Ce6–7), '*Zygorhiza*' *wanklyni* Seeley, 1876, BNSS0777, from the Bartonian of Barton-on-Sea, England. A1–3. Vertebra A (Ce2) in anterior (A1), in left lateral (A2) and in posterior (A3) view. B. Vertebra B (Ce'3') in anterior view. C. Vertebra C (Ce'4') in anterior view. D. Vertebra D (Ce'5') in anterior view. E. Vertebra E (Ce6) in anterior view. F. Vertebra F (Ce7) in anterior view. Ce'3'–'5' in quotation marks, because the position is not completely certain. Scale bar is 50 mm.

The epiphyseal ridges are rather shallow. The length and relative length are smaller than those of Ce'3' and Ce'4', and because this is also the case in cervical vertebrae of *D. atrox* (Uhen, 2004, appendix V), it is tentatively assigned to Ce'5' (Fig. 4, vert. D; Fig. 5D).

Vertebra E, Ce6, is broken into four parts; a part at the dorsal side is missing. The centrum is oval-shaped. The neural arch is missing. The epiphyses are partly fused with the centrum. The transverse processes are directed slightly anteriorly. Between the diapophysis and parapophysis of the transverse processes is a notch (better observed in the more completely preserved Ce6, NHMUK11090; see below). The diapophyses are missing the most lateral ends. The right vertebrarterial foramen is well-preserved; it is oval-shaped and is anteriorly 7.8 mm in (dorsoventral) length and 7.2 mm in width. There are two small ventral foramina, one to the right and one to the left of a thin median ridge. The parapophyses are robust; they are both broken, missing the tip of the process. They are also oriented slightly anteriorly (Fig. 4, vert. E; Fig. 5E).

Vertebra F, Ce7, is broken into four parts. The right part of the neural arch is present. There are traces of initiating epiphyseal fusion. The left vertebrarterial foramen is absent (Fig. 4, vert. F; Fig. 5F; Appendix Table A.1).

Post-cervical region. A series of at least 17 separate vertebral centra is present, eight of them are fragmentary. The vertebrae are ordered in increasing vertebral length and numbered vertebrae G–W (Fig. 4).

Vertebrae G–K (Th'1'–'5') are the anteriormost thoracic vertebral centra. They have a complete centrum and are heart-shaped in anterior and posterior view. The epiphyses and pedicles of the neural arches are not yet fused with these centra. These sutures have a surface of irregular ridges at the places of future fusion, indicating the former presence of

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cartilage. The onsets of the pedicles of the neural arches are remarkably thick, ranging between 21.8 mm (due to damage) and 29.8 mm with a median value of 25 mm. Dorsally, vertebra G (Th'1') has two large foramina, separated by a very thin median ridge. Each of these foramina consists of at least four confluent vascular canals. Vertebrae H–K (Th'2'–'5') have three (vert. H, Th'2') to five (vert. K, Th'5') dorsal foramina positioned on the right side and two on the left side of a thin median ridge. They are accompanied by several smaller foramina located more anteriorly and posteriorly. On the upper lateral sides, the five anteriormost centra have foveae for the ribs. Except for some small foramina, randomly scattered on the ventral surface, no ventral foramina near the midline are seen in vertebrae G–J (Th'1'–'4'). Vertebra K (Th'5') has small ventral foramina, as well as multiple small foramina near the epiphyseal sides. A ventral median ridge is absent. Vertebra I (Th'3') has a surface of whitish dust, which is ascribed to corrosion or degradation; when cleaned, the surface becomes black. Th'1'–'5' are in quotation marks, because the position is not completely certain (Fig. 4, verts. G–K; Fig. 6A1–2; Appendix Table A.2).

The dorsal sides of vertebrae L–W show damage and the thickness of the onsets of the pedicles cannot be measured in most of them. Epiphyses are lacking in all vertebrae, except for vertebra W. Vertebrae M (Th'7') has four or five dorsal foramina positioned on the right side and two on the left side, all obscured by matrix; the median ridge is absent due to breakage. In vertebrae M, N, O, Q and R the neural arch certainly is not fused with the vertebral centrum. Vertebra Q (Th'11') has at least two dorsal foramina plus two additional foramina positioned on the right side and at least one on the left side; the median ridge is absent due to breakage. Vertebra P has two ventral foramina, each positioned on one side of a thin median ridge. There are multiple smaller foramina, scattered on the surface near the two epiphyseal sides. The onset of a

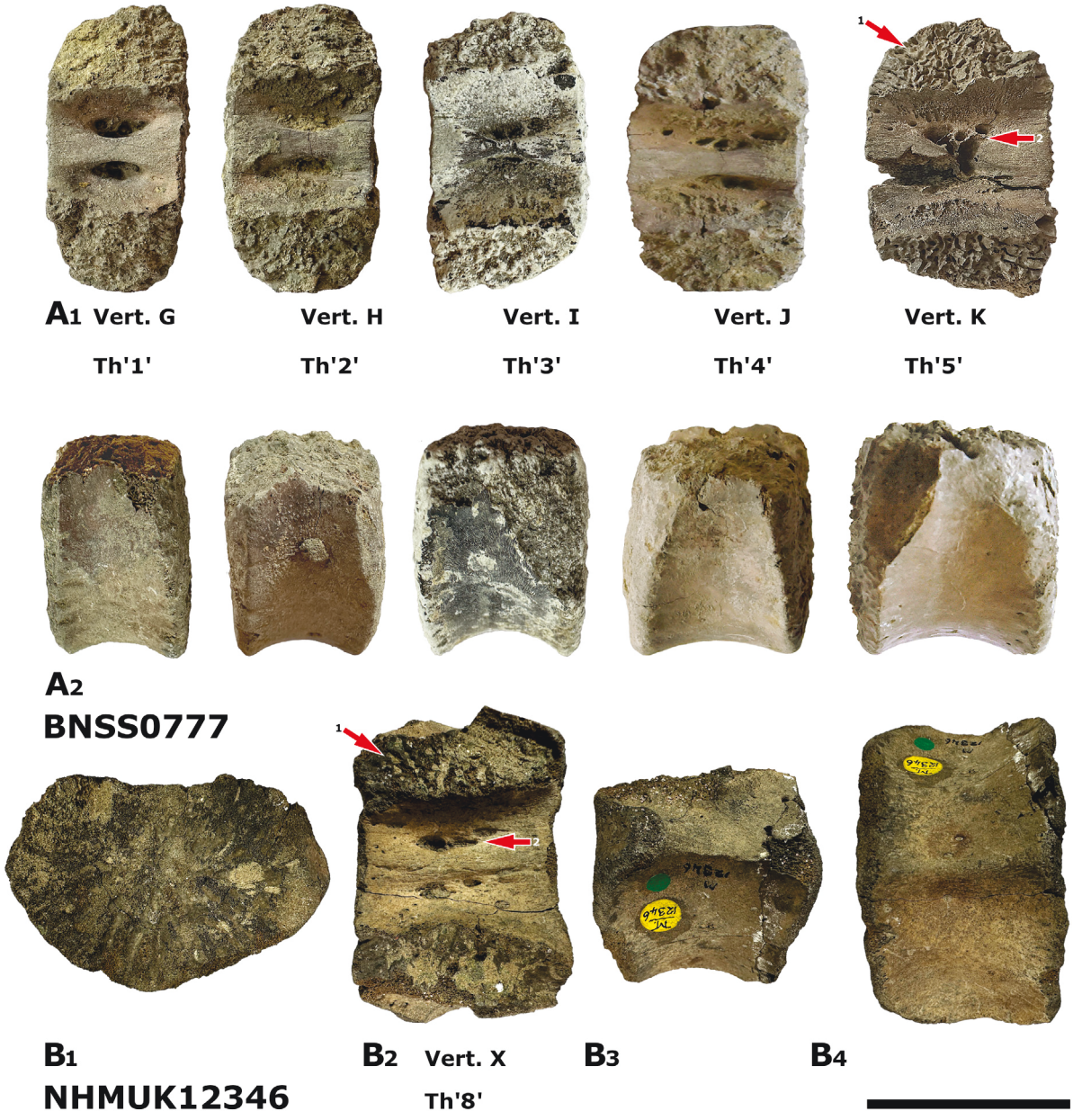


Fig. 6. Anteriormost thoracic vertebral centra, vertebrae G–K, '*Zygorhiza*' *wanklyni* Seeley, 1876, BNSS0777, compared with thoracic vertebra X (Th'8'), NHMUK12346 from the Bartonian of Barton-on-Sea, England. A1–2. Thoracic vertebrae, vertebrae G–K (Th'1'–'5'), BNSS0777 in dorsal (A1) and left lateral (A2) view. B1–4. Thoracic vertebra, vertebra X (Th'8'), NHMUK12346 in anterior (B1), dorsal (B2), left lateral (B3) and ventral (B4) view. This vertebra is slightly deformed as is seen in anterior view (B1). Oblique arrows with '1' in A1: vertebra K (Th'5'), BNSS0777 and B2: vertebra X (Th'8'), NHMUK12346 indicate the articulation site with the not-fused pedicles of the neural arch. Horizontal arrows in A1: vertebra K (Th'5'), BNSS0777 and B2: vertebra X (Th'8'), NHMUK12346 point to the dorsal foramina, which have a similar distribution. Th'1'–'5' and Th'8' in quotation marks, because the position is not completely certain. Scale bar is 50 mm.

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broad transverse process is located ventrally of the centrum. Vertebra R has two ventral foramina on the left side of a thin median ridge. The ventral side of vertebra U has two large and at least eight smaller foramina. The length of vertebrae V–W cannot be measured. The fragmentary vertebra W is the only (post-cervical) vertebra with a loosely fused epiphysis (Fig. 4, verts. L–W; Appendix Table A.2).

Other bones include: a partial neural arch, consisting of a large part of a neural spine, the right lamina and transverse process. Metapophyses, pre- and postzygapophyses are missing. It is ascribed to an anterior thoracic vertebra, but its exact position cannot be determined (Appendix Table A.3). Furthermore, there are some isolated epiphyseal discs. One epiphyseal disc is complete; a large part of two others is preserved. The latter two are oval-shaped. The first, complete one is circular. In *D. atrox* the epiphyses of the anterior thoracic vertebrae are oval-shaped and posteriorly become more circular (Uhen, 2004). The circular epiphysis of BNSS0777 was probably positioned posteriorly to the other two epiphyses (Appendix Table A.4). Finally, a single-headed fragment of a posterior rib is not described here in detail.

4.2. Palynological results

Facies. The palynological association of the studied sample is very rich in dinoflagellate cysts, spores and bisaccate pollen. The dinocysts are dominating (70% of the total sum) the microflora. The marine content is very diverse. Most prominent genera present are *Spiniferites* (30%) and *Homotryblium* (21%). Given the representation, number and variety in dinocysts, 30% presence of continental influence indicates near-coastal shallow marine conditions.

Age. The dinoflagellate cyst spectrum is interpreted as late Middle Eocene, mid-, maybe late-Bartonian, Zone E7b (Bujak and Mudge, 1994). The most important biostratigraphical events of age-diagnostic dinocysts are the LODs of *Areosphaeridium dictyoplokum*, *Areosphaeridium michoudii*, *Heteraulacacysta porosa*, and *Rottnestia borussica* and the FODs of *Areosphaeridium fenestratum*, *Corrudinium incompositum* and *Rhombodinium draco* (Fig. 3B).

Remarks. As the adhering sediments of the partial skeleton contain abundant glauconite grains, BNSS0777 originated from somewhere between Bed B and the lower part of Bed E of the Barton Clay Formation (Hooker, pers. comm., October 17, 2024). The dinocyst analysis as given in Figure 2B, which indicates dinocyst zonation E7b, seemingly suggests that the skeleton originated from Bed D, or maybe the lower part of Bed E, which would also suggest an age between 39.2 and 39.9 Ma. However, the beds in the Barton Clay Formation as depicted in Figure 2A–B approximately reflect their actual thickness, not their age. Because sedimentation rates may vary during deposition, BNSS0777 could also originate from Bed C or even B. Furthermore, as conflicting data are encountered in literature, the ages of *Areosphaeridium fenestratum* (and especially *Corrudinium incompositum*, here not figured) are considered by us as less certain, than that of *Rhombodinium draco*. Therefore, we tentatively assume a mid-Bartonian age between 39.5 and 40.5 Ma.

5. Discussion

5.1. Partial, postcranial skeleton BNSS0777

In the preserved cervical vertebrae, Ce2, Ce'4' and Ce6 have partly fused epiphyses, and in Ce7 the epiphyses are maybe beginning to fuse with the centra. The pedicles of the neural arches are fused in all cervical vertebrae. Of the post-cervical vertebrae, in at least ten thoracic vertebrae, the epiphyses and also the pedicles of the neural arches were not fused with the centra and are lacking. Only one fragment of a presumably caudal vertebra has a loosely fused epiphysis. Therefore, BNSS0777 apparently represents an ontogenetically very young individual. Surprisingly, there is only one rib fragment. Skull fragments are absent. Although the centra of many vertebrae are fragmentary, the length of most of them could be measured and used for determining an approximate position in the vertebral column. There can be no doubt that the bones of BNSS0777 belong to the same skeleton: all have the same preservation without signs of abrasion and all represent a very juvenile individual and show similar features (*e.g.*, distribution of dorsal foramina, at least ten post-cervical centra not fused with the neural arches) (Figs. 4–6). The plots of the vertebral lengths show no significant irregularities (Figs. 7–8).

Nevertheless, it is not certain that all vertebrae in the preserved series are present; some could have been missed during collection or may have been sold later. One vertebra (NHMUK12346, here indicated with 'vertebra X') could probably be part of the column (see Introduction and section about NHMUK12346 below). Also here, the neural arch is not yet fused with the vertebral centrum (Fig. 6B2). If NHMUK12346 belongs to the same individual as BNSS0777, then at least in the first eleven thoracic vertebrae the neural arches are not yet fused with the vertebral centra (Fig. 4).

5.1.1. Ontogenetic age of the postcranial skeleton BNSS0777

Determining of the ontogenetic age of BNSS0777 is hampered by the fact that no accurate data of the ontogenesis in archaeocetes are available. Uhen (2000) mentioned an ontogenetically very young individual of *D. atrox*, UM94814 consisting of amongst others six cervical

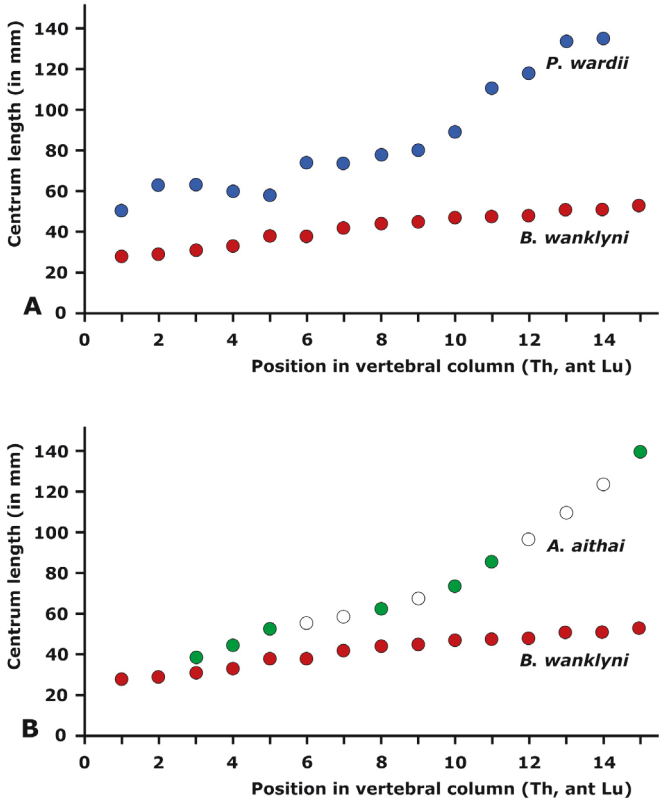


Fig. 7. Comparison of the vertebral lengths of '*Zygorhiza*' *wanklyni* Seeley, 1876, BNSS0777 with those of two small pachycetine basilosaurids. A. Plot of thoracic and anterior lumbar vertebrae of '*Zy.*' *wanklyni*, BNSS0777 (red circles) from the Bartonian of Barton-on-Sea, England, England and a small pachycetine basilosaurid, *Pachycetus wardii* Uhen, 1999, NCSM11284 (blue circles) from the Bartonian of North Carolina. B. Plot of thoracic and anterior lumbar vertebrae of '*Zy.*' *wanklyni*, BNSS0777 (red circles) and a small pachycetine basilosaurid, *Antaecetus aithai*, FSAC Bouj-200 (green circles) from the Bartonian of Morocco. NCSM11284 according to Uhen (2001, table 1); FSAC Bouj-200 according to Gingerich et al. (2022, table 4). The vertebral dorsal length is plotted against the position in the vertebral column of '*Zy.*' *wanklyni* and *A. aithai*, whereas the vertebral ventral length is used in *P. wardii*. All here figured vertebrae of '*Zy.*' *wanklyni* are lacking the epiphyses. All vertebrae of *P. wardii* are lacking one or both epiphyses, except Th6. It is unknown whether the vertebrae of *A. aithai* are lacking the epiphyses. Not-coloured circles of *A. aithai* are interpolated (Gingerich et al., 2022, table 4).

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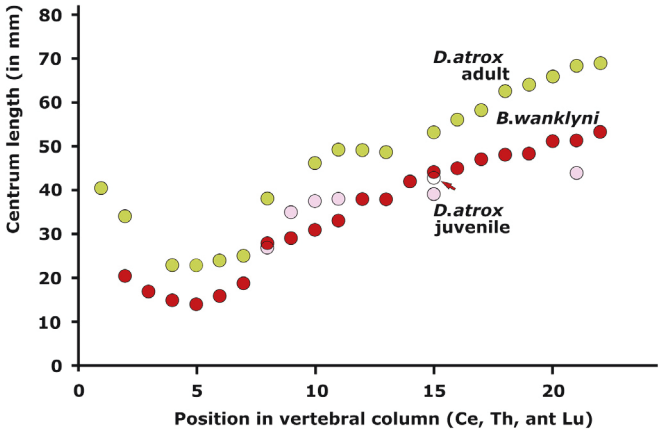


Fig. 8. Comparison of the vertebral lengths of '*Zygorhiza*' *wanklyni* Seeley, 1876, with those of an adult and juvenile individual of *Dorudon atrox*. A. Plot of cervical, thoracic and anterior lumbar vertebrae of '*Zy.*' *wanklyni*, BNSS0777 (red circles) from the Bartonian of Barton-on-Sea, England, cervical and thoracic vertebrae of a dorudontine basilosaurid, *D. atrox*, UM101215 adult individual (green circles), and thoracic vertebrae of *D. atrox*, No. 1904.XII.134e = Munich9, juvenile individual (pink circles), both from the Priabonian of Egypt. Open circle with arrow is vertebra X (Th'8'), NHMUK12346 from the Bartonian of England. UM101225 according to Uhen (2004, appendix V). Munich09, according to Kellogg (1936, table 56).

vertebrae with fused arches and epiphyses, but a neural arch of a thoracic vertebra, that is still not fused with the centrum (Uhen, 2000, 2004). BNSS0777, having cervical centra with fused neural arches but not-fused epiphyses, is apparently ontogenetically even younger than UM94814 and shows that in cervical vertebrae of this taxon, the neural arches fuse earlier in life with the centra than the epiphyses.

The ontogenesis of the extant *Stenella attenuata graffmani* Perrin, 1990 was studied in 64 individuals by Perrin (1975). Six classes of ontogenetic growth and development were discerned. Near-full-time foetuses belonged to Class I. Regarding the vertebral column, newborn individuals belong to Class II; left and right sides of the neural arches of the first 10–15 vertebrae were dorsally not ankylosed, neither were the arches fused with the centra. In Class II.5, left and right sides of the neural arches of the vertebrae were dorsally ankylosed and the arches were fused to the centra. Physically mature adults belonged to Class VI; in this class, all vertebral epiphyses were fused with the centra (Perrin, 1975, p. 42). One has to be careful with extrapolating data of neocetes to archaeocetes, but BNSS0777 clearly belongs to a very young individual. If the postcranial skeleton BNSS0777 belonged to *St. attenuata graffmani*, it would be regarded as an individual somewhere between Class II and Class II.5 (*sensu* Perrin, 1975), slightly older than newborn (Table 2).

The ontogenesis of the vertebral column in *Phocoena phocoena* Linnaeus, 1758 was studied in 350 individuals by Galatius and Kinze (2003). 17 classes of age were discerned. In the foetal stage, in the cervical region, only Ce1 and Ce2 had fused epiphyses and only in female individuals (not in males) fusion of the epiphyses with the centra was beginning. In Age Class 0, fusion of the epiphyses with Ce3–7 was beginning, as well as in the caudal region in some individuals. In Age Class 2, epiphyseal fusion in several caudal vertebrae was complete in some individuals. In Age Classes 1–3, epiphyseal fusion in the first thoracic vertebra was beginning in some individuals. In Age Class 4, epiphyseal fusion of the first thoracic vertebrae was progressing in all individuals (Table 2). In BNSS077, vertebrae Ce2 and Ce6 have partly fused epiphyses, the preserved part of Ce'4' has fused epiphyses, and Ce7 has maybe traces of beginning epiphyseal fusion. A presumably caudal vertebra (vertebra W) has a completely, but loosely fused epiphysis. If the postcranial skeleton BNSS0777 belonged to *Ph. phocoena*, it would be regarded as an individual somewhere between Age Classes 0 and 2 (*sensu* Galatius and Kinze, 2003), slightly older than newborn (Table 2).

5.1.2. Comparison of the postcranial skeleton, BNSS0777 with protocetids

The relative length of the cervical vertebrae Ce'3' and Ce'5'–Ce7, BNSS0777, varying between 0.27 and 0.32 (Appendix Table A.1) is far smaller than that of protocetids, with values between 0.47 and 0.73. (The protocetids examined are *Georgiacetus volgtensis* Hulbert et al., 1998, from the latest Lutetian or earliest Bartonian of Georgia; *Makaracetus bidens* Gingerich et al., 2005, GSP-UM3570 from the Lutetian of Pakistan; *Maiacetus inuus* Gingerich et al., 2009, GSP-UM3551 from the Lutetian of Pakistan; *Togocetus traversei* Gingerich

Table 2
Ontogenetic age of vertebrae, postcranial skeleton, BNSS0777 compared to vertebrae of *Dorudon atrox*, *Stenella attenuata graffmani* and *Phocoena phocoena*.

BNSS0777	*Stenella attenuata graffmani*	*Phocoena phocoena*
- Neural arches fused in Ce2–7; - Dens fused in Ce2; - Posterior epiphysis partly fused in Ce2; - Epiphyses (partly?) fused in Ce'4'; - Epiphyses partly fused in Ce6; - Maybe beginning epiphyseal fusion in Ce7 - Neural arches not fused in at least first 10 Th's; - No epiphyses fused in nearly all post-cervical vertebrae - One vertebra (caudal) with a loosely fused epiphysis	Six classes of growth discerned[a]: Class II, new born[a]: - Neural arches not ankylosed to centra - Halves of the neural arches dorsally not yet ankylosed in anterior 10–15 vertebrae - No ossified transverse processes developed on any vertebrae[b] Class II.5, juvenile[a] - Neural arches ankylosed to centra; - Neural arches dorsally ankylosed; - Ossified transverse processes on Ce1–2 and post-cervical centra - Ce1 reaches fully-grown dimensions; - Development transverse processes Ce2 similar to Ce1[b] Class V, sexually mature: - Not all epiphyses fused with centra[a] Class VI, fully-grown individuals: - All epiphyses fused with post-cervical centra[a]	17 age classes discerned (average life span 8–10 years)[c]: Foetuses: - No epiphyseal fusion except Ce1-2 and beginning in some other cervical vertebrae, but not in all individuals Age Class 0: - Epiphyseal fusion progressing in cervical vertebrae - Epiphyseal fusion beginning in 23rd–26th caudal vertebrae Age Classes 1–3: - Epiphyseal fusion beginning in first thoracic vertebra in some individuals Age Classes 7 to 12–14: - Epiphyseal fusion (nearly) complete in cervical and posterior caudal vertebrae - Complete fusion progressing to first thoracic vertebrae Age Class 15 and later: - Complete epiphyseal fusion in most females; in some males delayed

[a] Perrin (1975, p. 42).
[b] Perrin (1975, p. 62).
[c] Galatius and Kinze (2003, fig. 5).

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and Capetta, 2014, KPG-M110, KPG-M64, and KPG-M102, from the Lutetian of Togo; *Aegicetus gehennae* Gingerich et al., 2019, CGM60584 from the early Priabonian of Egypt (Gingerich et al., 2019, table 2).) (Appendix Table B).

More specifically, the relative length of Ce6, BNSS0777 (without epiphyses) is 0.30 and that of Ce6, NHMUK11090, '*Zy.*' *wanklyni* (with one fused epiphysis) is 0.35. With two fused epiphyses the relative length of Ce6 in '*Zy.*' *wanklyni* could have reached a value somewhere near 0.40. These values are significantly smaller than the relative length of Ce6 (with epiphyses) in *M. inuus*: 0.69. The small relative lengths of the cervical vertebrae of BNSS0777 compared to protocetids cannot be attributed to an ontogenetically young age and a protocetid is ruled out (Table 3; Appendix Table B).

5.1.3. Comparison of the postcranial skeleton, BNSS0777 with pachycetines

Cervical vertebrae of pachycetines are also longer. Vertebra NHMUK44968 (with epiphyses) from the Bartonian of Barton-on-Sea, England, assigned to a Ce3, 4 or 5 of the small *Pachycetus* cf. *humilis* Van Beneden, 1883 has a relative length of 0.56 (Van Vliet et al., 2025). In the small *A. aithai* from the Bartonian of Morocco, the relative length of two not-numbered cervical vertebrae is 0.50 and 0.60 (Gingerich et al., 2022, supplement table S1). The same is seen in cervical vertebrae of large pachycetines. In *P.* cf. *paulsonii* (*Basilotritus* sp. according to Gol'din and Zvonok, 2013) from the Bartonian of Ukraine, the relative length of Ce4, NMNH-P Ngr-6, Ce5, NMNH-P Ngr-7 and Ce7, NMNH-P Ngr-8 varies between 0.51 and 0.60 (Gol'din et al., 2014, appendix C). The small relative lengths of the cervical vertebrae, BNSS0777 compared to pachycetines cannot be attributed to an ontogenetically young age.

In Figure 7 the lengths of the thoracic and anterior lumbar vertebrae, BNSS0777 are plotted against a series of thoracic vertebrae of *Antaecetus aithai* Gingerich and Zouhri, 2015 (Fig. 7A) and *Pachycetus wardii* Uhen, 1999 (Fig. 7B). The vertebrae of the posterior part of BNSS0777 (posterior thoracic and lumbar vertebrae) are not-elongated, contrary to those of the pachycetines (Van Vliet et al., 2020). The short lengths of these torso vertebrae most probably cannot be due to the juvenile age of the individual involved. A torso vertebra of a small pachycetine from the Barton Clay Formation, ascribed to *P.* cf. ?*humilis* is, notwithstanding its apparent ontogenetically very young age, clearly elongated with a relative length of 1.37. It is seen on a fossil forum (https://www.dmap.co.uk/fossils/barton/vert/bartvert.htm) and will be described in a future paper.

For these reasons, BNSS0777 cannot be assigned to a pachycetine basilosaurid (Figs. 4, 5).

5.1.4. Comparison of the postcranial skeleton, BNSS0777 with dorudontines

In Figure 8, the lengths of the cervical, thoracic and anterior lumbar vertebrae of BNSS0777 are plotted against a series of thoracic vertebrae of *Dorudon atrox*, UM101215, adult specimen, and *D. atrox*, No. 1904.XII.134e = Munich9, juvenile specimen (according to Kellogg, 1936: *Dorudon stromeri*, which is a synonym of *Dorudon atrox* (Uhen, 2004, p. 15). The vertebral columns of *D. atrox*, Munich09 (without epiphyses) and BNSS0777 follow nearly the same curve. With fully grown vertebrae, the plot of BNSS0777 could have been more alike that of the adult specimen of *D. atrox*, UM101215. Without doubt, BNSS0777 displays vertebral proportions and size that are in line with a small dorudontine basilosaurid, the size of a juvenile *D. atrox*.

Table 3
Comparison of several vertebrae of *B. wanklyni* to comparable vertebrae of other dorudontine basilosaurids.

	'*Zygorhiza*' *wanklyni*[a]	*Dorudon atrox*	*Zygorhiza kochii*[h]	*Saghacetus osiris*[i]	*Stromerius nidensis*[j]	*Chrysocetus healyorum*[k]	*Chrysocetus fouadassi*[l]
Total W	**Ce2** 2ep)[a] 99.03 (ant) 100.63 (post)	**Ce2** 2ep)[d] me110.1	–	–	–	**Ce2** 2ep) 102.5	–
	Ce6 1ep)[b]	**Ce6** 2ep)[d]	**Ce6** 2ep)	–	–	**Ce6** 2ep)	**Ce6** 2ep)
L	20.50	me 29.4 min 24.6	33.3			22.3	26
W	58.24 (ant) 61.42 (post)	me 66.1 (ant) min 61.0 (ant)	55.3 (ant) 55.6 (post)			52.6 (ant) – (post)	39 (ant) 44 (post)
H	49.43 (ant) 47.82 (post)	me 61.3 (ant) min 61.0 (ant)	55.0 (ant) 52.0 (post)			48.0 (ant 45.9 (post)	38 (ant) 39 (post)
Rel L	0.3520	me 0.4448 0.4590[e] 0.3460[f] Me 2a–2b: 0.4025	0.6022			0.4240	0.6667
	Th/Lu 0ep)[c]	**Th16** 2ep)[g]	**Lu1** 2ep)	**Ant. Lu** 2ep)	**Th(n)** 2ep)	**Th13(?)** 1ep)	**Th14?** 2ep)
L	e53	me 71.6	66.0	54	51.3	56.8	65
W	e64 (ant) e71 (post)	me 82.6 (ant)	72.6 (ant) 73.4 (post)	53	59.3 (ant) 59.6 (post)	68.9 (ant) 71.2 (post)	59 (ant) 62 (post)
H	e52 (ant) e63 (post)	min 77.6 (ant)	66.7 (ant) 58.7 (post)	53	50.0 (ant) 48.2 (post)	59.4 (ant) 61.7 (post)	53 (ant) 54 (post)
Rel L	e0.8281	me 67.6 (ant) min 62.7 (ant) 0.8668	0.9091	1.0189	0.8651	0.8244	1.1017

0ep) without epiphyses.
1ep) with one epiphysis.
2ep) with two epiphyses.
[a] BNSS0777.
[b] NHMUK11090.
[c] NHMUK60000.
[d] Multiple individuals (Uhen, 2004, table 11).
[e] UM100146 (Uhen, 2004, appendix V).
[f] UM101215 (Uhen, 2004, appendix V).
[g] Multiple individuals (Uhen, 2004, table 12).
[h] *Zygorhiza kochii*, FMNH PM-459 (Gingerich, 2015, table 3).
[i] *Saghacetus osiris*, SMNS 11237a (Stromer, 1908, table IIIb (St. II)).
[j] *Stromerius nidensis*, UM100140 (Gingerich, 2007, table 1).
[k] *Chrysocetus healyorum*, SCSM87.195 (Uhen and Gingerich, 2001, table 2).
[l] *Chrysocetus fouadassi*, FSACBouj-2 (Gingerich and Zouhri, 2015, table 1).

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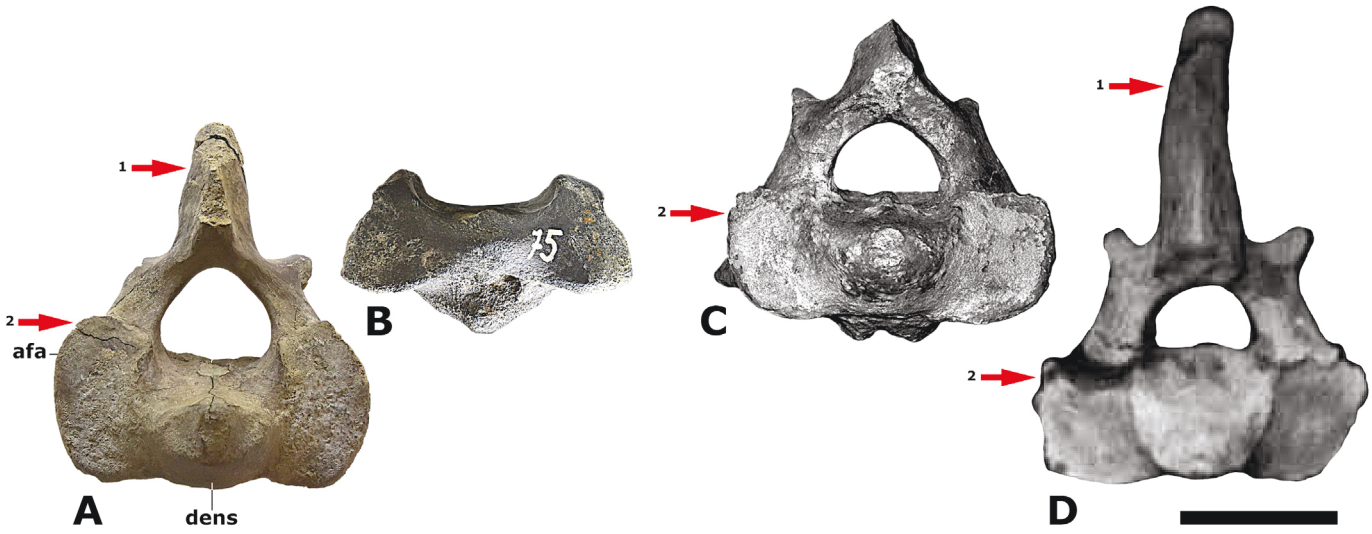


Fig. 9. Comparison of four cervical vertebrae, Ce2, axis of small dorudontine basilosaurids in anterior view. A. '*Zygorhiza*' *wanklyni* Seeley, 1876, BNSS0777 from the Bartonian of England. B. ?'*Zy.*' *wanklyni*, ID75-a from the Bartonian–Priabonian of Germany (after Van Vliet et al., 2020, plate 4, fig. C1). C. *Dorudon atrox*, UM93220 from the early Priabonian of Egypt (after Uhen, 2004, fig. 55a). D. *Chrysocetus healyorum*, SCSM87.195 from the late Bartonian to early Priabonian of South Carolina (after Uhen and Gingerich, 2001, fig. 6B). Arrows with '1' in A, '*Zy.*' *wanklyni* and D, *Ch. healyorum* indicate the neural spine, that is more robust in Ce6 of *Ch. healyorum*, than in Ce6 of '*Zy.*' *wanklyni*. Arrows with '2' in A, C–D indicate the articulation facet with the atlas, that is longer in Ce2 of '*Zy.*' *wanklyni* (A), than in Ce2 of *D. atrox* (C), and *Ch. healyorum* (D). afa: articulation facet of the axis with the atlas. Scale bar is 50 mm.

5.1.4.1. Comparison of cervical region BNSS077 with dorudontines. Vertebra Ce2, BNSS0777 (with anteriorly a fused dens and a partly fused posterior epiphysis, nearly fully grown), is somewhat smaller than the Ce2 of *D. atrox* and nearly equal in size with that of a juvenile to subadult *Chr. healyorum* (Table 3). The relative length of cervical vertebrae Ce4–7 of *D. atrox*, UM101215 varies between 0.346 and 0.378. These values are somewhat larger than in BNSS0777, but in UM101215 the epiphyses are fused with the cervical centra. As seen (Section 5.1.2), the relative length of Ce6 in '*Zy.*' *wanklyni* with two completely fused epiphyses could have reached a value somewhere near e0.40. Ce6 in *D. atrox* (with two fused epiphyses) has a mean relative length of 0.44 (0.35–0.46) (Uhen, 2004, table 11, two to four individuals), which is nearly the same (Table 3).

In Figure 9, Ce2, BNSS0777 is compared with Ce2, ID75-a from the Helmstedt region, Germany (see below, other finds from Germany), *D. atrox* (juvenile), UM93220 from Egypt, and *Chrysocetus healyorum*, SCSM87.195 (juvenile) from South Carolina, all in anterior view. The articulation facet with the atlas in BNSS0777 is ventrodorsally longer than in *D. atrox* and *Chr. healyorum*. Ce2, BNSS0777 has a less robust neural spine than Ce2 of *Ch. healyorum*.

In Figure 10, Ce2, BNSS0777 is compared with Ce2, ID75-a from Helmstedt and *D. atrox* (UM93220) from Egypt, all in posterior view. The distance between the diapophysis and the parapophysis of the transverse process is shorter (11.5 mm) in Ce2, BNSS0777 than in *D. atrox*, UM93220, e22 mm (estimated from Uhen, 2004, fig. 55b). The parapophyses of Ce2, BNSS0777 are positioned more dorsally on the vertebral centrum, than in *D. atrox* (UM93220). The diapophyses of Ce2, BNSS0777 are much smaller than in *D. atrox*, UM93220.

In Figure 11, Ce6, BNSS0777, Ce6 of *B. wanklyni*, NHMUK11090 (see 'other finds from England'), and Ce6, ID75-b from Helmstedt, Germany (see below, other finds from Germany) are compared with Ce6, *D. atrox*, UM93220 from Egypt, *Zy. kochii*, TM8501 from Alabama, and *Ch. healyorum*, SCSM87.195, from South Carolina, all in anterior view. Ce6, BNSS0777 and *B. wanklyni*, NHMUK11090 can be distinguished from Ce6 of *Zy. kochii* in having smaller vertebrarterial foramina and shorter parapophyses. The vertebrarterial foramina in Ce6, BNSS0777

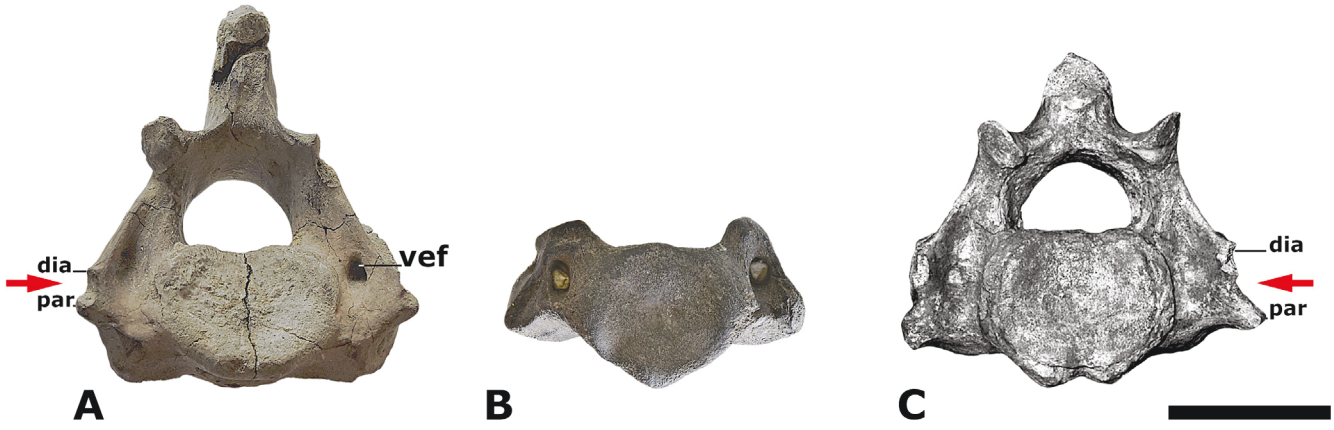


Fig. 10. Comparison of three cervical vertebrae, Ce2, axis of small dorudontine basilosaurids in posterior view. A. '*Zygorhiza*' *wanklyni* Seeley, 1876, BNSS0777, from the Bartonian of England. B. ?'*Zy.*' *wanklyni*, ID75-a from the Bartonian–Priabonian of Germany (after Van Vliet et al., 2020, plate 4, fig. C2). C. *Dorudon atrox*, UM 93220 from the early Priabonian of Egypt (after Uhen, 2004, fig. 55b). Arrows in A and C indicate the distance between the diapophysis and parapophysis of the transverse processes which is shorter in '*Zy.*' *wanklyni* (A), than in *D. atrox* (C). dia, diapophysis; par, parapophysis; vef, vertebrarterial foramen. Scale bar is 50 mm.

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and NHMUK11090 are also somewhat smaller than those of *D. atrox*. The prezygapophyses are directed slightly more upwardly than in Ce6 of *D. atrox*. Ce6, NHMUK11090 with a solidly fused posterior epiphysis representing an ontogenetic older individual than BNSS0777, is slightly smaller than Ce2 of *D. atrox* and slightly larger than Ce2 in *Chr. healyorum* (Table 3).

In Figure 12, the shape of the centrum of Ce6, BNSS0777 and *B. wanklyni*, NHMUK11090 (see below, other postcranial finds from England), and ID75-b from the Helmstedt region, Germany (see below, other postcranial finds from Germany) is schematically compared with that of several small, dorudontine basilosaurids. Only the Ce6, BNSS0777 and NHMUK11090 from Barton, England and ID75-b from Helmstedt, Germany, and *D. serratus*, MMNS VP130 from Mississippi are oval-shaped. Although the oval-shape could be due to post-mortem deformation, this seems not probable, because in that case, the (supposedly randomly occurring) deformation of Ce6, BNSS0777 and NHMUK11090 would have been practically the same. Ce3–7 of juvenile specimens of *D. atrox* are more oval-shaped, than those of older specimens (Uhen, 2004), but nevertheless, the centrum, Ce6 of the juvenile *D. atrox*, UM93220 is more circular than the centrum of Ce6, BNSS0777, NHMUK11090 and ID75-b. In the latter three vertebrae Ce6, BNSS0777, NHMUK11090 and ID75-b with zero, one, and two fused epiphyses, respectively, the oval shape remains more or less unchanged during ontogenetic ageing, although NHMUK11090, representing an older individual is slightly more circular than the very juvenile Ce6 in BNSS0777.

Ce7, BNSS0777 has only one vertebrarterial foramen. In *D. atrox*, the vertebrarterial foramina of Ce7 are small and unequal in size (Uhen, 2004, fig. 59). No vertebrarterial foramina seem to be present in the Ce7 of two protocetes (*Aegicetus gehennae* Gingerich et al., 2019; *Georgiacetus vogtlensis* Hulbert et al., 1998). The significance of only one vertebrarterial foramen in Ce7, BNSS0777 is uncertain (anomaly or plesiomorphic feature) (Fig. 4, vert. F; Fig. 5F).

5.1.4.2. Comparison of post-cervical region BNSS077 with dorudontines. The onset of the transverse process in post-cervical vertebra P is thick and is interpreted to have been an articulation site for the rib, whereas the twelfth post-cervical vertebra R is interpreted as a lumbar one, because the onset of the transverse process is rather thin. Vertebra W with fused epiphysis could have been a caudal vertebra, because the epiphyses in the cetacean vertebral column fuse from both the cervical region and the caudal region towards the thoracic region during ontogeny (Galatius and Kinze, 2003). But size alone is insufficient to tell thoracic and lumbar vertebrae apart: in two vertebral columns of *D. atrox* (CGM42813, UM101215), Th16 is slightly larger than Lu1 (Uhen, 2004, appendix V). Vertebrae S–V could either be thoracic or lumbar vertebrae. BNSS0777 could have had less thoracic vertebrae than *D. atrox* (17 thoracic vertebrae, Uhen, 2004), but the actual number is not known. The position of most vertebrae, being uncertain, is indicated with quotation marks in Appendix Table A.2. Multiple dorsal foramina are present in several thoracic vertebrae, BNSS0777, which is here attributed to a high metabolic rate, due to the juvenile age of the specimen. Thoracic vertebrae of BNSS0777 seem to differ from those of other small dorudontine basilosaurids regarding the ventral foramina from Th'5' and more posterior: they were not described in thoracic vertebrae of *Zy. kochii* and *D. serratus* (Kellogg, 1936) but present in all thoracic vertebrae of *D. atrox* (Uhen, 2004). The posterior thoracic or lumbar vertebra NHMUK60000 (without epiphyses) is slightly smaller than posterior thoracic vertebrae (with two fused epiphyses) of a small fully grown *D. atrox* and more or less equal in size with those (with one fused epiphysis) of a juvenile to subadult *Chr. haelyorum* (Table 3).

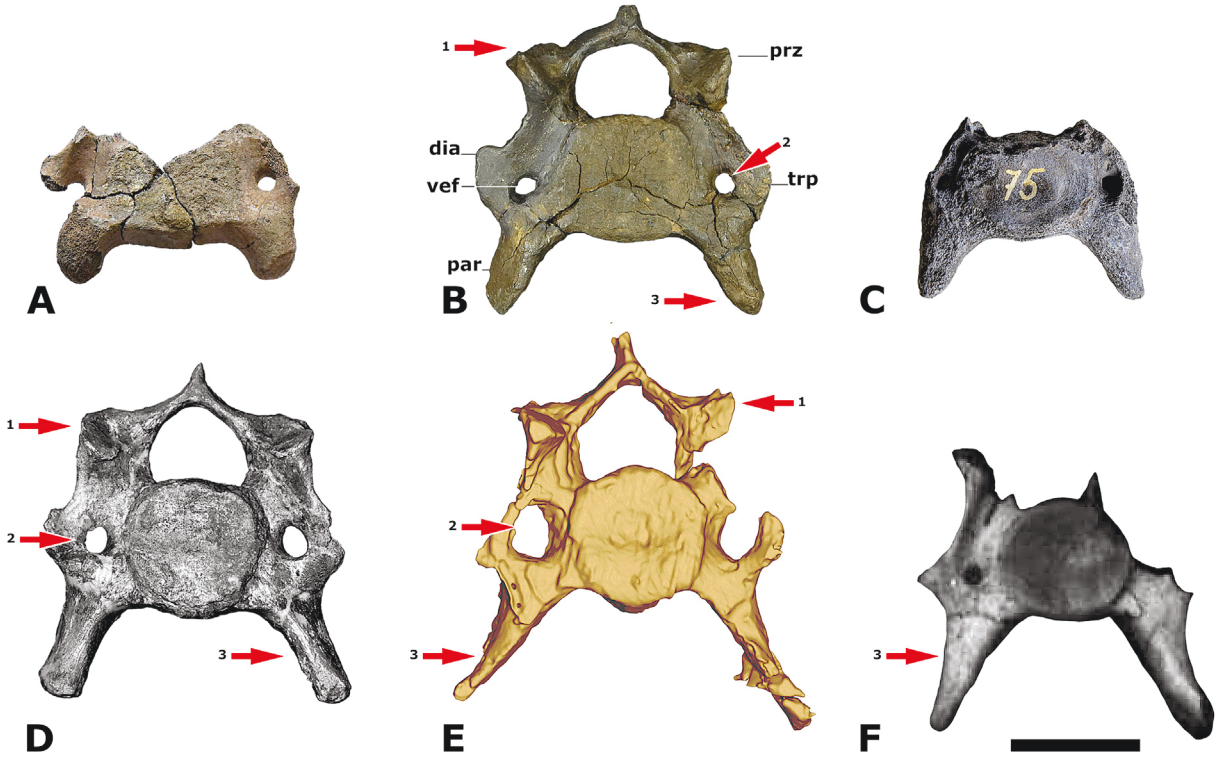


Fig. 11. Comparison of six cervical vertebrae, Ce6 of small dorudontine basilosaurids in anterior view. A. '*Zygorhiza*' *wanklyni* Seeley, 1876, BNSS0777. B. '*Zy.*' *wanklyni*, NHMUK110090; A–B from the Bartonian of England. C. ?'*Zy.*' *wanklyni*, ID75-b from the Bartonian–Priabonian of Germany (after Van Vliet et al., 2020, plate 4, fig. D1). D. *Dorudon atrox*, UM 93220 from the early Priabonian of Egypt (after Uhen, 2004, fig. 58a). E. *Zygorhiza kochii*, TM 8501 from the Priabonian of Alabama (as seen in a scan of the skull, Hakkens et al., (2026)). F. *Chrysocetus healyorum*, CSM87.195 from the late Bartonian of South Carolina (after Uhen and Gingerich, 2001, fig. 6F). Arrows with '1' in B, D–E show that the prezygapophyses of Ce6 in '*Zy.*' *wanklyni*, (B) are directed slightly more dorsally than in *D. atrox* (D), but less than in *Z. kochii* (E). Arrows with '2' in B, D–E indicate that the vertebrarterial foramina of Ce6 in '*Zy.*' *wanklyni* (B) are far smaller than in *Z. kochii* (E). Arrows with '3 in B, D–F indicate that the parapophyses of Ce6 in '*Zy.*' *wanklyni* (B) are protruding less ventrally than in *Z. kochii* (E) and *Ch. healyorum* (F). dia, diapophysis; par, parapophysis; prz, prezygapophysis; trp, transverse process; vef, vertebrarterial foramen. Scale bar is 50 mm.

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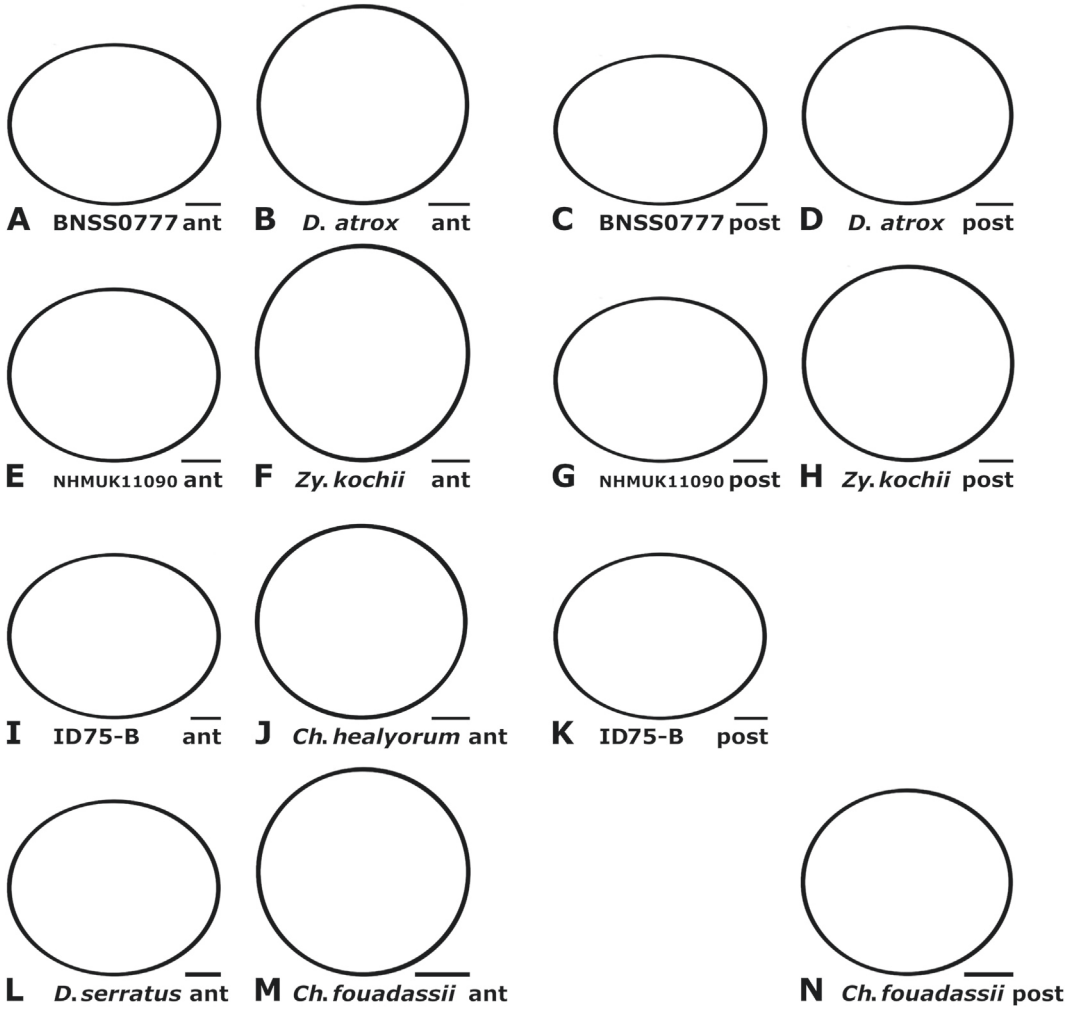


Fig. 12. Comparison of cervical vertebral centra, Ce6 of small dorudontine basilosaurids in anterior (ant) and posterior (post) view. A & I. '*Zygorhiza*' *wanklyni* Seeley, 1876, BNSS0777. B & J. '*Zy.*' *wanklyni*, NHMUK11090. A–B & I–J from the Bartonian of England. C & K. ?'*Zy.*' *wanklyni*, ID75-b from the Bartonian–Priabonian of Germany (Van Vliet et al., 2020, appendix table 6c). D. *Dorudon serratus*, MMNS VP130 from the late Bartonian of Mississippi (Daly, 1999, table 2). E & L. *Dorudon atrox*, UM 93220 from the early Priabonian of Egypt (Uhen, 2004, fig. 58). F & M. *Zygorhiza kochii*, TM 8501 from the Priabonian of Alabama (Hakkens et al., 2026). G. *Chrysocetus haelyorum*, SCSM 87.195 from the late Bartonian to early Priabonian of South Carolina (Uhen and Gingerich, 2001, table 2). H & N. *Chrysocetus fouadassii* (Gingerich and Zouhri, 2015), FSAC Bouj-2 from the Bartonian of Morocco (Gingerich and Zouhri, 2015, table 1). The centra of Ce6 of '*Zy.*' *wanklyni* (A–I, B–J) and ?'*Zy.*' *wanklyni* (C–K) are more oval-shaped, than those of the other small dorudontine species, except *D. serratus* (D). Scale bars are 10 mm.

5.1.4.3. 'Zygorhiza' juddi. A caudal vertebra, assigned to '*Zygorhiza*' *juddi* is known from the Priabonian Colwell Bay Formation in South Hampshire, England. As will be shown in a future article, this vertebra belongs to another, larger taxon than BNSS0777 (Van Vliet et al., in prep.).

5.1.5. Remarks on the geologic age of the postcranial skeleton, BNSS0777

With an estimated age between 39.5 and 40.5 Ma, BNS0777 is one of the oldest, well-dated small dorudontine basilosaurids presently known. *Tutcetus rayanensis* is slightly older (*ca.,* 41 Ma). *T. rayanensis* differs from other small, dorudontine basilosaurids in several aspects (*e.g.,* size of the teeth) (Antar et al., 2023, fig. 3, suppl. note 1), contrary to *B. wanklyni*, which shares features with *Dorudon* (Table 4). '*Zygorhiza*' sp. from the Bartonian of New Zealand is considered to be a pachycetine basilosaurid (Van Vliet et al., 2025). Some associated teeth (ID unknown) from the Lutetian of Austria can probably be assigned to a small species of *Pachycetus* too (Van Vliet et al., 2025).

5.2. Skull of 'Zygorhiza' wanklyni Seeley, 1876

Significant features of the lost skull of '*Zy.*' *wanklyni* are a posteriorly flattened sagittal crest, small rostrum, and very small diastemata. Premolars 2–3 have vertical striae at the lingual sides; each has four mesial and distal denticles which are 'faintly crenulated' (Seeley, 1876) (Fig. 13).

5.2.1. Comparison of the dentition of the lost skull with the pachycetine Antaecetus aithai

Gingerich et al. (2022) noted that dimensions of the preserved teeth of the lost skull of '*Zy.*' *wanklyni* Seeley, 1876 are close to those of deciduous teeth of *Dorudon serratus*, USNM16638 (Kellogg, 1936, table 32) (Table 1). This specimen, USMN16638, traditionally assigned to *Zygorhiza kochii* Reichenbach in Carus, 1847 is considered here to belong to *Dorudon serratus* Gibbes, 1845 because of the configurations of the posterior end of the nasals and premaxilla (Hakkens et al., 2026). In spite of this resemblance, Gingerich et al. (2022) remarked that the skull could belong to a species of *Pachycetus*, because the size of the teeth does not necessarily mean that they are deciduous and pachycetines are known from the Bartonian of western Europe. The skull of '*Zy.*' *wanklyni* would have been of a pachycetine as small as that of *Antaecetus aithai*, FSAC Bouj-200: both were coincidentally compared with the skull of the small *Saghacetus osiris* (Kellogg, 1936: skull of '*Zy.*' *wanklyni*; Gingerich et al., 2022: skull of *A. aithai*), but the dimensions of the teeth of '*Zy.*' *wanklyni* do not fit with those of *A. aithai* (Gingerich et al., 2022, table 3). The (mesiodistal) length of *e.*

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Table 4
Size comparison upper teeth of small basilosaurids (in mm).

Tooth position		*'Zy.' wanklyni*	*D. atrox*	*D. atrox*	*D. serratus*		*S. osiris*		*Chr. healyorum*		*T. rayanensis*	*A. aithai*
		DD[a]	DD[b]	PD[c]	DD[f]		PD[g]		PD[j]		PD[k]	PD[l]
					Le	Ri	Le	Ri	Le	Ri		
I1	L	–	me14.5	me21.8	–	–	20.5[h]	22[h]	15.6	15.8	–	15.2
	W	–	me11.2	me15.2 3a	–	–	–	–	11.1	10.5	–	10.5
	H	–	–	–	–	–	–	–	–	23.9	–	14.2
I2	L	–	me20.2	me22.9	–	–	~27	22.5[h]	–	–	11.2	18.9
	W	–	me12.8	me14.2	–	–	20[h]	–	–	–	5.6	–
	H	–	me32.3	me30.2[d]	–	–	–		–	–	–	25.1
I3	L	15.88	me16.1	me25.5	–	–	26[h]	27.2[h]	19.5	–	–	18.4
	W	12.70	me11.0	me15.7	–	–	–	–	12.4	–	–	–
	H	25.40 (Total H 69.84)	me22.5	me36.8[d]	–	–	–	–	27.3	–	–	17.6
C	L	Alv 22.23	me23.7	me31.0	–	–	21.5[h]	22.5	–	–	–	22.3
	W	Alv 15.88	me13.6	me18.3	–	–	–	18[h]	–	–	–	12.2
	H		–	me36.7[d]	–	–	–	–	–	–	–	27.2
Diastema		14.29	–	e33[e]	–	–	25[i]	30[i]	–	–	–	30.3
Pm1	L	Alv >25.4	me31.7	me23.6	–	–	–	22.8	22.2	22.1	–	18.4
	W	Alv <15.88	me16.0	–	–	–	–	17[h]	11.7	12.3	–	10.2
	H		–	me9.3[d]	–	–	–		26.4	–	–	19.0
Diastema		14.29	–	e34[e]	–	–	26[i]	32[i]	–		–	27.0
Pm2	L	44.45	me45.7	me53.2	–	41.5	41.2	47	–	41.6	–	32.4
	W	<12.70	me11.7	me15.9	–	10.0	–	16[h]	12.1	12.0	–	15.1
	H	<25,40	me25.0	me30.1[d]	–	–	–	–	27.8	29.0	–	28.5
Diastema		6.35	–	e14[e]	–	–	0[i]	12[i]	–	–	–	–
Pm3	L	44.45	me46.7	me49.1	–	43.5	50[h]	45[h]	46.7	–	28.3	–
	W	–	me12.0	me14.8	13	13.2	–	–	13.2	–	7.5	–
	H	~25.4	me24.3	me21.9[d]	–	–	–	–	29.0	–	21.2	
Pm4	L	<44.5	me43.0	me47.3	–	–	38.5	36[h]	38	–	29.6	39.8
	W	>12.70	me11.6	me14.6	–	–	~20[h]	–	11	–	6.8	15.0
	H	–	me18.0	me26.7[d]	–	–	–	–	–	–	22.7	32.1

alv, alveolus; C, upper canine; DD, deciduous upper dentition; H, height; I, upper incisor; L, mesiodistal length; le, left; me, mean; PD, permanent upper dentition; Pm, upper premolar; ri, right; W, width; –, unknown; >, more than; >>, far more than; <, less than.

[a] *'Zygorhiza' wanklyni* (Seeley, 1876), lost skull.
[b] *Dorudon atrox*, multiple individuals (Uhen, 2004, table 3).
[c] *Dorudon atrox*, multiple individuals.
[d] *D. atrox*, multiple individuals (Uhen, 2004, table 5).
[e] Estimated from Uhen (2004: fig. 7).
[f] *D. serratus*, USMN16638 (Kellogg, 1936, table 32).
[g] Permanent upper teeth *S. osiris*.
[h] SMNS11626 (Kellogg, 1936: table 53).
[i] Skull 'No. 1' (Stromer, 1903, table p. 80).
[j] Presumably permanent upper teeth *Chr. healyorum*, SCSM87.195 (Uhen and Gingerich, 2001: table 1).
[k] *Tutcetus rayanensis*, MUVP 501 (Antar et al., 2023).
[l] *Antaecetus aithai*, FSAC Bouj-200 (Gingerich et al., 2022, table 3).

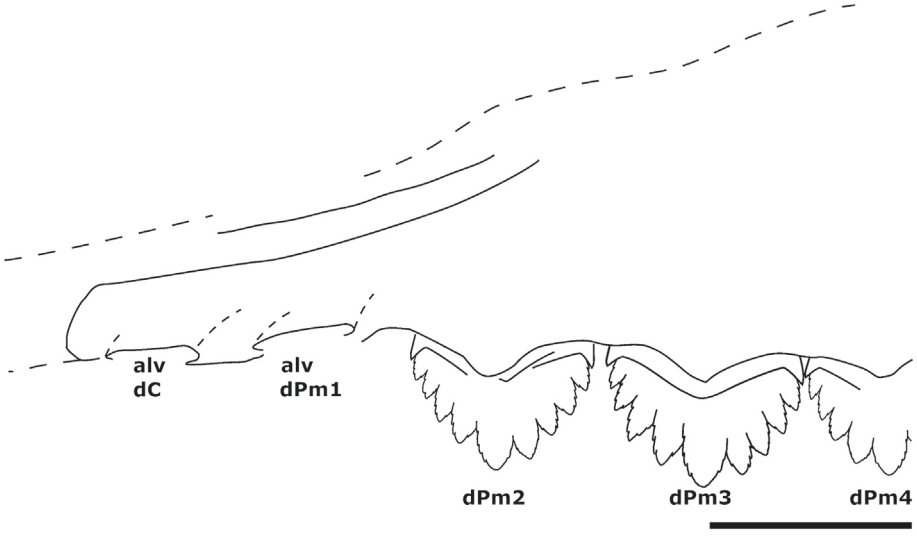


Fig. 13. Reconstruction of the maxilla fragment of '*Zygorhiza*' *wanklyni* (Seeley, 1876), gen. et comb. nov., according to the description of Seeley (1876). The dentition is considered to be deciduous. Contrary to what is seen in other small dorudontine basilosaurids, dPm2 has four mesial and distal denticles and the denticles in the premolars are crenulated (somewhat exaggerated in the illustration). Reconstruction (line drawing) by Mark Bosselaers, based on the original description. Scale bar is 50 mm.

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g., Pm2 in '*Zy.*' *wanklyni* is significantly larger than the length of Pm2 in *A. aithai*, whereas its width and height are smaller. Because of the mediodistal lengths of Pm2–3, very probably also the length of the damaged Pm4 in '*Zy.*' *wanklyni* was somewhat larger than the length of Pm4 in *A. aithai*. Finally, the mesiodistal lengths of Pm2 and Pm4 in *A. aithai* suggest a length of the missing Pm3 in *A. aithai*, that was smaller than the length of Pm3 in '*Zy.*' *wanklyni* (Table 4).

5.2.2. Comparison of the dentition of the lost skull with small dorudontine basilosaurids

Contrary to what is seen in the comparison with teeth of *A. aithai*, dimensions of the teeth of '*Zy.*' *wanklyni* are comparable to those of the corresponding teeth in several small dorudontine basilosaurids. Dimensions of teeth of '*Zy.*' *wanklyni* are close to those of *Chrysocetus healyorum* (Table 4), which was however presumed to be a permanent, not a deciduous dentition (Uhen and Gingerich, 2001). Dimensions of C1 to Pm4 of '*Zy.*' *wanklyni* are also close to the permanent C1 to Pm4 of *Saghacetus osiris*, but I1–3 of *S. osiris* are much larger in length than those of the presumed incisor of '*Zy.*' *wanklyni* (see below and Table 4). Furthermore, the diastemata in '*Zy.*' *wanklyni* are smaller than in *S. osiris*: between C1 and dPm1 'about half that' in *S. osiris*, and between dPm1 and dPm2 'less than three-fourth', according to Kellogg (1936), who probably referred to an adult specimen (Table 4). Dimensions of alveoli and upper teeth of '*Zy.*' *wanklyni* perfectly match those of deciduous upper teeth of *Dorudon atrox* (Uhen, 2004, table 3) and indeed, also of two deciduous upper premolars of *D. serratus* (Kellogg, 1936, table 32) (Table 2). An isolated tooth, discovered with the skull, was described as a possible canine (Seeley, 1876; Kellogg, 1936). The hollow pulp cavity is indicative for a deciduous tooth. The alveolus for the upper canine in the lost skull is however too large, being 6.34 mm (33.3%) longer in mesiodistal length, and 3.15 mm (25%) larger in mediolateral width than the tooth. The upper dC1 of *D. atrox* fits this alveolus much better (Table 4). If from the upper jaw, the isolated tooth with dimensions comparable to dI3 of *D. atrox* could be a dI3, or maybe a dI1 (Table 2). The small diastemata and dimensions of the teeth strongly suggest that the dentition of '*Zy.*' *wanklyni* represents deciduous teeth of a small dorudontine basilosaurid, the size of a juvenile *D. atrox* (Table 4).

5.2.3. Ontogenetic age of the lost skull

Some fragments of the lost skull were described by Seeley (1876). Sutures of the parietal with the frontal were 'well seen' and 'deeply impressed', indicative for incomplete fusion. The anterior end of the maxillae seems to have been incompletely fused too or even not-fused with the premaxillae ('perfect and rounded convexly' according to Seeley, 1876), indicative for absence of fractures. In skulls of juvenile specimens of *D. atrox*, the sutures close from posterior to anterior and the fronto-parietal sutures fuse earlier, than the premaxilla and maxilla (Uhen, 2000). In a juvenile individual of *D. atrox*, UM93220, the frontoparietal sutures were beginning to fuse and other cranial sutures were partially fused. These data were compared with the extant neocete *Neophocaena phocaenoides*. Cuvier, 1829. As in *N. phocaenoides* all cranial sutures were completely closed at an ontogenetic age of 12 months, and it was concluded that in *Neophocaena* years, UM93220 was less than one year old (Uhen and Gingerich, 2001, fig. 11).

Because the diastemata of the lost skull are small and because its teeth were in size comparable to deciduous teeth of *D. atrox*, these and other features of the skull are investigated by comparing them to juvenile and fully grown individuals of *D. atrox* and *Saghacetus osiris*. Added to *D. atrox* is the extant *Stenella attenuata graffmani* Perrin, 1990. Three juvenile (CGM 9317; RGM.74261; Munich.1904.XII.134e) and three adult (UMMP VP118139; Munich 1904.XII.134a; NHMUK M.10173) individuals of *D. atrox* were investigated by Hakkens et al. (2026). The nuchal and sagittal crests of juvenile specimens were less prominent than those of older individuals of *D. atrox*, whereas the rostrum was shorter and diastemata were smaller or lacking. An ontogenetic young age of the lost skull is indicated by the posteriorly flattened sagittal crest, and the small maxillae, with small diastemata, but relatively large teeth. No signs of tooth replacement were described by Seeley (1876), although the presumably deciduous dentition seems to have been already fully erupted. Moreover, the cranial bones were probably incompletely fused or not-fused.

The skull was said to be 'even smaller than the smallest skulls of *S. osiris*' (Kellogg, 1936). A skull of *S. osiris* had a CBL of 680 mm (Stromer, 1903). This is 72% of the CBL of adult specimens of *D. atrox* (Uhen, 2004: 941.3 mm); it can be assumed that the lost skull had a CBL of at best 70% that of a fully grown *D. atrox*. The length of a part of the maxilla (>178 mm) in the lost skull was 64% that of fully grown individuals of *D. atrox* (277 mm, as estimated from Uhen, 2004, fig. 23). Rostrum breadth near the canines was 66% that of fully grown individuals of *D. atrox*. For these and other features indicating a young ontogenetic age of the lost skull, see Table 5.

In 64 specimens of the extant neocete *St. attenuata graffmani*, dimensions of the skulls of new-born individuals, Class II in *St. attenuata graffmani* appeared to be a maximum of 67% those of fully grown individuals (Perrin, 1975). The rostrum length of individuals in Classes II–II.5 in *St. attenuata graffmani* was 60% and rostrum breadth at mid-length 70% that of fully grown individuals (Perrin, 1975). With teeth the size of deciduous teeth of *D. atrox* and with cranial dimensions varying between 65 and 70% of that of a fully grown *D. atrox*, the lost skull without doubt belonged to a very young individual. If assigned to *St. attenuata graffmani*, it would have belonged to an individual with an ontogenetic age far less than one year old, somewhere between Classes II and II.5 (*sensu* Perrin, 1975) (Table 5). This is similar to what is seen in the postcranial skeleton BNSS0777 and we assume that skeleton and lost skull had the same ontogenetic age.

5.2.4. Working assumption a: the partial, postcranial skeleton BNSS0777 and the lost skull represent one and the same taxon

The partial, postcranial skeleton, BNSS0777 and the lost skull, '*Zygorhiza*' *wanklyni* can be both referred to small dorudontine basilosaurids, in size comparable to a juvenile *Dorudon atrox*. When fully grown, this taxon could have reached the size of a small, fully grown *D. atrox*, or maybe a large fully grown *Chrysocetus healyorum*. Of old, since Seeley's description of the lost skull in 1876, remains of small dorudontine basilosaurids from Barton-on-Sea have been referred to *Zeuglodon wanklyni*. Labels attached to BNSS0777 also bear the name *Zeuglodon wanklyni*. This assignment was likely done at least 90 years ago, as Kellogg (1936) with regard to the lost skull and the isolated Ce6, NHMUK11090, obviously considering it a valid taxon, changed the name to *Zygorhiza wanklyni*. Hooker (1986) also assigned BNSS0777 to the same taxon as the lost skull.

Although it cannot be proven with complete certainty, we have made it probable that the assignment of BNSS0777 to this taxon was correct. There are no indications for the hypothetical possibility that a second small dorudontine taxon lived in the same geological age in the same area; this is even deemed improbable, as '*Zygorhiza*' *wanklyni* is one of the oldest dorudontine taxa known worldwide. Nevertheless, it cannot be completely excluded that future finds will show that BNSS0777 and the lost skull represent different species. For the time being, instead of assigning BNSS0777 to a new dorudontine species or leaving it unnamed, we adhere to the working assumption that this skeleton represents the same taxon as the lost skull, as was supposed in the past, if only to avoid taxonomic confusion. This taxon combines several unique features, different from other dorudontine taxa, importantly also from *Zygorhiza*. Given the fact that the name '*Zygorhiza*' apparently is doubtful, a new genus is here erected, named *Bartoncetus wanklyni* (Seeley, 1876) gen. et comb. nov. BNSS0777 is declared the neotype of this taxon.

5.2.5. Naming a juvenile individual

The partial, postcranial skeleton, BNSS0777 and the lost skull represent very young individuals of probably the same ontogenetic age; if

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Table 5
Ontogenetic age of the lost skull, '*Zygorhiza*' *wanklyni* compared to *Dorudon atrox* and *Stenella attenuata graffmani*.

'*Zygorhiza*' *wanklyni*	*Dorudon atrox*	*Stenella attenuata graffmani*
Skull:[a]	Skulls of fully-grown individuals: mean **941.3 mm**[c]	Six classes of growth discerned:
'Smaller than smallest skulls of *Saghacetus osiris*' = **<680 mm** in length[b] ⇒**<e72%** of a fully-grown *D. atrox*		- Condylobasal length Class II: **221 to 242 mm**; - Condylobasal length Class VI: **360 to 404 mm** (Perrin, 1975: p. 42)[h] Condylobasal length skulls Class II/Class VI Minimum **54.7%**; maximum **67.2%**
Posteriorly flattened sagittal crest **d)**	Nuchal and sagittal crests in juvenile individuals less prominent[d]	
Deeply impressed parietal–frontal sutures: incomplete fusion **d)**	Fusion frontal–parietal suture early in ontogenetic age[e]	Closure and obliteration sutures braincase from Class II.5[i]
Maxillae anteriorly incompletely or not fused with premaxillae	Fusion sutures premaxillae and frontals later than frontal–parietal suture[e]	Distal fusion premaxillae–maxillae from Classes IV–V[i]
Short rostrum[a]	Shorter rostrum in juvenile individuals[d]	Rostrum fully-grown in length from Class IV[i]
Left maxilla (anterior–posterobasal angle dPm3):	Left maxilla (anterior–posterobasal angle Pm3) in fully-grown individuals: **e277 mm** in length[f]	Rostrum length:
>**178 mm** in length[a] ⇒>**e64%** of a fully-grown *D. atrox*		- Class II: mean 114,6 mm; - Class II.5: mean 176 mm; - Classes II–II.5: mean **145.3 mm**; - Class VI: mean **236.2 mm**[j] Rostrum length Classes II–II.5/Class VI ⇒**61.5%** of fully-grown individuals
Rostrum breadth anteriorly near canines: **57.15 mm**[a]	Mean rostrum breadth at canines in fully-grown individuals: **86.9 mm**[g]	Rostrum breadth at mid-length:
⇒**66%** of fully-grown *D. atrox*		- Class II: mean 26 mm; - Class II.5: mean 34.5 mm; - Classes II–II.5: mean **30.25 mm**; - Class VI: mean **43.1 mm**[k] Rostrum breadth Classes II–II.5/Class VI ⇒**70.2%** of fully-grown individuals
Small diastemata, but relatively large teeth[a]	Diastemata smaller or lacking in juvenile individuals[d]	

[a] '*Zygorhiza*' *wanklyni*, lost skull (Seeley, 1876).
[b] *Saghacetus osiris* (Stromer, 1903, p. 80).
[c] Uhen (2004, table 7).
[d] Hakkens et al. (2026).
[e] Uhen (2000).
[f] Estimated from Uhen (2004, fig. 7).
[g] Uhen (2004, table 7).
[h] Perrin (1975, p. 42).
[i] Perrin (1975).
[j] Perrin (1975, fig. 16).
[k] Perrin (1975, fig. 17).

belonging to the extant *St. attenuata graffmani*, both would have been attributed to calves of Classes II–II.5 (*sensu* Perrin, 1975). This is remarkable, as remains of very young archaeocetes (except *D. atrox* and *Z. kochii*) are rarely found (Uhen, 2000). A possible objection against naming a new taxon could be, that it is based upon juvenile individuals, for it would be difficult to recognise fully grown individuals that are discovered later on. This objection is opposed with regard to the postcranial skeleton BNSS0777 by the following arguments. During ontogeny it is the atlas, Ce1 that gets its fully grown dimensions early on (Table 2). Although the atlas in BNSS0777 is missing, the well-preserved axis with fused epiphyses has nearly reached its fully grown dimensions. Ce6 is known by the isolated vertebra, NHMUK11090, with a fused posterior epiphysis, which apparently had nearly reached its fully grown dimensions too. Both Ce2 and Ce6 have diagnostic features.

5.2.6. Working assumption b: post-cranial skeleton BNSS0777 and the lost skull belong to one individual

BNSS0777 seems to be the only find of associated remains thus far known from Barton-on-Sea. Remains with similar preservation and ontogenetic age have never been found here over more than 100 years, except NHMUK12346 (see Introduction and below). BNSS0777 comprises the anterior part of the vertebral column, but no skull fragments are present and on the other hand, no vertebrae were mentioned by Seeley (1876) in his description of the lost skull. In fact, the finds are complementary. The post-cranial skeleton BNSS077 and the lost skull have been found in cliffs in a rather restricted area of about 3 km in length. As all archaeocete remains for which stratigraphical details are known have been derived from the whale-bearing Beds B to the lower part E of the Barton Clay Formation, the lost skull, as BNSS0777, probably had been discovered in the same beds. These beds have been deposited in estimated less than 1 Ma. Given the rarity of finds of associated vertebrae (postcranial skeleton BNSS0777) from the Barton Clay Formation of Barton-on-Sea and a skull (one of the very few basilosaurid skulls known from Europe), and given the rarity of finds with a comparable young ontogenetic age, both discovered in roughly the same period of time, the possibility is not excluded that they belonged to one and the same individual. Because this is maybe too audacious a hypothesis, we refrain from declaring BNSS0777 the syntype of *Bartoncetus wanklyni*.

5.2.7. Other finds from Barton-on-Sea, England

An overview of finds, ascribed to small, mostly or all dorudontine archaeocetes from the Barton Clay Formation, Barton, England is given in Appendix Table C.

A dental root from the Barton Clay Formation and housed in the Natural History Museum of London (NHMUK85421). The root is not hollow and buccolingually compressed. Its dimensions (mesiodistal

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length 23.16 mm; width 14.25 mm) seem to match several cheek teeth (the single-rooted upper or lower dC1, the lower dpm1 or the upper Pm1) of *D. atrox* (Uhen, 2004, tables 3–5), but also those of the upper C1 of *A. aithai* (Gingerich et al., 2022, table 3). It was collected by Mr Steve Lamb and donated to the Natural History Museum London in 2010 (Appendix Table C.1).

A rather complete Ce6 of *B. wanklyni* (Seeley, 1876) gen. et comb. nov. from the Barton Clay Formation and housed in the Natural History Museum of London (NHMUK11090). It was assigned to *Zeuglodon wanklyni* by Andrews (1907). The centrum is oval-shaped (Fig. 12E, G). The posterior epiphysis is solidly fused with the centrum. Anteriorly, there are some signs of beginning epiphyseal fusion. The parapophysis is larger than the diapophysis and becomes broader distally. The left postzygapophysis is well-preserved. The right side of the neural arch and the right diapophysis have been restored. It is not-abraded, black in colour and not mineralised. It has been derived from Beds B to D (Hooker, 1986). With the posterior (but not the anterior) epiphyseal disc fused with the centrum, NHMUK11090 is from an ontogenetically slightly older individual than BNSS0777. It was donated by Mr or Mrs Walton to the Natural History Museum London in 1915 (Figs. 11B, 12E, G; Appendix Table C.2).

A thoracic vertebra and an epiphyseal disc fragment from the Barton Clay Formation, assigned to *Zy. wanklyni* by Halstead and Middleton (1972), housed in the Natural History Museum London (NHMUK12346). Halstead and Middleton (1972) noted that it is similar to Th6–7 of *Zy. kochii*, but the position of the lateral ridges is more alike that in Th8–9 of *Zy. kochii*, or *D. atrox*. Dimensions of NHMUK12346 (43.10 mm in dorsal, 43.32 mm in ventral length) indicate that this vertebra had a position between Th'7' and Th'8' in BNSS0777. Having a relative length of only 0.62, it can certainly be ascribed to a small dorudontine basilosaurid. The relative width of 1.51 is large, resembling a vertebra of *Pachycetus* at first sight, but the vertebral centrum is slightly deformed (Fig. 6B1). The relative width of the not-deformed five anteriormost vertebrae of BNSS0777 is about 1.3 (Appendix Table A.2). With pedicles of the neural arch not yet fused with the vertebral centrum, the very young ontogenetic age of NHMUK12346 is similar to that of the specimen BNSS0777. There are multiple dorsal foramina, located in the same positions (Fig. 6B3) as those of Th'4', Th'5' and Th'7' in BNSS0777 (Fig. 6A1, verts. I–K). Two ventral foramina are present on the left side and one at the right side of a thin median ridge. Colour and preservation differ from other vertebrae from the Barton Clay Formation in the collections of the NHM London but are rather similar to BNSS0777 (grey-brownish in colour, not-abraded). The adhering matrix contains abundant glauconitic grains, indicating that, like BNSS0777, the vertebra has been derived from Beds B to D, or maybe the lower part of Bed E. Because of the similarities, NHMUK12346 originally could have been part of BNSS0777. It was donated by Mr R. Egerton-Godwin to the Natural History Museum London in 1923 (Fig. 4, vert. X; Fig. 6B1–4; Appendix Table C.2).

Finally, a posterior thoracic or lumbar vertebra from the Barton Clay Formation, also housed in the Natural History Museum London (NHMUK60000), has not been previously described. The vertebral centrum is broken into two parts and due to fractures the neural arch is detached from the vertebral centrum, but the vertebra is essentially complete. The epiphyses are lacking. The onsets of the pedicles of the neural arch are pachyostotic. It is slightly abraded and black in colour; judging by its weight, it is thoroughly petrified. Having a small size and a relative length of 0.83, it undoubtedly can be assigned to a small dorudontine and is regarded to represent the same taxon as BNSS0777. Its preservation is clearly different from that of BNSS0777. It was collected by Mrs Sally Richardson and donated to the Natural History Museum London in 1994 (Fig. 14; Appendix Table C.2).

5.3. Finds from Germany

An overview of finds, ascribed to small dorudontine archaeocetes, mostly or all the size of those of *B. wanklyni* from the Bartonian and

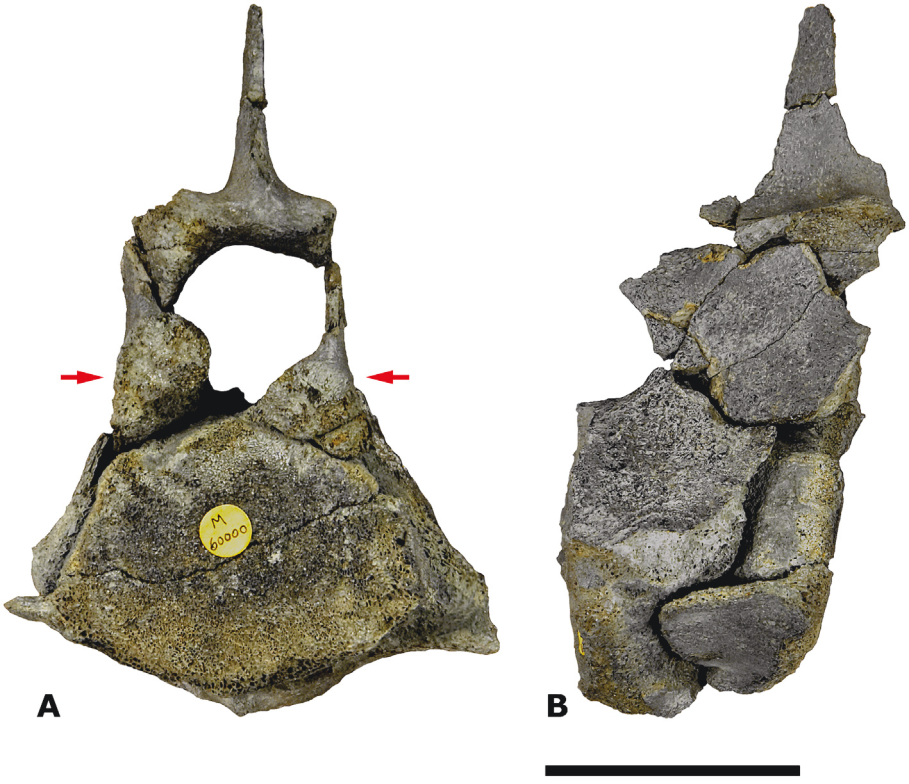


Fig. 14. A–B. Presumably posterior thoracic vertebra *Bartoncetus wanklyni* (Seeley, 1876) gen. et comb. nov., NHMUK60000 (not earlier figured) from the Bartonian of Barton-on-Sea, England in anterior (A) and right lateral (B) view. Arrows point to the pachyostotic part of the pedicles of the neural arch. Scale bar is 50 mm.

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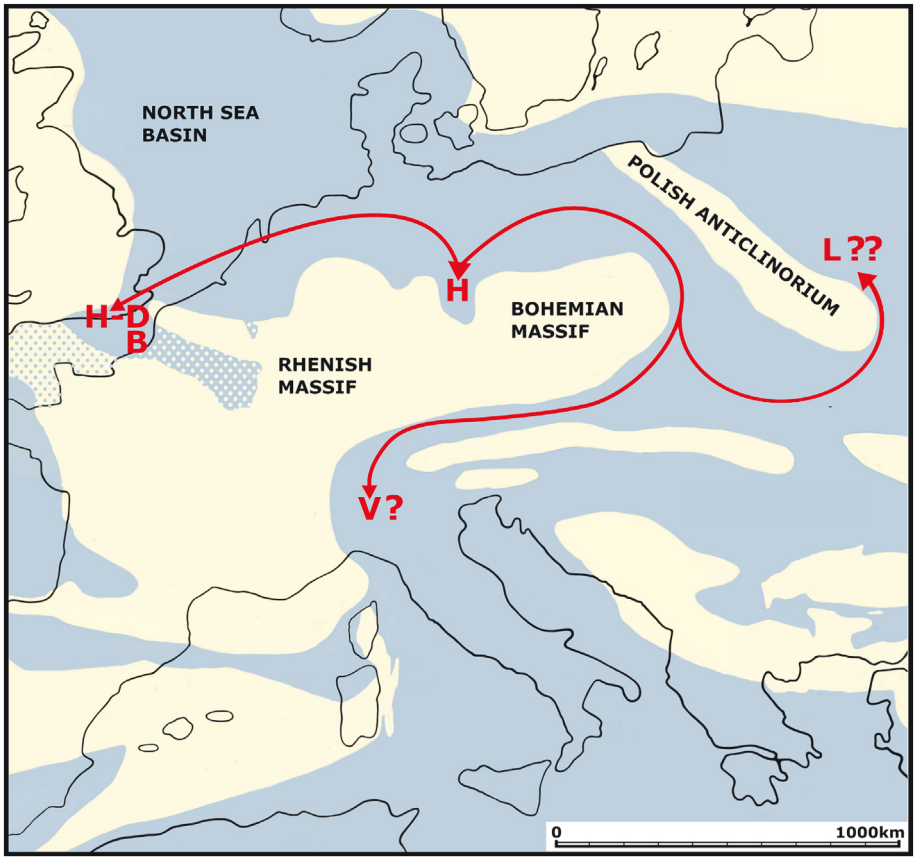


Fig. 15. Map of the western and southwestern parts of the European continent in the Bartonian, showing the locations, where remains of small dorudontine archaeocetes have been found. The North Sea Basin was connected with the Tethys and the later Paratethys Oceans through amongst others a south-eastern passage east of the Bohemian Massif, but was probably separated from the Atlantic Ocean by a land bridge between Normandy, France and Southwest England. Map based on Curry and Smith (1975), Smith and Curry (1975), Rögl (1999, fig. 1), Popov et al. (2004), Marandat et al. (2012), Gol'din and Zvonok (2013, fig. 1), Gibbard and Lewin (2014, figs 1–3), de Lapparent de Broin et al. (2018, fig. 1), and Lenz et al. (2021, fig. 1). H, region of Helmstedt, Germany; H-D B, Hampshire–Dieppe Basin, England; L, Lubartów, Poland; V, Italy: Varano, Italy.

Priabonian of the Helmstedt region, Germany is given in Appendix Tables D.1–D.2. The isolated and often abraded remains could, because of their dimensions, be doubtfully assigned to ?*B. wanklyni*.

5.4. Find from Italy

Pilleri and Fulgosi (1989) described a most fragmentary skeleton, amongst others 12 fragments of teeth from the late Eocene of Varano, Italy. The (pre)molar fragments comprise crenulated denticles, reminiscent of cheek teeth of *B. wanklyni*. Dimensions point to a small dorudontine archaeocete (Appendix Table E).

5.5. Find from Poland

A mandibular fragment of a small basilosaurid from the Bartonian–Priabonian boundary of Lubartów, Poland was described by Tyborowski et al. (2026). It is however not possible to determine whether it belonged to a pachycetine or a dorudontine basilosaurid.

5.6. Distribution in Europe

Vectors in Figure 15 show the possible passages of small dorudontine archaeocetes in the North Sea Basin between the Eocene Hampshire (or Hampshire–Dieppe) Basin in the eastern part of the Channel between England and France, and *via* the North Sea Basin to the Helmstedt region, Germany. They could reach the region of Varano, Italy, through a channel at the east of the Bohemian Massif (Rögl, 1999). Archaeocete passages from the present-day Atlantic Ocean to the south-western part of the North Sea Basin could have been blocked by land connections between present-day England and France from the Lutetian to at least the Priabonian, although transgressions occurred onto the Armorican platform from the Atlantic Ocean towards the east, maybe even reaching the Channel Islands (Curry and Smith, 1975; Smith and Curry, 1975; Popov et al., 2004; Hooker, 2007; Marandat et al., 2012; Gibbard and Lewin, 2014). Passages from the north-west along present-day Scotland could have been hampered by the presence of a land bridge, the Highland Shetland, reaching from Scotland to more than 150 km to the northwest of the Shetland Isles, probably too far towards the North to be an archaeocete passage (Gibbard and Lewin, 2014, figs.1–4[1]).

6. Conclusions

The partial, postcranial skeleton, BNSS0777 of a small archaeocete from the Bartonian part of the Barton Clay Formation at Barton-on-Sea and Highcliffe, England comprises 23 vertebral centra and multiple vertebral fragments of the anterior part of the vertebral column. It belongs to a very juvenile individual with cervical vertebrae having only partly fused epiphyses or no fusion at all, with nearly all post-cervical vertebrae (except a caudal vertebra fragment) lacking the epiphyses and at least the first ten post-cervical vertebral centra not fused with

[1] *When this article was in press, a cervical vertebrae Ce3 or 4 from the Bartonian of Ukraine was published by Davydenko et al. (2026). Width and height are similar to Ce'3' and '5', BNSS0777 from Barton-on-Sea, England; in addition, the vertebra is remarkably oval in shape like those of Bartoncetus wanklyni. It could be maybe assigned to ?Bartoncetus wanklyni, which would considerably expand its distribution in Europe.*

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the neural arches. The length of the cervical vertebrae, as well as the not-elongated posterior thoracic and lumbar vertebrae indicate a small, dorudontine basilosaurid, the size of a juvenile *Dorudon atrox*.

Although the skull of '*Zygorhiza*' *wanklyni* Seeley, 1876 from the Barton Clay Formation at Barton-on-Sea was lost, it was adequately described by Seeley (1876). A very juvenile age of the specimen is indicated by the small diastemata, the short rostrum with maxillae probably not fused with the premaxillae, the posteriorly flattened sagittal crest and still deeply incised frontoparietal sutures. The dentition perfectly matching the deciduous dentition of *D. atrox* indicates that the skull can be assigned to a small, dorudontine basilosaurid.

Working assumption a, that the partial, postcranial skeleton BNSS0777 and the lost skull, both from the same formation and location, represent one and the same taxon has been made probable. Lithological and dinocyst analyses of sediments adhering to BNSS0777 reveal an age of 39.5 to 40.5 Ma; BNSS0777 is one of the oldest well-dated dorudontine basilosaurids presently known. Of old, remains of small dorudontine basilosaurids from the Bartonian Clay Formation have been assigned to '*Zygorhiza*' *wanklyni*; there are no indications for the hypothetical possibility of the co-occurrence of two species of dorudontine basilosaurids in the same region and formation. The vertebrae of BNSS0777 and the teeth of the lost skull differ from that of other small dorudontines in several aspects. A new genus is here erected, named *Bartoncetus wanklyni* (Seeley, 1876) gen. et comb. nov., with the vertebral column, BNSS0777 designated the neotype of the genus and species.

Working assumption b that the post-cranial skeleton BNSS0777 and the lost skull belong to the same individual is possible. Both were found in the same, rather small area of cliffs, maximum less than 3 km in length, in more or less the same period of time. In the postcranial skeleton BNSS0777, skull fragments are absent. Seeley (1876) did not mention having seen any postcranial material in his description of the lost skull. BNSS0777 and the lost skull belong to very juvenile individuals of probably the same age. Nevertheless, working assumption b cannot be proven with enough certainty. BNSS0777 is not declared the syntype of *Bartoncetus wanklyni*.

A tooth and several vertebrae from the Bartonian to Priabonian of Helmstedt, Germany, as well as dental fragments of a very fragmentary skeleton from the Late Eocene of Varano, Italy share characters with the dorudontine remains from Barton-on-Sea, England and could possibly be assigned to *Bartoncetus wanklyni*, potentially bridging a gap in understanding the patchy fossil record of small dorudontine remains from Europe.

CRediT authorship contribution statement

Henk Jan van Vliet: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation, Conceptualization. **Jonas Hakkens:** Writing – review & editing, Visualization, Investigation. **Theo M. Paijmans:** Writing – review & editing, Visualization, Investigation. **Charles J. Underwood:** Writing – review & editing, Conceptualization. **Ivo Verheijen:** Writing – review & editing, Investigation. **Mark E.J. Bosselaers:** Writing – review & editing, Visualization, Investigation. **David J. Ward:** Writing – review & editing. **Dirk K. Munsterman:** Writing – review & editing, Formal analysis. **Jelle W.F. Reumer:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pgeola.2026.101201.

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