An archaeocete vertebra re-examined: indications for a small-sized species of *Pachycetus* from Spain, Europe

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ABSTRACT

A cetacean vertebra from presumably Bartonian strata near Taradell, Northeastern Spain, described by Pilleri in 1989, is here re-examined. Also a description of the local stratigraphy is given. Notwithstanding the rather severe damage of the vertebral centrum, it shows the same characteristics as vertebrae ascribed to *Pachycetus* ('*Platyosphys*'; '*Basilotritus*') sp. from, amongst others, Ukraine, Germany and Belgium. The characteristics are: the combined presence of a compact, circumferential multi-layered cortex, the pock-marked surface of the vertebral centrum, the pachyostotic pedicles of the neural arch and finally the probable elongation of the vertebral centrum, the transverse processes and the pedicles of the neural arch. The compactness of the midpart of the vertebral centrum has been measured and is compared with that of other taxa. The find extends the geographic distribution of this genus to Southwestern Europe. The vertebra appears to belong to a small species of *Pachycetus*, which was until now not known with certainty from Europe, although some similar-sized vertebrae from the Southern Bight of the North Sea have recently been described.

Keywords archaeocetes, Basilosauridae, Eocene, Vic Area

INTRODUCTION

During his investigations on sirenian remains from the Barcelona area in the collections of the Museo Geológico del Seminario de Barcelona (MGSB), Pilleri came upon a vertebral centrum, apparently of an archaeocete, that had been found in Bartonian strata of Taradell, Northeastern Spain. In 1989, he published a short description of this vertebra (Pilleri 1989) in which he gave special attention to the multi-layered cortex of the vertebra by quoting Müller (1849). The latter author had described the conspicuous cortical layering in basilosaurid vertebrae already in 1849. Pilleri compared the vertebral centrum from Taradell with the caudal vertebrae Ca10-12 of *Zygorhiza kochii* Carus, 1847, with the connotation that the former is larger than the vertebrae of *Zygorhiza* (Pilleri 1989). In the present paper we redescribe the vertebra, which appears to belong to a small species of *Pachycetus*, contrary to most other, larger vertebrae assigned to this genus known from Europe.

By publishing a manuscript by Paulson, it was Brandt (1873) who for the first time mentioned two finds of vertebrae of *Pachycetus* (as *Zeuglodon paulsonii* Brandt, 1873), that had been found near Tschigirin, Ukraine. Kellogg (1936) renamed the genus to *Platyosphys* (*Platyosphys paulsonii*) and mentioned two other finds from Ukraine. All these finds have been lost, but they had been neatly described and figured by Brandt (1873) and Fedorovsky (1912). Gol'din & Zvonok (2013) brought the somewhat forgotten taxon *Platyosphys* back to scientific attention. They introduced a new genus and species, *Basilotritus uheni* Gol'din & Zvonok, 2013 for newly found remains with similar vertebral characteristics from Ukraine. Moreover, they showed that '*Eocetus*' *wardii* Uhen, 1999 from the Middle Eocene of North Carolina and Virginia, USA, represents another, yet smaller species of this genus. A few years later, Gingerich & Zouhri (2015) described another small species, *Platyosphys aithai* Gingerich & Zouhri, 2015 from the Bartonian of Morocco, Africa. In 2020 it was found that Van Beneden (1883) was actually the first who had named this genus, by assigning the name *Pachycetus robustus* Van Beneden, 1883 to a large vertebra, NsT90 and a rib fragment, NsT92 from the region of Helmstedt, Germany (kept in Senckenberg Naturhistorische Sammlungen, Dresden). This vertebra appeared to represent the same genus as the finds from Ukraine, long before Kellogg's denomination of *Platyosphys* in 1936 (Van Vliet *et al.* 2020). Recently, Gingerich *et al.* (2022) erected a new basilosaurid subfamily, Pachycetinae, for the different species of *Pachyce*-
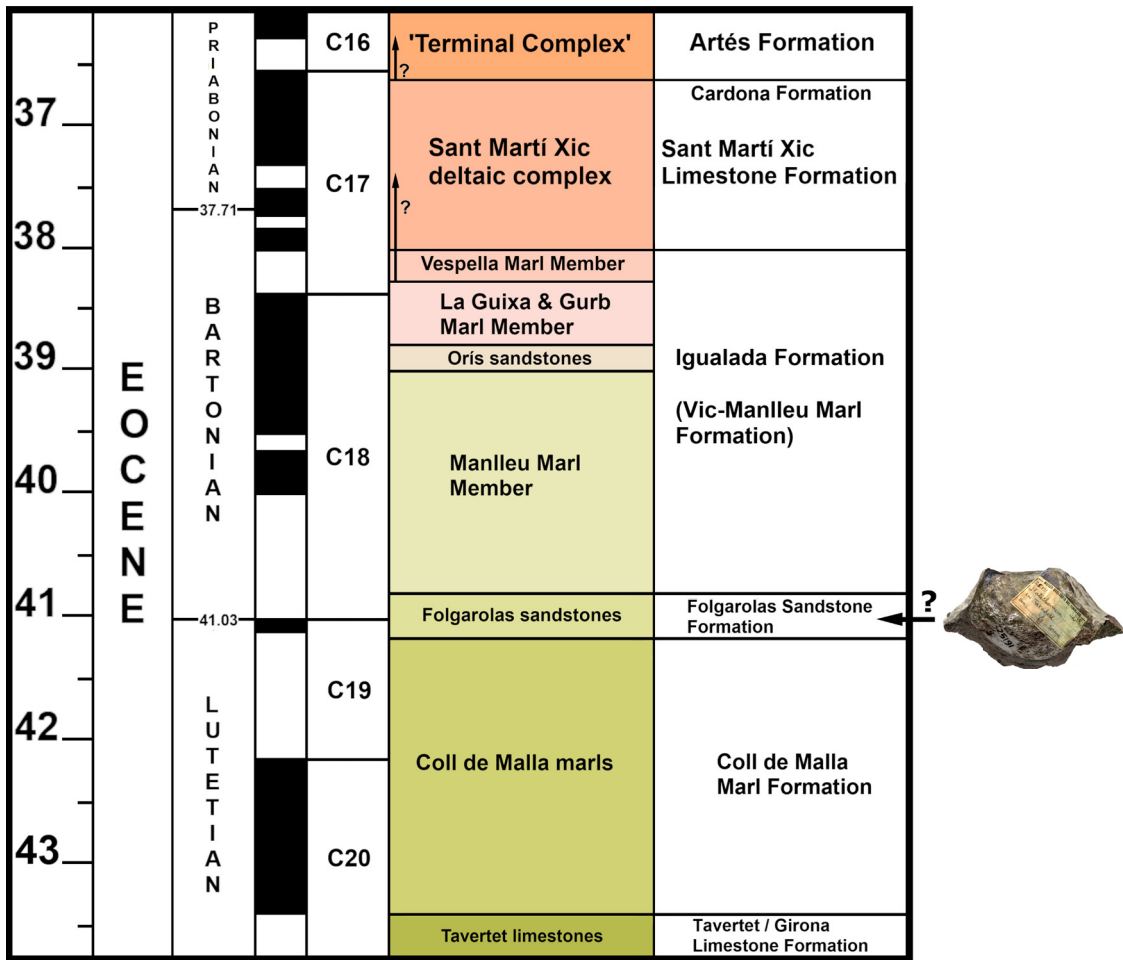
tus. Moreover, they renamed the taxon *Pachycetus aithai* to *Antaecetus aithai*.

Pachycetus is thus far poorly known and no complete skeleton or even skull has been described from Europe. The excact vertebral count of *Pachycetus* spp. from Europe is unknown, but the related *Pachycetus wardii* from the Bartonian of North Carolina has a thoracic vertebral count of 12 and a lumbar count of 6 (Uhen 2001) reflecting the artiodactyl vertebral configuration (Uhen 2014: fig. 8). *Antaecetus aithai* could have had more than 13 thoracic vertebrae and at least 10 lumbar vertebrae (Gingerich *et al.* 2022). More derived basilosaurids, like *Basilosaurus cetoides* Owen, 1839, and *Cynthiacetus peruvianus* Martínez-Cáceres & de Muizon, 2011 have a larger number of thoracic and lumbar vertebrae (Zalmout *et al.* 2009, Martínez-Cáceres *et al.* 2017). The cheek teeth have smaller denticles, than the large and prominent denticles of *Basilosaurus* species (Gol'din *et al.* 2014, Van Vliet *et al.* 2020).

Adding up to the relatively poor fossil record of archaeocetes in Europe, new finds have been published over the last years (Gol'din & Zvonok 2013, Gol'din *et al.* 2014, Van Vliet *et al.* 2019, 2020, 2022). Many finds are isolated, fragmentary fossils, mostly postcrania. Nevertheless, postcrania of archaeocetes have more taxonomic relevant important characteristics than those of neocetes, by which determining the genus is sometimes possible (Van Vliet *et al.* 2022), and indeed, vertebrae of *Pachycetus* have quite characteristic features (Gingerich & Zouhri 2015). The new finds comprise
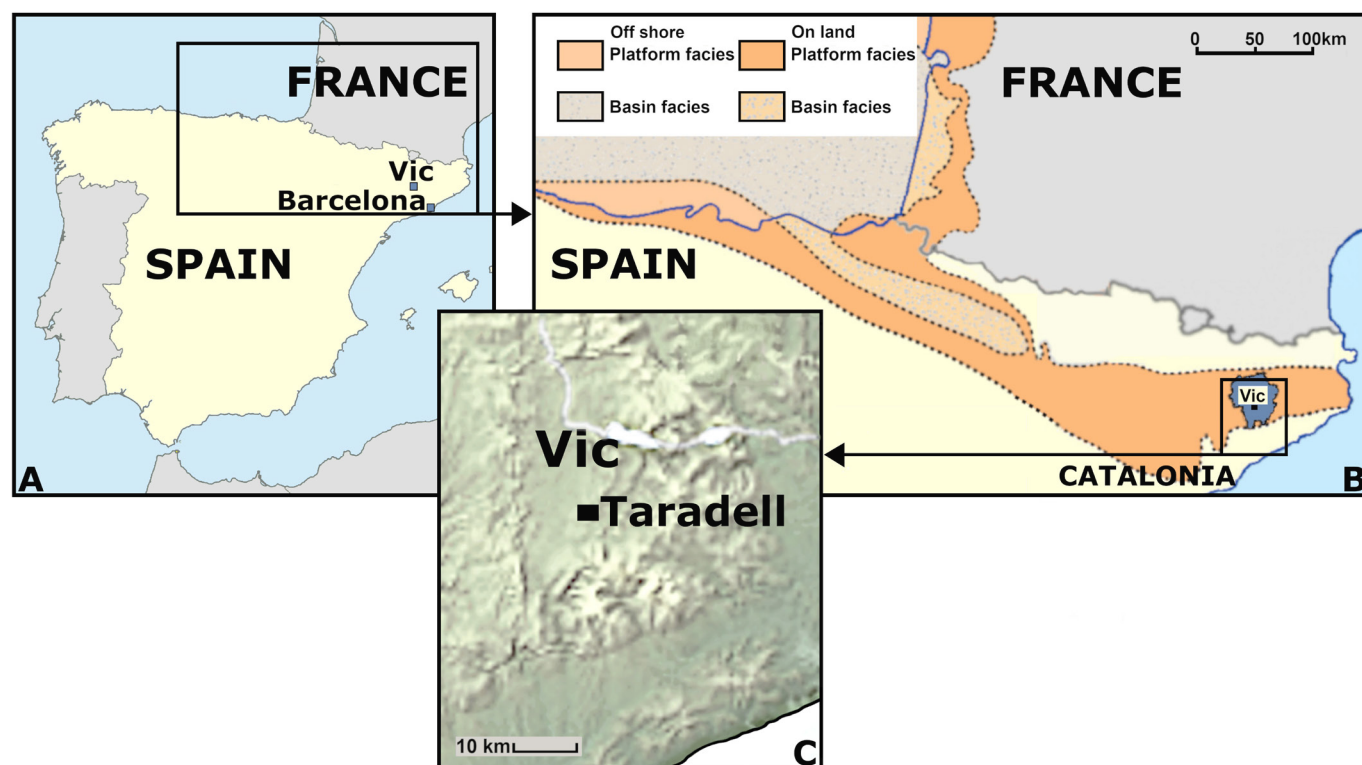
Figure 1 Study site. **A** Map of Spain, Portugal and a part of France, with the village of Vic near Barcelona, Catalonia, Spain. **B** The Ebro Basin in the Eocene with the Vic Area, modified after de Lapparent *et al.* (2018). **C** The Vic Area, with the village of Taradell. [H.J. van Vliet]

DEINSEA

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Figure 2 Section through the Eocene sediments of the Vic Area, Catalonia, Spain. Figure based on Serra-Kiel *et al.* (2003: fig. 10) and the timescales of Gradstein *et al.* (2020). Vertebra and horizontal arrow indicate that vertebral centrum, MGSB No. 25.191 probably originated from the Folgaroles Sandstone Formation. Vertical arrows in the upper parts of the section indicate that these are considered to be younger in age by some authors, with the Bartonian-Priabonian boundary lying below or within the Vespella Marl Member (Cascella & Dinarès-Turell 2009, Lapparent de Broin *et al.* 2018). [H.J. van Vliet]

to date more than 30 isolated bones and teeth that can be attributed to *Paychetus* from Germany (Uhen & Berndt 2008, Van Vliet *et al.* 2022), Ukraine (Gol'din & Zvonok 2013) and the Belgian-Dutch border (Van Vliet *et al.* 2022), as well as six associated remains or partial skeletons, all from Ukraine (Gol'din & Zvonok 2013; Goldin *et al.* 2014; Davydenko *et al.* 2021). Most or all finds (new and older) represent large species of *Pachycetus*, which is clearly the most abundant, large archaeocete taxon in Europe. It cannot be completely excluded that more than one taxon with more or less similar vertebral characteristics did exist in the Bartonian of Europe (Davydenko *et al.* 2021), but due to the fragmentary, often badly preserved remains, this is up to now only hypothetical.

MATERIAL AND METHODS
The studied vertebra is housed in the Museo Geológico del Seminario de Barcelona, Spain. All measurements were taken with digital calipers. All values were rounded to a millimetre. As we presume that the only preserved epiphyseal side of the partial vertebral centrum, MGSB No. 25.191 is the posterior one, its relative length (Rel L) is here calculated by the dorsal length divided by the presumed posterior width: Rel L = Ldors/Wp. Its relative width (Rel W) is calculated by the presumed posterior width divided by the presumed posterior height: Rel W=Wp/Hp.

The vertebra was cross-sectioned into two inequal pieces by Pilleri in or before 1989. The large piece is 75.5 mm and small piece 39 mm in dorsal length. By estimation, at least 3 mm (anteroposteriorly) of the vertebra was lost in this way (Fig. 3C). Traces of the sawing are still to be seen on surface of the small piece; the saw blade used, was maybe about 30 cm in diameter. The surface of the large piece has been polished, just like Pilleri (1989) remarked. Judged by the details of the picture provided by Pilleri (1989: plate II) the section surface seems to have been much higher in contrast than nowadays; it has become dull yellowish-brown to grey, although the structures are still visible (Figs 3A-B). This could be due to oxidation of the surface over 30 years, but maybe the contrast of details in the picture had been enhanced by other factors, like the use of an orthochromatic film, liquids to embrighten the surface, etc.

The picture of Pilleri (1989) was slightly manipulated by
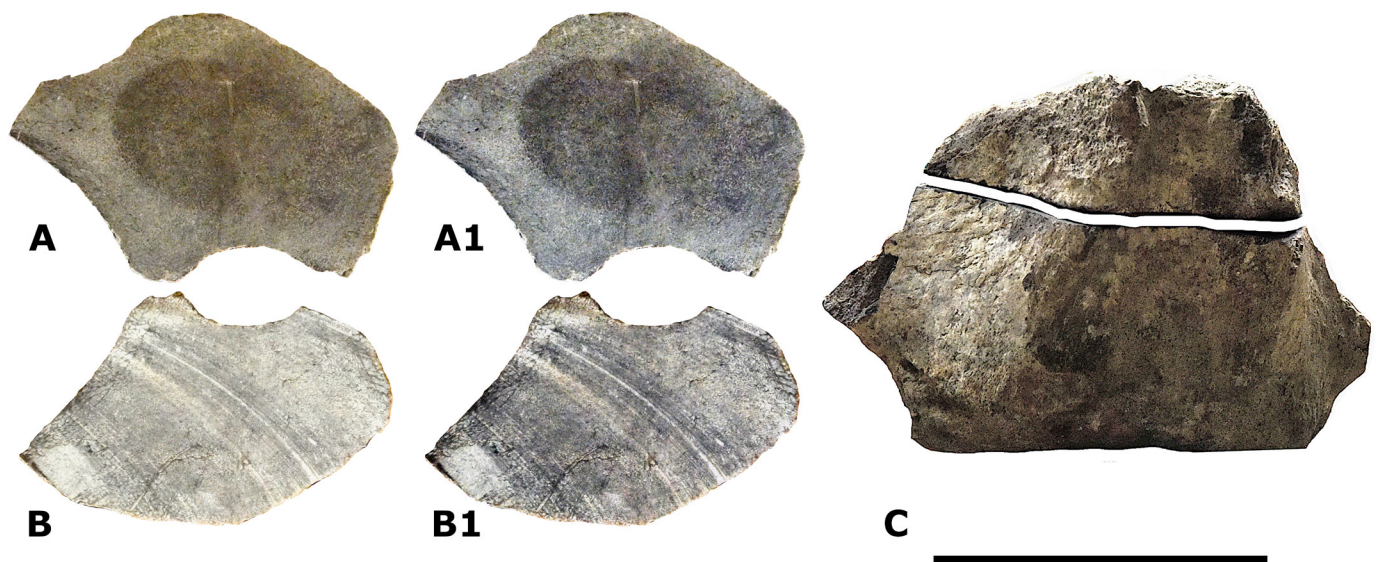
Figure 3 Sections of the partial, caudal vertebral centrum, MGSB No. 25.191, from Taradell, Catalonia, Spain, showing the axial cross-sections (in present-day condition) of the large posterior piece (**A-A1**) and the small anterior piece (**B-B1**), as well as the estimated part of the vertebra that is missing by the sectioning process (white zone in **C**). Both A1 and B1 have been manipulated by Photoshop to give a better impression of the inner structures of the vertebra. Note that the cross-sections seen in A and B have become rather dull yellowish-brown to grey over the years. Scale bar 10 cm. [Th. Paijmans]

the authors with Adobe Photoshop, to heighten the contrast between the dark and white parts. The bone compactness ('compacity') of several sections of this picture was calculated with the program 'boneprofiler' from the University of Montpellier, France (Girondot & Laurin 2003).

Anatomical abbreviations

ant, anterior; CCMC, compact, circumferential, multi-layered cortex; Ca, caudal vertebra; dors, dorsal; gen, genus; H, height; Hp, posterior height; NA, neural arch; Th, thoracic vertebra; L, length; Ldors, dorsal length of vertebral centrum; Lvent, ventral length of vertebral centrum; Lu, lumbar vertebra; post, posterior; Rel L, relative length; Rel W, relative width; sp., species (singular); spp., species (plural); vent, ventral; vert, vertebra; W, width; Wp, posterior width.

Institutional abbreviations

FSAC-Bouj, Faculty of Sciences Aïn Chock, Boujdour collection, Casablanca, Morocco. ID, identification number Heimatmuseum Schöningen, Germany. MGSB, Museo Geológico del Seminario de Barcelona, Spain. M, Museum in the monastery of Montserrat, Spain. MPZ, Paleontological Museum, Zaragoza University, Spain. NCSM, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA. NMR, Natural History Museum Rotterdam, Rotterdam, the Netherlands. RGM, registration number of the collections of Naturalis Biodiversity Center, Leiden, the Netherlands. UM, University of Michigan Museum of Natural History. USNM, United States National Museum of Natural History, Washington DC, USA.

Terminology

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

GEOLOGICAL SETTING

The Ebro Basin, the southern Foreland Basin of the Pyrenees, is located in Northern Spain, south of the Pyrenees (Lapparent de Broin *et al.* 2018) (Fig. 1). In the Palaeogene, this basin was a large marine gulf opening to the west into the Atlantic Ocean, with the eastern part of this gulf temporarily opening to the Tethys Ocean (Lapparent de Broin *et al.* 2018). Taradell, the find locality of the cetacean vertebra, is part of the Vic Area (Plana de Vic), the easternmost part of the Ebro Basin (Cascella & Dinarès-Turell 2009). This region is rich in Eocene sediments (Fig. 1). In the Lutetian to Priabonian strata, several transgressive and regressive phases or sedimentary cycles are recognised (Serra-Kiel *et al.* 2003).

Reguant (1967: 242) pointed to two characteristics of the Eocene marine sedimentation of the Vic Area: both its monotony and its variability, manifested in rapid changes of thickness and lithology. For these reasons, stratigraphic series have a very local value (Reguant 1967). Nevertheless, the following

Table 1a Dimensions vertebral centrum MSGB No. 25191, *Pachycetus* sp. (in mm)

Taxon	Vert	Length	Width NA	Width	Height	Rel W Wp/ Hp	Rel L Ldors/ Wp	References
MGSB25.191 Archaeoceti, gen. et sp. indet.	Ca (10-12?)	110	60 (ant) 37 (post)	115	105			Pilleri, 1989
Pachycetus sp.	Ant Ca	>115 (dors) >110 (vent) e138	37 (ant) 50 (post)	>110 (ant) 112 (post)	>77 (ant) 104 (post)	1.08	e1.23	This article

Table 1b Dimensions lumbar and caudal vertebral centra of several pachycetine species (in mm)

Taxon	Vert	Length	Width NA	Width	Height	Rel W W/H	Rel L Ldors/W	References
USNM310633 *P. wardii* Uhen, 1999	LuB Fig. 5: C1	164 (dors) 165 (vent)	?	110 (ant) 120 (post)	93 (ant) 96 (post)	1.18	1.49	Uhen 1999: appendix 1
USNM449549 *P. wardii*	LuC Fig. 5: C2	~164 (dors) ~163 (vent)	?	119 (ant) ~137 (post)	~109 (ant) ~112 (post)	~1.09	~1.38	Uhen 1999: appendix 1
USNM310633 *P. wardii*	CaA (ant)	?	?	? (ant) 98 (post)	? (ant) 125 (post)	?	?	Uhen 1999: appendix 1
NCSM11284 *P. wardii*	Ca (post) **)	106	?	?	?	?	?	Uhen 2001
FSAC-Bouj-11 *A. aithai* Gingerich & Zouhri, 2015	Lu2? Fig. 5: B1	158	44	104 (ant) 111 (post)	87 (ant) 94 (post)	1.20	1.52	Gingerich & Zouhri 2015: table 2
FSAC-Bouj-11 *A. aithai*	Lu3? Fig. 5: B2	175	42	111 (ant) 108 (post)	101 (ant) 102 (post)	1.10	1.58	Gingerich & Zouhri 2015: table 2
P. paulsonii Brandt, 1873	Lu '1' *) Fig. 5: D1	269 (vent)	126	~173 (ant)	~162 (ant)	~1.07	~1.55 (Lvent)	Fedorovsky 1912, Kellogg 1936: table 24
P. paulsonii	Lu '5' Fig. 5: D2	274 (vent)	107	164 (ant)	157 (ant)	1.04	1.67 (Lvent)	Fedorovsky, 1912, Kellogg 1936: table 24
P. paulsonii	Ca '9' **) Fig. 5: D3	190 (vent)	~e32 (post)	146 (ant)	138 (ant)	1.06	1.30 (Lvent)	Fedorovsky 1912, Kellogg 1936: table 24
P. paulsonii	?Ca '10' Fig. 5: D4	220 (vent)	?	~137 (ant)	~127 (ant)	~1.08	~1.61 (Lvent)	Fedorovsky 1912, Kellogg 1936: table 24

*) One epiphysis missing; **) Both epiphyses missing

Abbreviations: A., *Antaecetus*; ant, anterior; Ca, caudal vertebral centrum; dors, dorsal; e, estimated; H, height; Hp, posterior height; indet., indeterminable; L, length; Ldors, dorsal length; Lvent, ventral length; Lu, lumbar vertebral centrum; NA, neural arch; P., *Pachycetus*; post, posterior; rel, relative; sp, species; vent, ventral; W, width; Wp, posterior width; ?, unknown; ~, about; >, more than; /, fraction

Table 2a Thickness trabecular struts of the Taradell vertebra, MSGB No. 25.191 (mean value of the trabecular struts at six places, in μm)

MGSB 25.191	Mean thickness
Cortex ri-lateral dorsal	334
Cortex pr.transv. dorsal	299
Cortex pr.transv. ventral	330
Cortex ventral inner part	347
Cortex ventral outermost part	330
Midpart dorsal	351
Midpart Ventral	322
Midpart lateral	364

Table 2b Compacity of the Taradell vertebra, MSGB No. 25.191

Region	Section	Compacity	Surface (in mm)	Sum value	Mean value
Central part	B	0.640	13 × 8	0.666	
	C	0.549	10 × 10	0.549	
	D	0.498	10 × 10	0.498	
	E	0.610	10 × 10	0.610	
	F	0.454	10 × 10	0.454	
B-F			50.4	2.7766	0.551
Inner cortex (ventral)	G	0.502	10 × 10	0.502	
	H	0.551	20 × 8	0.882	
G-H			26.0	1.3836	0.532
Outer cortex (ventral)	I	0.569	10 × 10	0.569	
	J	0.594	10 × 10	0.594	
	K	0.538	20 × 12	1.291	
I-K			44.0	2.4542	0.558
Lateral cortex	L	0.615	10 × 10	0.615	
	M	0.513	10 × 13	0.667	
	N	0.611	7 × 20	0.855	
L-N			37	2.1394	0.578
Total compacity B-N			15.74	8.7538	0.556

Abbreviations: pr.transv., processus transversus; ri-lateral, right-lateral

strata and formations are discerned, albeit that the age and naming of the formations show a rather high variability in literature too. The whole section reaches a thickness of 1200 m (Lapparent de Broin *et al.* 2018).

The Lutetian Banyoles Marls are encountered at the base of the section in the Vic Area, and above it the Tavertet Limestones (Cascella & Dinarès-Turell 2009). These are followed by the late Lutetian to early Bartonian sandstones of the Folgarolas (Folgueroles) Formation (Serra-Kiel *et al.* 2003, Cascella & Dinarès-Turell 2009, Lapparent de Broin *et al.* 2018). At Aguaitallops, near Taradell, these deposits reach a thickness of about 12 m with molluscs in its middle and upper parts (Abad 2001: 273). The lithology is suggestive for a near-coastal environment. These deposits are capped by the Igualada Formation (or Vic-Manlleu Marl Formation), about 200 m thick (Serra-Kiel *et al.* 2003, Farrés & Fierstine 2009), in which four members are discerned. The first members of this formation contain invertebrate fossils (Farrés & Fierstine 2009) and turtles in the La Guixa & Gurb Member (Lapparent de Broin *et al.* 2018). The Vespella Marl Member is the last marine member, with in its lower parts molluscs and vertebrate fossils, e.g. chondrichthyans and turtles (Farrés and Fierstine, 2009, Lapparent de Broin *et al.* 2018). The age of the Vic-Manlleu Marls Formation has been disputed. The whole formation was thought to be Bartonian in age with the Bartonian-Priabonian boundary above the Vespella Marls Member (Serra-Kiel *et al.* 2003). Other authors reckon the upper parts of the formation to the Priabonian with the Bartonian-Priabonian boundary between the upper part of the Manlleu Member and the lower part of the Vespella Marl Member (Cascella & Dinarès-Turell 2009). At the top, the Vespella Marl member gradually gives way to lacustrine sediments of the Priabonian Sant Martí Xic deltaic complex and the Cardona Formation (Cascella & Dinarès-Turell 2009, Farrés & Fierstine 2009). It is followed by the continental Priabonian Artés Formation (Farrés & Fierstine 2009) (Fig. 2).

SYSTEMATIC PALAEONTOLOGY
Order Cetacea Brisson, 1762
Unranked clade Pelagiceti Uhen, 2008
Family Basilosauridae Cope, 1868
Subfamily Pachycetinae Gingerich, Amane & Zouhri, 2022
Genus *Pachycetus* Van Beneden, 1883

Type species: *Pachycetus robustus* Van Beneden, 1883

***Pachycetus* sp.**

Material
MGSB No. 25.191, from Taradell, Spain; partial vertebral centrum (Figs 3-6).

DESCRIPTION
MGSB No. 25.191 is a vertebral centrum, with the pedicles of the neural arch and the base of the transverse processes only partly preserved. On what is thought to be the anterior side, a large part of about 30 mm is missing, which includes the epiphyseal side. Measurements are given in Tables 1 and

2. The vertebral centrum consists nowadays of two parts. The vertebral centrum appears to be somewhat deformed by external pressures during the fossilisation process. Judging by its weight, it is permineralised. The centrum is abraded and yellowish-brown to grey in colour. Some sediments are still adhering to the vertebral centrum, especially on the ventral surface. The presumed posterior epiphysis is fused with the vertebral centrum. The epiphyseal surface is concave, with the deepest point of the epiphysis slightly off-center towards the dorsal side of the vertebra. The pedicles of the neural arch are at their base about 21 mm thick. Dorsal and ventral foramina seem to be absent; see 'Discussion'. The transverse processes are broken; only the bases of the processes are preserved on the (presumed) posterior half of the lateral sides. The left transverse process has a fresh break surface; it appears to consist at its base nearly completely of the CCMC. The break surface of the right transverse process is abraded. The bases of the transverse processes, 27 mm thick, are slightly deflected ventrally. On the ventral side, two shallow longitudinal ridges are running anterior-posteriorly with a distance of about 40 mm from each other. They become broader and more prominent towards the (presumed) posterior epiphyseal side, forming here two shallow protuberances (Fig. 4).

The sectioning done by Pilleri (1989) revealed the inner structure with two rather large vascular canals. In the section surface of the large piece, a part of the (presumed) right canal is running dorsoventrally at the central region (Fig. 4C, left); a part of another rather large one is located more to the ventral side of the cross-section (Fig. 4C, right). Some smaller canals are seen ventrally to the left (Fig. 4C, right). In the section surface of the small piece only a small part of the latter ventrally located vascular canal is seen, but traces seem to show that it was also running through the midpart of the vertebral centrum. Therefore, and because of the similar breadth and the more or less opposite places, the left, ventral vascular canal and the right, dorsoventral canal could be a pair as described below ('Discussion'). The surface of the small piece reveals also some other ventrally located vascular canals at the left side (Figs 3B & B1). The CCMC as seen in the cross-section has a thickness of maximum 16 mm at the ventral side, 4 mm at the dorsal side, and 8 mm at the lateral side. There are about 18-20 layers, each consisting of a compact and a more spongy layer (Fig. 4C). At many places, the outermost layer(s) of the CCMC are missing. Multiple, small elongate punctae are present on the whole surface of the vertebra, but are especially abundant on the dorsal side, between the pedicles of the neural arch. Where the outermost layers are missing, it is seen that the cortex consists of multiple tiny vascular canals, running antero-posteriorly (Figs 5A & A1).

STRATIGRAPHIC ASSIGNMENT
Vertebra MGSB No. 25.191 was part of a paleontological collection, given to the MGSB by the Solé brothers around 1985. They lived near Taradell. No more geographic or stratigraphic details have been given, than that the here described vertebra was collected in Bartonian sediments of Taradell. Taradell (N 41°52'3'' – W 2°17'1''), is located about 68 km north of Barcelona, Catalonia, Spain and about 9 km
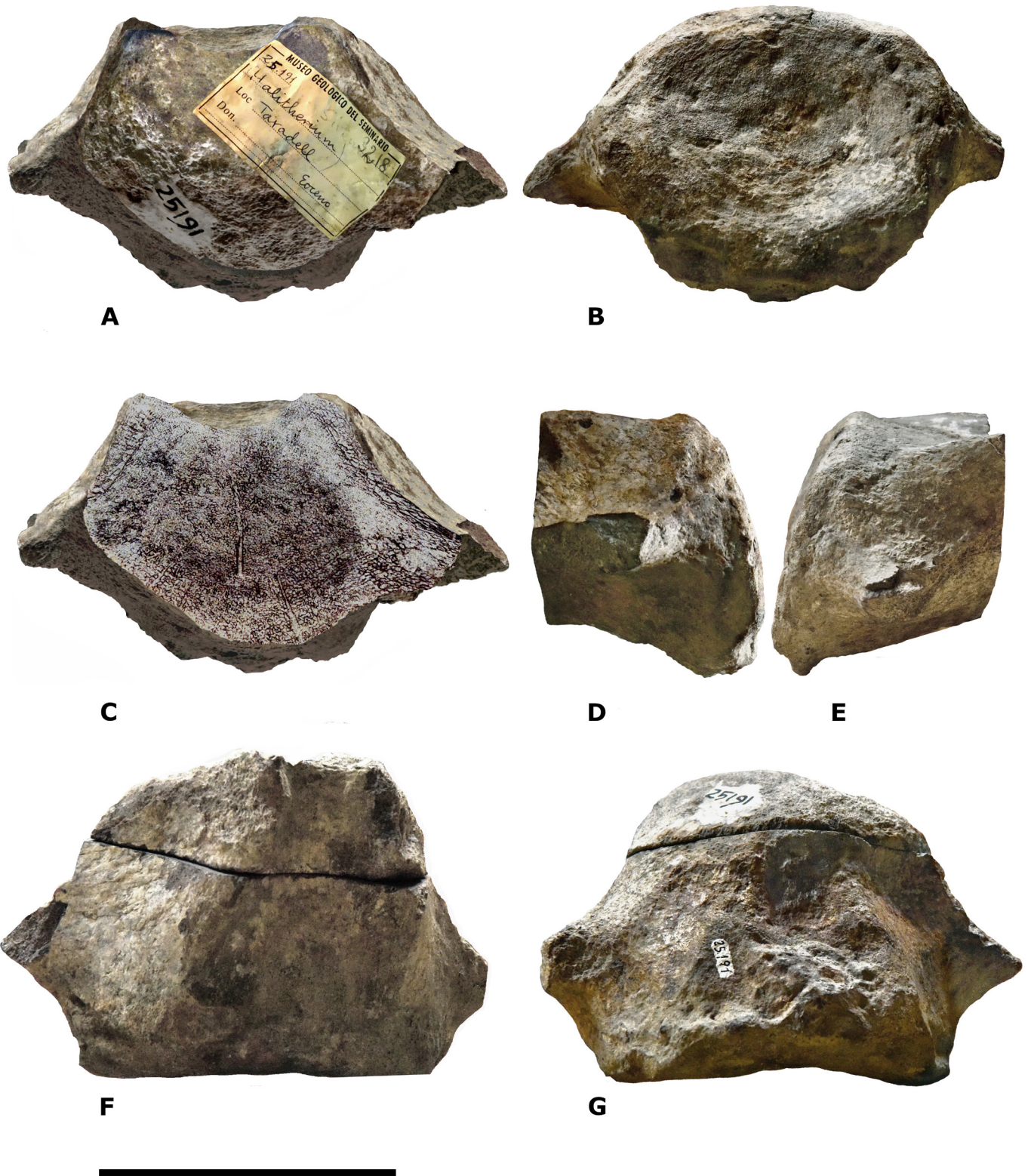
Figure 4 Partial, caudal vertebral centrum, MGSB No. 25.191, from Taradell, Catalonia, Spain, in anterior (**A**), posterior (**B**), axial cross-section (**C**), left lateral (**D**), right lateral (**E**), dorsal (**F**) and ventral (**G**) view. The cross-section in C shows the multiple layers of the cortex, the compact bone in the central area, as well as two large and some smaller vascular canals. It is right through the midpart of vertebra MGSB No. 25.191, as proved by the vascular canals. The vertebra as it is now, with superimposed the section as figured by Pilleri (1989: plate II). Note that in F, the dorsal foramina and in G, the ventral foramina are hardly or not visible, probably due to the cross-sectioning. Scale bar 10 cm. [Th. Paijmans]

Table 3 Dimensions of anterior caudal vertebrae in some Eocene sirenians (in mm)

Taxon	Vert	Length	Width	Height	References
Sirenia from Catalonia, Spain					
'P4' *) 'Prototherium montserratense' Pilleri et al., 1989	Ca	36	40	37	Pilleri et al. 1989: table XII & plate XXII
'P5' *) 'Prototherium montserratense'	Ca	35	40	30	Pilleri et al. 1989: table XII
MGSB 41.159 ? Prototherium sp.	Ca	38	50	30	Pilleri et al. 1989: p. 49 & fig 19
MGSB 43.468 ? Prototherium sp.	Ca	43	75	40	Pilleri et al. 1989: table XV
MGSB 43.468 ?Prototherium sp.	Ca	45	65	35	Pilleri et al. 1989: table XV, fig 21
M 325 ?Prototherium sp.	Ca	32	53	30	Pilleri et al. 1989: table XXI, fig 30
M 325 ?Prototherium sp.	Ca	35	45	28	Pilleri et al. 1989: table XXI, fig 30
Sirenia from Bay of Biscay Spain					
MPZ 2017/20 Sobrarbesiren cardieli Díaz-Berenguer et al., 2018	ant Ca	53	70	40	Díaz-Berenguer et al. 2018
Sirenia from France					
RGM 814737 Prototherium taulannense Sagne, 2001	ant Ca	42	65	44	Own measurements
RGM 814737 Prototherium taulannense	ant Ca	43	63	41	Own measurements
Sirenia from Egypt					
UM 101226 Eosiren libyca Andrews, 1902b	Ca1	51	-	-	Zalmout & Gingerich 2012: table 33
UM 101226 Eosiren libyca	Ca3	48	72	-	Zalmout & Gingerich 2012: table 33
UM 97514 Eotheroides clavigerum Zalmout & Gingerich, 2012	Ca2	41	63	38	Zalmout & Gingerich 2012: table 8
UM 97514 Eotheroides sandersi Zalmout & Gingerich, 2012	Ca1	42	62	-	Zalmout & Gingerich 2012: table 33
UM 97514 Eotheroides sandersi	Ca3	40	-	-	Zalmout & Gingerich 2012: table 33
UM 101224 Protosiren smithae Domning & Gingerich, 1994	Ca1	53	70	-	Zalmout & Gingerich 2012: table 33
UM 101224 Protosiren smithae	Ca3	46	71	-	Zalmout & Gingerich 2012: table 33

*) Technician's numbering according to Pilleri (1989)
Abbreviations: Ant, anterior; Ca, caudal
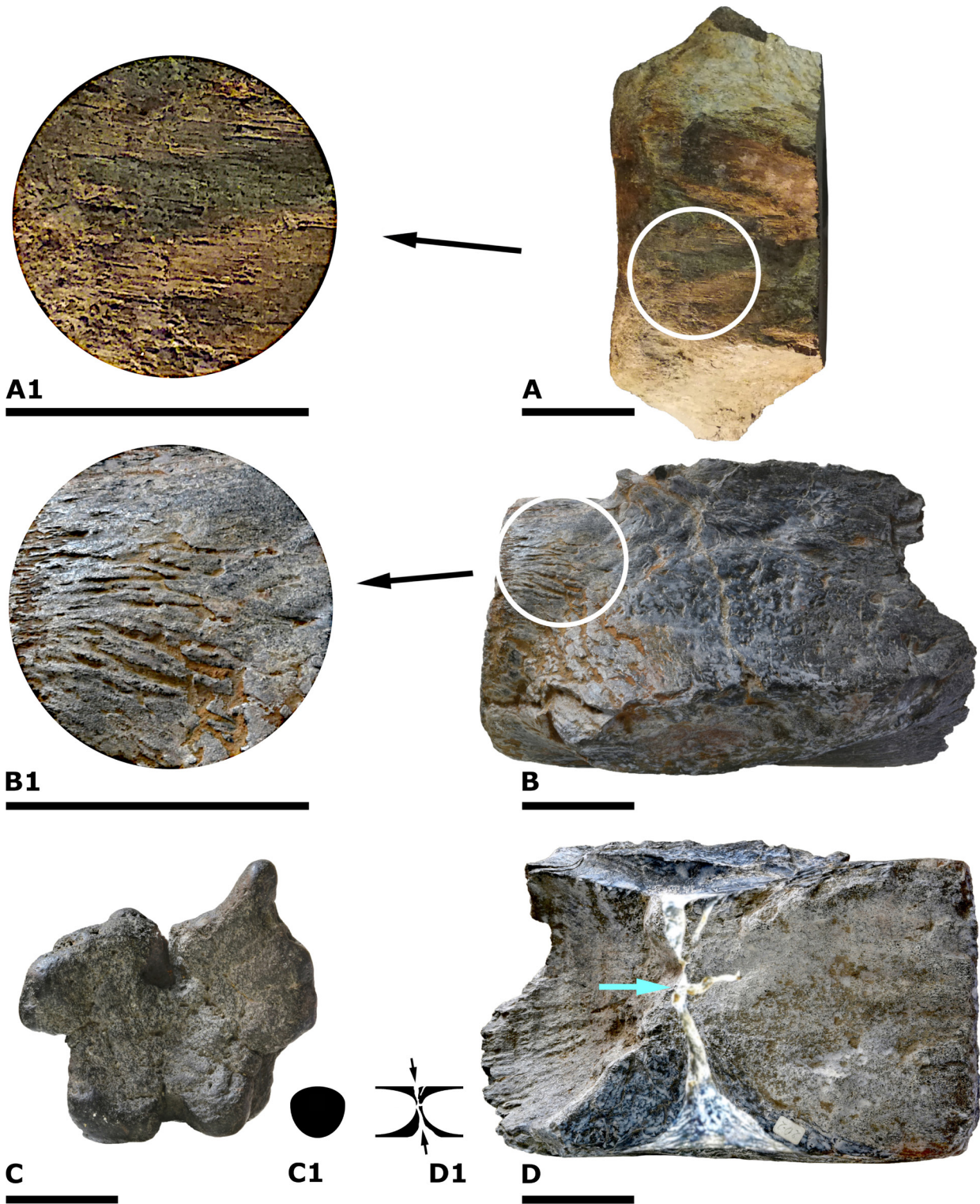
Figure 5 Comparison of the cortex and midpart of some vertebral centra, assigned to *Pachycetus*.
A Caudal vertebral centrum, MGSB No. 25.191, from the Taradell, Vic Area in Catalonia, Spain, in dorsal view. White circle indicates the part of the vertebra that is magnified in **A1**, showing the tiny longitudinal vascular canals in the cortex. The outer parts of the cortex are missing. **B** Lumbar vertebral centrum, ID20-2 (Van Vliet *et al*. 2020), assigned to *Pachycetus* sp. from Alversdorf, Helmstedt region, Germany in right lateral view. White circle indicates the part of the vertebra that is magnified in **B1**, showing longitudinal vascular canals in the cortex, comparable with those of 'A'. **C** Partial posterior thoracic or lumbar vertebral centrum, ID20-3, assigned to *Pachycetus* sp. Alversdorf, Helmstedt region in axial view, consisting of only the midpart of the original vertebral centrum. **C1** Schematic drawing of this midpart. ID20-3 was described, but not figured by Van Vliet *et al*. (2020). **D** Lumbar vertebra, ID20-2 (Van Vliet *et al*. 2020), assigned to *Pachycetus* sp. from Alversdorf, Helmstedt region, Germany in midsagitttal view, showing the multi-layered cortex, the midpart, the posterior conus and the place of the missing anterior conus of the vertebral centrum. The dorsoventral vascular canals running through the midpart of the centrum have been made brighter. Blue arrow indicates the central midpoint of the midpart of the vertebral centrum through which the dorsoventral vascular canals are running. **D1** Schematic drawing of the cortex and the vertebral midpart. White lines indicate the dorsoventral vascular canals. Black arrows indicate the probable direction of sectioning of MGSB No. 25.191. Scale bars 5 cm. [Th. Paijmans]

south of Vic (Fig. 1 and section 'Geologic setting'). Adhering sediments (from the ventral side of the vertebra) have been investigated for age-diagnostic microfossils, but appeared to contain only large, essentially non-diagnostic plant remains (S. Louwye, pers. comm. 2020). According to Abad from the MGSB, the studied vertebra could have been derived from the late Lutetian to early Bartonian Folgarolas Formation (A. Abad, pers. comm. 2020).

DISCUSSION

In Table 3, some measurements of Eocene sirenian vertebrae are given; these vertebrae are indeed significantly smaller than MGSB No. 25.191 as was remarked by Pilleri (1989). The pock-marked surface of the vertebra and a thick CCMC underneath, the elongation of the centrum, as indicated by the estimation of its original length, as well as the apparent anterior-posteriorly elongated and pachyostotic pedicles of the neural arch, are considered specific for the archaeocete genus *Pachycetus* (Gol'din & Zvonok 2013, Van Vliet *et al.* 2020).

Because the base of the pedicles of the neural arch begins at about 37 mm from the epiphyseal side and because of the gently forward sloping angle of the transverse processes on this side, the preserved epiphysis is interpreted as the posterior part of the vertebra. The low relative width of 1.08 probably excludes a thoracic position; the width of thoracic vertebrae in *Pachycetus* is considerably larger than the height (Gol'din & Zvonok 2013). The two shallow and abraded protuberances on the presumably posterior ventral side of the vertebral centrum are interpreted as facets for the haemal arch. The transverse processes in MGSB No. 25.191 arise near the dorsoventral midpart of the lateral sides, not ventrally as in lumbar vertebrae assigned to this genus (Davydenko *et al.* 2021, Van Vliet *et al.* 2022); see Figs 4 A-C. Also in *Cynthiacetus peruvianus* and *Dorudon atrox* Andrews, 1906, the transverse processes of caudal vertebrae arise at a more dorsal level on the lateral sides, than seen in lumbar vertebrae (Martínez-Cáceres *et al.* 2017: p.104, Uhen 2004: figs 85 & 92). For these reasons, a caudal position for MGSB No. 25.191 is the most probable.

Due to damage, the original length of the centrum MGSB No. 25.191 can only be estimated. This estimation is based on the following two observations:

First, in the natural sagittal cross-section of two lumbar vertebrae, vertebra ID20-2 (Figs 5D & D1) and NMR999100151795 of *Pachycetus* sp. from the Helmstedt region, Germany, it is seen that only dorsoventral vascular canals lie in the anatomical midpart of the vertebral centrum and pass in a straight line through the central point of this midpart. See for NMR999100151795, and also ID20-2 with anterior and posterior coni, Van Vliet *et al.* (2020: plate 3A & C). The dorsoventral vascular canals however can have oblique branches towards the dorsal (and in caudal vertebrae probably also towards the ventral) vertebral surface (Figs 5D & D1). The distance of the central point of the anatomical midpart to the posterior epiphyseal side of vertebra ID20-2 is about 53% of the total vertebral length (with anterior and posterior coni).

Secondly, in caudal and lumbar vertebrae of *Pachycetus paulsonii* and *Pachycetus* sp. the vascular ventral foramina

(the orifices of the dorsoventral vascular canals) are lying at the midpart of the vertebral centra. In two caudal vertebrae of *Pachycetus paulsonii*, figured by Fedorovsky (1912), the distance of the ventral foramina to the posterior epiphyseal side is also about 54 % of the total vertebral length. See for the two caudal vertebrae of *P. paulsonii*, Figs 6C-F; Fedorovsky (1912: plate 3 15-18) and Kellogg (1936). (It has to be remarked that, although Kellogg (1936: p.99) mentioned, that the second vertebra, described by Fedorovsky (1912: plate 3 17-18) (Figs 6E-F), could be a lumbar one, it is here assigned to a caudal position in accordance with Fedorovsky. This, because of the more dorsal position of the transverse processes on the lateral sides of the vertebral centrum, instead of a ventral position as in lumbar vertebrae; the presence of protuberances for the hemal arch; the apparent indentation for the spinal arteries at the anterior edges of the transverse processes and the ventral foramina being smaller than in the other caudal vertebra (Figs 6C-D). The last feature points to a more posterior position than the first caudal vertebra).

The right dorsoventral vascular canal, seen in the cross-section of MGSB No. 25.191, is most probably one of the two main vascular canals, because it goes in a straight line through the central point of the midpart, obviously without bending anteriorly or posteriorly. Therefore, it must have been positioned at the anatomical midpart of the vertebral centrum. The dorsal length of the presumed posterior part of MGSB No. 25.191 is 75.5 mm, the ventral length 71 mm. The length from the central midpoint (through which the right dorsoventral vascular canal is running) to the posterior epiphyseal side is slightly more than 73.3 mm, because this midpoint is probably located slightly more to the dorsal vertebral surface (see Figs 5D & D1). If the distance of this midpoint to the posterior epiphyseal side is also here 53% of the total vertebral length, the original length of MGSB No. 25.191 would have been slightly more than 138 mm, with an estimated relative length of 1.23. This indicates a moderate elongation.

The dimensions of ventral foramina in caudal vertebrae of *P. paulsonii* (Figs 6C & E and Table 1B) are smaller, than the very large ventral formina in lumbar vertebrae of *Pachycetus* spp (Figs 4D & D1). The seemingly absence of dorsal and ventral foramina, openings of the vascular canals seen at the surface of the cross-section, can be possibly explained by infill of sediments (matrix) and by adhering sediments, but maybe also a part of the relatively small foramina was lost by the process of sawing.

The relative width of the two caudal vertebrae of *P. paulsonii* (Figs 6C-F) as described by Fedorovsky (1912) is more or less the same as that of MGSB No. 25.191 (Tables 1A-B). The relative length of the second one (with both epiphyses) is with 1.61 larger than that of MGSB No. 25.191. The relative length of the first vertebra is almost similar to MGSB No. 25.191, but here the epiphyses are lacking. Because of the width of the neural arch (50-37 mm), MGSB No. 25.191 is assigned an anterior caudal position. For comparison, the posterior width of the neural arch in the first caudal vertebra (without epiphyses), figured by Fedorovsky (1912) (Fig. 6D) is estimated to be about 32 mm.

With an estimated length of 138 mm and an anterior caudal
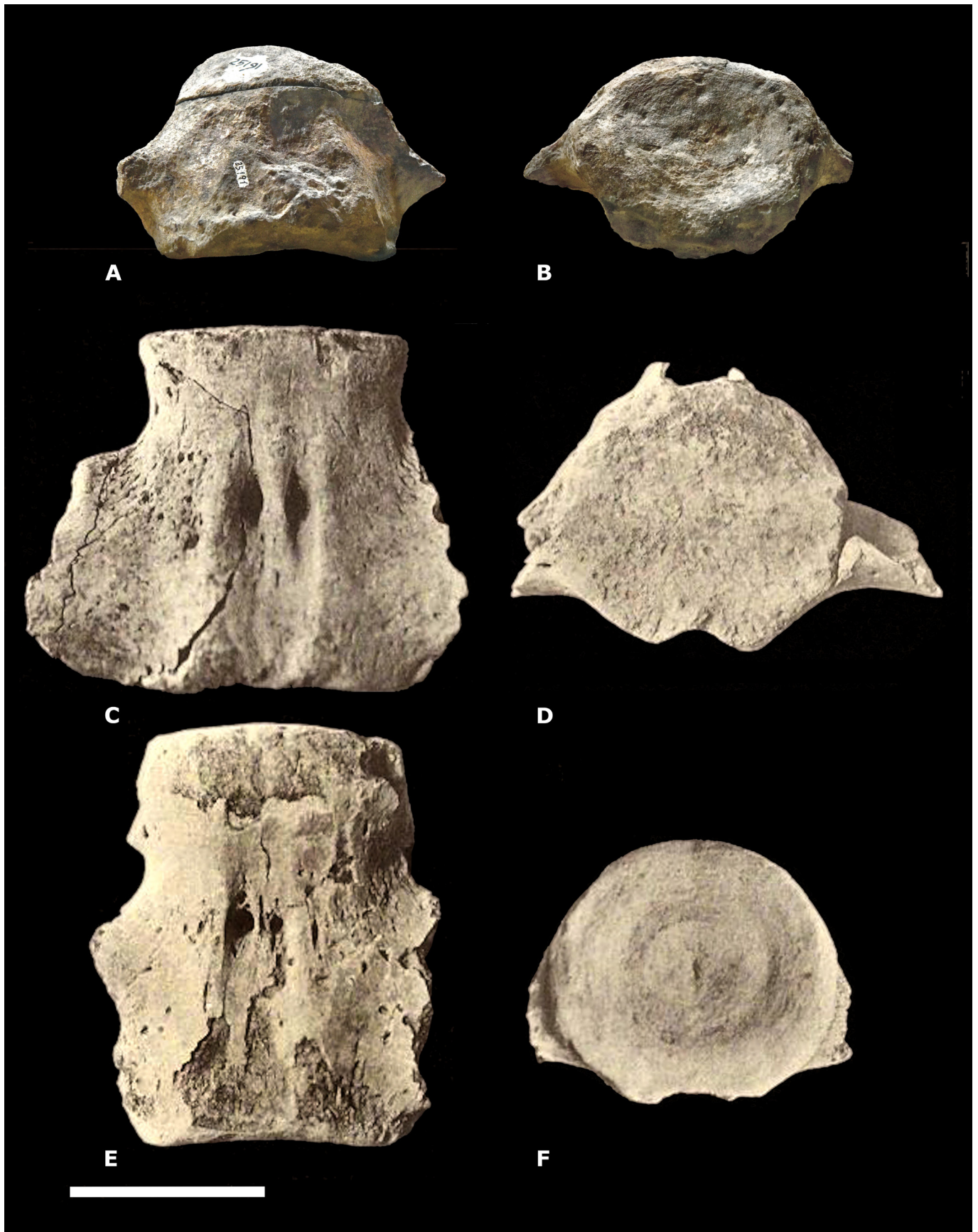
Figure 6 Comparison of the presumed anterior caudal vertebral centrum, MGSB No. 25.191 with two caudal vertebrae of *Pachycetus paulsonii* Brandt, 1873, described and figured by Fedorovsky (1912). MGSB No. 25.191 in ventral (**A**) and posterior (**B**) view. Caudal vertebra of *Pachycetus paulsonii,* no. 1 in ventral (**C**) and posterior (**D**) view. Caudal vertebra of *Pachycetus paulsonii,* no. 2 in ventral (**E**) and posterior (**F**) view. Note that the ventral foramina in C and E are located at the midpart of the total vertebral length. The epiphyses are present in caudal vertebra no. 2 of *Pachycetus paulsonii,* but absent in caudal vertebra no. 1. The largest vertebra (E-F) is here, in accordance with Fedorovsky (1912), considered a caudal one. Figure C-F modified after Fedorovsky (1912: fig. 3). Scale bar 10 cm. [H.J. van Vliet]

Figure 7 Scatter diagram with width plotted against length of vertebral centra, all assigned to pachycetine species, showing two different clusters of vertebrae. The circles A-C within the ellipse to the left, represent vertebrae, presumably belonging to small-sized species. **A** caudal vertebra, MGSB No. 25.191 from Taradell; **B1-2** anterior lumbar vertebrae of *Antaecetus aithai* Gingerich & Zouhri, 2015 from Morocco; **C1-2** lumbar vertebrae of *Pachycetus wardii* Uhen, 1999 from North Carolina. **D1-2** within the ellipse to the right, represent two presumably posterior lumbar vertebrae, **D3-4** two anterior caudal vertebrae, all belonging to one specimen, *Pachycetus paulsonii* Brandt, 1873 (Fedorovsky 1912, Kellogg 1936) from Ukraine. The lumbar vertebra D3 is missing both epiphyses, which can explain its smaller length than D4. Note that the caudal vertebrae D3-4 are smaller in length than the two lumbar vertebrae D1-2, which seems to be also the case in the caudal vertebra form Taradell compared to the lumbar vertebrae of the other small species of *Pachycetus* (B and C). Dimensions and other information of the here plotted vertebrae B-J are given in Table 1b. [H.J. van Vliet]
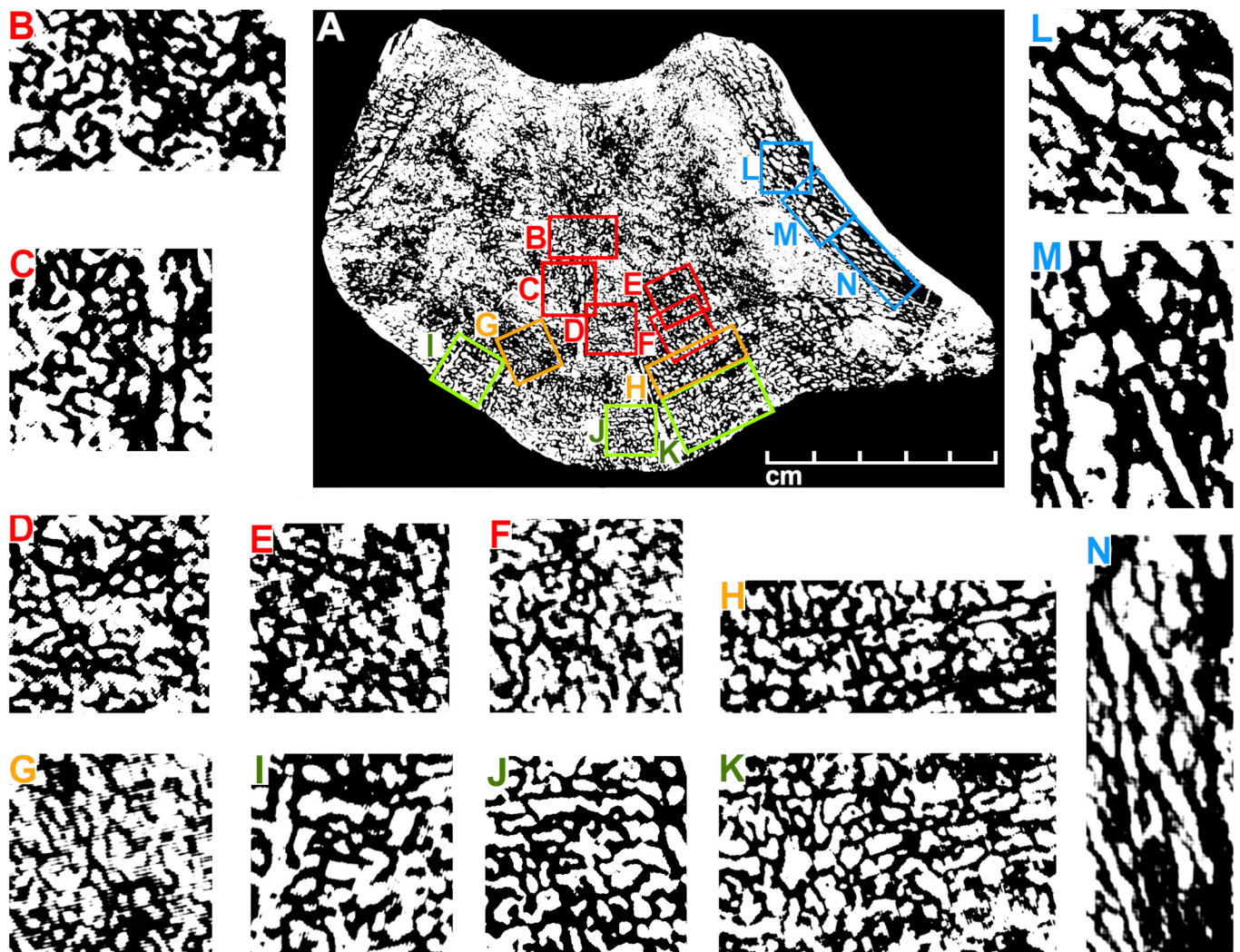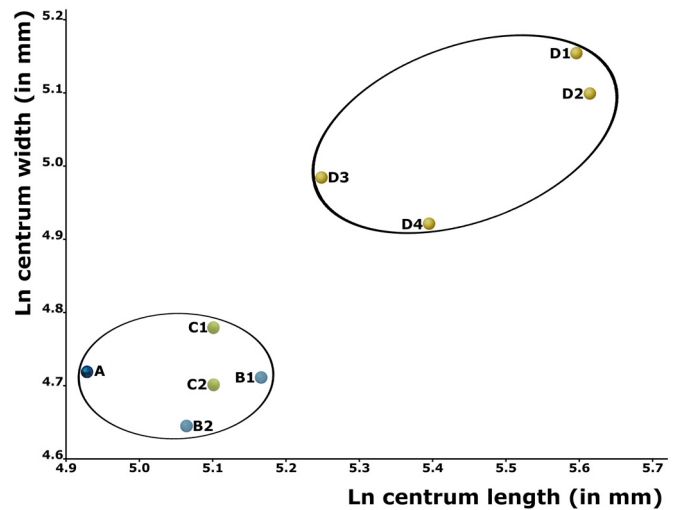
Figure 8 Sections used to calculate the bone compactness. **A** Axial cross-section of caudal vertebral centrum, MGSB No. 25, modified after Pilleri (1989: plate II). The contrast between dark and light areas has been enhanced. The sections used in the compactness calculation, are magnified and shown alongside and below 'A'. Colours of the rectangles indicate the particular areas from which the sections have been chosen; the numbers of the sections are in corresponding colours. The colour red (sections **B-F**) indicates the central area of the vertebra; amber (sections **G-H**) indicates the ventral inner cortex; green (sections **I-K**) indicates the ventral outer cortex and blue (sections **L-N**) indicates the presumed left lateral cortex. Separate compactness values and total mean values are given in Table 2. [M. Bosselaers and H.J. van Vliet]

position, MGSB No. 25.191 is significantly smaller than the caudal vertebrae assigned to *Pachycetus* from Ukraine (Table 1B and Fig. 7). Because of the fused epiphysis, the vertebral centrum has reached its fully-grown size. This size is more comparable to lumbar vertebral centra of *P. wardii* from North Carolina and Virginia, and *Antaecetus aithai* from Morocco (Table 1B and Fig. 7), indicating that MGSB No. 25.191 was from a small species as well. From the Southern Bight of the North Sea at least one lumbar vertebral centrum (NMR999100150839) could possibly belong to a small species of *Pachycetus* too (Van Vliet *et al.* 2022).

Contrary to the vertebra MGSB No. 25.191 with a fused epiphysis, none of the vertebral centra of *Pachycetus* from the Helmstedt Region, Germany has fused epiphyses (Van Vliet *et al.* 2020), nor the seven vertebrae assigned to the genus *Pachycetus* from the southern North Sea, at the Belgian-Dutch border (Van Vliet *et al.* 2022). Also in *Pachycetus* vertebrae from Ukraine (Gol'din *et al.* 2014), only some vertebrae have fused epiphyses (Van Vliet *et al.* 2020). This can be due to a relatively high frequency of young individuals dying in these regions. On the other hand, Gol'din *et al.* (2014) proposed, that the high frequency of vertebrae of *Pachycetus* lacking epiphyses could be ascribed to neoteny in which adult specimens still retain juvenile features. As in cetaceans, caudal and cervical vertebrae are the first in which the epiphyses get fused (Moran *et al.* 2015), it is yet possible, that also the Taradell cetacean still retained thoracic and lumbar vertebrae with unfused epiphyses at the time of its death.

Microstructure
The thickness of the trabecular struts has been measured at eight places: five from the cortex and three from the midpart of the vertebral centrum. Six measurements at each place have been conducted; the mean value of each set of six measurements is given in Table 2A. The thicknesses of the trabeculae appear to be remarkably uniform, without significant differences between the trabecular thicknesses of the cortex or those of the vertebral midpart. The mean value of the trabeculae of the cortex is 328 μm and that of the vertebral midpart 346 μm. The mean value of the trabeculae at these eight places is 335 μm. These values point to a moderate degree of osteosclerosis, compared with the values of Gray *et al.* (2007: table 2), in which the trabecular thicknesses of ribs of several archaeocetes, as well as some extant aquatic, semiaquatic and terrestrial mammals are given, all measured with the program BIOQUANT.

The compactness of 13 sections from four regions of the cross-section at the vertebral midpart has been calculated: five sections from the central region, two from the ventral inner cortex, three from the ventral outer cortex and three from the presumed left lateral cortex (Fig. 8). These regions have a rather similar compactness with mean values ranging between 0.551 to 0.578 (Table 2A). The mean compactness of the 13 sections in MGSB No. 25.191 is 0.556 (Table 2B) which can be called moderate. An extreme compactness of 0.952 was for instance seen in the proximal part of a rib of *Basilosaurus isis* Andrews, 1904 (Houssaye *et al.* 2015). The moderate

compactness of the centrum will be elaborated upon in another publication.

The mean compactness of vertebral centrum MGSB No. 25.191 is however significantly higher than that of a mysticete caudal vertebra from the Miocene of Belgium (*private collection* MB) which was found by us to be only 0.301. This is similar to the mean vertebral compactness of 0.318 in the Recent dolphin *Delphinus delphis* Linnaeus, 1758, whereas that of the lion (*Panthera leo* Linnaeus,1758) was found to be 0.460 (de Buffrénil *et al.* 1986). The vertebral compactness of this terrestrial mammal thus appears to be almost exactly intermediate between the lower compactness of derived neocetes, indicative of bone mass decrease, and the higher compactness of MGSB No. 25.191, suggestive for bone mass increase. Bone mass decrease in neocetes is associated with a hydrodynamic buoyancy control; bone mass increase in archaeocetes with a hydrostatic buoyancy control, which is considered an early adaptation to a marine environment (de Buffrénil *et al.* 1990, Gray *et al.* 2007).

CONCLUSIONS
The vertebral centrum MGSB No. 25.191, described by Pilleri in 1989, probably has been derived from the late Lutetian to early Bartonian Folgarolas Formation. It is ascribed to an anterior caudal position. With at least one fused epiphysis, it had most probably reached its full-grown size. The compactness of the axial cross-section, right through the midpart of the centrum is higher than that of vertebrae of Neogene and Recent cetaceans, or that of the terrestrial *Panthera leo*. It is thus far the only find of an archaeocete described from Spain. Its dimensions point to a small species of *Pachycetus*, but assignment on species level is not possible. At least one vertebral centrum from the North Sea could also belong to a small species of *Pachycetus*. New finds are needed to elucidate the distribution of small species of *Pachycetus* in Europe.

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