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HOW TO BREAK A SPERM WHALE'S TEETH: DENTAL DAMAGE IN A LARGE MIOCENE PHYSETEROID FROM THE NORTH SEA BASIN

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ABSTRACT—In contrast to the suction-feeding, predominantly teuthophagous extant sperm whale, several Miocene physeteroids display proportionally larger teeth, deeply embedded in both upper and lower jaws. Together with other osteological features, these differences lead to the functional interpretation of these taxa as macroraptorial predators, using their teeth to capture and process large marine vertebrates. However, the assumption that strong forces applied to macroraptorial physeteroid teeth during powerful bites and contacts with bone material should result in major dental damage has not yet been tested. In the present work, we analyzed a large collection of physeteroid teeth with an enameled crown from the Miocene of the North Sea Basin. We especially focused on a set of 45 teeth of *Scaldicetus caretti* discovered in Antwerp (Belgium, southern North Sea Basin) and tentatively dated to the Tortonian (early late Miocene). Visual inspection and computed tomography (CT) scans revealed dental damage, including wear and breaks. The latter could be interpreted as chipping fractures, occurring along the crown, and vertical root fractures, observed along the apical part of the massive root. Chipping fractures are most likely due to contacts with hard material, whereas vertical root fractures may result from the application of strong and repetitive bite forces and/or contacts with hard material. Such results further support the interpretation of a series of Miocene physeteroids with proportionally large teeth as macroraptorial (rather than suction-feeding) top predators. Considering the size of the teeth of *S. caretti*, its most likely prey items were other large marine vertebrates.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

The extant sperm whale *Physeter macrocephalus* (Physeteroidea, Physeteridae) is the largest modern toothed whale (Cetacea, Odontoceti), with adult males reaching a body length of 18 m (Rice, 1989). This giant among odontocetes is also one of the most ecologically specialized toothed whales: it feeds nearly exclusively upon cephalopods, which are detected by the echolocation system and captured in deep meso- to benthopelagic regions worldwide, at depths ranging between 400 and 1,200 m (Caldwell et al., 1966; Rice, 1989; Watwood et al., 2006; Fais et al., 2016). Whereas details of the prey capture process are currently poorly understood (Fais et al., 2016), *Physeter* is proposed to be a highly efficient, although aberrant, suction feeder, an interpretation based on morphological features (lack of functional upper dentition, slender lower jaw, peculiar shape and position of the tongue), the observation of otherwise healthy individuals with deformed or broken mandibles, and stomach contents showing complete squids with no tooth marks (Caldwell et al., 1966; Rice, 1989; Werth, 2004, 2006).

Contrasting with the deep-diving and suction-feeding extant sperm whale, a number of Miocene physeteroids (e.g., *Acrophyseter*, *Albicetus*, *Brygmophyseter*, *Livyatan*, and

Zygophyseter) display proportionally much larger teeth on the more robust upper and lower jaws, leading to the suggestion that these early relatives of *Physeter* did use their teeth to capture and possibly process large prey, such as other marine mammals (Bianucci and Landini, 2006; Lambert et al., 2010, 2017; Boersma and Pyenson, 2015). Until now, such a macroraptorial interpretation of these ancient sperm whales has been based on the comparison of size and proportions of cranial and dental features with the extant suction-feeding *Physeter* and the macroraptorial delphinid *Orcinus orca* (killer whale) (Bianucci and Landini, 2006; Lambert et al., 2010, 2017), whereas more direct evidence such as stomach contents or bite marks on other marine mammal bones is still lacking.

The present work starts with a hypothesis: strong forces applied to physeteroid teeth during powerful bites and/or bites on hard material (i.e., bone) should lead to specific dental damage, as observed in large terrestrial carnivores (e.g., Van Valkenburgh and Hertel, 1993; Lawn et al., 2013). In a previous work, bony outgrowths observed around posterior upper alveoli of one of these Miocene physeteroids were interpreted as the result of intense occlusal forces, thus providing further support for a macroraptorial interpretation (Lambert et al., 2014). Here, we focus on the teeth to test our premise. To do so we analyze a large sample of physeteroid teeth from the Neogene of Antwerp (southern margin of the North Sea Basin, Belgium) and describe dental damage on some of the teeth that we interpret as resulting from stresses related to strong bites and contact with hard material.

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Institutional Abbreviation—IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.

MATERIALS AND METHODS

The main sample used in this work is a set of 45 physeteroid teeth, IRSNB M.512 (numbered from A to 1S; Fig. 1; Table 1), discovered in Miocene deposits of the southern margin of the North Sea Basin (Borgerhout, Antwerp suburbs, Belgium) and used by du Bus (1867) to define the species *Scaldicetus caretti* (see also comments in Abel, 1905). Because physeteroid teeth do not bear enough diagnostic information, the genus and species *Scaldicetus caretti* were later restricted to this type material (Bianucci and Landini, 2006). Because these teeth

were found together (du Bus, 1867), display a similar shape, state of preservation, and color, and were most likely not reworked (considering the preservation of the thin edges of their pulp cavity), they most likely belong to a single individual. The fact that no cranial or mandibular elements were collected with the teeth may sound surprising. However, most of the fossil marine mammal remains discovered in the Antwerp area during the 1860s were not collected by researchers, but by soldiers, during the construction of fortifications around the city (du Bus, 1867). It is possible that highly fragmented skull material (a condition frequently encountered in nonconsolidated sand deposits of the area; e.g., type material of *Physeterula dubusi*; Lambert, 2008) was associated with the teeth but not collected due to its poor state of preservation.

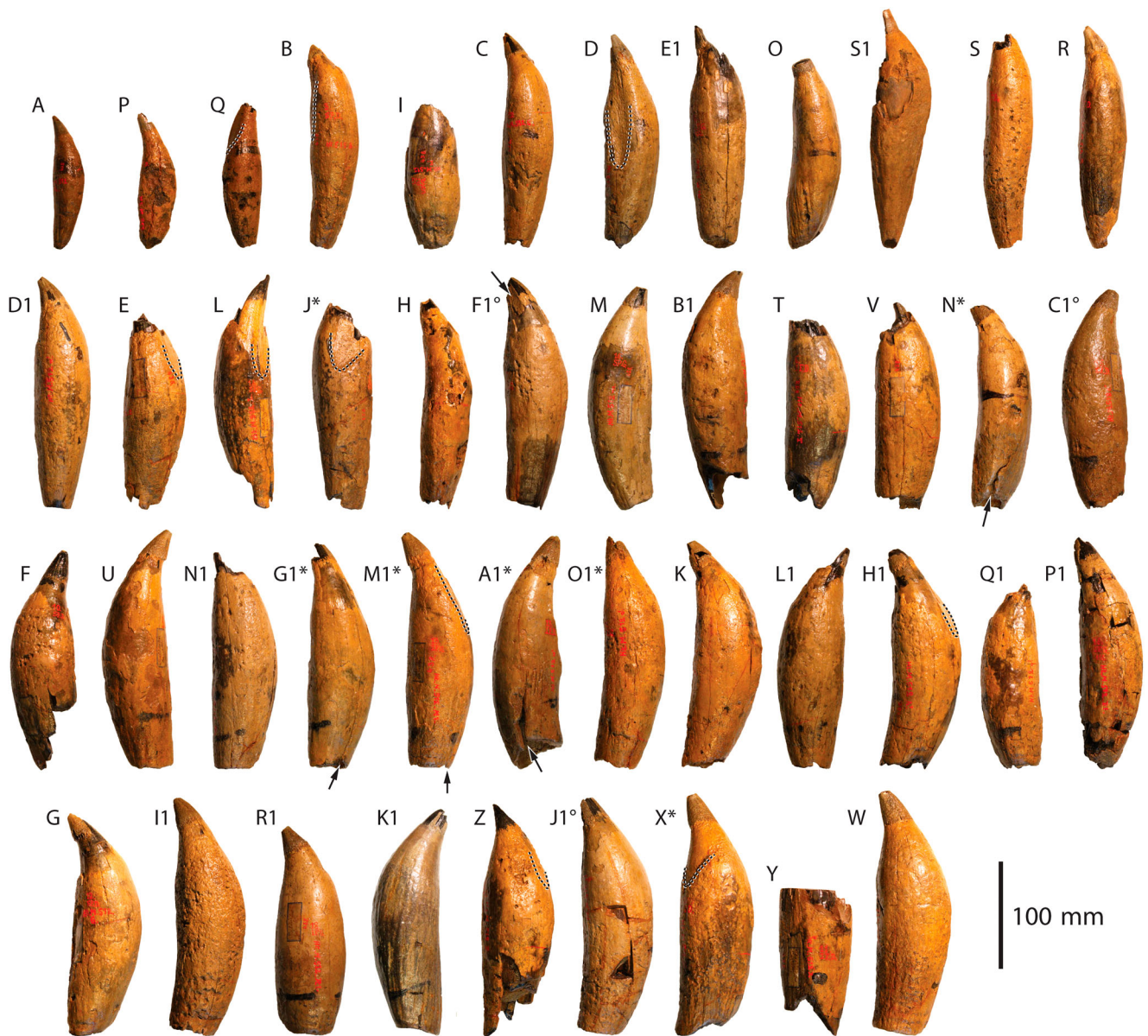


FIGURE 1. Forty-five teeth of the physeteroid *Scaldicetus caretti* IRSNB M.512 (lectotype), Miocene of Borgerhout, Antwerp, Belgium. Teeth are illustrated in a view perpendicular to their strongest curvature plane, and the sequence goes from the upper left with the smallest teeth (lowest root diameter) to the lower right with the largest teeth (greatest root diameter). Letters and numbers above the individual teeth are collection identifiers, not corresponding to a meaningful sequence along the jaws. * indicates teeth with a vertical root fracture (if visible in the view, marked with a black arrow); ° indicates teeth with a chipping fracture on the crown (if visible in the view, also marked with a black arrow); black and white dotted lines indicate occlusal facets.

TABLE 1. Measurements (in mm) and summary of dental damage on the teeth of the physeteroid *Scaldicetus caretti* IRSNB M.512 (lectotype), Miocene of Borgerhout (Antwerp, Belgium).

Tooth letter	Max. length as preserved	Max. diameter of crown base	Max. length of root	Max. diameter of root	Max. length of occlusal facet	Comments on tooth damage
A	128.0	16.0	106.9	32.1	—	
B	203.0	21.1	179.0	47.8	68.0	
C	212.0	23.3	183.5	54.8	77.5	
D	208.0	22.7	+180.0	56.5	130.0	
E	194.0	—	—	61.2	+91.5	2 occlusal facets
F	215.0	+28.3	—	65.1	—	
G	212.0	+24.2	187.0	68.5	—	
H	209.0	+22.1	184.0	62.0	—	
I	141.5	—	—	54.6	—	
J	198.0	—	—	61.9	+69.5	Vertical root fracture
K	224.0	+26.7	190.5	66.1	—	Pocket-like occlusal facet
L	227.0	—	198.0	61.5	+113.0	2 occlusal facets
M	219.0	25.7	193.5	62.7	—	
N	205.0	27	186.0	64.8	—	Vertical root fracture
O	187.0	24.8	169.0	57.4	—	
P	134.0	16.4	114.7	39.1	—	
Q	144.0	18.5	131.0	41.8	+65.5	
R	218.0	24.6	190.5	58.7	—	
S	208.0	—	199.0	58.1	—	
T	184.0	—	—	64.5	—	
U	228.0	+26.6	200.0	65.1	—	
V	200.0	—	—	64.8	+71.5	
W	235.0	33.0	199.0	72.3	—	
X	235.0	31.4	203.0	72.0	—	Vertical root fracture
Y	138.0	—	—	72.1	—	
Z	226.0	—	—	70.6	—	
A1	230.5	29.5	196.0	65.8	—	Vertical root fracture
B1	233.0	26.8	203.5	63.0	—	
C1	210.0	27.5	188.4	65.1	—	Chipping fracture
D1	229.0	25.2	198.7	58.9	—	
E1	219.0	—	—	56.7	—	
F1	229.0	27.8	191.5	62.3	—	Chipping fracture
G1	224.5	—	195.3	65.2	+100.5	Vertical root fracture
H1	216.0	—	+186.0	67.5	—	
I1	231.0	31.4	192.6	68.9	—	
J1	227.5	32.5	194.0	70.7	—	Chipping fracture
K1	218.0	—	187.2	70.4	—	
L1	214.0	—	192.0	66.6	—	
M1	233.0	27.5	194.0	65.3	—	Vertical root fracture
N1	209.5	—	—	65.1	—	
O1	226.0	28.9	190.5	65.8	—	Vertical root fracture
P1	224.5	+29.6	+188.7	68.5	—	
Q1	183.0	—	+166.8	67.8	—	
R1	203.0	27.3	173.0	69.0	—	
S1	221.0	23.7	197.0	57.5	91.0	Pocket-like occlusal facet

+ = incomplete.

In addition to this set of teeth, a sample of 262 isolated physeteroid teeth from the Neogene of the same region, also collected during the second half of the 19th century, was observed. Due to the low diagnostic value of isolated physeteroid teeth, these other specimens are identified here as *Physeteroidea* indet., although some of them could belong to the same taxon (or a closely related species) as IRSNB M.512.

Three teeth (two from *Scaldicetus caretti* IRSNB M.512 and one from *Physeteroidea* indet. IRSNB M.516) were computed tomography (CT)-scanned at the Royal Belgian Institute of Natural Sciences with an EasyTom 150 microCT Scanner to reveal details of the outline (and more specifically inner extent) of the longitudinal fractures first observed during external visual inspection of their root. The CT scanning yielded cross-sections of the teeth, for which contrast and lighting were manually adjusted to optimize observations of cementum and dentin outlines.

GEOLOGICAL CONTEXT

Large physeteroid (*Scaldicetus*-like) teeth with an enamel-covered crown from the Miocene of Antwerp are generally recorded as originating from the 'Boldérien' (Bolderian) or 'Anversien' (Antwerpian) (Vanden Broeck, 1874; Abel, 1905; Misonne, 1958); these now disused regional stages roughly correspond to the late early to middle Miocene Berchem Formation (Louwye et al., 2000; Laga and Louwye, 2006). However, first hand data on the lithological units where these teeth were found during the second half of the 19th century are rarely available, and part of the material probably originates from reworked deposits. Furthermore, at least a few more recently found teeth were discovered in late Miocene deposits of the Diest Formation (O.L., pers. observ.; Louwye et al., 2007). The sediment retained in the pulp cavity of teeth from specimen IRSNB M.512 unfortunately did not yield any biostratigraphically informative microfossils. However, the sediment's aspect differs markedly from what is

found in the Borgerhout district for the Antwerpen Sands Member of the Berchem Formation, being much lighter with a significantly lower quantity of glauconite grains (Fig. 2) and sharing more similarities with sediment from the Deurne Sands Member of the Diest Formation (see De Meuter et al., 1976). Among the geological sections taken in Borgerhout, several revealed the presence of the Deurne Sands just above the Antwerpen Sands (De Meuter et al., 1976). An early late Miocene age (Tortonian) is thus tentatively proposed for at least a part of the sample, including *Scaldicetus caretii* IRSNB M.512. Such an age is further supported by the observation of holes at the surface of several teeth of IRSNB M.512 (Fig. 1), similar to holes tentatively interpreted as aborted molluscan drillings in skulls of the ziphiid *Ziphirostrum marginatum*, also originating from the Deurne Sands Member in the Antwerp area (Lambert, 2005).

PHYSETEROIDEA incertae sedis
SCALDICETUS CARETTI du Bus, 1867
(Figs. 1–5)

Lectotype—IRSNB M.512, a set of 45 teeth.

Type Locality—Borgerhout, Antwerp suburbs, Belgium.

Age and Horizon—Probably Deurne Sands Member of the Diest Formation. Probably early late Miocene (Tortonian) (see Geological Context).

Comment—As discussed above, because isolated physeteroid teeth lack diagnostic information, the genus and species *Scaldicetus caretii* are restricted to this type material (Bianucci and Landini, 2006). Other large physeteroid teeth from the Antwerp area mentioned here are thus referred to Physeteroidea indet.

SYSTEMATIC PALEONTOLOGY

CETACEA Brisson, 1762
NEOCETI Fordyce and Muizon, 2001
ODONTOCETI Flower, 1867
PHYSETEROIDEA Gray, 1821

DESCRIPTION

General Morphology

The exact position of the teeth IRSNB M.512, having been found detached from the jaws, cannot be established. Because some of them display long occlusal facets (see below), there is no doubt that both upper and lower teeth were originally present. The

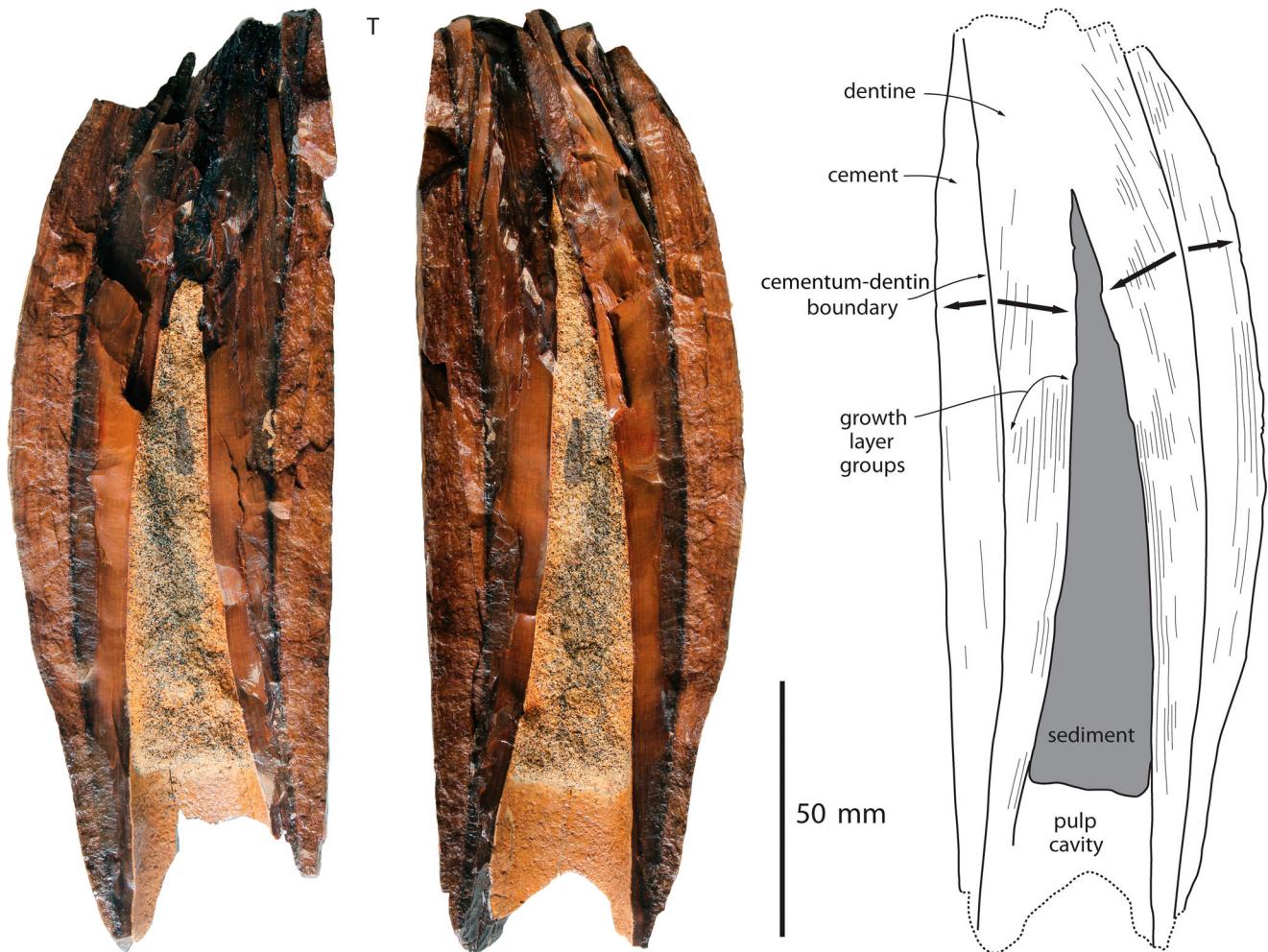


FIGURE 2. Growth layer groups in one tooth of the physeteroid *Scaldicetus caretii* IRSNB M.512 (lectotype). Tooth IRSNB M.512T, split into two halves with a fracture plane roughly along the center of the large conical pulp cavity and showing the cementum-dentin boundary as well as a series of growth layer groups (20–25). Thick black arrows indicate the direction of growth for the cementum (outward) and dentin (inward). Dark gray shading for sediment partly filling the pulp cavity.

tooth count for each row varies from nine to 14 in other known Miocene macroraptorial physeteroids (Bianucci and Landini, 2006; Lambert et al., 2017). With a minimum total of 45 teeth, IRSNB M.512 possessed at least 11 teeth per row, which is a higher tooth count than in *Livyatan melvillei* (Lambert et al., 2010). The minimum total tooth count of *Scaldicetus caretii* is in the upper range of the extant *Physeter macrocephalus*, but in the latter functional teeth are only present on the mandible (between 17 and 29 per row and no functional upper teeth; Rice, 1989). As in other physeteroids, tooth dimensions vary markedly in this specimen: the total length of the root ranges from 106.9 to 203.5 mm, the maximum diameter of the root from 32.1 to 73.3 mm, the maximum diameter of the crown at its base from 16.0 to 32.5 mm, and the maximum total length reaches 233 mm (Table 1; Fig. 1). Maximum total length is in the upper range of adult male *P. macrocephalus*; teeth of some very old males of the latter can reach up to 250 mm in length (Boschma, 1938; Rice, 1989). The smallest teeth most likely originate from the posterior part of the jaws, as seen in *Acrophyseter deinodon* (although in the latter size differences between anterior and posterior teeth are not as great; see Lambert et al., 2017), whereas some teeth intermediate in size could also originate from the anterior region, as seen in *L. melvillei* and *P. macrocephalus* (Boschma, 1938; Lambert et al., 2017). Among Miocene macroraptorial physeteroids, larger teeth are only found in *L. melvillei*, whereas the largest alveolar dimensions of *Albicetus oxymycterus* (which retains some broken tooth roots in the alveoli) also correspond to somewhat larger teeth (Boersma and Pyenson, 2015). All the teeth are subcylindrical and moderately curved, with a maximum diameter at about mid-length. Roots of large *P. macrocephalus* teeth are more flattened along the tooth row (maximum, roughly mesiodistal diameter is considerably greater than the diameter perpendicular to it; e.g., Boschma, 1938; O.L., pers. observ.). Only some of the teeth described here are more significantly labiolingually flattened and may possibly correspond to posterior lower teeth, as in *Acrophyseter deinodon* and *Zygophyseter varolai*. The conical crown is short relative to the root length (a diagnostic feature of physeteroids). Contrasting markedly with *P. macrocephalus*, which has teeth devoid of enamel, the crown is covered with a thick layer of enamel. Maximum enamel thickness is consistent throughout the sample, ranging from 1.2 to 1.3 mm; thickness gradually diminishes at crown base and is less in regions with conspicuous wear, including the crown tip and occlusal facets (see below). The enamel surface is conspicuously ornamented with anastomosed, roughly longitudinal ridges and grooves. In some of the teeth, some remnants of a thin layer of black material with a rough surface cover the cementum in the proximal part of the root (Fig. 1). As in *Zygophyseter varolai*, this dark coating is interpreted as marking the part of the root outside the bony alveolus and originally covered by gum (gingival collar in Bianucci and Landini, 2006). The coating may correspond to calculus (dental plaque) deposition between tooth and gum, as seen in extant odontocetes (Loch et al., 2011), including *P. macrocephalus* (O.L., pers. observ.; Fig. S2 in Supplemental Data). The pulp cavity is wide open (Figs. 2, 4), a feature that is observed in adult specimens of other physeteroids, including the extant *P. macrocephalus* (Boschma, 1938; Pierce and Kajimura, 1980: fig. 1; Lambert et al., 2017).

Growth Layer Groups and Age

The tooth IRSNB M.512T (previously figured in Marx et al., 2016:fig. 6.25) has been preserved as two halves, with the longitudinal fracture surface passing roughly through the center of the large conical pulp cavity (Fig. 2). Furthermore, the break surface is smooth in the dentin area, contrasting markedly with the rougher surface in the cement area.

Based on a comparison with sections in extant *Physeter macrocephalus* teeth and other fossil physeteroid teeth (e.g., Pierce and Kajimura, 1980; Gilbert et al., 2018; Hohn, 2018), growth layer groups (GLGs) can be detected in both the cementum and dentin but are more easily spotted in the latter. Combining data from different parts of the section, a minimum of 20–25 GLGs is counted in the dentin (Fig. 2). For the extant *P. macrocephalus*, animals older than 16 years are considered sexually mature, whereas growth can continue up to 25–60 years of age (Rice, 1989). Based on the available evidence, the individual represented by the IRSNB M.512 teeth was most likely at least sexually mature.

As seen in longitudinal section (Fig. 2) and cross-section (Figs. 5, 6), in IRSNB M.512 the cementum and dentin roughly display the same thickness; in longitudinal sections of large adult teeth of *Physeter macrocephalus* (e.g., Boschma, 1938:pl. 13; Pierce and Kajimura, 1980:fig. 1; Hohn, 2018:fig. 3; O.L., pers. observ.), the outer cementum layer is significantly thinner than the inner dentin layer.

Apical Damage, Occlusal Facets, and Collar Wear

Different types of tooth wear/damage are observed. First, when preserved, the crown tip has been removed in vivo (as indicated by the smoothed surface, differing from postmortem breaks) in 24 teeth. Only one smaller tooth actually displays a nearly complete crown tip. In teeth with a truncated tip, the apical surface of the crown is generally subhorizontal, but in a few cases it slopes distolingually or mesiolingually. The diameter of the truncated surface varies markedly from one tooth to another (Figs. 1, 3), suggesting that this apical damage not only results from progressive abrasive wear (from friction against exogenous material; see Loch and Simões-Lopes, 2013), differing from some populations of *Orcinus orca* (Ford et al., 2011:fig. 3c) and the highly specialized, suction-feeding *Physeter macrocephalus* (Boschma, 1938: figs. 10–13), in which successive teeth along a specific portion of the tooth row display roughly the same extent of apical wear, more developed in anterior teeth in *O. orca* and more developed in posterior teeth in *P. macrocephalus*. In IRSNB M.512, this apical damage may at least partly be due to a break of the crown tip, such as following a contact with hard material. This interpretation is further supported by an observation made on three teeth (IRSNB M.512C1, F1, and J1) of a subvertical facet resulting from the removal of a larger portion of the crown (Fig. 3). In these teeth, the smoothed facet ends abruptly proximally, either at the crown-root boundary or 20 mm below, with a marked horizontal, 2.5–3.0 mm deep step. In two of these three teeth (IRSNB M.512C1 and F1), a shallow occlusal facet is observed reaching farther along the root surface on the same side of the tooth (Fig. 3), meaning that the subvertical facet cannot be identified as an occlusal facet. We thus interpret the facet and associated step as a chipping fracture, resulting from the abrupt removal of part of the crown (e.g., Lawn et al., 2013).

Second, when preserved, the apical part of the crown always displays an attenuated ornamentation as compared with the basal region of the crown (a feature reflected in the thinner enamel mentioned above). Although we cannot exclude that such a reduced ornamentation is a genuine feature of a given taxon (as proposed elsewhere for other fossil physeteroid teeth; Hampe, 2006), it is tempting to propose that it is at least partly related to superficial abrasion, resulting from repeated contact with food items.

Third, long occlusal (attritional, tooth-to-tooth contact) facets are observed on the proximal part of the root in 20 of the 45 teeth of IRSNB M.512 (Figs. 1, 3). Several teeth (e.g., IRSNB M.512E and L) display two occlusal facets, one distal (= posterior in cetaceans) and one mesial (= anterior in cetaceans), indicating a close spacing of opposing teeth. Parts of the ends of these facets

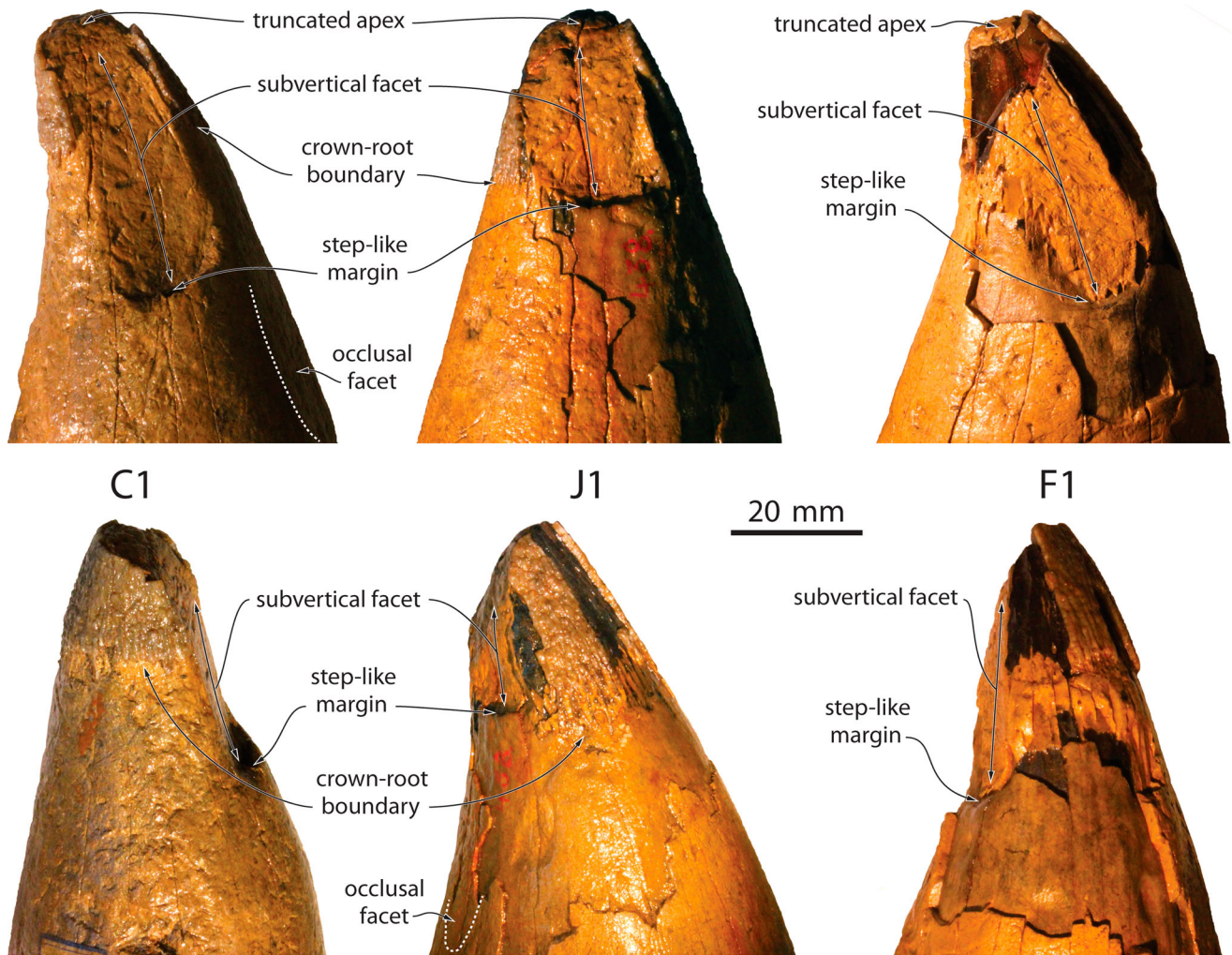


FIGURE 3. Chipping fractures on the teeth of the physeteroid *Scaldicetus caretti* IRSNB M.512 (lectotype). Detail of the crown and proximal part of the root in three teeth (IRSNB M.512 C1, J1, and F1, in two different views each), to show the extent (compared with crown-root boundary) and morphological features (subvertical facet and step-like margin) of chipping fractures. Shallow occlusal facets are outlined with white dotted lines.

are pocket-shaped, as described, for example, in *Acrophyseter deinodon* and *Zygophyseter varolai* (Bianucci and Landini, 2006; Lambert et al., 2017). Short occlusal facets are only rarely observed in the extant *Physeter macrocephalus*, due to the absence of functional upper teeth in the latter; upper teeth only rarely erupt and thus generally do not contact lower teeth (see Boschma, 1938). Originally receiving the tip of the opposing tooth, such a pocket thus provides a maximum length for the contact between upper and lower teeth of up to 130 mm in IRSNB M.512D. Like in *Zygophyseter varolai*, occlusal surfaces often reach beyond the boundary of the gingival collar (Bianucci and Landini, 2006:fig. 8), meaning that the opposing tooth's tip entered deeply into the gum during jaw adduction. Interestingly, remains of the dark coating (probably calculus) marking the gingival collar are generally preferentially preserved along the edges of the occlusal surface (e.g., IRSNB M.512E).

Fourth, in addition to the occlusal facets, the proximal-most part of the root is superficially worn all around the contact with the enameled crown. A similar wear type has been described in teeth of other extinct physeteroids, being in some cases much more advanced (e.g., Hampe, 2006; Marra et al., 2016:fig. 2f), ultimately leading to the loss of the crown (e.g., Bianucci and Landini, 2006:fig. 8d).

Vertical Root Fractures

Seven of the teeth of *Scaldicetus caretti* IRSNB M.512 (J, N, X, A1, G1, M1, and O1) display a major longitudinal break along the root, starting proximally from the thin apical edge of the open pulp cavity (Figs. 1, 4, 5, S1). The length of these breaks ranges from 26 to 60 mm, only taking into account the part with a clear gap (corresponding to material loss) between the two edges of the fracture. Indeed, in some cases, the break extends proximally as a gradually narrowing thin line. In five teeth, the break follows the longitudinal axis of the tooth in a regular fashion, whereas the other two teeth display a much more irregular path. A maximum gap of 6.4 mm is observed between the two edges of the fracture in one of these two latter teeth, compared with a maximum gap of 3.7 mm in a tooth with a more rectilinear break. The edges of the fracture zone are rounded and display a color similar to the outer surface of the tooth farther from the break. In at least five teeth, the inner edges (in the pulp cavity) of the break are noticeably thickened, a feature observed either by direct finger manipulation of the inner surface or via visual inspection of CT scan cross-sections (Figs. 4, 5, S1). In most of the observed teeth, dentin deposition in the pulp cavity partly closes the fracture from the inside (Figs. 4, 5); this inner closure

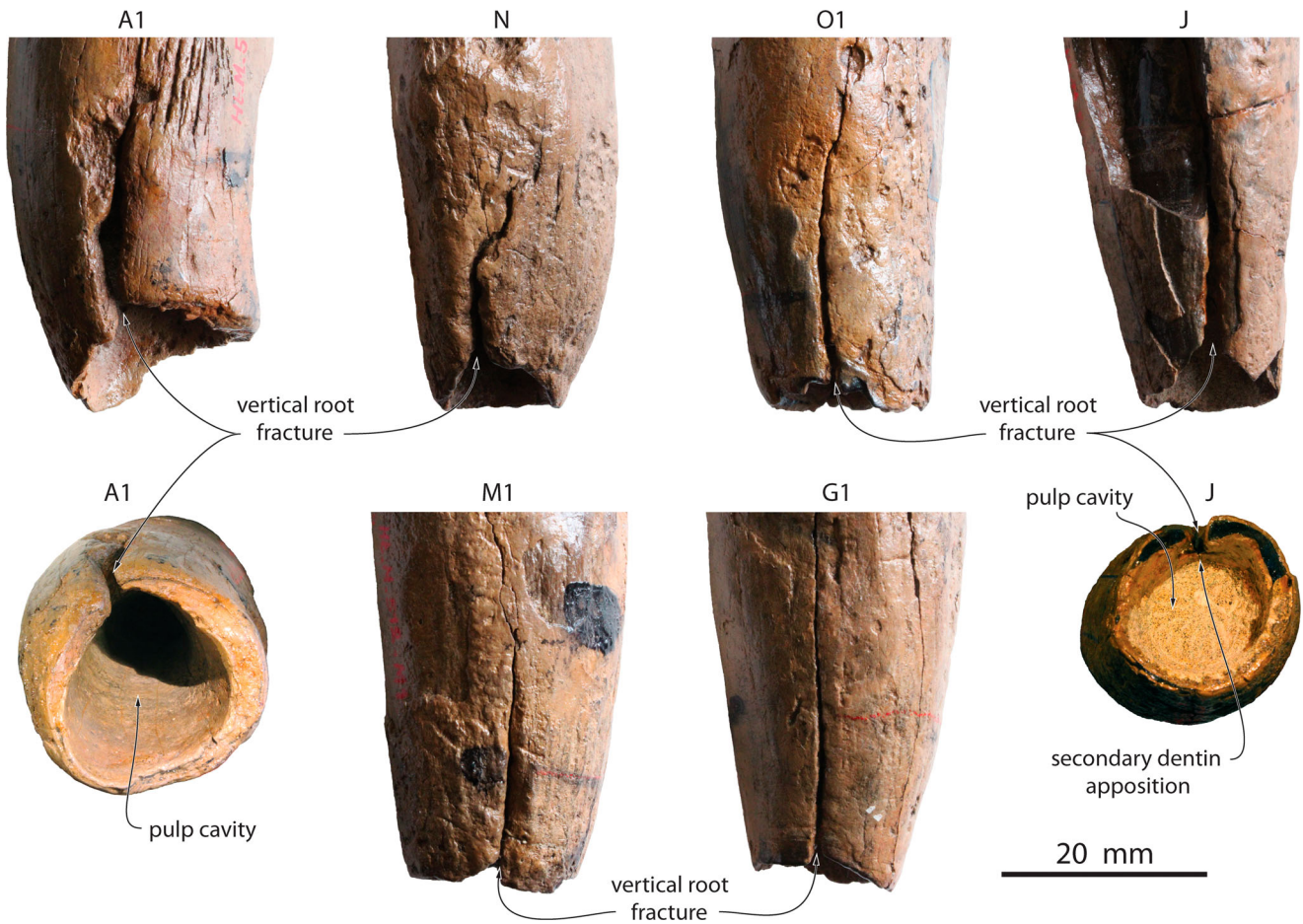


FIGURE 4. Vertical root fractures on the teeth of the physeteroid *Scaldicetus caretti* IRSNB M.512 (lectotype). Detail of the apical part of the root in six teeth (IRSNB M.512 A1, N, O1, J, M1, and G1), showing vertical root fractures. Additional coronal views showing the open pulp cavity are provided for IRSNB M.512 A1 and J.

is less advanced apically in teeth displaying the widest gap on the outer surface. Similar breaks were observed in at least 10 other isolated physeteroid teeth of varying sizes (maximum root diameter ranging from 25 to 72 mm) from the Miocene of Antwerp (e.g., IRSNB M.516; Fig. 6; also displaying secondary dentin apposition, see below), meaning that this kind of break is not unique to a single specimen.

A first interpretation would be that these longitudinal breaks along the root occurred after the death of the animal, in relation to preburial movements on the sea floor, burial, or early stages of diagenesis. Fossil cetacean teeth are made of very brittle material and are often found fractured (e.g., Hampe, 2006; Lambert et al., 2017). When combined, however, some of the morphological features of the teeth IRSNB M.512 listed above contradict this interpretation:

First, the color of the studied break surfaces differs markedly from other, obvious postmortem breaks seen on the same teeth; as mentioned above, the color is the same as on the external surface of the root, contrasting with the generally much darker color of other breaks. Second, surfaces along these breaks are smooth, contrasting with the more angular surfaces of postmortem break surfaces. Third, and more importantly, the slight to moderate thickening of the inner edges of these breaks does not occur in postmortem breaks. Fourth, additional deposition of dentin inside the pulp cavity also does not occur in postmortem breaks, which generally do not produce a significant gap to be filled.

All these features strongly support the hypothesis that the longitudinal breaks described here instead occurred during the animal's life. The thickening of the inner edges may then correspond to a 'callus' formed during healing, and the deposition of dentin on the inner side of the break to another healing response, namely, secondary dentin apposition (Walton et al., 1984; Heithersay and Kahler, 2013). In humans, the type of dental damage that by far best matches the location, direction, extent, and healing response observed in teeth of *Scaldicetus caretti* is called vertical root fracture (Pitts and Natkin, 1983; Walton et al., 1984; Moule and Kahler, 1999; Heithersay and Kahler, 2013; Khasnis et al., 2014). Similar to the condition of IRSNB M.512, some of the vertical root fractures detected in humans are incomplete, meaning that they do not extend on the opposite side of the pulp cavity and do not necessarily propagate in the crown either (Walton et al., 1984). Considering, on the one hand, the extent of the root fractures in a considerable thickness of the cementum and dentin and, on the other hand, the thin layer of secondary dentin apposition and callus, we can propose that the breaks occurred after sexual maturity, but some time before death, meaning that the animal could keep feeding with such dental damage.

As mentioned above, the breaks described in IRSNB M.512 are followed proximally by a thin fracture running to the crown, without any significant gap. Similar fractures are present elsewhere in these teeth (Figs. 1–4), and we propose that postmortem

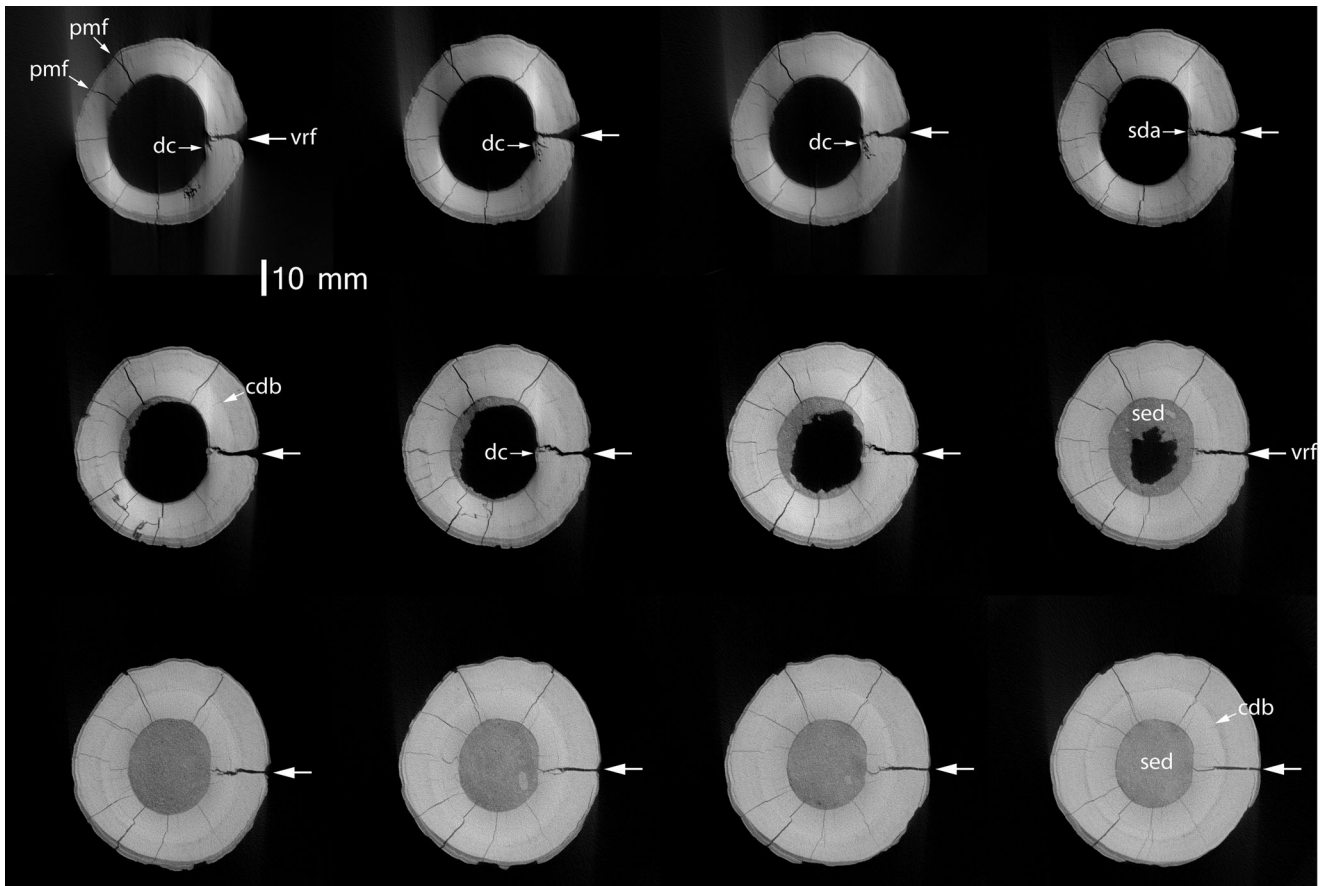


FIGURE 5. CT scan images of a vertical root fracture on the tooth of the physeteroid *Scaldicetus caretti* IRSNB M.512 M1 (lectotype). Cross-sections resulting from the CT scanning of the tooth. Sequence starts from the upper left with the most apical part of the root and proceeds toward the lower right. Each slice is separated from the adjoining slice by 3 mm. Large arrows indicate vertical root fractures. **Abbreviations:** **cdb**, cementum-dentin boundary; **dc**, dentin callus; **pmf**, postmortem fracture; **sda**, secondary dentin apposition; **sed**, indurated sediment in pulp cavity; **vrf**, vertical root fracture.

breaks may have developed preferentially from the mechanically weaker vertical root fracture area.

DISCUSSION

All the observed features of the longitudinal breaks on the roots of the teeth of IRSNB M.512 as well as other isolated physeteroid teeth from the Miocene of Antwerp point to their interpretation as vertical root fractures, dental damage that to our knowledge has never been previously recorded from the extant *Physeter macrocephalus* and has not been observed by us in studied specimens of the latter species. In humans, this dental damage is relatively uncommon in teeth without endodontic treatment, and its occurrence has been tentatively related to factors such as excessive vertical forces from mastication or occlusion and the tendency to chew harder food (Chan et al., 1998; Wang et al., 2012). More specifically, in some human populations, vertical root fracture may be associated with a given diet or chewing habit (e.g., chewing of bones in meat, nuts, dry meat, etc.), leading to the postulate that chewing of hard food and/or the application of excessive and repetitive masticatory forces could initiate cracks at the apex of the root, the latter region being the weakest (Chan et al., 1998; Khasnis et al., 2014).

We thus hypothesize that the most likely explanation for the occurrence of vertical root fractures in these Miocene physeteroid teeth is the application of strong and repetitive bite forces and/or

bites on hard food items. Considering that chipping fractures provide strong evidence for contact with hard material (Lawn et al., 2013), our hypothesis gains further support from the observation of structures interpreted as resulting from large chipping fractures on the crowns of three IRSNB M.512 teeth. In a marine tetrapod, hard material could originate from different prey types, including shelled invertebrates, but considering the size of the teeth of IRSNB M.512, the corresponding animal was undoubtedly large. We strongly suspect that other medium- to large-sized marine vertebrates with robust bones, for example, marine mammals, were preyed upon by this large physeteroid, as proposed for other Miocene macroraptorial sperm whales (Bianucci and Landini, 2006; Lambert et al., 2010, 2014).

Finite element analysis (FEA) on human tooth models demonstrates the combined impact of dentin thickness, curvature of the root surface, canal size (pulp cavity diameter), and shape on fracture susceptibility (Sathorn et al., 2005). It is thus not surprising that vertical root fractures are initiated along the thin apical edge of the widely open pulp cavity in these Miocene physeteroids. To our knowledge, there is no published record of vertical root fracture in *Orcinus orca* (killer whale), the main extant macroraptorial cetacean. Although this lack of a record could be related to the fact that root fractures are less easy to observe when teeth remain in situ in their alveoli and can be more easily confused with frequently observed postmortem longitudinal cracks related to drying dental tissue (see Fig. S3, displaying

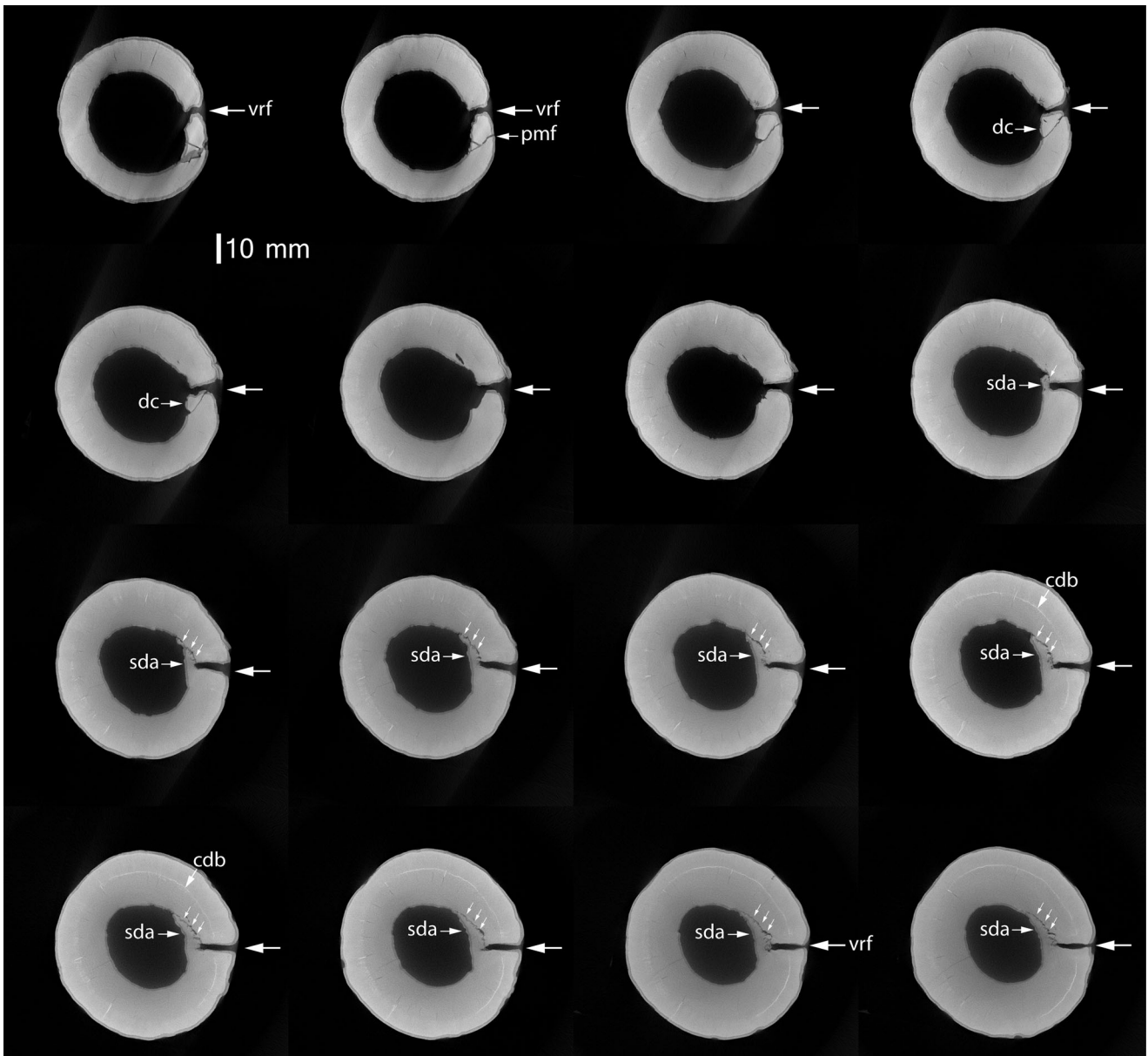


FIGURE 6. CT scan images of a vertical root fracture on the tooth of *Physeteroidea* indet. IRSNB M.516. Cross-sections resulting from the CT scanning of the tooth. Sequence starts from the upper left with the most apical part of the root and proceeds toward the lower right. Each slice is separated from the adjoining slice by 3 mm. Three small parallel arrows indicate a thin space retained between secondary dentin apposition and unmodified part of the inner surface of the pulp cavity. Large arrows indicate vertical root fractures. **Abbreviations:** *cdb*, cementum-dentin boundary; *dc*, dentin callus; *pmf*, postmortem fracture; *sda*, secondary dentin apposition; *vrf*, vertical root fracture.

desiccation-related cracks on all the teeth of a very young *O. orca* mandible and on an adult tooth of the same species), we suspect that the smaller pulp cavity with thicker edges in *O. orca* (lacking the continuous cementum deposition of physeteroids), as compared with the sperm whale teeth studied here, reduces fracture susceptibility during predation. Furthermore, not all *O. orca* populations feed on other marine tetrapods, and a large variation in tooth wear is consequently observed among populations (Caldwell and Brown, 1964; Massare, 1987; Ford et al., 2011; Foote et al., 2009), to an extent greater than what has been observed until now in any given stem physeteroid genus (but with much smaller sample sizes in the latter; O.L., pers. observ.).

The very specific morphological features of these physeteroid teeth (pulp cavity remaining open in mature individuals, thin

edges of the cavity, and large part of the root outside the bony alveolus, all related to continuous cementum and dentin deposition; Figs. 2, 4–6, S1) potentially increase the risks of longitudinal breaks in roots and may thus also explain why vertical root fractures are not reported in large terrestrial carnivorous mammals, whereas other dental damage related to their feeding strategies and prey types has been described (Van Valkenburgh and Ruff, 1987; Van Valkenburg, 1988; Van Valkenburgh and Hertel, 1993; Lawn et al., 2013). Similarly, a faster closure of the pulp cavity during ontogeny may have allowed other stem physeteroids (e.g., *Zygophyseter*) to reduce vertical root fracture susceptibility.

Studies on large terrestrial carnivore dental damage nevertheless provide useful results for the interpretation of macroraptorial

physeteroid teeth. Indeed, large carnivores that eat bone display higher frequencies of dental fracture, and species that consume particularly hard food tend to develop stronger teeth, with larger roots (Van Valkenburgh, 1988; Kupczik and Stynder, 2012). Interestingly, carnivores preying upon larger animals also have proportionally larger root surface areas (Kupczik and Stynder, 2012). Considering the enormous, subcylindrical dental roots of macroraptorial physeteroids, it is tempting to propose that such voluminous roots are useful for the dissipation of stresses during strong bites and/or predation on large, powerful animals, as suggested for carnivores (Christiansen and Wroe, 2007; Kupczik and Stynder, 2012).

To conclude, despite the aforementioned considerable strengthening of the mechanical properties of the teeth (including a proportionally thicker cementum layer, as compared with the extant *Physeter*), at least some of the large Miocene macroraptorial physeteroids display relatively frequent root damage. We propose that the vertical root fractures and chipping fractures described here for the first time in an extinct sperm whale can be correlated with the production of powerful bites when feeding on large prey with hard parts (namely, other marine vertebrates). Prey was captured and probably processed so as to produce smaller pieces for ingestion, as performed by *Orcinus orca* when preying upon other marine mammals, and as proposed for other macroraptorial sperm whales. Processing of the prey item by successive strong bites increases the risk of contacting bone and, consequently, the risk of dental damage. Stable isotope analyses and finite element analysis on extinct physeteroid teeth and jaws will allow further testing of our interpretation of their feeding ecology, which contrasts markedly with the ecology of the suction-feeding and deep-diving extant sperm whale.

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