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Trace fossil evidence for *Osedax* Rouse et al., 2004 exploiting shark tooth dentine on a Pliocene seafloor: broadening our understanding of a major taphonomic agent

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Abstract

The zombie worm genus *Osedax* Rouse et al. 2004 is part of a peculiar group of organisms that thrive at whale fall localities on the ocean floor. In addition to feeding on whale bones, extant *Osedax* spp. are known to feed on the bones of other marine and terrestrial mammals, birds, and reptiles, and have recently been found to also feed on shark tooth dentine under experimental conditions. The efficacy of *Osedax* spp. as bioeroders is such that they are thought to have significantly affected both the quantity and the quality of the marine vertebrate fossil record. Here, we report on the occurrence of single-entry borings consistent with those produced by *Osedax* on fossil shark teeth from the Lower Pliocene offshore deposits of Tuscany, central Italy. Micro-CT investigations reveal that the worms excavated the dentine of the tooth roots, leaving the enameloid-coated crowns seemingly unaltered. The borings in question are assigned to the *Osedax*-related ichnogenus *Osspecus* Higgs et al., 2012, which to date had been found on a variety of marine vertebrate fossils, but not on shark teeth. This ichnological record provides the first fossil evidence for zombie worms exploiting shark tooth dentine and serves as a powerful demonstration that such behaviour can and does occur in the wild. Root exploitation by *Osedax* may contribute to explain the high frequency of rootless teeth in some shark tooth accumulations from modern deep-sea floors and time-averaged horizons inland. Over the past 100 million years, shark teeth have likely served as critical ecological stepping stones between remote marine vertebrate fall localities and may even have provided a suitable substrate for ancient zombie worms during the Cretaceous–Paleogene (K–Pg) extinction event.

Key Words

Biostratinomy, ichnology, *Osspecus*, palaeobiology, Siena-Radicofani Basin, Zanclean, zombie worms

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* Joint first authorship.

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Introduction

Since the discovery of a peculiar assemblage of chemolithoautotrophic organisms on a balaenopterid skeleton on the deep seafloor off California (Smith et al. 1989), which unexpectedly resembled the then newly-found communities at hydrothermal vents and cold seeps, the fate of deep-sea marine vertebrate carcasses have been the subject of intense research by biologists and palaeontologists alike (Smith et al. 2015). One of the major findings of whale fall research was the discovery of the bone-eating siboglinid polychaetes of the genus *Osedax* Rouse et al., 2004, which are known as 'zombie worms' (Ferber 2005). Although these organisms were first described only some 20 years ago, subsequent studies have recovered as many as thirty-four formally named species of *Osedax* in all the major oceanic basins (WoRMS Editorial Board 2025), suggesting a high diversity as well as a worldwide distribution (Rouse et al. 2018; Berman et al. 2023).

Osedax worms exhibit a bizarre body morphology that resembles a palm tree; a crown of palps is usually well-developed (either reddish or yellowish/greenish in colour), the trunk is covered with mucus, and bulbous, branching, root-like structures are present, corresponding to large ovisacs that enter the substrate the worm lives and feeds on (Rouse et al. 2004; Glover et al. 2005). *Osedax* spp. lack a digestive tract and rely on colonies of bacterial symbionts (Oceanospirillales) hosted in a trophosome for nutrition. These symbionts are found in the highly vascularised 'roots' rather than in the elongated trunk as observed in other siboglinids (Katz et al. 2011). The bacteria produce enzymes for digesting collagen and lipids from bone, thus nourishing both themselves and their *Osedax* host (Goffredi et al. 2005, 2007; Katz et al. 2010; Moggioli et al. 2023). Such exploitation of bony tissues for nutrition, coupled with the peculiar anatomy of the symbiont-bearing root-like system, make this form of bacterial endosymbiosis unique (Rouse et al. 2004).

The bone-eating activity of *Osedax* is not without remarkable taphonomic consequences. Extant *Osedax* spp. are known to excavate distinctive borings into the bones they feed on (Rouse et al. 2004; Fujikura et al. 2006; Higgs et al. 2010). These borings display a single, circular to sub-circular aperture, lacking any rim or platform, which extends into the bone as a uniformly thick canal, generally perpendicular to the outer surface, ending with a globular or irregularly shaped chamber (Higgs et al. 2012). Although the borings produced by the living members of *Osedax* display significant variations in terms of size and shape (Higgs et al. 2014), their overall morphology is nonetheless consistent, reflecting as it does a signature trait of this bone-eating genus, namely, the development of the branching roots that host the trophosome (Jamison-Todd et al. 2025b).

The unique morphology of the borings made by *Osedax* has allowed for these bioerosional modifications to be readily recognised on fossil whale bones (Kiel et al. 2010). Such trace fossils have been subsequently assigned to their own ichnogenus, *Osspecus* Higgs et al., 2012. At the same time, whale fall research has shown that dense, long-lasting colonisation by *Osedax* can result in extensive pitting and significant degradation of the supporting bone(s) (Higgs et al. 2010, 2012), and even in the destruction of entire whale skeletons (Braby et al. 2007; Lundsten et al. 2010; Higgs and Pokines 2013). Thus, some researchers have proposed that the bone-eating activity of *Osedax* has significantly affected both the quantity and the quality of the cetacean fossil record — a notion that has entered the palaeontological literature as the '*Osedax* effect' (Kiel et al. 2010; Dominici et al. 2020).

Osedax was first recorded dwelling in cetacean skeletons and bones on deep seafloors (Baco-Taylor 2002, where specimens belonging in this genus were referred to as a 'snot worms'; Rouse et al. 2004; Glover et al. 2005), which explains the widespread understanding of zombie worms as whale fall specialists (Glover et al. 2008). Occurring on two cetacean specimens from Oligocene bathyal deposits of the U.S. Pacific coast, the first trace fossils to be interpreted as reflecting the feeding activity of *Osedax* seemingly lent support to this interpretation (Kiel et al. 2010). However, other studies have shown *Osedax* to be able to live and feed on experimentally deployed terrestrial mammal bones (Jones et al. 2008) as well as on naturally occurring seal bones (Taboada et al. 2015). Further deployment experiments have revealed that *Osedax* can also exploit the bones of non-mammalian vertebrates, including those of bony fishes (Rouse et al. 2011), turtles (Rouse et al. 2018), birds (Rouse et al. 2018) and alligators (McClain et al. 2019). Moreover, at least one *Osedax* species has been observed inhabiting decaying cetacean soft tissues in addition to bone (Fujiwara et al. 2007; but see also Fujikura et al. 2006), while another has been shown to rely on small bone shards buried in the sediment adjacent to whale falls (Rouse et al. 2018).

Similarly, palaeontological investigations have led to identifying the occurrence of *Osedax*-related trace fossils on a diverse array of organogenic phosphatic substrates, including the bones of birds (Kiel et al. 2011) and bony fishes (Kiel et al. 2013), and even whale tooth roots (Kiel et al. 2013). Furthermore, the survey of pre-Cenozoic materials has revealed the occurrence of similar bioerosional features on plesiosaur and marine turtle bones from strata as old as the mid-Cretaceous (Danise and Higgs 2015). This has led to an expanded understanding of the '*Osedax* effect' — one that regards the taphonomic significance of *Osedax* as likely extending to various marine vertebrate lineages as well as back to Cretaceous times (Danise and Higgs 2015). That some zombie worms have been found inhabiting the present-day marine shallows (up to some 15 m water depth; Taboada et al. 2015) matches well with the relatively shallow depositional settings that yielded most of the geologically oldest examples of *Osspecus* (Jamison-Todd et al. 2025a), thus further suggesting that the '*Osedax* effect' cannot be regarded as a strictly deep-water phenomenon.

Recently, the substrate and feeding habits of zombie worms have been shown to be even more catholic than previously recognised, extending to the skeletal and dental remains of most major clades of Cretaceous marine reptiles (Jamison-Todd et al. 2024, 2025b), and even to shark teeth, the latter behaviour being evidenced by the discovery of representatives of two different *Osedax* species on tooth roots from experimentally deployed jaws of *Alopias vulpinus* (Bonnaterre, 1788) in the vicinity of a large whale fall off Monterey, California (Rouse and Goffredi 2023). To date, such behaviour has not been observed in the wild, nor has it ever been inferred based on the trace fossil record. The present paper reports on the first occurrence of *Osspecus* on fossil shark teeth based on specimens from Pliocene offshore deposits of Tuscany (Northern Apennine hinterland, central Italy). It demonstrates that *Osedax* can and does exploit shark tooth dentine in the wild, i.e., outside experimental conditions. The taphonomic and palaeobiological relevance of these findings is discussed with special reference to the impact that the unique feeding habits of *Osedax* may have had in shaping the marine vertebrate fossil record over the past 100 million years or so.

Geological and palaeoenvironmental setting

The tectonics of the Mediterranean region are dominated by the convergence between the African and European plates, which is further complicated by the occurrence of various intervening minor plates. This convergence scenario has led to the formation of the Alpide orogenic belts, including the Alps and Apennines, as well as to the development of the many sub-basins that make up the present-day Mediterranean Sea. Among the latter are the 'neoautochtonous' basins that began to form on the Tyrrhenian side of the Northern Apennine chain and gradually developed eastward as the orogen migrated toward the foreland (Martini and Sagri 1993). This process resulted in the progressive formation of various sets of tectonic depressions parallel to the rising Apennines and bordered seawards by fringes of topographic highs. These basins have been categorised as either 'central' or 'peripheral'; the former are typically home to Miocene and Pliocene marine deposits, while the latter are mostly filled with Pliocene and Pleistocene continental deposits (Martini and Sagri 1993).

For several centuries, the Neogene successions of the central basins have yielded remarkable finds of marine vertebrate fossils, which have gained international recognition since the latter half of the 19th century. These fossils include countless specimens of bony and cartilaginous fishes (among which are sharks, rays and chimaeras), cetaceans (both toothed and baleen-bearing whales), sirenians, pinnipeds, seabirds, and sea turtles (e.g., Dominici et al. 2018, and the many references therein). Interestingly, some of the first trace fossils to show evidence of the feeding activity of *Osedax* come from the Northern Apennine hinterland. They occur as single-entry borings and pits on an isolated cetacean radius from the historic palaeontological locality of Orciano Pisano, and include the holotype of *Osspecus tusciae* Higgs et al., 2012, which in turn represents the type ichnospecies of *Osspecus* (Higgs et al. 2012). Unfortunately, the exact geographic and stratigraphic context of the find in question remains uncertain, as is the case for most of the fossils from Orciano Pisano (Landini 1977; Cigala Fulgosi et al. 2009).

The fossil shark teeth dealt with herein originate from clayey badlands at Lucciola Bella (indicative geographic coordinates: 43°02'00"N, 011°45'30"E) and Selvoli (indicative geographic coordinates: 43°03'00"N, 011°40'00"E), two sites in the vicinity of Pienza (Siena Province, Tuscany, central Italy). Both localities (Fig. 1A) belong in the Siena-Radicofani Basin, one of the 'central' basins of Tuscany, which is shaped as a NNW-trending tectonic depression that preserves a valuable record of post-collisional deposition in the Northern Apennine hinterland (Martini et al. 2021).

Specifically, both Lucciola Bella and Selvoli are located in the Radicofani sub-basin, which corresponds to the southern portion of the Siena-Radicofani Basin, south of the so-called Pienza high (Brogi 2011; Brogi et al. 2014; Martini et al. 2017). The sedimentary fill of the Radicofani sub-basin includes some 1,000 m of continental and marine Pliocene deposits that unconformably overlie continental sediments of Miocene age (Martini et al. 2021, and the many references therein). Two distinct depositional cycles have long been identified within this Pliocene succession. The older cycle is characterised by siliciclastic sediments, including sandstones and mudstones, which transition basinward into offshore mudstones punctuated by turbidites. This cycle spans throughout the Zanclean, corresponding to the biozones MPl1 to MPl4a (as per the zonal scheme of Iaccarino et al. 2007). The younger cycle, which only crops out close to the eastern basin margin, is mostly comprised of *Amphistegina* d'Orbigny, 1826-rich limestones and nearshore sandstones deposited during the Piacenzian, corresponding to the biozones MPl4b to MPl5a. At Lucciola Bella and Selvoli, the fossiliferous outcrops consist of offshore mudstones that belong in the Zanclean cycle, specifically in the Argille Azzurre Formation (Regione Toscana 2006–2009).

Detailed sedimentological and palaeontological data are available for the Pliocene succession exposed at Lucciola Bella (Fig. 1B), which consists of massive, pervasively bioturbated silty clays with interbeds of normally graded sands (Pascucci et al. 2006; Bianucci et al. 2009). Analyses of the foraminiferal assemblages from the Lucciola Bella section have led to the identification of either the zones MPl 2–3 (Pascucci et al. 2006) or the zones MPl 3–4a (Bianucci et al. 2009), which belong in the Lower Pliocene. Micropalaeontological observations have also resulted in reconstructing an outer shelf/upper slope depositional environment with relatively low oxygen levels and high concentrations of organic matter at the seafloor (Bianucci et al. 2009). Marine vertebrate finds from this site include a skeleton of the extinct delphinid *Etruridelphis giulii* Bianucci et al., 2009, a rostral spine of a pristid sawfish (Collareta et al. 2017), a dentary beak of an ocean sunfish (Collareta et al. 2025), and a

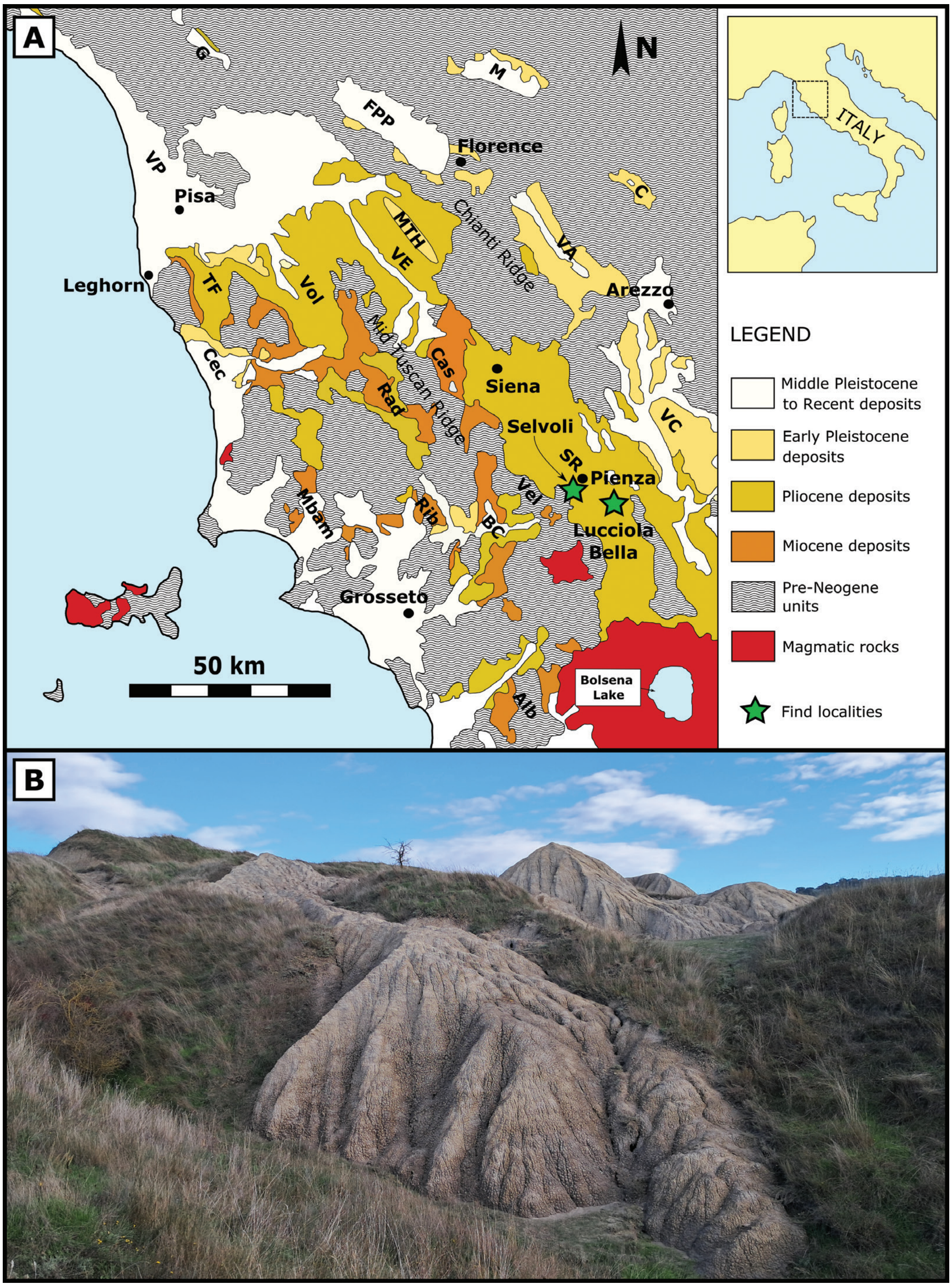

Figure 1. Geographic and geological setting. **A.** Schematic geological map of Tuscany, showing the location of the study sites (Lucciola Bella and Selvoli, indicated by stars). Redrawn and modified from Benvenuti et al. (2014). Abbreviations: **Alb** – Albegna Basin; **BC** – Baccinello-Cinigiano Basin; **C** – Casentino Basin; **Cas** – Casino Basin; **Cec** – Cecina Basin; **FPP** – Firenze-Prato-Pistoia Basin; **G** – Garfagnana Basin; **M** – Mugello Basin; **Mbam** – Montebamboli Basin; **MTR** – Montespertoli-Tavernelle Ridge; **Rad** – Radicondoli Basin; **Rib** – Ribolla Basin; **SR** – Siena-Radicofani Basin; **TF** – Tora-Fine Basin; **VA** – upper Valdarno Basin; **VC** – Valdichiana Basin; **VE** – Valdelsa-lower Valdarno Basin; **Vel** – Velona Basin; **Vol** – Volterra Basin; **B.** Landscape view of the marine clays outcropping at Lucciola Bella.

large number of shark teeth whose systematic analysis is still in progress. Macro-invertebrate (mollusc) fossils from the same site were previously noted by Pascucci et al. (2006), and later examined in detail by Spadini and Manganelli (2010) and Spadini (2022).

During the Early Pliocene, the Radicofani sub-basin was shaped as a semi-enclosed embayment sheltered seaward by an emerging structural high (Pascucci et al. 2006). That said, the depositional settings were rather deep, though relatively close to the continent, as evidenced by the local occurrence of nearshore (shoreface to shallow-deltaic), coarse-grained deposits representing the proximal equivalent of the offshore mudstones that are found at the study sites (Martini et al. 2021).

Material and methods

The fossil materials dealt with herein consist of four fossil carcharhiniform teeth that were surface collected by means of hand-picking. These specimens are housed in the publicly accessible palaeontological collections of Gruppo AVIS Mineralogia e Paleontologia Scandicci (= GAMPS) at Badia a Settimo (Scandicci, Florence Province, Italy) under the catalogue numbers GAMPS-01970 to GAMPS-01973. Specifically, the lower teeth GAMPS-01970, GAMPS-01972 and GAMPS-01973 feature a narrow, suberect cusp flanked by heels, finely serrated cutting edges, a mesiolaterally extended root with widely separated root lobes, and a nearly straight ventral root edge. The upper tooth GAMPS-01971 exhibits a triangular, distally bent cusp, complete, thoroughly serrated cutting edges, well-individualised, subhorizontal heels, and a root with a well-developed basal furrow. Both the uppers and lowers have the lingual root surface bisected by a distinct nutrient groove. Based on these characters, the four teeth in question are assigned herein to the widespread requiem shark genus *Carcharhinus* Blainville, 1816 (see also Compagno 1988; Cappetta 2012), which in Pliocene times was represented by at least eight different species inhabiting the Mediterranean Sea (Collareta et al. 2021).

High-resolution microphotographs were taken at Dipartimento di Scienze della Terra dell'Università di Pisa (Pisa, Italy) with a Zeiss AXIO Zoom.V16 macroscope by using the automated focus stacking and extended depth of focus (EDF) functions.

Micro-CT scans were performed at the Istituto di Fisica Applicata "Nello Carrara" (CNR-IFAC; Sesto Fiorentino, Italy) with a Cheetah EVO X-ray inspection system (Comet Yxlon GmbH, Germany) equipped with a Multifocus X-ray tube (FeinFocus FXT-160.51, tungsten target) and a flat-panel detector (1004 × 1004 pixels, 127 µm pitch). This instrument has proven effective for the successful tomographic imaging of fossil shark teeth (Amendola et al. 2025). The distances between the source, object, and detector can be adjusted as needed to achieve the desired field of view and magnification. The system can reach a maximum spatial resolution of approximately 0.9 µm. Samples were placed within a dense polystyrene foam shell and clamped to the rotary stage using a plastic support for scanning. The parameters of the micro-CT acquisitions (i.e., tube voltage, tube current, number of projections, and voxel size) are reported in Table 1. Projection images obtained during the scanning were subsequently processed using the VG Studio Max® (Version 3.5, Volume Graphics GmbH, Heidelberg, Germany) and 3D Slicer (version 5.8.1, retrieved from https://www.slicer.org/) programs for the tomographic reconstruction of the analysed volumes as well as for the extraction of 2D slices and 3D models. On a side note, it should be noted that some volume reconstructions involved mental three-dimensional interpolation due to some minor interference between the original porosity of dentine and the superimposed borings.

Measurements were taken using 3D Slicer and Blender (version 4.4.3, retrieved from https://www.blender.org/). In some cases, Blender was also used to post-process the 3D models for presentation purposes. All figures were assembled using Inkscape (version 1.0.2, retrieved from https://inkscape.org/).

The most informative traces detected on the studied teeth were identified with Greek letters ('α', 'β', etc.). They were further classified based on the ichnotaxonomic framework proposed by Higgs et al. (2012) and subsequently expanded by Jamison-Todd et al. (2025a, b), whereby traces consistent in shape with those left by extant *Osedax* spp. on bony and dental substrates are assigned to the ichnogenus *Osspecus*. On the other hand, fossil examples of *Osspecus* spp. are invariably interpreted as reflecting the feeding activity of *Osedax* as no other organisms are known to make borings in hard organogenic phosphatic substrates with this distinctive morphology (Jamison-Todd et al. 2025b). In fairness, a caveat must be mentioned, as there is no reason to exclude the possibility that similar traces may have also been produced by other osteophagous worm genera, either ancestral to or convergent with *Osedax*. That said, it is worth noting here that the oldest molecular age estimates for the origin of *Osedax* and the geologically oldest examples of *Osspecus* are in good agreement with each other, both suggesting an Early Cretaceous timing for the emergence of the zombie worm clade (see Discussion below). For the sake of simplicity, we will continue to refer to *Osspecus* and other cognate bioerosional features as '*Osedax*-related'.

To date, as many as nine ichnospecies of *Osspecus* have been formally described, sometimes based on traits such as subtle differences in size that are commonly rejected as ichnotaxobases (Bertling et al. 2022). Notwithstanding some reservations, reference is made here to all the nominal ichnospecies of *Osspecus* as per Jamison-Todd et al.'s (2025a, b) diagnoses. It should be noted that structural and compositional differences exist between bone and dentine, so much so that an organism producing traces of a particular morphology on the former substrate may generate different trace patterns on the latter. The corollary of such an observation is that caution should be exercised when extrapolating species-level information on ancient

Table 1. Parameters of the micro-CT acquisitions.

Catalogue number	Number of projections	Tube voltage (kv)	Tube current (µa)	Magnification	Voxel size (µm)
GAMPS-01970	1420	110	182	5.6	23
GAMPS-01971	1420	110	227	6.8	19
GAMPS-01972	1420	110	219	7.2	18
GAMPS-01973	1420	110	219	7.2	18

zombie worm communities (as done e.g. by Jamison-Todd et al. 2025b) based on assemblages of *Osspecus* ispp. originating from different substrates such as bone and dentine.

Results

Two different types of likely cognate bioerosional features – namely, well-preserved *Osspecus* borings and 'pockmarks' – have been detected on the studied teeth and are herein dealt with separately.

Osspecus borings

Specimen GAMPS-01970 from Lucciola Bella is an 11.8-mm-high, 11.3-mm-wide lower tooth (Fig. 2A, B). Macroscopically, GAMPS-01970 is remarkably complete but for some wear of the thin enameloid layer at the crown base on the labial tooth surface as well as for some sparse, very minor pitting of the root exterior. A subcircular hole ('α' in Fig. 2C), approximately a quarter of a millimetre in maximum diameter, pierces the labial root surface along the distal root lobe, slightly below

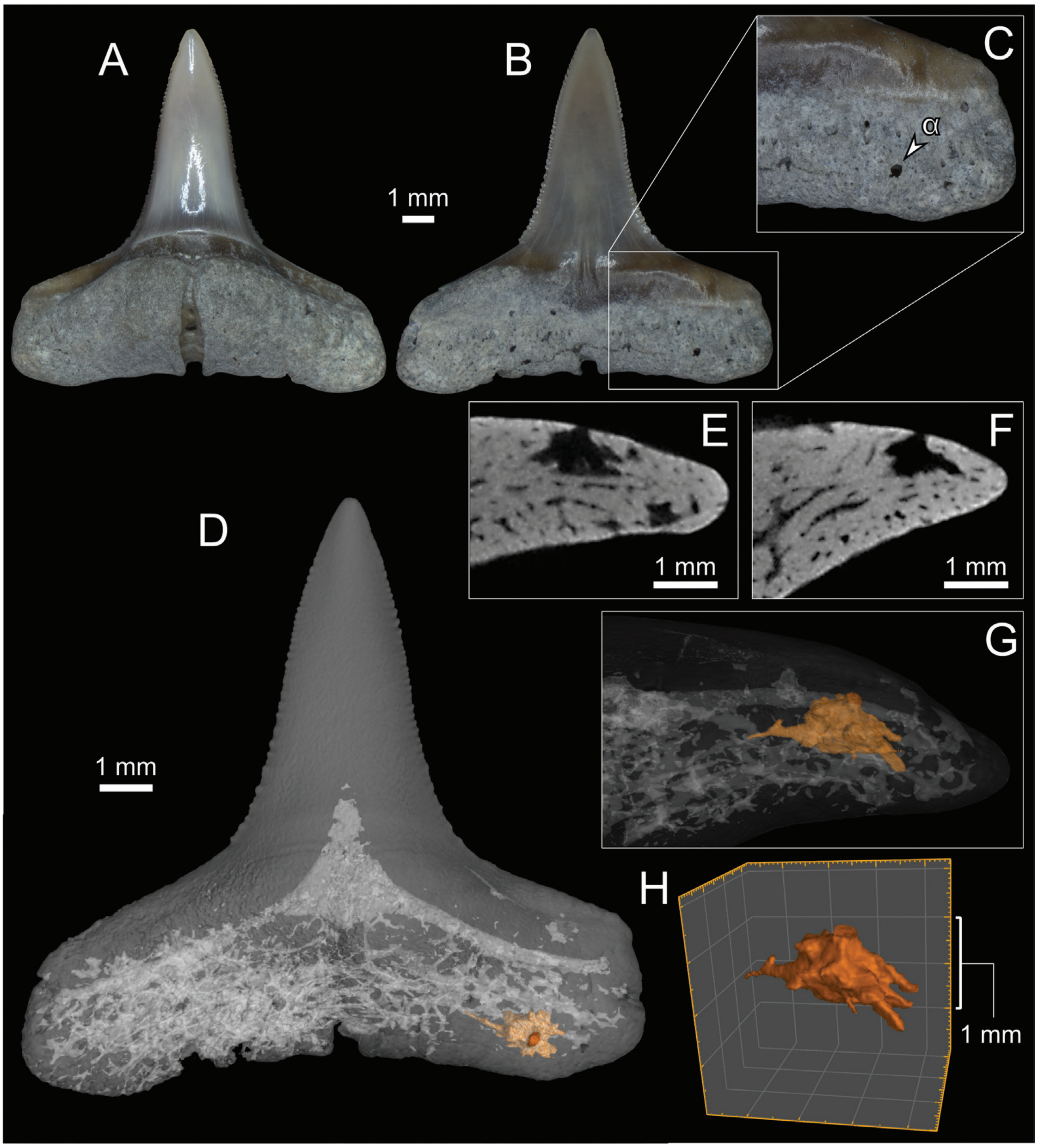

Figure 2. GAMPS-01970, lower tooth of *Carcharhinus* from the Lower Pliocene of Lucciola Bella, overview and close-ups of the associated *Osspecus* boring (i.e., trace 'α'). **A, B.** Microphotographs of GAMPS-01970 in lingual (**A.**) and labial (**B.**) views; **C.** Close-up of (**B.**), showing the location of the external opening of the *Osspecus* boring α; **D.** Transparent 3D model of GAMPS-01970 and superimposed opaque 3D volume reconstruction of the *Osspecus* boring α. The whitish areas represent the vascular cavities developing within the tooth dentine (note the large, open pulp cavity); **E, F.** Two microtomographic cross-sections of the *Osspecus* boring α; **G.** Close-up of (**D.**), taken from a different point of view; **H.** 3D model of the *Osspecus* boring α. The external opening of the boring is oriented upward.

and beyond the mid-height and mid-length of the latter, respectively. Under the macroscope, the hole in question is readily distinguishable from the minor foramina that pierce the labial root surface as well as from other nearby, smaller, seemingly shallower pits. Micro-CT analyses demonstrate that this hole represents the single external opening of a well-defined, tree-like cavity, which differs from the surrounding dentine pores both in terms of size and shape (Fig. 2D). Below the subcircular aperture, a very short neck expands into a much larger internal chamber, leaving only a thin layer of surface dentine on top (Fig. 2E, F). The chamber is roughly ellipsoidal in shape and sends around a variety of exploratory branches (Fig. 2G, H). These branches range from short to long (sensu Jamison-Todd et al. 2025b), most of them being short and incipient. Some branches are bulbous, but others are lobate and tapering, with the longest narrowing into a point. A short, acutely pointed branch is observed projecting downwards from the trace floor. Measurements of trace α are reported in Table 2.

Specimen GAMPS-01971 from Lucciola Bella is an 11.0-mm-high, 14.1-mm-wide upper tooth (Fig. 3A, B). Like GAMPS-01970, it is remarkably complete but for some missing enameloid in occurrence of the distal notch. The labial root surface features four subcircular holes. Two large such holes pierce the distal root lobe, one of them being filled with sediment (‘γ’ in Fig. 3C). Micro-CT analyses reveal that these holes, too, represent the external openings of much larger borings. The boring associated with the sediment-free hole (‘β’ in Figs 3C, 4A) is shallow, its deepest point being located less than one millimetre below the external opening, but not much so considering the limited thickness of the distal root lobe at its distal end. The chamber develops subhorizontally. When viewed apically, its outline is roughly trapezoidal, its long axis being aligned with the root lobe itself (Fig. 4D). There are a few exploratory branches, which are short and substraight (Fig. 4E, G). The boring associated with the sediment-filled hole (‘γ’ in Fig. 4B) is strongly eccentric, developing as it does toward the middle of the root (Fig. 4D).

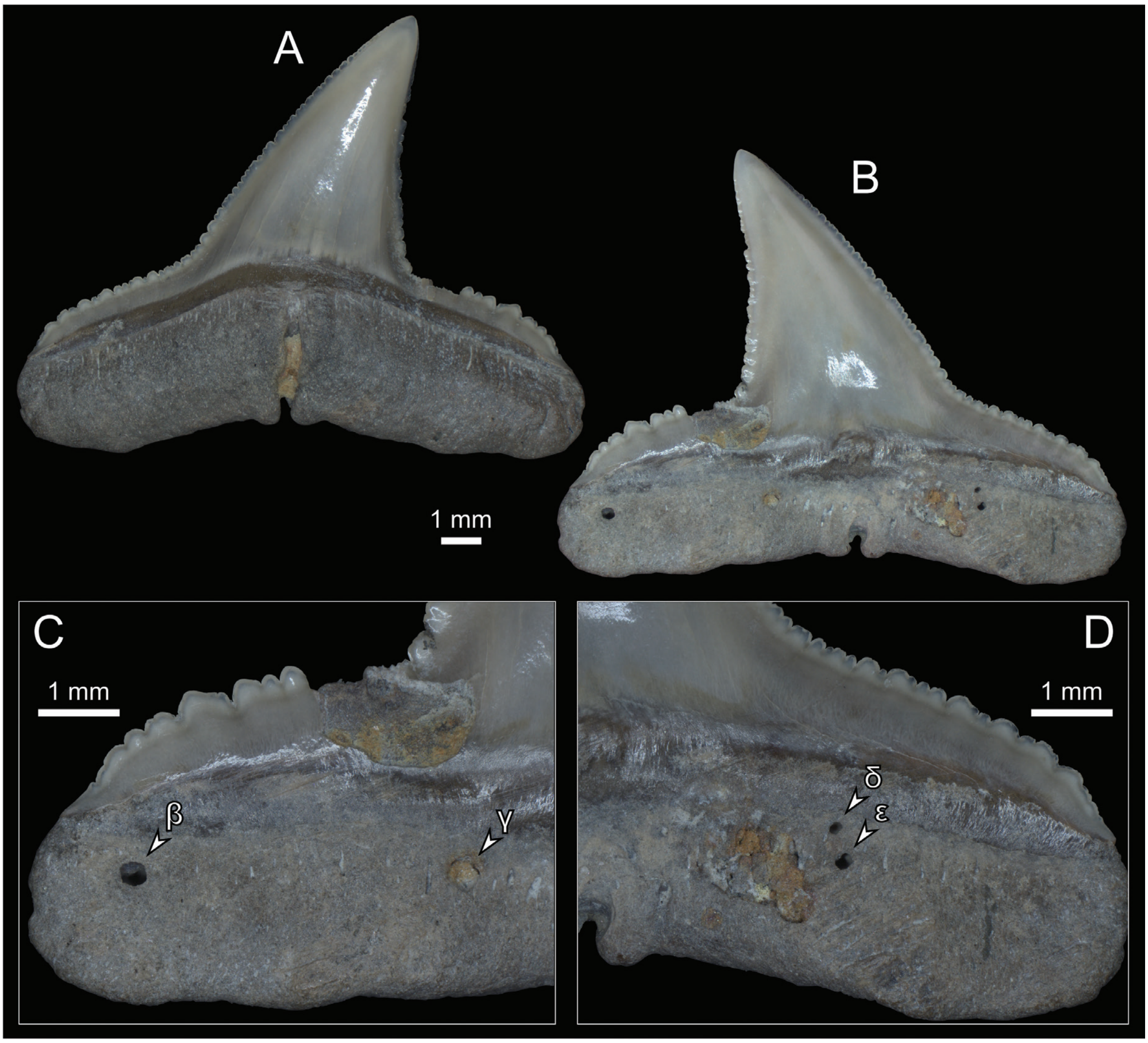

Figure 3. GAMPS-01971, upper tooth of *Carcharhinus* from the Lower Pliocene of Lucciola Bella, overview. **A, B.** Microphotographs of GAMPS-01971 in lingual (**A.**) and labial (**B.**) views; **C, D.** Close-ups of (**B.**), showing the location of the external openings of the *Osspecus* borings β and γ (**C.**), and δ and ε (**D.**).

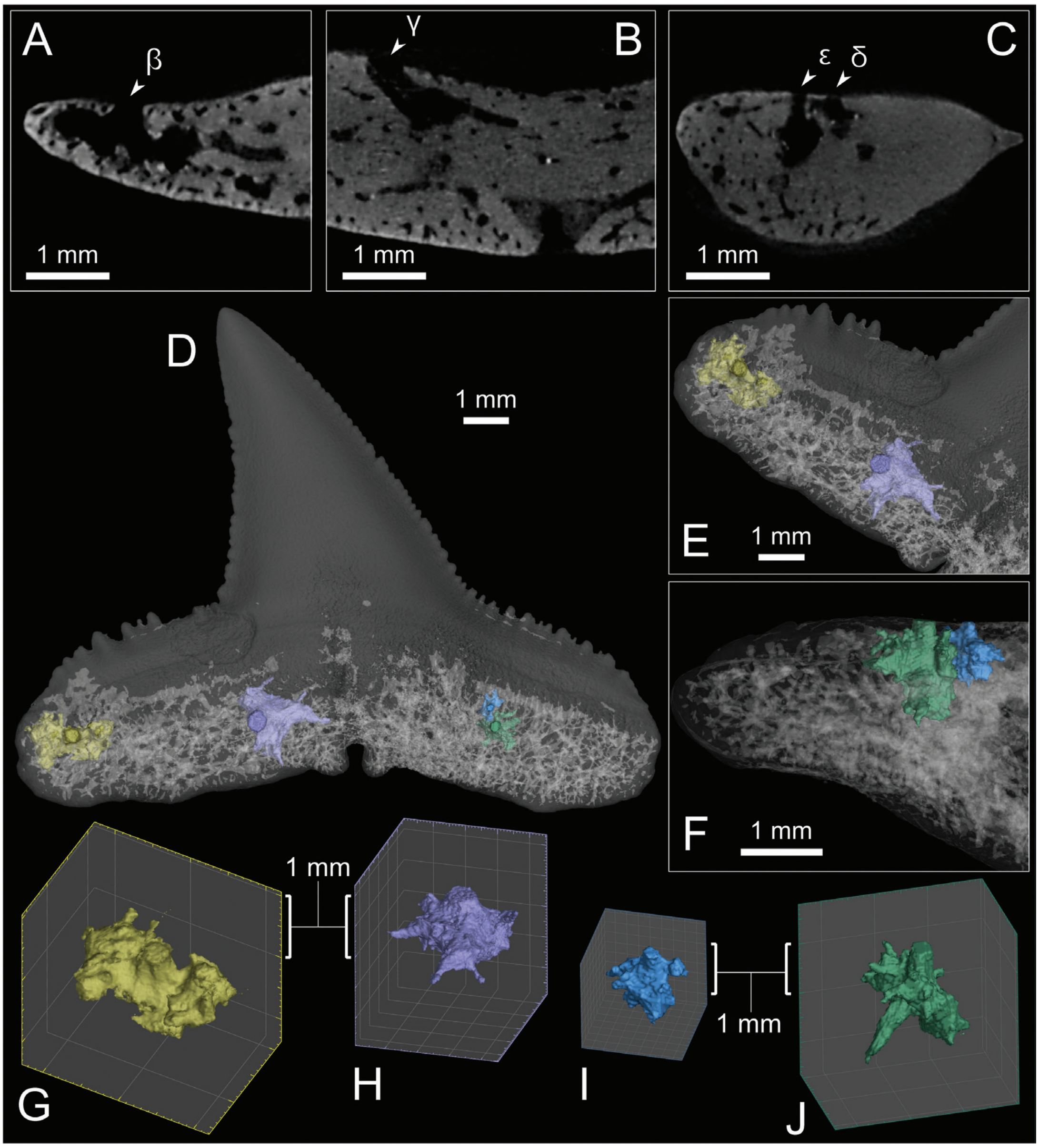

Figure 4. Close-ups of the four *Osspecus* borings (i.e., traces 'β', 'γ', 'δ' and 'ε') occurring on GAMPS-01971, upper tooth of *Carcharhinus* from the Lower Pliocene of Lucciola Bella. **A–C.** Microtomographic cross-sections of the *Osspecus* borings β (**A.**), γ (**B.**), and δ and ε (**C.**). **D.** Transparent 3D model of GAMPS-01970 and superimposed opaque 3D volume reconstructions of the *Osspecus* borings β (yellow), γ (purple), δ (blue) and ε (green). The whitish areas represent the vascular cavities developing within the tooth dentine (note that the pulp cavity is most likely filled with a dense mineral deposit); **E, F.** Close-ups of (**D.**), taken from different points of view. The colour legend is the same as in panel (**D.**). **G–J.** 3D models of the *Osspecus* borings β (**G.**), γ (**H.**), δ (**I.**), and ε (**J.**). The external openings of the borings are oriented upward.

The neck is stout and gradually expands into an oblique-oriented chamber (Fig. 4B). The latter sends around some thin, acutely pointed exploratory branches (Fig. 4D, E, H). Each of the two small borings that pierce the mesial root lobe ('δ' and 'ε' in Fig. 3D) also connects with an internal chamber through a short neck (Fig. 4C). Said chambers are closely interdigitated yet still separated from each other by a thin wall of dentine (Fig. 4B, D, F). Their overall shape is bulbous, with short exploratory branches, but for a single, long, pointed branch associated with trace ε (Fig. 4I, J). Measurements of traces β, γ, δ and ε are reported in Table 2.

Specimen GAMPS-01972 from Selvoli is a 12.3-mm-high, 12.5-mm-wide lower tooth (Fig. 5A, B). It is well preserved but for some missing dentine and enameloid at its mesial end as well as for a smaller, crater-like damage along the lingual surface of the mesial root lobe (see description below). The basal end of the sediment-filled nutrient groove appears somewhat widened mesially ('ζ' in Fig. 5C). Under the Micro-CT, this broadened sector of the groove is shown to connect with a largely irregular chamber through a short neck (Fig. 5D). A number of stout, rounded exploratory branches depart from the trace floor. Because it is continuous with the

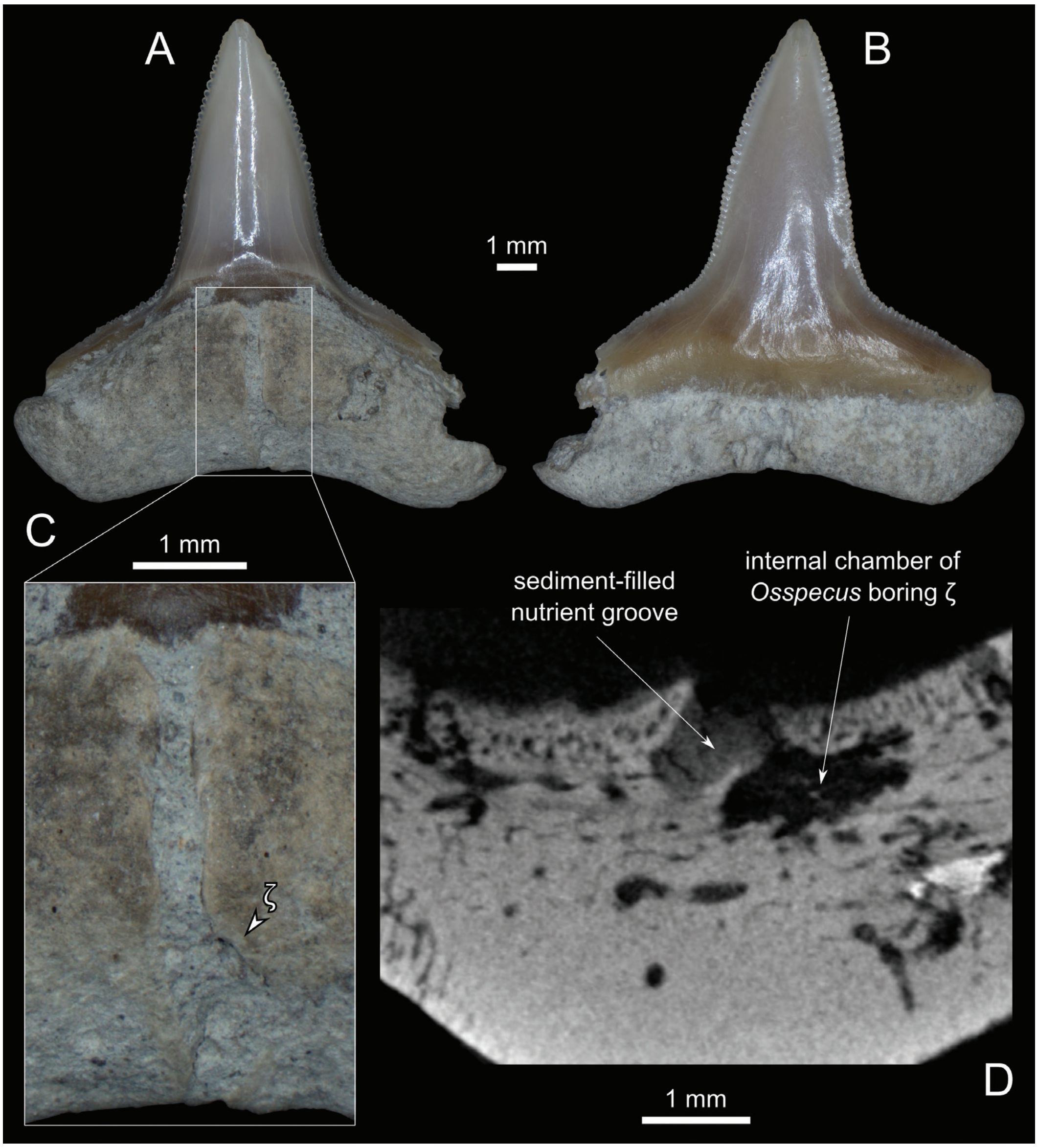

Figure 5. GAMPS-01972, lower tooth of *Carcharhinus* from the Lower Pliocene of Selvoli, overview and close-ups of the associated *Osspecus* boring (i.e., trace 'ζ'). **A, B.** Microphotographs of GAMPS-01972 in lingual (**A.**) and labial (**B.**) views; **C.** Close-up of (**B.**), showing the location of the external opening of the *Osspecus* boring ζ within the nutrient groove; **D.** Microtomographic cross-section of the nutrient groove and associated *Osspecus* boring ζ.

nutrient groove and intersects multiple vascular cavities within the root dentine, this trace could not be reliably segmented to produce a 3D reconstruction.

Each of the above described traces — numbering one in GAMPS-01970, four in GAMPS-01971, and one in GAMPS-01972 — may be described as consisting of a single, circular to sub-circular aperture, lacking any rim or platform, extending into the substrate as a short, subvertical canal that leads to a much larger, globular or irregularly shaped chamber provided with a variety of exploratory branches. Owing to these characters, the borings in question are unambiguously assigned to the ichnogenus *Osspecus*. The next closest match would be *Entobia* Bronn, 1838, which is commonly attributed to the boring action of endolithic clionid sponges (Wisshak et al. 2019). Entobian borings have been recently discovered on teeth of Jurassic marine crocodylomorphs (Serafini et al. 2024) as well as of Neogene cetaceans (Jamison-Todd et al. 2025a) and sharks (Maisch IV et al. 2020). However, *Entobia* commonly consists of networks of chambers and galleries (Tapanila 2006), while our examples of *Osspecus* are typically found isolated from each other.

Based on the observation of short, tapering necks as well as of far-from-spherical chambers, the traces for which volume reconstructions are available (i.e., those occurring on GAMPS-01970 and GAMPS-01971) are further referred to *Osspecus tuscia*, whose holotype also comes from the Tuscan Pliocene (Higgs et al. 2012). The next closest match would be *Osspecus eunicefootia* Jamison-Todd et al., 2025, which, however, typically features exploratory branches that are thin and wavy.

Table 2. Measurements of the five *Osspecus* borings observed on the shark tooth specimens GAMPS-01970 (trace ‘α’) and GAMPS-01971 (traces ‘β’, ‘γ’, ‘δ’ and ‘ε’).

Trace code	Aperture diameter (mm)	Maximum length of chamber (mm)	Transverse width of chamber (mm)	Depth of chamber (mm)	Trace volume (mm^3)	Trace surface area (mm^2)
α	0.25	1.93	0.90	0.84	0.23	3.28
β	0.42	1.98	1.35	0.64	0.44	6.16
γ	0.47	2.11	1.12	1.04	0.49	5.82
δ	0.16	0.76	0.29	0.49	0.04	0.87
ε	0.25	0.98	0.64	0.66	0.13	2.41

Pockmarks

Besides the above described *Osspecus* specimen, GAMPS-01970 also features the occurrence of three similar-sized cavities along the basal margin of the mesial root lobe, just lateral to the nutrient groove (Fig. 6B). Compared to traces α to ε, these cavities exhibit a much larger, irregular external opening, which results in a crater-like morphology (Fig. 6C). These crater-like structures are best interpreted as *Osspecus* borings in which the thin layer of dentine that originally roofed the traces themselves has been largely lost through collapse. Such structures have been described by several authors, including Higgs et al. (2012), Boessenecker and Fordyce (2015) and Bosio et al. (2024), and termed ‘pockmarks’.

Pockmarks are commonly found on otherwise reasonably well-preserved shark teeth collected at the study site, including GAMPS-01972 (Fig. 6A) as well as GAMPS-01973 (Fig. 6D, E), the latter being a 12.8-mm-high, 11.8-mm-wide, fairly complete lower tooth from Selvoli. While most such craters are similar in size to the above examples of *Osspecus*, others are significantly larger, extending as they do along the root lobes (Fig. 6E). This is best explained as due to the coalescence of adjacent *Osspecus* borings followed by the collapse of the delicate roofs thereof (see also Higgs et al. 2014 and Boessenecker and Fordyce 2015).

Discussion

Behavioural inferences

The *Osspecus* specimens described above are most parsimoniously regarded as indicative of feeding by zombie worms, as no other organisms are known to produce borings with such distinctive morphology in hard organogenic phosphatic substrates (Jamison-Todd et al. 2025b). That all these traces excavate the root dentine, leaving the enameloid-coated crowns seemingly unaltered, is consistent with the behaviour of extant *Osedax* spp. feeding on artificially deployed shark teeth, as is the observation of a single boring opening within the nutrient groove of GAMPS-01972 (Rouse and Goffredi 2023). It is worth noting here that shark tooth roots are comprised of osteodentine – a rather porous, organic-rich, and overall bone-like variety of dentine (Berkovitz and Shellis 2017).

Extant *Osedax* spp. are believed to exploit both lipids and collagen for nutrition. Although small quantities of lipids may occur in the shark tooth dentine (López-Álvarez et al. 2016), the main nutrition source of past and present shark tooth-inhabiting zombie worms is most likely collagen, which abounds in the organic-rich shark tooth roots (LeGeros 1981; Enax et al. 2012).

To the best of our knowledge, the putative occurrence of *Osedax*-related bioerosional features on fossil shark materials has been evoked by as few as three previous works. Specifically, Amalfitano et al. (2019) interpreted some circular borings on a vertebral centrum from a partially articulated skeleton of *Cretoxyrhina mantelli* (Agassiz, 1835) from the Upper Cretaceous (Turonian) of northeastern Italy as possibly due to the feeding activity of zombie worms. However, this inference is contentious, as the 3D morphology of the traces in question remain unknown, and there is no evidence at present for extant *Osedax* spp. colonising the endoskeletal elements of sharks from observations in the wild, nor from deployment experiments (Rouse and Goffredi 2023). Feichtinger et al. (2020) tentatively referred some microborings on teeth of *Cretacladoides noricum* Feichtinger et al., 2018 from the Lower Cretaceous (Berriasian–Valanginian) of Upper Austria as possibly related to *Osedax* or some *Osedax*-like organism. Here again, nothing is known on the 3D morphology of the traces in question, which are characterised by very small aperture diameters (< 0.1 mm) and significantly predate the earliest unambiguous occurrences of *Osspecus*. Lastly, a Megalodon tooth collected at an as-yet unnamed deep-sea locality close to Johnston Atoll (northern Pacific Ocean) has recently been hypothesised to lack the root due to bioerosion by *Osedax* (Pollerspöck et al. 2025). No ichnological features that may either support or falsify this fascinating, if speculative, hypothesis appear to be preserved on the tooth in question. All things considered, our bioeroded *Carcharhinus* teeth from the Italian Pliocene provide the first fossil evidence for *Osedax* exploiting shark tooth dentine – and, more broadly, any shark-derived material.

Taphonomic implications

Osedax is a major taphonomic agent in the marine environment owing to its remarkable capability of eroding whale bones, which in turn is due to the acid secretion that accompanies the absorption of bone-trapped nutrients

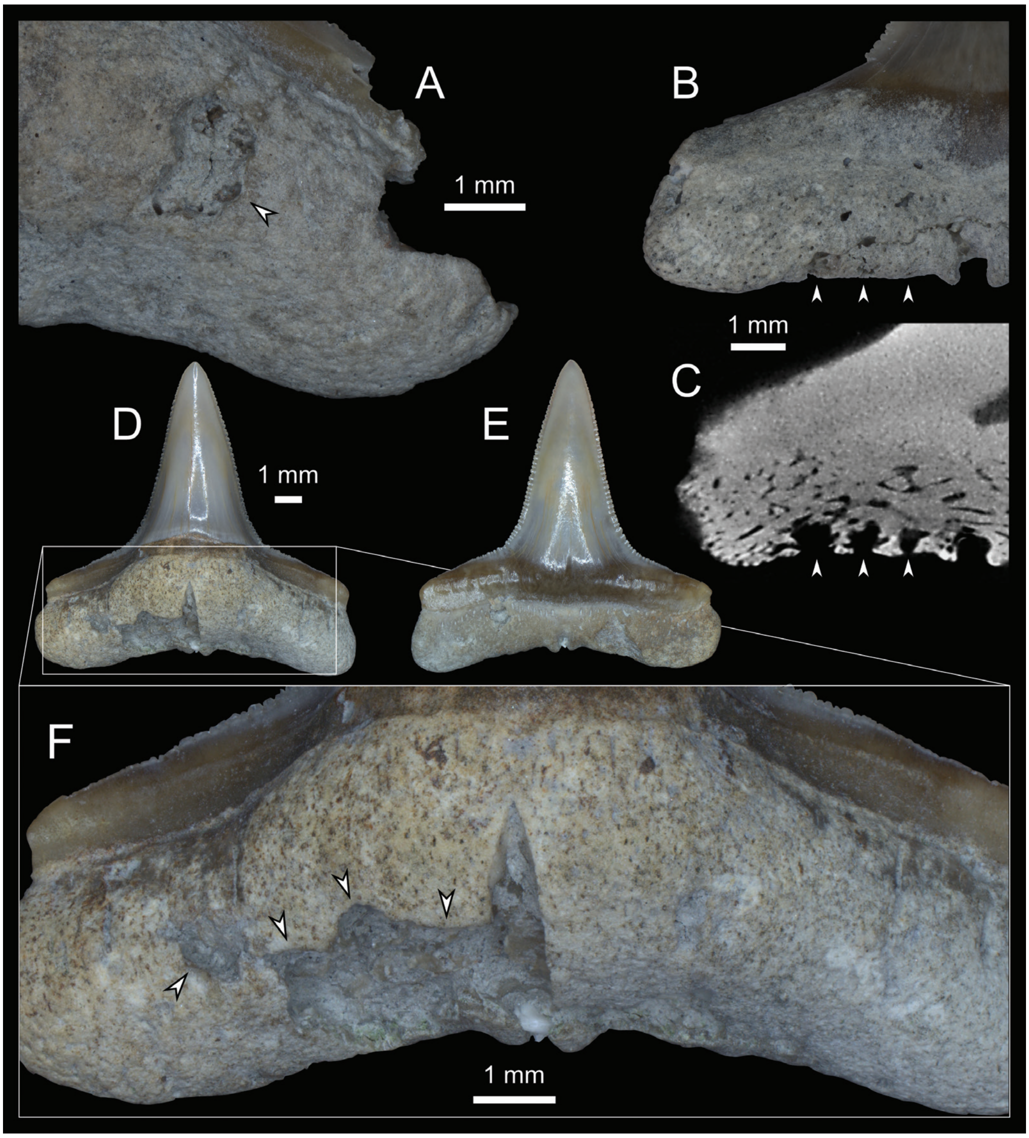

Figure 6. Crater-like 'pockmarks', indicated by arrowheads, on shark teeth from the Lower Pliocene of Lucciola Bella and Selvoli. **A.** Isolated pockmark on the lingual surface of the mesial root lobe of GAMPS-01972; **B.** Three small pockmarks piercing the basal margin of the mesial root lobe of GAMPS-01970; **C.** Microtomographic cross-section of the same pockmarks as in (**B.**). **D; E.** GAMPS-01973, lower tooth of *Carcharhinus* from the Lower Pliocene of Selvoli, microphotographs in lingual (**D.**) and labial (**E.**) views; **F.** Close-up of (**D.**), showing an isolated pockmark and a large, crater-like damaged area along the lingual surface of the distal root lobe.

(Higgs et al. 2011; Tresguerres et al. 2013). Where *Osedax* worms are abundant, bioerosion by these bone-eating siboglinids may even induce the rapid destruction of entire whale skeletons. Thus, it is widely believed that the feeding habits of *Osedax* have had a prominent role in shaping the cetacean fossil record over most of the Cenozoic. Now, however, considering the well-established occurrence of *Osedax*-related borings on the skeletal remains of other marine vertebrates (including Cretaceous marine reptiles such as plesiosaurs and mosasaurs), the '*Osedax* effect' — whatever its actual extent — is unlikely to have solely impacted the cetacean fossil record. This interpretation is further strengthened by the fact that multiple deployment experiments have shown various extant members of *Osedax* to be able to be feed on the bones of other marine and terrestrial mammals, birds, and reptiles, and lately also on shark teeth, exploiting the latter's dentine. By documenting the occurrence of *Osspecus* on fossil teeth of *Carcharhinus*, the present paper serves as a powerful demonstration that feeding on shark tooth dentine can and does occur in at least some wild populations of *Osedax*. Thus, we are led to ponder whether an '*Osedax* effect' may exist with respect to the selachian fossil record.

Sharks have inhabited the Earth's oceans for some 250 million years (Maisey 2012), leaving behind a substantial palaeontological record (Cappetta 2012), most of which consists of dental and dermal remains due to the fact that teeth and scales are heavily mineralised in sharks, while the endoskeleton is largely cartilaginous, and as such, poorly suited for fossil preservation. The fossil record of selachians is further enhanced by their unique dental replacement pattern, whereby teeth are shed and replaced continuously throughout their lives (Kemp 1999; Gillis and Donoghue 2007; Tucker and Fraser 2014; Berkovitz and Shellis 2017), so much so that some modern sharks can lose thousands or even tens of thousands of teeth during their lifetime (Brisswalter 2009), which in turn results in the accumulation of abundant dental remains on the seafloor (Litvinov 2007).

Considering such an abundant fossil record, and taking into account that zombie worms and sharks appear to have coexisted for at least 100 million years (Danise and Higgs 2015; Jamison-Todd et al. 2025b), how could the occurrence of *Osedax*-related modifications on shark teeth go unnoticed for such a long time? That *Osedax*'s capability to bore into and feed on shark tooth dentine has been disclosed only recently does certainly contribute to explain this widespread invisibility, in that *Osspecus*-like traces may have simply not been searched for, at least not routinely, on fossil shark teeth. However, search bias alone is unlikely to account for the pattern, as the discovery of *Osspecus* on fossil bones of marine turtles and birds (Kiel et al. 2011; Danise and Higgs 2015) has predated the identification of *Osedax* on their modern counterparts (Rouse et al. 2018).

The point we would like to make here is that *Osspecus* borings represent somewhat self-destroying evidence for ancient *Osedax* populations. Indeed, *Osspecus* borings are unlikely to be preserved on bones (or teeth for that matter) that are not buried halfway through biostratinomy, as *Osedax* itself progressively consumes its own substrate through feeding (Jamison-Todd et al. 2024). In this regard, it is noteworthy that the *Osspecus* borings dealt with herein are remarkably small-sized compared to those made by extant *Osedax* spp. on bone, with total volumes falling well below 1 mm^3 (Table 2), versus maximum boring volumes of up to some tens of cubic millimetres in many living zombie worm species (Higgs et al. 2014: tab. 2). Also remarkable is the fact that the volume of the largest individual *Osedax*-related boring recorded by Higgs et al. (2014: tab. 2) significantly exceeds that of the root of e.g. GAMPS-01970 (99 mm^2 vs 76 mm^2), and even the total volume of the same tooth (98 mm^2). Therefore, our Italian Pliocene specimens of *Osspecus* were either excavated by an idiosyncratic, likely miniaturised *Osedax* species that produced very small-sized borings, or they represent ichnogenetically incomplete (sensu Belaústegui et al. 2016) examples of traces that could have grown much larger. Since there is no indication that the exploitation of shark tooth dentine is exclusive to highly specialised members of *Osedax* (Rouse and Goffredi 2023; but see also Smith et al. 2015), the latter hypothesis is the most promising. Furthermore, considering that some large-sized species of *Osedax* have roots that can penetrate the substrate by several centimetres (Smith et al. 2015), destruction by zombie worms is likely very efficient, and often completely successful, in the case of inconspicuous food items such as shark tooth roots.

The fossil record, both offshore and inland, may preserve some evidence of the root-destroying effectiveness of *Osedax*. As mentioned, an otodontid tooth from the midst of the Pacific Ocean has been recently hypothesised to lack the root due to the feeding activity of *Osedax* (Pollerspöck et al. 2025). Rootless specimens are also known to comprise approximately one half of the shark teeth trawled from the seafloor at the Nazca and Sala-y-Gomez seamounts, in the southern Pacific Ocean (Litvinov 2007). Many other shark tooth assemblages from deep seafloors are known to include a large fraction of rootless specimens (e.g., Belyaev and Glickman 1970). Moving inland, some time-averaged marine vertebrate accumulations have been reported to be home to rootless shark teeth, with some specimens even missing most of the dentine 'core' of the tooth crowns while invariably featuring essentially well-preserved enameloid cusps (e.g., Boessenecker et al. 2014). That this peculiar preservation style is exclusive to certain shark tooth-rich beds is suggestive of the local action of a specific taphonomic agent (Boessenecker et al. 2014). Although widespread phenomena of root destruction are often ascribed to fungal and/or bacterial bioerosion (e.g., Underwood et al. 1999; Bosio et al. 2022), it is possible that a prominent role is also played by zombie worms.

That said, we must emphasise that although *Osedax* is no longer regarded as a whale bone specialist (Rouse et al. 2011), large natural populations of this siboglinid have hitherto been reported only from whale bones and skeletons (Smith et al. 2015). Furthermore, there is no indication at present that *Osedax* may live and feed on the largely cartilaginous elements that comprise the selachian endoskeleton (Rouse and Goffredi 2023), such that the '*Osedax* effect' is not expected to affect the preservation of these materials. Also, shark teeth are often small and lightweight, so much so that those lying on the seafloor in high-energy depositional settings may be easily mobilised by bottom currents, thereby hindering the successful colonisation by zombie worms. On a different but related note, due to their inconspicuous volume and organic content, very small teeth such as those of many deep-sea sharks are unlikely to be frequently colonised by *Osedax* spp. On the other hand, we may expect *Osedax* to be able to exploit large, modified dermal denticles such as the fin spines of some shark species, which share the same general architecture as teeth, featuring a dentine base and 'trunk' coated by an enameloid-bearing 'cap' (Tovar-Ávila et al. 2008). Further deployment experiments may shed more light on this and other aspects of *Osedax*'s exploitation of shark-derived dental and dermal tissues.

All things considered, an '*Osedax* effect' likely exists in relation to sharks in the form of a progressive destruction of the dentine portions of the teeth, including the root and the 'core' of the crown. However underinvestigated this selachian-related '*Osedax* effect' may be, it is likely less generalised than hypothesised for whales and other marine tetrapods, as it appears to leave the largely cartilaginous shark endoskeleton essentially unaffected.

Palaeobiological implications

The recent observation of *Osedax* colonising and feeding on modern shark tooth roots under experimental conditions has raised the question whether the shark tooth dentine represents the primordial nutrition source of this peculiar siboglinid genus (Rouse and Goffredi 2023). By demonstrating that such a behaviour can and does occur in the wild (i.e., outside experimental conditions), our discovery of *Osspecus* on Pliocene shark teeth gives this hypothesis some credibility, especially in relation to an early Mesozoic or Palaeozoic scenario for the origin of *Osedax* (Rouse and Goffredi 2023). Such a scenario is at least consistent with the fossil history of sharks, which have wandered the Earth's seas for some 250 million years, with the palaeontological record of chondrichthyan-like teeth being even deeper, extending as it does back some 425 million years (e.g., Andreev et al. 2022). Although the rates of tooth replacement of the Palaeozoic 'sharks' were much lower than those characterising the present-day selachians (Botella et al. 2009), which in turn would imply a more limited availability of teeth on the seafloor, the remarkable antiquity of the cartilaginous fishes could still provide a reasonable context for a deep-time scenario for the emergence of the zombie worms, which nonetheless may also have taken place on bony fish skeletons (Rouse and Goffreddi 2023). In principle, a systematic search for *Osedax*-related borings on fossil marine vertebrate remains (including shark teeth) from lower Mesozoic and Paleozoic deposits may thus reveal that the zombie worm lineage is much older than thought (Rouse and Goffreddi 2023). However, this tantalising hypothesis is not without some major problems.

First and foremost, we are to remember that extensive natural populations of *Osedax* are only known to occur on the skeletal remains of cetaceans, and that the same appears to hold true for the Cenozoic record of *Osspecus*. However limited the Cretaceous evidence for *Osedax* may be, it seems to conform to a similar pattern, where *Osspecus* concentrates on marine reptile bones. Considering all the published occurrences of both *Osspecus* and *Osedax*, there is no evidence at present for a widespread diffusion of the latter on substrates other than the bony remains of marine tetrapods. This pattern is not particularly suggestive of *Osedax* having originated on shark teeth, exploiting the latter's dentine as its original nutrition source.

Secondly, and perhaps more importantly, although the timing of the main evolutionary events within the siboglinid clade remains largely unexplored by means of molecular clocks, the available estimates suggest that *Osedax* did not originate prior to the Cretaceous (Vrijenhoek et al. 2009; Rouse et al. 2011; Taboada et al. 2015). These estimates are broadly consistent with the chronostratigraphic distribution of *Osspecus*, which has its first appearance in the Albian (uppermost Lower Cretaceous) (Danise and Higgs 2015; Jamison-Todd et al. 2024) (Fig. 7). That said, the recent discovery of multiple *Osspecus* ichnospecies on bones from Cenomanian (lowermost Upper Cretaceous) deposits has been taken as evidencing a similarly high number of co-occurring *Osedax* species, which in turn would be indicative either of a rapid diversification of the zombie worms after their emergence in Albian times or of an origin older than previously thought (Jamison-Todd et al. 2024). Although it is somewhat likely that *Osedax* originated earlier than the Albian first occurrence of *Osspecus*, that the latter has never been reported to occur on marine vertebrate remains from the reasonably well-prospected Jurassic (Jamison-Todd et al. 2024) is quite suggestive of a genuine absence before the beginning of the Cretaceous. Ultimately, that the molecular clocks and the fossil record converge in suggesting a Cretaceous age for the emergence of *Osedax* (Fig. 7) is hard to dismiss. If a Cretaceous origin is assumed for *Osedax*, then hypothesising that such an origin occurred on a substrate other than the bony tissues of (large) marine vertebrates may not be the most parsimonious solution. All things considered, shark tooth roots are unlikely to have been the ancestral substrate and nutrition source of *Osedax*.

At this point, it can be speculated that the colonisation of inconspicuous substrates such as loose shark teeth would generally begin in the vicinity of large whale falls, as an offshoot (as it were) of the whale fall community, and that the same could have happened in Mesozoic times starting from large marine reptile skeletons. By becoming home to small, peripheral *Osedax* colonies, the colonised teeth would act as critical benthic islands as well as ecological stepping stones between remote whale falls, which in turn have long been regarded as serving as dispersal and evolutionary stepping stones for a variety of chemotrophic deep-sea invertebrates (Smith et al. 2015, and the many references therein). Ultimately, that many ocean floors are known to be covered with a 'carpet' of shark teeth (e.g., Litvinov 2007) is at least consistent with this hypothesis.

A major stratigraphic gap still exists between the youngest Mesozoic occurrence of *Osspecus*, which dates back to the latest Cretaceous (Jamison-Todd et al. 2024), and its oldest Cenozoic occurrence, which dates back to the late middle Eocene (Ibrahim et al. 2025) (Fig. 7). Whether the near-ubiquitous availability of shark teeth at the seafloor helped *Osedax* to survive through the end-Cretaceous (K–Pg) mass extinction is an open question. On the one hand, considering that sea turtles are the only extant group of marine vertebrates whose Mesozoic fossil record has hitherto yielded evidence of colonisation by *Osedax* (Danise and Higgs 2015), such survival may have been possible first and foremost on chelonioid skeletons and bones. On the other hand, considering that the K–Pg event has been recently shown to have had little impact on at least some elasmobranch communities (Feichtinger et al. 2025), deep-sea accumulations of shark teeth may well have played a role in permitting the post-Cretaceous survival of zombie worms.

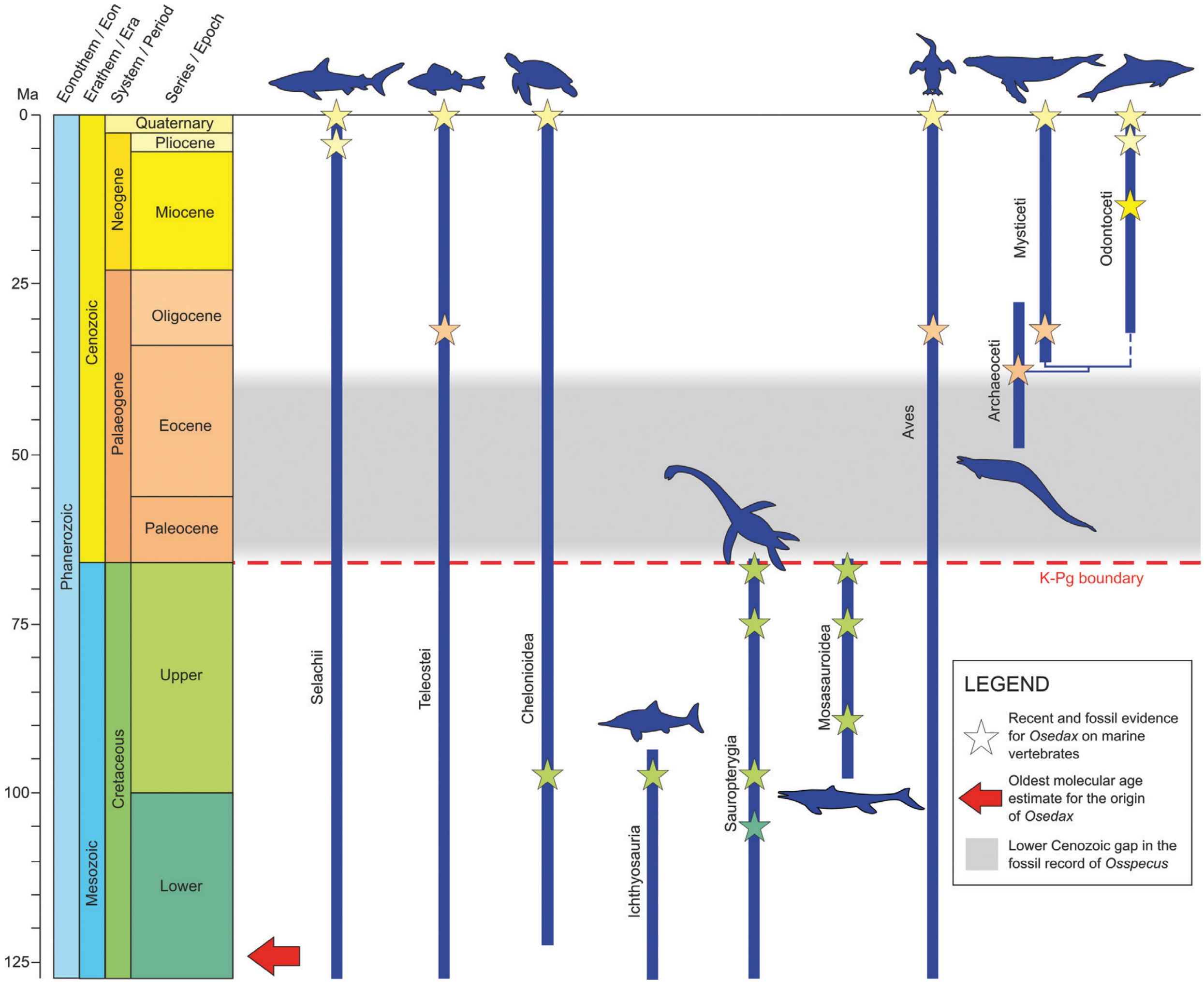

Figure 7. Stratigraphic range of marine vertebrate groups associated with trace fossil evidence for ancient *Osedax* populations. The molecular age estimate for the origin of *Osedax* is after Vrijenhoek et al. (2009). Data on modern and fossil occurrences of *Osedax* are after Danise and Higgs (2015), Rouse et al. (2018), Jamison-Todd et al. (2023, 2024, 2025a, b), Ibrahim et al. (2025) and the present work. Note that only reports substantiated by microtomographic analyses are included here, and that *Osspecus* occurrences originating from roughly coeval deposits were subsumed into a single record if relative to the same marine vertebrate group.

Conclusions

We documented the presence of *Osspecus* borings on fossil shark teeth recovered from Lower Pliocene offshore deposits of the Siena-Radicofani Basin (Tuscany, central Italy). Micro-CT scans revealed that these traces penetrate the dentine of the tooth roots, while the enameloid-coated crowns remain essentially unaffected. Although many such borings have turned into poorly defined pockmarks due to the collapse of the thin layer of dentine that originally roofed the traces themselves, some of them retain a well-preserved three-dimensional morphology, thus allowing for unambiguous ichnotaxonomic identification.

Occurring as they do on Pliocene shark teeth, the borings in question represent the first fossil evidence for *Osedax* exploiting shark tooth dentine. Moreover, they compellingly demonstrate that such behaviour is not restricted to deployment experiments but can and does occur in the wild. The exploitation of tooth roots by zombie worms may also account for their absence from some modern deep-sea shark tooth assemblages and time-averaged horizons. Shark teeth are unlikely to have been the ancestral substrate and nutrition source of *Osedax* but may have had a role in enabling the survival of zombie worms across the end-Cretaceous mass extinction. Furthermore, they may have served as critical benthic islands and ecological stepping stones between distant marine vertebrate fall sites, a role that likely dates back to the late Mesozoic, some 100 million years ago.

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References

Amalfitano J, Giusberti L, Fornaciari E, Dalla Vecchia FM, Luciani V, Kriwet J, Carnevale G (2019) Large deadfalls of the ‘ginsu’ shark *Cretoxyrhina mantelli* (Agassiz, 1835) (Neoselachii, Lamniformes) from the Upper Cretaceous of northeastern Italy. Cretaceous Research 98: 250–275. https://doi.org/10.1016/j.cretres.2019.02.003

Amendola M, Barucci A, Baucon A, Zini C, Borrelli C, Casati S, Di Cencio A, Fiore S, Agresti J, Siano S, Agresti J, Neto de Carvalho C, Bernardini F, Lo Russo G, Collareta A, Bosio G (2025) Exploring how micro-computed tomography imaging technology impacts the preservation of paleontological heritage. Heritage 8: 310. https://doi.org/10.3390/heritage8080310

Andreev PS, Sansom IJ, Li Q, Zhao W, Wang J, Wang CC, Peng L, Jia L, Qiao T, Zhu M (2022) The oldest gnathostome teeth. Nature 609: 964–968. https://doi.org/10.1038/s41586-022-05166-2

Baco-Taylor AR (2002) Food-web structure, succession and phylogenetics on deep-sea whale skeletons. PhD Thesis, University of Hawaii, Honolulu.

Belaústegui Z, Muñiz F, Mángano MG, Buatois LA, Domènech R, Martinell J (2016) *Lepeichnus giberti* igen. nov. isp. nov. from the upper Miocene of Lepe (Huelva, SW Spain): evidence for its origin and development with proposal of a new concept, ichnogeny. Palaeogeography, Palaeoclimatology, Palaeoecology 452: 80–89. https://doi.org/10.1016/j.palaeo.2016.04.018

Belyaev GM, Glikman LS (1970) Shark teeth on the bottom of the Pacific Ocean [in Russian]. Trudy Instituta Okeanologii 88: 252–277.

Benvenuti M, Del Conte S, Scarselli N, Dominici S (2014) Hinterland basin development and infilling through tectonic and eustatic processes: latest Messinian–Gelasian Valdelsa Basin, Northern Apennines, Italy. Basin Research 26: 387–402. https://doi.org/10.1111/bre.12031

Berkovitz B, Shellis P (2017) The teeth of non-mammalian vertebrates. Academic Press, Cambridge, 342 pp.

Berman GH, Johnson SB, Seid CA, Vrijenhoek RC, Rouse GW (2023) Range extensions of Pacific bone-eating worms (Annelida, Siboglinidae, *Osedax*). Biodiversity Data Journal 11: e102803. https://doi.org/10.3897/BDJ.11.e102803

Bertling M, Buatois LA, Knaust D, Laing B, Mángano MG, Meyer N, Mikuláš R, Minter NJ, Neumann C, Rindsberg AK, Uchman A, Wisshak M (2022) Names for trace fossils 2.0: theory and practice in ichnotaxonomy. Lethaia 55: 1–19. https://doi.org/10.18261/let.55.3.3

Bianucci G, Vaiani SC, Casati S (2009) A new delphinid record (Odontoceti, Cetacea) from the Early Pliocene of Tuscany (Central Italy): systematics and biostratigraphic considerations. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 11: 275. https://doi.org/10.1127/0077-7749/2009/0018

Boessenecker RW, Fordyce RE (2015) Trace fossil evidence of predation upon bone-eating worms on a baleen whale skeleton from the Oligocene of New Zealand. Lethaia 48: 326–331. https://doi.org/10.1111/let.12108

Boessenecker RW, Perry FA, Schmitt JG (2014) Comparative taphonomy, taphofacies, and bonebeds of the Mio-Pliocene Purisima Formation, Central California: strong physical control on marine vertebrate preservation in shallow marine settings. PLoS ONE 9: e91419. https://doi.org/10.1371/journal.pone.0091419

Bosio G, Bianucci G, Collareta A, Landini W, Urbina M, Di Celma C (2022) Ultrastructure, composition, and $^{87}Sr/^{86}Sr$ dating of shark teeth from lower Miocene sediments of southwestern Peru. Journal of South American Earth Sciences 118: 103909. https://doi.org/10.1016/j.jsames.2022.103909

Bosio G, Bajo-Campos I, Collareta A, Ros-Montoya S, de la Torre D, Coletti G, Bianucci G (2024) Taphonomy of a mysticete whale from the Lower Pliocene of the coast of Cádiz (Spain). Journal of Marine Science and Engineering 12: 17. https://doi.org/10.3390/jmse12010017

Botella H, Valenzuela-Ríos JI, Martínez-Pérez C (2009) Tooth replacement rates in early chondrichthyans: a qualitative approach. Lethaia 42: 365–376. https://doi.org/10.1111/j.1502-3931.2009.00152.x

Braby CE, Rouse GW, Johnson SB, Jones WJ, Vrijenhoek RC (2007) Bathymetric and temporal variation among *Osedax* boneworms and associated megafauna on whale-falls in Monterey Bay, California. Deep Sea Research Part I: Oceanographic Research Papers 54: 1773–1791. https://doi.org/10.1016/j.dsr.2007.05.014

Brisswalter G (2009) Inventaire des Élasmobranches (requins, raies, chimères) des dépôts molassiques du Sud-Luberon (Miocène supérieur), Cabrières d’Aigues (Vaucluse) France. Courriers scientifiques du Parc naturel Régional du Lubéron, Hors Série: 1–100.

Brogi A (2011) Bowl-shaped basin related to low-angle detachment during continental extension: the case of the controversial Neogene Siena Basin (central Italy, Northern Apennines). Tectonophysics 499: 54–76. https://doi.org/10.1016/j.tecto.2010.12.005

Brogi A, Capezzuoli E, Martini I, Picozzi M, Sandrelli F (2014) Late Quaternary tectonics in the inner Northern Apennines (Siena Basin, southern Tuscany, Italy) and their seismotectonic implication. Journal of Geodynamics 76: 25–45. https://doi.org/10.1016/j.jog.2014.03.001

Cappetta H (2012) Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In: Schultze HP (Ed.) Handbook of Paleoichthyology, Volume 3E. Pfeil, Munich, 512 pp.

Collareta A, Casati S, Di Cencio A (2017) A pristid sawfish from the lower Pliocene of Lucciolabella (Radicofani Basin, Tuscany, central Italy). Atti della Società Toscana di Scienze Naturali, Memorie, Serie A 124: 49–55.

Collareta A, Merella M, Casati S, Di Cencio A (2021) First fossils of the extant blacktip shark *Carcharhinus limbatus* from Europe and the Mediterranean Basin. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 301: 109–118. https://doi.org/10.1127/njgpa/2021/1002

Collareta A, Casati S, Mulè F, Pieri A, Di Cencio A, Bianucci G (2025) A fossil mola from the Mediterranean Pliocene. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 313: 341–351. https://doi.org/10.1127/njgpa/2025/1238

Compagno L (1988) Sharks of the Order Carcharhiniformes. Princeton University Press, Princeton, 486 pp.

Danise S, Higgs ND (2015) Bone-eating *Osedax* worms lived on Mesozoic marine reptile deadfalls. Biology Letters 11: 20150072. https://doi.org/10.1098/rsbl.2015.0072

Dominici S, Danise S, Cau S, Freschi A (2020) The awkward record of fossil whales. Earth-Science Reviews 205: 103057. https://doi.org/10.1016/j.earscirev.2019.103057

Enax J, Prymak O, Raabe D, Epple M (2012) Structure, composition, and mechanical properties of shark teeth. Journal of Structural Biology 178: 290–299. https://doi.org/10.1016/j.jsb.2012.03.012

Feichtinger I, Lukeneder A, Topa D, Kriwet J, Libowitzky E, Westall F (2020) Fossil microbial shark tooth decay documents in situ metabolism of enameloid proteins as nutrition source in deep water environments. Scientific Reports 10: 20979. https://doi.org/10.1038/s41598-020-77964-5

Ferber D (2005) Whaling endangers more than whales. Science 307: 1190–1191. https://doi.org/10.1126/science.307.5713.1190c

Fujikura K, Fujiwara Y, Kawato M (2006) A new species of *Osedax* (Annelida: Siboglinidae) associated with whale carcasses off Kyushu, Japan. Zoological Science 23: 733–740. https://doi.org/10.2108/zsj.23.733

Fujiwara Y, Kawato M, Yamamoto T, Yamanaka T, Sato-Okoshi W, Noda C, Tsuchida S, Komai T, Cubelio SS, Sasaki T, Jacobsen K, Kubokawa K, Fujikura K, Maruyama T, Furushima Y, Okoshi K, Miyake H, Miyazaki M, Nogi Y, Yatabe A, Okutani T (2007) Three-year investigations into sperm whale-fall ecosystems in Japan. Marine Ecology 28: 219–232. https://doi.org/10.1111/j.1439-0485.2007.00150.x

Gillis JA, Donoghue PC (2007) The homology and phylogeny of chondrichthyan tooth enameloid. Journal of Morphology 268: 33–49. https://doi.org/10.1002/jmor.10501

Glover AG, Kallstrom B, Smith CR, Dahlgren TG (2005) World-wide whale worms? A new species of *Osedax* from the shallow North Atlantic. Proceedings of the Royal Society B 272: 2587–2592. https://doi.org/10.1098/rspb.2005.3275

Glover AG, Kemp KM, Smith CR, Dahlgren TG (2008) On the role of bone-eating worms in the degradation of marine vertebrate remains. Proceedings of the Royal Society B 275: 1959–1961. https://doi.org/10.1098/rspb.2008.0177

Goffredi SK, Johnson SB, Vrijenhoek RC (2007) Genetic diversity and potential function of microbial symbionts associated with newly-discovered species of *Osedax* polychaete worms. Applied and Environmental Microbiology 73: 2314–2323. https://doi.org/10.1128/AEM.01986-06

Goffredi SK, Orphan VJ, Rouse GW, Jahnke L, Embaye T, Turk K, Lee R, Vrijenhoek RC (2005) Evolutionary innovation: a bone-eating marine symbiosis. Environmental Microbiology 7: 1369–1378. https://doi.org/10.1111/j.1462-2920.2005.00824.x

Higgs ND, Pokines JT (2013) Marine environmental alterations to bone. In: Pokines JT, Symes SA (Eds) Manual of Forensic Taphonomy. CRC Press, Boca Raton, 143–179. https://doi.org/10.1201/b15424

Higgs ND, Glover AG, Dahlgren TG, Little CTS (2010) Using computed-tomography to document borings by *Osedax mucofloris* in whale bone. Cahiers de Biologie Marine 51: 401–405.

Higgs ND, Glover AG, Dahlgren TG, Little CTS (2011) Bone-boring worms: characterizing the morphology, rate, and method of bioerosion by *Osedax mucofloris* (Annelida, Siboglinidae). Biological Bulletin 221: 307–316. https://doi.org/10.1086/BBLv221n3p307

Higgs ND, Little CTS, Glover AG, Dahlgren TG, Smith CR, Dominici S (2012) Evidence of *Osedax* worm borings in Pliocene (~3 Ma) whale bone from the Mediterranean. Historical Biology 24: 269–277. https://doi.org/10.1080/08912963.2011.621167

Higgs ND, Glover AG, Dahlgren TG, Smith CR, Fujiwara Y, Pradillon F, Johnson SB, Vrijenhoek RC, Little CTS (2014) The morphological diversity of *Osedax* worm borings (Annelida: Siboglinidae). Journal of the Marine Biological Association of the United Kingdom 94: 1429–1439. https://doi.org/10.1017/S0025315414000770

Iaccarino SM, Premoli Silva I, Biolzi M, Foresi LM, Lirer F, Turco E, Petrizio MR (2007) Practical manual of Neogene Planktonic Foraminifera. International School on Planktonic Foraminifera, 6° Course - Late Miocene to Holocene. Tipografa Pontefelcino, Perugia, 124 pp.

Ibrahim ES, El Hedeny MM, El-Sabbagh AM, El-Kheir GAA, Osman AG, Mahdy A, Ahmed EA (2025) Shallow-water whale-fall communities: Evidence from the middle–late Eocene basilosaurid whale bones, Wadi El-Hitan, Fayum, Egypt. Palaeoworld 34: 100863. https://doi.org/10.1016/j.palwor.2024.06.006

Jamison-Todd S, Upchurch P, Mannion PD (2023) The prevalence of invertebrate bioerosion on Mesozoic marine reptile bone from the Jurassic and Cretaceous of the United Kingdom: new data and implications for taphonomy and environment. Geological Magazine 160: 1701–1710. https://doi.org/10.1017/S0016756823000651

Jamison-Todd S, Mannion PD, Upchurch P (2025a) The earliest fossil cetacean with *Osedax* borings: narrowing the spatiotemporal gap between Cretaceous marine reptiles and late Cenozoic whales. Royal Society Open Science 12: 250446. https://doi.org/10.1098/rsos.250446

Jamison-Todd S, Mannion PD, Glover AG, Upchurch P (2024) New occurrences of the bone-eating worm *Osedax* from Late Cretaceous marine reptiles and implications for its biogeography and diversification. Proceedings of the Royal Society B 291: 20232830. https://doi.org/10.1098/rspb.2023.2830

Jamison-Todd S, Witts JD, Jones ME, Tangunan D, Chandler K, Bown P, Twitchett RJ (2025b) The evolution of bone-eating worm diversity in the Upper Cretaceous Chalk Group of the United Kingdom. PLoS ONE 20: e0320945. https://doi.org/10.1371/journal.pone.0320945

Katz S, Klepal W, Bright M (2010) The skin of *Osedax* (Siboglinidae, Annelida): an ultrastructural investigation of its epidermis. Journal of Morphology 271: 1272–1280. https://doi.org/10.1002/jmor.10873

Katz S, Klepal W, Bright M (2011) The *Osedax* trophosome: organization and ultrastructure. Biological Bulletin 220: 128–139. https://doi.org/10.1086/BBLv220n2p128

Kemp NE (1999) Integumentary system and teeth. In: Hamlett W (Ed.) Sharks, Skates and Rays. The Biology of Elasmobranch Fishes. Johns Hopkins University Press, Baltimore, 43–68.

Kiel S, Kahl WA, Goedert JL (2011) *Osedax* borings in fossil marine bird bones. Naturwissenschaften 98: 51–55. https://doi.org/10.1007/s00114-010-0740-5

Kiel S, Kahl WA, Goedert JL (2013) Traces of the bone-eating annelid *Osedax* in Oligocene whale teeth and fish bones. Paläontologische Zeitschrift 87: 161–167. https://doi.org/10.1007/s12542-012-0158-9

Kiel S, Goedert JL, Kahl WA, Rouse GW (2010) Fossil traces of the bone-eating worm *Osedax* in early Oligocene whale bones. Proceedings of the National Academy of Sciences of the United States of America 107: 8656–8659. https://doi.org/10.1073/pnas.1002014107

LeGeros RZ (1981) Apatites in biological systems. Progress in Crystal Growth and Characterization 4: 1–45. https://doi.org/10.1016/0146-3535(81)90046-0

Litvinov FF (2007) Foundations of the method of dating global fluctuations of abundance of oceanic sharks on the basis of the amount of fossil teeth in bottom sediments. Journal of Ichthyology 47: 267–270. https://doi.org/10.1134/S0032945207040029

López-Álvarez M, Pérez-Davila S, Rodríguez-Valencia C, González P, Serra J (2016) The improved biological response of shark tooth bioapatites in a comparative in vitro study with synthetic and bovine bone grafts. Biomedical Materials 11: 035011. https://doi.org/10.1088/1748-6041/11/3/035011

Lundsten L, Schlining KL, Frasier K, Johnson SB, Kuhnz LA, Harvey JB, Clague G, Vrijenhoek RC (2010) Time-series analysis of six whale-fall communities in Monterey Canyon, California, USA. Deep Sea Research Part I: Oceanographic Research Papers 57: 1573–1584. https://doi.org/10.1016/j.dsr.2010.09.003

Maisch IV HM, Becker MA, Chamberlain Jr JA (2020) Macroborings in *Otodus megalodon* and *Otodus chubutensis* shark teeth from the submerged shelf of Onslow Bay, North Carolina, USA: implications for processes of lag deposit formation. Ichnos 27: 122–141. https://doi.org/10.1080/10420940.2019.1697257

Maisey JG (2012) What is an 'elasmobranch'? The impact of palaeontology in understanding elasmobranch phylogeny and evolution. Journal of Fish Biology 80: 918–951. https://doi.org/10.1111/j.1095-8649.2012.03245.x

Martini IP, Sagri M (1993) Tectono-sedimentary characteristics of Late Miocene–Quaternary extensional basins of the Northern Apennines, Italy. Earth-Science Reviews 34: 197–233. https://doi.org/10.1016/0012-8252(93)90034-5

Martini I, Ambrosetti E, Sandrelli F (2017) The role of sediment supply in large-scale stratigraphic architecture of ancient Gilbert-type deltas (Pliocene Siena–Radicofani Basin, Italy). Sedimentary Geology 350: 23–41. https://doi.org/10.1016/j.sedgeo.2017.01.006

Martini I, Ambrosetti E, Brogi A, Aldinucci M, Zwaan F, Sandrelli F (2021) Polyphase extensional basins: interplay between tectonics and sedimentation in the Neogene Siena–Radicofani Basin (Northern Apennines, Italy). International Journal of Earth Sciences 110: 1729–1751. https://doi.org/10.1007/s00531-021-02038-4

McClain CR, Nunnally C, Dixon R, Rouse GW, Benfield M (2019) Alligators in the abyss: the first experimental reptilian food fall in the deep ocean. PLoS ONE 14: e0225345. https://doi.org/10.1371/journal.pone.0225345

Moggioli G, Panossian B, Sun YA, Thiel D, Martin-Zamora FM, Tran M, Clifford AM, Goffredi SK, Rimskaya-Korsakova N, Jekely G, Tresguerres M, Qian PY, Qiu JW, Rouse GW, Henry LM, Martin-Duran JM (2023) Distinct genomic routes underlie transitions to specialised symbiotic lifestyles in deep-sea annelid worms. Nature Communications 14: 2814. https://doi.org/10.1038/s41467-023-38521-6

Pascucci V, Costantini A, Martini IP, Dringoli R (2006) Tectono-sedimentary analysis of a complex, extensional, Neogene basin formed on thrust-faulted, Northern Apennines hinterland: Radicofani Basin, Italy. Sedimentary Geology 183: 71–97. https://doi.org/10.1016/j.sedgeo.2005.09.009

Pollerspöck J, Cares D, Ebert DA, Kelley KA, Pockalny R, Robinson RS, Wagner D, Straube N (2025) First in situ documentation of a fossil tooth of the megatooth shark *Otodus* (*Megaselachus*) *megalodon* from the deep sea in the Pacific Ocean. Historical Biology 37: 120–125. https://doi.org/10.1080/08912963.2023.2291771

Regione Toscana (2006–2009) Carta geologica regionale in scala 1:10.000. www502.regione.toscana.it/geoscopio/cartoteca.html

Rouse GW, Goffredi SK (2023) *Osedax* (Siboglinidae: Annelida) utilizes shark teeth for nutrition. Journal of the Marine Biological Association of the United Kingdom 103: e35. https://doi.org/10.1017/S0025315423000243

Rouse GW, Goffredi SK, Vrijenhoek RC (2004) *Osedax*: bone-eating marine worms with dwarf males. Science 305: 668–671. https://doi.org/10.1126/science.1098650

Rouse GW, Goffredi SK, Johnson SB, Vrijenhoek RC (2011) Not whale-fall specialists, *Osedax* worms also consume fish bones. Biology Letters 7: 736–739. https://doi.org/10.1098/rsbl.2011.0202

Rouse GW, Wilson NG, Worsaae K, Vrijenhoek RC (2015) A dwarf male reversal in bone-eating worms. Current Biology 25: 236–241. https://doi.org/10.1016/j.cub.2014.11.032

Rouse GW, Goffredi SK, Johnson SB, Vrijenhoek RC (2018) An inordinate fondness for *Osedax* (Siboglinidae: Annelida): fourteen new species of bone worms from California. Zootaxa 4377: 451–489. https://doi.org/10.11646/zootaxa.4377.4.1

Serafini G, Danise S, Maxwell E, Martire L, Amalfitano J, Cobianchi M, Thun Hohenstein U, Giusberti L (2024) Of his bones are crinoid made: taphonomy and deadfall ecology of marine reptiles from a pelagic setting (Middle-Upper Jurassic of Northeastern Italy). Rivista Italiana di Paleontologia e Stratigrafia 130: 97–128. https://doi.org/10.54103/2039-4942/22314

Smith CR, Kukert H, Wheatcroft RA, Jumars PA, Deming JW (1989) Vent fauna on whale remains. Nature 341: 27–28. https://doi.org/10.1038/341027a0

Smith CR, Glover AG, Treude T, Higgs ND, Amon DJ (2015) Whale-fall ecosystems: recent insights into ecology, paleoecology, and evolution. Annual Review of Marine Science 7: 571–596. https://doi.org/10.1146/annurev-marine-010213-135144

Spadini V (2022) La famiglia Pectinidae nel Pliocene senese (Italia, Toscana). Quaderni della Sezione di Studi e Notizie di Storia Naturale della Romagna 55: 67–136.

Spadini V, Manganelli G (2010) A large clavatulid species first reported from the Early Pliocene of Italy (Gastropoda, Neogastropoda, Conoidea). Journal of Conchology 40: 189–192.

Taboada S, Riesgo A, Bas M, Arnedo MA, Cristobo J, Rouse GW, Avila C (2015) Bone-eating worms spread: insights into shallow-water *Osedax* (Annelida, Siboglinidae) from Antarctic, Subantarctic, and Mediterranean waters. PLoS ONE 10: e0140341. https://doi.org/10.1371/journal.pone.0140341

Tapanila L (2006) Devonian *Entobia* borings from Nevada, with a revision of *Topsentopsis*. Journal of Paleontology 80: 760–767. https://doi.org/10.1666/0022-3360(2006)80[760:DEBFNW]2.0.CO;2

Tovar-Ávila J, Izzo C, Walker TI, Braccini JM, Day RW (2008) Dorsal-fin spine growth of *Heterodontus portusjacksoni*: a general model that applies to dorsal-fin spines of chondrichthyans? Canadian Journal of Fisheries and Aquatic Sciences 65: 74–82. https://doi.org/10.1139/f07-146

Tresguerres M, Katz S, Rouse GW (2013) How to get into bones: proton pump and carbonic anhydrase in *Osedax* boneworms. Proceedings of the Royal Society B: Biological Sciences 280: 20130625. https://doi.org/10.1098/rspb.2013.0625

Tucker AS, Fraser GJ (2014) Evolution and developmental diversity of tooth regeneration. Seminars in Cell and Developmental Biology 25: 71–80. https://doi.org/10.1016/j.semcdb.2013.12.013

Underwood CJ, Mitchell SF, Veltkamp CJ (1999) Microborings in mid-Cretaceous fish teeth. Proceedings of the Yorkshire Geological Society 52: 269–274. https://doi.org/10.1144/pygs.52.3.269

Vrijenhoek RC, Johnson SB, Rouse GW (2009) A remarkable diversity of bone-eating worms (*Osedax*; Siboglinidae; Annelida). BMC Biology 7: 74. https://doi.org/10.1186/1741-7007-7-74

Wisshak M, Knaust D, Bertling M (2019) Bioerosion ichnotaxa: review and annotated list. Facies, 65: 24. https://doi.org/10.1007/s10347-019-0561-8

WoRMS Editorial Board (2025) World Register of Marine Species. https://www.marinespecies.org [Accessed 15 May 2025]