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Osedax (Siboglinidae: Annelida) utilizes shark teeth for nutrition

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Abstract

We deployed jaws of the common thresher shark (*Alopias vulpinus*) on the seafloor at ~1000 m depth off Monterey California for 8 months. The jaws disintegrated, with all the hyaline cartilage disappearing, leaving some fragments of tessellated cartilage and the teeth. Two different *Osedax* species, *O. packardorum* and *O. talkovici* were found to have bored into the roots of some of the teeth, and were using the dentin pulp, which is rich in collagen, as a food source. The enameloid crowns of the shark teeth and the tessellated cartilage showed no signs of *Osedax* activity. This is the first demonstration of *Osedax* exploiting a source of food that is not bone. This raises questions as to the original food source of *Osedax* 'bone worms'. Examination for the presence of *Osedax* in the skeletons and teeth of Mesozoic and possibly even Palaeozoic fossil sharks, bony fish and reptiles is warranted.

Introduction

Members of *Osedax* are well known for relying, with the aid of symbiotic bacteria, on sunken vertebrates for their nutrition (Rouse *et al.*, 2004; Goffredi *et al.*, 2005). Initially found living on whale bones (Rouse *et al.*, 2004; Glover *et al.*, 2005; Fujikura *et al.*, 2006), it has subsequently been shown that *Osedax* can live off the exposed bones of a range of vertebrates, including teleost fish (Jones *et al.*, 2008; Rouse *et al.*, 2011, 2018; McClain *et al.*, 2019). While one of the early descriptions, by Fujikura *et al.* (2006), reported that *Osedax japonicus* was found living 'on the surfaces of tainted spermaceti' no details were provided. There have been no subsequent reports of extant *Osedax* living on any other substrate apart from bone, though the unusual *Osedax jabba* is known to live off buried fragmented pieces of bone buried in the sediment (Rouse *et al.*, 2018). With reference to fossil evidence for *Osedax* activity that is not bone-related, Kiel *et al.* (2013) showed bore holes and cavities within the teeth of an Oligocene toothed mysticete whale. Amalfitano *et al.* (2019) also suggested that circular boreholes in the fossil vertebrae of the shark *Cretoxyrhina mantelli*, dating to the Upper Cretaceous, could represent the action of *Osedax*. However, evidence to support this via internal microCT scans as performed on other fossils to support the presence of *Osedax* borings (Kiel *et al.*, 2010; Danise & Higgs, 2015), were lacking.

Osedax obtain nutrition via the symbiotic heterotrophic bacteria that live in their roots, which are in contact with the bone matrix. The inorganic component of the bone (calcium hydroxyapatite) is dissolved by acid secreted by the roots (Tresguerres *et al.*, 2013) allowing access to the organic components. The food source was initially hypothesized to be the major organic components of bone such as proteins (e.g. collagen) and hydrocarbons (e.g. cholesterol) (Goffredi *et al.*, 2005). Subsequent studies narrowed this down to the food source likely being collagen (Goffredi *et al.*, 2007, 2014; Miyamoto *et al.*, 2017).

Given the apparent reliance on *Osedax* and their symbionts on collagen it seems reasonable to examine non-bone marine food sources that they might exploit. Collagen is a primary component of the cartilage of non-bony fishes such as elasmobranchs (Merly & Smith, 2013). Parts of shark cartilaginous skeletons, such as the jaws, may be mineralized as tessellated cartilage (Balaban *et al.*, 2015), allowing resistance to rapid degradation by scavengers. It was hypothesized that this would provide time for colonization and growth of *Osedax*, which can occur in less than 2 months (Rouse *et al.*, 2008). Also, the teeth of sharks contain various forms of dentin (or dentine), a bone-like matrix with an organic content that is largely collagen (Enax *et al.*, 2012). The dentin of the tooth is surrounded by an extremely hard enameloid 'crown' that does not extend over the tooth root (Salomon, 1969; Enax *et al.*, 2012; Jambura *et al.*, 2020). Osteodentine is porous, cellular dentin, harder than bone and is found in the root (base) of all shark teeth (Whitenack *et al.*, 2010). The teeth of most sharks and rays have hollow pulp cavities surrounded by another form of dentin, orthodentine, beneath the enameloid. However, in the clade Lamniformes (and some rays) the pulp cavity is missing, and space beneath the enameloid is filled with osteodentine. These latter teeth are referred to as osteodont or pseudoosteodont (Whitenack *et al.*, 2010; Schnetz *et al.*, 2016; Jambura *et al.*, 2020).

Rouse *et al.* (2011) reported the deployment of the jaw and several vertebrae of a juvenile mako shark (*Isurus oxyrinchus*, Lamniformes) for 5 months at ~1000 m depth, but the vertebrae and jaws had disintegrated except for some calcareous elements. The teeth were intact and showed no signs of *Osedax*. Here we report on a deployment of jaws of the common thresher shark (*Alopias*

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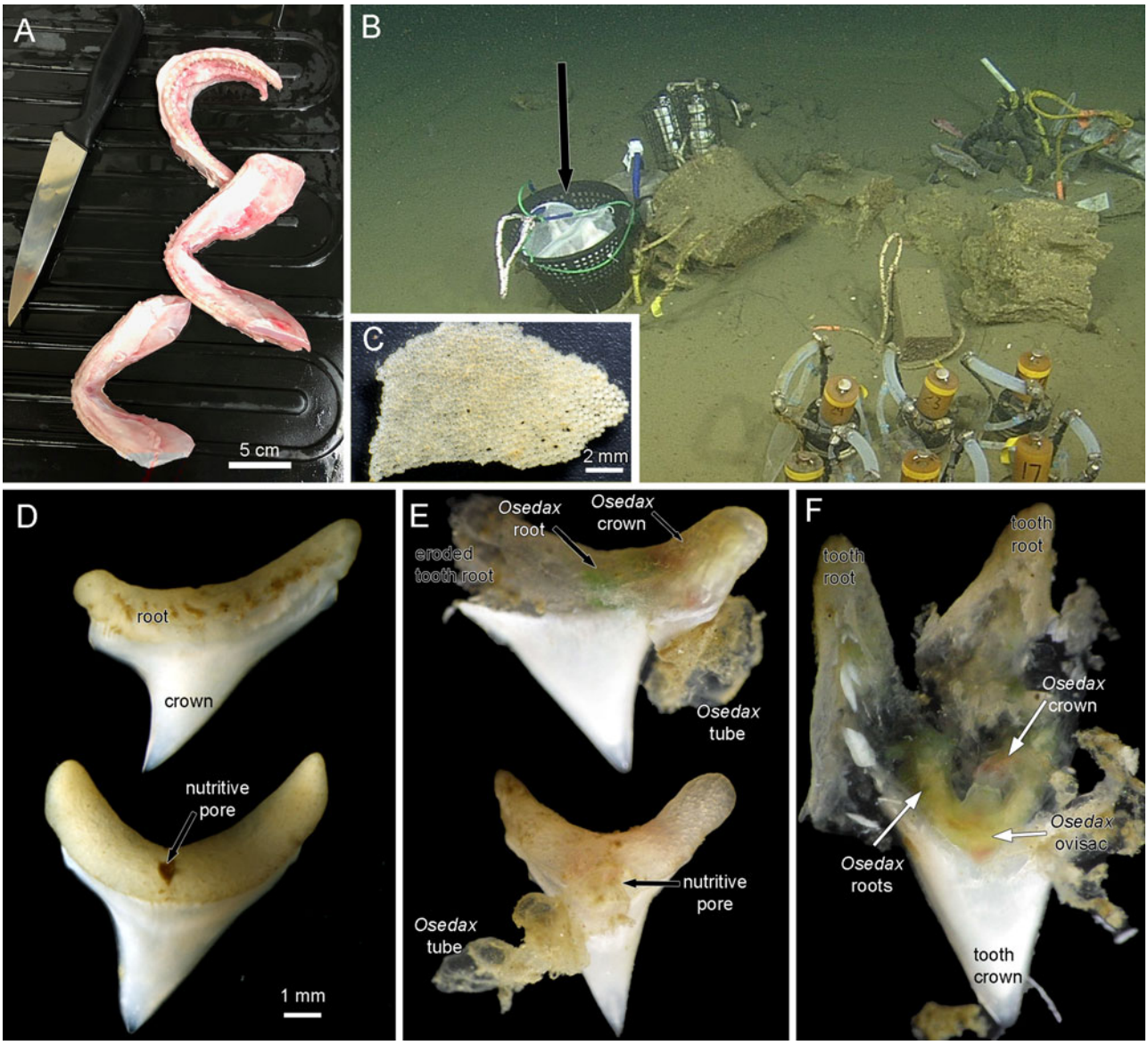


Figure 1. (A) Jaws of thresher shark *Alopias vulpinus* prepared for deployment. (B) Jaws in mesh bags in a weighted basket (black arrow) deployed near a whale fall at 1018 m depth in Monterey Submarine Canyon. (C) Tessellated cartilage fragment from mesh bags recovered after 8 months on the sea floor. The hyaline cartilage had disappeared. There were no obvious signs of *Osedax* activity on these fragments. (D) Most of the ~40 recovered teeth were intact. (E) Two teeth photographed on the initial recovery before fixation. Each has an obvious *Osedax* inside the tooth root and an emergent tube. (F) A tooth root dissected on the initial recovery showing a live *Osdax*, probably *O. talkovici*. Most of the dentin pulp has been digested, though the enameloid crown of the tooth was untouched.

vulpinus, Lamniformes) for 8 months, and document the occurrence of two known *Osedax* species using shark teeth as a food source.

Materials and methods

Heads of *Alopias vulpinus* had been donated to the NOAA Southwest Fisheries Science Center, La Jolla, California by anglers as part of the Oceanside Anglers' Club thresher shark sport fishing tournament in May 2018. Frozen heads were then provided for this project. Three jaws were dissected, two lower and one upper (Figure 1A) and placed in mesh bags and then into a half of a minnow trap that was weighted (Figure 1B), in order to prevent the teeth from being buried in the sediment, as in a previous deployment of mako shark jaws. The trap was deployed near a whale fall 'Francisco' at 1018 m depth in Monterey Submarine Canyon (36.77°N 122.08°W) by the ROV 'Doc Ricketts' from the R/V 'Western Flyer' on 13 December 2018, dive 1105, and recovered on 8 August 2019, dive 1172. Upon collection the remains of the jaws and teeth were removed from the mesh bags and examined for *Osedax* traces with a Leica S8APO stereomicroscope with a Pentax WG-III handheld camera. Some teeth were dissected open at this point and then fixed and preserved in 95% ethanol. All remains of the jaws and all other teeth including some with *Osedax* traces were also fixed and preserved in 95% ethanol. These samples were examined further with a Leica MZ9.5 stereomicroscope and photographed with a Canon Rebel T6s camera. A dwarf male found in the tube of one *Osedax* specimen was photographed with a Leica DMR compound microscope. *Osedax* specimens were subsampled for DNA analysis and the remaining tissue accessioned into the Benthic Invertebrate Collection at Scripps Oceanography. Mitochondrial cytochrome c subunit I (COI) sequences were obtained following methods outlined previously (Vrijenhoek *et al.* 2009).

Results

There was no trace of any hyaline cartilage after the 8 months on the seafloor. There were some fragments of the outer layer of

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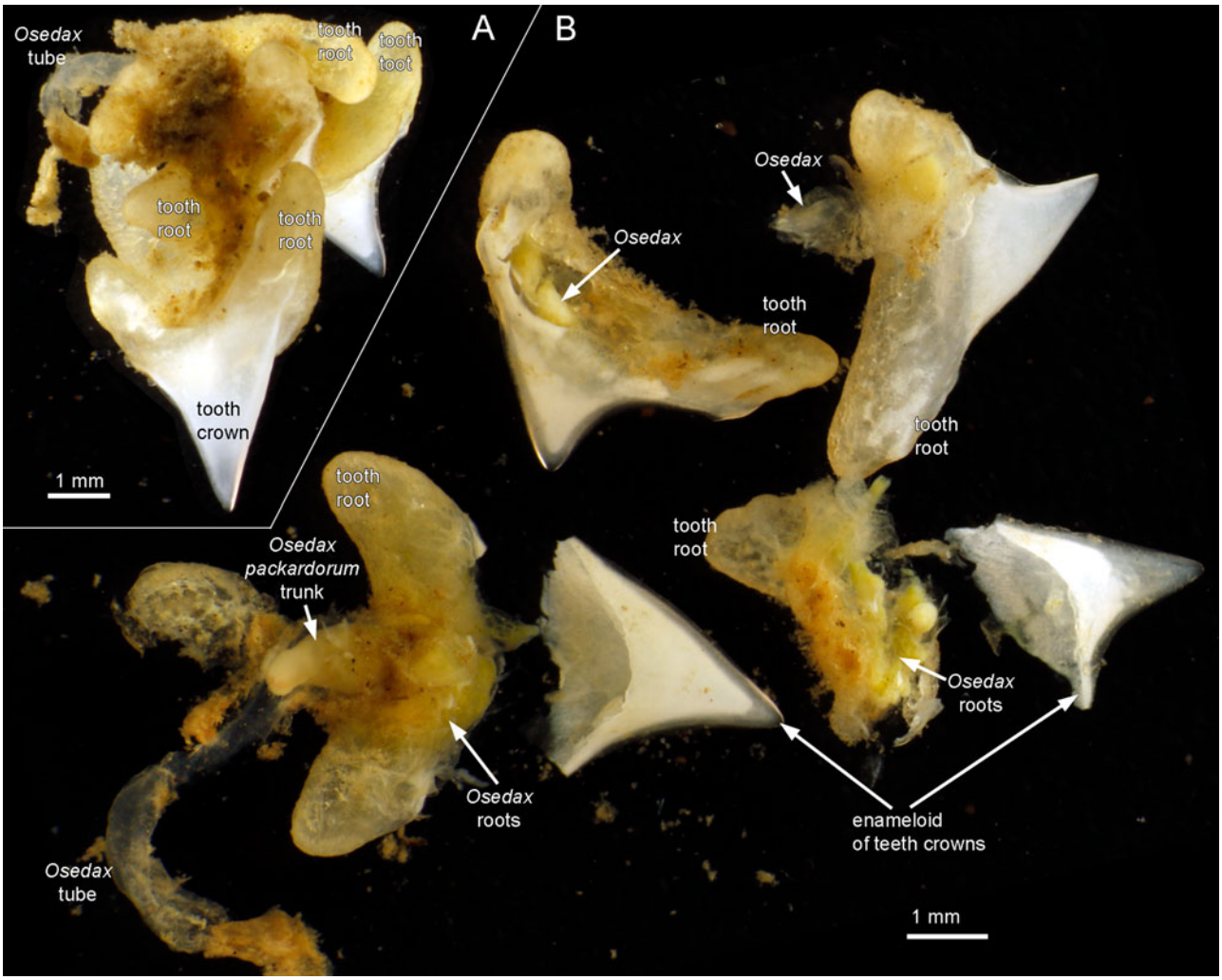


Figure 2. Preserved thresher shark teeth with *Osedax*. (A) A cluster of four teeth that were stuck together. One obvious *Osedax* tube is present. (B) The four teeth separated, and each was occupied by an *Osedax*. The specimen labelled *Osedax packardorum*, missing its crown of palps, was sequenced (GenBank OQ814199).

tessellated cartilage that showed no traces of *Osedax* (Figure 1C). Of the ~40 teeth that were recovered most showed no obvious traces of *Osedax* (Figure 1D). These intact teeth, which had a width of up to 8 mm across the root section, showed a distinct nutritive pore on one side (Figure 1D). Ten teeth were found to have obvious *Osedax* occupying the root area of the tooth and we obtained COI sequences for six of these (GenBank OQ814198-OQ814203), identified as either *Osedax packardorum* or *O. talkovici*. Several teeth that were observed and photographed on the initial recovery (Figure 1E) showed the typical gelatinous tubes of *Osedax* attached to the root portion. The *Osedax* specimens had all retracted, with colours visible inside the tooth root suggestive of *Osedax* roots (green) and crown (red). The outer surfaces of the tooth roots were relatively intact (Figure 1E) but on dissection of one specimen there was no little to no dentin visible inside the root, or the crown of the tooth (Figure 1F).

In one case there was a cluster of four teeth bound together (Figure 2A) and all four showed evidence of *Osedax* (Figure 2B) in their respective roots. One of these specimens was sequenced for COI (GenBank OQ814199) and was found to be *Osedax packardorum* Rouse *et al*., 2018, with a 98.6% similarity to the sequence of the holotype (EU223341). Another tooth dissected in the laboratory showed a tube emerging from the side of the tooth root (Figure 3A). On dissection, the tooth was largely empty, except for a female *Osedax* with a distinctive yellow patch (Figure 3B), like that seen in *Osedax talkovici* Rouse *et al*., 2018. The COI sequence for this specimen had a 99.4% similarity to the sequence of the holotype of *Osedax talkovici* (MG262313). Four other *Osedax talkovici* were also found in other teeth (GenBank OQ814200-OQ814203). The tube of the female specimen in Figure 3A, B was examined, and a single dwarf male was present (Figure 3C, D). The enameloid crowns of the teeth were unaffected with no trace of *Osedax* borings.

Discussion

This study provides the first direct evidence for *Osedax* to exploit a substrate other than bone for nutrition. The worms appear to have used the inner parts of the shark teeth, composed of osteodentine and orthodentine (Goto, 1991; Whitenack *et al*., 2010). The root surfaces were largely intact with erosion only near the *Osedax* tubes. This appears to be a general strategy of *Osedax*, where surface regions of bone are left alone while the roots ramify inside (Rouse & Goffredi, pers. obs.). It was notable that one tooth at least was penetrated by *Osedax* via the nutritive pore (Figure 1E), though based on the position of the tubes, other *Osedax* accessed the interior via other parts of the tooth root, such as the lateral region (Figures 1E, 2B & 3A). Dentin has a similar hardness to bone and its organic matrix is also largely composed of collagen (MacDougall & Javed, 2010). The dentin of shark teeth is about 20% organic matrix (Enax *et al*., 2012), comparable to that seen in sperm whales (Brault *et al*., 2014)

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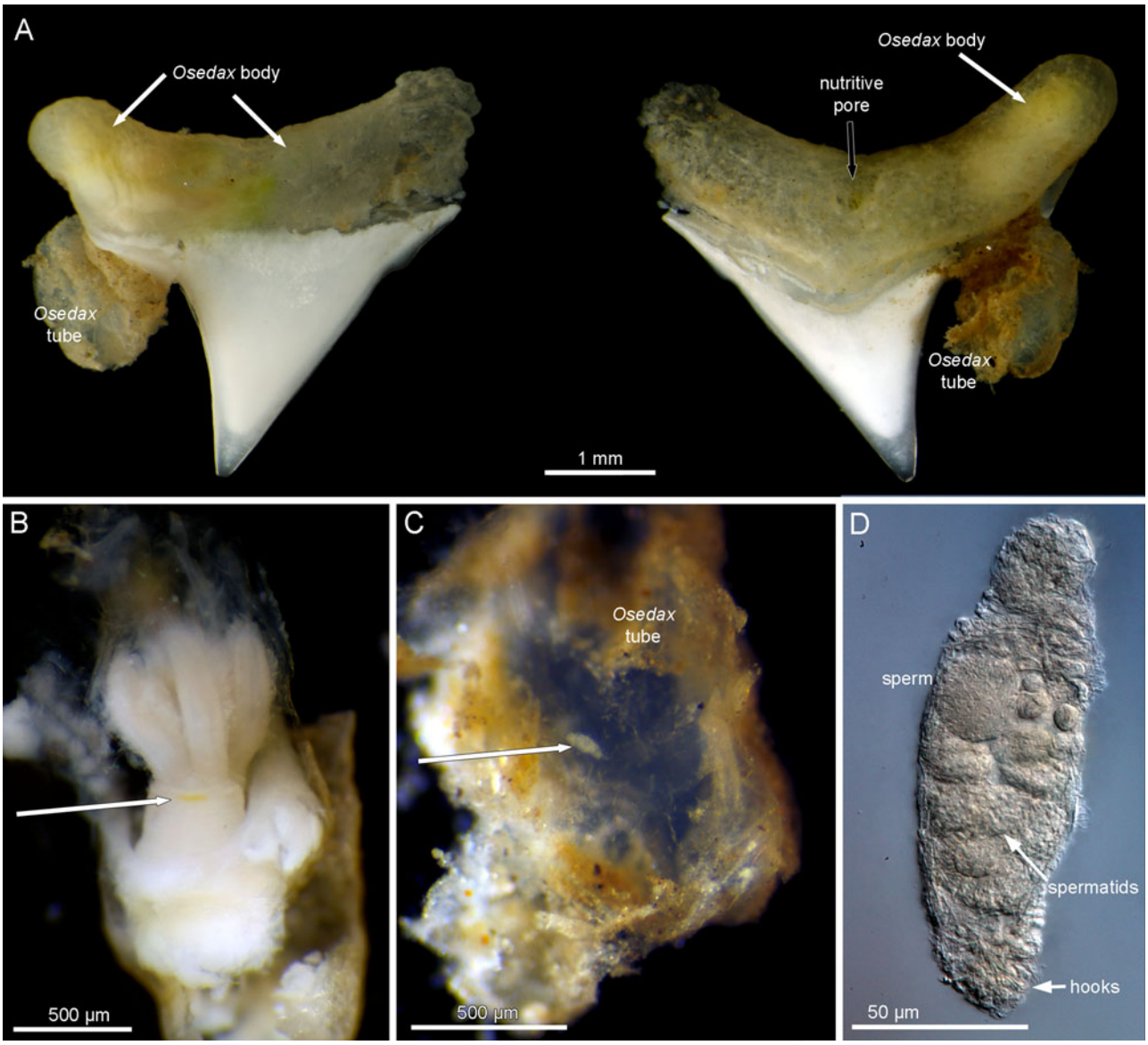


Figure 3. Preserved thresher shark tooth with *Osedax.* (A) Both sides of a tooth with the root filled with an *Osedax* specimen and an emergent tube on one side. (B) The *Osedax* female dissected from the tube with the yellow patch found on one side of the trunk that is distinctive is *Osedax talkovici*. The specimen was sequenced (GenBank OQ814198). (C) The tube had a single dwarf male present. (D) The dwarf male viewed with a compound microscope showing sperm, spermatids and posterior hooks.

and humans (LeGeros, 1981). This makes dentin an obvious food source for *Osedax* if accessible. The teeth of *Alopias vulpinus* studied here had roots that obviously could be penetrated by *Osedax*. In a previous experiment using the jaws of a juvenile mako shark (*Isurus oxyrinchus*), deployed at a similar depth, no *Osedax* occurrences were found after 5 months of deployment (Rouse *et al.*, 2011). Both these sharks belong in Lamniformes and so have similar osteodont teeth with the crown full of dentin and no pulp cavity (Jambura *et al.*, 2020). It may be that *Osedax* larvae simply did not recruit to the mako shark teeth during the deployment period, since they fell to the bottom of the deployment trap and may have been buried, while the teleost vertebrae in the experiment were secured above the sediment (see Figure 1A in Rouse *et al.*, 2011). For the present experiment the thresher shark jaws were placed in mesh bags (Figure 1A), which stopped the teeth being buried when the jaws disintegrated.

There was no evidence of *Osedax* boring through the outer tooth crown, which is made up of enameloid, a much harder substrate than dentin or bone, and with a much lower proportion of organic matrix (Enax *et al.*, 2012). Also, shark enameloid incorporates significant amounts (2.5% or more) of fluoride (LeGeros, 1981; Miake *et al.*, 1991) and this may resist the acid deployed by *Osedax* (Tresguerres *et al.*, 2013). These factors could preclude *Osedax* larvae from surviving long enough to bore through the enameloid crown to access the organic-rich dentin beneath. Kiel *et al.* (2013) showed evidence of boreholes in the teeth of Oligocene whales, and these also appeared to be restricted to the root with little evidence of boring into enamel crown. Tessellated cartilage, with its collagen matrix (Maisey *et al.*, 2021), is a possible food source for *Osedax*, however, there was no evidence of *Osedax* utilizing this calcified sheath that surrounded the hyaline cartilage of the jaw. Further study on the possible utility of the various forms of cartilage found in skeletons of sharks and rays is warranted.

Osedax was discovered living on a whale skeleton and two species were initially described (Rouse *et al.*, 2004). Subsequently *Osedax* species were shown to be able to utilize other mammal bones, initially with the deployment of cow bones (Jones *et al.*, 2008). This was dismissed as not being ecologically relevant and that *Osedax* was most likely a whale fall specialist (Glover *et al.*,

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2008). Further deployment experiments revealed that *Osedax* could colonize the bones of marine teleosts (Rouse *et al.*, 2011), seals (Rouse *et al.*, 2015), marine turtles birds (Rouse *et al.*, 2018) and alligators (McClain *et al.*, 2019), rendering the whale fall specialist argument untenable. Also *Osedax* appears to have evolved well before the appearance of whales (Vrijenhoek *et al.*, 2009; Danise & Higgs, 2015) and so its original nutritional choice remains unknown. The two species of *Osedax* found to exploit dentin in this study, *O. packardorum* and *O. talkovici*, are phylogenetically quite separated in the context of the overall diversity of the clade, belonging to subclades IV and I, respectively (Rouse *et al.*, 2018). The ability of disparate *Osedax* lineages to exploit bones as well as dentin suggests calcified collagenous tissues may be an ancestral preference, rather than bone as previously proposed. Rouse *et al.* (2018) summarized the various bone substrates that had been specifically colonized by different *Osedax* up to that time. *Osedax talkovici* was notable for having been found on the widest range of bones deployed at 600–1000 m depth (cow, whale, elephant seal, teleost, turkey, turtle) and to this can now be added shark teeth. *Osedax packardorum* lives across a similar depth range as *O. talkovici* (600–1000 m depth) but had only been found on whale and cow bones until now.

The discovery that *Osedax* can exploit the dentin of teeth raises the obvious question of the evolutionary origin of the group and its original nutrition source. Modern sharks (crown group Elasmobranchii) have a fossil record extending back into the Devonian (Frey *et al.*, 2019), with bony fishes (Osteichthyes) even older. Thus, bones and teeth have been available as food sources in the sea for over 400 million years. Sharks notably show substantial turnover of teeth in their lifetimes (Botella *et al.*, 2009) with shed teeth falling to the seafloor and potentially being available for *Osedax*. *Osedax* is nested within Siboglinidae, which contains taxa such as Frenulata, *Sclerolinum* and Vestimentifera, taxa that also utilize symbiotic bacteria for their nutrition, though their energy source is hydrogen sulphide or methane from seeps and/or vents (Rouse *et al.*, 2022). Estimates of the origin of Siboglinidae based on molecular clocks have yet to be fully explored, though such estimates for the origin of crown group *Osedax* and Vestimentifera both fall in the late Cretaceous (Vrijenhoek *et al.*, 2009; Vrijenhoek, 2013; Taboada *et al.*, 2015). The presence of fossils attributed to *Osedax* and Vestimentifera date to the mid-Cretaceous and Jurassic, respectively (Danise & Higgs, 2015; Georgieva *et al.*, 2019), suggest an earlier origin of Siboglinidae as a whole. Close examination for *Osedax* traces in fossilized marine bones and teeth from earlier in the Mesozoic and possibly back into the Paleozoic may well be warranted.

Data. All relevant data are within the manuscript or on GenBank.

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Ethical standards. Not applicable.

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