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http://hdl.handle.net/10026.1/3329

10.1098/rsbl.2015.0072
Biol Lett

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Bone-eating *Osedax* worms lived on Mesozoic marine reptile deadfalls

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Keywords: Siboglinidae, taphonomy, Cretaceous, marine reptile, whale-fall
Abstract

We report fossil traces of Osedax, a genus of siboglinid annelids that consume the skeletons of sunken vertebrates on the ocean floor, from Early-Late Cretaceous (~100 million years, Myr) plesiosaur and sea turtle bones. Although plesiosaurs went extinct at the end-Cretaceous mass extinction (66 Myr), chelonioids survived the event and diversified, and thus provided sustenance for Osedax in the 20 Myr gap preceding the radiation of cetaceans, their main modern food source. This finding shows that marine reptile carcasses, before whales, played a key role in the evolution and dispersal of Osedax, and confirms that its generalist ability of colonizing different vertebrate substrates, like fishes and marine birds, besides whale bones, is an ancestral trait. A Cretaceous age for unequivocal Osedax trace fossils also dates back to the Mesozoic the origin of the entire siboglinid family, which includes chemosynthetic tubeworms living at hydrothermal vents and seeps, contrary to phylogenetic estimations of a late Mesozoic-Cenozoic origin (~50-100 Myr).
1. Introduction

The exploration of the deep sea in the last decades has led to the discovery of many new species with unique adaptations to extreme environments, raising important questions on their origin and evolution through geological time (1, 2). *Osedax* is a genus of marine worms that colonize the bones of marine vertebrates, mostly whales, sunken to the deep sea-floor (3). It belongs to the Siboglinidae family of annelids that, as adults, lack mouth and digestive system and are nutritionally dependent on endosymbiotic bacteria (4). Among siboglinids, *Osedax* has developed a unique metazoan-bacteria symbiosis that exploits the organic material sequestered within the bones of dead vertebrates as an energy source. The posterior body of *Osedax* penetrates into the bone using root-like structures (figure 1a-b). The root epithelium absorbs bone collagen and lipids, which are possibly metabolized by heterotrophic symbiotic bacteria that serve for *Osedax* nutrition (3, 5). The anterior part of the body, the trunk, extends into the water and is crowned with respiratory palps (6).

*Osedax* is a highly speciose clade, found at depths ranging from 21-4000 m, with a near global geographic distribution (7, 8). The origins and causes of this diversity are an unresolved aspect of its biology and evolution. Molecular age estimations suggest that either *Osedax* split from its siboglinid relatives ~45 Myr ago, possibly coincident with the origins of large archeocete cetaceans during the Eocene (3, 7), or ~125 Myr ago in the Cretaceous, when it could have lived on the bones of large marine Mesozic reptiles (7, 9). Only direct fossil evidence of the trace fossil left by *Osedax* worms can confirm which of these scenarios is correct, as it is unlikely for the soft-bodied animal itself to be
preserved. The oldest Osedax traces known to date come from ~30 Myr whale and fish bones, indicating a generalist ability to thrive on different vertebrate substrates (10, 11).

Here we show that Osedax colonized the bones of plesiosaurs and cheloniids in the Cretaceous, validating the hypothesis of a Mesozoic origin of the clade, and provide important implications for the evolution of the entire Siboglinidae family.

2. Materials and Methods

Traces resembling those created by recent Osedax species were found on (i) one isolated plesiosaur humerus from the Cenomanian (~100-93.9 Myr) Cambridge Greensand Member, UK, whose fossil fauna is mainly reworked from the top of the underlying late Albian Gault Formation (~100 Myr); and (ii) two fragmentary bones (rib and costal plate) belonging to a marine turtle, family Cheloniidae, originally referred to Chelone camperi? Owen 1851, collected from the Cenomanian Grey Chalk Subgroup (Burham, Kent, UK) (figure 1). Specimens are curated in the Sedgwick Museum of Earth Sciences, University of Cambridge, UK. No invertebrate remains are associated with them. The bones were investigated using micro computed tomography (CT), a well-established method that allows the morphology of subsurface bone structures to be quantitatively described, providing their three-dimensional reconstruction (12) (see electronic supplementary material, ESM, for details on the specimens, figure S1; geological setting; and analytical methods).

3. Results
Digital removal of the matrix overlying the plesiosaur humerus revealed that *Osedax* bioerosion is concentrated in the center of the bone (figure 1d). Two intact individual borings were identified on the periphery of the bioeroded area (figure 1d). The borings consist of circular surficial openings (diameter 0.56 & 0.36 mm) with a uniform tube section that expands to an irregularly shaped chamber inside the bone (figure 1, figure S2, Table 1). Similar borings were identified on the cheloniid fragments (figure 1i-k, figure S3). The costal plate, even if heavily eroded, shows some intact borings. The largest example consists of a small circular surface opening (diameter 0.20 mm) with a laterally expansive, but shallow subsurface chamber (figure 1j-k). The rib shows 15 small subcircular holes that extend as long tubes into the bone, terminating in expanded irregular chambers (figure S3). These chambers are generally smaller than those identified on the plesiosaur skeleton (Table 1).

*Osedax* often colonize bones in such dense aggregations that the cavities formed by their root systems merge together under the bone surface (13). Therefore only cavities with a single borehole reflect the shape of the root system of an individual animal and are of particular diagnostic value (13). The tube section represents the trunk of *Osedax*, partially embedded within bone matrix in modern specimens (14), whereas the chamber represents the hole left by the ovisac and root structure (figure 1b-c). Although modern *Osedax* borings display a diverse range of morphologies (12), the combination of a narrow opening with laterally-expansive irregular subsurface chambers are diagnostic features of *Osedax* activity (13). Once buried, larger borings may collapse, leaving behind rounded pockmarks in the bones, as shown in our samples (figure 1d,i). The intact borings identified here are relatively small, but their sizes are within the range of known *Osedax*...
borings (12) and consistent with other fossil Osedax traces (Table 1). In modern Osedax, the morphology of the borings of a single species is consistent in the same bone but changes between bone types (12), suggesting that each of the fossil bones in this study was colonized by a single species, although it is not possible to estimate the total number of species.

4. Discussion

Together with chemosynthesis–based associations of molluscs found on Late Cretaceous plesiosaurs (15), our discovery confirms that vertebrate deadfall communities developed several times in the geological past, not only on whale-falls, and had a key role in the dispersal and evolution of specialized fauna (16). Plesiosaurs were a group of diverse, cosmopolitan marine reptiles fully secondary adapted to aquatic life, with largest species reaching up to 15 meters in length, a size comparable to that of modern sperm whales (17). Whereas they could have contributed to the evolution and dispersal of Osedax during the Cretaceous, they went extinct at the Cretaceous-Paleogene boundary, together with other large marine reptiles such as mosasaurs, leaving an almost 20 Myr gap for Osedax to survive before the evolution of whales (figure 3). Our finding of Osedax traces also on Late Cretaceous sea turtles reinforces the hypothesis of Osedax survival and diversification through the Paleogene, as suggested by phylogenetic analyses (7). Differently from other marine reptiles originated in the Mesozoic, sea turtles show their highest diversity during the Late Cretaceous–Early Paleogene, when they were represented by a large number of taxa with diverse ecological adaptations to aquatic life (18). Thereafter, sea turtles, together with teleost fishes, whose most modern clades
diversified during the Paleogene (19), might have provided sustenance for Osedax through this time interval. The finding of bone-eating limpets (Osteopelta), typical of whale-falls, on an Eocene leatherback turtle (20), supports the hypothesis that sea turtles sustained organisms later adapted to live on whale bones.

Our finding has also important implications for the debated age of the entire Siboglinidae family and their evolutionary leap from conventional heterotrophic annelids to specialized forms adapted to extreme chemosynthetic environments, such as hydrothermal vents, cold seeps and whale-falls (4). Molecular data indicate a late Mesozoic or Cenozoic (~50-100 Myr) origin for the siboglinids (1, 21), whereas their fossil record goes back to the Mesozoic or even to the Paleozoic (22). The Cretaceous Osedax traces presented here provide a firm calibration point for the molecular clock of the siboglinid phylogenetic tree, placing a common siboglinid ancestor as far back as the mid-Cretaceous, and the origin of the Siboglinidae family even earlier still. This adds to the growing evidence that the Cretaceous was a key period for the evolution of modern chemosynthetic communities (1, 23).

The evolution of Osedax has been viewed as an extreme adaptation to deep-sea environments since most species of Osedax have been discovered at bathyal depths, but shallower species have been documented from the Antarctic, Japan and the Northeast Atlantic (24). *O. mucofloris* has been found at multiple sites from 30-125 m depth and is the only species known from the North Atlantic (14). Our findings show that Osedax species occupied similarly shallow waters (*see Geological setting in ESM*) in this region early on in the clade’s evolutionary history. The increasing evidence for Osedax in shelf-depth settings combined with their propensity to rapidly consume a wide range of
vertebrate skeletons, suggests that Osedax may have had a significant negative effect on the preservation of marine vertebrates in the fossil record. The true extent of this “Osedax effect”, previously hypothesized only for the Cenozoic (10), now needs to be assessed for Cretaceous marine vertebrates.
Acknowledgements. We thank M. Riley for access to specimens, D. Sykes for micro-CT scan acquisition, R.J. Twitchett and C.T.S. Little for advices on the first drafts, and three reviewers for helpful comments.

Author Contributions. SD designed the research. NDH analyzed the micro-CT scan images and created the 3D reconstructions. SD and NDH wrote the paper.

Data accessibility. Data for this study are available at Dryad (doi:10.5061/dryad.k4d0q).

Funding Statement. This work was founded by a Palaeontological Association Research Grant to SD.

Competing interests. The authors declare that they have no competing interests.
Figure Legends

Figure 1. Modern and fossil Osedax borings. (a) Osedax trunk and palps emerging from whale bone. (b) Osedax ovisac and root tissue. (c) CT reconstruction of a modern boring created by O. frankpressi. (d) CT reconstruction of plesiosaur bone (semi-transparent), with two Osedax borings reconstructed in orange. (e-f) Boring-1 digitally dissected and close up in situ. (g-h) Boring-2 digitally dissected and close up in situ. (i) CT reconstruction of cheloniid bones. Arrow indicates borings in j & k. (j-k) Boring in cheloniid costal plate. (c) modified from Higgs et al. (12). Scale bars are 1 cm and scale meshes have spacing of 1 mm.

Figure 2. Stratigraphic range of marine vertebrates (Cetacea, Plotopteridae, teleost fishes, Plesiosauria, Cheloniaioea) associated with modern and fossil evidence of Osedax worms. Molecular age estimations of the origin of the Osedax clade from Vrijenhoek et al. (7). Data on modern and fossil occurrence of Osedax from Smith et al. (8); Kiel et al. (10, 11, 25), Higgs et al. (13).
References


**Table 1.** Quantitative morphometrics of individual *Osedax* borings in fossil Mesozoic reptile bones (this study) compared with *Osedax* borings in Cenozoic fossil bones.

<table>
<thead>
<tr>
<th>Fossil bone</th>
<th>Age</th>
<th>Aperture diameter (mm)</th>
<th>Length (mm)</th>
<th>Width (mm)</th>
<th>Depth (mm)</th>
<th>Volume (mm³)</th>
<th>Surface Area (mm²)</th>
<th>Source</th>
</tr>
</thead>
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<tr>
<td>Plesiosaur humerus (1)</td>
<td>Albian</td>
<td>0.56</td>
<td>3.50</td>
<td>2.30</td>
<td>1.93</td>
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<td>29.78</td>
<td>This study</td>
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<td>Plesiosaur humerus (2)</td>
<td>Albian</td>
<td>0.36</td>
<td>2.04</td>
<td>1.31</td>
<td>1.20</td>
<td>0.65</td>
<td>6.32</td>
<td>This study</td>
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<td>Cheloniid rib (1)</td>
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<td>2.44</td>
<td>1.69</td>
<td>0.94</td>
<td>0.54</td>
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<td>1.19</td>
<td>1.19</td>
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<td>Cheloniid rib (3)</td>
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<td>0.62</td>
<td>0.62</td>
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<td>1.17</td>
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<tr>
<td>Cheloniid costal plate (7)</td>
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<td>0.20</td>
<td>1.25</td>
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<td>1.44</td>
<td>0.23</td>
<td>3.21</td>
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<td>-</td>
<td>-</td>
<td>1.7</td>
<td>-</td>
<td>-</td>
<td>Ref. 10</td>
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<tr>
<td>Avian bone</td>
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<td>&lt;0.3–1.5</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Ref. 25</td>
</tr>
<tr>
<td>Whale teeth</td>
<td>Oligocene</td>
<td>max 0.50</td>
<td>max 3.00</td>
<td>-</td>
<td>2.3</td>
<td>-</td>
<td>-</td>
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<tr>
<td>Fish bone</td>
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<td>~0.1</td>
<td>-</td>
<td>6.5</td>
<td>2</td>
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<td>-</td>
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<tr>
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<td>2.3–4.5</td>
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<td>-</td>
<td>Ref. 13</td>
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</tbody>
</table>
Figure 1
**FIGURE 2**

- **Modern and fossil evidence of Oseax on marine vertebrates**
- **This study**
- **Two alternative molecular age estimations of the origin of the Oseax clade**
- **Gap between the evolution of the first mysticetes and the extinction of large Mesozoic marine reptiles**

- **End-Cretaceous Mass Extinction**

- **Miozene**
- **Neogene**
- **Quaternary**
- **Pliocene**
- **Miocene**
- **Oligocene**
- **Eocene**
- **Paleocene**
- **Cenozoic**
- **Mesozoic**
- **Lower Cretaceous**
- **Upper Cretaceous**
- **Cenomanian**
- **Turonian**
- **Santonian**
- **Campanian**
- **Maastrichtian**
- **Paleogene**

- **Archaeoceti**
- **Misticeti**
- **Odontoceti**
- **Pliopteridae penguin-like birds**
- **Teleost - bony fishes**
- **Chelonoidea - sea turtles**
- **Plesiosauro - marine reptiles**