Bone-eating Osedax worms lived on Mesozoic marine reptile deadfalls

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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 (approx. 100 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 (approx. 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 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 [3,6]. The anterior part of the body, the trunk, extends into the water and is crowned with respiratory palps [7].

Osedax is a highly speciose clade, found at depths ranging from 21 to 4000 m, with a near global geographical distribution [8,9]. 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 approximately 45 Ma, possibly coincident with the origins of large archeocete cetaceans during the Eocene [3,8], or approximately 125 Ma in the Cretaceous, when it could have lived on the bones of large marine Mesozoic reptiles [8,10]. 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 approximately 30 Myr whale and fish bones, indicating a generalist ability to thrive on different vertebrate substrates [11,12]. 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 we provide important implications for the evolution of the entire Siboglinidae family.

2. Material and methods

Traces resembling those created by recent Osedax species were found on: (i) one isolated plesiosaur humerus from the Cenomanian (approx. 100–93.9 Myr) Cambridge Greensand Member, UK, whose fossil fauna is mainly reworked from the top of the underlying Late Albian Gault Formation (approx. 100 Myr); and (ii) two fragmentary bones (rib and costal plate) belonging to a marine turtle, family Cheloniidae, originally referred to *Chelone campesi* 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

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**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 *Osedax 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) Adapted from [5]. Scale bars are 1 cm and scale meshes have spacing of 1 mm. (Online version in colour.)
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>
<tbody>
<tr>
<td>Pleiosaur humerus (1)</td>
<td>Albian</td>
<td>0.56</td>
<td>3.50</td>
<td>2.30</td>
<td>1.93</td>
<td>2.70</td>
<td>29.78</td>
<td>this study</td>
</tr>
<tr>
<td>Pleiosaur 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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<tr>
<td>Cheloniid rib (1)</td>
<td>Cenomanian</td>
<td>0.83</td>
<td>2.44</td>
<td>1.69</td>
<td>0.94</td>
<td>0.54</td>
<td>2.88</td>
<td>this study</td>
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<td>Cheloniid rib (2)</td>
<td>Cenomanian</td>
<td>0.53</td>
<td>1.19</td>
<td>1.19</td>
<td>0.88</td>
<td>0.14</td>
<td>2.57</td>
<td>this study</td>
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<tr>
<td>Cheloniid rib (3)</td>
<td>Cenomanian</td>
<td>0.18</td>
<td>0.62</td>
<td>0.62</td>
<td>0.62</td>
<td>0.07</td>
<td>1.17</td>
<td>this study</td>
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<td>Cheloniid costal plate (7)</td>
<td>Cenomanian</td>
<td>0.20</td>
<td>1.25</td>
<td>0.51</td>
<td>1.44</td>
<td>0.23</td>
<td>3.21</td>
<td>this study</td>
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<td>Whale bone</td>
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<td>0.10–0.45</td>
<td>—</td>
<td>—</td>
<td>1.7</td>
<td>—</td>
<td>—</td>
<td>[11]</td>
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<td>Avian bone</td>
<td>Oligocene</td>
<td>&lt;0.3–1.5</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>[13]</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>
<td>[12]</td>
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<tr>
<td>Fish bone</td>
<td>Oligocene</td>
<td>approximately 0.1</td>
<td>—</td>
<td>6.5</td>
<td>2</td>
<td>—</td>
<td>—</td>
<td>[12]</td>
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<tr>
<td>Whale bone</td>
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<td>—</td>
<td>—</td>
<td>2.3–4.5</td>
<td>—</td>
<td>—</td>
<td>[14]</td>
</tr>
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The morphology of subsurface bone structures to be quantitatively described, providing their three-dimensional reconstruction [5] (see the electronic supplementary material 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 centre 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 and 0.36 mm) with a uniform tube section that expands to an irregularly shaped chamber inside the bone (figure 1 and table 1; electronic supplementary material, figure S2). Similar borings were identified on the cheloniid fragments (figure 1i–k; electronic supplementary material, 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 sub-circular holes that extend as long tubes into the bone, terminating in expanded irregular chambers (electronic supplementary material, 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 [14]. Therefore, only cavities with a single borehole reflect the shape of the root system of an individual animal and are of particular diagnostic value [14]. The tube section represents the trunk of *Osedax*, partially embedded within bone matrix in modern specimens [15], 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 [5], the combination of a narrow opening with laterally expansive irregular subsurface chambers are diagnostic features of *Osedax* activity [14]. 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 [5] 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 [5], suggesting that each of the fossil borings 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 [16], 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 [17]. Plesiosaurs were a group of diverse, cosmopolitan marine reptiles fully secondary adapted to aquatic life, with largest species reaching up to 15 m in length, a size comparable to that of modern sperm whales [18]. Whereas they could have contributed to the evolution and dispersal of *Osedax* during the Cretaceous, they went extinct at the Cretaceous–Palaeogene 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 2). Our finding of additional *Osedax* traces on Late Cretaceous sea turtles reinforces the hypothesis of *Osedax* survival and diversification through the Palaeogene, as suggested by phylogenetic analyses [8]. In contrast to other marine reptiles that originated in the Mesozoic, sea turtles show their highest diversity during the Late
Cretaceous–Early Palaeogene, when they were represented by a large number of taxa with diverse ecological adaptations to aquatic life [19]. Thereafter, sea turtles, together with teleost fishes, whose most modern clades diversified during the Palaeogene [20], 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 [21], 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 (approx. 50–100 Myr) origin for the siboglinids [1,22], whereas their fossil record goes back to the Mesozoic or even to the Palaeozoic [23]. 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 [1,24].

The evolution of Osedax has been viewed as an extreme adaptation to deep-sea environments as most species of Osedax have been discovered at bathyal depths, but shallower species have been documented from the Antarctic, Japan and the Northeast Atlantic [25]. Osedax mucofloris has been found at multiple sites from 30 to 125 m depth and is the only species known from the North Atlantic [15]. Our findings show that Osedax species occupied similarly shallow waters (see Geological setting in the electronic supplementary material) 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 [11], now needs to be assessed for Cretaceous marine vertebrates.

Data accessibility. Data for this study are available at Dryad (doi:10.5061/dryad.k4d1q).

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Author contributions. S.D. designed the research. N.D.H. analysed the micro-CT scan images and created the three-dimensional reconstructions. S.D. and N.D.H. wrote the paper.

Conflict of interests. The authors declare that they have no competing interests.

References


