

Osedax borings in fossil marine bird bones

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Abstract The bone-eating marine annelid *Osedax* consumes mainly whale bones on the deep-sea floor, but recent colonization experiments with cow bones and molecular age estimates suggesting a possible Cretaceous origin of *Osedax* indicate that this worm might be able to grow on a wider range of substrates. The suggested Cretaceous origin was thought to imply that *Osedax* could colonize marine reptile or fish bones, but there is currently no evidence that *Osedax* consumes bones other than those of mammals. We provide the first evidence that *Osedax* was, and most likely still is, able to consume non-mammalian bones, namely bird bones. Borings resembling those produced by living *Osedax* were found in bones of early Oligocene marine flightless diving birds (family Plotopteridae). The species that produced these boreholes had a branching filiform root that grew to a length of at least 3 mm, and lived in densities of up to 40 individuals per square centimeter. The inclusion of bird bones into the diet of *Osedax* has interesting implications for the recent suggestion of a Cretaceous origin of this worm because marine birds have existed continuously since the Cretaceous. Bird bones could have enabled this worm to survive times in the Earth's history when large marine

vertebrates other than fish were rare, specifically after the disappearance of large marine reptiles at the end-Cretaceous mass extinction event and before the rise of whales in the Eocene.

Keywords Whale fall · Bioerosion · Trace fossils · Deep sea · Siboglinidae · Micro-CT

Introduction

Osedax is a marine annelid (family Siboglinidae) that consumes bones on the seafloor (Rouse et al. 2004). Its evolutionary origin and the range of substrates that it is able to consume are still unclear (Glover et al. 2008; Jones et al. 2008; Vrijenhoek et al. 2008, 2009). Using molecular clock estimates, its origin has been linked to the Cenozoic rise of whales (Rouse et al. 2004), recently supported by the discovery of fossil traces of *Osedax* in Oligocene whale bones (Kiel et al. 2010). Using an alternative calibration for the molecular clock, however, a Cretaceous origin also seems possible (Vrijenhoek et al. 2009). In this case, *Osedax* might have consumed bones of large marine reptiles such as plesiosaurs and mosasaurs and after their extinction at the end of the Cretaceous it was suggested (Vrijenhoek et al. 2009) that bones of turtles, marine crocodiles, and perhaps large fishes could have been utilized. Although the bacterial symbionts that provide *Osedax* with nutrition can survive on collagen and lipids as sole carbon sources (Goffredi et al. 2007), there was no evidence so far that *Osedax* consumes anything other than mammalian bone. Here, we show that *Osedax* colonized bones of large, flightless marine birds in the early Oligocene and discuss the evolutionary implications of this discovery.

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Material and methods

Bones of two penguin-like birds (family Plotopteridae) collected from the Pysht Formation in northwestern Washington State were investigated: a partial skeleton of an unnamed species (University of Washington, Burke Museum, UWBM 86875), including femora and other fragments and a partial skeleton of *Tonsala hildegardae* Olson, 1980 (UWBM 86873) that includes a humeral fragment, femora, tibiotarsi, pelvis, and fragments of ribs and vertebrae (Goedert and Cornish 2002). The specimens were preserved in concretions found near the mouth of Murdock Creek along the Strait of Juan de Fuca, in Clallam County (UWBM loc. C0667). These sediments were deposited in bathyal depth on an oxygenated seafloor during the early Oligocene (Goedert et al. 1995). The bones were extracted by etching with dilute (10% or less) formic and acetic acid.

The X-ray microcomputed tomography scans of a vertebra with boreholes were done using the SkyScan1172 system (SkyScan, Belgium). The bone was scanned with a beam energy of 70 kV, a flux of 141 μ A, and a copper–aluminum filter at a detector resolution of 8.0 μ m per pixel using a 360-degree rotation with a step size of 0.75 degrees. The scan to survey the bone fragment (480 transmission images) was reconstructed in a 2,376 \times 2,668 matrix of 1,935 slices with a resolution of 8.0 μ m per voxel using the SkyScan software NRecon running on a cluster of three networked PCs. The program uses a modified Feldkamp algorithm. The segmentation of bone and boreholes was done with the SkyScan software CT Analyser. For the study of cavity morphology details, a volume of interest in a 511 \times 547-matrix of 314 slices was chosen. Visualization of the 3D models was done by the SkyScan software CTvol.

Results

Many of the bones of UWBM 86873 and 86875 show significant corrosion (Goedert and Cornish 2002), and almost all of the bones have at least a few boreholes. Protruding edges of some bones are corroded to the extent that much of the smooth surface has been corroded away, exposing the trabecular bone underneath (Fig. 1b). The bones also show scrape marks most likely produced by scavenging sharks. Boreholes are widely scattered on some of the bones, especially on the femora and tibiotarsi where they are restricted to the bone shaft and are absent from the more dense proximal and distal surfaces. The pelvis has a number of widely distributed boreholes, some in very thin bone such as portions of the ilium and ischium. A high density of boreholes (35 borings per square centimeter), some of them fused, with a maximum diameter of 0.3 mm, was seen on the smooth surface of the micro-CT scanned

vertebra of *T. hildegardae* (Fig. 1b). Just below the head of the femur of *T. hildegardae*, the density reaches 40 borings per square centimeter.

The micro-CT scans show that these boreholes lead into a network of cavities underneath the surface (Fig. 1d). A regular cavity of the trabecular bone was also penetrated (Fig. 1e). The surface layer above the network of cavities is often only 0.1 to 0.2 mm thick (Fig. 1f). Most holes on the investigated bones do not exceed 0.3 mm in diameter. Exceptions include one hole on the proximal end of a femur of *T. hildegardae*, which reaches nearly 1 mm in diameter (near top of Fig. 1a), and one hole that reaches 1.5 mm in diameter near the distal end of the femur (UWBM 86875). Both of these large holes are situated at the transition zone between shaft and the head.

Discussion

The boreholes and cavities documented here in bones of the early Oligocene plotopterid bird *T. hildegardae* resemble those in whale bones from the same strata and those produced by *Osedax* today (e.g., Figs. 1d, 2a in Kiel et al. 2010). Plotopterid bones have neurovascular foramina that can be of similar size as boreholes produced by *Osedax*, but they have smooth edges or start as a small sulcus whereas *Osedax* boreholes have sharp edges, as if made by a drill. Borings and cavities produced by other deep-sea invertebrates such as sipunculids, sponges, or bivalves differ in shape from *Osedax* borings (see discussion in Kiel et al. 2010) and from those reported here. Microbes can substantially damage bones in deep water, but their activities affect mainly the surface layer of the bone rather than the interior and individual borings are only a few micrometers in diameter (Allison et al. 1991; Kiel 2008). The borings documented here are thus interpreted as *Osedax* borings.

Compared to *Osedax* borings in Oligocene whale bones those reported here reach significantly higher densities, up to 40 borings per square centimeter in the bird femur compared to a maximum of 15.5 borings per square centimeter on a whale dentary (Kiel et al. 2010). The size of most borings in the bird bones is within the range of those on the whale bones (up to 0.45 mm in diameter), except for the two extremely large borings (up to 1.5 mm in diameter) on the bird femora. The shape of the cavities suggests that the producing *Osedax* species had a branching filiform root like the extant *O. roseus* (Rouse et al. 2008, their Fig. 4b) and the species that attacked Oligocene whale bones (Kiel et al. 2010). The maximum size of an individual specimen of *Osedax* in the bird bones is difficult to determine because all boreholes on the surface lead into interconnected cavities; however, an elongate tunnel

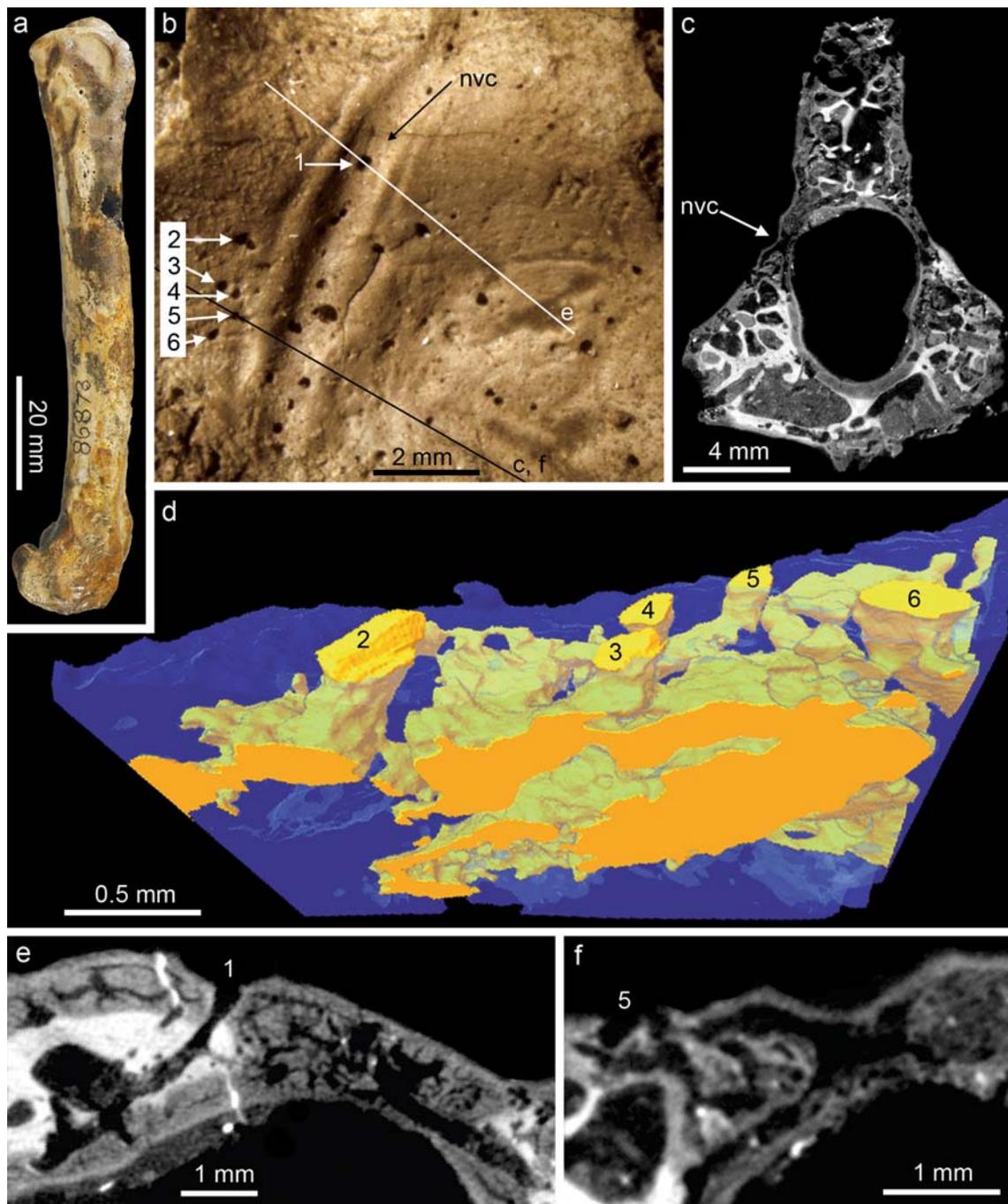


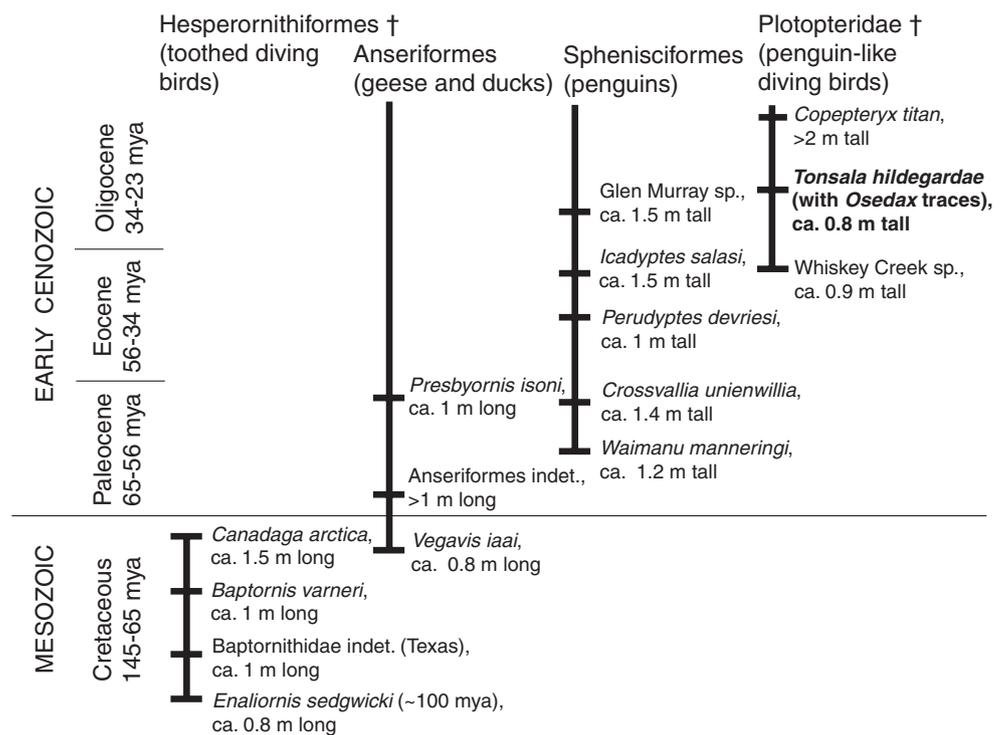
Fig. 1 *Osedax* borings in early Oligocene bones of the plotopterid bird *T. hildegardae* (UWBM 86873). **a** Femur showing numerous small holes, and a corrosion pit on the upper half. **b** Smooth lateral surface of a vertebra with a neurovascular channel (*nvc*) in the middle and a high density of *Osedax* borings; numbers indicate the boreholes shown in **d**, **e**, and **f**; lines indicate the positions of the micro-CT scans shown in **c**, **e**, and **f**. **c** Reconstructed image of a micro-CT scan

horizontally through the vertebra, bone material (*white to gray*), holes and cavities (*black*). **d** Micro-CT-based rendering of the trace fossils, bone material in *transparent blue*, borings and cavities in *yellow*. **e**, **f** Micro-CT scan images of the vertebra, showing a relatively straight boring that penetrated a regular cavity of the trabecular bone (**e**) and a cavity with only a thin “roof” of bone material (**f**)

(Fig. 1e) most likely produced by a single individual is 3 mm long. This is almost twice as large as the *Osedax* holes from coeval whale bones, which reach a maximum dimension of 1.7 mm (Kiel et al. 2010).

The trace fossils reported here provide the first evidence that *Osedax* was (and probably still is) able to consume non-mammalian bones. Plotopterids like *T. hildegardae* were large, flightless, wing-propelled diving seabirds found

Fig. 2 Cretaceous to early Cenozoic marine bird lineages, their geologic ranges and examples of large-sized taxa. Records younger than Oligocene (~23 mya) are not shown because whale bones were readily available for *Osedax* by Oligocene time. Data from Hou (1999), Galton and Martin (2002), Martin and Cordes-Person (2007), Everhart and Bell (2009), Mayr (2009) and references therein. *Dagger*, extinct; *mya*, million years ago



mainly in Eocene to Miocene deep-water sediments around the northern Pacific. Their bones had thick cortices and dense trabecular bone, they share several morphologic adaptations with penguins, and likely had similar foraging habits (Mayr 2009). The inclusion of bird bones into the diet of *Osedax* has significant evolutionary implications. A Cretaceous origin of *Osedax*, as suggested by some molecular clock estimates (Vrijenhoek et al. 2009), is problematic because it implies that *Osedax* was able to consume reptile and/or fish bones, but there is currently no evidence supporting this (Vrijenhoek et al. 2009). These food sources would have been especially important during the Paleocene when large Mesozoic marine reptiles other than turtles and crocodylians had already gone extinct and whales had not yet evolved; however, large marine birds originated in the Cretaceous, survived the end-Cretaceous mass extinction event, and existed during the recovery interval after the mass extinction (Fig. 2). If *Osedax* indeed originated in the Cretaceous it could have avoided extinction by using bird bones as a food source during the earliest Cenozoic, at least until whales became widely distributed in the Oligocene.

Figure 2 summarizes the geologic ranges and maximum body sizes of marine bird clades that we consider a potential food source for *Osedax* because they had generally thick and dense non-pneumatic bones like ptopteraids (Mayr 2009). A clade of large extinct birds (with wing spans up to 6 m) that is not included in this compilation is the Pelagornithidae, albatross-like marine birds with a nearly worldwide distribution from Paleocene

to Pliocene time (Mayr 2009). In contrast to ptopteraid bones, those of pelagornithids are extremely thin-walled and lightweight and thus may not have been attractive for *Osedax*. Indeed, pelagornithid bones recovered from Late Eocene to Early Miocene deep-water strata in Oregon (Goedert 1989) do not show *Osedax* traces (JLG, pers. obs.). Bone consumption by *Osedax* (the “*Osedax* effect”) may be one reason why bird fossils are generally rare in deep marine strata; they were much smaller and could be consumed in much shorter time than whale bones. Only those with dense bones like ptopteraids had a chance at surviving.

Conclusions

The boreholes documented here in fossil marine bird bones provide the first evidence that *Osedax* may be capable of growing on non-mammalian bones and to colonize carcasses as small as 80 cm in length. A possible Cretaceous origin of *Osedax* as suggested by molecular clock estimates was thought to require its ability to grow on fish or reptile bones, for which there is currently no evidence. The Oligocene traces documented here do not provide evidence for a Cretaceous origin of *Osedax*; however, marine birds have existed continuously since the Cretaceous and could thus have, in theory, provided an alternative food source for *Osedax* since that time. Our finding underpins the need for experimental studies on the range of substrates that *Osedax* is able to colonize. In

addition, fossil bones of a wide range of vertebrates and of all sizes should be investigated for similar boreholes to clarify the age of this extraordinary bone-eating worm.

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