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Microborings in mid-Cretaceous fish teeth

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SUMMARY: Fish teeth and other remains from the British Cretaceous contain abundant evidence for post-mortem colonization by endolithic organisms. The borings are here recognised as occurring in three morphotypes, including a flask-shaped form not previously recorded. There is strong evidence to suggest that each of these boring types shows a strong preference for a particular substrate histology. The damage and destruction of vertebrate remains by microborings is here considered to exert a major taphonomic control on microvertebrate assemblages. The relationships between the intensity of colonization of vertebrate material by endolithic organisms and palaeoenvironment have implications for using these bone microborings as palaeoenvironmental indicators.

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Fish teeth and other small vertebrate remains from marine sequences show the almost ubiquitous presence of small endolithic trace fossils. These have been recorded in fish remains (e.g. Roux 1887, Mägdefrau 1937, Gouget and Locquin 1979, Martill 1989) as well as reptile bones (e.g. Bystrov 1956), but relatively few morphotypes have been reported. Fish teeth from Cretaceous (Albian and Cenomanian) sections in Britain show surface and internal borings of several distinct morphologies.

1. GEOLOGICAL SETTING

Disarticulated fish material was collected from three mid Cretaceous sections in eastern England: Speeton, South Ferriby and Folkestone. The coastal section at Speeton, North Yorkshire, has a near complete sequence through the Cretaceous from Berriasian to Turonian. Bulk samples yielding fish material were collected from the Speeton Clay, Hunstanton and Ferriby Chalk Formations, concentrating on the Hunstanton Formation (Red Chalk). The Speeton Clay Formation consists of a condensed succession of marine clays, some levels being rich in carbonate and phosphate nodules and glauconite. Fish remains were obtained from the Hauterivian (beds D2D, D1 and C7H: for details see Neale 1960, Lamplugh 1889 and Doyle 1989) basal Barremian (bed C2A: for details see Mitchell 1992), Aptian (for details see Ennis 1937), and Lower Albian. The Hunstanton Formation consists of a series of marls and limestones, mostly reddened (Mitchell 1996a), spanning the Middle Albian to basal Cenomanian, with fish remains recorded from most levels. The Cenomanian Ferriby Chalk Formation consists largely of hard white chalks. Fish remains were recovered from the Crowes Shoot Member at the base (Mitchell 1996a) and a level (bed SLC11C: see Mitchell 1996b) in the Middle Cenomanian.

Fish remains were collected at South Ferriby Quarry, north Lincolnshire, from the Hunstanton Formation. This is more condensed than at Speeton (Mitchell and Langner 1995) and exclusively Albian in age. All the marly units were sampled and yielded fish material.

Material from the Gault Clay Formation was collected from Copt Point, Folkestone, Kent from levels throughout the Lower Gault and basal part of the Upper Gault (*dentatus* to lower *inflatum* Zones) (see Owen 1975 for details). Material was bulk sampled and sieved by Andrew Gale and David Ward.

Additional fish teeth have been studied from the Rhaetic of Somerset and Avon, Bathonian of Gloucestershire, Kimmeridgian of Dorset, 'Purbeck' of Dorset, 'Wealden' of Sussex and the Isle of Wight and the Upper Eocene of Hampshire.

Specimens were coated with gold-palladium alloy and observed under a scanning electron microscope. Figured specimens are deposited in Liverpool City Museum (National Museums and Galleries on Merseyside).

2. MICROBORING MORPHOTYPES

Endolithic borings are present in a large proportion of vertebrate remains preserved in marine environments (during this study, they were present within at least 95% of fish bones and teeth studied at high magnification). These have been assigned to either the ichnogenus *Mycelites* Roux 1887 or *Abeliella* Mägdefrau 1937 (for meandering and regular branching morphologies respectively) where borings have been considered post-mortem, or *Mycobystrovia* Gouget and Locquin 1979 for supposed parasitic fungal remains and borings. There is no evidence that any of the borings described here represent anything but post-mortem activity, and the ramifying morphologies of most of the borings compare well with figured examples of *Mycelites* and *Abeliella* . *Mycelites* is very widely distributed (Bystrov 1956), but individual occurrences appear to show substrate specificity. *M. ossifragus* Roux 1887 and *Mycobystrovia* are recorded from primarily the dentine-enamel boundary in fish material, borings referred to *Mycelites ossifragus* also having been recorded from fish dermal elements and in internal parts of ichthyosaur bone (Bystrov 1956). *Mycelites enameloides* Martill 1989 has a similar morphology, but is restricted to selachian enameloid. *Abeliella riccioides* Mägdefrau 1937 was originally recorded from bony fish scales, although identical borings are also present in shark tooth roots (e.g. Siverson 1993, p. 13). The affinities of the makers of these borings are unknown, with fungal hyphae being likely (Gouget and Locquin 1979, Martill 1989). Although substrate specificity has been used to distinguish microboring ichnotaxa of similar morphology (Martill 1989), differences in substrate preference is not considered here to be sufficient grounds for erecting ichnospecies. Despite this, individual microboring networks are rarely seen crossing histological boundaries within the bone material (e.g. Bystrov 1956, Figs. 7, 12). It is therefore likely that although individual endolithobionts or species of endolithic organisms may have been substrate specific, their borings, and hence ichnospecies, are not morphologically distinguishable.

SYSTEMATIC PALAEONTOLOGY

Ichnogenus **MYCELITES** Roux 1887.

Mycelites ossifragus Roux 1887.

Mycelites ossifragus Roux 1887
Borings of *Mycobystrovia lepidographa* Gouget and Locquin 1979, Plate 1, figs. 1-6,
      Plate 4, Figs. 1-2
 Mycelites enameloides Martill 1989

Trabecular bone borings

Figure 1. **b-e**.

Material. Extremely common, seen in most (over 200) of the mid Cretaceous selachian teeth examined in detail, as well as several teeth of enchodonts and *?Caturus*. Borings of this type were recorded in fish remains from all of the marine or quasi-marine sites studied.

Description. The borings are relatively parallel sided and round in cross section, generally about 5 to 7 μm in diameter. They trace a path which varies from irregular and sharply angled to gently sinuous, the morphology probably largely dependant on the substrate type. Where colonisation is light, the borings run along the surface of the bone substrate, with the top exposed to the sediment, and continue for up to 200 μm before penetrating deeper into the interior of the substrate. Branching is bifurcate but irregular, generally every 50 to 100μm. Where the degree of boring is more intense, the original surface of the tooth is destroyed and the borings form a more irregular ramifying mass.

Discussion. These borings are almost ubiquitous, but show a strong degree of substrate preference, being commonest within more porous bone and tooth tissues. Where borings assigned to this type are seen in other tissues, they retain the same morphology and preference for boring the bone surface. In selachian teeth, the root is preferentially colonized. Dentine of the tooth interior is also often extensively bored. These borings are generally only seen in enameloid in cases of intense colonization, and then is largely limited to the area near the junction of the crown and root where the enameloid is thin. In bony fish material, this microboring morphology is often present in the root and dentine of *?Caturus* teeth, as well as on the surface of enchodont teeth, but it is rarely as

extensively developed as in selachian teeth. It is rare in bony fish 'flat bones', ganoid scales and robust teeth of pycnodonts and seminotids.

Orthodentine borings

Figure 1. **f-h**.

Material. Seen in only one tooth of the batoid *Squatirhina* from the Hunstanton Formation of Speeton. The substrate specificity of this boring for the inner parts of teeth, however, make it easily overlooked, and as such it may be far more common than so far recognized.

Description. Morphologically this boring shows a strong similarity to the preceding type, probably differing only in its selected substrate. Within the tooth where it has been recorded, the borings are almost entirely restricted to the orthodentine, only reaching the surface of the tooth where the overlying enameloid is very thin near the crown-root junction. In the higher parts of the crown, neither the enameloid nor the thin lining of the pulp cavity are penetrated. The borings are round in cross section and about 7 μm across. Bifurcations are present and irregular. Within the crown the borings very sinuous, and despite their proliferation, do not appear to intersect.

Discussion. The network seen shows a very strong preference for boring the orthodentine interior of the root separates the borings in this tooth from the usual borings which preferentially colonize the surface layers of the osteodentine root, only penetrating the orthodentine in intense colonizations when much of the root has been destroyed. Although this boring may be separated from that described above due to preferences both for a different substrate (orthodentine as opposed to trabecular bone) and site (tooth interior as opposed to surface), the similar morphology prevents it from being classified as a separate ichnotaxon.

Abeliella riccioides Mägdefrau 1937

Figure 2. **a-d**.

Abeliella riccioides Mägdefrau 1937

Material. Boring networks seen on several enchodont teeth, bony fish jaw and bone fragments and more rarely shark teeth from Folkestone and Speeton. Also seen in bony fish material from the Bathonian of Gloucestershire.

Description. These borings have a distinctive radial pattern, with regular dichotomous bifurcations. The central point of the boring network is usually just below the surface of the substrate. Two, or more rarely three, initial branches contact the surface of the bone and thereafter stay as surface borings. The borings are either round or flattened in cross section, and between 3 and 7 μm across, retaining a constant width throughout the network. These borings bifurcate at intervals of 20 to 40 μm , with each branch dichotomously bifurcating at a similar distance, giving a very regular pattern. On a flat substrate, the proximal bifurcations enclose angles of between 90 and 120 degrees, although the angle between the more distal branches of the boring tends to be more acute, down to about 30 degrees.

Discussion. As with other microborings of vertebrate material, *Abeliella riccioides* appears to show a strong preference for certain substrates. It is especially common on bony fish material, being originally described in a bony fish scale. During this study, it was seen on the surface of the majority of enchodont teeth, where it is the dominant boring. It is also the dominant boring on bony fish jaw and skull elements. *A. riccioides* was also seen in fish jaw elements and teeth of *Belonostromus* from the English Bathonian. It is rarer in selachian material, but is present in shark tooth roots and, in one specimen of *Squatina*, in enameloid near the crown-root junction. This morphology of microboring has previously been figured in Upper Cretaceous shark tooth roots (e.g. Siverson 1993, p13). A variety of superficially similar radially branched microborings have been described from carbonate substrates (e.g. Mägdefrau 1937, Vogel *et al*. 1987, Tavernier *et al*. 1992). These differ not only in the substrate colonised, but also are generally of far less regular branching form, are largely buried below the substrate surface, and are generally of a far larger boring diameter.

Flask-shaped boring
Figure 2, **a, e-f.**

Material. Several borings of this morphology seen on a single enchodont tooth from the Gault Clay Formation, *cristatum* Zone, Copt point, Folkestone.

Description. These are hemispherical to flask shaped unbranched borings penetrating normal to the substrate surface. The entrance hole is circular and between 30 and 50 μm in diameter. In shallow borings, this is the top of a hemispherical pit with smooth sides. In deeper borings, the boring may be up to 200μm deep and widens gradually downwards to about 70μm across, again with a hemispherical base. One specimen shows a slight constriction. Branching was not seen, but in one case two borings were seen to intersect.

Discussion. This boring appears very distinct from the branching microborings, and probably represents the activities of a different boring organism. The overall morphology is superficially similar to that of boring bivalve crypts, and likewise probably represents a living or encysting chamber of an organism which is neither branched or colonial. The general form of the boring is similar to that of *Tremichnus* Brett 1985, which forms parabolic or flask-shaped borings in echinoderms. This differs morphologically in not increasing in boring diameter with depth and by being of a far greater overall size (0.5 to 4mm diameter). *Tremichnus* also differs developmentally from this boring in representing a host specific epibiont of living echinoderms, the growth of the pit apparently related to growth of the stereom.

3. OCCURRENCE

Borings of hyphate morphologies are abundant in marine vertebrate material, (e.g. Roux 1887, Mägdefrau 1937, Bystrov 1956, Gouget and Locquin 1979, Martill 1989) being seen during this study in at least 90% of marine micovertebrate specimens studied with high powered microscopy. The frequency and mode of occurrence, however, varies with both bone histology and sedimentological setting.

The histology of vertebrate material greatly effects the frequency of microborings. Of the material studied, the trabecular bone of the roots of shark and ray teeth appears the most prone to endolith colonization, with microborings seen in almost all of the specimens studied; the root having been completely destroyed in a large proportion of teeth (e.g. Fig. 1. a.). There appears to be some connection between shark taxa and the degree of tooth root destruction, presumably related to minor variations in histology. This is well demonstrated within the Hunstanton Formation at South Ferriby, where the roots of 'lamnids' are extremely rarely preserved, whilst the roots of co-occurring squalids and hexanchids are regularly present. Shark orthodentine is also often extensively bored, but is often present in teeth where the root has been destroyed, suggesting that it is less

readily bored. Selachian enameloid was only rarely seen to be bored (contra Martill 1989), and then generally only where it is thin near the basal edge. Bony fish remains also vary in their frequency of bioerosion. Flat bone elements, such as skull and girdle bones, enchodont teeth and the tooth roots of fishes such as ?*Caturus*, all regularly show microborings, but these appears to be considerably less common than in selachian tooth roots. No boring were seen in the clear enamel tip of seminotid and ?*Caturus* teeth. Although not studied in detail here, the variations in abundance of bony fish vertebrae are similar to that of selachian tooth roots, suggesting a similar degree of destruction by bioerosion.

As well as histological variations, the intensity of endolithic bioerosion varies with the degree of marine influence at the site of deposition, sedimentation rate and general quantity of phosphate within the depositional environment. Teeth from non-marine and quasi-marine environments (such as within the Rhaetic, Purbeck and Wealden) generally show relatively low degrees of bioerosion. Many of the teeth within these sediments are of types which appear to be relatively resistant to bioerosion within open marine settings (such as teeth of hybodont sharks, and seminotid and pycnodont bony fish). However, where teeth are present of types that tend to be heavily bioeroded in marine settings (such as from rhinobatid rays and ?*Caturus*), these are still generally lightly or un-eroded.

As with bioerosion of shelly fossils, slower sedimentation rates result in higher degrees of damage to vertebrate remains. This is largely simply a function of time spent on, or immediately below, the sea floor allowing more time for endolith colonization. This variation in degree of bioerosion with sedimentation rate is clearly evident when comparing fish teeth from hiatus nodule beds and interbedded clays in the Speeton Clay and Gault, in which the (more abundant) fish teeth within the nodule bands have generally suffered greater bioerosion. This variation is also seen when material from the Hunstanton Formation sites at Speeton and South Ferriby are compared, with fish remains from the more expanded Speeton section being consistently less bored. Teeth from the more condensed sediments at South Ferriby are so heavily bioeroded that under 5 % of teeth still have well preserved roots, and no teeth were seen with no bioerosion. At one hiatal marl horizon (Bed 9 of Mitchell and Langner 1995), there was no root material preserved on any of the approximately 200 shark teeth collected.

The degree to which teeth are bored by endoliths also appears to vary with the quantity of diagenetic calcium phosphate in the sediment. This is particularly evident when the high degree of endolith boring in teeth from the Hunstanton Formation at Speeton (which contains no diagenetic phosphate) is compared with the far lower degree

of boring in teeth from the phosphate-rich Speeton and Gault Clays, despite the Speeton Clay showing lower sedimentation rates than the Hunstanton Formation.

4. SIGNIFICANCE OF MICROBORINGS

As there appears to be a strong relationship between the degree of microboring of vertebrate material and both sedimentation rate and amount of available phosphate, there is great potential in using microboring frequency as an aid to palaeoenvironmental analysis. It is therefore likely that within homogeneous sediments the frequency of endolithic borings in vertebrate fossils could be of use in identifying minor changes in sedimentation rates and degree of marine influence. The connection between the intensity of boring and phosphate concentration within the marine system may also prove useful in the analysis of ancient marine productivity. As suggested by Martill (1989), it is probable that endolithic borings are important in the marine phosphate cycle, releasing vertebrate phosphate back into the seawater. Within nutrient-deprived systems, such as the mid to late Cretaceous of the North Sea Basin (Mitchell 1996b), it is therefore likely that vertebrate material would be extensively recycled and undergo considerable taphonomic loss. The poor preservation of selachian fossils and rarity of other vertebrate remains within the Hunstanton Formation and Chalk Groups of the northern region appear to bear this out.

The taphonomic loss of vertebrate fossils due to destruction by microborings almost certainly imposes a strong bias on the composition of fossil fish faunas. It is unlikely that selachian and many bony fish teeth are commonly completely destroyed by bioerosion, due to the tenacity of enameloid and enamel. It is likely, however, that these teeth are regularly rendered indeterminate by the loss of the root, added to which their greater fragility is likely to render then far more prone to physical breakage during any reworking events or during collection by sieving. The complete destruction of other skeletal remains by microborings is probably a frequent occurrence, resulting in the bias against fish taxa with small or specifically indeterminate teeth within recorded fossil fish assemblages.

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FIGURE CAPTIONS

Fig. 1

a) Tooth of *Protosqualus* showing severe damage caused by endolithic boring organisms. Note that the root has been destroyed whilst the basal edge of the crown is severely damaged. Width of tooth 1.3 mm. Hunstanton Formation, South Ferriby, bed 6a. LIVCM 1997 51E.

b) Tooth of juvenile *Notorhynchus* showing damage caused by endolithic boring organisms. Note that the root is largely destroyed and *Mycelites* can be seen extending into the basal part of the crown enameloid. Width of tooth 1.2 mm. Hunstanton Formation, Speeton,Weather Castle Member. LIVCM 1997 51H.

c) Apical view of a tooth of *Squatina* showing *Mycelites ossifragus* Roux 1887 on the upper surface of the root. Width of tooth 1.2 mm. Hunstanton Formation, Speeton,Weather Castle Member. LIVCM 1997 51F.

d) Enlargement of above showing typical sinuous *Mycelites ossifragus*. Width of view 310 µm.

e) Rather irregular *Mycelites ossifragus* on the surface of an enchodont tooth. Width of view 370 µm. Speeton Clay Formation, Speeton, bed A1. LIVCM 1997 51B.

f) Lateral view of a tooth of *Squatirhina* showing endolithic borings near the crown-root junction. Height of tooth 1.1 mm. Hunstanton Formation, Speeton,Red Cliff Hole Member. LIVCM 1997 51G.

g) Enlargement of crown-root junction of above. Note that *Mycelites ossifragus* are only just reaching the surface of the tooth, not selectively colonising the surface. Width of view 350 μm.

h) Broken crown of above. Note the intense development of *Mycelites ossifragus* is restricted to the osteodentine. Width of view 270 μm.

Fig. 2

a) *Abeliella riccioides* Mägdefrau 1937 and entrance to a flask-shaped boring on the surface of an enchodont tooth. Width of view 370 μm. Gault Formation, Folkestone, *cristatum* Zone. LIVCM 1997 51A.

b) *Abeliella riccioides* on the surface of an enchodont tooth. Width of view 550 μm. Hunstanton Formation, Speeton, Red Cliff Hole Member. LIVCM 1997 51C.

c) Detail of branching in the distal parts of a large *Abeliella riccioides* network. Width of view 270 μm. Same specimen as above.

d) Rather less regular *Abeliella riccioides* on the surface of a small fish jaw. Note the primary triradial branching. Width of view 350 μm. Hunstanton Formation, Speeton, Speeton Beck Member. LIVCM 1997 51D.

e) Two flask-shaped borings on the surface of an enchodont tooth, with a shallow hemispherical boring and the entrance to a deeper boring. Width of view 130 μm. Gault Formation, Folkestone, *cristatum* Zone. LIVCM 1997 51A.

f) Flask-shaped boringsin a broken enchodont tooth. Note the expanded crypt and intersection with a second example.Width of view 260 μm. Same specimen as above

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