Borings, bodies and ghosts: spicules of the endolithic sponge *Aka akis* sp. nov. within the boring *Entobia cretacea*, Cretaceous, England

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Abstract. The fossilised borings of endolithic sponges are generally abundant in marine sediments since the Jurassic, and sparse occurrences date back to the Lower Palaeozoic. However, the zoological identity of the boring sponge is not revealed by the morphology of the boring alone. The preservation potential of the boring is far greater than that of the spicular skeleton of the endolithic sponge. The spicules are opaline silica, which is readily soluble in seawater. Thus, while the borings are abundant and diverse, we have almost no knowledge of the bioeroding sponges that produced them.

In situations where early diagenetic cementation of the sediment occurs before the dissolution of the silica, the spicules may be preserved as casts. Such a case exists in association with hardground formation. A hardground in the Upper Cretaceous (Turonian) Chalk Rock of Buckinghamshire, SE England, yielded an intraclast containing a sponge boring referable to *Entobia cretacea* Portlock, 1843. Many of the chambers contain sparite-filled casts of sponge spicules. Only megascleres are present, comprising smooth oxeas about 2 mm in length and 74 µm in width, indicating an extinct species of the phloeodictyid genus *Aka*. No part of the original skeleton of the sponge is preserved, only very accurate external moulds of the spicules, representing little more than the ghost of the animal. But this is not unusual in palaeontology and, as it appears that this body fossil is new to science, it is herein named *Aka akis* sp. nov. This is only the fifth account of fossilised *Aka* spp. where spicule morphology and erosion traces can be observed. It is hoped that further search for spicules preserved within *Entobia* will allow an investigation of the endolithic sponge communities of the Mesozoic and Tertiary seas, about which almost nothing is known at present.

Keywords. *Entobia cretacea*, chalk hardgrounds, Chalk Rock, sponge body fossil, oxeas, *Aka akis* sp. nov.

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Introduction

Borings attributable to endolithic sponge bioerosion are uncommon in the Palaeozoic (e.g., Mikuláš 1994; Schönberg and Tapanila 2006; Tapanila 2006), but are generally abundant since the Jurassic. However, we still have little understanding of which biological genera they represent (e.g., Bromley 2004), because the preservation potential of the boring is far greater than that of the spicular skeleton of the tracemaker. Spicules of endolithic sponges are composed of hydrated, amorphous, opaline silica, which is soluble in seawater (Siever 1962; Lang and Steiger 1985; Uriz et al. 2003). Owing to the common lack of spicular remains, many palaeontologists simplistically consider as synonyms 'boring sponge' and 'clionid sponge' (or, after the revision by Rützler [2002] of the family name, 'clionaid sponge'). However, although the family Clionaidae may be the dominant and most diverse family of endolithic sponges today, it is not the only one, and the families represented in, for example, the Cretaceous are hardly understood at all, despite the great abundance of their borings. It would also appear that the clionaids have a shorter history than *Aka* de Laubenfels, 1936, at least in their boring habit.

Spicule preservation

Spiculation is the basic means of sponge taxonomy (e.g., Uriz et al. 2003), but the opaline spicules are rarely preserved in fossil material. After the death of an endolithic sponge, however, it is unlikely that all the spicules would be physically washed out of the intricately chambered forms of boring. Instead, the most usual cause of loss is apparently through early diagenetic dissolution of the silica.

Preservation of the spicules requires special taphonomic conditions. An early diagenetic cementation is required that will cement the matrix of the spicules before they are dissolved. Their subsequent dissolution will create a void that may later be filled with cement. Such a diagenetic environment is found in hardgrounds, in which calcitic cement is precipitated from the marine pore water of the seafloor (e.g., Bathurst 1971; Bromley 1975). It might be pointed out that the use of 'preservation' in this scenario is somewhat misleading. The spicules themselves are not preserved; only their external shape is preserved, like a ghost of the original sponge. But this is a common phenomenon in palaeontological material, and the ghosts are herein regarded as body fossils.

Material and methods

In the Upper Cretaceous Chalk Group of northern Europe, the pure, white, micritic chalk is weakly lithified and generally preserves sponges poorly, and at many levels, not at all. Their original presence is divulged, however, by borings of endolithic sponges in skeletal fossils such as oysters and belemnites (e.g., Bromley 1970). Spicules have not been found in these borings, except where these are embedded within flint concretions, but here visibility of the spicules is generally poor.

However, in the Turonian Chalk Rock Formation of southern England (Bromley and Gale 1982), sometimes regarded as a diachronous member of the Lewis Nodular Chalk Formation (Mortimore et al. 2001; Woods and Aldis 2004; Hopson et al. 2006), the topmost of a group of hardgrounds, the Hitch Wood Hardground,

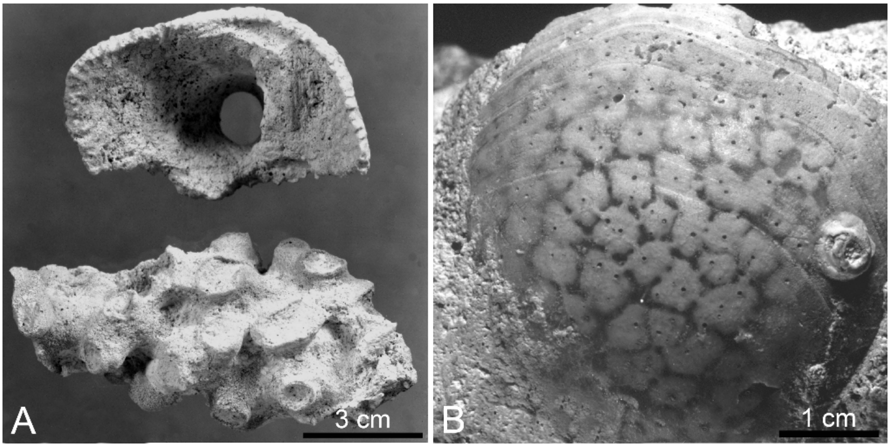

Fig. 1 Preservation of sponges and their borings in the Hitch Wood Hardground at Hitch Wood quarry. **A** Two hexactinellid sponges preserved as phosphatic body fossils, the spicules as empty or cement-filled cavities. Extracted from the matrix using acetic acid. **B** The transparent shell of a terebratulid brachiopod, *Gibbithyris* sp, containing the post mortem boring *Entobia cretacea*

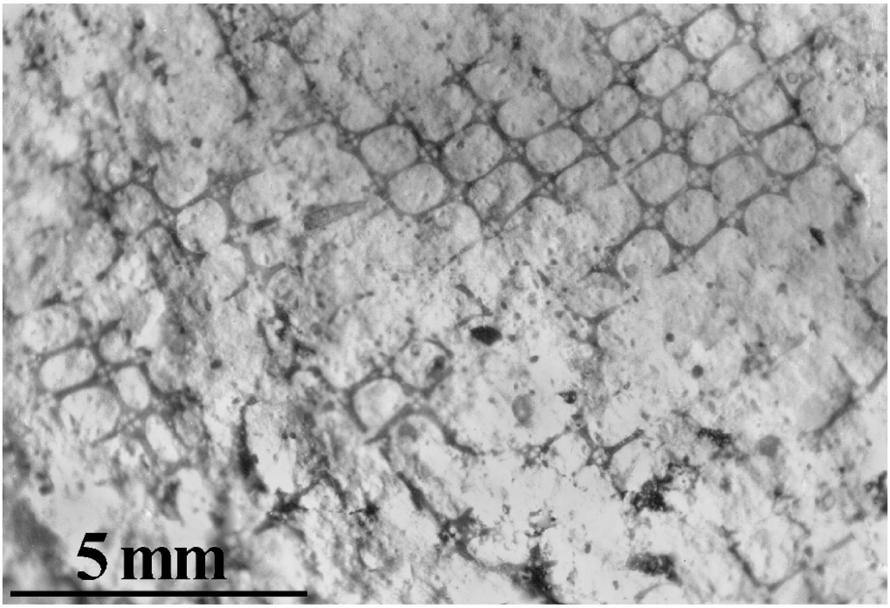

Fig. 2 The skeleton of a lychniscosan hexactinellid sponge, the silica replaced by glauconite. Hitch Wood Hardground, Chalk Rock, Hitch Wood quarry

contains abundant non-boring sponge body fossils as well as *Entobia* Bronn, 1837 (Fig. 1). The hardground is well mineralised with phosphates and glauconite. The spicular skeleton of the non-boring sponges is well preserved by early cementation of the sediment followed by phosphatisation and glauconitisation at or close to the seafloor. In some cases, the spicules themselves are replaced by glauconite (Fig. 2). Intraclastic pebbles and mollusc shells commonly contain *Entobia*.

At an old quarry at The Frogmore, High Wycombe, Buckinghamshire, England (Bromley and Gale 1982), an intraclast, containing *Entobia cretacea*, was collected from the Hitch Wood Hardground. Using a rock saw, the intraclast was sectioned (Fig. 3), and was found to contain spicules in several of the chambers of the boring (Figs. 4-6). Parallel serial surfaces were ground and polished, about 30-50 µm apart, and an acetate peel of each was taken (17 peels labelled A to Q). The specimen was illustrated by Bromley (1970: pl. 5a) as it was before the peels were taken.

Measurements of spicules were taken from enlarged images obtained from peels (Figs. 4-6). From consecutive images, the widest diameters were used for the erosion traces. Spicule widths were defined as the smallest diameters of bright circular areas representing spicule cross-sections seen in Figures 4-6, because slightly diagonal sections would artificially increase diameters. Where spicules were sectioned longitudinally, the widest diameters were used, as the opposite effect took place. Spicule lengths were measured in a straight line from tip to tip, always assuming to underestimate, as the spicule was unlikely to be sectioned in a plane that allowed viewing of the full length. Photographs of acetate peels and spicules of recent sponges were taken with a ColorView I digital camera for microscopy, using

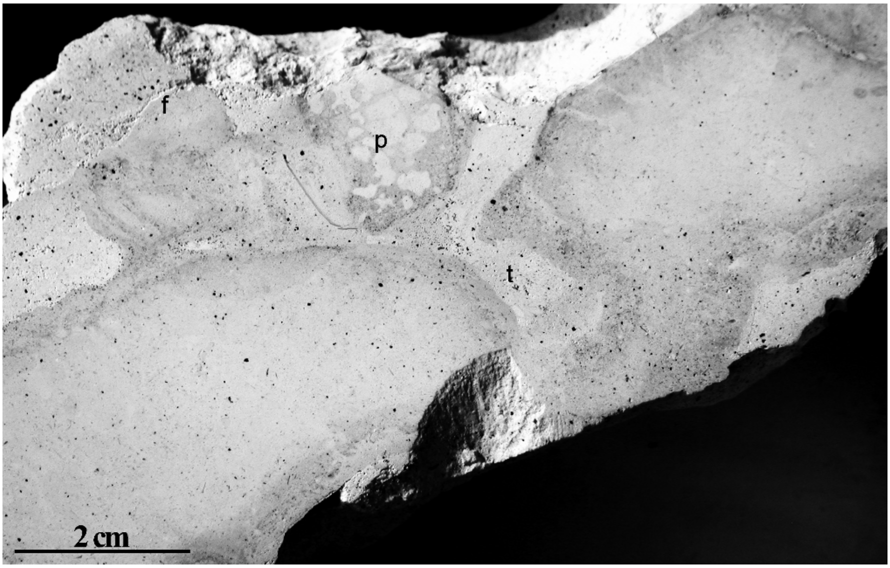

Fig. 3 Sample of the Hitch Wood Hardground from High Wycombe quarry, sawn and polished surface. The framework of the hardground, some distance below seafloor (f) shows no bioerosion. Omission-suite, pre-cementation *Thalassinoides* penetrate the cemented chalkstone (t). The bioeroded pebble (p) has fallen into the *Thalassinoides* network with the filling sediment

the software AnalySIS 3.2, a Heerbrugg dissecting microscope and a Leica phase contrast microscope at Oldenburg University.

Type material is housed in the Geological Museum of the University of Copenhagen, Denmark. Photographs of recent sponge spicules were taken from preparations in the Schönberg collection.

Results and discussion

The intraclast revealed sponge erosion traces filled with heterogeneous, cemented chalk sediment (Fig. 4). The morphology of the boring corresponded to that of *Entobia cretacea* Portlock, 1843 in having rather small, well-inflated chambers 2-6.5 mm in diameter that maintained a fairly thick interchamber wall of about 360 µm (Figs. 4, 5A). The chambers were connected by rather few intercameral canals of widths around 350 µm, and the surface apertures also were slender but not accurately measurable. The wall of *Entobia cretacea* has well-developed chip-ornament (Bromley 1970; Ekdale et al. 1984: fig. 10-6) and this was clearly visible in sections in the studied intraclast (Fig. 5B-D, arrows). Sponge chips are unlikely to survive, as they lie unattached within the soft endosomal tissues and presumably become dislodged when the tissue disintegrates. If chips were preserved in the present sample, they would be in the darker colour of the eroded calcareous substrate. It may be possible that we located sponge chips in two instances (Fig. 5E, circles). Bright areas of similar diameters and shapes did not represent sponge chips, but cross sections through sponge spicules (Fig. 5F).

The spicules were very uniform and appeared to represent only one type (Figs. 4-6). They tended to lie geopetally on the floors of the larger chambers closer to the substrate surface (Fig. 4), but the sections were not taken in the original vertical plane. In some cases the spicules had a more ordered distribution, e.g., in parallel alignment or as fan-shaped structures, almost suggesting their position as in life (Fig. 4B-F, i.e., in chambers deeper within the substrate). We can assume that spongin originally held the spicules in place and allowed them to form bands and bundles typical for *Aka* (see Rützler 1971). Spongin does not as easily break down in water as opal will and thus may have held some of the spicules in their former position, especially in the chambers more remote from the surface. There can be no doubt that the spicules originated within the boring and were not washed in allochthonously. They are the skeleton of the borer.

The spicules pictured here represent casts of dissolution cavities after silica, filled with sparry calcite cement. It is important, therefore, to remember that we are looking at random sections of them, not at the spicules themselves. The shapes seen in the peels are not those of the whole spicules. In most cases, what appears to be the termination of the spicule is spurious, and merely represents the place where the plane of section passed out of the spicule. In only very few cases is anything resembling the full length revealed (Figs. 4F-G, 6E-F). The true morphology of the terminations is seen only where the plane of section passes longitudinally through the termination of the spicule (Fig. 6E-G). For these reasons, lengths given in earlier studies may be underestimates (Reitner and Keupp 1991).

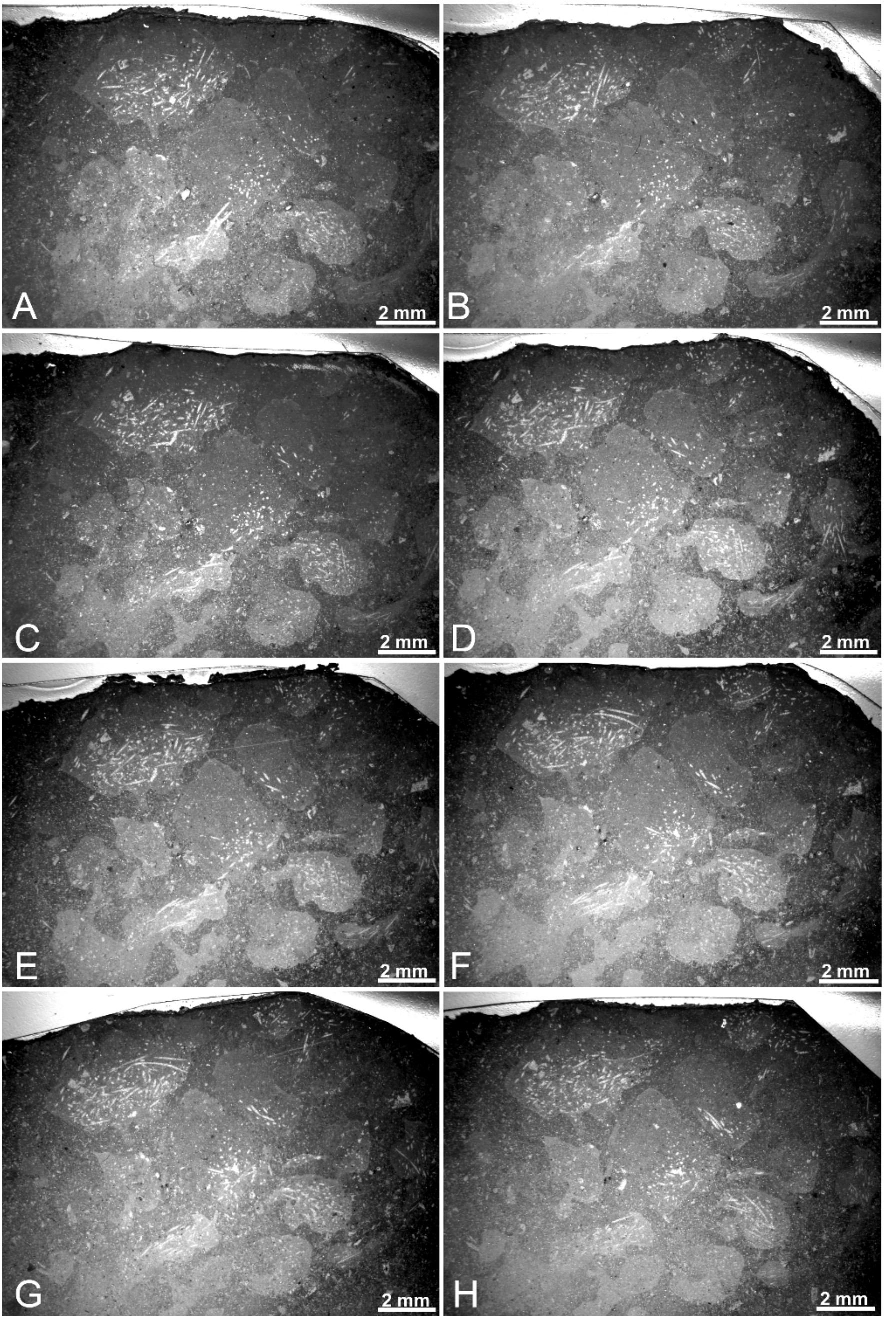

Fig. 4 A-H Consecutive peels of a section through the Hitch Wood Hardground intraclast seen in Figure 3 (MGUH 28734), allowing some understanding of the three-dimensional arrangement of the chambers and spicules. Peels show the pale fill of the *Entobia cretacea*, itself containing sparry cement-filled dissolution casts of spicules of the endolithic sponge

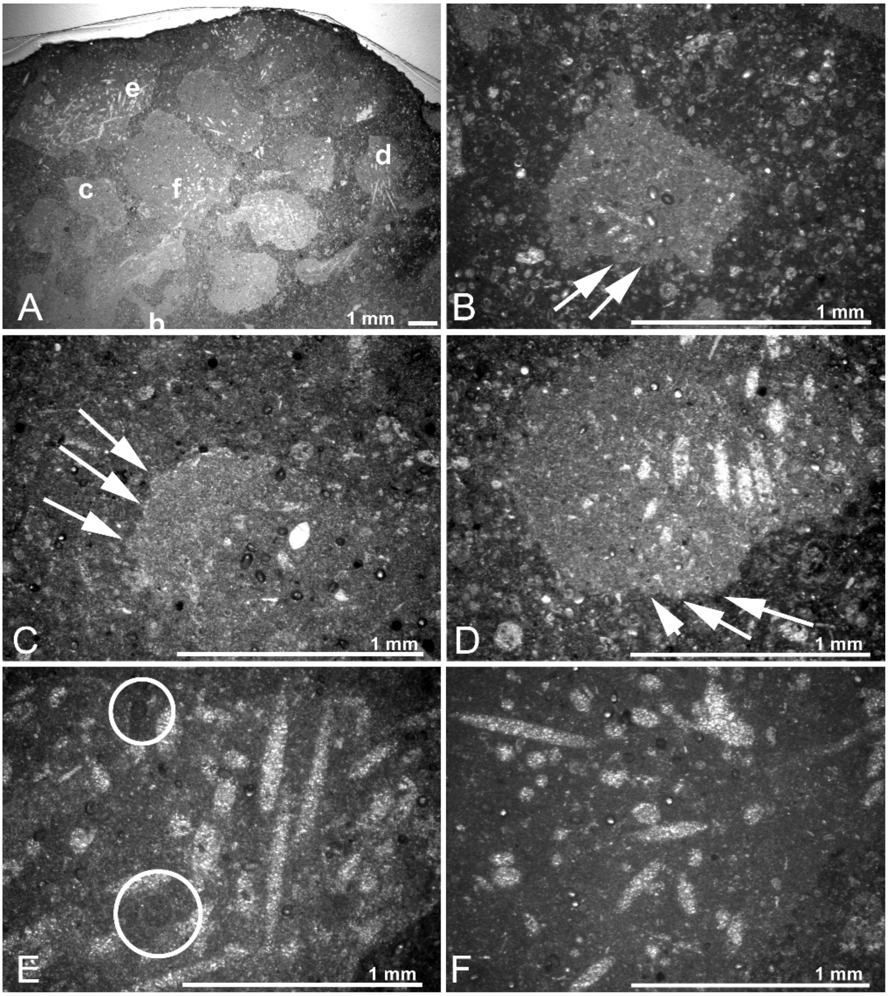

Fig. 5 Bioerosion traces observed in the Hitch Wood Hardground intraclast (MGUH 28734). **A** Overview indicating locations of the following images. **B** (Peel E). **C** (Peel L). **D** (Peel L). Occurrence of scalloped sponge scars along the sectioned walls of the erosion chambers (arrows), providing conclusive evidence for sponge bioerosion. **E** Possible sponge chips as indicated by the slightly darker colour than the fill of the bioerosion chambers (peel C; circles). **F** Bright areas of similar diameters and round outlines do not represent sponge chips, but cross sections through the spicules at more or less a right angle (peel F)

Aka, in white. Chambers of the multicamerate boring were more or less oval, but irregular in outline, connected to each other by slim, short ducts. The largest chamber in the upper left contained most spicule casts. In the figured peels they had the appearance of having fallen to the bottom without apparent order. However, in the largest chamber in the middle, spicules were all arranged at right angles to the section, and in the chamber underneath to the left, they are parallel with the chamber walls, being partly lodged in the connecting duct between the two chambers (A). **D** Fan-shaped arrangements of spicules can be seen on the right of the image. **F**-**G** Peels F and G, top left chamber, the longest spicule sections about 2 mm long

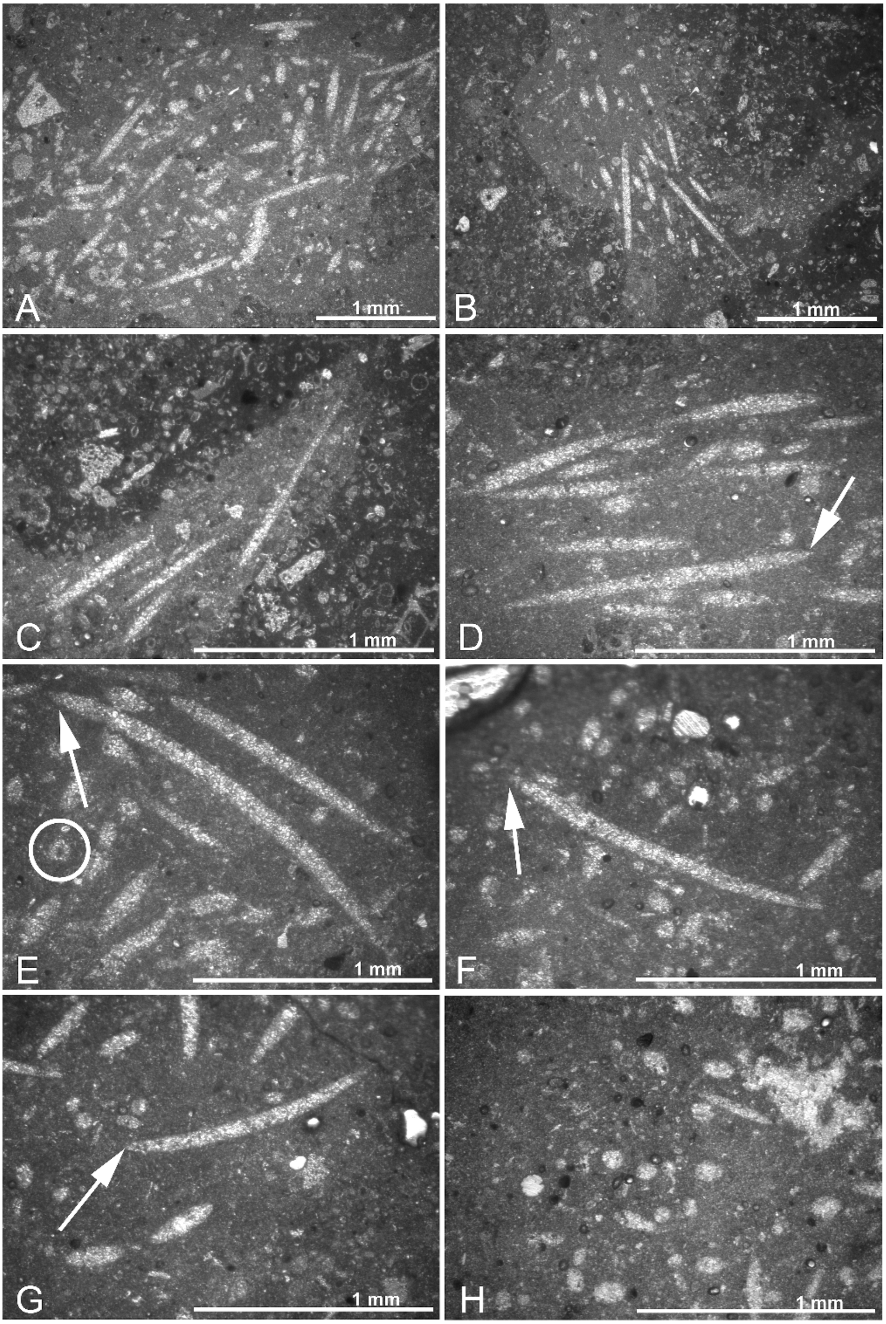

Fig. 6 Cement-filled spicule casts in the Hitch Wood Hardground intraclast (MGUH 28734). **A** Distribution of spicules in the largest chamber near the surface appeared without order in the uppermost 8 peels. **B**-**C** However, fan-shaped arrangement indicated that some spicules might have been preserved in their original position (peel D). **D**-**E** Spicule arrangement in

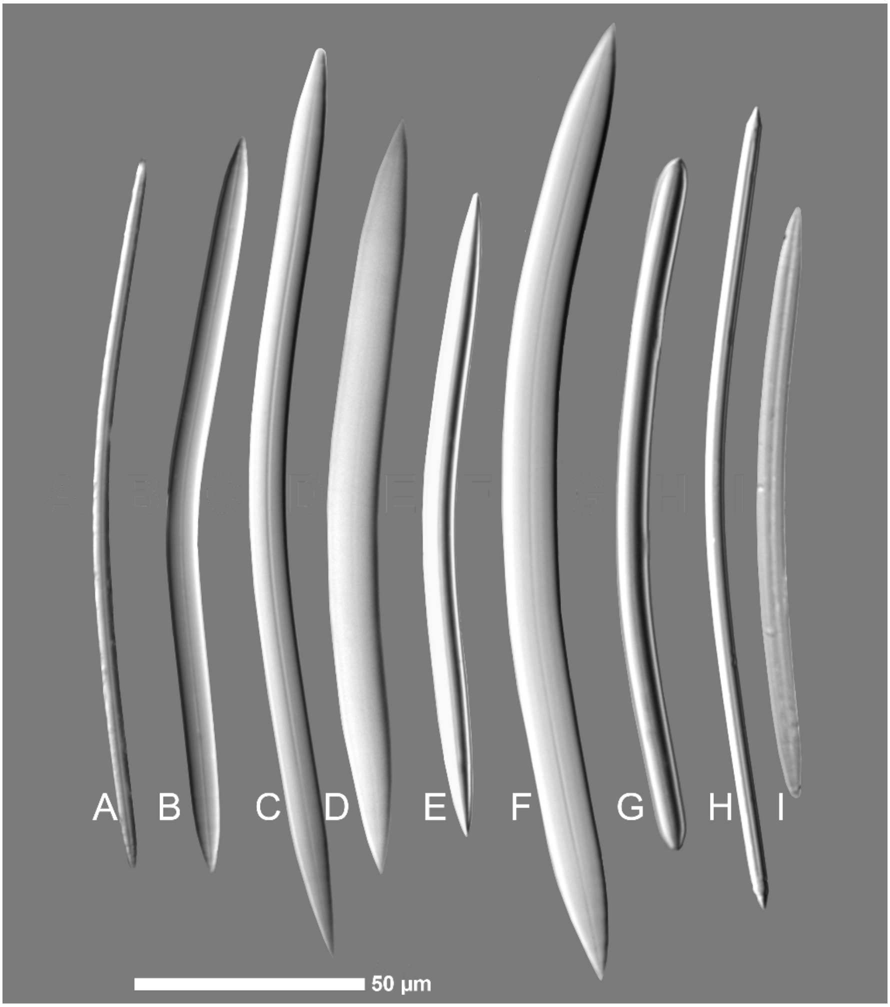

Fig. 7 Oxeas of living *Aka* spp. **A** *Aka brevitublata* (Pang, 1973) (Caribbean, from Calcinai sample Clio 75). **B** *Aka cachacrouense* (Rützler, 1971) (Dominica, from holotype USNM 24094). **C** *Aka coralliphaga* forma *typica* (Rützler, 1971) (Jamaica, from holotype USNM 24095). **D** *Aka infesta* (Johnson, 1899) (Adriatic, Schönberg collection CR-73-1). **E** *Aka minuta* Thomas, 1972 (central Great Barrier Reef, QM G322595). **F** *Aka mucosa* (Bergquist, 1965) (Palau, from holotype USNM 23697). **G** *Aka paratypica* Fromont, 1993 (central Great Barrier Reef, Schönberg collection LPB TS-1.3). **H** *Aka siphona* de Laubenfels, 1949 (Bahamas, from USNM 24107). **I** *Aka xamaycaense* (Pulitzer-Finali, 1986) (Jamaica, from holotype MSNG 47907)

parallel suggested preservation of original orientation (peel F). One cross section in E may display an open axial canal of the spicule (circle). **F-G** Curvature of spicules was similar to oxeas of living *Aka* (peel O). **H** Cross sections of spicules more or less at right angles, from the central large cavity (peel L). The best longitudinal sections were observed in peels F and G (E), where the spicule may be displayed more or less at maximum length (peel F).

The spicules appeared to be smooth, curved oxeas, suggesting the phloeodictyid genus *Aka*, the only endolithic genus in this family (Desqueyroux-Faúndez and Valentine 2002). Microscleres were not seen, but microscleres are not present in living species of *Aka*. Comparison with the often short-tipped, acerate shape of oxeas of living species was close (Figs. 7, 8A), showing little tapering of the shaft. There was a superficial likeness to the acanthoxeas of the clionaid *Pione vastifica* (Hancock, 1849). These, however, have long, tapering (i.e., hastate) terminations, and are covered with small spines (Fig. 8B, left inset). These spines appeared to be absent in the fossil material. Also absent were the tylostyles that categorise clionaid sponges (Fig. 8B), and the microrhabds of the genus *Pione* Gray, 1867 (Fig. 8B, right inset).

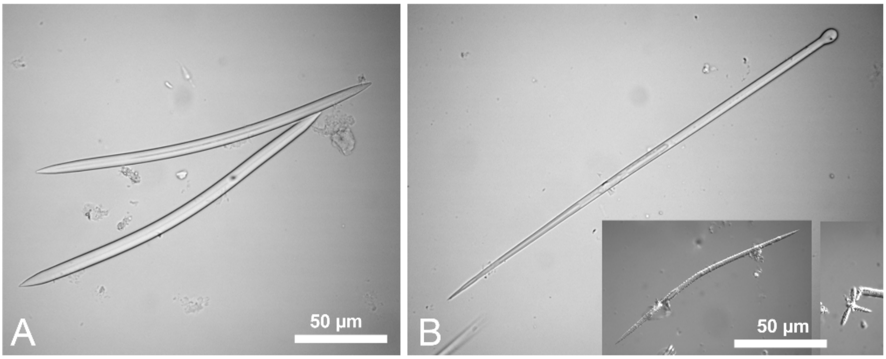

Fig. 8 Spicules from living sponges, from Little Pioneer Bay, Orpheus Island, central Great Barrier Reef. All spicules to scale. **A** Oxeas from *Aka mucosa* (Bergquist, 1965), Schönberg sample LPB-14. **B** Spicules from *Pione vastifica* (Hancock, 1849), Schönberg sample LPB-1.130, with a tylostyle (large), an acanthoxea (left inset) and a cluster of 3 cigar-shaped microspined microrhabds (right inset)

Spicule dimensions of the sponge in the intraclast are about ten times larger than those known for living species of *Aka* (e.g., Rützler 1971). Mean oxea width is 73.6 µm (minimum 47.6 µm, maximum 103.2 µm, standard deviation 13.0, for n = 50). Spicule lengths were difficult to estimate, as we had to assume that we had only incomplete spans, due to oblique sectioning. Measuring the lengths of the ten longest spicule sections, we obtained a mean length of 1327.2 µm, an obvious underestimate owing to the oblique section planes of the spicules. A length / width ratio of 18 is typical for an oxea as displayed in Figure 7D. Dividing the longest and probably most complete spicule length (of the spicule in Fig. 6E) by the mean width gives a ratio of 25.9, which is more typical of *Aka* spp. (Schönberg and Beuck, in press). Common ratios in *Aka* are approximately 23, therefore we can assume that the spicule in Figure 3E shows a section in more or less full length and that the putative mean spicule length in this fossil *Aka* was likely around 2 mm. Of the measured oxeas, about a tenth may represent immature spicules that were still in the process of formation when the sponge died and was buried, because a histogram of spicule widths showed a slightly bimodal distribution on the side of the slimmer spicules (Fig. 9).

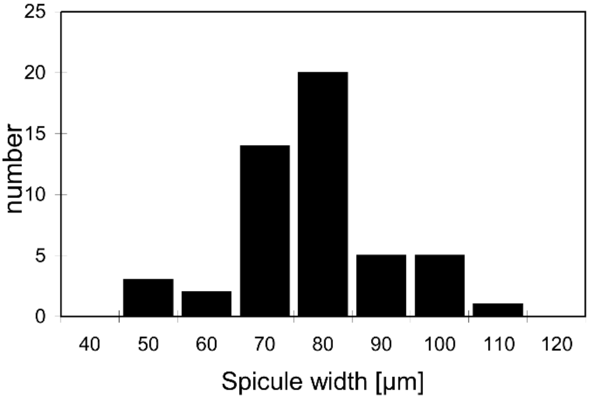

Fig. 9 Size frequency distribution of oxea width from spicules in the Hitch Wood Hardground intraclast (MGUH 28734). The slight bimodality with a secondary, smaller peak on the left indicates the occurrence of a few immature oxeas that were unusually slim compared to the other oxeas and may have been unfinished when the sponge died

Systematics

Phylum Porifera Grant, 1826
Class Demospongiae Sollas, 1885
Family Phloeodictyidae Carter, 1882
Genus *Aka* de Laubenfels, 1936

Diagnosis: Boring sponges, excavating calcareous substrates (molluscs, coral rocks); externally visible by their fistulose tubes. Skeleton formed only of spicule-bundles in sinuous bands, not in a network, lining walls of fistules. Spicules short, slender, curved oxeas. Without microscleres. (From Desqueyroux-Faúndez and Valentine 2002).

Aka akis sp. nov.

Diagnosis: *Aka* having very large, smooth oxeas, mean width ca. 74 µm, approximate length 2000 µm. Other spicule types absent. Tips of the oxeas acerate, shafts with only little curvature, soft, not angular.

Differential diagnosis: The herein described *Aka* has oxeas that are about ten times the size of those of extant *Aka* spp. It has similar spicule characters compared to *Aka cassianensis* Reitner and Keupp, 1991 from the Italian Triassic and *Aka boltanaensis* Reitner and Keupp, 1991 from the Spanish Tertiary. This new sponge is from a different period and location, and differs from the above species in the larger size of its spicules. We therefore describe it as *Aka akis* sp. nov.

Etymology: *akis*, Greek, needle.

Type material, locality and horizon: The holotype is a bioeroded hardground intraclast containing sparry calcite cement-filled casts of spicules, MGUH 28734, together with a series of 17 peels made from successive sections of the same specimen, respectively MGUH 28734 A-Q. Repository: the Geological Museum, University of Copenhagen, Denmark. Quarry at The Frogmore, High Wycombe, Buckingham, SE England (Bromley and Gale 1982), no longer exposed. Hitch Wood Hardround, Chalk Rock Formation, Upper Chalk Group, Turonian, Cretaceous.

Description: Spicules of holotype occurring within sponge boring *Entobia cretacea*. The only spicule present, a smooth oxea, mean width 73.6 µm, maximum width recorded 103.2 µm. Spicules observed in section only, leaving measurement of length uncertain, but 10 measurements resulting in mean of 1327 µm. Considering length : width ratios typical for *Aka*, a spicule length of 2000 µm appears more likely. Most spicules observed straight, some with subtle, soft, evenly formed curve. Shaft only with little tapering. Short, acerate terminations where points appeared complete. Skeletal arrangement partly preserved, showing fan-shaped and band-like formations. No epilithic structures preserved.

Conclusions

The present account of *Aka akis* sp. nov. as a tracemaking species producing *Entobia cretacea* is the first positive identification of an *Entobia*-maker in the geological record that preserves the trace fossil and the (ghosts of) spicules in combination. Earlier accounts of fossil *Aka* described the sponges without naming the trace fossils (Reitner and Keupp 1991) or did not have spicules at their disposal, preserved in the bioerosion chambers (Schönberg and Tapanila 2006). The Hitch Wood Hardground contains other (unnamed) forms of *Entobia*. If further examples can be found containing autochthonous spicules, an idea at last may be developed of the ecology, evolution and systematics of endolithic sponges through time. However, there are important questions that still require answering. What was the diversity of endolithic sponges in the Mesozoic? When did the Clionaidae arise? Hardgrounds may supply the answers.

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