

The Fossil Record of the Haplosclerid Excavating Sponge *Aka* de Laubenfels

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Introduction

Only few publications deal with Recent species of the genus *Aka* or *Siphonodictyon*, a younger synonym of *Aka* (Johnson 1899; de Laubenfels 1936; Bergquist 1965; Rützler 1971; Thomas 1972; Pang 1973). In the literature, only two publications figure and describe fossil *Aka* spicule arrangements – Müller (1978) and Reitner (1987a). *Aka* spicules are commonly found within burrows in Jurassic and Cretaceous shallow marine carbonates.

The present chapter will document the stratigraphic occurrences, systematic and phylogenetic implications, as well as ecological interpretations, of fossil *Aka* species (Fig. 1).

Systematic Position of the Genus *Aka*

The excavating sponge *Aka* is classified within the order Haplosclerida, family Adociidae, based on the oxea spicule type and its arrangement in bundles or brushes. The spicules of the inner parts of the sponge exhibit a typical adociid arrangement. Spongin is reduced and cortical spicule tracts are arranged perpendicular to the central spicule bundles. The whole sponge lives wholly inside calcareous material. Only prominent chimneys with apertures protrude from surfaces.

Systematics and Stratigraphic Distribution of Fossil *Aka*

Systematic Description of Early Carnian Aka

Aka cassianensis n.sp. (Fig. 2a-d)

Derivatio nominis: After the Lower Carnian Cassian Formation, named after the type locality, a small village near Cortina d'Ampezzo (Northern Italy).

Holotype: Deposited in the Institut für Paläontologie der Freien Universität Berlin (IPFUB, JR5/89)

Locus typicus: Seelandalpe near Schluderbach

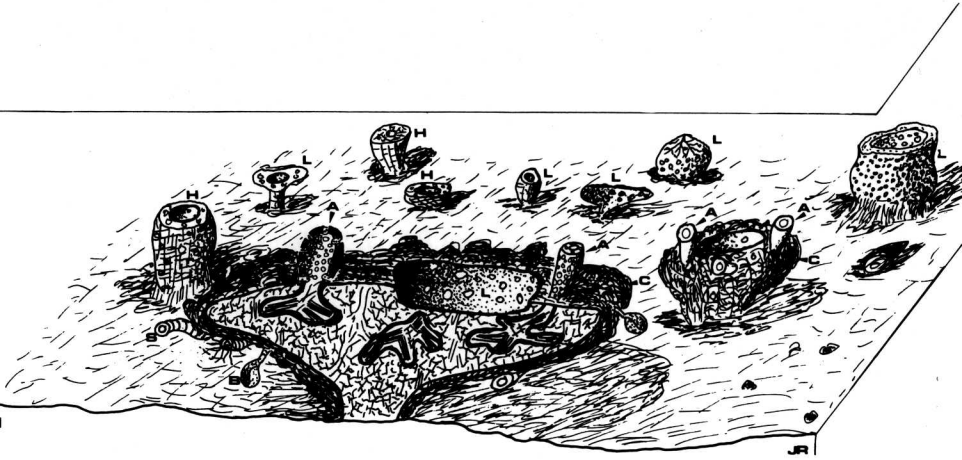


Fig. 1. Sketch of living *Aka* within Late Jurassic siliceous sponge habitats. Most sponges are dead and covered by bacterial crusts. The entire spicular skeleton is altered to calcareous material. *H* Hexactinellid; *L* lithistid; *A* *Aka*; *C* micritic crust

Stratum typicum: Triassic, Early Carnian, Cassian Formation

Material: 4 specimens

Diagnosis: Encrusting and excavating *Aka* with relative short, but thick oxeas, arranged in brushes. Spicules connected with their end points as seen in *Adocia*

Description of the holotype (Fig. 2a-d): *Aka* bores in a small chaetetid sponge. Six round-shaped to elongated boring cavities are visible. In two of these cavities cross-cut monaxonic spicules are visible. On the outer surface of the chaetetid sponge, *Aka* is cut obliquely. The sponge protrudes from the surface of the chaetetid sponge. The thick short oxeas are similar to those seen in the cavities. Therefore a close relationship between the excavations and the protruding sponge is probable. The entire sponge is encrusted by dark, micritic, bacterial crusts.

Spicule measurements: length: 620–900 μm , mean 740 μm ; width: 80–65 μm , mean: 70 μm .

Diameter of the burrows: 1600–400 μm

Diameter of the entire sponge: ca. 1.5 cm

Description of the paratype (Fig. 3a-c): The described sponge is encrusting. Spicule type and arrangement are typical for *Aka*. The sponge is cut perpendicular to the axis of the spicule bundles and exhibits mostly cross-cut spicules. Only a few spicules retain the entire shape. Within the center of the sponge, a hole is visible. The sponge remains are covered by dark, cloudy, stromatolitic structures. The spicules are smaller than those measured in the holotype.

Spicule measurements: length: 700–850 μm , mean 775 μm ; width: 75 μm

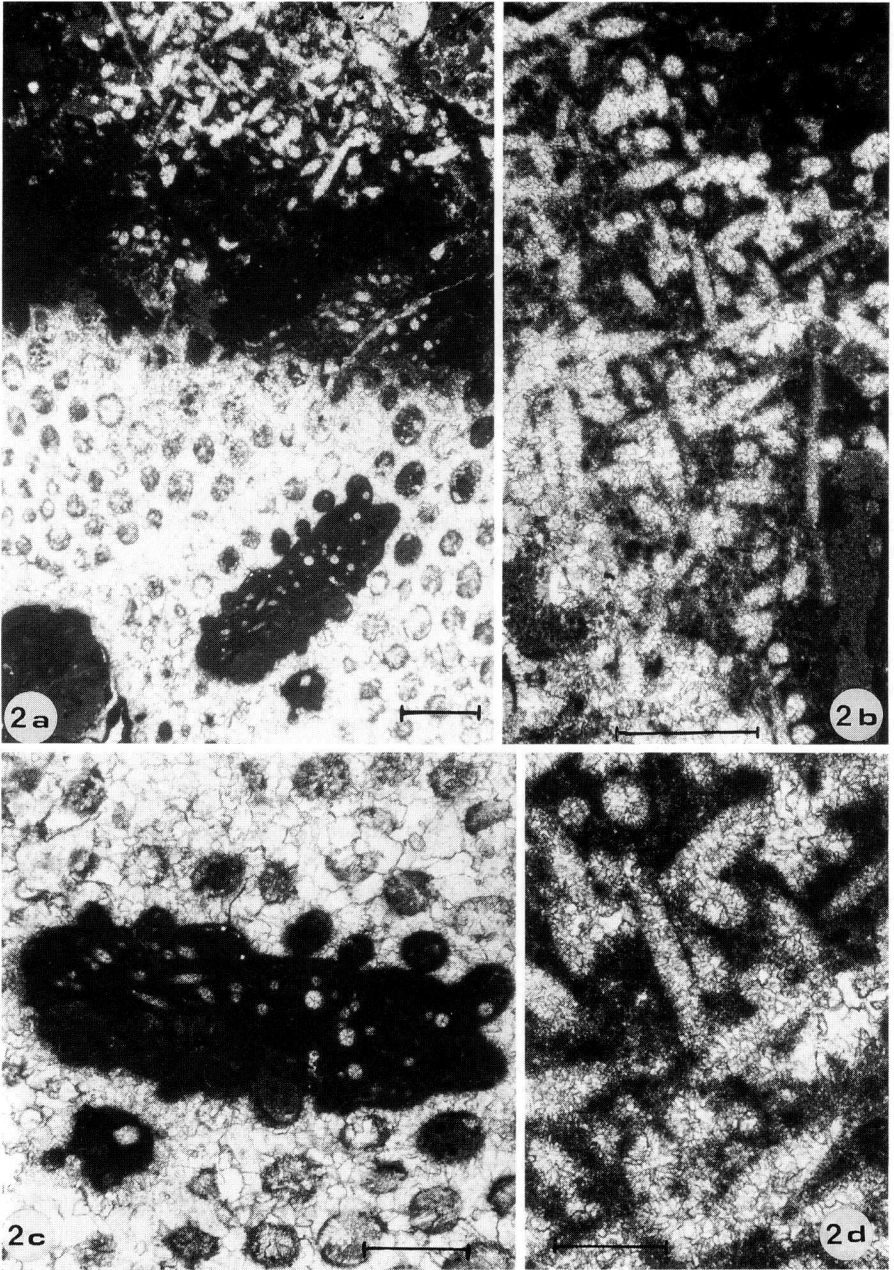


Fig. 2. *Aka cassianensis* n.sp. holotype; Cipit Boulders from the Cassian Beds near Seeland Alpe (Schluderbach, Northern Italy). **a** Entire sponge with boring cavities inside a small chaetetid sponge. Scale: 1 mm. **b** Spicular arrangement of the encrusting outer part of the sponge. Scale = 1 mm. **c** Elongated burrowing cavity with cross-sectioned spicule tracts. Scale = 500 μ m. **d** Detail of **b** showing the short thick oxeas. Scale = 500 μ m

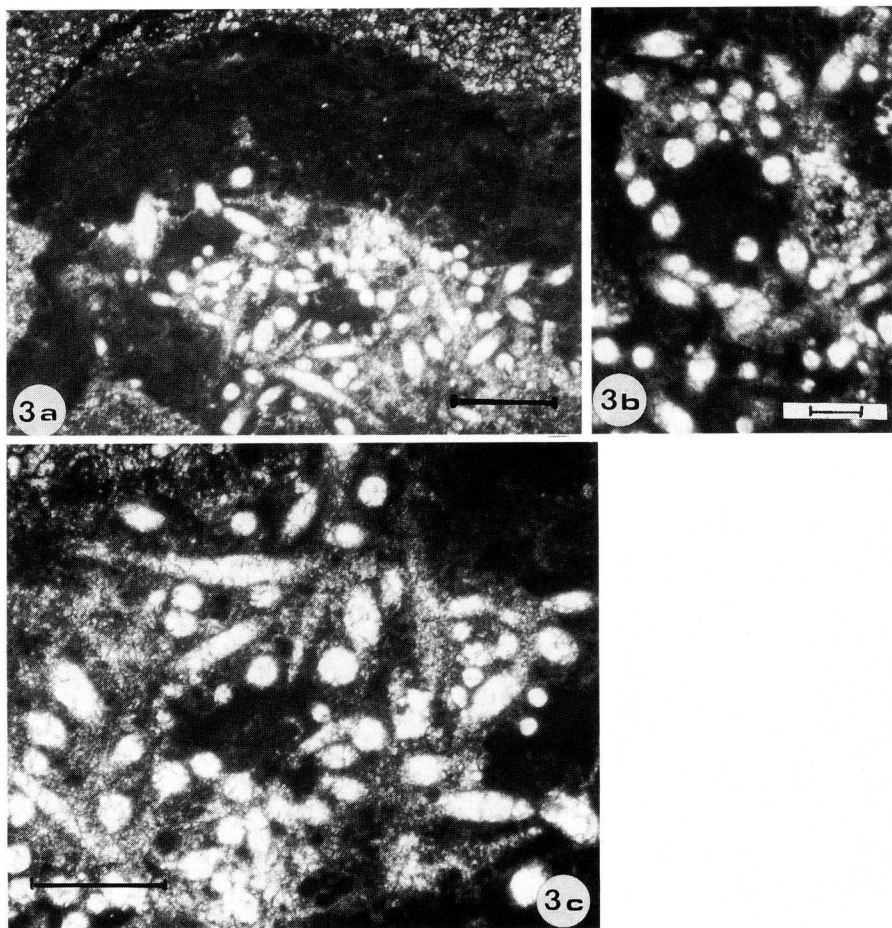


Fig. 3. *Aka cassianensis* n.sp. paratype; Cipit Boulders from the Cassian Beds near Seeland Alpe (Schluderbach, northern Italy). Specimen is covered by a dark micritic layer with stromatolitic affinities. Scale = **3a** 400 μm , **3b** 100 μm , **3c** 200 μm

Diameter of the entire sponge: ca. 10 mm

Diameter of the central hole: 5 mm

Differential diagnosis: The new species differs from all modern species by exhibiting significantly larger scleres. In modern *Aka* the spicules size varies from 100–200 μm . Within fossil *Aka* this particular type of short and thick oxea seen in *Aka cassianensis* is never observed.

Remarks. From the Lower Carnian Cassian Formation of the Dolomites near Cortina d'Ampezzo (northern Italy), fore-reef debris flows are common containing excellently preserved coralline sponges. Most of these sponges are pre-

served with their original mineralogy (aragonite, high Mg calcite) (Fürsich and Wendt 1977; Wendt 1979; Reitner 1987b; and others). The associated siliceous sponges are badly preserved because the siliceous spicules are dissolved very early. Only in few thin sections can the characteristic *Aka* spicules arranged in brushes and bundles be seen (Figs. 2–5).

Systematic Descriptions of Jurassic and Cretaceous Aka

Remarks. Most post Triassic *Aka* species possess a burrowing ability. Some encrusting specimens are observed within Bathonian siliceous sponge build-ups from St. Aubin-sur-Mer (Normandy). The spicule types and spicule arrangement of the encrusting and boring type are nearly similar. Only two new main types of *Aka* are described here. Based on the lack of characters found in fossil specimens,



Fig. 4. *Aka cassianensis* n.sp.; same locality as Fig. 2. Scale = 200 μ m

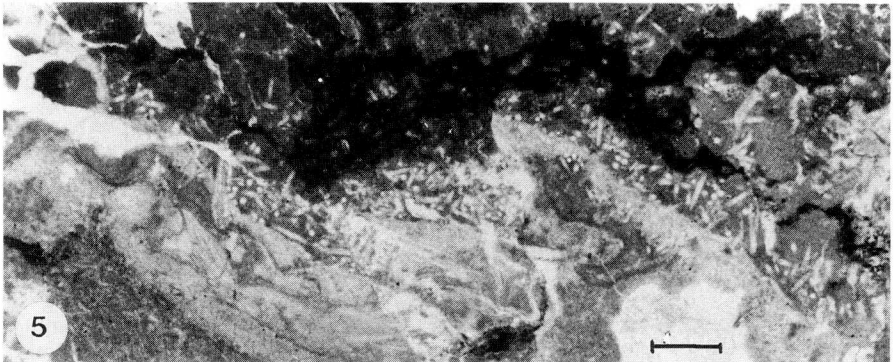


Fig. 5. *Aka cassianensis* n.sp.; encrusting specimen. Same locality as Fig. 2. Scale = 2 mm

it is always very difficult to erect new species, but the new observed forms significantly differ from modern ones and new species are justified.

Aka muelleri n.sp. (Figs. 6–8)

Derivatio nominis: After Walter Müller, a paleospongiologist who found and described the first, fossil *Aka*.

Holotype: Deposited in the IPFUB, JR6/89

Locus typicus: Roßbach, north part of the Frankenalb in Bavaria

Stratum typicum: Lower Kimmeridgian sponge mound facies

Material: Numerous specimens from Jurassic and Cretaceous carbonate platforms and from calcareous organisms.

Stratigraphic distribution: Bajocian-Late Cretaceous

Geographical distribution: Middle and Western Europe, Arizona/Northern Mexico (Aptian/Albian Mural Limestone).

Diagnosis: Irregularly shaped sponges of various sizes which live exclusively in excavated burrows. The burrows are large and possess generally only one or two openings. The spicules (oxeas) are big and arranged in bundles and brushes. Smaller ectosomal oxeas are observed in few specimens. Within the probable choanosomal area, the spicules exhibit typical haplosclerid arrangements. The sponge bores only in calcareous material, such as corals, diagenetically altered siliceous sponges, coralline red algae, bivalves, and belemnites.

Description of the holotype (Fig. 6): The sponge is located in an oyster shell which is settled by thecidean brachiopods. The microfacies of the host rock is mudstone/wackestone. The micrite is cloudy and exhibits irregularly shaped clasts and tuberoids. Seven spicule tracts are visible which are cut vertically and obliquely. A single spicule tract possesses more than 50 spicules. Two types of oxeas are observed: a rare smaller type in the outer part of the sponge remains, probably representing ectosomal scleres, and a bigger more common one in the center of the sponge. Small spicule types are observed also within the larger spicule tracts (bundles).

Measurements:

Big oxeas (3x): length: 1000–1600 μm ; width: 60 μm

Small oxeas (2x): length: 800 – 1200 μm ; width: 20–25 μm

Differential diagnosis: *Aka muelleri* n.sp. differs from *Aka cassianensis* n.sp. in the absence of an encrusting growth form and the possession of much larger scleres. The Recent *Aka* species have much smaller spicules (10 \times smaller).

Aka minima n.sp. (Figs. 9,10)

Derivatio nominis: After the Latin word “minimus” small

Holotype: IPFUB, JR7/89

Paratype: IPFUB, JR8/89

Locus typicus: Kasendorf, SW of Kulmbach, northern Bavaria (MFS 188); leg. T. Steiger, Munich

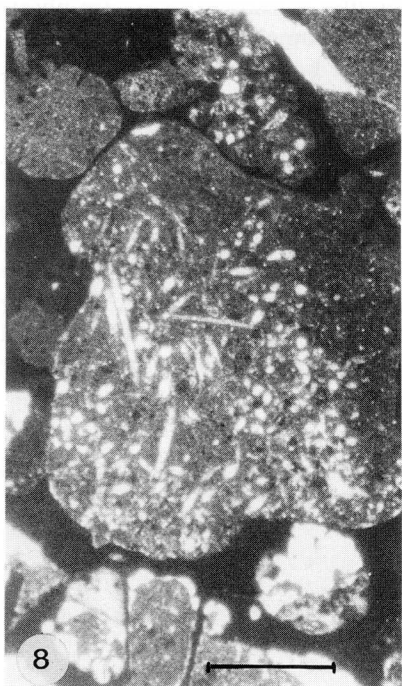
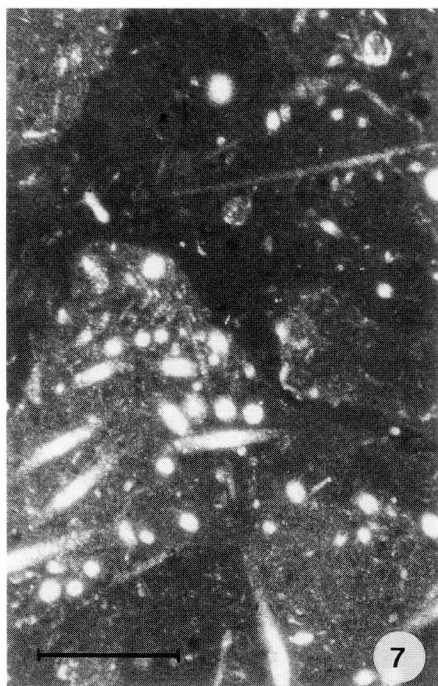
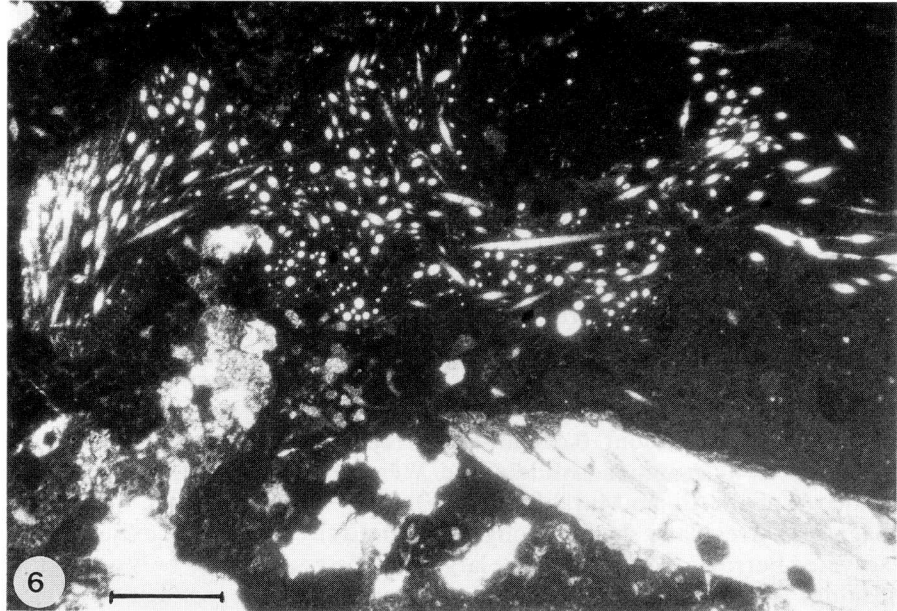


Fig. 6. *Aka muelleri* n.sp. holotype; Kimmeridgian sponge mounds from Roßbach northern Franconian Alb (southern Germany, Bavaria). Scale = 1 mm

Fig. 7. *Aka muelleri* n.sp. from Bajocian/Bathonian sponge biostromes of Vilviestre (Sierra de la Demanda, northern Spain). Scale = 500 μ m

Fig. 8. *Aka muelleri* n.sp. from a Late Albian reef (Albeniz/Eguino reef) near Araya (Prov. Alava, northern Spain). *Aka* bored within a specimen of *Acanthochaetetes* (deep fore-facies). Scale = 1 mm

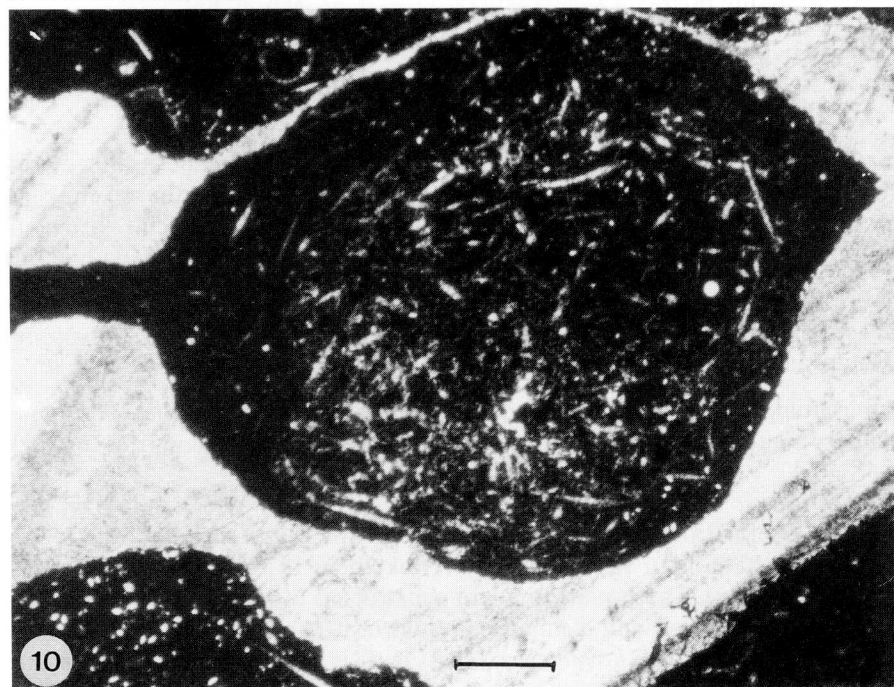
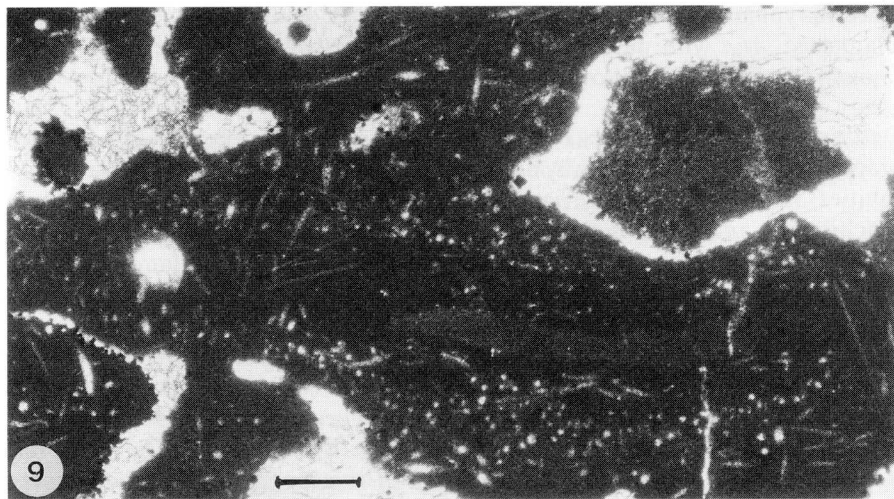


Fig. 9. *Aka minima* n.sp. holotype; Kimmeridgian sponge mounds near Kasendorf (Southern Germany, Bavaria). Scale = 200 μ m

Fig. 10. *Aka minima* n.sp. paratype; Oxfordian/Kimmeridgian from Laibarös (northern Frankenalb, South Germany, Bavaria). *Aka* bored in a belemnite guard. Scale = 500 μ m

Stratum typicum: Sponge mounds of the Kimmeridgian

Diagnosis: *Aka* with narrow long oxeas forming spicule bundles. Burrowing cavities elongated and in some cases branched.

Description of the holotype (Fig. 9): *Aka minima* n.sp. is located within a thick brachiopod shell which is totally bored with only thin walls between single sponge cavities. The new species *Aka muelleri* n.sp. is also common. Other fossils include brachiopods and lithistid sponges. The biogenetic pore space of the sponges filled up with pellets. The host microfacies is a tuberculitic filament-bearing wackestone/mudstone. Most bioclasts are surrounded by dark micritic crusts.

The new *Aka* species is located in a large bore cavity of a brachiopod and all cross-sections are visible. The spicules are arranged in loose bundles. The cavity is elongated in contrast to the *Aka muelleri* cavities, which are sack-shaped. The oxeas are thin and relatively long. Other spicule types are not observed. The inner zone of the sponge exhibits a dark micritic halo with rare spicules. The innermost zone of the halo is spicule free. The center of the sponge shows an elongated cavity, probably the main excurrent canal (spongocoel?).

Measurements:

Spicules: length: 300–600 μm , mean 400 μm ; width: 15–25 μm , mean: 20 μm

Cavity: length: ca. 10 mm; diameter: 1–5 mm

Paratype (Fig. 10): The paratype is located in a totally bored belemnite guard from the Oxfordian/Kimmeridgian boundary of Laibarös (northern Frankenalb, Bavaria). The sponge is relatively badly preserved. The spicules are concentrated in thick bundles. Only *Aka minima* n.sp. is observed within the belemnite guard.

Measurements:

Spicules: length: 400–640 μm , mean 500 μm ; width: 15–25 μm , mean: 20 μm

Differential diagnosis: *Aka minima* n.sp. differs from *Aka muelleri* in having smaller spicules and more elongate burrowing cavities.

Middle Jurassic Occurrences of Aka

In the Celtiberic Ranges and the northern part of Spain, vast carbonate platforms of Bajocian/Bathonian age are present (Hinkelbein 1975; Wilde 1988; Scheer 1988; and others). These platforms are constructed of rigid siliceous sponges, lithistid demosponges, and a smaller amount of hexactinellid sponges. Within these sponge build-ups *Aka muelleri* n.sp. (Fig. 7) is a common boring organism.

Measurements:

Bigger oxeas: length: 1000–1500 μm ; width: 50–55 μm

Smaller oxeas: length: 850–1000 μm ; width: 50 μm

Late Jurassic

Build-ups of siliceous rigid sponges are very common at this time in all of Europe (especially in southern Germany) (Fritz 1958; Wagenplast 1972; Trammer 1982; Gaillard 1983; Flügel and Steiger 1981; Schorr and Koch 1985; and others). The main facies belts are more or less the same as those observed in the Dogger of Spain. The Late Jurassic occurrences are mostly in mud mounds and in some cases in mud banks ("Treuchtlinger Marmor"). The Oxfordian mounds are constructed mainly of hexactinellid sponges. The Kimmeridgian and Tithonian mounds and banks are composed mostly of lithistid demosponges. In both cases *Aka* is a common excavator within sponge skeletons. *Aka muelleri* n.sp. is the most common boring sponge. The smaller *Aka minima* n.sp. is rare and mostly associated together with *Aka muelleri* n.sp.

Müller (1978) has reported *Aka minima* n.sp. within the lithistid sponge *Pyrgochonina acetabulum* (Goldf.) from the Lower Kimmeridgian of the Schwäbische Alb (southern Germany). He has found this new sponge also in hexactinellids, and therefore, he interpreted the new sponge as a parasitic organism. His observation was the first report of fossil *Aka* species.

Aka bores exclusively in calcareous material. Therefore *Aka* is a postmortem inhabitant of siliceous sponges after a very early diagenetic replacement of the opal or cristobalite of the siliceous spicules into calcite. *Aka* bores in diagenetically altered sponge skeletons and in belemite guards.

Measurements of *Aka muelleri* n.sp. (excl. holotype):

Bigger oxeas:

length: 1300–1550 μm , mean: 1450 μm ; width: 55–60 μm , mean: 50 μm

Smaller oxeas:

length: 700–1000 μm , mean: 900 μm ; width: 15–20 μm , mean: 17 μm

Measurements of *Aka minima* n.sp. (excl. holotype):

Oxeas of Müller specimen: length: 350–470 μm , mean 450 μm ; width: 15 μm

Oxeas of further specimens: length: 320–620 μm , mean 500 μm ; width: 20 μm

Early Cretaceous

In the Lower Cretaceous of the Tethyan realm of Europe, as well as in the north part of the Cretaceous Gulf of Mexico, shallow marine carbonate platforms and reefs are widespread and called "Urgonian". The Urgonian facies of northern Spain is well studied, especially the facies distributions and the sponge communities (Pascal 1985; Reitner 1982, 1986, 1987a, 1987c; Reitner and Engeser 1983, 1985, 1987). The boring sponge *Aka* is common in the deeper part of the coralgall facies belt, within the *Microsolena* deeper water coral facies and within the *Spirastrella* (*Acanthochaetetes*) biofacies (Reitner 1987a, Pl. 15, Figs. 5,6) (Fig. 8). Further occurrences of *Aka* are within micritic mud mounds which were formed by siliceous sponges, comparable with the Jurassic ones, and rarely in rudist mud mounds. Within the beach facies and other permanently wave-agi-

tated facies zones, typical pearl band borings of the hadromerid burrowing sponge *Cliona* are observed. *Cliona* borings are never seen within quiet water facies in which *Aka* is dominant. Spicule type and spicule arrangements are characteristic for the species *Aka muelleri*. The spicules are slightly smaller but they have the same shape and thickness.

Measurements:

Oxeas: length: 800–1000 μm , mean 900 μm ; width: 50–55 μm , mean 52 μm

Middle Eocene

Early Tertiary coral reefs are rarely exposed and only few localities are known. Generally the deeper parts of the fore-reefs of these distinct reefs are not preserved or exposed. From the Boltaña anticline in the southern Pyrenees Middle Eocene debris flows are exposed, which bear components of deeper fore-reef mud mound facies. A strong freshwater diagenesis has dissolved out most of the aragonitic organisms, as evidenced by preserved ghost structures. The facies is characterized by flat corals, different encrusting coralline red algae, encrusting rotaliid foraminifera, bryozoa, and sponges. A *Spiraastrella* (*Acanthochaetetes*) community composed of small *S.(A.) eocena* (Rios & Almela), different unidentified lithistid demosponges and *Aka* is observed.

Nearly all larger calcareous organisms are intensively bored by *Aka* and often only a vague relict is preserved. The *Aka* cavities are often elongated or rarely sack-shaped. The living cavities of *Aka* exhibit a length of > 10 mm. Each possesses one narrow opening. The spicules are enormous (1.5–2 mm) and are arranged in bundles. The number of spicule-bundles is highly variable and has therefore no taxonomic significance. Two oxea size categories are observed. A differentiation of spicules to dermal or choanosomal scleres are not seen. The spicule-bundles are covered by dark micritic halos.

The sponge differs from all other fossil *Aka* in cavity size and shape, spicule size, and habitat. Therefore a new species is created.

Systematic Description

Aka boltanaensis n.sp. (Figs. 11–13)

Derivatio nominis: After the locus typicus the village Boltaña in the southern Pyrenees.

Holotype: Deposited within IPFUB, JR9/89

Locus typicus: Base of the Boltaña-anticline near a parking lot on the south side of the river.

Stratum typicum: Middle Eocene debris flow

Material: 5 specimens

Diagnosis: Very big *Aka* excavating single elongated or sack-shaped borings, opened at one end. The spicules exhibit two sizes, a large one with a mean size of

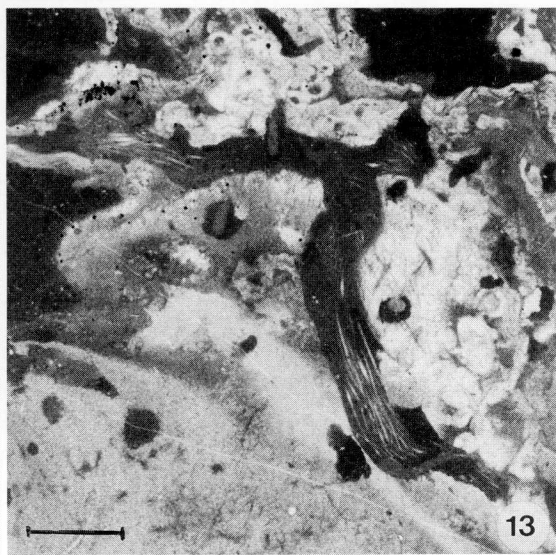
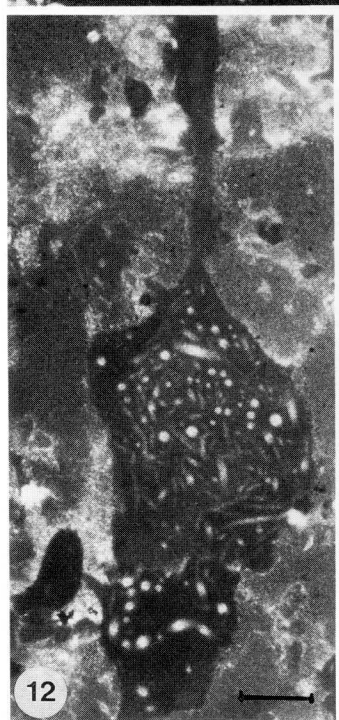
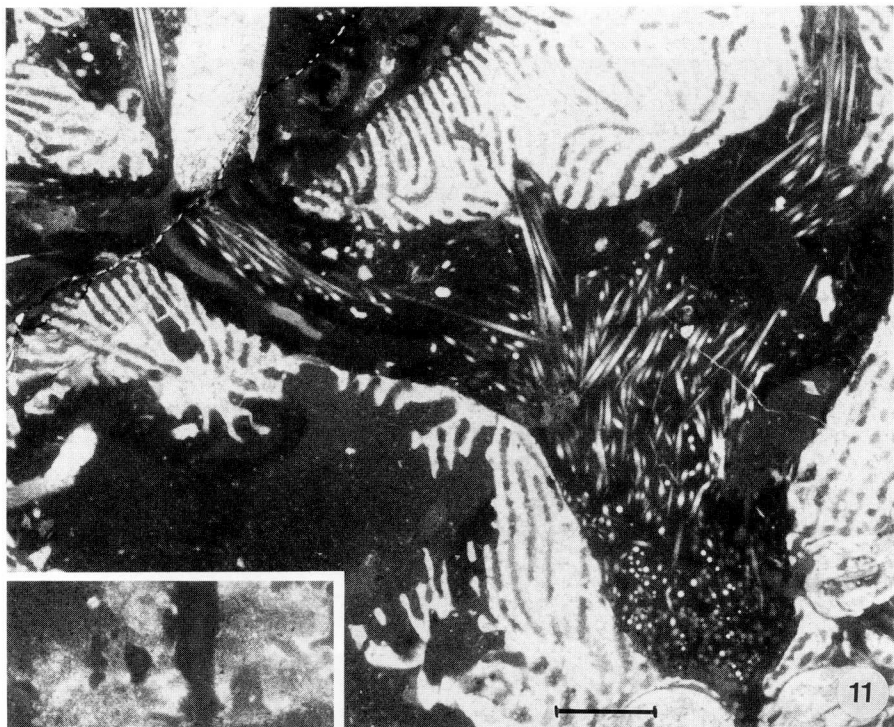


Fig. 11. *Aka boltanaensis* n.sp. holotype; Middle Eocene clast within a debris flow of the same age from the Boltaña Anticline near Boltaña (southern Pyrenees). *Aka* boring in a large coral. Scale = 1 mm

Fig. 12. *Aka boltanaensis* n.sp. Living cavity with a prominent bottle neck canal which serves as the connection between the outer and inner sponge tissue. Same locality as Fig. 10. Scale = 500 μ m

Fig. 13. *Aka boltanaensis* n.sp. Characteristic elongated canals in the living cavity of this particular species. Scale = 2 mm

1600 μm and a smaller one with a mean size of 500 μm . The thickness of the spicules varies from 80–20 μm . The ratio of length to thickness shows a long narrow spicule character.

Description of the holotype (Fig. 11): The holotype of *Aka boltanaensis* is in a thin section from the *Spirastrella (Acanthochaetetes)* community mud mound facies. Flat coral remains are common, as well as larger rotaliid foraminifera (*Nummulites* sp.), and coralline red algae. The holotype is found in the remains of a thamnasteroid scleractinian coral. The coral is totally bored. The coral skeleton is preserved in granular neomorphic calcite. The big *Aka*-boring (living cavity) has a measured length of 2 cm and a maximum diameter of 9 mm. Several smaller blind cavities are observed extending from the main cavity are observed. These blind cavities are filled with spicules and probably served as mining areas for the sponge immediately before its death. The living cavity of the sponge is a complicated three dimensional network, as evidenced by vertical and oblique cuts of the spicule-bundles and Y-shaped areas connecting the cavities.

Measurements:

Bigger oxeas: length: 1400–2200 μm , mean 1700 μm ; width: 60–80 μm , mean 75 μm

Smaller oxeas: length: 300–1000 μm , mean: 560 μm ; width: 20–40 μm , mean 35 μm

Differential diagnosis: *Aka boltanaensis* n.sp. differs in first order from all known *Aka* species in having very large, elongated two size categories oxeas. *Aka muelleri* n.sp. has similar-sized spicules and also possessing two sizes of oxeas. The measured dimensions are slightly smaller and the length/thickness ratio is smaller, than in *Aka boltanaensis*. Nevertheless, both species are closely related. The living cavity of *Aka boltanaensis* is much more complicated than seen in other fossil *Aka*. All Recent *Aka* have spicules with length of 100–300 μm .

Recent *Aka*

Aka in *Petrobiona massiliana* Vacelet and Levi, 1958

One species is a common boring sponge inside the dead body of a pharetronid sponge *Petrobiona massiliana* Vacelet and Levi (Figs. 16,17) from submarine caves near Marseille (Mediterranean Sea). The spicule shape is typical for *Aka minuta* Thomas, a Pacific species, but the spicule size is bigger (mean 205 μm), as

Fig. 14. *Aka coralliphaga* (Rützler). Spicule bundles of the central part of an outdoor chimney. Curacao, Playa Kalki (10–20 m) Collected by van Soest. (Scanning electron microscope (SEM) micrograph)

Fig. 15. *Aka* aff. *coralliphaga* inside the coralline sponge *Astrosclera willeyana* Lister exhibiting a pitted surface caused by boring activity. The dissolution marks are similar to those observed in *Cliona*. (SEM) micrograph)

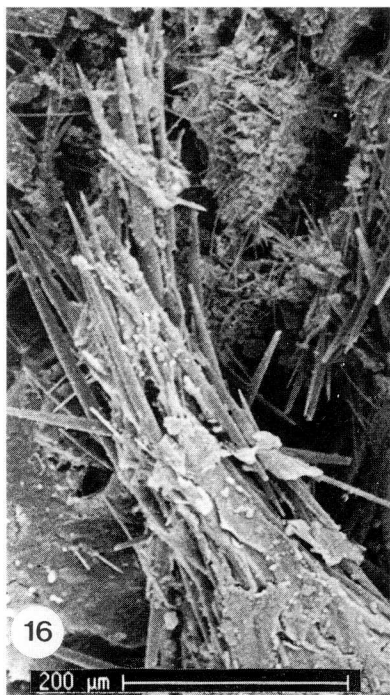
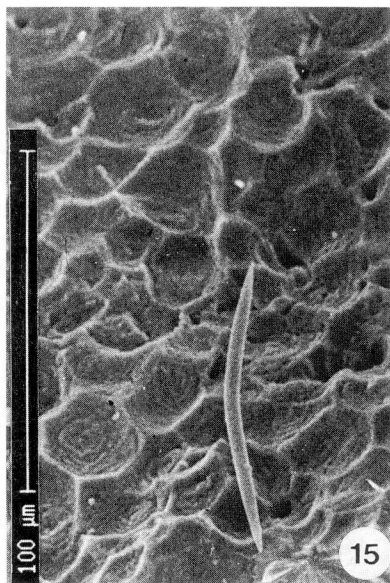


Fig. 16. *Aka* cf. *minuta* Thomas inside the dead portion of *Petrobiona massiliana* Vacelet & Levi. Submarine cave near Marseille. (SEM micrograph)

Fig. 17. *Aka* cf. *minuta* Thomas inside the basal skeleton of *Petrobiona* with living sponge in an endolithic chamber and narrow incurrent and outcurrent canals. Submarine cave near Marseille. Scale = 200 μ m

observed within the type material of *Aka minuta* (mean size of 120 μm) (Thomas 1972). Therefore *Aka* in *Petrobiona* are classified as *Aka cf. minuta*. The spicules are arranged in bundles and brushes and the entire shape is comparable with the fossils species.

Within the dead skeleton of *Petrobiona*, many endolithic sponges are present. Beside *Aka*, *Cliona* is a rare excavating sponge. In cavities caused by the boring activity of excavating sponges, parasitic nonburrowing sponges settled. In the studied material *Agelas* sp., *Geodia* sp., and *Clathrina* sp. are found. The spicules of *Aka cf. minuta* are much smaller than those observed in all described fossil *Aka*. The shape of the living cavities are comparable. In most cases sack-shaped cavities are observed.

Measurements:

Spicules: length: 170–215 μm , mean 200 μm ; width: 7.5–10 μm , mean 8 μm

Aka coralliphaga (Rützler)

In Caribbean reefs *Aka coralliphaga* (Rützler) dominantly bores in flat corals (Fig. 14). The species was erected by Rützler (1971) and described as "*Siphonodictyon*" *coralliphagum* (p. *Siphonodictyon* Bergquist 1965 is a younger synonym of *Aka* de Laubenfels 1936). *Aka coralliphaga* is also very common inside the dead parts of Indopacific coralline sponges, e.g., *Astrosclera willeyana* (Fig. 15). Rützler (1971) has described different morphotypes of this species which he called "*S.*" *coralliphagum* forma *typica*, forma *obruta*, forma *tubulosa*, and forma *incrustans*. These morphotypes indicate that, as he considered, the various forms are different growth stages outside the living cavities. Beside ontogenetic growth stages an adaptation to water currents is probable. The morphotype forma *tubulosa* is here selected. The forma *tubulosa* is characterized by having a chimney-like main excurrent opening (spongocoel). The spicules in this area are arranged in thick bundles from which perpendicular smaller spicule tracts derive, forming the dermal layer. The center of the sponge exhibits typical adociid spicules connections. The spicules are arranged in bundles. For further descriptions see Rützler (1971).

Measurements:

Spicules: length: 150–200 μm , mean 170 μm ; width: 7–9 μm , mean 7.5 μm

Paleoecology and Biostratigraphic Implications

All observed fossil and modern occurrences of *Aka* are more or less found in protected habitats far from very turbulent water. Rützler (1971) noticed that the main depth distribution of *Aka* from the Caribbean is between 10–70 m, below the direct influence of normal wave action. Steady water currents were measured and are probably important for feeding. *Aka* is sometimes found in protected shallower water environments (1–2 m water depth), e.g., *Aka coralliphaga* is often found in boulder-like corals which are bored by *Cliona* spp.

Within the turbulent zones, the most species of the genus *Cliona* occupies the ecological niche of *Aka*. *Cliona* is rarely observed in deeper water (*Cliona viridis*, *Leptoseris* reefs, 90 m), and within West Indies reefs *Cliona delitrix*, *C. agrica*, *C. langue*, and *C. schmidtii* is common at 20 m water depth. The main depth distribution of *Cliona* is between 0–10 m (Rützler 1973, 1974; Schwarz 1981). *Cliona* is also observed in cooler, temperate water.

Temperature seems also to be an important limiting factor of the Caribbean *Aka* communities. Within the northern Bermuda reefs *Aka* is not observed. From the Mediterranean, *Aka* is observed only in underwater caves, which are characterized by communities comparable with some Tethyan Cretaceous and modern Indopacific ones. These communities are primary Tethyan relicts (Reitner 1989). Perhaps *Aka* in *Petrobiona* is part of the primary Tethyan sponge community. This idea is supported by the existence of *Aka* as part of the Eocene *Spirastrella/Acanthochaetetes* community from the southern Pyrenees. *Aka* in *Petrobiona* is a probable Tethyan survivor and specially adapted to moderate temperate water.

Aka bores calcareous material, like *Cliona*. *Aka* produces the same type of boring chip as seen with *Cliona* and its boring method is comparable to *Cliona* (Pomponi 1980). The diameter of the etching chips of *Aka* varies from 14–40 μm , mean 30 μm and therefore comparable with the sponge chips of *Cliona* (Pomponi 1980). Similar ecological paleoenvironments of *Aka* are observed in all fossil *Aka* examples. *Aka* is also missing from high turbulent water facies zones. In this particular zone *Cliona* borings rarely exist (Reitner 1987a). *Aka* is common within the reef core, fore-reef, and mud mound facies which are always below normal wave base. In two reefs from the Late Albian Albeniz/Eguino platform in northern Spain, water depth of the coralgall reef core to fore-reef slopes was calculated as 30–100 m (Reitner 1987a) – the main distribution of *Aka*.

The Late Carnian *Aka* are part of the highly diverse coralline sponge community of the Cassian reefs. These sponge communities are normally located in mound structures of the deeper fore-reef. The platforms are constructed of algae and oolite shoals.

The bathymetric position of the Jurassic siliceous sponge mounds is still under discussion. The first studies on these build-ups mentioned a deeper water position based on the lack of true algae, and the presence of micritic sediments. Also the sedimentary megacycle of the Malm of southern Germany indicates a regressive sequence. On the top of sponge mounds, coral reefs were established during the Tithonian and demonstrate shallow marine water conditions. Based on "J. Walther's law" the sponge mounds must be situated in deeper waters (Fritz 1958; Gwinner 1962; Nitzopoulos 1974; Ziegler 1977). New studies on the diagenetic sequences of these mounds and bank facies indicate a contradictory bathymetric position within extremely shallow marine waters (intertidal). These conclusions are mainly based on marine vadose cements (Koch and Schorr 1986). Lang (1988) and Kott (1989) postulated a paleobathymetric position for the Oxfordian and Kimmeridgian sponge biostromes and mounds, based on sedimentological criteria, between normal wave base and storm wave base. All

these interpretations, however, indicate a restricted water movement: the optimal environment for *Aka*.

Of special importance is the boring activity of *Aka* in dead siliceous sponges which are often still in original life position. *Aka* and *Cliona* bore only in calcareous material; therefore, the siliceous skeletons of sponges must be altered into calcite before *Aka* starts excavating. Most of the siliceous sponges are surrounded by dark micritic, partially stromatolitic halos. This feature indicates a reduced sedimentation rate; the siliceous sponges are not totally covered by sediment during this stage. The micritic crusts are called "Kalkmumien" (Fritz 1958). These micritic covers are cemented very early before the siliceous spicules are dissolved (cf. Brachert et al. 1987; Lang and Steiger 1984). The micritic layers are probably bacterial crusts decomposing the sponge soft tissue. One characteristic of these bacteria crusts is the *synvivo* lithification outside their cell walls. The dissolution of the siliceous scleres occurred after this early diagenetic event. Then the organic axial filaments were also decomposed by bacteria. These processes produced high pH values which probably were responsible for dissolving the spicule cristobalite (Land 1976; Reitner 1986). The sclere molds were cemented rapidly by granular or single calcite crystals. After this diagenetic stage, *Aka* was able to bore inside the "siliceous" sponges. *Aka* is an important post mortem organism of siliceous sponge mounds. This diagenetic process is found in Jurassic as well as Cretaceous deeper water mud mound. *Aka* is therefore an excellent indicator for a very early submarine cementation and diagenesis.

The common *Aka* within the Middle Eocene reef rocks also indicate quiet water conditions of this particular biofacies. This biofacies is characterized by *Spirastrella* (*Acanthochaetetes*), a sponge which prefers dark and/or deeper water conditions.

Conclusions

1. The new Lower Carnian species *Aka cassianensis* is a dominantly encrusting sponge. Borings are only known from the holotype. Spicule shape and arrangement are similar to those in the modern genus *Aka* but the size is different.
2. Jurassic to Recent *Aka* are dominantly excavating sponges.
3. Two new species are described from the Jurassic and Lower Cretaceous, *Aka muelleri*, and *Aka minima*. *Aka muelleri* n.sp. is the most common species.
4. From Middle Eocene fore reef sediments of the southern Pyrenees a further new species is described (*Aka boltanaensis*).
5. Recent species of *Aka* differ in having much smaller oxeas (100–200 μm) in relation to fossil ones (300–2200 μm).
6. *Aka* prefers deeper, moderately agitated water conditions (20–100 m), as evidenced by modern occurrences and by facies analyses of fossil occurrences. The niches for boring sponges in shallower more agitated environ-

ments are preferred occupied by certain species of the hadromerid genus *Cliona*.

7. *Aka* is an excellent indicator for very early carbonate cementation and replacement of the siliceous spicules in calcite in fossil siliceous sponge mud mounds. *Aka* is an important post-mortem faunal element in these particular build-ups (Fig. 1).

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