

ICHTNOLOGICAL STUDY OF SHALLOW MARINE ENDOLITHIC SPONGES FROM THE ITALIAN COAST

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Riassunto. Spugne perforanti viventi, appartenenti a 8 specie dei generi *Siphonodictyon*, *Cliona* e *Clionosia*, sono state prelevate dal fondo marino calcareo delle coste della Puglia, per analizzarne le spicole e i modelli delle perforazioni praticate sul substrato.

Le perforazioni, esaminate ichnotassonomicamente, sono risultate corrispondenti a quelle dell'ichnogenere *Entobia* e sono state attribuite a 11 ichnospecie, di cui alcune nuove per la scienza (*Entobia gigantea*, *E. magna*, *E. parva*).

Abstract. Living boring sponges belonging to eight species of the genera *Siphonodictyon*, *Cliona* and *Clionosia*, were collected from the limestone seafloor of the Apulian coast. Samples were taken in zero to -20 m water depth. Spicule preparations from the sponges, and epoxy casts of the borings, facilitated a comparison of the animal and its work. The borings were analyzed ichnotaxonomically and attributed to 11 ichnospecies of *Entobia*. Direct correlation between biospecies and ichnospecies was not found in all cases.

Several ichnospecies are new, and some of these are named using Pleistocene material. The new ichnospecies are *Entobia gigantea*, *E. magna* and *E. parva*.

Introduction.

Borings of sponges are common in the Mesozoic and Cenozoic palaeontological record. As the work of animals, these structures are treated as trace fossils and mostly have been assigned to the ichnogenus *Entobia* Bronn, 1837. Many ichnospecies have been described on the basis of the morphology of the borings in fossil material (e.g., by Fischer, 1868 and Bromley & D'Alessandro, 1984).

Endolithic sponges are active bioeroders of carbonate substrates in marine environments today, and numerous biological species have been assigned in particular to genera of the family *Clionidae* on the basis of their spiculation and soft-part anatomy. Relatively little is known of the characteristics of borings of different species; only a few

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sponge taxonomists have mentioned these (Hancock, 1849, 1867; Volz, 1939; Rützler, 1974). Some palaeontologists have examined the borings of individual species (e.g., Bromley, 1970, 1978; de Groot, 1977; Ward & Risk, 1977) but a clear idea of morphological range within and among species is not available. Spicules (the body fossil) are generally not preserved in fossil material, and so the sole information available to the palaeontologist is the morphology of the boring. It is not known, however, to what extent trace fossil taxa (shapes of borings) are correlatable with biological species of sponges. For example, in what degree different species can excavate identical borings, or individual species can create different types of borings.

Methods and material.

Shallow water localities were examined along the coast of Puglia in order to find places where suitable substrates of limestone occur that were not excessively covered by epilithic encrustation. Four localities were chosen (Fig. 1): the harbour entrance of



Fig. 1 - Map showing the position of the four sampled localities.

Polignano; the shallow limestone platform at Cala Corvino, Monopoli; and the cliff-foot ramps 3 km north of Novaglie and at La Montagna Spaccata, north of Gallipoli. At these places, relatively compact, impermeable Mesozoic and Tertiary micrites are being bioeroded. Pleistocene calcarenite and recent red algal encrustation are generally too porous to produce successful casts.

Samples were collected from zero to -19 m by diver; deeper than this the sediment cover and algal encrustation become excessive. Both loose boulders as well as massive bedrock were sampled. Before collection, sponges were photographed *in situ*. Some sponges were discovered later, however, during processing in the laboratory. Samples were divided to provide material for spicule analysis and for casting the boring of the same sponge. The subsamples for borings were placed in hydrogen peroxide to remove

organic material, and cast in epoxy resin. Casts were coated in aluminium chloride for photography. Samples for spicules were dried. Sponge material was plucked from papillae, chambers and intercameral canals and placed in chromic sulphuric acid or hydrogen peroxide to remove organic material. The spicules so released were examined by SEM.

The borings as entobians.

The morphology of the sponge borings corresponds to the ichnogenus *Entobia* and, although they cannot be considered fossil (the trace-maker was alive when collected), the material may be classified in terms of *Entobia* ispp. Representatives of the following ichnospecies occur: *Entobia cateniformis*, *E. geometrica*, *E. laquea*, *E. megastoma*, *E. ovula*, and *E. volzi*. The morphologies of these forms correspond to the descriptions by Bromley & D'Alessandro (1984), although in slightly modified expression in some cases. Borings are also present that have not received formal designation as trace fossils. Three of these, *E. gigantea*, *E. magna* and *E. parva*, are named formally herein on the basis of fossil material whereas three others are named informally as entobians A, B and C, because fossil equivalents are not available (1).

Entobia gigantea isp. n.

Pl. 28, fig. 1; Pl. 32, fig. 5, 6; Text-fig. 2

Derivation of name. Latin, *Gigas, gigantis*: giant.

Type series. Holotype MGUH 19003 (Pl. 32, fig. 5); paratypes MGUH 19004 (Pl. 28, fig. 1); MGUH 19005 (Pl. 32, fig. 6).

Horizon and age. Sgourou Formation, Pleistocene.

Type locality. Ancient sea cliff behind the bay of Ladiko, Rhodes, Greece.

Collocation. Geological Museum, University of Copenhagen, Denmark.

Material. Several further specimens from the type locality.

Diagnosis. Large, coarsely camerate entobian coalescing in late ontogeny to produce a single, flat, rounded cavity. Chambers irregularly amoeboid in growth phase C (Bromley & D'Alessandro, 1984, pp. 232-233). Active surfaces of whole boring bear numerous long, much-branched apophyses, some cylindrical, some blade-shaped. Chamber roofs vermiculated by passage of innumerable blade-shaped apophyses. Wall ornament verrucose, ranging from coarse to fine in different individuals.

Description of fossil material. The material comprises only ontogenetic phases D and E. In phase E, a single giant chamber is developed; the holotype measures 83 x 82 x

(1) Abbreviations ichnogen. and ichnosp. are rendered as igen. and isp. respectively (see Bromley & D'Alessandro, 1987, p. 388).

23 mm. Larger individuals have been observed. In phase D the growing margins of the flat discoid cavity are lobed or amoeboid and comprise discrete chambers in partially fused state (Fig. 2).

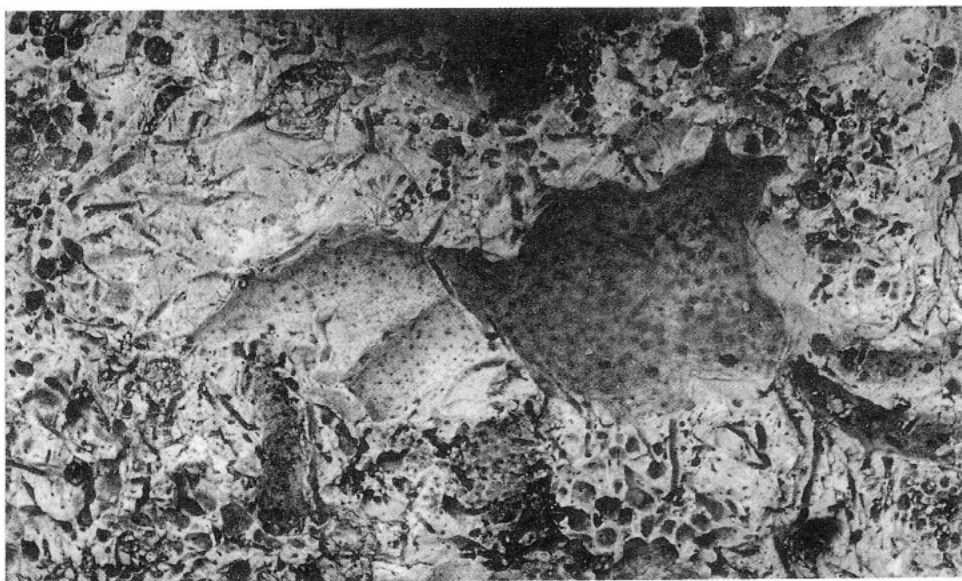


Fig. 2 - Field photograph of a Pliocene *Entobia gigantea* isp. n., in growth phase D, together with other entobians in the limestone basement at Vallone Impiso (see Bromley & D'Alessandro, 1987). Natural size.

The surface of the boring has a characteristic warty sculpture that varies considerably in degree of relief in different individuals (Pl. 28, fig. 1). Conical pits are abundant within this sculpture, and from there, apophyses extend as much as a centimetre into the substrate. Density of these apophyses varies. In the floor they are spaced about 1 mm apart and have a circular basal cross section. In parts of the roofs the apophyses are far more crowded and have a flattened cross section (Pl. 32, fig. 6). So close are the perforations as to give roof a vermiculated texture. At a smaller scale, the walls bear the chip microsculpture characteristic of sponge borings, but the individual chip scars are smaller than in most entobians. Owing to collapse of almost all roofs, apertures have not been observed.

Where two chambers, probably of different individuals, approach each other with growth, a thin partition of substrate is retained. Similarly, the earlier borings of other organisms in the same substrate are bored up to very closely, leaving them surrounded by a translucent pellicle of limestone suspended within the *E. gigantea* cavity.

Description of recent material. A recent boring, invariably occupied by *Siphonodictyon* sp. (Pl. 22), presents all the characteristic features of *E. gigantea*. Details of the apophyses and of phases A and B are available in addition and the growth history of the boring is more clearly discernible than in the fossil material (Fig. 3).

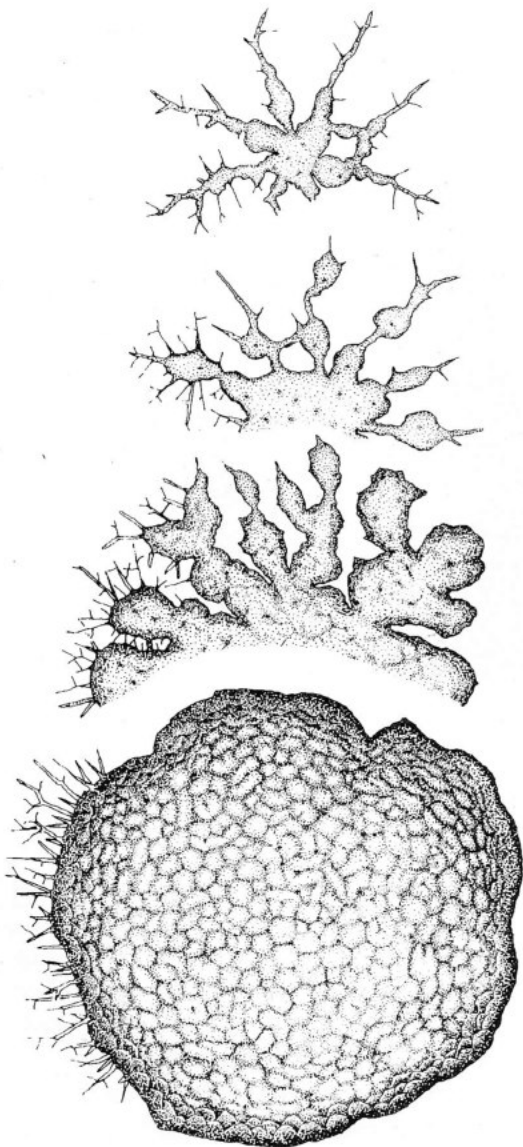


Fig. 3 - Diagrammatic sketches of the ontogeny of the boring of *Siphonodictyon* sp., based on many specimens. The borings are viewed as if lacking a roof. From top to bottom: phases A - B; phases A - C; fusion of chambers in phase D; and the final complete coalescence in phase E. Natural size.

Well developed apophyses are an essential feature of this boring and are present in all growth phases of the system. They resemble a thick carpet of long, bifurcating and anastomosing threads, which are larger and more numerous than in any other entobian. They may reach a length of well over 10 mm (Fig. 4). These apophyses are highly characteristic in their branching morphology and also in their tendency to fuse laterally to produce flat, blade-like structures (Pl. 32, fig. 7). Between these major apophyses, the wall bears many fine, short, generally unbranched minor apophyses. In places, exploratory canals may be generated by the fusion of several major apophyses.

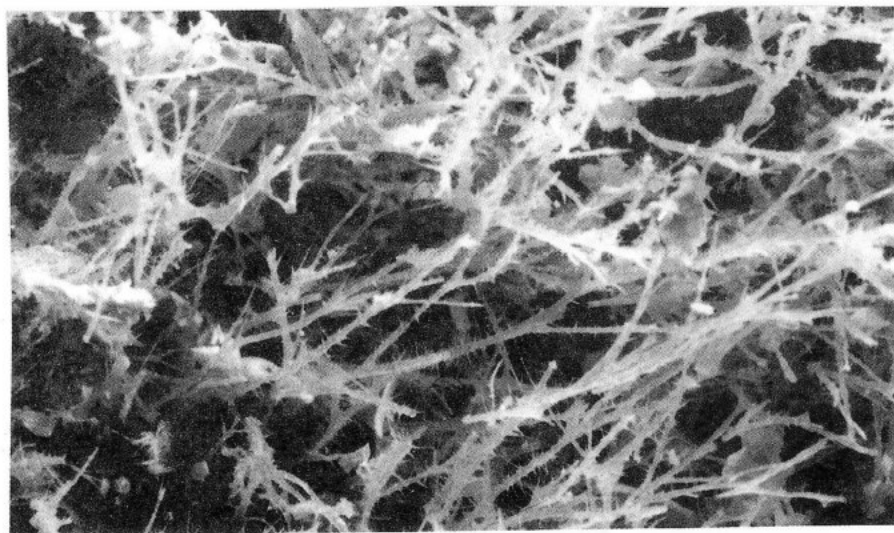


Fig. 4 - Epoxy cast of the boring of *Siphonodictyon* sp. The chamber is obscured by a forest of branching and anastomosing apophyses bearing slender side-threads. From Novaglie at -16 m. MGUH 19012; x 5.

Phase A appears to consist of long, often curved exploratory canals that extend 10 - 20 mm and support shorter needle-like side branches. Locally and at varying intervals, these exploratory threads swell to produce irregularly globular or elongated chambers in phase B. These may be far apart and connected by long, curving intercameral canals.

In phase C, these small chambers swell to centimetre size, and begin to coalesce. This fusion may be brought about either by the enlargement of the wide intercameral canals or by multiple fusion of the slender interconnecting apophyses. This results in irregularly ovoid to amoeboid bodies of complex shapes (Pl. 30, fig. 5; Pl. 32, fig. 3).

In phase D, further expansion causes still more fusion to produce irregular chambers several centimetres in diameter. These become flattened parallel with the substrate surface, as growth continues laterally but is reduced downwards. The lateral growth causes phase C chambers to develop around the central phase D bodies. Ultimately, the system is fused completely in phase E so as to comprise a single giant chamber. As

growth downward ceases, the warty wall ornament may become smoother, although the lateral margins always remain verrucose, and the roof vermiculate.

In gerontic individuals where lateral growth is slow, the outline becomes more rounded or entire (Pl. 30, fig. 3). Thus phases A to C are suppressed in the adult sponge and are only present in actively exploring stages.

The structure of the roof is weakened through the dense penetration by apophyses (Pl. 30, fig. 2; Pl. 32, fig. 2), but roofless borings are all empty: breakage of the roof exposes the sponge to predation. Apertures are difficult to observe. Large openings for exhalant papillae are sparse (Pl. 22, fig. 4). A few inhalant papillae were observed under water (Pl. 22, fig. 2), but were not recognized in the dry material. Normally, the *Siphonodictyon* sp. occupies a tier beneath a continuous layer of another boring sponge. Commonly this is *Cliona viridis* (Schmidt), through the dense system of which the large white papillae of the *Siphonodictyon* sp. must connect with the surface. In dry material the corresponding apertures are unrecognizable among those of *C. viridis*.

The boring of the white sponge avoids truncation of other borings within the limestone (Pl. 32, fig. 4). In rare cases, however, larger abandoned borings in the substrate are occupied by the sponge, as for example those of *Lithophaga lithophaga* (Linné). These become filled with sponge tissue and apophyses extend from the surface of the bivalve boring.

Observations. Pleydell & Jones (1988) erected the ichnogenus *Uniglobites* for single-chambered borings having otherwise the characteristics of *Entobia*. In the present case however, owing to the multicamerate earlier growth phases, we place the new ichnospecies in *Entobia*.

Occurrence. The trace fossil *E. gigantea* isp. n. is abundant in Pleistocene bioerosion of the Sgourou Formation at many localities on Rhodes, Greece. It has been observed also in Pliocene bioerosion sculptures underlying the Gravina Formation at Valone Impiso (Fig. 2) (Bromley & D'Alessandro, 1987).

Siphonodictyon sp. has been found only in shaded situations in water depths between -7.5 and -19 m along the eastern coast of Puglia.

***Entobia magna* isp. n.**

Pl. 27, fig. 1, 3, 4, 5; Text-fig. 5, 6

1987 *Entobia* isp. B. Bromley & D'Alessandro, p. 394, pl. 46, fig. 1.

Derivation of name. Latin, *Magnus*: large.

Type series. Holotype MGUH 19006 (Pl. 27, fig. 5); paratype MGUH 19007 (Pl. 27, fig. 3).

Horizon and age. Sgourou Formation, Pleistocene.

Type locality. The ancient sea cliff behind the bay of Ladiko, Rhodes, Greece.

Collocation. Geological Museum, University of Copenhagen, Denmark.

Material. Further specimens from the type locality.

Diagnosis. Strongly camerate entobian fusing in phase D to produce many large, flattened, interlocking, rounded to irregular chambers; these are connected by numerous intercameral canals, mostly slender. Chamber wall relatively smooth, giving rise to abundant thin unbranched apophyses. Apertures large and numerous. The system is dominated by phase D and may extend to cover large areas, but remains generally within a single tier.

Description of fossil material. Phase A comprises strong, branched exploratory canals, commonly palmate at branching points. In phase B, these threads swell at irregular distances as elongate or round chambers. Phase B rapidly proceeds to phase C, where chambers of varying shape and roundness enlarge to about 10 mm in diameter. These are interconnected with many canals. The surfaces are covered with numerous needle-like, slender apophyses (Pl. 27, fig. 1). In phase D, fusion of chambers produces large amoeboid cavities that in the holotype reach 38 x 28 x c.10 mm. There are smaller chambers between these, leaving little unoccupied substrate (Pl. 27, fig. 5). Partitions between chambers are narrow, crossed by numerous canals, but complete fusion of the

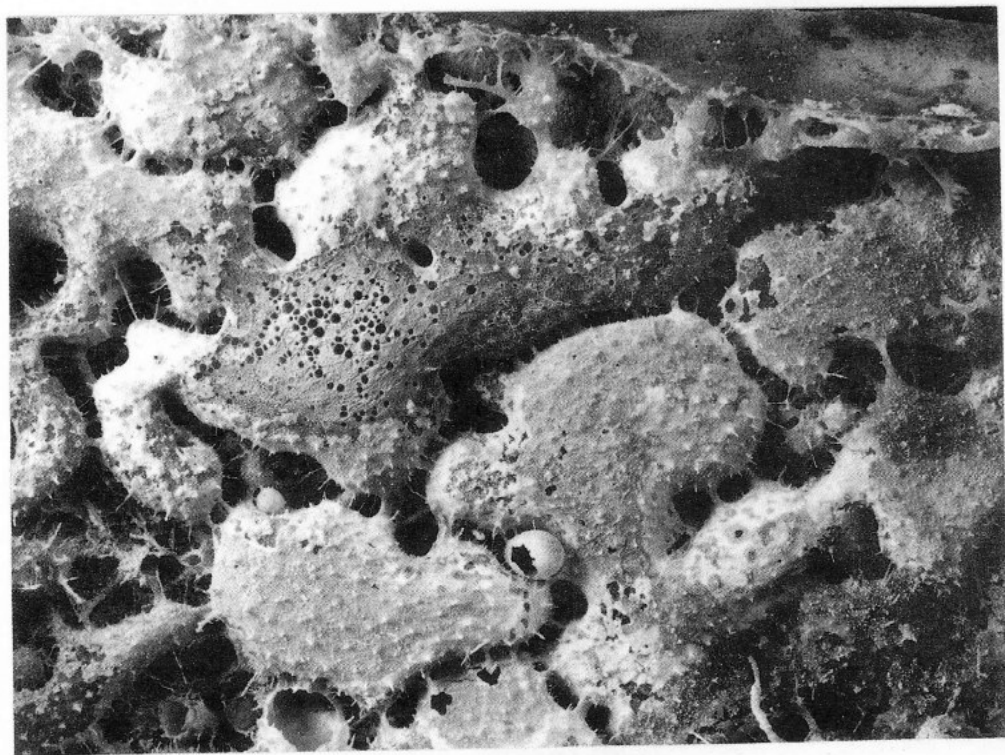


Fig. 5 - Epoxy cast of the boring of *Cliona rhodensis* (Rützler & Bromley), phase D, corresponding to *Entobia magna* isp. n. Note the large, interlocking chambers bearing numerous fine apophyses and numerous intercameral canals. From Polignano at -9 m. MGUH 19013; x 1.7.

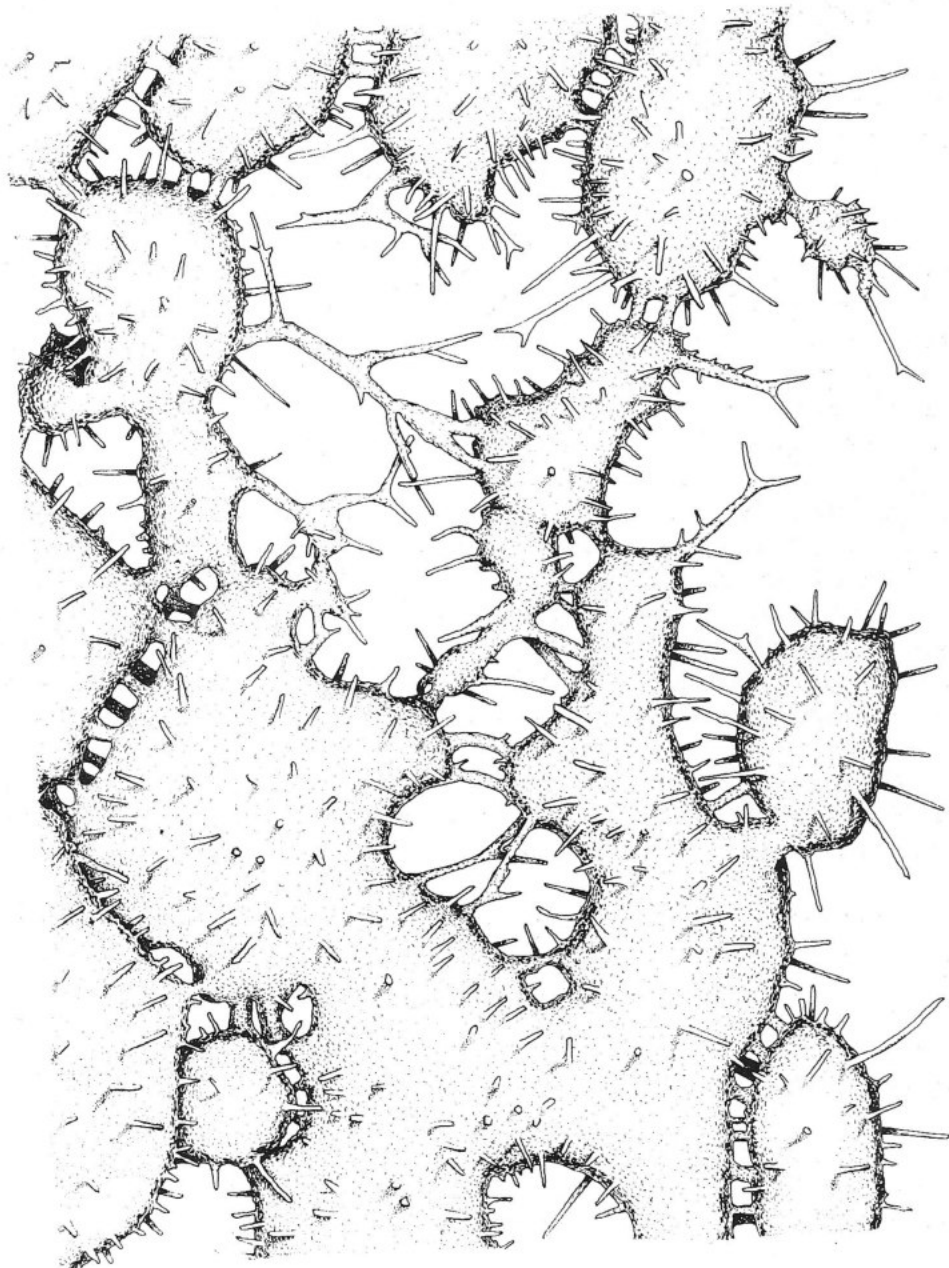


Fig. 6 - Camera lucida sketch of part of the boring of *Cliona rhodensis* (Rützler & Bromley) showing growth phases A to D. Seen from within the substrate; x 2.

whole system has not been seen. Compound chambers rarely exceed 40 mm in length.

The walls are relatively smooth (Pl. 27, fig. 4). Fine punctae represent bases of apophyses, and in some cases these are seated in small depressions. The entobian micro-sculpture of the boring surface is well developed. Apertures vary in size (Pl. 27, fig. 3); in phase D they are round and numerous and may reach 3 mm in diameter, but most are 1-2 mm. Fusion of neighbouring apertures is unusual.

Description of recent material. Recent borings corresponding to *E. magna* isp. n. are more complete than the fossil and allow a fuller description of the ontogenetic development and variation. In phase A (Pl. 27, fig. 2), exploratory canals branch and anastomose abundantly; they are powerfully developed and can reach several centimetres in length. Phase B develops as seen in the fossil material. Where growth is slow the small chambers remain scattered within a tangle of exploratory threads. In regions of more active growth they swell rapidly to produce a C-phase of rounded to irregular chambers.

In phase C, chambers become interconnected by several canals as they swell and approach each other. New canals are initiated by apophyses and exploratory threads.

Phase C is transient to the dominant D-phase, in which expansion and further partial fusion lead to a compact system of interlocking, large chambers separated by incomplete, thin wall partitions (Fig. 5, 6). Partial fusion of groups of chambers produces flattened, highly lobed compound cavities. Each original chamber of the C-phase possesses several apertures and the compound chambers of the D-phase therefore bear many.

The system normally develops only a single tier close beneath the surface; apertural canals are 1-3 mm long. A second tier develops only locally, where the substrate surface bends round a corner or becomes irregular.

Observations. Phases A, B and early C somewhat resemble *E. paradoxa* (Fischer). However, they are usually accompanied by *E. magna* phase D, so the two forms are unlikely to be confused. The paradoxoid phases of *E. magna* are much reduced.

E. magna remains rigorously camerate, in contrast to *E. gigantea*. These ichnospecies differ also in the smaller size of *E. magna* and the presence of the characteristic verrucose wall in *E. gigantea*.

Occurrence. As for *E. gigantea* isp. n. The red-orange sponge, *Cliona rhodensis* Rützler & Bromley, that produces its recent equivalent, occurs commonly in shallow waters of the Mediterranean (Rützler & Bromley, 1981).

Entobia megastoma (Fischer, 1868) and **E. cf. paradoxa** (Fischer, 1868)

Large networks of *E. megastoma* are common in the recent material (Pl. 27, fig. 6; Pl. 29, fig. 1). Morphology agrees well with the emended diagnosis of Bromley &

D'Alessandro (1984). In phase D the diameter of the gallery reaches 7 mm, and locally the maze fuses to produce large cavities representing phase E. Passage from phase A to E is smoother than suggested by the composite sketch in Bromley & D'Alessandro (1984, fig. 8). The full diameter is reached rapidly in phase C and remains more-or-less unchanged until the galleries coalesce in phase E.

Locally, two tiers may be developed, but normally the idiomorphic borings are emplaced within the substrate as a single tier 1 - 2 mm below the surface. In a few specimens, however, nodal points are unusually swollen to such a degree that ichnologically the system here is comparable to *E. cf. paradoxa* (Pl. 29, fig. 2). The size of these galleries is larger, however, than is normal for *E. paradoxa*, and intercameral divisions are very poorly defined. Clearly, these camerate portions must be regarded as variants of the *E. megastoma* systems.

Entobla parva isp. n.

Pl. 28, fig. 3, 4, 5; Pl. 29, fig. 3, 5, 6; Text-fig. 7

Derivation of name. Latin, *Parvus*: small.

Type series. Holotype MGUH 19008 (Pl. 29, fig. 6; Fig. 7); paratype MGUH 19009 (Pl. 28, fig. 5)

Limhamn Quarry, Malmö, Sweden, Upper Danian; paratypes MGUH 19010 and 19011 from type locality and horizon.

Horizon and age. Monte della Torre calcarenite, Upper Pliocene.

Type locality. Monte della Torre, San Giorgio Morgeto, Calabria, Italy.

Collocation. Geological Museum, University of Copenhagen, Denmark.

Material. Several specimens from the localities of the type series.

Diagnosis. Diminutive, camerate entobian comprising in phase D a compact boxwork of inflated chambers connected by enlarged intercameral canals. The distal chambers are characterized by a number of tapering, branching projections that give them an irregular or angular appearance. Phases A and B are extremely reduced, the exploratory threads very short; the system has an abruptly closed growth front. Wide canals opening by large apertures cross the chamber boxwork in all directions.

Description of fossil material. This entobian comprises dense, small-scale, camerate systems forming patches or bushes reaching over 10 mm or 20 - 30 chambers deep beneath the substrate surface. The growth front is abrupt and closed. The chamber networks are cut by larger canals 2 - 4 mm wide, orientated in all directions and interconnected with smaller canals (Pl. 28, fig. 5). Apertures are correspondingly large (Fig. 7). In coral skeleton the system is far smaller than in limestone (Pl. 29, fig. 6; Fig. 7), but the characteristics and scale of the chambers are the same. The chambers are inflated and possess bluntly tapering processes that give the cavities a somewhat irregular pillow

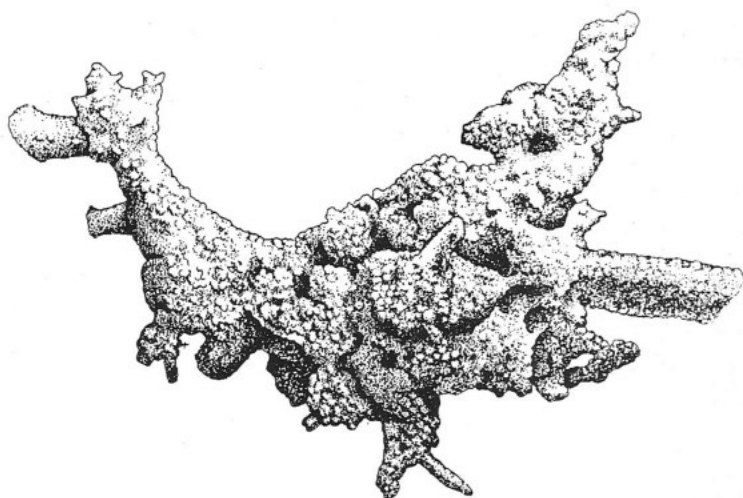


Fig. 7 - Holotype of *Entobia parva* sp. n. sketched from a different angle from Pl. 29, fig. 6, showing the large apertural canals; x 13.

shape. Some chambers are in direct contact, others connected by long canals. Exploratory canals consist of blunt outgrowths, and are extremely short. Fusion of such neighbouring projections creates intercameral canals.

Description of recent material. Phase A is composed of short, stout exploratory canals that bear a few narrower but similar, short side branches. Anastomosis also occurs and nodal points are non-palmate. Inflation of these canals to produce full-sized chambers is so rapid that phase B is reduced to a single ovoid cavity. Phase C is more-or-less non-existent, the system abruptly becoming densely crowded (Pl. 28, fig. 3, 4; Pl. 29, fig. 5).

Diameter of chambers is 0.3 - 0.5 mm on average, and fusion occurs rarely. The blunt processes on each chamber are either intercameral canals or elsewhere stunted exploratory threads (Pl. 29, fig. 5). Extremely fine, short apophyses radiate sparsely from the chambers. It seems that, within the compact boxwork, the intercameral connections become larger towards the substrate surface so that the chambers become a complex network of passages. The large canal apertures presumably are accompanied by numerous small openings for inhalant papillae, but these have not been observed. Echinoid grazing of the surface of the boring has rendered any such apertures indistinguishable. The microsculpture of the wall of the boring is finer than in most entobians.

Observations. In empty borings and casts of these, *E. parva* may easily be distinguished from *E. volzi* Bromley & D'Alessandro. Phase A is well developed in *E. volzi*, the exploratory canals being palmate at nodal points; the chambers in phase D are

rounded and coalesce in clusters. The tapering processes on the chambers are lacking in *E. volzi*. In cross section, however, the only visible difference between these two ichnospecies is one of scale: the constructional module of *E. parva* is half the size of that of *E. volzi*.

E. parva may be mistaken for small scale development of entobian A. The latter is nevertheless larger in chamber size, and the development of apophyses is characteristically different. A small-scale entobian preliminarily described as "J-form C-1" by Glaub (1988) from the Jurassic shows similar features to *E. parva*. The description was based on a single specimen, however, so we shall not attempt further comparison here.

Occurrence. Common in bathyal coral at the type locality (Upper Pliocene); a few pleistocenian examples from the circalittoral red coral at Pescoluse. A group of borings in the hardground beneath the base of the Upper Danian at Limhamn (Sweden). In the recent material two empty systems collected at -17 m depth at Novaglie.

Entobian A

Pl. 28, fig. 2; Pl. 31, fig. 1, 4, 5, 6

Description. System highly camerate, small in scale but extending over large areas. Short apophyses, widening at the base, are common over most of the system (Pl. 31, fig. 1, 6).

Phase A of young borings comprises long, thick, much-branched, contorted exploratory threads that extend several millimetres ahead of the system in actively growing areas. These threads may end in a minute aperture at the substrate surface. A few of the characteristic apophyses arise from these threads.

In phase B, the exploratory threads either swell in their entirety to produce exhalant canals, or locally as chambers. Rows of these may lie along longer threads at varying distances. The chambers are not spherical, but are irregularly nodular, somewhat angular. The number of apophyses increases and their wide bases enhance the impression of irregular angularity.

The chambers are fully developed in phase C (Pl. 31, fig. 4, 6), having a diameter of about 1 - 1.5 mm and may fuse locally, thereby increasing the diameter. Large canals leading towards exhalant apertures bear nodules or half chambers on their surfaces. Phase C may survive without further growth, even in systems of many tiers' thickness. In other individuals or regions of systems the phase passes rapidly to phase D.

Phase D dominates many systems and comprises crowded, subrounded chambers richly provided with short apophyses. The intercameral walls of substrate are reduced to extreme thinness, and other groups of chambers fuse to produce larger ones up to 3 mm wide. Thus two sizes of chamber, fused and unfused, occur together (Pl. 28, fig. 2; Pl. 31, fig. 5) but greater degrees of coalescence are not seen. At this phase, the exhalant

canals enlarge to 4 mm in diameter and cut into the surrounding chambers, thereby obtaining a mammillated surface.

In well-grown borings, the system extends many tiers into the substrate, to as much as 10 mm (about 10 chambers), and may extend laterally over many centimetres. At the inward margin of these systems a closed front is produced, few or no exploratory threads extending further into the substrate, and phases A and B here are suppressed.

The large canals open onto the surface by apertures of equivalent size. Smaller apertures also occur, as well as extra large ones formed by fusion of neighbouring openings.

Details of the morphology commonly vary considerably in different parts of the system in regard to chamber-size (scale), closeness of crowding, and development of apophyses.

Distinction from other entobians. In parts of some systems, networks of the B and C phases can have some resemblance to *E. laquea* Bromley & D'Alessandro, while small-scale, compact systems converge on *E. volzi* Bromley & D'Alessandro morphology. Despite these similarities, the entobian A remains distinctive. The chambers in phases B and C have an angular form, exaggerated by the short, stout apophyses, that is not seen in either *E. laquea* or *E. volzi*. Furthermore, *E. laquea* has a more open network than the entobian A, while the chambers in any one system of *E. volzi* are more constant in diameter than in the present boring.

The enlarging canals of phases C and D resemble somewhat *E. retiformis* (Stephenson) and *E. mammillata* Bromley & D'Alessandro respectively, but the chamber configuration of the remainder of the system is entirely different. The tubercles on the walls of *E. mammillata* must not be confused with the chambers of entobian A, although morphologically they resemble each other closely. Naturally, therefore, the special, narrow intercameral constrictions characteristic of *E. mammillata* are never seen in entobian A. The chamber fusion seen in entobian A is not imitated by the tubercular surface of *E. mammillata*.

Occurrence. Abundant at all localities and water depths investigated. Considering the ubiquity of this boring today in shallow water, it is surprising that it has not been observed in Pleistocene material. *E. ovula* form A (Bromley & D'Alessandro, 1984) is the only form that approaches the morphology of entobian A, but its individuals are extremely small and rare.

Entobian B

Pl. 31, fig. 2, 3

The borings of this type proved to be difficult to cast, and our material is inadequate for a detailed description.

A small-scale, camerate entobian having reduced A and B phases. In phase A, very short, branched exploratory threads extend from the swelling chambers of phase B. As inflation increases to produce phase C, the chambers already fuse in part to produce clusters of small soap-bubble-like chambers (Pl. 31, fig. 2). Thus the intercameral junctions are broad and no canal is seen. In phase D, the chambers apparently begin to coalesce at the substrate surface (Pl. 31, fig. 3). There is a general resemblance here to phase D of entobian A. The lower remains of the chambers become crowded and somewhat polygonal in shape. Further development of the sponge is as an epilithic crust (Pl. 26, fig. 1, 3) and seems to entail no change to the boring.

Occurrence. Abundant in shallow water of the Apulian coast but not recognized in fossil material.

Entobian C

Pl. 29, fig. 4

A single example of a large sponge boring was collected that shows morphological features and size similar to *E. magna* isp. n. In some details, however, it is distinctive. Entobian C has greater inflation of the compound chambers; few, large intercameral canals; and a considerable reduction of the apophyses.

The system is camerate, the chambers inflated and entirely lacking apophyses on the under surface. Phase A closely resembles that of *E. magna*. The exploratory threads swell as elongated to rounded chambers in phase B and these in turn fuse in groups to produce the large, compound chambers of phase C. Thick, contorted intercameral canals connect these large chambers and probably further coalescence takes place. There is a tendency to form two tiers but later fusion has disturbed this organisation. Apertures appear to be similar to those of *E. geometrica*.

Occurrence. A single example from Polignano, -1.8 m, in a small boulder.

The trace makers

Examination of the sponges inhabiting the borings has been limited to the gross morphology, colour and spiculation. The following species of sponge were identified. The borings and species are interrelated in Table 1.

Cliona celata Grant (Pl. 25).

The spiculation of this species is much reduced, the microscleres entirely lacking. Simplified spiculation of this sort, comprising only tylostyles, was found in sponges occupying three entobians. Tylostyles in sponges from *E. geometrica* have the size and proportion typical of *C. celata*. Entobian C contained a sponge that yielded somewhat stouter tylostyles than those in *E. geometrica*, but referable to the same species (Pl. 25,

fig. 2). Sponges in *E. megastoma*, and chambered variants of these, yielded more slender tylostyles (Pl. 25, fig. 1, 3).

The sponges in the three entobians are all similar in appearance, being large and bright yellow coloured in life.

C. celata in the North Sea has been reported to produce *E. megastoma* (Bromley, 1970). However, de Groot (1977) found it associated with *E. geometrica* in limestone and *E. megastoma* (locally showing a tendency to poor cameration) in shell substrates. In the present study it is interesting to find it in both ichnotaxa in limestone.

Cliona nigricans (Schmidt) (Pl. 23, fig. 4; Pl. 24, fig. 2; Pl. 26, fig. 1, 3).

Extensive areas of substrate are covered by an abundant greenish brown sponge having a rubbery consistency. Large exhalant papillae are conspicuous on its surface (Pl. 26, fig. 3). This is the beta-stage of a boring sponge that Rützler (1973) considered to belong to *C. nigricans*. The examples we saw ranged to a much larger overall size than those reported by Rützler (1973), however, reaching over 500 cm². Beneath and peripheral to the crust, the borings comprise entobian B.

Cliona rhodensis Rützler & Bromley (Pl. 23, fig. 2; Pl. 26, fig. 4).

This bright red or orange-red sponge is particularly common at the studied localities. As noted by Rützler & Bromley (1981), it produces large camerate borings. These have exclusively the morphology of *E. magna*, although passing through a phase B that superficially resembles *E. paradoxa*.

Cliona schmidti (Ridley) (Pl. 23, fig. 1).

This vividly coloured vermilion sponge does not grow to any great size. Normally it covers less than 10 cm² of substrate. The boring is camerate and inflated, in some individuals resembling entobian A, but more generally producing *E. ovula* (Pl. 31, fig. 1; Pl. 32, fig. 1).

Cliona vastifica Hancock (Pl. 24, fig. 1, 3, 4).

The orange sponge has small papillae and is common in our material. The small scale boring may cover extensive areas reaching over 100 cm². The sponge produces borings of several types, having been found in systems of *E. cateniformis* (Fig. 8), *E. ovula* (Pl. 31, fig. 6; Pl. 33, fig. 1, 3) and *E. laquea* (Pl. 33, fig. 5). Some of its borings show an incomplete distinction between the morphologies of *E. laquea* and *E. ovula* (Pl. 33, fig. 2, 4).

Cliona vermifera Hancock (Pl. 23, fig. 5).

This species appears to be relatively uncommon in the area studied. We obtained a single specimen in *E. ovula*. De Groot (1977) reported the species in *E. cateniformis*. Thus the overlap with the borings of *C. vastifica* is almost complete.

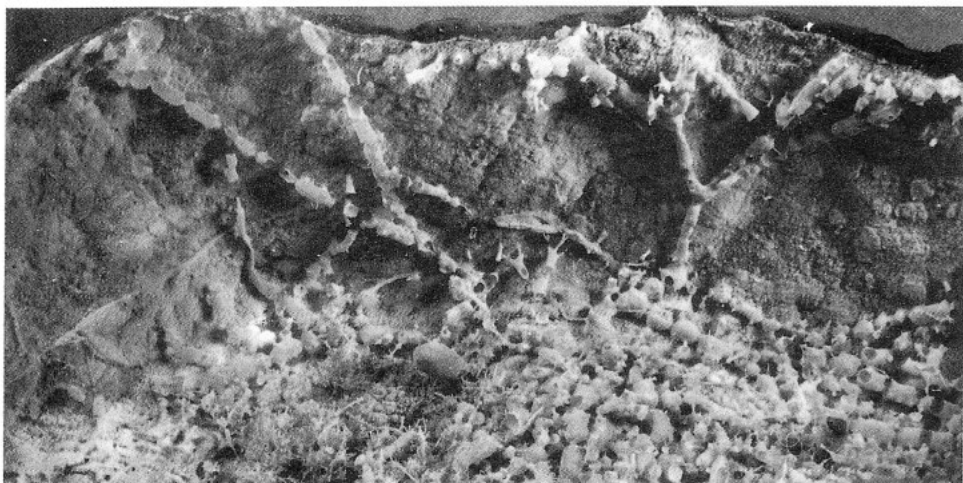


Fig. 8 - Epoxy cast of the boring of *Cliona vastifica* Hancock, corresponding to *Entobia cateniformis* Bromley & D'Alessandro. From Polignano at - 4 m. MGUH 19014; x 2.

Cliona viridis (Schmidt) (Pl. 23, fig. 3; Pl. 26, fig. 2).

The borings of this extremely abundant sponge are distinctive but variable. Generally they are entobian A, but local variation may approach *E. laquea* and *E. volzi*. De Groot (1977, fig. 21, 22) also illustrated entobian A as the work of *C. viridis*.

Cliothosa hancocki (Topsent).

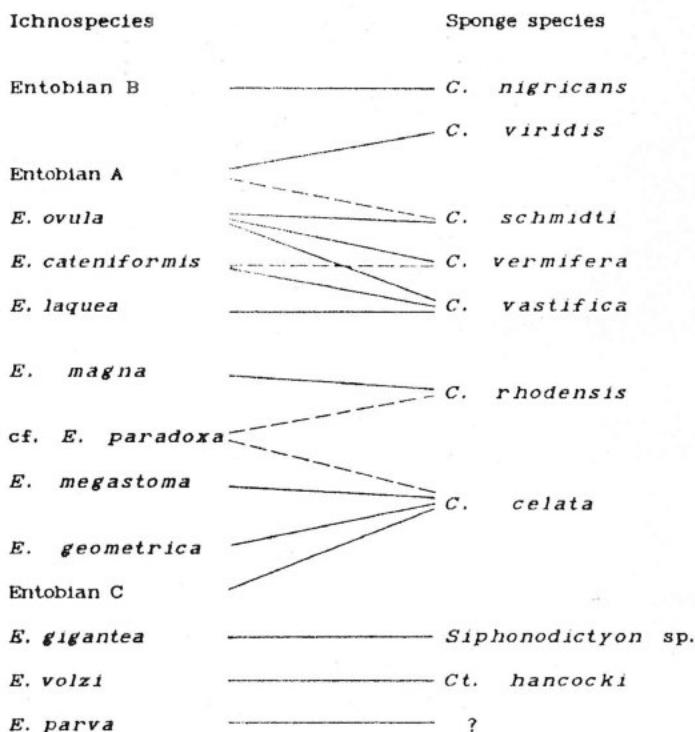
This abundant sponge produces an unmistakable boring, as indicated by Volz (1939). The morphology is exclusively that of *E. volzi* (Pl. 30, fig. 1, 4) and little variation has been recorded.

Siphonodictyon sp. (Pl. 22).

A large whitish boring sponge was found at two localities: Polignano and Novaglie from -7.5 to - 19 m depth. Spicules indicate this to be a species of *Siphonodictyon*. Few, well separated, large oscula protrude from the substrate as stiff but brittle chimneys about 10 mm high (Pl. 22, fig. 4). Ostia appear to be distributed on separate, large but inconspicuous papillae (Pl. 22, fig. 2). The choanosome is soft and mucous and fills the boring. This species exclusively constructs *E. gigantea*. Species of this genus have been reported from other parts of the world (not in the Mediterranean Sea) as producing large single cavities of this type (Rützler, 1971).

Unidentified sponge.

The diminutive entobian *E. parva* isp. n. has not yielded us any spicules. The largest specimen was empty on collection, and others were not recognized until epoxy cast processing had removed any organic contents. Collected at Novaglie in -15 m.



Tab. 1 - Relationship between ichnotaxa and zootaxa of the boring sponges.

Conclusions.

The present work supports the general discrepancy between the biological and trace fossil taxonomies. This is somewhat surprising, since borings are a result of growth behaviour and as such are conceptually closer to biological species than are trace fossils expressing movement.

Table 1 lists the three genera and nine species (plus one unidentified) of sponge that were collected, and the 13 entobian systems represented by their borings. In the case of only 4 ichnospecies is there a direct relationship with a sponge species: entobian B is produced by *Cliona nigricans*, *Entobia gigantea* by *Siphonodictyon* sp., *E. magna* by *C. rhodensis*, and *E. volzi* by *Cliothosa hancocki*. Entobian A is almost restricted to *Cliona viridis*, although similar borings can be produced by *C. schmidti*. The relation-

ship between sponge species and the diminutive *E. parva* is unknown.

There is a complicated interrelationship with the remaining ichnotaxa and sponge species. *C. vastifica* produces *E. ovula*, *E. cateniformis* and *E. laquea*, but *E. ovula* also is constructed by *C. schmidti* and *C. vermifera* which latter produces *E. cateniformis* as well. *C. celata* also excavates at least three radically different boring morphologies: *E. geometrica*, *E. megastoma* and entobian *C.*

Reasons for this are obscure. The integrity of the sponge taxa might be questioned. This is especially likely for *C. celata*, the simplified spiculation of which may conceal several morphologically convergent species. *E. geometrica* in particular is an unmistakable boring having extremely constant morphology. It contrasts strongly with entobian *C.*, yet the two are found in the closest juxtaposition in the same small boulder (Pl. 29, fig. 4). This is not the case for the three ichnospecies produced by *C. vastifica*, which share many features and may be difficult to distinguish, and thus more easily might be considered behavioural variants of the same species under the influence of minor environmental differences. Again, *E. laquea* and *E. ovula* occurring in the same pebble both contained *C. vastifica*.

Thus, while the entobian ichnospecies remain distinctive and potentially valuable in environmental interpretation, they cannot be used directly to indicate biological diversity of organisms that are not bodily preserved.

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PLATE 22

Siphonodictyon sp.

- Fig. 1, 3 - Oxeas, the only type of spicule present, from a specimen from Novaglie, -18 m. 1) x 390; 3) x 540.
- Fig. 2, 4 - Underwater photographs of a sponge at Polignano, -9 m. Fig. 2 shows a group of "hairy" inhalant papillae and fig. 4 a typical, large osculum; x 2.

PLATE 23

Spirasters from different species of clionid sponges; x 2000.

- Fig. 1 - *Cliona schmidti* (Ridley) from La Montagna Spaccata, -8 m.
- Fig. 2 - *Cliona rhodensis* Rützler & Bromley from Cala Corvino, -4 m.
- Fig. 3 - *Cliona viridis* (Schmidt) from Polignano, -4 m.
- Fig. 4 - *Cliona nigricans* (Schmidt) from Cala Corvino, -4 m.
- Fig. 5 - *Cliona vermifera* Hancock from the same pebble as fig. 3.

PLATE 24

Spicules of *Cliona vastifica* Hancock and *Cliona nigricans* (Schmidt).

- Fig. 1 - Tylostyles and oxeas of *Cliona vastifica* from Polignano, -5 m; x 290.
 Fig. 2 - Tylostyles and spirasters of *Cliona nigricans* from Cala Corvino, -4 m. Same specimen as Pl. 23, fig. 4; x 240.
 Fig. 3 - Microrhabd of *Cliona vastifica* from Polignano, -9 m; x 6400.
 Fig. 4 - Microspined oxeas and microrhabds of *Cliona vastifica* from Polignano, -9 m; x 790.

PLATE 25

Spicules of sponges referred to *Cliona celata* Grant.

- Fig. 1 - Tylostyles from a boring corresponding to a "paradoxoid" *Entobia megastoma* (Fischer) (see Pl. 29, fig. 2), from Polignano at -4 m; x 200.
 Fig. 2 - Tylostyles from the globose boring named entobian C, shown in Pl. 29, fig. 4, from Polignano at -2 m; x 200.
 Fig. 3 - Tylostyles from a boring corresponding to *Entobia megastoma* (Fischer) (see Pl. 29, fig. 1) from Polignano at -5 m; x 240.
 Fig. 4 - Subterminal head of a tylostyle from the same boring as fig. 3; x 5600.

PLATE 26

Underwater photographs of bioeroding sponges as they appear at the substrate surface.

- Fig. 1 - *Cliona nigricans* (Schmidt). Endolithic juvenile phase that is only just beginning to extend over the surface of the substrate. Several porous inhalant regions are visible and some open oscula. Cala Corvino at -4 m; x 0.5.
 Fig. 2 - *Cliona viridis* (Schmidt) at La Montagna Spaccata in -8 m. Many porous, irregular inhalant papillae and a few open oscula are seen; x 1.
 Fig. 3 - *Cliona nigricans* (Schmidt) in its mature development at La Montagna Spaccata in -8 m. Note the two large oscula and the porous patches on the rubbery surface; x 1.
 Fig. 4 - *Cliona rhodensis* Rützler & Bromley at Novaglie -8 m. The gnawing by echinoids on the surrounding limestone surface has produced a characteristic sculpture corresponding to the trace fossil *Gnathichnus pentax* Bromley; x 1.

PLATE 27

- Fig. 1-5 - *Entobia magna* isp. n. and its equivalent, the boring of *Cliona rhodensis* Rützler & Bromley.
 Fig. 1 - Epoxy cast of a rather small-scale *Entobia magna* isp. n. from the Pleistocene of Vallone Impiso in a limestone boulder. Note in the lower right corner a small *Entobia mammillata* Bromley & D'Allesandro. MGUH 19015; x 2.
 Fig. 2 - Epoxy cast of a boring of *Cliona rhodensis* Rützler & Bromley, phases A to C, from Polignano at -9 m. MGUH 19016; x 1.5.
 Fig. 3 - *Entobia magna* isp. n. Paratype, in limestone showing large apertures of varying size from the Pleistocene of Ladiko, Rhodes. MGUH 19007; x 1.5.
 Fig. 4 - *Entobia magna* isp. n. showing large, fused chambers and rather smooth walls containing fine punctae, the bases of apophyses. Pleistocene of Ladiko, Rhodes. MGUH 19003; nat. size.
 Fig. 5 - *Entobia magna* isp. n. Holotype, a detail. Note the numerous intercameral canals. Sgourou Formation, Pleistocene. Bay of Ladiko, Rhodes. MGUH 19006; x 1.4.
 Fig. 6 - Epoxy cast of a boring of *Cliona celata* Grant corresponding to the initial phases of *Entobia megastoma* (Fischer); x 2.

PLATE 28

- Fig. 1 - *Entobia gigantea* isp. n. Paratype, showing the variation from individual to individual in the warty sculpture and conical pits of the wall. Sgourou Formation, Pleistocene. Bay of Ladiko, Rhodes. MGUH 19005; x 3.5.
The chamber having smooth, punctate sculpture at the lower left is *Entobia magna* isp. n.
- Fig. 2 - Epoxy cast of the boring of *Cliona viridis* (Schmidt) representing an entobian A system in growth phase D. Fused and unfused chambers coexist side by side. From Polignano at -4 m. MGUH 19018; x 4.
- Fig. 3 - *Entobia parva* isp. n. in growth phase D, showing the abrupt, closed growth front and minute scale of the boring. Sawn section of empty boring, from Novaglie at -17 m. MGUH 19019; x 2.
- Fig. 4 - Epoxy cast of *Entobia parva* isp. n., the counterpart of the specimen shown in fig. 3. MGUH 19020; x 2.
- Fig. 5 - *Entobia parva* isp. n. Paratype showing two large canals cutting through the chamber network. Upper Danian limestone from Limhamn Quarry, Malmö, Sweden. MGUH 19009; x 3.

PLATE 29

- Fig. 1 - Epoxy cast of an *Entobia megastoma* (Fischer) that was bored by *Cliona celata* Grant (see Pl. 25, fig. 3). From Polignano at -5 m. MGUH 19021; x 1.5.
- Fig. 2 - Epoxy cast of an *Entobia megastoma* (Fischer) that was bored by *Cliona celata* Grant (see Pl. 25, fig. 1). The system shows a tendency to cameration and so is somewhat reminiscent of *Entobia paradoxa* (Fischer). From Polignano at -5 m. MGUH 19022; x 2.
- Fig. 3 - Epoxy cast of the tiny system of *Entobia parva* isp. n. nestled in amongst the relatively enormous chambers of *Entobia magna* isp. n. MGUH 19023; x 4.
- Fig. 4 - Epoxy cast of entobian C, produced by a sponge apparently referable to *Cliona celata* Grant. Its spicules are shown in Pl. 25, fig. 2. The boring to the left has the form of *Entobia geometrica* Bromley & D'Alessandro and that to the right has the form of *Entobia laquea* Bromley & D'Alessandro. From Polignano at -2 m. MGUH 19024; x 1.
- Fig. 5 - Epoxy cast of *Entobia parva* isp. n., a detail of Pl. 28, fig. 4; x 5.
- Fig. 6 - *Entobia parva* isp. n. Holotype. A natural cast in the skeleton of the coral *Lophelia pertusa* (see Text-fig. 7). Monte della Torre calcarenite, Upper Pliocene. San Giorgio Morgeto, Calabria. MGUH 19008; x 6.5.

PLATE 30

Borings of *Siphonodictyon* sp. and *Cliothosa hancocki* (Topsent).

- Fig. 1 - Epoxy cast of the boring of *Cliothosa hancocki* (Topsent) corresponding to *Entobia volzi* Bromley & D'Alessandro, showing ontogenetic phases B to D. From Polignano at -1.5 m. MGUH 19025; x 1.
- Fig. 2 - Detail of the roof sculpture of the boring of *Siphonodictyon* sp. Compare with the fossil equivalent, *Entobia gigantea* isp. n., Pl. 28, fig. 1. From Novaglie at -15 m. MGUH 19026; x 8.
- Fig. 3 - Floor of the boring of a large individual of *Siphonodictyon* sp. from Novaglie at -18 m. MGUH 19027; x 1.
- Fig. 4 - A detail from the *Cliothosa hancocki* (Topsent) boring shown in fig. 1. Note the well developed exploratory canals and a large exhalant canal (left); x 1.7.
- Fig. 5 - Epoxy cast of the lobed edge (phase D) of a large boring of *Siphonodictyon* sp. denuded of its long apophyses. From Novaglie at -18 m. MGUH 19028; x 1.5.

PLATE 31

- Fig. 1 - Epoxy cast of initial phases of entobian A produced by the work of *Cliona viridis* (Schmidt). Note the characteristic short, spiky apophyses and exploratory canals. At the lower left there is a fragment of a boring corresponding to *Entobia ovula* Bromley & D'Alessandro; to judge from the colour of the boring sponge that produced this, it is presumably the work of *Cliona schmidti* (Ridley). From Novaglie at -15 m. MGUH 19029; x 4.
- Fig. 2 - Epoxy cast of entobian B, produced by *Cliona nigricans* (Schmidt). Note the absence of intercameral canals. Chambers fuse increasingly toward the right, the surface of the substrate, where the sponge emerged as an epilithic "rubber mat" covering the limestone (see Pl. 26, fig. 3). From Cala Corvino at -4 m. MGUH 19030; x 6.
- Fig. 3 - Same individual as fig. 2, showing the coalescence of chambers in phase D at the substrate surface; x 6.
- Fig. 4 - Epoxy cast of entobian A in phases C (upper right) and D (centre and left). From Polignano at -9 m. MGUH 19031; x 2.
- Fig. 5 - Epoxy cast of entobian A, the boring of *Cliona viridis* (Schmidt) (spicules of this individual are shown in Pl. 23, fig. 3). At the top, the cross section shows how little substrate is retained as partitions between chambers. From Polignano at -5 m. MGUH 19032; x 2.
- Fig. 6 - Epoxy cast showing the contact zone between the borings of *Cliona viridis* (Schmidt) (entobian A) and of *C. vastifica* Hancock, equivalent to *Entobia ovula* Bromley & D'Alessandro (right). Same pebble as fig. 5; x 3.

PLATE 32

- Fig. 1 - Epoxy cast of the boring of *Cliona schmidti* (Ridley) seen in section, corresponding to *Entobia ovula* Bromley & D'Alessandro. From Novaglie at -15 m. MGUH 19033; x 3.5.
- Fig. 2 - Epoxy cast of the short, bladed apophyses characteristic of the roof of borings of *Siphonodictyon* sp., compare Pl. 30, fig. 2. From Novaglie at -16 m. MGUH 19034; x 8.
- Fig. 3 - Epoxy cast of the boring of *Siphonodictyon* sp., showing growth phases B and C, denuded of its apophyses. From Novaglie at -18 m. MGUH 19035; x 1.5.
- Fig. 4 - Boring of *Siphonodictyon* sp. which has grown around earlier borings in the substrate. These earlier borings are now suspended within the lumen of the giant chamber, separated from it by a pellicle of remnant limestone. The suspended borings visible here resemble *Entobia laquea* Bromley & D'Alessandro (behind) and *Caulostrepsis* isp. (broken off in the foreground). From Novaglie at -15 m. MGUH 19027; x 2.
- Fig. 5 - *Entobia gigantea* isp. n. Holotype. Sgourou Formation, Pleistocene. Bay of Ladiko, Rhodes. MGUH 19003; x 0.8.
The chambers at the bottom centre and high right belong to *Entobia magna* isp. n.
- Fig. 6 - *Entobia gigantea* isp. n. Paratype. Detail of the roof showing numerous blade-like apophyses (cf. Fig. 2 and Pl. 30, fig. 2). Sgourou Formation, Pleistocene. Bay of Ladiko, Rhodes. MGUH 19005; x 8.
- Fig. 7 - The lobed edge of an epoxy cast of a *Siphonodictyon* sp. boring. The dense development of apophyses has been removed from the nearer surface to reveal the morphology of the boring. From Novaglie at -15 m. MGUH 19036; x 2.7.

PLATE 33

- Fig. 1, 5 - Epoxy casts of borings that have yielded spicules of *Cliona vastifica* Hancock; see also Text-fig. 4.
- Fig. 1 - *Entobia ovula* Bromley & D'Alessandro from Polignano at -4 m. MGUH 19037; x 2.
- Fig. 2 - An entobian showing chamber fusion in the manner of *Entobia laquea* Bromley & D'Alessandro but chamber shape like *Entobia ovula* Bromley & D'Alessandro. Spicules are shown in Pl. 24, fig. 1, 4. From Polignano at -4 m. MGUH 19038; x 2.
- Fig. 3 - *Entobia ovula* Bromley & D'Alessandro from Polignano at -5 m. MGUH 19039; x 3.

- Fig. 4 - A boring showing features of both *Entobia laquea* Bromley & D'Alessandro and *Entobia ovula* Bromley & D'Alessandro from Polignano at -9 m. Spicule from this boring is shown in Pl. 24, fig. 3. MGUH 19040; x 2.5.
- Fig. 5 - A boring showing typical *Entobia laquea* Bromley & D'Alessandro morphology from Polignano at -5 m. MGUH 19041; x 1.8.
- Fig. 6 - A boring produced by *Cliona celata* Grant having *Entobia geometrica* Bromley & D'Alessandro morphology. Cala Corvino. MGUH 19042; x 1.5.

