Riv. It. Paleont. Strat.	v. 90	n. 2	pp. 227–296	tav. 16–29	Ottobre 1984

THE ICHNOGENUS *ENTOBIA* FROM THE MIOCENE, PLIOCENE AND PLEISTOCENE OF SOUTHERN ITALY

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Key–words: Trace fossils, Taxonomy, *Entobia*, Sponge boring, Miocene–Pleistocene, Puglia–Italy.

Riassunto. La tassonomia di *Entobia* Bronn, 1837 è stata riesaminata sulla base di un ricco materiale raccolto nel territorio pugliese, in differenti formazioni di età comprese fra il Miocene superiore e il Pleistocene inferiore. In questo ichnogenere sono raggruppate strutture di bioerosione, che nell'insieme possono essere attribuite all'attività di Spugne perforanti; la revisione di 23 ichnotaxa finora istituiti ha portato alla conclusione che solo 6 possono essere considerati validi. Nel materiale italiano sono state riconosciute *Entobia megastoma* (Fischer) e *E. paradoxa* (Fischer); inoltre sono state istituite le seguenti nuove ichnospecie: *E. cateniformis, E. geometrica, E. laquea, E. mammillata, E. ovula, E. volzi.*

Abstract. The taxonomy of the ichnogenus *Entobia* Bronn, 1837 is investigated on the basis of Miocene, Pliocene and Pleistocene material from localities in Puglia (Italy). The ichnospecies of *Entobia* generally may be ascribed to the work of boring sponges; a survey of the twenty–three ichnospecies hitherto erected indicates that only six of these may be regarded as valid. Of these, *Entobia megastoma* (Fischer) and *E. paradoxa* (Fischer) occur in the Italian material. In addition to these, six new ichnospecies are erected: *E. cateniformis, E. geometrica, E. laquea, E. mammillata, E. ovula, E. volzi.*

Introduction.

Tertiary and Quaternary basal conglomerates in transgressive sequences generally show evidence of active bioerosional processes in the form of hard substrate trace fossils. This is the case, for example, for the *Calcarenite di Gravina.* Both the transgressed Mesozoic limestone pavement, and boulders derived from this, are riddled with borings. Mollusc shells within the *Calcarenite di Gravina* have likewise served as substrates for endolithic organisms.

Part of this trace fossil assemblage has been treated in a previous paper (Bromley & D'Alessandro, 1983), namely the ichnogenera *Caulostrepsis* and *Maeandropolydora.* In the present study, this treatment is extended to cover the ichnogenus *Entobia*, and in order to give this complex taxon more complete

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With grants from the Italian C.N.R., from the Ministero della Pubblica Istruzione and from the University of Bari.

treatment, material has been included from Miocene and Pliocene formations of the Apulian area (Fig. 1).

The ages of the respective localities are given in Table 1 on the basis of previous literature, together with a code by which each sampled horizon is referred to in the text. The age of the *Calcarenite di Gravina* at La Murgetta Grande, however, requires some further comment. Iannone and Pieri (1979, 1980a) dated the formation here as Santernian to Emilian (Lower Pleistocene), owing to the presence of *Arctica islandica* and *Hyalinea balthica.* However, we believe the basal deposits of the formation here to be older on the basis of the abun-

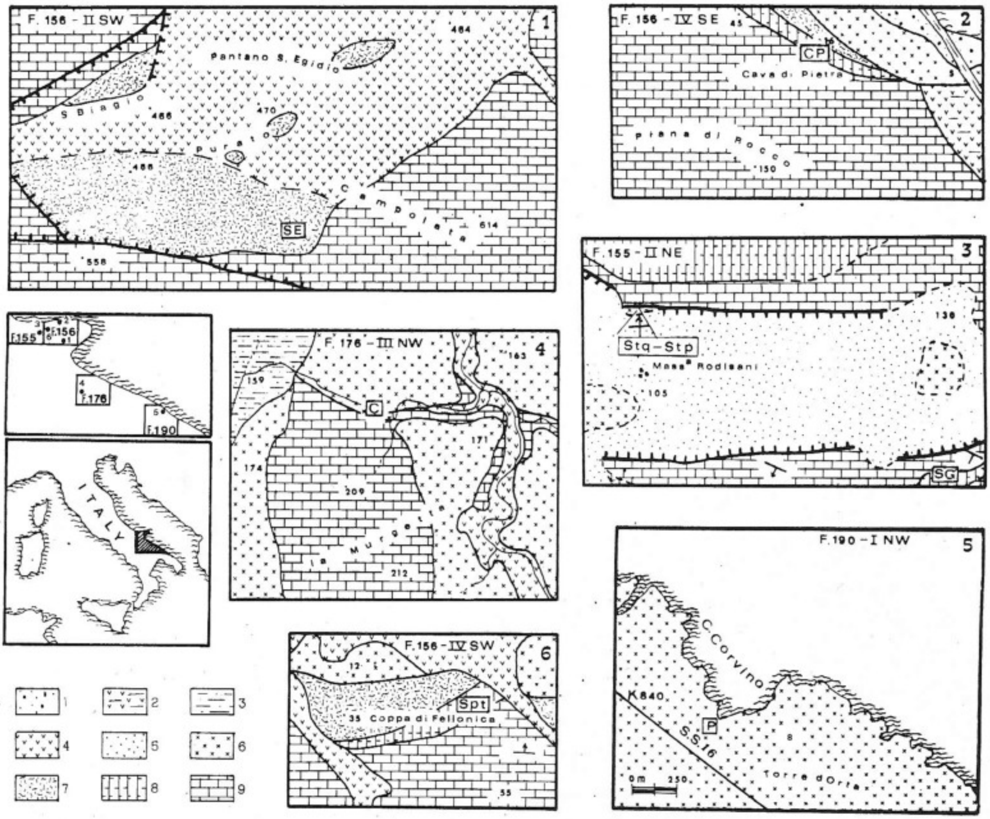
F. 156 - II SW
1
Pantano S. Egidio
S. Biagio
Purato
Cambolata
SE
484
466
470
468
614
558
F. 156 - IV SE
2
CP
Cava di Pietra
piana di Rocco
45
150
F. 155 - II NE
3
Stq–Stp
Mass.a Rodisani
SG
138
105
F. 155
F. 156
F. 176
F. 190
ITALY
F. 176 - III NW
4
C
La Murgetta
159
163
171
174
209
212
F. 156 - IV SW
6
Spt
Coppa di Fellonica
12
35
55
F. 190 - I NW
5
C. Corvino
K840
S.S. 16
P
Torre d'Orta
0m
250
1
2
3
4
5
6
7
8
9

Fig. 1 – Location of the sampled outcrops, showing the Italian geological map sheet numbers and locality codes used in the text.
Legend: 1) Recent beach sand and gravel; 2) Holocene lacustrine mud and clay; 3) Post–Calabrian marine sediments, locally terraced, composed of thin sands or coarse calcarenite; 4) terraced lacustrine gravel, sand and clay and alluvial pebble–sand and clay; 5) *Sabbie di Serra Capriola* formation, Upper Pliocene to Lower Pleistocene; 6) *Calcarenite di Gravina* formation, Middle Pliocene to Lower Pleistocene; 7) *Pietra Leccese* formation, Middle and Upper Miocene; 8) *Calcarenite di Apricena* formation, Middle (?) and Upper Miocene; 9) Mesozoic limestone.

Locality	Italian Geological map (C.G.I.)	Formation	Outcrop ages	Substrate	Codes
1. Pantano S. Egidio	F° 156 "S. Marco in Lamis"	*Pietra leccese* (D'Alessandro et al., 1979) = Calcarenite di Apricena *pro parte* (M_{c}^{2-3},II ed. C.G.I.)	Tortonian	Limestone pebbles	SE
2. Capoiale	F° 156 "S. Marco in Lamis"	*Calcarenite di Apricena* (D'Alessandro et al., 1979) = Calcarenite di Apricena *pro parte* (M_{br}^{2-3} ,II ed. C.G.I.)	Tortonian	Bivalve shells	CP
3. Coppa Fellonica	F° 156 "S. Marco in Lamis"	*Calcarenite di Apricena* (D'Alessandro et al., 1979) = Calcarenite di Apricena *pro parte* (M_{br}^{2-3} ,II ed. C.G.I.)	Tortonian	Limestone pebbles Mollusc shells	Spt
4. Cave di pietra	F° 155 "S. Severo"	*Calcarenite di Apricena* (D'Alessandro et al., 1979) = Calcarenite di Apricena *pro parte* (M_{b}^{3}; M^{3}, II ed. C.G.I.)	–––	Mesozoic limestone beds	St
			Tortonian	Madreporare, barnacle, bivalve skeleton	SG, Stp
		Calcarenite di Gravina = Calcarenite di Apricena *pro parte* (M^{3}, II ed. C.G.I.)	Middle Pliocene	Mollusc shells	Stq
5. La Murgetta grande	F° 176 "Barletta"	*Calcarenite di Gravina* (II ed. C.G.I.)	Upper Pliocene	Mesozoic limestone beds Limestone pebbles Mollusc and barnacle skeleton	C
6. Torre d'Orta	F° 190 "Monopoli"	*Calcarenite di Gravina* (Iannone & Pieri, 1980b; D'Alessandro & Iannone, 1982) = Biocalcarenite di Gravina (Iannone & Pieri, 1979) = Tufi delle Murge (Q_{ca}^{c} ,II ed. C.G.I.)	Lower Pleistocene (?)	Limestone pebbles Ostreid shells	P

Table 1 – Names of the investigated areas and formations, the ages of these formations at the localities sampled, the type of substrate containing bioerosional trace fossils, and codes of reference to each locality and horizon.

dant presence of taxa that are considered typically Pliocene, or that have only exceptionally been mentioned in lower Pleistocene assemblages: these are *Aphelesia bipartita* (Brocchi), *Chlamys seniensis* (Lamarck), *Chlamys latissima* (Brocchi), *Hinnites crispus* (Brocchi), *Pecten flabelliformis* (Brocchi) and beds of *Isognomon maxillatus* (Lamarck).

At all the examined localities, the body fossil assemblages indicate palaeocommunities that are comparable to Recent Mediterranean biocoenoses associated with the infralittoral zone.

Taxonomy of entobians.

The taxonomy of the ichnogenus *Entobia* Bronn is poorly understood, largely because of extreme morphological variation between borings at the individual level. This variation has severely hampered the search for taxobases on which to subdivide the ichnogenus into meaningful ichnospecies. The best defined form is the type–ichnospecies, *Entobia cretacea* Portlock, 1843 (see Bromley, 1970), and the most recent emendation of the ichnogenus (Häntzschel, 1975) is based alone on that ichnospecies.

The morphologies of *E. cretacea* and related entobians fall within the range of those of borings produced by sponges in present seas, and although these trace fossils and sponge borings cover a wide range of morphology, the many forms are united by the possession of a number of common features. It is on these common features that the ichnogenus *Entobia* may be defined, and by critical evaluation of the individual features, a number of distinctive ichnospecies may be established. Before we attempt this on the basis of the Miocene to Pleistocene material from Italy, however we need to discuss the numerous factors that influence the morphology of sponge borings.

Factors influencing morphology.

The factors that influence the morphology of (fossil) entobians and (present day) sponge borings are complex and partly interdependent, but may be summarized under the following heads:

1) *Nature and structure of the substrate.* Boring sponges are restricted to fully lithified calcareous substrates (calcite and aragonite). Where pure, homogeneous limestone is exposed to seawater, colonizing sponges may extend their borings freely within the substrate to produce an idiomorphic (see glossary) boring system. If, however, the substrate is physically restricted as, for example, a thin mollusc shell or the carbonate cement of a non–carbonate beachrock, the form of the boring will become stenomorphic, following the constraints of the space available. Such morphological traits are imposed by individual

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substrate peculiarities and obviously are not suitable as taxobases. Likewise, inhomogeneities in the structure of calcareous substrates may also strongly influence boring morphology. In oyster shell, for example, thin sheets of conchiolin, which are less easy to penetrate than the surrounding calcite, constitute partial barriers to the progress of the sponge, and impose a spurious tiering upon the morphology of the system as a whole (Warburton, 1958, p. 559). Again, natural void systems, as occur in coral skeleton, may be occupied by the sponge and the boring morphology thereby comes to follow the fabric of the substrate instead of the idiomorphic model (e. g. Ward & Risk, 1977).

2) *Quality of the surrounding environment.* Not all calcareous substrate surfaces are equally suitable for sponge colonization. Local variation in the suitability of surfaces depends on such factors as liability to become covered in sediment; degree of illumination; hydrodynamic energy; presence of encrusting organisms and predators; and proximity of other endoliths. If a larva of a boring sponge metamorphoses on an unsuitable surface it may penetrate through the substrate and reach more suitable areas where it will concentrate its growth. In high quality areas a sponge may complete its ontogenetic growth rapidly whereas less fortunately located sponges may use their energy in constructing long exploratory threads in search of better living conditions. The borings in these contrasting situations show markedly different morphologies. For example, *Cliona viridis* (Schmidt) having algal symbionts within its papillary tissue, seeks well illuminated sites. In small cobbles, the borings of this sponge always show remarkably different development on the upper, illuminated side and the lower, shaded side of the substrate respectively. Likewise, in a shell

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partly buried in fine–grained sediment, the sponge abruptly ceases to extend its boring beyond the sediment line, beneath which freely circulating water is not available.

Epilithic organisms coating the substrate may hinder the sponge in obtaining access to the surface, and thus alter the boring strategy of the endobiont. Furthermore, predation by e. g. echinoids also causes boring sponges to alter their growth pattern. It is clear, therefore, that such morphological variation resulting from variation in local environment is also unsuitable for the purpose of taxonomy.

3) *Proximity of other endoliths.* Other endoliths sharing the substrate with a boring sponge influence the strategy of the sponge in three ways. Large, open voids in the substrate, vacated by their originators (e. g. borings of bivalve molluscs such as *Lithophaga*) are commonly used as extensions of the surface of

the substrate in which to emplace apertures for papillae. However, more restricted borings such as *Trypanites* or *Caulostrepsis*, where vacated by their original inhabitants, are commonly occupied by the sponge, which then modifies them by additional boring. In this case, the sponge boring becames xenomorphic, following the shape of the occupied boring instead of reflecting its own idiomorphic form.

Where borings such as *Trypanites* and *Caulostrepsis* are still occupied by endobionts, the sponge avoids contact with them and, where such worm borings are abundant, the out–competed sponge is forced to produce a stenomorphic system between and around them.

Finally, where two endolithic sponges, of the same or different species, simultaneously are competing for occupation of the substrate, it is common that each individual extends an abnormally large number of short, exploratory canals towards the other within the zone of proximity between two sponges, thus drastically changing the normal form of their borings (Bromley & Tendal, 1973).

4) *Species of the boring sponge.* To a varying degree, the species of the boring sponge is reflected in the morphology of its boring. Some species, e. g. *Cliothosa hancocki* Topsent, seem to produce highly characteristic borings (e.g. Volz, 1939). Other species, such as *Cliona celata* Grant, appear to produce entirely different borings in limestone and shell respectively (de Groot, 1977). Borings of the majority of living sponges have been insufficiently investigated, however, and it is not known how species–dependent boring morphology will show itself to be. However, it must be emphasized that the ichnospecies of *Entobia* are trace fossils and are in no way to be confused with biological species (Bromley, 1970). It is already quite clear that the relationship of biological species and ichnospecies is not simple.

5) *Ontogeny of the borer.* The morphology of sponge borings is a function of growth and varies continuously as they are extended; there is thus extreme discrepancy in shape between the juvenile and gerontic areas within individual borings. Yet, despite the great variety in form between different types of sponge boring, it has been possible, nevertheless, to distinguish five phases of growth through which most sponge borings pass.

Growth phase A. After larval settlement, the initial penetration of the substrate by the juvenile sponge produces slender exploratory canals which commonly radiate and branch out from the point of entry. Likewise, in the youngest zone of a mature sponge boring, where linear growth is most active, the morphology is of fine exploratory canals.

Growth phase B. Behind the zone of linear growth, the diameter of the boring is increased by lateral growth. Normally at this stage, camerate forms begin to swell locally to form chambers, whereas non–camerate forms take on a characteristic antler–like shape.

Growth phase C. Ultimately a relatively stable morphology is attained, commonly represented by large areas of the boring having characteristic traits such as chamber size, intercameral canal dimensions etc. The radiating form of the system may still be obvious at this stage. Many sponges progress no further.

Growth phase D. Continued lateral growth inflates the chambers or branches until little intervening substrate survives. New branches continue to be inserted in the spaces between main branches until the radiating pattern is obscured. In some camerate forms a phase of fusion of neighbouring chambers ensues in which large, compound cavities are produced.

Growth phase E. Some sponges continue lateral growth until extensive fusion has obliterated most of the characteristic traits of the form to produce either a single or few large cavities or a non–camerate tunnel system of great size.

Different types of sponge borings distinguished on the basis of morphology of their parts, further distinguish themselves in showing different emphasis of the individual growth phases; some phases are completely supressed, others exaggerated. In general, phases A and E possess the fewest distinguishing characteristics and it is normally necessary to study material containing growth phases C and D in order to reach a satisfactory taxonomic identification. Sponges growing in unsatisfactory habitats lag behind developmentally; thus they may reach a reasonable size yet not advance to the growth phase normal for that form at that size.

Available ichnospecies for Entobia.

Previous workers applied a number of names to fossil borings of sponges. In most cases it is clear that the authors intended the name to cover the unpreserved organism, but since the description is entirely based on the work of the animal, the name may be considered an ichnotaxon. In addition, a number of names have been based on good descriptions of empty sponge borings in recent material, but in such cases, since the boring is vacated and the description is based exclusively on ichnological criteria, these names may also be considered available as ichnotaxa. Entobian ichnospecies are listed in Table 2. Many of the names are based on unsatisfactory material. Either the morphology of the boring is inadequately visible (e. g. *Cliona praecursor* Fischer) or poorly preserved, or the specimens are stenomorphs (e. g. *Cliona cerithiorum* Fischer) or misidentification of other borings (*Clionites mantelli* Wetherell). In some cases unsuitable characters have been selected as taxobases: e. g. *Cliona microtuberum* Stephenson is distinguished chiefly on the basis of its having a microtuberculate ornament (Stephenson, 1941), but this feature is characteristic of almost all sponge borings.

Taxobases used in the present study.

It is clear from the foregoing that not all morphological features of entobians are suitable as taxobases for ichnospecies. As with trace fossils in general, and indeed body fossils as well, a relatively complete understanding of the whole structure is necessary before meaningful taxonomy can be proposed and applied. Too often in the past, names have been based on fragmentary material, including mixtures of different forms, or on individual stenomorphic borings. In the present material, the majority of entobians having shell as a substrate show some degree of stenomorphism. Such examples, belonging to ichnospecies that have a maximum diameter greater than the thickness of the shell, show malformed or incomplete growth features and premature crowding that have interfered with their natural ontogenetic development. Only a few such steno-

Ichnotaxa	Synonymy / Availability	Remarks
Cliona cerithiorum Fischer, 1868		Unrecognizable stenomorph
Clionites conybearei Morris, 1850	*Entobia cretacea*	Bromley, 1970
Entobia conybearei Bronn, 1848	*Entobia cretacea*	Bromley, 1970
Entobia cretacea Portlock, 1843	* *Entobia cretacea*	Type–ichnospecies: Bromley, 1970
Cliona cretacica Fenton & Fenton, 1932 a	? *Entobia megastoma*	
Cliona distans Étallon, 1860		? Acrothoracican borings dubious: Fischer, 1868
Cliona falunica Fischer, 1868		Unrecognizable stenomorph
Vioa glomerata Michelin, 1846		Unrecognizable fragment
Clionites glomerata Morris, 1851	* *Entobia glomerata*	
Clionites mantelli Wetherell, 1852		Acrothoracican borings (*Rogerella* ichnosp.: Bromley, 1970)
Cliona megastoma Fischer, 1868	* *Entobia megastoma*	
Vioa michelini Nardo, 1844		Recent, empty boring: Michelin, 1847
Cliona microtuberum Stephenson, 1941	? *Entobia megastoma*	
Cliona multicava Étallon, 1860		? Acrothoracican borings dubious: Fischer, 1868
Vioa nardina Michelin, 1846		Recent, empty boring: Michelin, 1847
Cliona ovata Étallon, 1860		? Acrothoracican borings dubious: Fischer, 1868
Cliona paradoxa Fischer, 1868	* *Entobia paradoxa*	
Cliona parisiensis Fischer, 1868	* *Entobia parisiensis*	
Vioa pasichea Nardo, 1839	*Nomen nudum*	Recent empty borings
Cliona praecursor Fischer, 1868	*Nomen dubium*	Inadequate material (lost)
Cliona retiformis Stephenson, 1952	* *Entobia retiformis*	
Vioa typica Nardo, 1847	*Nomen nudum*	Recent empty borings
Vioa typus Nardo, 1839	*Nomen nudum*	Recent empty borings

Table 2 — Ichnotaxa referred by earlier workers to the work of sponges, or considered body fossils of sponges, or based on Recent, empty sponge borings. Ichnospecies marked with * are considered valid herein. Ichnospecies belonging to the ichnogenera *Clionoides*, *Clionolithes*, *Filuroda* and *Topsentopsis* are not included, see p. 238.

morphs preserve sufficient diagnostic characters to allow ichnospecies determination.

In this work, therefore, a large number of specimens of each form have been studied in order to gain a full picture of its range of variation and ontogenetic progress. In this way it has been possible to distinguish between variable features that differ from individual to individual, and stable features that are common to all members of a morphological group and which consequently are suitable as taxobases. Stenomorphic and xenomorphic individuals have been avoided. In particular, the relative development of ontogenetic phases was found to be a useful means of distinguishing between and describing sponge–boring ichnospecies. The possession of a camerate versus a non camerate form is generally useful. However, it should be noted that some ichnospecies are camerate at certain growth stages only, and some individuals of generally non–camerate ichnospecies may exhibit weak inflation as incipient chambers in growth phase B.

The basic distinction of entobian ichnospecies nevertheless relies chiefly on the description and dimensions of their basic parts, and for these a set of terms is required; the terms used here are discussed in the following section. The chief criteria examined in the material are as follows:

1) size of apertures;
2) presence and length of apertural canals;
3) camerate/non–camerate;
4) arrangement of chambers;
5) presence and dimensions of intercameral canals;
6) fusion/non–fusion of chambers;
7) maximum dimensions of chambers;
8) ontogenetic development;
9) depth of penetration into the substrate.

Terminology.

Many different terms have been applied to the anatomical parts of sponge borings. Synonyms are included in the following glossary to assist in correlation with the work of other authors. The basic organization of sponge borings is shown in Fig. 2.

Apertural canal. The subcylindrical or slightly conical canal that connects the chambers or gallery with the aperture at the surface of the substrate. (*Papillargänge*; Volz, 1939; *papillary canal*; Rützler, 1974).

Aperture. The opening at the substrate surface connecting the lumen of the boring with the exterior. The aperture and apertural canals housed the papillae of the living sponge. (*Osculis*; Fischer, 1868; *Papillarlöcher*; Volz, 1939; *pores*; Boekschoten, 1966; *papillar opening*; Bromley, 1970; *papillary perforation*; Rützler, 1974).

Apophyses. Minute pin–prick or hair–like extensions that commonly extend from all parts of the sponge boring. In casts, these give the system a minutely spinose or hairy appearance. (*Punctures*; Hancock, 1867; *rootlet*; de Groot, 1977).

Camerate. Entobians in which any stage of growth is characterized by inflation or swelling of discrete parts of the system to produce chambers. In casts such systems resemble strings of beads or bunches of grapes. (*Nodular gallery*; Lawrence, 1969).

Chambers. Discretely swollen, fusiform or globular portions of boring sponge systems. (*Lobes*; Hancock, 1849, 1867; *loculis, loges*; Fischer, 1868; *chamberlets*; Boekschoten, 1966).

Exploratory thread. The most juvenile portion of the boring system where linear growth predominates, consists of slender branching thread–like canals. Such threads are produced in order to locate the boundaries of the substrate and to investigate cavities within it. Apophyses are probably a stunted form of exploratory process, and where the advancing sponge approaches another sponge, the apophyses of each individual, in the zone of proximity of the two sponges, are greatly extended and much branched as a network of exploratory threads, as if to map the progress of the competitor. (*Twigs*; Hancock, 1849; *branching rootlets*; de Groot, 1977).

Gallery. The main passageways of the sponge boring, used particularly for non–camerate forms. (*Branch*; Hancock, 1849; *tube*; Fenton & Fenton, 1932a; *canal*; Fenton & Fenton, 1932b; Stephenson, 1941).

Idiomorphic. The natural, uninhibited, full growth–form of a sponge boring in an extensive, homogeneous carbonate substrate. Cf. *stenomorphic, xenomorphic*. Commonly used for bioturbation structures (e.g. Bromley, 1975) but not previously for sponge borings.

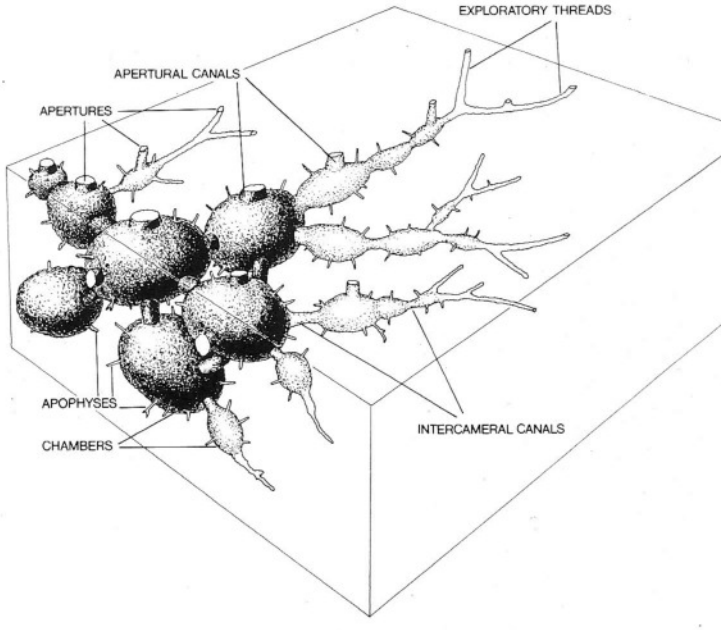


Fig. 2 – Portion of a sponge boring showing growth phases A (unshaded), B (pale) and C (dark), and the terminology used in this paper.

Intercameral canal. Subcylindrical canals that interconnect chambers. (*Stems*; Hancock, 1849; *interconnecting canal*; Bromley, 1970; *stems*; Pang, 1973; cf. *foramina*; Rützler, 1974; *rootstock, interconnecting canal;* de Groot, 1977).

Irregular boxwork. Three–dimensional network as defined in soft substrate trace fossils (cf. Frey, Howard & Pryor, 1978, fig. 2D).

Irregular maze. Network of irregularly developed horizontal components (cf. Frey, Howard & Pryor, 1978, fig. 2F).

Microsculpture. The mode of boring by sponges, involving the removal of discrete particles of the substrate (sponge–chips) produces a characteristic facetted sculpture on the boring walls (e. g. Pomponi, 1977). Although facets may be less than 20 μm in width, this pattern is commonly well preserved in fossil material as a botryoidal or micro-tuberculate ornament on cast surfaces. (*Shagreened sculpture of pits*; Hancock, 1867; *wall ornament*; Bromley, 1970).

Stenomorphic. As opposed to idiomorphic, a boring the form of which is affected by physical restriction in substrates such as thin mollusc shell or limestone that has been riddled previously by other endoliths.

Tiers. The depth to which different types of sponge boring extend into the substrate is variable. In some cases, a single tier of chambers is developed immediately below the surface; in others, two or more tiers may be developed beneath each other. Commonly the chambers or galleries are not distinctly tiered, but occur within a homogeneous zone of boring.

Xenoglyph. A foreign sculpture imposed on a boring by the fabric of the substrate (Bromley, Pemberton & Rahmani, 1984). (*Fremdskulptur*; Voigt, 1971).

Xenomorphic. As opposed to idiomorphic, of a boring that has been initiated within another boring, the morphology of which therefore overprints that of the later boring. *Entobia* commonly can be seen to have incorporated *Trypanites* and the branching pattern of the entobian is thereby strongly modified. Similarly, in heterogeneous substrates such as oyster shell, the fabric of the matrix may induce the sponge to alter its boring strategy and the morphology of the system correspondingly will be altered.

Taxonomy

Ichnogenus *Entobia* Bronn, 1837

Selected synonymy. After 1854, entobians commonly have been referred to living sponge genera such as *Cliona, Vioa* etc. (e. g. Radwanski, 1964, 1969).

1808 Bodies Parkinson, pp. 75, 76, 151, pl. 8, fig. 8, 10; pl. 12, fig. 3.
1814 Cavities Conybeare, pl. 14, fig. 1–8.
1822 Parasitical bodies Mantell, p. 218, pl. 27, fig. 7.
1837 *Entobia* Bronn, p. 34, fig. 12 inf.
1838 *Entobia* – Bronn, p. 691.
1843 *Entobia* – Portlock, pp. 359, 360.
1850 *Clionites* Morris (in Mantell), p. 100.
1868 *Cliona* – Fischer (non Grant), p. 161.
1962 *Entobia* – Häntzschel, p. W230.
1970 *Entobia* – Bromley, p. 78.
1975 *Entobia* – Häntzschel, p. W127.

The following four Palaeozoic ichnogenera have been ascribed by several authors to the work of sponges. Their morphology and diagnosis are very poorly understood, however, and we shall not attempt to relate them here to *Entobia*. This must await detailed re–examination of the type–material of these four ichnogenera.

Clionolithes Clarke, 1908 is very small. It has a single central cavity giving off radiating dichotomously branched galleries to all sides.

Clionoides Fenton & Fenton, 1932a is an irregularly branched open system of cylindrical galleries, bearing many apertures.

Filuroda Solle, 1938 is an irregularly winding system of borings close beneath the substrate surface.

Topsentopsis de Laubenfels, 1955 has a central cavity and fine radiating canals.

Emended diagnosis. Boring in carbonate substrates comprising a single chamber or networks or boxworks of galleries connected to the surface by several or numerous apertures. Morphology changes markedly with ontogeny. The galleries show progressive increase in diameter during growth; in some forms, inflation at more or less regular distances produces a system of closely interconnected chambers; in other forms, chamber development is restricted to only a brief ontogenetic stage; in still other forms, no cameration is developed. The surface of the boring bears a cuspate microsculpture that may be lost in gerontic specimens. Fine apophyses arise from all or most surfaces of the system.

Type–ichnospecies: *Entobia cretacea* Portlock, 1843

Entobia cateniformis ichnosp. nov.

Pl. 16, fig. 1, 3, 4, 5; Pl. 17, fig. 3; Pl. 27, fig. 3; Text–fig. 3

Derivation of name. Latin, *catena*, chain.

Type–series. Holotype no. MGUH 16413 (14 P), Pl. 17, fig. 3; paratypes no. MGUH 16414 (216 P), Pl. 16, fig. 3, 5; no. MGUH 16415 (221 P), Pl. 16, fig. 1; no. MGUH 16416 (223 C), Pl. 16, fig. 4; no. MGUH 16417 (224 P).

Horizon. Calcarenite di Gravina formation.

Type–locality. Cala Corvino (P), Monopoli, Bari.

Collocation. Geological Museum, University of Copenhagen, Denmark.

Diagnosis. Entobian developed as an open camerate system, comprising long rows of cylindrical chambers forming an irregular maze through branching and anastomosis. Many chambers elongated, commonly T–, L– or cross–shaped where rows intersect. Elsewhere, no fusion of chambers. Intercameral canals reduced to constrictions. Apertures small, irregularly distributed; apertural canals well developed. Ontogenetic phases A, B and C well developed, D reduced.

Description. Apertures small (average 0.5 – 1.0 mm), subcircular, uncrowded and distributed irregularly. From each of these openings arises a distinct apertural canal (average 0.8 – 1.0 mm long), weakly tapering outwards; only a few chambers are connected in this way to the exterior.

Phase A is represented by well developed exploratory threads, diameter up to about 0.2 mm, branched and anastomosed, with minor swellings at nodal points. These threads lie more or less perpendicular to the surface, but flow together into larger galleries (about 0.7 mm in diameter), rarely branched, that run subparallel to the surface. When present at bounderies of mature individuals, the exploratory threads are shorter and more densely branched as a poorly developed boxwork. There are numerous slender apophyses.

In phase B, constrictions of greater or lesser accentuation define cylindrical chambers having a length of two or three times the diameter ranging to a little less than the diameter. These are disposed in long rows, rarely branched, commonly resembling chains arranged in festoons, lying subparallel to the surface to which, at the attachment between the festoons, there are connections by long apertural canals. In some samples, growth stops at this phase, the chambers reaching a size comparable to that reached by phase C (see Table 3).

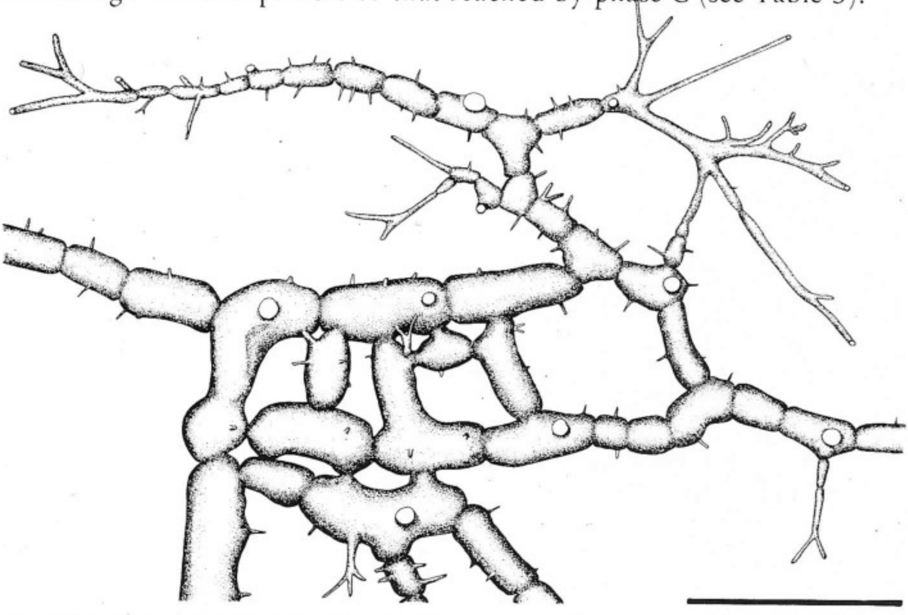


Fig. 3 – Part of an *Entobia cateniformis* ichnosp. nov. showing growth phases A to C and early stages of D at centre. Compound camera lucida drawing of artificial casts in limestone. Scale bar = 1 cm.

Phase C is characterized by development of a network produced by anastomosis and dichotomy of long sublinear chains of elongated cylindrical chambers. Dimensions of phase C chambers are on average 2.0 – 5.3 mm in length, 1.3 – 3.4 mm in width. Between these chambers are interposed others having length less than diameter. When two rows cross, the chambers commonly coalesce and take the shape of a cross, a T or an L. At a more advanced stage, new rows are intercalated, descending somewhat, to give rise to a second, poorly separable tier. Exploratory threads are well developed at the advancing boundary of the system, whereas between rows they are little larger than apophyses.

Phase D has been reached by a single specimen, the holotype (Pl. 17, fig. 3), but this appears to be unusual in this ichnospecies, which normally retains an open character.

Individual tiers are poorly developed, the system interweaving within the 25 mm that represents its maximum depth of boring.

Observations. The characteristic elongation of the chambers in *E. cateniformis* and its open branching system render this ichnospecies highly distinctive. These features are normally present in borings of *Cliona vermifera* Hancock, the chambers of which are generally described as oval or elongated (Hancock, 1867; Pang, 1973; Rützler, 1974; de Groot, 1977, fig. 27).

Specimen no.	Substrate	Preservation	Ø Apertures			Length of apertural canal			Ø Constrictions			number constrictions /chamber	Length of chamber			Ø chamber			Fusion of chambers	Phase	Depth
			Average	Range	n	Average	Range	n	Average	Range	n		Average	Range	n	Average	Range	n			
14	Ls	Ac	0.7	0.5–1.2	22				0.9	03–20	40		3.4	1.3–6.6	39	1.8	0.8–3.3	39	R	C	10
216	Ls	Ac	0.8	0.3–1.0	11	0.8	0.7–1.0	7	0.8	05–13	22		2.6	1.5–3.6	18	1.3	0.8–2.7	18	A	A–C	25
223	Ls	Ac		0.5–0.7	3				1.0	05–18	19		5.3	3.3–8.3	21	2.5	1.5–3.6	21	A	A–C	7
221	Ls	Ac	1.0	0,5–2,2	22	0.9	0.3–1.7	10	0.9	07–15	12	2–3 4–5	6.6 5.2	4.6–10 3.3–5.8	10 5	1.6 3.4	1.0–2.7 2.2–5.3	10 5	A A	B C	8
135	Ls	Ac	0.5	0,3–0,7	7	1.0	0,5–1,5	11	1.0	03–15	14	3–4	2.0	0.8–3.3	16	1.9	0.7–2.5	16		B–C	
165	Ls	Ac							1.4	07–23	11		2.8	1.8–3.5	12	2.0	1.5–3.2	12		B,D	

Table 3 – Numerical data for *Entobia cateniformis* ichnosp. nov. Abbreviations in this and the following tables are as follows: A = abundant; Ac = artificial cast; B = bivalvia indet.; Bg = *Glycymeridae*; Bv = *Veneridae*; Cv = cavity; F = frequent; Ls = limestone; Nc = natural cast; O = *Ostreidae*; P = partially fused; R = rare; VF = very frequent.
«Number constrictions/chamber» = number of contiguous chambers in communication.

Material. In addition to the type–material, fifteen artificial casts in limestone have been examined, 11 from P and 4 from C.

Entobia geometrica ichnosp. nov.

Pl. 18, fig. 1; Pl. 19, fig. 1, 3; Pl. 20, fig. 1; Pl. 21, fig. 1, 4, 5; Pl. 22, fig. 1, 2, 5; Text–fig. 4

Derivation of name. Latin, *geometricus*, geometrical, for the general appearance of phase D in limestone.

Type–series. Holotype no. MGUH 16419 (7 C), Pl. 18, fig. 1; Pl. 19, fig. 3; Pl. 20, fig. 1; paratypes no. MGUH 16422 (10 P), Pl. 22, fig. 2; no. MGUH 16423 (23 P), Pl. 22, fig. 1, 5; no. MGUH 16421 (3 P), Pl. 21, fig. 1; no. MGUH 16420 (1 P), Pl. 19, fig. 1; no. MGUH 16424 (240 P); no. MGUH 16425 (2 P).

Horizon. Calcarenite di Gravina formation.

Type–locality. Cala Corvino (P), Monopoli, Bari.

Collocation. Geological Museum, University of Copenhagen, Denmark.

Diagnosis. Camerate entobian. Apertures of two markedly different sizes; the larger generally unfused, variable in diameter; the smaller spread among the larger ones. Apertural canals very short. Chambers wide, generally polygonal in section in mature growth–phases, separated by thin walls perforated by numerous short intercameral canals that may be fused together. In more juvenile phases the chambers are oval or subspherical, always joined by a distinct intercameral canal. Chambers disposed in weakly developed rows, tending to form a subrectangular network. The dominant growth phase is D; B and C are usually much reduced. The system is developed parallel to the external substrate surface, in usually only one or two tiers.

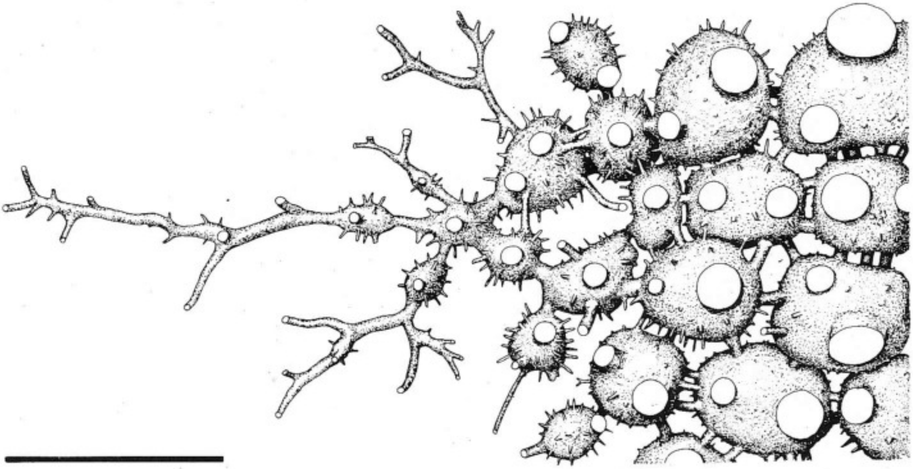


Fig. 4 – Part of an *Entobia geometrica* ichnosp. nov. showing growth phases A to D from left to right. Compound camera lucida drawing of artificial casts in limestone. Scale bar = 1 cm.

Description. Apertures of two distinct size groups. The large apertures are circular, only rarely in contact or fused, wide but variable in size, differing greatly within the same sample, and having a range in diameter of 0.7 to 3.8 mm. Between these apertures there are others, distinctly smaller (range 0.3 – 1.5 mm, average 0.7 – 1.0 mm). From each of these apertures arises a cylindrical apertural canal, the length of which is not easily observed in our material. The chambers appear to grow closely beneath the surface, and the apertural canal is consequently commonly shorter than wide. If the chambers are organized in a single tier, it is usual that each is connected to the outside by a single canal, more rarely by two.

Phase A, normally reduced, consists of bifurcating exploratory threads of variable length. Phase B represents weak swellings along these threads. At the close of phase B, the chambers assume an oval shape (range of diameter 1.0 – 3.2 mm) joined by only two or three distinct intercameral canals, and arranged in very short rows. In phase C the chambers become more rounded to subspherical in the initial stage (average 2.4 – 3.7 mm). The intercameral canals appear to be fewer than eight.

In phase D which dominates the system, the chamber walls have almost flat surfaces, with rounded corners, and in section the shape of the chambers varies from subrectangular to subtriangular (average 4.9 – 6.8 mm). Thus, although the chambers are expanded greatly and partitions between become thin, fusion generally does not occur. The intercameral canals are circular in cross section. In a few cases the intercameral canals fuse together in pairs or bundles to produce canals of a larger size. The intercameral walls between neighbouring chambers are penetrated by more than ten such canals, frequently more than twenty, rendering the walls seive–like (Pl. 22, fig. 2, 5). Chambers are disposed in weakly developed rows, tending to form a subrectangular network and, within main rows, they become very inflated and closely spaced before the interrow areas are occupied.

In all phases, the apophyses are long and numerous, usually unbranched but rarely bifurcated.

In our material up to three tiers are developed, but in most cases only one or two. Maximum depth of penetration 15 mm.

Stenomorphic material (Pl. 21, fig. 4, 5). The chambers are considerably flattened and have variable sizes in the other dimensions (average length 4.0 – 9.1 mm). The shape is more irregular than in idiomorphs. Intercameral canals are usually short (average 0.2 – 0.9 mm) and more variable in diameter than in idiomorphs (average 0.7 – 2.6 mm), owing to fusion of neighbours. There are no more than four or five intercameral canals between chambers. The apertures, usually one per chamber, range from 0.5 to 2.0 mm. The most significant difference between idiomorphic and moderately stenomorphic shapes, related to the flattening of the chambers, is the alteration of the position of the canals (restricted in the stenomorph to a single plane) and their fusion, as well as the smaller apertures.

Observations. Borings of this ichnospecies are closely similar in morphology and size to artificial casts of borings in limestone made by *Cliona celata* Grant, as figured by de Groot (1977, fig. 15–17).

Entobia geometrica differs from *E. cretacea* in several respects. The apertures of *E. geometrica* are larger; the chambers to a greater extent leave thinner dividing walls than *E. cretacea* and the chambers are normally connected by single intercameral canals in *E. cretacea.* The stenomorphs of these two ichnospecies resemble each other more closely (cf. Bromley, 1970, pl. 5 c). However, here also, *E. geometrica* has larger, more closely spaced chambers and larger apertures than *E. cretacea.*

Material. In addition to the type–material we have fifteen artificial casts (14, P; 1, C) in limestone, two artificial casts in shells of *Ostrea edulis* Linnaeus (P) and eleven in limestone (P). Less well preserved specimens come from Monopoli, Barletta (C), S. Severo (St), S. Marco in Lamis (SE); numerous natural casts occur in shells of *Glycymerys insubricus* (Brocchi) and *Venus multilamella* Lamarck from S. Severo (Stq).

Specimen no.	Substrate	Preservation	ø Apertures			Length of apertural canal			Number apertures/ chamber	Length of intercameral canal			ø intercameral canal			Fusion of intercameral canals	Length of chamber			Width of chamber			Phase
			Average	Range	n	Average	Range	n		Average	Range	n	Average	Range	n		Average	Range	n	Average	Range	n	
7	Ls	Ac															2.0	1.6–2.5	3	1.5	1.0–1.7	3	B
										1.0	0.5–1.7	4				A	2.4	1.7–3.5	12				C
			1.7	1.0–2.3	14				0–2	0.36	0.2–0.7	7				R	5.6	2.0–8.5	14				D
1	Ls	Ac	2.1	1.7–2.5	5		0.3	3	0–1		< 1	5	0.7	0.3–1.0	8	R	4.9	2.0–8.5	15	4.4	3.0–5.9	15	D
2	Ls	Ac	2.0	1.3–3.7	50	1.3	0.7–2.7	15	0–2	0.4	0.2–1.0	19	0.6	0.2–1.0	11	A	5.9	2.3–9.8	18				D
5	Ls	Ac	1.5	1.0–1.7	4	1.3	1.2–1.7	3	1	0.4	0.3–0.5	3				A	6.8	5.1–8.5	5				D
6	Ls	Ac	1.1	0.8–1.4	6	1.0	0.8–1.2	6	0–2	1.2	0.7–2.0	7	0.5	0.3–0.9	7	A	5.5	2.5–8.5	7				D
64	Ls	Cv	1.6	0.8–3.8	26					0.4	0.2–0.7	9	0.5	0.2–0.8	9	R	5.3	2.3–7.0	6	4.4	2.2–6.3	6	D
10	Ls	Cv	1.4	0.7–1.8	32						≃ 0.4		0.5	0.1–1.9	40	R	6.5	3.0–10	15				D
15	Ls	Ac								1.6	0.8–2.5	4		0.3	4	A	2.2	1.7–3.0	3	2.1	1.5–3.2	4	B
17	Ls	Ac	1.3	1.0–1.7	4		0.8, 1.0		1	0.7	0.3–1.0	7	0.5	0.3–0.7	4	A	3.7	2.0–6.0	9	3.5	2.2–4.2	8	C
23	Ls	Ac	1.5	1.3–3.7	11	0.6	0.3–0.8	13	1–2	0.4	0.3–0.7	15	0.4	0.2–0.7	34	F	6.6	4.3–10	4	6.6	5.6–7.1	4	D
	Stenomorphs																						
30	Bg	Nc	0.7	0.5–0.8	8				1	0.2	0.12–0.25	5	0.7	0.5–0.8	8	VF	4.0	2.5–6.6	12	3.1	1.7–5.0	12	D (A)
31	Bg	Nc	1.4	1.0–2.0	6				1	0.9	0.7–1.2	6	1.4	0.8–1.7	6	VF	6.9	5.0–8.3	6	5.8	4.0–8.0	6	D
32	Bg	Nc	0.9	0.6–1.3	7				1–2	0.6	0.5–0.8	7	0.7	0.2–1.2	6	VF	6.8	5.3–8.3	7	5.6	4.6–6.6	7	D
35	Bv	Nc	1.3	0.8–1.8	7				1–2	0.5	0.3–0.8	13	2.6	1.3–4.2	15	VF	9.1	5.0–15	10	7.4	4.0–12	3	D (B)

Table 4 – Numerical data for *Entobia geometrica* ichnosp. nov. Abbreviations as in Table 3.

Entobia laquea ichnosp. nov.

Pl. 17, fig. 2; Pl. 19, fig. 2; Pl. 23, fig. 1; Text–fig. 5, 6

Derivation of name. Latin, *laqueus*, noose, from which the English name «lace» is derived, refering to the lace–like appearance of phases B and C of the boring.

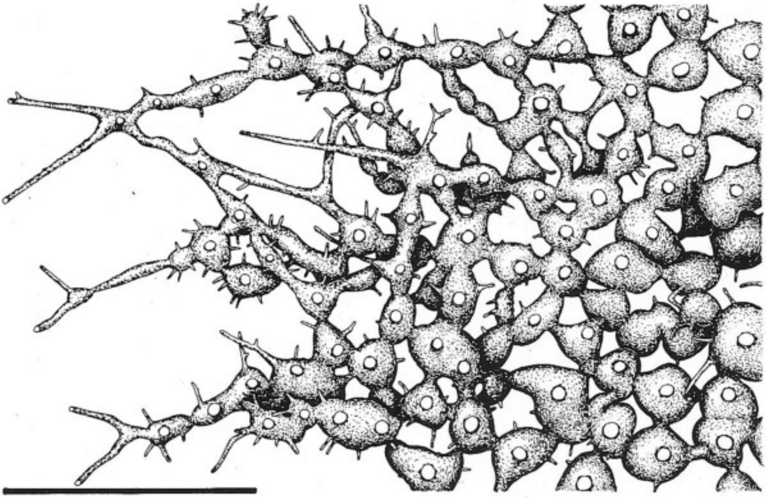
Type–series. Holotype no. MGUH 16428 (102 C), Pl. 23, fig. 1; paratypes no. MGUH 16429 (125 C). Pl. 19, fig. 2; no. MGUH 16430 (128 P), MGUH 16431 (132 C).

Horizon. Calcarenite di Gravina formation.

Type–locality. La Murgetta Grande (C), Barletta, Bari.

Collocation. Geological Museum, University of Copenhagen, Denmark.

Diagnosis. A camerate entobian composed in mature stages of networks of small chambers arranged in several tiers subparallel to the substrate surface. The chambers, variable in shape, taper abruptly near the constrictions that separate them from neighbours. They are organized in short, more or less arcuate chains that encircle small spaces in a way that resembles lace. The apertures, circular in shape, rarely fused, are small, numerous and distributed irregularly. Phase A well represented by branched exploratory threads that anastomose early to produce a slender network. Furthermore, phase A is usually present at the periphery, even in mature specimens. Phase B is greatly reduced or absent, the enclosed meshes passing almost directly into phase C. The most characteristic growth phase of the ichnospecies is C.



Description. Apertures circular (average 0.5–0.7), more rarely oval in shape, in some cases fused, numerous and irregularly disposed, opening directly into the chamber or to very short apertural canals. The chambers are organized in many networks arranged in interconnected tiers (up to six) lying parallel to the surface; maximum depth 15 mm.

Phase A (Pl. 17, fig. 2) is represented by numerous exploratory threads, the slender canals of which (⩽0.3 mm in diameter) are generally arcuate and branched, flowing together again into wider tubules about 0.7 mm. These also branch and anastomose, so that a closed mesh of varying width can arise. There may be weak swelling at nodal points. Phase A is usually present at the perifery of mature individuals; in such cases the exploratory threads are shorter and more densely branched, so that the meshes are smaller.

Phase B, usually reduced, is represented by small chambers varying in shape from irregularly oval to subtriangular and subquadrate, the vertices elongated in necks of greater or lesser length. Normally only a simple constriction separates each neck from neighbours. More rarely this is replaced by a very short intercameral canal. The chambers are arranged in short rows, irregularly in patterns, commonly like strings of beads, or closed in a network.

In phase C, the arrangement of the chambers in the network becomes distinctly lace–like, with more or less narrow meshes (often delimited by 5 or 6 small chambers), the meshes arranged in several tiers. The chambers (average 1.7 – 3.5 mm in length), somewhat equidimensional, have a subglobose to sub–pyramidal appearance, tapering in a short neck connecting directly to neighbouring chambers. Apophyses are present in all phases: they are long and commonly forked but not numerous. Phase C is the best developed and most characteristic of the ichnospecies and in several specimens represents the final phase.

Transition to phase D is gradual. The small chambers tend towards a more globose shape. The meshes become narrower, and the system resembles a boxwork. In extreme cases, the diagnostic character becomes obliterated and it is not possible to separate this ichnospecies from phase D of *E. ovula.*

Stenomorphic and xenomorphic material. Owing to the small size of the chambers and the characteristic growth form of the network, the stenomorphic shape is generally restricted to the oldest stages where the number of tiers increases. The chambers of the different network tiers, normally separated in idiomorphic examples, become closely interlaced, flattened and partially fused in stenomorphs (Fig. 6). The exploratory threads are very numerous, short and branched; extreme stenomorphs are not always separable from those of *E. ovula*.

In xenomorphs in *Ostrea*, the arrangement in planes becomes exaggerated and the chambers have a xenoglyphic sculpture inherited from the laminar substrate. Such chambers are flattened parallel to lamination and partially fused together. Xenomorphs can be separated from *E. ovula* only if they possess a developmental stage where the chambers are not influenced by shell structure, and where surface–parallel sections of the boring may be viewed. In artificial casts of xenomorphs in limestone, where the morphology is altered by the presence of earlier borings (e. g. *Trypanites* sp. or *Caulostrepsis contorta*), the constrictions are replaced by rather wide canals and the chambers have a knot–like shape.

Observations. This ichnospecies is one of the most numerous in the examined material from the Calcarenite di Gravina formation. Morphologically it shows similarities with excavations in limestone illustrated by de Groot (1977, fig. 21, 22) and ascribed to *Cliona viridis* (O. Schmidt) Gray. *Entobia laquea*, however, has smaller and more numerous apertures (1). *E. laquea* differs from *E. paradoxa* (Fischer) in having smaller size both of chamber and of apertures; in the less irregular shape of the chambers and particularly in the ubiquitous presence of exploratory threads in phase C. This last feature greatly assists recognition of stenomorphic individuals of *E. laquea.*

Material. Idiomorphs: twenty–four artificial casts in limestone (C, SE, P), three artificial casts in shells of *Pecten jacobaeus* (C) and *Ostrea edulis* (P), six natural casts in shells of *Veneridae* and *Glycymeridae* (Stq), and *Ostrea edulis lamellosa* (CP), and two in corals (SG, Stp). Stenomorphs: seven natural casts in *Glycymeris insubricus* (Stq), one in indeterminable bivalve (CP). Xenomorphs: one in *Ostrea edulis* and one in limestone (P).

Entobia mammillata ichnosp. nov.

Pl. 20, fig. 3; Pl. 24, fig. 1; Pl. 25, fig. 1, 2, 4; Pl. 26, fig. 2; Pl. 27, fig. 3; Text–fig. 7

Derivation of name. Latin, *mammillatus*, mammillated, in accordance with the surface sculpture.

Type–series. Holotype no. MGUH 16435 (47 P), Pl. 24, fig. 1; paratypes no. MGUH 16436 (56 C), Pl. 25, fig. 1; Pl. 26, fig. 2; no. MGUH 16437 (62 C), Pl. 25, fig. 2; no. MGUH 16438 (66 C), Pl. 20, fig. 3; no. MGUH 16439 (46 C).

Horizon. Calcarenite di Gravina formation.

Type–locality. Cala Corvino (P), Monopoli, Bari.

Collocation. Geological Museum, University of Copenhagen, Denmark.

Diagnosis. Camerate entobian in juvenile phases, non camerate in mature phases. Network of sublinear cylindrical chambers, later fusing to galleries, organized in an irregular maze of a single tier, anastomosed and branched at wide angles to a right angle. Surface ornamented with hemispherical tubercles, each bearing a long terminal apophysis, or by a cluster of partially fused tubercles. Phase C well developed, phase D absent. Phase E represented by wide, shallow, surface grooves, the ornamentation locally lost. Apertures extremely variable, in two sizes; a few relatively large and wide, sparsely distributed; among these, minute apertures of much smaller size.

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(1) It should be noted that casts of *C. viridis* borings made by us of material from Rhodes, Greece, have a quite different morphology from that illustrated by de Groot, and from *E. laquea.*

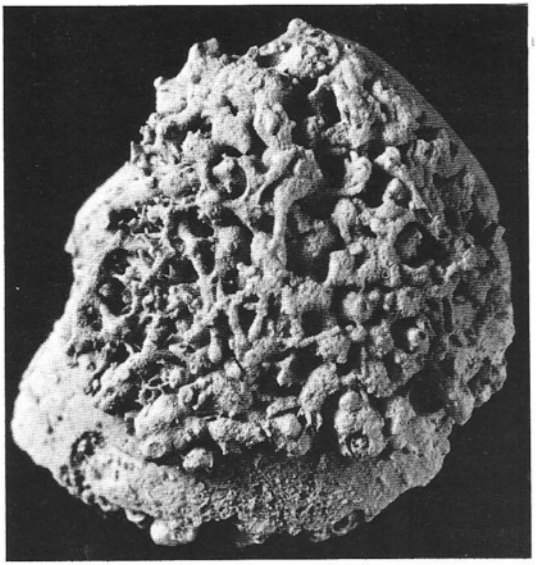

Fig. 6 – *Entobia laquea* stenomorphic in *Glycymeris* sp. No. MGUH 16434 (104 Stq); x 2.

Specimen no.	Substrate	Preservation	ø Apertures			Number constrictions / chamber	ø Constrictions			Tiers	Length of chamber			Width of chamber			Fusion of chambers	Phase	Depth
			Average	Range	n		Average	Range	n		Average	Range	n	Average	Range	n			
102	Ls	Ac	0,5	0,3−0,8	84	2−4	0.4	0,2−0.7	30	1−5	2,2	0,7−3,0	43	1,6	0.7−2,2	38	F	C(D)	7
128	Ls	Ac	0,5	0,2−0.7	7	2		≃0.16		1	2,4	1,7−3,3	8	1,3	0,7−2,5	8	A	B	
						3−5	0,4	0,2−0,6	19	3	3,0	2,0−4,0	13	2,1	1,2−2,5	13	R	C	4
125	Ls	Ac		≤0.7	4	3−5	0,5	0,2−0,8	20	1−5	2,2	1,7−2,9	12	1,6	0,9−2,1	12	F	C,D	7
111	Ls	Ac	0,5	0,2−0,8	36	2−4	0,5	0,2−0,6	24	1−3	2,0	1,3−3,5	19	1,5	1,2−2,7	19	F	C(D)	15
101	Ls	Ac	0.7	0,2−1,3	15	2−3				1−2	1.7	1,3−2,0	4	1,5	1,3−1.7	4	R	B,C	5
118	Ls	Ac	0,7	0,5−0,8	7	3−7	0,5	0,3−0,8	19	>5	3,5	2,2−5,0	9	2,6	1,7−4,6	9	F	D	12
103	Ls	Ac				2−5	0,8	0,5−1,0	13	5	2,9	2,0−3,3	7	2,1	1,8−2,3	7	F	(B)C	8

Table 5 – Numerical data for *Entobia laquea* ichnosp. nov. Abbreviations as in Table 3.

Description. Camerate entobian in phase B, partially in phase C, to totally uncamerated in phase E. Phase A is represented by a system of thin, cylindrical galleries (about 1 mm wide), running in straight lines, rarely immediately beneath the surface but usually plunging in a curve to a few millimetres into the substrate. These galleries bifurcate repeatedly in several decreasing orders of size, distally arriving at the surface as minute apertures. The angle of bifurcation is wide, approaching a right angle. Weak enlargement occurs at nodal points. Very long arcuate capillary galleries ($\simeq 0.3$ mm in diameter) interconnect different parts of the same gallery system. Apophyses long, numerous and robust (Pl. 25, fig. 1, 2).

Phase B appears abruptly and has a highly characteristic development. It is initiated by the differentiation of a turnip–shaped chamber (3 mm in diameter, length variable), which is succeeded by one or two subcylindrical ones, and these in turn by clearly cylindrical chambers (average 3.2 – 5.8 mm in length). These are connected by intercameral canals that become gradually shorter until the chambers are separated only by a narrow, deep constriction. The chambers are disposed in an approximately straight chain of constant diameter varying in different rows from 1.7 to 5 mm. Perpendicularly to a few of the chambers, side branches are given off that represent the initiation of a new row;

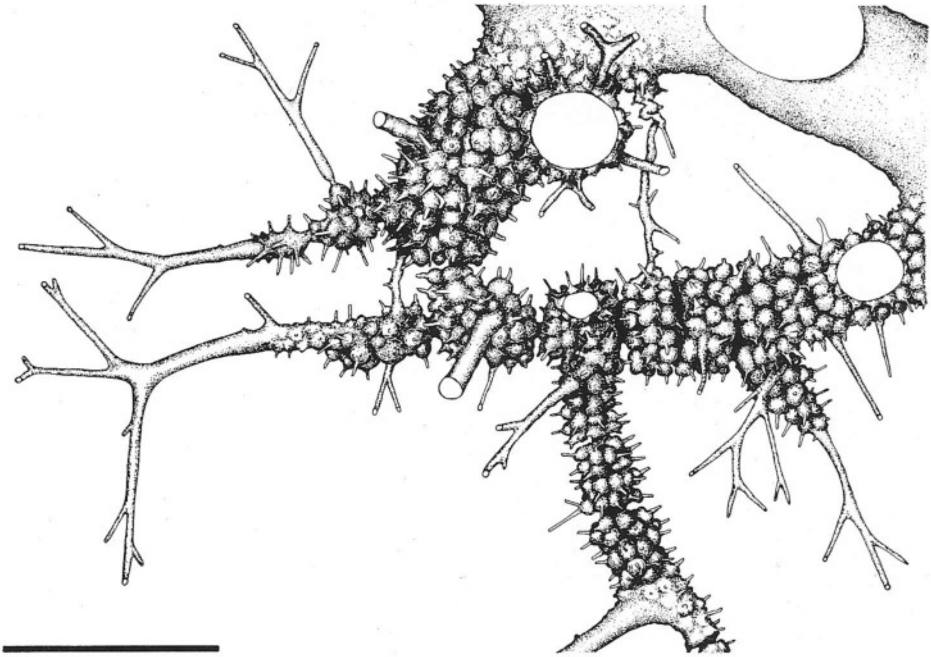

Fig. 7 – Part of a large *Entobia mammillata* ichnosp. nov. showing growth phases A to C, and a little of phase E at top right. Compound camera lucida drawing of artificial casts in limestone. Scale bar = 1 cm.

these normally start as a long, little–branched, exploratory thread, less commonly as a narrow, elongate, cylindrical chamber. The surface is characterized by numerous hemispherical tubercles or chamber–like outgrowths (in the cast; pits in the original). These are crowded close together, are constant in size, and the centre of each bears a robust, terminal apophysis. In addition, normal, small apophyses arise from all surfaces of the outgrowths. In a few samples, growth stopped at this stage.

In phase C, the constrictions tend to become obliterated, although in a few cases parts of them may remain. The different galleries of the same system have a relatively constant diameter, branching and anastomosing at short intervals. In some cases they are interconnected by narrower galleries. The chamber–like tubercles become partially fused in clusters of two or three to produce larger, compound tubercles, which again can fuse partially in still more complex structures. Fusion is not complete, and the position of the original tubercles remains clear, as do their single terminal apophyses. In the extreme form, the complex tubercle clusters come to resemble an irregular half–chamber. There is a tendency for these to be arranged in rings encircling the gallery perpendicular to its axis. The apertures in phase C have two sizes. The largest are few and widely separated, round to oval, 0.7 – 7.5 mm in diameter. Among these there are interposed numerous minute apertures.

From phase C we pass directly to phase E, in that no stage is reached in which the borings become crowded (except in stenomorphic situations). The E stage is represented by wide canals. In our material these are open as shallow grooves at the surface (5 – 10 mm deep) but this may not have been the case when the sponge was living. In peripheral areas, short galleries descend beneath the surface to re–emerge as wide apertural openings. This gerontic phase (Pl. 25, fig. 4) of the ichnospecies can be recognized where the characteristic tubercular sculpture of the wall is present in at least some parts of the system. However this sculpture is commonly lost in phase E over large areas, and the boring then comes to resemble phase E of *E. megastoma* (Fischer). Depth of boring 20 mm.

Stenomorphic material. Owing to its extensive form, this ichnospecies tends to become stenomorphic in its mature phases, even in relatively large substrates. The galleries become relatively short in comparison with diameter, which in turn is more variable; the galleries become more branched than in the idiomorphic form, and a D–phase is formed that almost completely consumes the substrate. Nevertheless, the ichnospecies remains distinctive on account of its characteristic tuberculous structure.

Observations. This entobian ichnospecies is highly distinctive on account of its large size, the cylindrical chambers and their mode of fusion as galleries, and in particular the unique tuberculous ornament. The microsculpture, an order of size smaller, is like that of other sponge borings.

Material. Fifteen idiomorphic artificial casts in limestone, three stenomorphic (P, C), and four limestone pebbles (P).

Specimen no.	Substrate	Preservation	ø Apertures (Large)			ø Apertures (Small)		ø Main gallery	Length of chamber			ø chamber			ø cluster	Phase
			Average	Range	n	Range	n	Range	Average	Range	n	Average	Range	n		
46	Ls	Ac							4.6	2.5−6.6	7	2.7	1.7−3.8	7		B
47	Ls	Ac	1.4	1.2−1.7	3	≤ 0.2	>50		5.8	5.0−7.5	6	3.2	2.8−5.0	6		B
52	Ls	Ac	0.9	0.7−1.2	3											B
54	Ls	Ac	1.4	1.2−2.3	9	0.05−0.2	>50									B
58	Ls	Ac	1.2	0.8−1.7	7	0.2−0.4	20									B
49	Ls	Ac							3.2	2.3−5.0	11		2.3−3.7			B
48	Ls	Ac	2.7	1.0−6.6	6	≤ 0.3	>20	4.1 − 4.3							1.1 − 1.7	C
51	Ls	Ac		7.0 , 7.5		≤ 0.3	>20	5.0 − 7.5							1.3 − 2.7	C
53	Ls	Ac	1.6	0.8−2.3	9			5.0,5.0,4.2								C
55	Ls	Ac	1.5	0.7−2.5	32	< 0.5	>50	5.0,5.8,7.5								C
57	Ls	Ac						≃ 10							>2.0 or obsolete	E
63	Ls	Ac						≃ 20							>2.0 or obsolete	E

Table 6 — Numerical data for *Entobia mammillata* ichnosp. nov. Abbreviations as in Table 3.

Entobia megastoma (Fischer, 1868)

Pl. 23, fig. 3; Pl. 24, fig. 2, 3; Pl. 26, fig. 1; Pl. 27, fig. 2; Text–fig. 8

1866 *Cliona megastoma* Fischer, p. 198 (*nomen nudum*?)
1868 *Cliona megastoma* Fischer, p. 165, pl. 24, fig. 2, 2a.
? 1932b *Cliona cretacica* Fenton & Fenton, p. 55, pl. 7, fig. 8, 9.
? 1941 *Cliona microtuberum* Stephenson, p. 54, pl. 3, fig. 1, 2, 4 (non 3, 5); pl. 5, fig. 1, 2.

Diagnosis follows the original (Fischer, 1868) closely but refines certain points on the basis of more complete material.

Diagnosis. Non–camerate entobian, organized in an irregular boxwork system becoming more or less complexly intermeshed in the mature stages. The galleries are subcylindrical, frequently bifurcated, swollen at nodal points where, usually, several galleries conjoin. Apertures large and numerous, circular or oval in shape, rarely fused, disposed irregularly. Phase A reduced; phases B–D well developed.

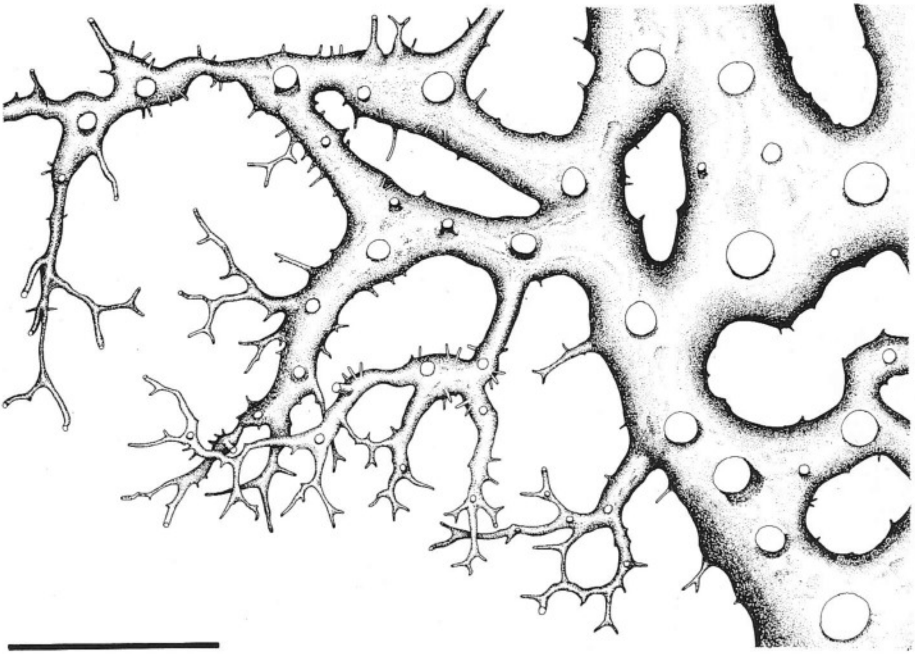

Fig. 8 – Part of a large *Entobia megastoma* (Fischer) showing growth phases A to D. Compound camera lucida drawing of artificial casts in limestone. Scale bar = 1 cm.

Description. Non–camerate form comprising a complex gallery including parts having widely differing diameters. The apertures are large (average 0.6 – 1.7 mm), circular or suboval in shape, numerous, close together, rarely fused. Apertural canal subcylindrical or, especially in oyster shell, tapering distally, not always distinctly separated from the gallery.

Phase A, usually reduced, begins with slender tubules having variable diameter, about 1 mm, which merge with wider, hand–like cavities. The cavities continue in more tubular galleries, about 1.5 mm wide, running in irregular patterns and having very variable diameter, swelling at nodal points (the swellings are too irregular and poorly defined to be considered chambers). This system is connected with the exterior by short canals of about the same size as the main gallery itself.

In phase B (Pl. 27, fig. 2) the complexity of the system increases, owing to anastomosis between the main galleries, which become further interconnected by arcuate canals. Diameter is more variable owing to the construction of tuber–like expansions ($\simeq$2.5 mm in diameter) where several galleries interconnect. In advanced phase B the development begins of a three–dimensional system, penetrating more deeply into the substrate. In both phases, thin apophyses occur (these are not visible in more mature stages).

Phase C (Pl. 23, fig. 3) is characterized by an irregular boxwork system formed by subcylindrical galleries frequently bifurcating and flowing together in numerous and large cavities. A few, fine exploratory canals still occur in this stage. In some samples only phase D is present, in which the boxwork system may still be recognized, but the main galleries are wider and internodal lengths shorter in relation to width. The boxwork becomes very closed and labyrinthine. In late phase D the substrate is removed extensively, becoming restricted (Pl. 24, fig. 2) in places to thin struts and columns (Fig. 8). Maximum depth 20 mm.

In our material, gerontic forms occur that may represent phase E of this form, but are indistinguishable from some gerontic *Entobia mammillata*. These comprise large tuber–like galleries up to 30 mm wide, sharing narrower side branches that show a morphology like *E. megastoma*.

Stenomorphic material (Pl. 26, fig. 1). Natural and artificial casts show gallery systems that probably represent a stenomorphic development of *E. megastoma*. In each sample, diameter of the gallery is variable. In the limestone they are well developed mazes parallel to and immediately under the outer surfaces. In the shells the galleries are not cylindrical, but clearly flattened by the restriction of the substrate.

Observations. Characteristics of this form in our material closely fit the morphological description and dimensions given by Fischer for *Cliona megastoma*.

Specimen no.	Substrate	Preservation	Ø Apertures			Length of apertural canal			Ø apertural canal			Ø Swelling	Ø Gallery	Phase	Depth
			Average	Range	n	Average	Range	n	Average	Range	n	Range	Range		
27	Ls	Ac	0.8	0.5–1.0	14							≤ 2.5	0.3 - 1.5	A B	
28	Ls	Ac	0.6 1.2	0.3–1.3 0.6–1.7	6 20	1.8 3.7	0.8–5.0 1.3–5.9	5 9	1.3	0.6–2.0	7	6.0 - 7.5	0.8 - 3.2	B C	
25	O	Ac	0.61 1.64	0.3–1.2 0.5–2.5	14 23	0.8	0.5–1.4	11					10	D	20
40	Ls	Ac	1.7	1.0–2.5	24							15	1.0 - 5.0	D	
	Stenomorphs														
41	B	Nc		0.8–1.2	3								1.5 - 4.0	C	1.2
30	B	Nc											1.5 - 2.5	C	1.8

Table 7 – Numerical data for *Entobia megastoma* (Fischer). Abbreviations as in Table 3.

Boekschoten (1966) placed in synonymy with *C. megastoma* another ichnospecies of Fischer's, *Cliona cerithiorum*, after having examined topotype material of the same substrate species as Fischer's, i. e. *Campanile giganteum*. However, because different ichnospecies may occur within the same substrate, it is essential to examine the holotype itself before such a decision can be made. Fischer's types, however, are now lost. *C. cerithiorum*, on the basis of Fischer's illustrations, is a small–chambered camerate form clearly distinct from *Entobia megastoma*. Among the examples illustrated by Boekschoten (1966) as *Cliona megastoma*, one is camerate (pl. 2, D); another (pl. 2, E) is not clear in this respect. The other two (pl. 2, B, C) show only their apertures.

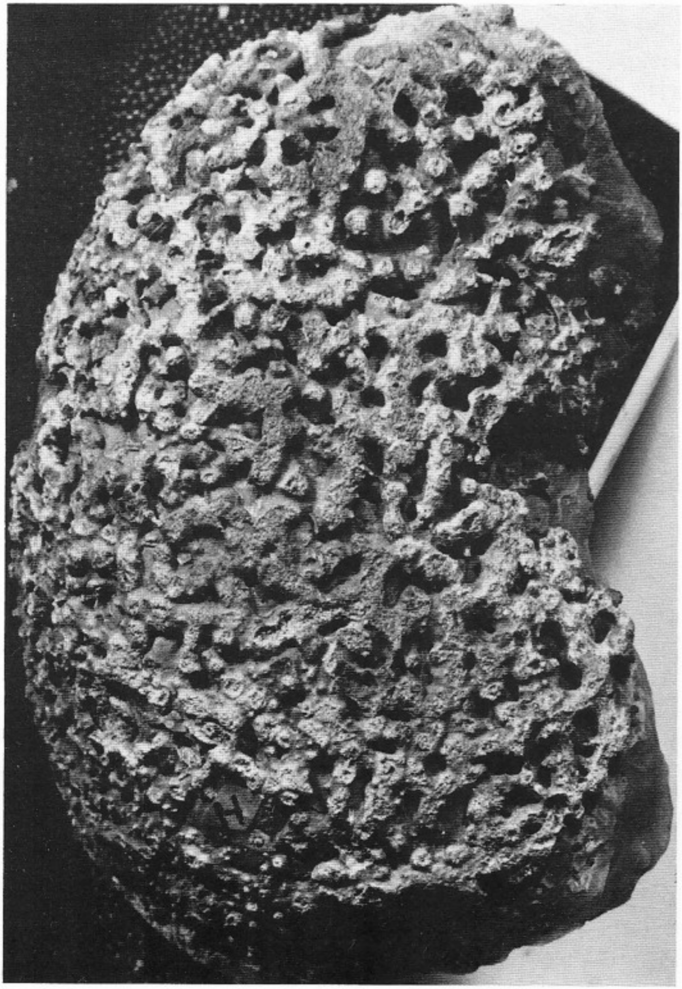

Fig. 9 – *Cliona microtuberum* Stephenson. Holotype slightly enlarged. U. S. National Museum no. 76266.

Size of aperture alone is not diagnostic of entobian ichnospecies (in our material several other ichnospecies have apertures as large as those of *E. megastoma*). For this reason we have not placed Boekschoten's (1966, 1967) examples in synonymy with *E. megastoma.*

Cliona cretacica Fenton & Fenton, 1932 b, may be a distinct form owing to regularity of the system due to the absence of large tuber–like cavities, and also to more constant diameter of the gallery which increases gradually from juvenile to more mature stages. The apertures seem smaller and more uniform in size than *E. megastoma*. Fenton & Fenton's holotype is lost, and the paratype poorly exposes the interior (pl. 29, fig. 2, 5). Possibly there is a resemblance between our stenomorphic examples (Pl. 26, fig. 1) and *C. cretacica* but synonymy cannot be considered certain.

The holotype of *Cliona microtuberum* Stephenson (1941, pl. 3, fig. 1, 2; pl 5, fig. 1) (Fig. 9) and two paratypes (pl. 3, fig. 4; pl. 5, fig. 2) correspond closely in morphology to *E. megastoma*. Slight differences are probably due to stenomorphy, Stephenson's material occurring in shells. A further possible difference is the tendency for the gallery in phase D to produce a rounded swelling immediately beneath the aperture, giving the spurious impression of a camerate system. This swelling has not been seen in our material, in limestone, but possibly occurs in *Ostrea* (not seen in cast). Stephenson's paratype (1941, pl. 3, fig. 3) is a different entobian, showing distinct cameration.

Material. Idiomorphs: ten artificial casts in limestone (P, C, SE), one in *Ostrea edulis* (P). Stenomorphs: three natural casts in *Glycymeris insubricus* (Stq); two artificial casts in small limestone pebbles (3.5 cm maximum size, P).

Entobia ovula ichnosp. nov.

Pl. 17, fig. 1,4; Pl. 18, fig. 2; Pl. 21, fig. 3; Pl. 23, fig. 2; Pl. 26, fig. 3;
Pl. 27, fig. 1; Pl. 28, fig. 4; Pl. 29, fig. 3; Text–fig. 10

Derivation of name. Latin, *ovulum* (technical neologism), egg–shape, after the fish–egg or snail's egg appearance of phase D.

Type–series. Holotype no. MGUH 16445 (195 P), Pl. 23, fig. 2; Pl. 27, fig. 1; paratypes, no. MGUH 16446 (181 P), Pl. 18, fig. 2; no. MGUH 16447 (177 C), Pl. 21, fig. 3; Pl. 28, fig. 4; no. MGUH 16448 (172 C); no. MGUH 16449 (179 P); no. MGUH 16450 (180 SE).

Horizon. Calcarenite di Gravina formation.

Type–locality. Cala Corvino (P), Monopoli, Bari.

Collocation. Geological Museum, University of Copenhagen, Denmark.

Diagnosis. A camerate entobian composed in the mature stage of small chambers of globose to ovoid shape, greatly crowded, arranged in a boxwork.

The chambers are separated from neighbours by a very short intercameral canal, usually reduced to a constriction. In phase C, the chambers are arranged in straight strings, forked at variable angles and anastomosed, giving rise to a network in one or two, poorly distinguishable tiers. A and B phases are reduced. Apertural canals distinct, tapering distally, or slightly inflated as a barrel. The openings are relatively small, numerous, rather regularly disposed, rarely fused.

Description. Camerate entobian developing a crowded boxwork arrangement in mature stages. The apertures are somewhat small (average 0.5 – 0.8 mm), circular, numerous and distributed rather regularly, in some cases in lines. From these arise short but distinct apertural canals, usually tapering outward or weakly inflated and barrel–like. Each chamber connects with the surface by a single canal, rarely two.

Phase A is represented by exploratory threads, little–branched, weakly swollen at nodes. This phase does not show clear diagnostic characteristics and is usually poorly developed. With the swelling of the fine canals and the appearance of constrictions we enter phase B, which is also very reduced. This comprises sub–cylindrical or oval chambers organized in rows and branched at variable angles. The rows may be parallel with the substrate surface, but commonly plunge into the matrix. In phase C (Pl. 21, fig. 3), the chambers range from globose to ovoid in shape and are separated by an extremely short intercameral canal or by a single constriction. They are arranged in straight rows like beads that intersect and branch to produce a network in one or two poorly distinguishable tiers. Slender apophyses, not really numerous; exploratory threads are rare and poorly developed (Pl. 28, fig. 4).

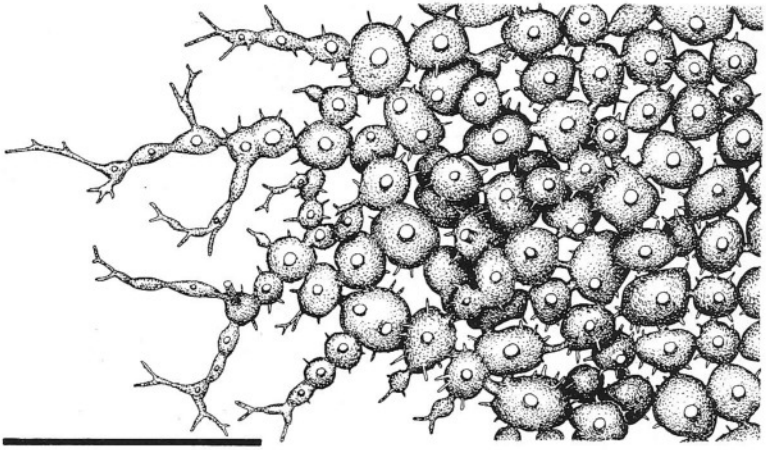

Fig. 10 – Part of an *Entobia ovula* ichnosp. nov. showing growth phases A to D. Compound camera lucida drawing of artificial casts in limestone. Scale bar = 1 cm.

Transformation to phase D involves multiplication of chambers in all directions. From the existing chamber a bud–like growth is differentiated, separated at first by a long intercameral canal and bearing long apophyses which rapidly connect it to nearby chambers. Next, the swelling of the chamber determines the disappearance of the intercameral canal; in this way the growth of the system as a whole proceeds as a compact, closed front, giving rise to a very crowded boxwork. However, even at this stage, the chambers still tend to be arranged in straight lines, but these rows are obscured at short intervals by the close crowding of the chambers. Each chamber is connected to six or seven others. They usually have distinct boundaries even where virtually in contact, avoiding fusion; but the shape consequently becomes more irregular, sub–prismatic. This phase is rarely present in the same sample as the earlier phases.

Stenomorphic and xenomorphic material. The stenomorphic form (Pl. 29, fig. 3) may not always be distinguished from stenomorphic *Entobia geometrica* because depression of the chambers causes them to become correspondingly broader, which reduces the characteristic size difference between these two forms. In xenomorphic forms in ostreids, the boxwork pattern is obliterated because the chambers tend to be developed along the laminae of the substrate. In transverse section, however, they show a strong tendency to be arranged in columns (Pl. 26, fig. 3).

Observations. This ichnospecies is separated from *E. laquea* by greater regularity in chamber shape; the mode of growth of the system like buds on a com-

			ø Apertures			ø Apertural canal			Length of apertural canal				Length of intercameral canal			ø constrictions			Length of chamber			Width of chamber					
Specimen no.	Substrate	Preservation	Average	Range	n	Average	Range	n	Average	Range	n	Number intercam. canal/chamber	Average	Range	n	Average	Range	n	Average	Range	n	Average	Range	n	Fusion of chambers	Phase	Depth
195	Ls	Ac				0,7	0,3–1,3	14	0,6	0,3–1,4	14	3–6				0,5	0,2–0,8	20	2,3	1,5–3,7	29	1,9	1,2–3,0	29	P–R	D	9
177	Ls	Ac	0,6	0,3–0,8	27	0,5	0,4–0,7	15	0,6	0,4–0,9	15	2–4				0,7	0,5–1,0	30	1,8	1,3–2,5	33	1,7	1,0–2,3	33	P–R	C(B)	5
180	Ls	Ac	0,5	0,3–0,8	16							5–6				0,7	0,2–1,2	30	2,0	0,8–3,0	26	1,7	0,8–3,0	26	P–R	D(C)	8
138	Ls	Ac	0,8	0,5–1,5	9							5–6				0,6	0,3–0,8	17	2,4	1,0–2,8	15	2,2	1,0–2,8	15	P–R	D	7
181	Ls	Ac	0,6	0,2–2,0	58	0,6	0,3–0,8	14	0,6	0,3–1,0	14	≤ 7				0,5	0,2–1,0	24	2,4	0,8–4,8	27	2,0	0,8–2,7	27	P–R	D	11
179	Ls	Ac	0,6	0,3–0,8	5	1,3	1,2–1,7	11	1,2	0,7–1,7	11	4–6				0,6	0,3–0,9	31	2,1	1,0–2,7	32	1,8	1,0–2,5	32	P–R	D	8
168	Ls	Ac	0,6	0,3–0,9	25														2,0	0,8–3,0	22	1,7	0,8–2,2	22	P–R	D	
S.G.	Ls	Cv	0,6	0,3–1,4	55														1,8	1,0–3,2	33				As		
	Form A																										
144	Ls	Ac	0,5	0,1–0,7	21							5–6	0,2	01–0,3	1,2	0,4	0,15–0,5	24	1,6	0,8–2,5	27	1,4	0,8–2,2	27	P–R	D	7
4	Ls	Ac														0,3	0,2–0,5	16	2,2 1,3	1,5–2,9 0,7–2,0	5 12	1,0 1,2	0,7–1,3 1,0–1,7	5 12	A P–R	B D	4
159	Ls	Ac											0,2	0,1–0,3	5	0,3	0,15–0,6	12	1,7	1,2–2,5	18	1,4	1,0–1,8	18	P–R	D	
150	Ls	Ac	0,6	0,5–0,7	4							5–6	0,3	0,2–0,4	4	0,4	0,15–0,5	4	1,3	1,0–1,6	7	1,1	0,8–1,3	7	P–R	D	
147	Ls	Ac	0,9	0,3–1,2	12									≤ 0,3	10	0,6	0,3–1,0	10	1,8	1,0–2,5	13	1,6	1,0–2,0	13	A	D	

Table 8 – Numerical data for *Entobia ovula* ichnosp. nov. Abbreviations as in Table 3.

pact front without the prior development of exploratory threads; and the greater crowding of chambers owing to the absence of necks before constrictions. In *E. ovula*, the juvenile phases are reduced and phase D is reached rapidly.

There is even greater difficulty in distinguishing *E. ovula* phase D idiomorphs from *E. laquea* phase C stenomorphs as crowding imposed by stenomorphy causes the two forms to resemble each other; however, *E. laquea* has a continued presence of phase A into late stages which is lacking in *E. ovula.*

Among the fossil forms illustrated by Fischer (1868) the natural cast of *Cliona glomerata* Michelin in a shell of *Exogyra columba* could be compared in size and morphology with our xenomorphic form.

The excavations of living *Cliona vastifica* Hancock resemble *E. ovula* in arrangement, form and size of chambers. This is especially clear if we compare borings of *C. vastifica* in phase C in limestone (de Groot 1977, fig. 24, 25).

Identical borings occur in oysters in the Maastrichtian Prairie Bluff Chalk (Selma Group) of Alabama, U.S.A. (unpublished observation).

E. ovula differs from *E. cretacea* Portlock in degree of crowding. *E. cretacea* retains markedly thicker dividing walls between chambers and clearly developed intercameral canals are always visible.

Material. Idiomorphs: thirteen artificial casts in limestone (C, P), three in pebbles (P); one natural cast in *Glycymeris bimaculata* (CP). Xenomorphs: three in *Ostrea edulis lamellosa* (SG); one artificial cast in *Ostrea edulis* (P). Stenomorphs: one in indeterminable bivalve (Stq).

Entobia ovula ichnosp. nov. form A

Pl. 17, fig. 1; Text–fig. 11

Description. A camerate entobian organized, in phase D, in clusters restricted to limited area. Phase A is well developed and presents generally very long, slender canals, a little arcuate, rarely branched. These slender canals fuse to form galleries the size of which varies owing to weak swelling at intervals. Phase B is represented by linear, sparsely branched rows of chambers from subovoid to subcylindrical shape resembling strings of beads. These rows connect different D–phase clusters of chambers. Phase C has not been recognized. Phase D consists of small chambers that are more or less ovoid to subspherical in shape, separated by short intercameral canals, or by constrictions preceded by a weak tapering. In a few cases, the chambers are partially fused. Extension of the system in this phase occurs by the appearance of rounded, small, bud–like growths from earlier chambers, the buds bearing very long apophyses. Another mode of growth is the development in the exploratory threads of constrictions and swellings at regular intervals.

In all phases there are numerous, long apophyses, simple or forked.

Observations. The main characteristic of this form of camerate entobian is the narrowly localized distribution of small clusters of chambers. The locations of these clusters are characteristically around and among the chambers of different ichnospecies of *Entobia.* For this reason it is difficult to recognize apertures and to distinguish these from those of the adjacent entobian. The present entobian shows affinity to *E. ovula*, commonly having the same chamber morphology and growing similarly with a compact front. Nevertheless, on average it has slightly smaller chambers and rarely shows the crowded characteristic of *E. ovula*, owing to the general presence of necks before the constrictions. This feature and the possession of numerous apophyses and exploratory threads, connects this form to *E. laquea.*

These differences are insufficient for the establishment of a separate ichnospecies, and we therefore treat it tentatively as a form of *E. ovula*, to which we judge it as having closest affinity.

Material. Fourteen artificial casts in limestone (P, C).

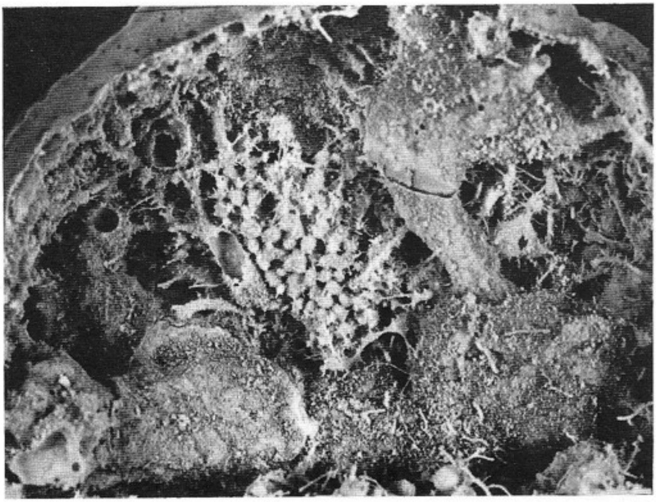

Fig. 11 – *Entobia ovula* form A, nestling in indeterminateerontic sponge boring. No. MGUH 16454 (162 P); x 2.

Entobia paradoxa (Fischer, 1868)

Pl. 20, fig. 2; Pl. 26, fig. 4; Pl. 28, fig. 3; Pl. 29, fig. 1, 4; Text–fig. 12

1868 *Cliona paradoxa* Fischer, p. 169, pl. 25, fig. 8.

Fischer founded *Cliona paradoxa* on a natural cast of an excavation in a single example of *Cyclolites elliptica* deriving from «la craie à *Hippurites* des Corbières». The author placed together in the same species two contrasting systems, the one composed of irregular chambers and the other composed of long, cylindrical galleries. Fischer explained the difference in morphology as differences in ontogenetic stages. In our material, however, more mature phases, having the chambers partially fused as a gallery, invariably retain some constrictions. In still older forms the diameter becomes very variable, as indeed is shown in another part of Fischer's picture of the type of *Cliona paradoxa* (1868, pl. 25, fig. 8 right top). The long and regular gallery, on the other hand, might be explained either as belonging to the same system and representing a xenomorphic form, following structural features in the coral substrate, or it could have been produced by a different borer. In either case these regular galleries cannot be considered diagnostic of *Cliona paradoxa.* Owing to these inconsistencies, it is necessary to emend Fischer's original diagnosis.

Emended diagnosis. A camerate entobian composed, in mature stages, of a

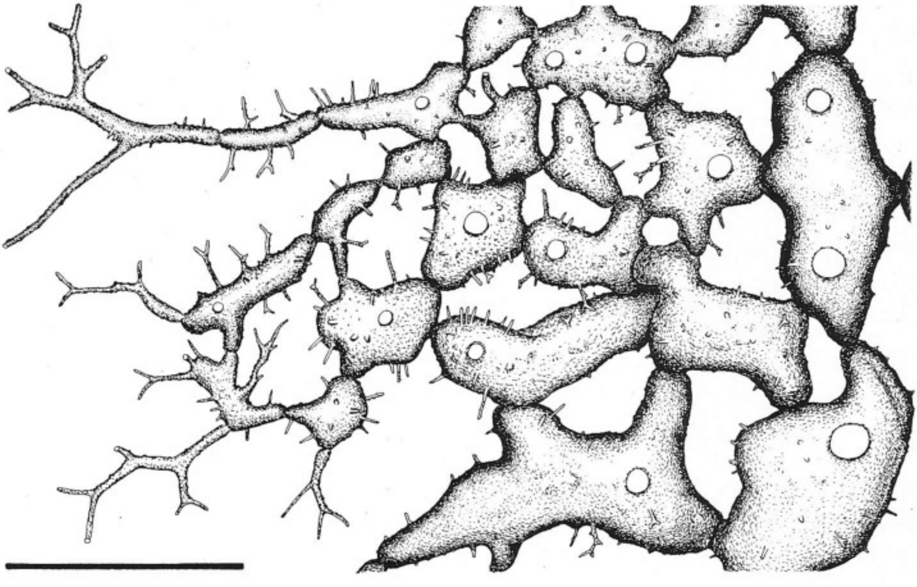

Fig. 12 – Part of an *Entobia paradoxa* (Fischer) showing growth phases A to D. Camera lucida drawing of an artificial cast in limestone. Scale bar = 1 cm.

network of very irregular chambers, somewhat amoeboid in shape, usually arranged in two tiers parallel to the substrate surface. Each chamber is connected to several others; the shape becomes extremely irregular owing to tapering as necks of varying lengths, before the constrictions that separate each chamber from its neighbours. In gerontic forms, a partial fusion among the chambers leads to the development of non–camerate galleries, usually variable in diameter and lacking diagnostic character. Apertures circular in shape, usually relatively small, uncrowded.

Description. Apertures relatively small (0.6 – 1.2 mm in average), circular, rarely fused, more or less uncrowded. From each of these arises a very short apertural canal which connects certain chambers with the outside. Not every chamber is so connected but those that are possess up to three apertural canals. Length of the apertural canal in phase C is up to 0.5 mm. The chambers are arranged in a network developed in one or two tiers, lying subparallel to the substrate surface. Maximum depth 8 mm.

Phase A (Pl. 26, fig. 4; Pl. 29, fig. 1) is represented by exploratory threads that continue in galleries (about 1 mm wide), running in irregular pattern. Diameter is variable owing to the existence of weak swellings along the gallery, particularly at branching points. At the beginning of phase B the swellings become more accentuated and take on an elongate amoeboid shape. Several galleries branch off from such swellings. Weak constrictions become evident. In more advanced phase B, the enlargement of the cavities produces distinct chambers of extremely irregular shape, elongated strictly parallel to the external surface. The more diagnostic feature is the gradual tapering of the chambers to constrictions that separate them from neighbouring chambers. This characteristic becomes better developed in phase C.

In phase C the chambers increase in height, and become more or less isometric in the plane parallel to the surface; the chambers are very variable in shape, ranging from triangular or polygonal to star–shaped. Each chamber is connected with up to 6 or 7 others, in the same plane or in two tiers, to produce a network having a relatively large mesh. In all these phases, slender apophyses are present, some of them bifurcated. Phase C is the most characteristic and best developed phase of the ichnospecies.

Passage to phase D is gradual: the meshes become narrower by the addition of new chambers and the swelling of old ones, which approach the shape of a tuber. After this they begin to fuse together, obliterating the characteristic amoeboid shape and the two–tiered network becomes a boxwork system. In more extreme form the chambers tend to resemble phase D of *E. megastoma.* Phase E has not been identified.

Stenomorphic material. In stenomorphic form this ichnospecies is still recognizable while the irregular shape of the chambers is preserved and in particular the tapering towards the constrictions (Pl. 29, fig. 4). When the chambers become more numerous (phase D) the crowding and flattening of the system obliterates the diagnostic form of the ichnospecies, which tends to approach that of *E. geometrica*; or if the chambers are partially fused, to that of *E. megastoma.*

Observations. In phase A and the beginning of B, until the swellings are clearly delimited by constrictions, it is not possible to separate this ichnospecies from the juvenile form of *E. megastoma.* Furthermore, one can never be quite certain of the taxonomic attribution of gerontic individuals if they are not still connected to mature phases; the complete fusion of chambers leads to a morphology comparable to that of *E. megastoma.*

Material. Idiomorphs: two natural casts in shell of Veneridae and *Glycymeris* sp. (Stq), one in undeterminable bivalve shell (C P); twelve artificial casts in limestone (SE, C, P). Stenomorphs: five natural casts in shell of Veneridae and *Glycymeris* sp. (Stq).

			Ø Apertures (large)			Ø Apertures (small)		Length of apertural canal		Ø gallery	Ø constrictions			Length of chamber.			Width of chamber			
Specimen no.	Substrate	Preservation	Average	Range	n	Range	n	Range	Number foramina / chamber	Range	Average	Range	n	Average	Range	n	Average	Range	n	Phase
77	Ls	Nc	0.7	0.2-1.2	31				1-3		0,5	0.2-0.7	17	5,8	2,3-10	15	3,1	1,5-4,7	15	C
70	Ls	Ac	0.6	0.2-1.3	51	<1	>50	≤0.5	1-3		0,8	0.2-1.3	22	6,8	4,6-10	22	4.4	2,3-5,6	20	C
71	Ls	Ac	0.8	0.4-1.8	24	<1.5	>50		1-3		0.6	0.2-1,2	12	4,3	2,3-6,3	12	2,6	1,7-40	13	C
76	Ls	Ac	1,2	0,8-1.7	10			1.7-2.5		2.8-6.6		1,6-5,0	3							D

Table 9 – Numerical data for *Entobia paradoxa* (Fischer). Abbreviations in Table 3. In the measurement of chamber dimensions, the longest dimension parallel to the surface is considered the length, and the next–longest in the same plane, the width, measured from constriction to constriction.

Entobia volzi ichnosp. nov.

Pl. 22, fig. 3, 4; Pl. 25, fig. 3; Pl. 28, fig. 1, 2; Text–fig. 13

Derivation of name. Named in honour of Peter Volz, who made the first detailed description (Volz, 1939) of the boring of *Cliothosa hancocki* (Topsent).

Type–series. Holotype no. MGUH 16460 (208 SE), Pl. 22, fig. 3, 4; paratypes no. MGUH 16461 (209 SE), Pl. 25, fig. 3; Pl. 28, fig. 2; no. MGUH 16462 (206 SE); no. MGUH 16463 (207 P).

Horizon. Pietra Leccese formation (= Calcarenite di Apricena *pro parte*).

Type–locality. Pantano S. Egidio (SE), Gargano, Foggia.

Collocation. Geological Museum, University of Copenhagen, Denmark.

Diagnosis. Diminutively camerate entobian consisting, in phase D, of chambers connected by wide intercameral canals or partially fused, taking a form resembling an irregular, close framework. This system is crossed in all direction by relatively wide, subcylindrical canals that connect with the substrate surface through large apertures. Growth front compact. Phases B and C are considerably reduced, characterized by appearance of irregular chambers or clusters of chambers as small swellings on the walls of the wide canals. Phase A comprises long, slender canals arranged irregularly and branched as a boxwork, having palmate expansions at nodal points. Apertures of two sizes, circular to oval, very irregularly distributed.

Description. In phase A of this entobian, long canals (0.3 – 0.4 mm wide), varying from slightly arcuate to sublinear, a few forked, connect with the surface, normally at high angle. At a more advanced stage the canals become wider (about 0.8 mm) but in some cases the diameter becomes extremely variable owing to palmate expansion at nodal points. The wider canals are destined to become major passageways leading to large apertures while the galleries having variable diameter give rise to the camerate portion of the boring. The pattern at this stage is an irregular boxwork. Passage to phase B (usually reduced) is recognized by differentiation of subglobose swellings, most commonly where the gallery is bent as an elbow, or laterally on the sides of the gallery.

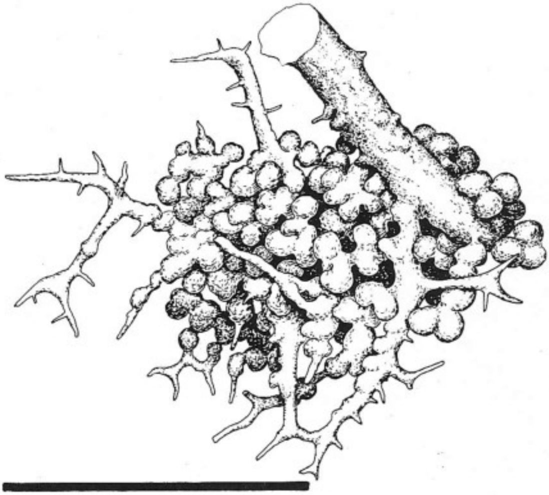

Fig. 13 – Part of an *Entobia volzi* ichnosp. nov. showing growth phases A to D and a single apertural canal. Camera lucida drawing of an artificial cast in limestone. Scale bar = 1 cm.

In phase C, the galleries become obviously wider (about 1.2 mm), in some cases bearing side branches forking acutely in a direction away from the substrate surface. From these galleries, yet smaller galleries arise in all directions bearing numerous apophyses. The surface of the main galleries becomes irregularly gnarled owing to the growth of numerous small chambers. The canals are then gradually covered by clusters of such chambers, particularly around nodal points. In many cases they are partially fused in irregular shape or connected by relatively wide intercameral canals.

Phase D is characterized by wide, subcylindrical canals, the space between them being completely occupied by numerous small chambers, partially fused, presenting a complicated, crowded framework formed by irregular interlacing of contorted columns. The tubercles of the microsculpture are particularly clearly visible (about 0.04 mm).

Apertures of two sizes. The largest (Tab. 10) are sparsely and irregularly distributed, circular to oval, amongst which are scattered distinctly smaller apertures. Maximum depth 25 mm.

Specimen no.	Substrate	Preservation	ø Apertures (large)			ø Apertures (small)			ø Main canals	Length of intercameral canal			ø intercameral canal			Length of chamber			Width of chamber			Fusion of chamber		
			Average	Range	n	Average	Range	n	Range	Average	Range	n	Average	Range	n	Average	Range	n	Average	Range	n		Phase	Depth
208	Ls	Cv	1.3	08-27	31	0.3	0.1-0.9	20	1.5,2.5,3.5							0.8	0,5-1,5	12	07	0,5-1.1	12	P	D	>18
209	Ls	Ac								0,3	0,1-0,6	20	0,5	0,2-1,2	23	1.1	0,8-1.5	25	07	0,5-1,1	25	P	A-D	20
Cliothosa hancocki (Topsent)																								
210	Ls	Ac	1.5	0,8-2,5	9	0.2	0,1-0,3	5		0,3	0,1-0,5	15	0,4	0,2-1,2	23	0.9	0,6-1,4	23	08	0,5-1,2	23	P	A-D	>20

Table 10 – Numerical data for *Entobia volzi* ichnosp. nov. Abbreviations as in Table 3.

Observations. The ichnospecies is easily distinguishable in all phases and in all kinds of preservation (in the original substrate, Pl. 22, fig. 3; Pl. 28, fig. 1; and as casts). We have observed identical perforations both in Danian limestone (Pl. 28, fig. 1) and in Campanian and Maastrichtian belemnite rostra from many localities in the NW European chalk.

Among Recent boring sponges, the excavations of *Cliothosa hancocki* (Topsent) correspond to *Entobia volzi* (Pl. 16, fig. 2), as clearly illustrated by Volz (1939, pl. 4, fig. 2, 3).

Material. Two borings in calcareous pebbles (CP).

Conclusions.

This study represents the first attempt in recent years to examine the taxonomy of the ichnogenus *Entobia*, following a reexamination of the type–ichnospecies, *Entobia cretacea* Portlock, by Bromley (1970). It was found that, although borings of this kind are extremely abundant in Mesozoic, Tertiary and Quaternary strata, it is only with material preserved in a particular way that sufficient diagnostic characters can be observed for full taxonomic evaluation. Ideally, natural or artificial casts of idiomorphic borings should be available. Only a slight degree of stenomorphism in restricted substrates, or xenomorphic deformation by foreign structures is sufficient to obscure the diagnostic characters of most of the ichnospecies. Commonly, moreover, a misleading impression of the morphology is gained from cross sections, even where the borings are not filled with lithified sediment or cement. Nevertheless *E. geometrica, E. volzi,* and some specimens of *E. megastoma* and *E. mammillata* can be identified readily in cross sections of empty borings. *E. volzi* is so distinctive that it may commonly be recognizable also in sections of sediment–filled borings.

Taxobases on which entobians have been distinguished include the detailed anatomy of the boring and the ontogenetic phases through which it passes.

Acknowledgements.

We thank J. C. Fischer, Muséum National d'Histoire Naturelle, Paris, for searching for P. Fischer's type–material. Jan Aagaard (Geological Central Institute, University of Copenhagen) applied his unusual skills to the photography of very difficult material. We thank N. Folco (Dipartimento di Geologia e Geofisica, Università di Bari) for helping in preparation of casts.

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PLATE 16

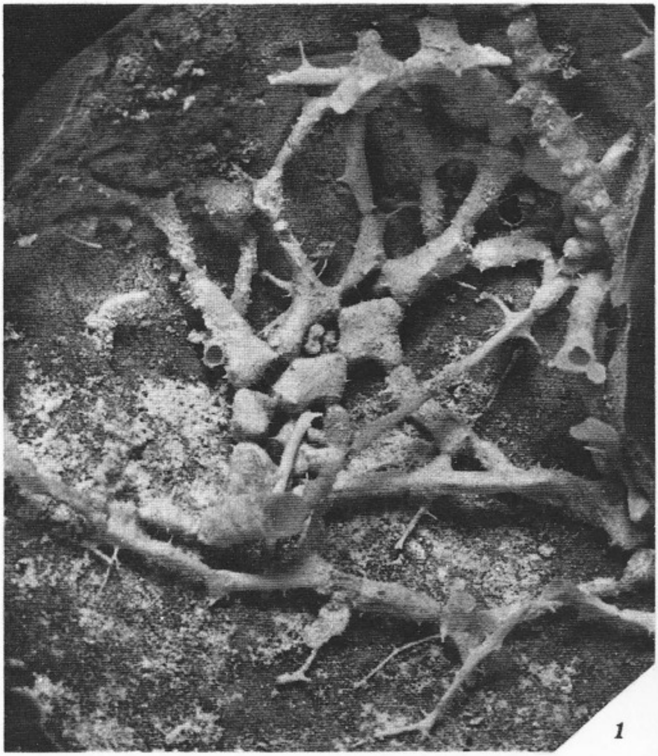
Fig. 1 – *Entobia cateniformis* ichnosp. n. Paratype. No. MGUH 16415 (221 P).

Fig. 2 – *Cliothosa hancocki* (Topsent) boring (= *E. volzi*), artificial cast, limestone from –2 m water at Lindos, Rhodes, Greece. No. MGUH 16465 (210).

Fig. 3, 5 – *Entobia cateniformis* ichnosp. n. Paratype. No. MGUH 16414 (216 P).

Fig. 4 – *Entobia cateniformis* ichnosp. n. Paratype. No. MGUH 16416 (223 C).

All samples x 2.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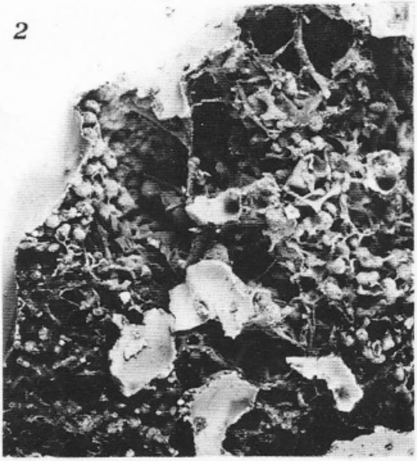
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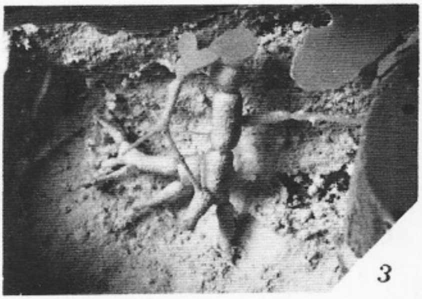
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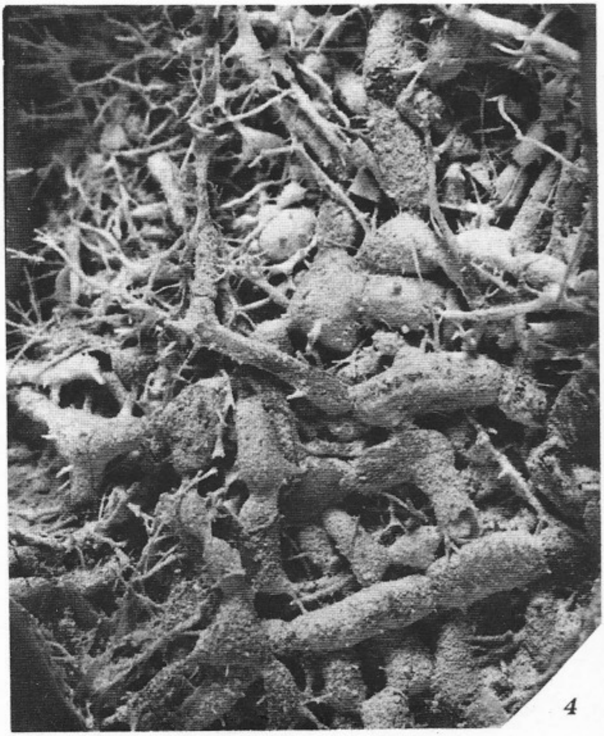
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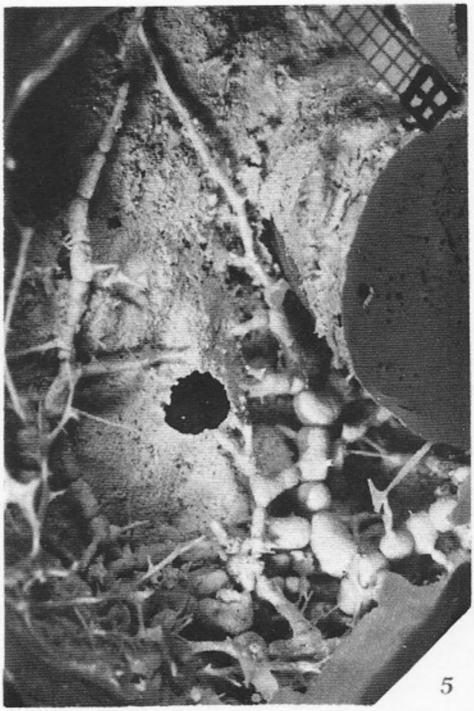
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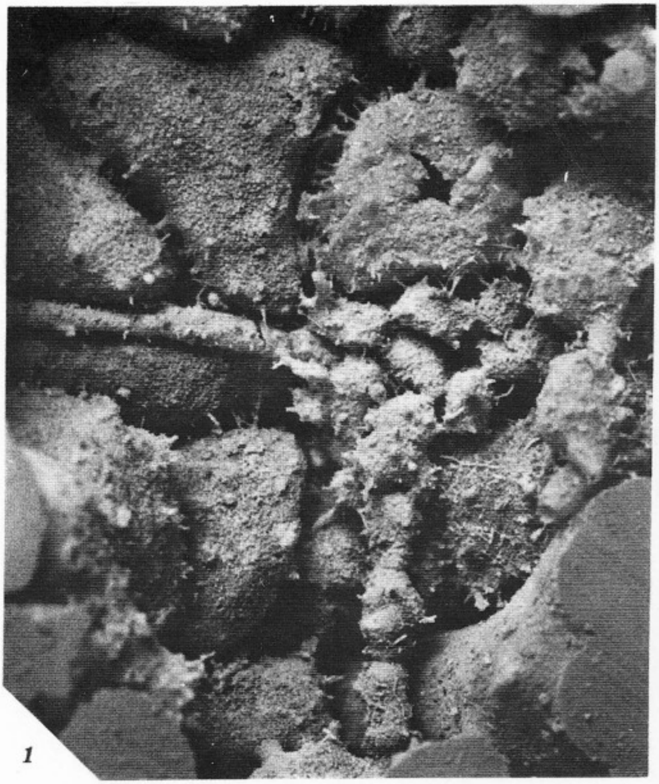
PLATE 17

Fig. 1 – *Entobia ovula* ichnosp. n. Form A, nestling among chambers of *E. geometrica*; microsculpture of walls of both species has about the same size. No. MGUH 16455 (4 P); x 5.

Fig. 2 – *Entobia laquea* ichnosp. n. Phase A (B). No. MGUH 16432 (108 P); x 2.

Fig. 3 – *Entobia cateniformis* ichnosp. n. Holotype. No. MGUH 16413 (14 P); x 2.

Fig. 4 – *Entobia ovula* ichnosp. n. No. MGUH 16451 (144 P); x 2.



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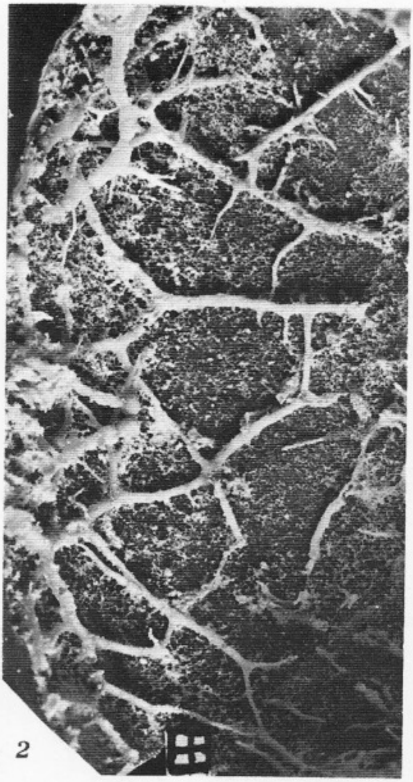

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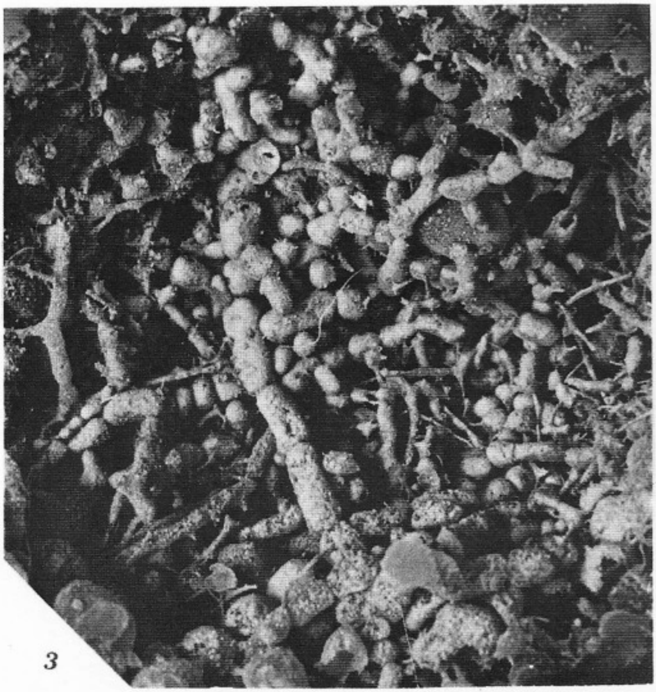

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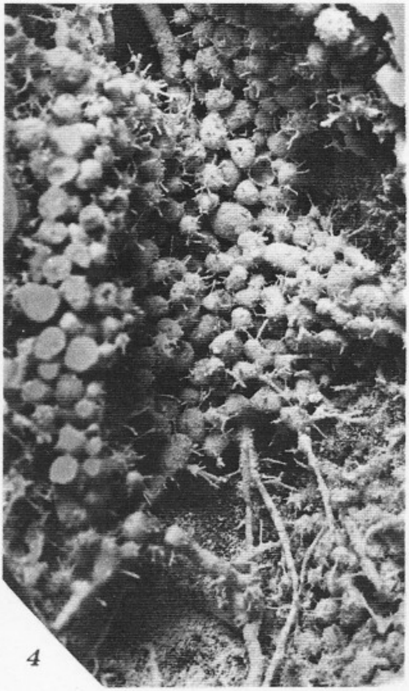

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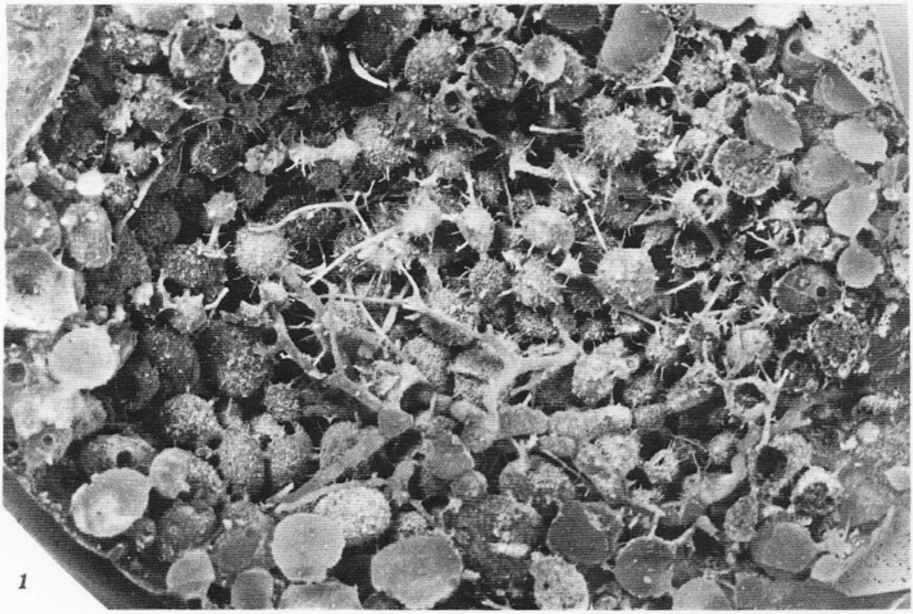
PLATE 18

Fig. 1 – *Entobia geometrica* ichnosp. n. Holotype. No. MGUH 16419 (7 C); x 2.

Fig. 2 – *Entobia ovula* ichnosp. n. Paratype. No. MGUH 16446 (181 P); x 5.



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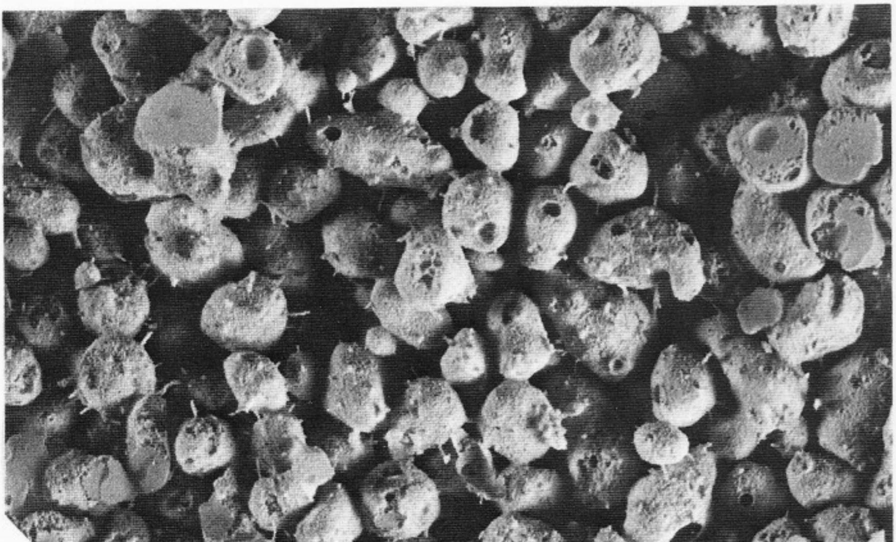

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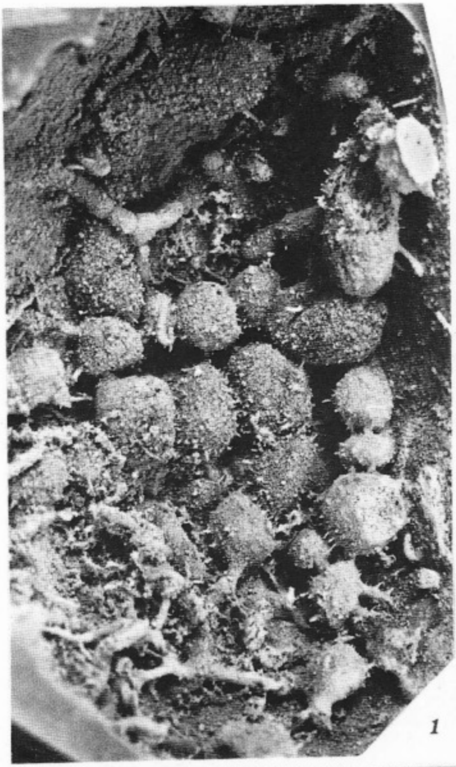
PLATE 19

Fig. 1 – *Entobia geometrica* ichnosp. n. Paratype. No. MGUH 16420 (1 P); x 2.

Fig. 2 – *Entobia laquea* ichnosp. n. Paratype. No. MGUH 16429 (125 C); x 2.

Fig. 3 – *Entobia geometrica* ichnosp. n. Holotype. No. MGUH 16419 (7 C); x 5.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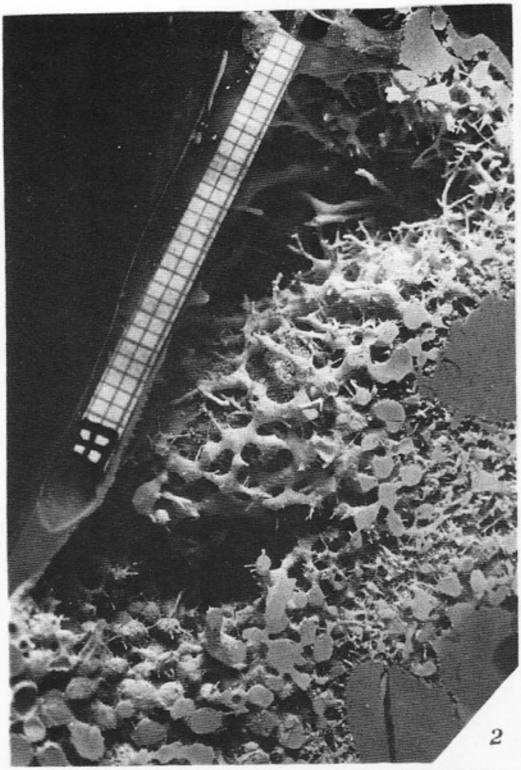
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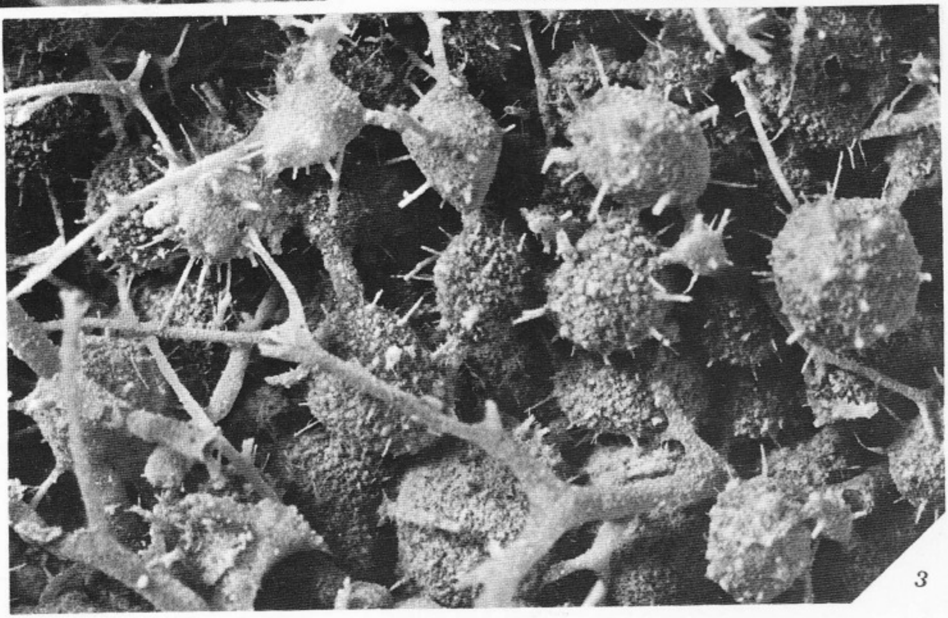
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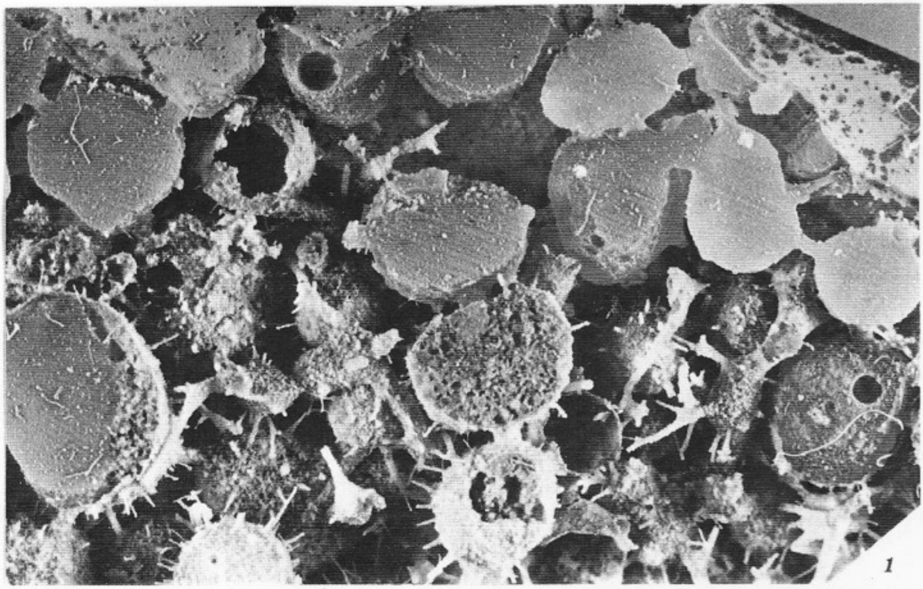
PLATE 20

Fig. 1 – *Entobia geometrica* ichnosp. n. Holotype. No. MGUH 16419 (7 C). Cast chambers sectioned to show intercameral canals; x 5.

Fig. 2 – *Entobia paradoxa* (Fischer) in indeterminable bivalve shell. Natural cast. No.MGUH 16456 (81 Spt); x 2.

Fig. 3 – *Entobia mammillata* ichnosp. n. Paratype. No. MGUH 16438 (66 C); x 2.



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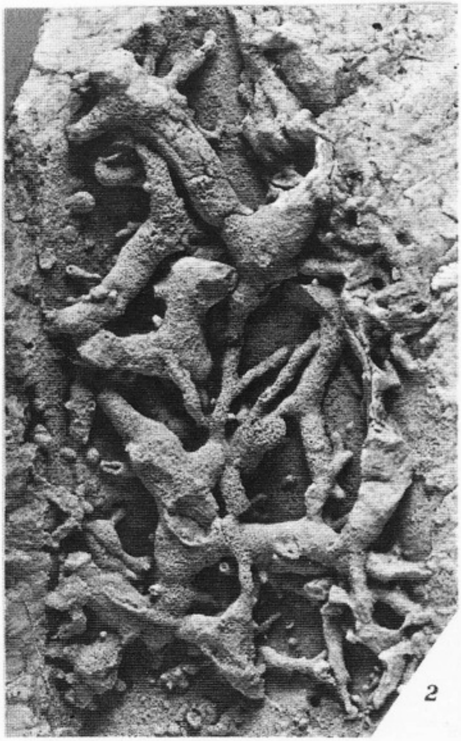

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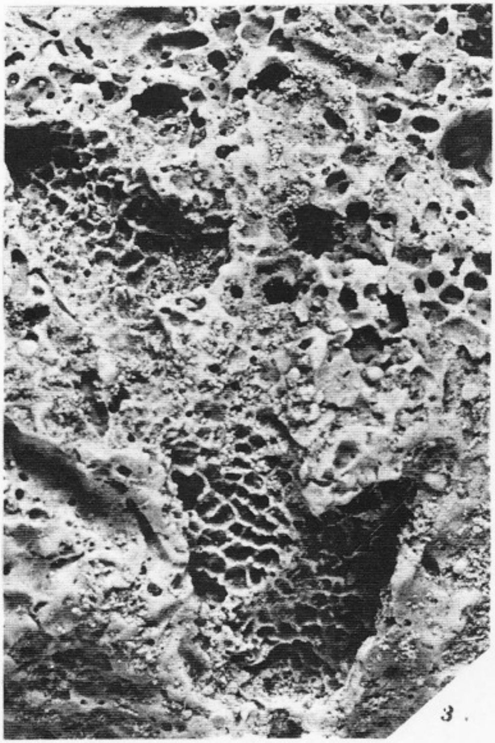

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PLATE 21

Fig. 1 – *Entobia geometrica* ichnosp. n. Paratype. No. MGUH 16421 (3 P).

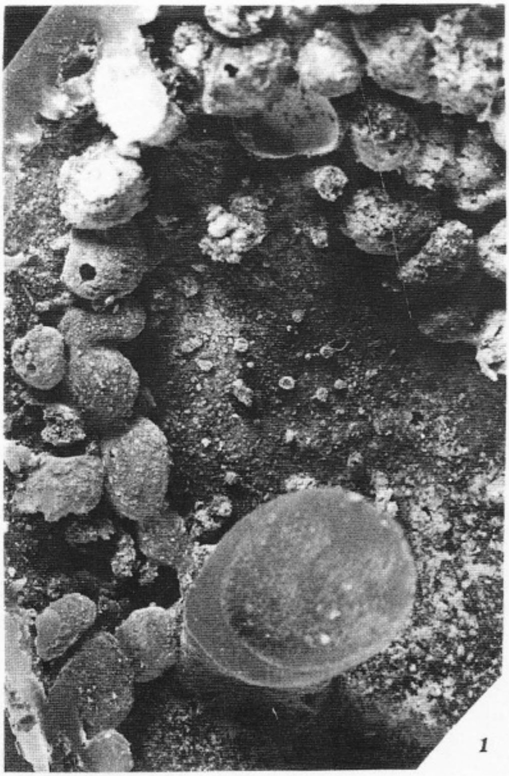
Fig. 2 – *Entobia laquea* ichnosp. n. in venerid shell. Natural cast. No. MGUH 16433 (131).

Fig. 3 – *Entobia ovula* ichnosp. n. Phase C. Paratype. No. MGUH 16447 (177 C).

Fig. 4 – Stenomorphic *Entobia geometrica* ichnosp. n. Natural cast. No. MGUH 16426 (35 Stq).

Fig. 5 – Stenomorphic *Entobia geometrica* ichnosp. n. Natural cast. No. MGUH 16427 (34 Stq).

All samples x 2.



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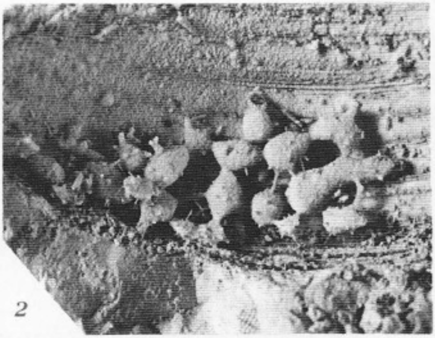

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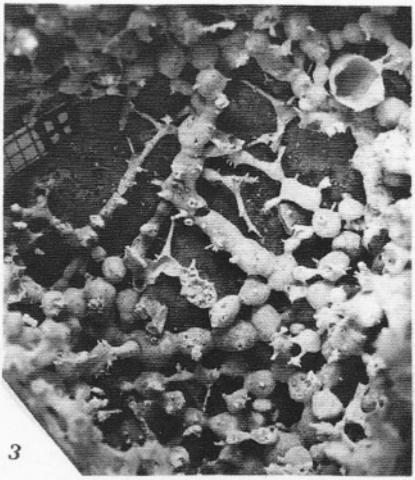

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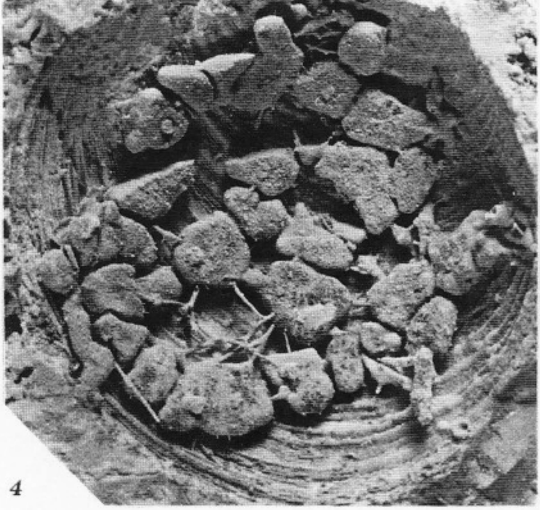

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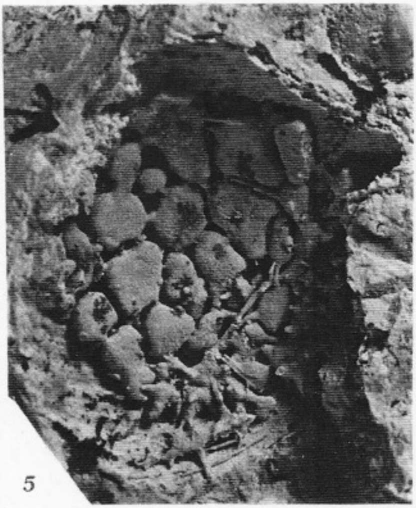

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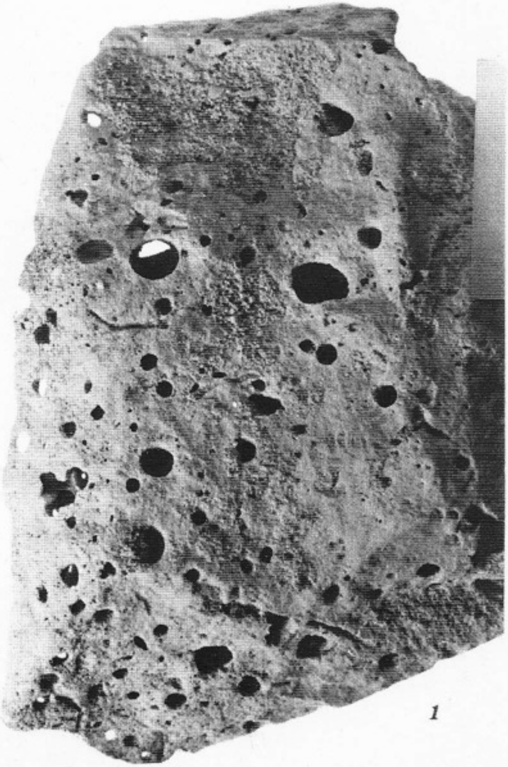
PLATE 22

Fig. 1, 5 – *Entobia geometrica* ichnosp. n. Paratype. No. MGUH 16423 (23 P).

Fig. 2 – *Entobia geometrica* ichnosp. n. Paratype. No. MGUH 16422 (10 P).

Fig. 3, 4 – *Entobia volzi* ichnosp. n. Holotype. No. MGUH 16460 (208 SE). Note large apertures visible through the specimen on under side in fig. 3.

All samples x 2.



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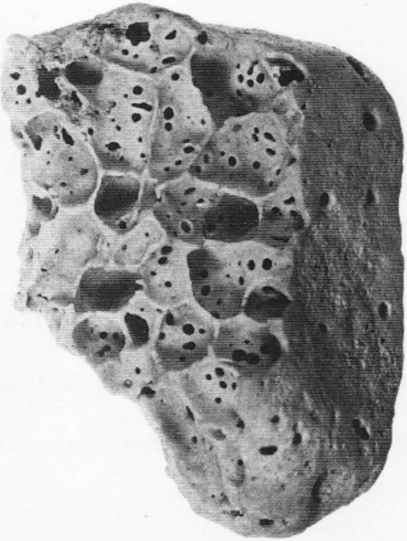

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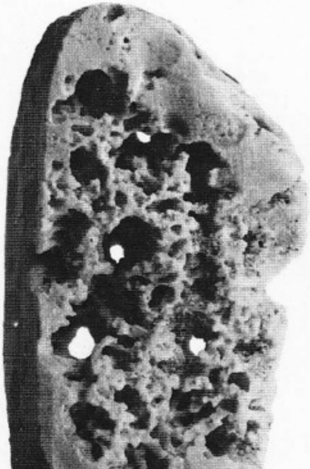

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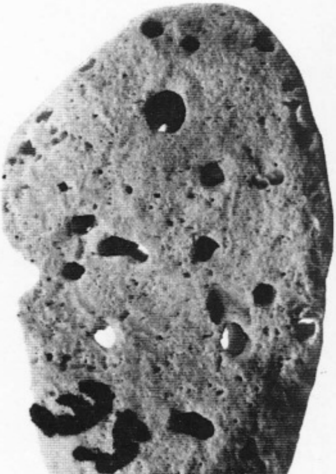

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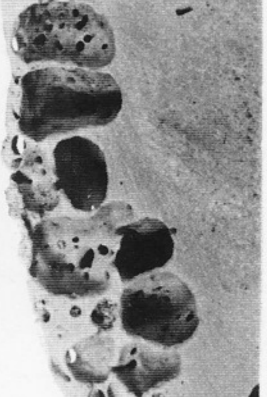

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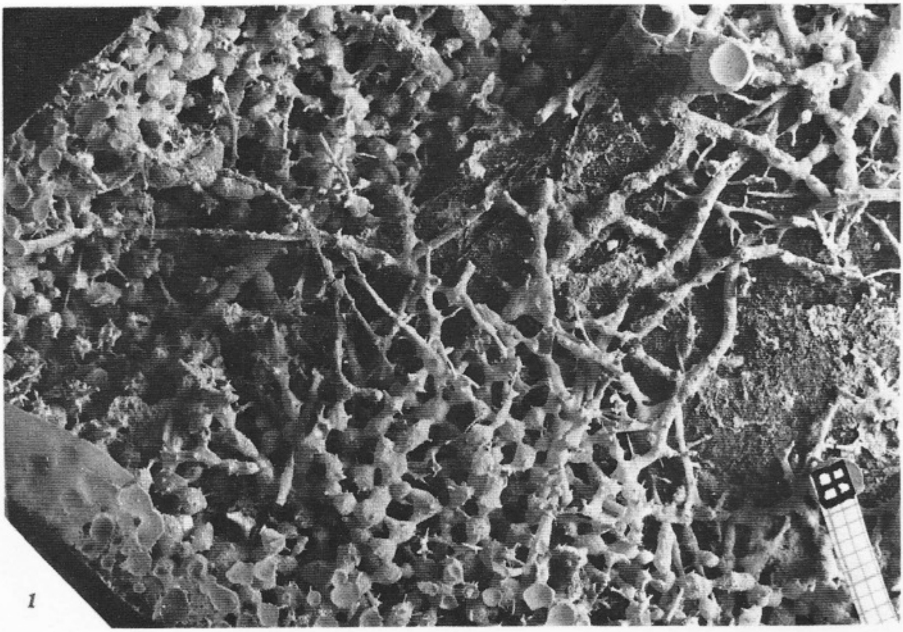
PLATE 23

Fig. 1 – *Entobia laquea* ichnosp. n. Holotype. No. MGUH 16428 (102 C); x 2.

Fig. 2 – *Entobia ovula* ichnosp. n. Holotype. No. MGUH 16445 (195 P); x 5.

Fig. 3 – *Entobia megastoma* (Fischer). Phase C. No. MGUH 16441 (29 C); x 2.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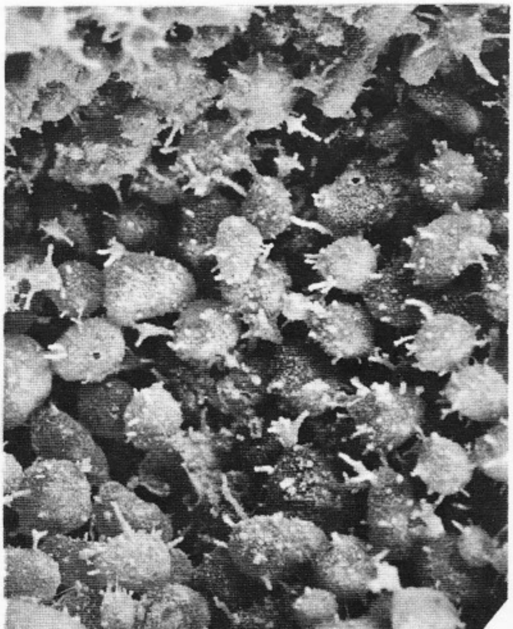
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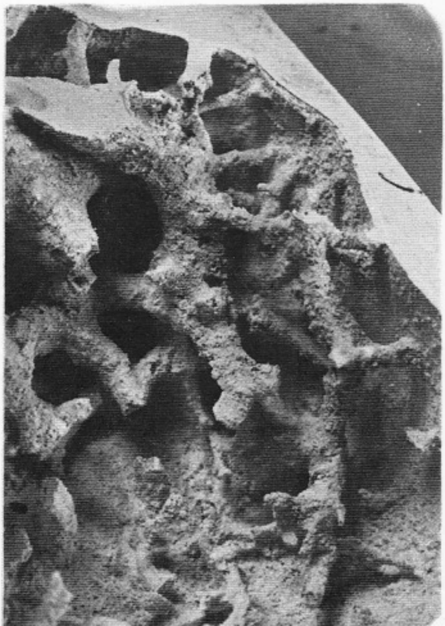
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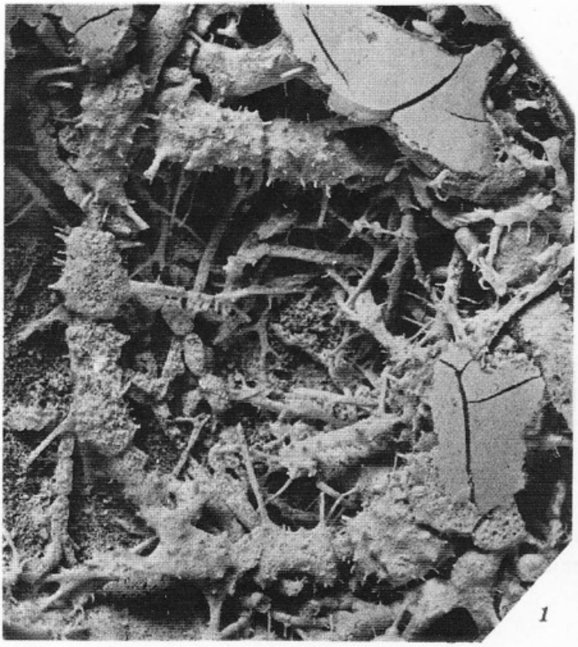
PLATE 24

Fig. 1 – *Entobia mammillata* ichnosp. n. Holotype. No. MGUH 16435 (47 P).

Fig. 2, 3 – *Entobia megastoma* (Fischer) in *Ostrea edulis* Linnaeus. No. MGUH 16442 (25 P).

Fig. 4 – Indeterminable stenomorph. No. MGUH 16466 (231 CP).



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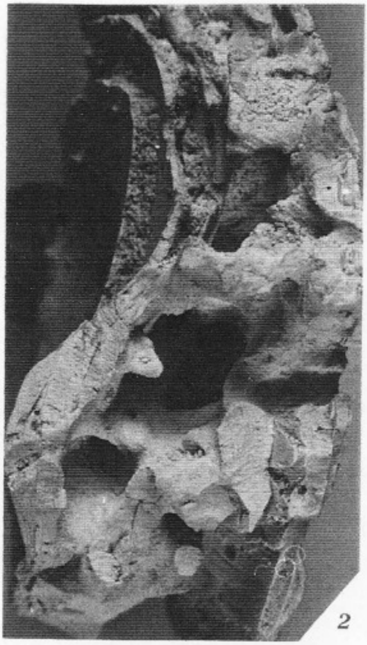

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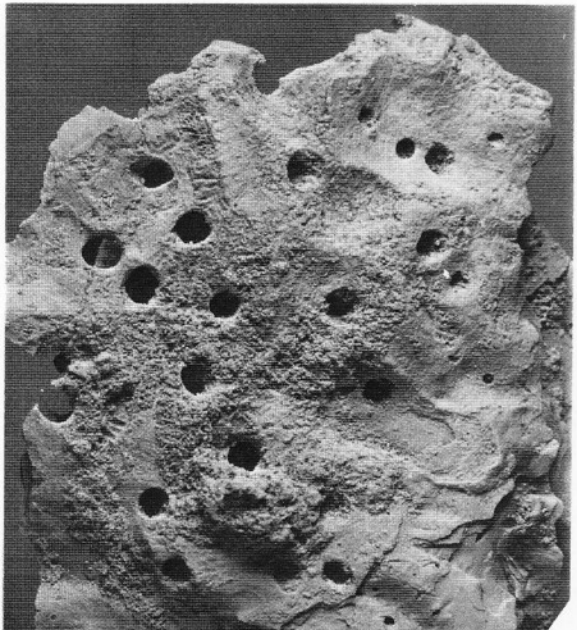

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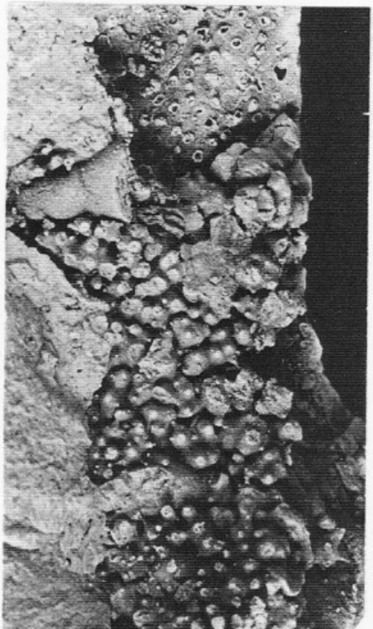

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PLATE 25

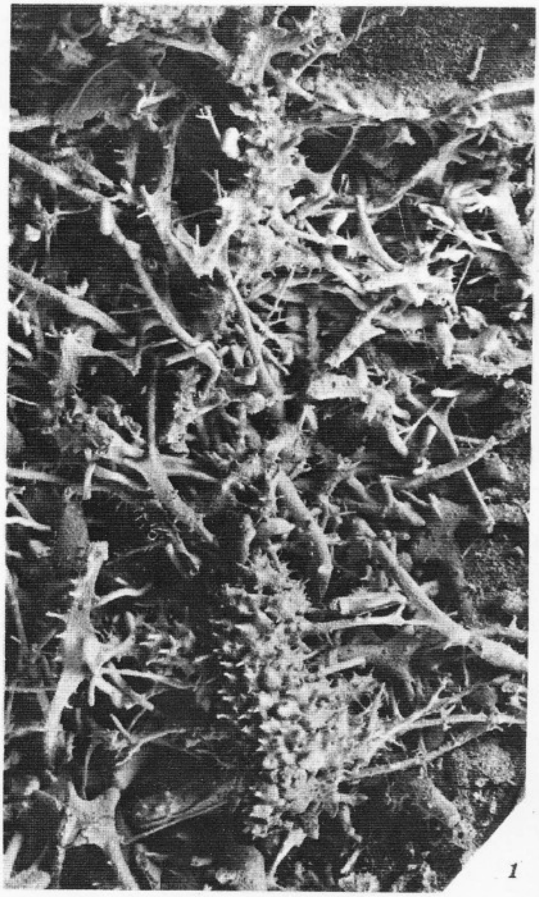
Fig. 1 – *Entobia mammillata* ichnosp. n. Early growth phases. Paratype. No. MGUH 16436 (56 C).

Fig. 2 – *Entobia mammillata* ichnosp. n. Phases A–B. Paratype. No. MGUH 16437 (62 C).

Fig. 3 – *Entobia volzi* ichnosp. n. Paratype. No. MGUH 16461 (209 SE).

Fig. 4 – Gerontic *Entobia mammillata* ichnosp. n. The tubercular sculpture is present only in some parts (left) of the system. No. MGUH 16440 (57 P).

All samples x 2.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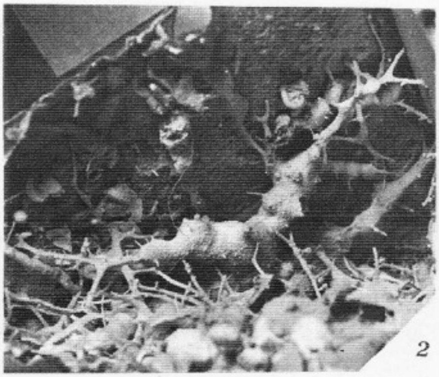
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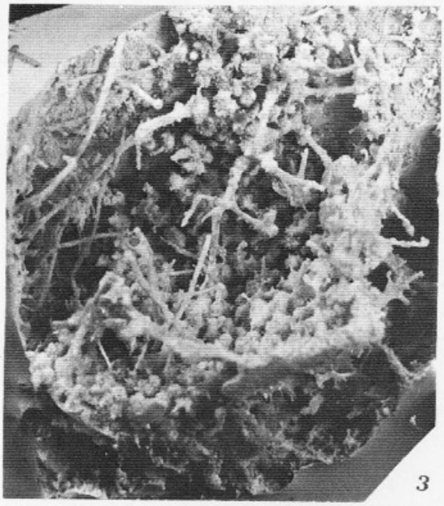
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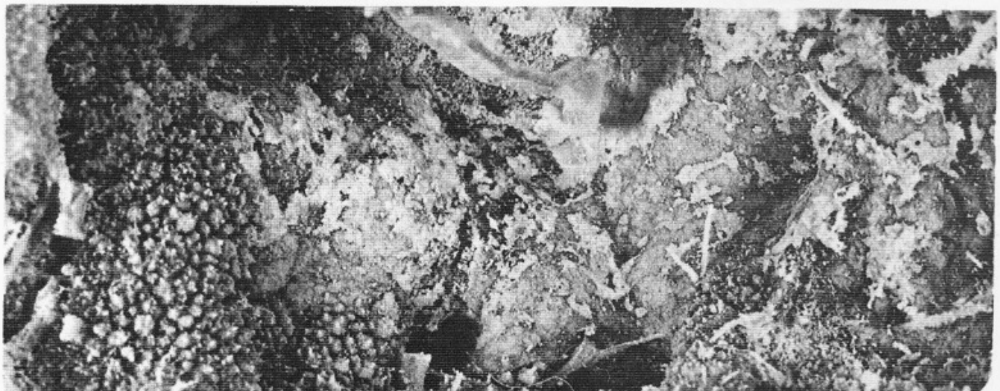
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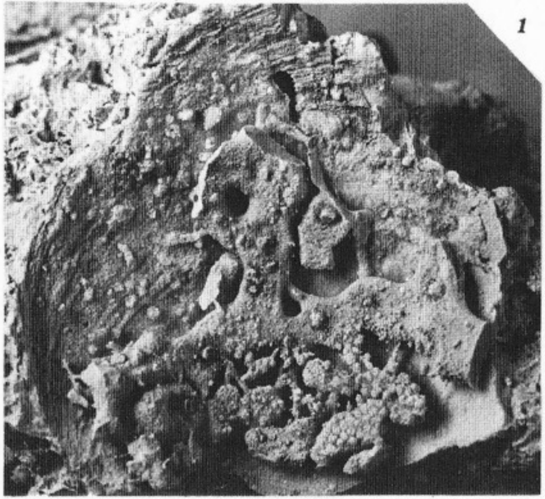
PLATE 26

Fig. 1 – *Entobia megastoma* (Fischer). Stenomorph. No. MGUH 16444 (41 Stq); x 2.

Fig. 2 – *Entobia mammillata* ichnosp. n. Paratype. No. MGUH 16436 (56 C); x 5.

Fig. 3 – *Entobia ovula* ichnosp. n. Xenomorphic in indeterminable bivalve. No. MGUH 16452 (200 CP); x 2.

Fig. 4 – *Entobia paradoxa* (Fischer). Phases A to C. No. MGUH 16457 (70 C); x 2.



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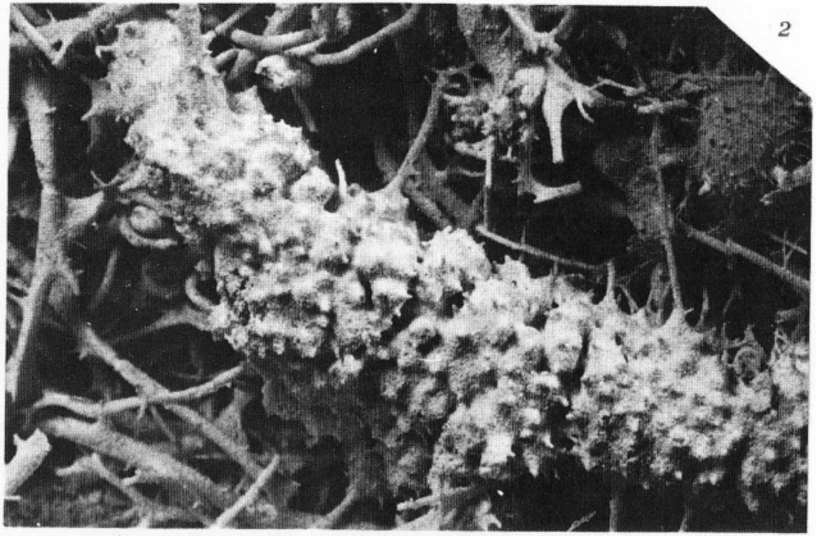

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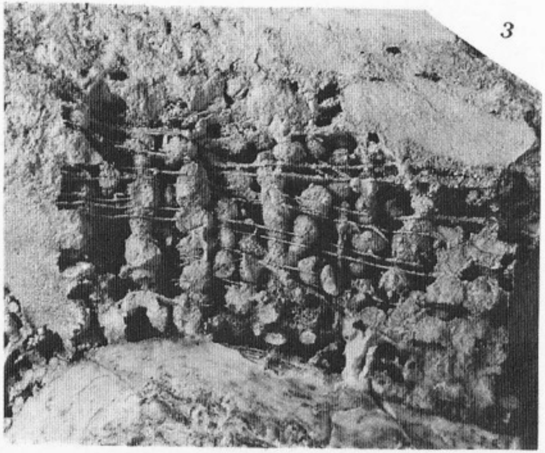

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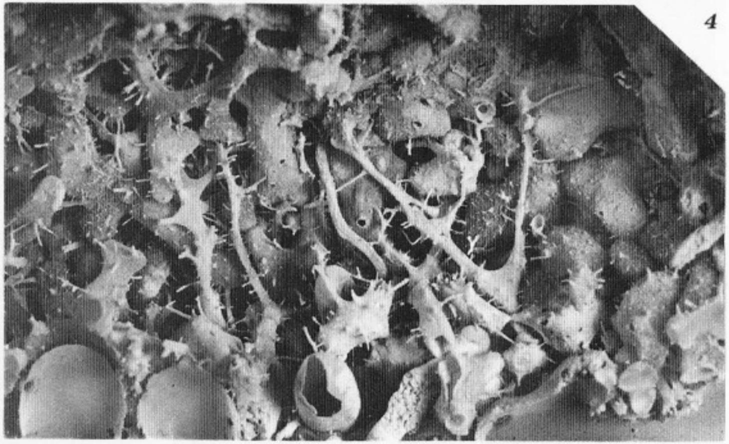

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PLATE 27

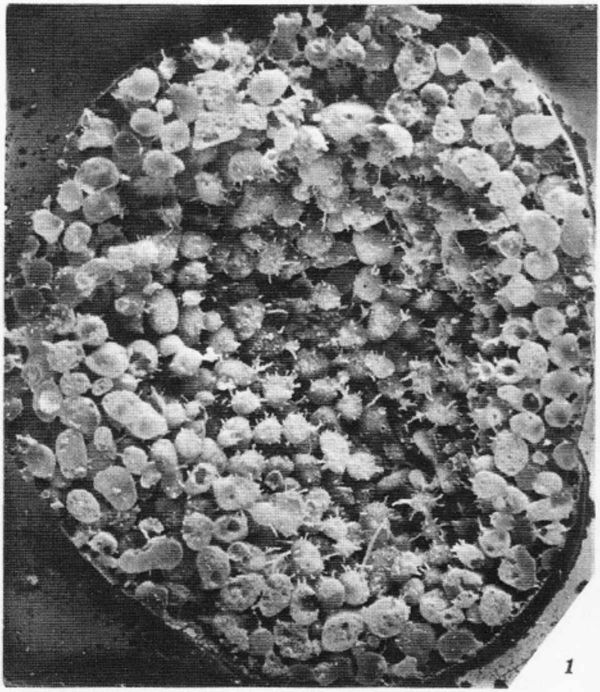
Fig. 1 – *Entobia ovula* ichnosp. n. Holotype. No. MGUH 16445 (195 P).

Fig. 2 – *Entobia megastoma* (Fischer). Phases A–B. No. MGUH 16443 (26 P).

Fig. 3 – *Entobia mammillata* ichnosp. n. (right) meets and reacts towards *Entobia cateniformis*. No. MGUH 16418 (61 C).

Fig. 4 – Indeterminable stenomorphic entobian in *Conus* sp. No. MGUH 16467 (230 Spt).

All samples x 2.



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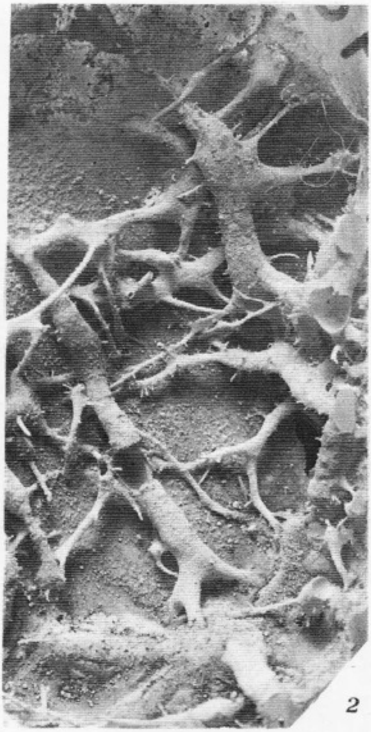

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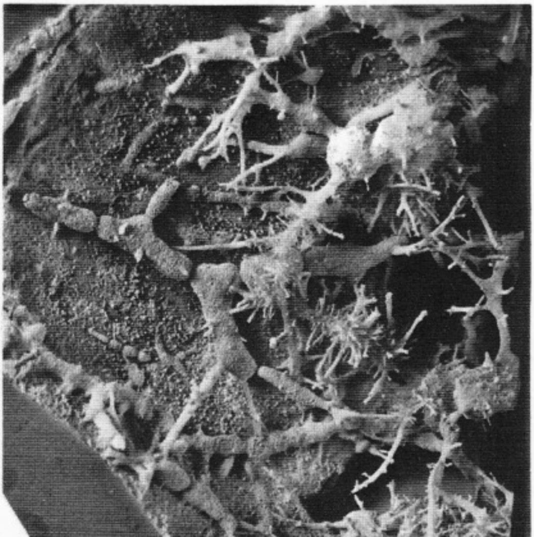

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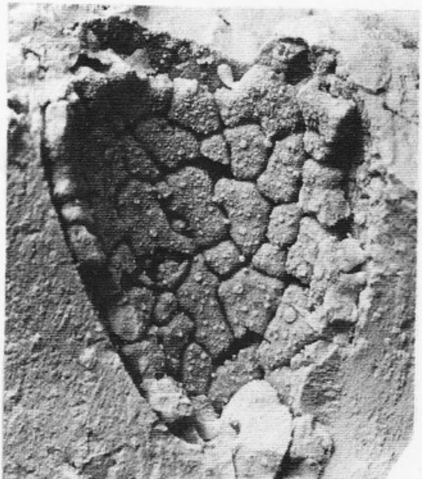

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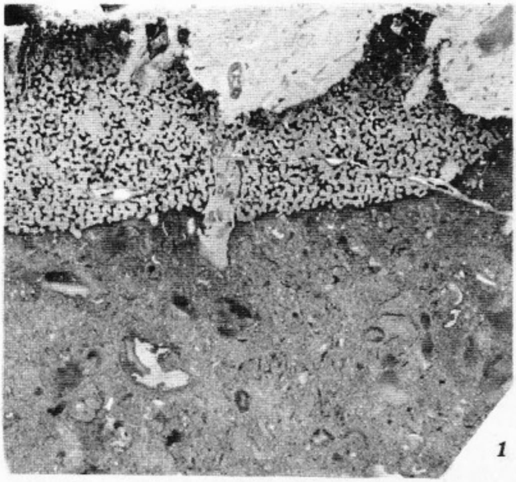
PLATE 28

Fig. 1 – *Entobia volzi* ichnosp. n. Hardground at junction Middle–Upper Danian, Limhamn Quarry, Malmö, Sweden. No. MGUH 16464; nat. size.

Fig. 2 – *Entobia volzi* ichnosp. n. Paratype. No. MGUH 16461 (209 SE); x 2.

Fig. 3 – *Entobia paradoxa* (Fischer). No. MGUH 16458 (77 P); x 5.

Fig. 4 – *Entobia ovula* ichnosp. n. Phase C. Paratype. No. MGUH 16447 (177 C); x 2.



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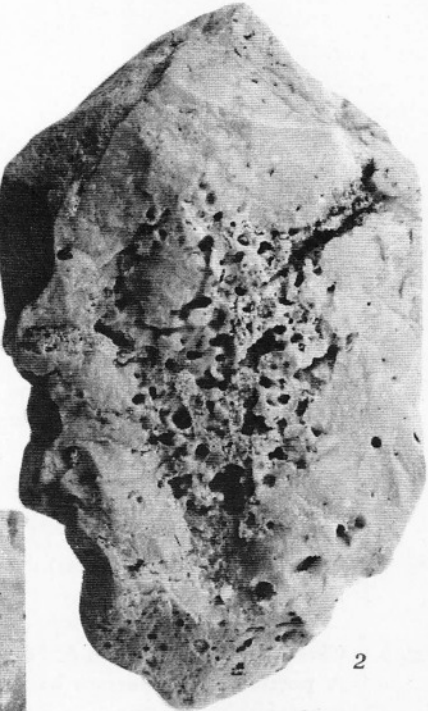

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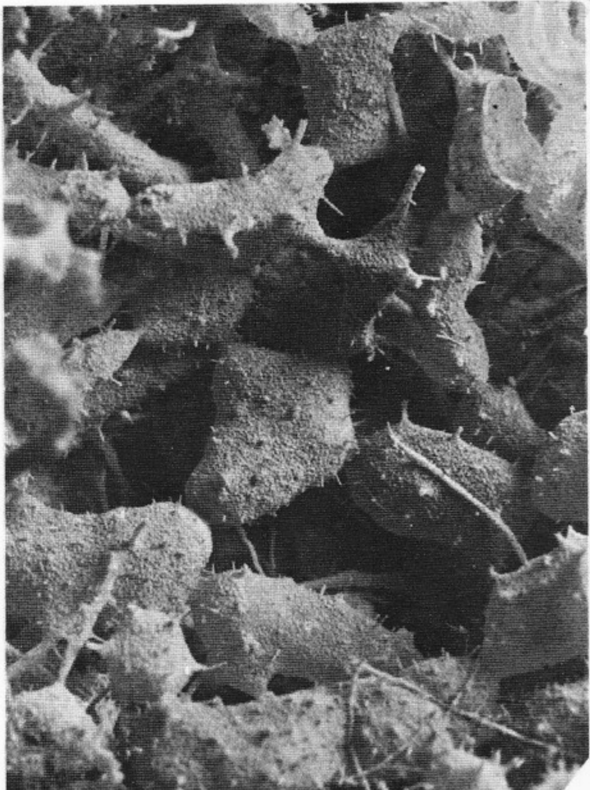

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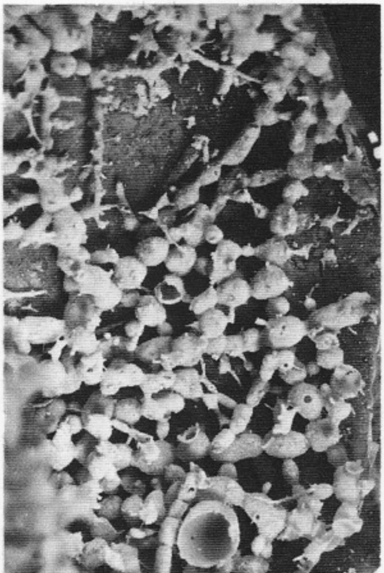

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PLATE 29

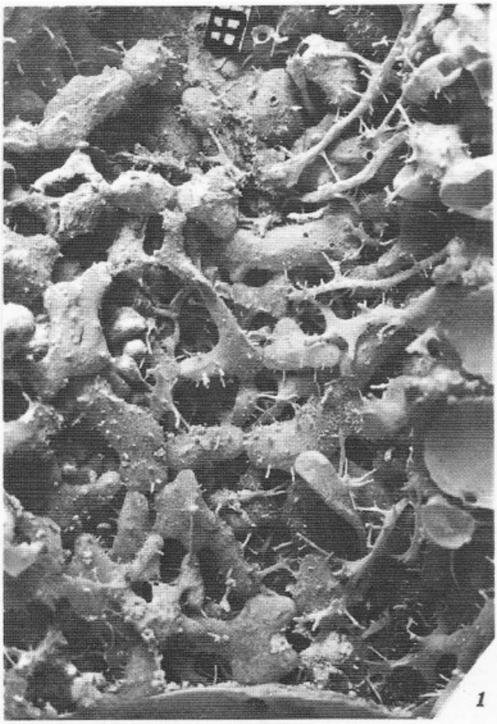
Fig. 1 – *Entobia paradoxa* (Fischer). Phases A to C. No. MGUH 16457 (70 P); x 2.

Fig. 2 – X–ray radiograph of paratype of *Cliona cretacica* Fenton & Fenton showing the non–camerate galleries; nat. size.

Fig. 3 – *Entobia ovula* ichnosp. n. Stenomorph in bivalve shell. No. MGUH 16453 (230 Stq); x 2.

Fig. 4 – *Entobia paradoxa* (Fischer). Stenomorph in *Glycymeris* sp. No. MGUH 16459 (86 Stq); x 2.

Fig. 5 – *Cliona cretacica* Fenton & Fenton. Paratype (New Jersey State Museum no. 8185). A portion of the surface has been sectioned and polished so as to expose the galleries within; nat. size.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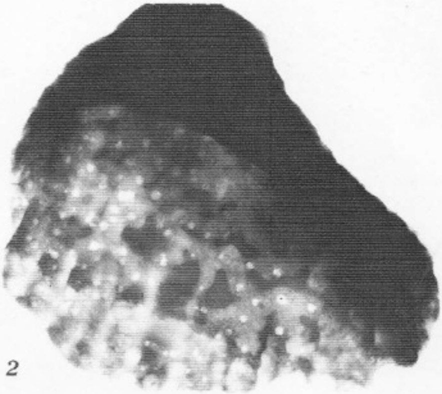
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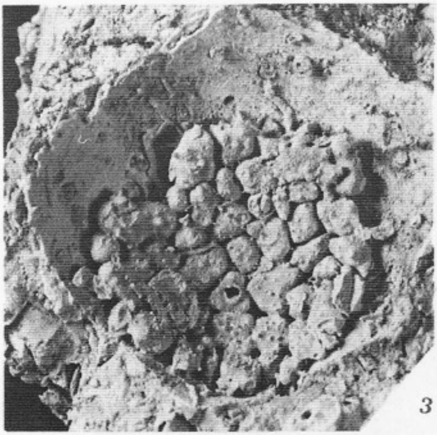
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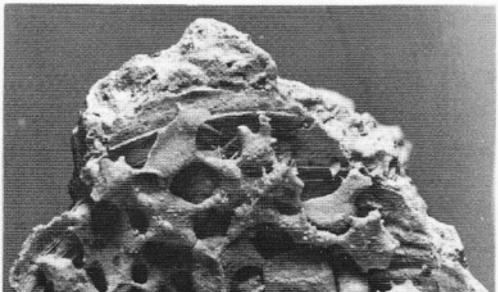
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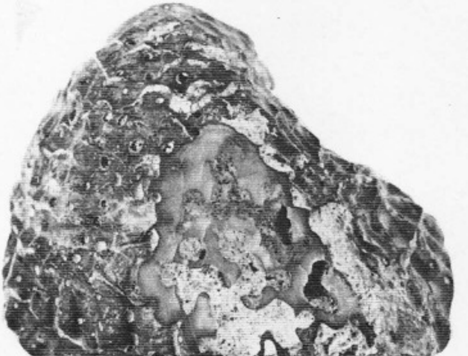
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