

Taxonomic revision of Late Triassic “*Lithocodium aggregatum* ELLIOTT” (Northern Calcareous Alps, Austria)

FELIX SCHLAGINTWEIT*

4 Text-Figures, 2 Tables, 5 Plates

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Northern Calcareous Alps
Norian–Rhaetian
Bioerosion
Boring Sponges
Lithocodium
Entobia

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Taxonomische Revision obertriassischer „*Lithocodium aggregatum* ELLIOTT“ (Nördliche Kalkalpen, Österreich)

Zusammenfassung

Die obertriadischen Exemplare von *Lithocodium aggregatum* ELLIOTT werden anhand von Dünnschliff-Material aus dem Oberrhät der Steinplatte, Tirol, und Adnet, Salzburg, taxonomisch revidiert. Sie werden als Bohrgänge (Kammern und Kanäle) von Schwämmen interpretiert, die in mikrobiellen-onkoidischen Krusten und Gerüstbildnern bohren (Ichnogattung *Entobia*). Von den Dächern dieser Kammern reichen sich verzweigende und dabei verjüngende Kanäle in die mikrobiellen Krusten, während von deren Basis pionierende Bohrfilamente das bioklastische Substrat durchsetzen. Spuren dieser Tätigkeit sind in Form eines mikritischen Netzwerkes erhalten. Irregulär globuläre Körper mit einer dünnen mikrokristallinen Wand, die im Innern der zementgefüllten Kammern auftreten, werden als Überreste der Bohrschwämme (Ektosom) interpretiert. Das gehäufte Auftreten bohrender Schwämme in der ausgehenden Trias könnte im Kontext mit der postulierten biologischen Krise im Bereich der Trias-Jura-Grenze, respektive den sie verursachenden Faktoren, jedoch nicht in ursächlichem Zusammenhang mit dem signifikanten Absterben von Korallen-Riffen in diesem Zeitraum stehen.

Abstract

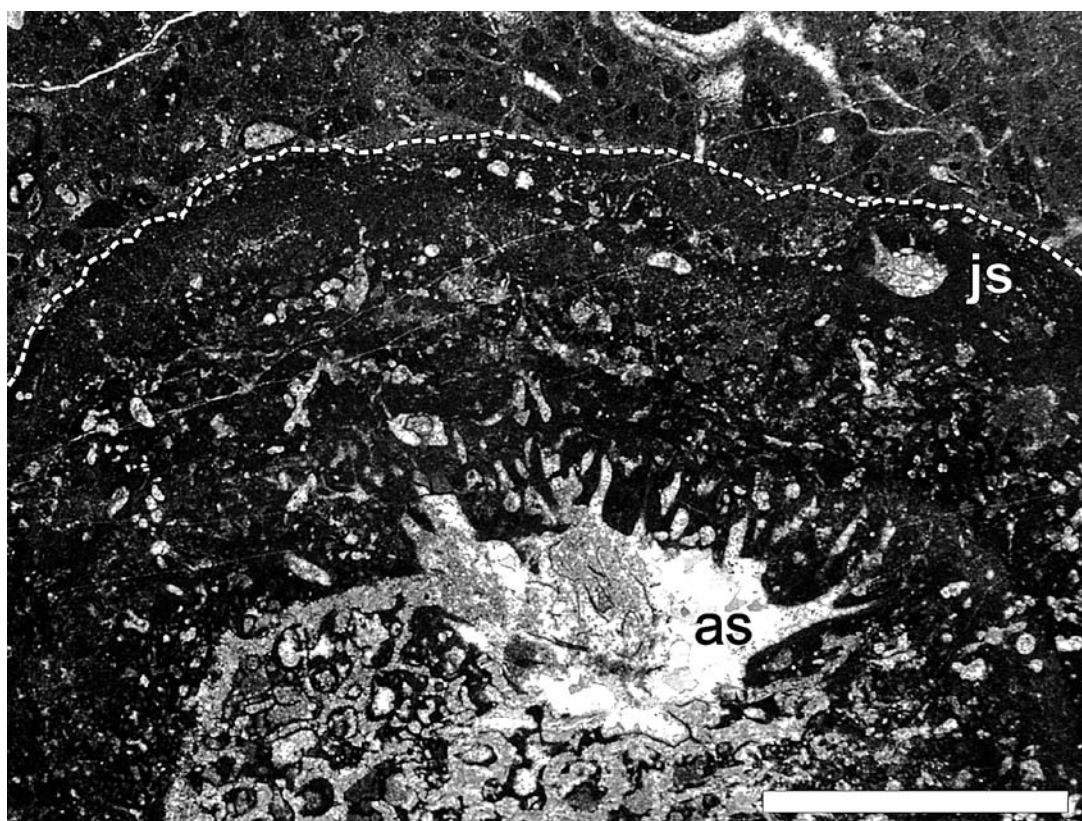
Late Triassic forms of *Lithocodium aggregatum* ELLIOTT are revised taxonomically based on thin-section material from the Late Rhaetian of Mount Steinplatte, Tyrol, and Adnet, Salzburg. They are interpreted as the boring galleries (chambers and canals) of sponges (ichnogenus *Entobia*), excavating into microbial-oncoid crusts and framebuilders. From the roof of these chambers, branching canals exhibiting successively decreasing diameters transect the crusts, while pioneering filaments bored downwards from the chamber bases into the bioclastic substrate. The traces of this activity are preserved as a micritic network. Irregular globular bodies displaying a thin microcrystalline wall occur inside the cement-filled chambers. These are interpreted as remnants of the former sponges (ectosome). The occurrence of abundant boring sponges in Late Triassic times could be linked to the biological crisis postulated around the Triassic-Jurassic boundary.

*) FELIX SCHLAGINTWEIT: Lerchenauerstraße 167, 80935 München. ef.schlagintweit@t-online.de

Introduction

In his PhD thesis, “The Steinplatte reef complex of the alpine Triassic (Rhaetian) of Austria”, OHLEN (1959) described a microfossil of unknown taxonomic position as “Problematicum A”. This microproblematicum has thereafter been recorded as “Problematicum A OHLEN” by other studies of the Rhaetian reefal limestones within the Northern Calcareous Alps of Germany and Austria (ZANKL, 1969; FLÜGEL, 1972, 1981). In later times, it has been illustrated as *Lithocodium* sp. (SENOWBARI-DARYAN & SCHÄFER, 1979; SENOWBARI-DARYAN, 1980; DULLO, 1980; SCHÄFER & SENOWBARI-DARYAN, 1981) referring to the genus with the type-species *L. aggregatum* described by ELLIOTT (1956) from the Early Cretaceous of Iraq and interpreted as an encrusting codiacean (= udoteacean) green alga. SADATI (1981) was the first author to propose the identity of the Late Triassic “Problematicum A” and the Early Cretaceous *Lithocodium aggregatum* ELLIOTT. However, given that some authors only referred to *Lithocodium* sp. being monospecific at this time, it can be assumed that they recognized structural differences to the type-species. Since then, it has become general consensus to ascribe the Late Triassic forms to *Lithocodium aggregatum* (WURM, 1982; SENOWBARI-DARYAN, 1984; SCHMID & LEINFELDER, 1996; KOCH et al., 2002; CHERCHI & SCHROEDER, 2006) or the *Lithocodium-Bacinella* complex or group (KUSS, 1983; EHSSES & LEINFELDER, 1988; STANTON & FLÜGEL, 1989; BORSATO et al., 1994; TOMAŠOVÝCH, 2004). This grouping refers to another incertae sedis described by RADOIČIĆ (1959): *Bacinella irregularis*. For the long-lasting controversial discussion

about the biogenic nature and a possible identity of both taxa, see for example MAURIN et al. (1985), FENNINGER (1972), SCHMID & LEINFELDER (1996), BANNER et al. (1990) and SCHLAGINTWEIT et al. (2010). In the often cited work of BANNER et al. (1990, p. 22), the “confirmed recorded range” of *Lithocodium aggregatum* was indicated as “Late Jurassic – Middle Cretaceous” excluding the Triassic records in the literature, that were surely known to them. An equivalent confirmed stratigraphic record was stated also recently by SCHLAGINTWEIT et al. (2010) reinterpreting *Lithocodium aggregatum* as a crust-forming green alga with heterotrichale thallus organization. Furthermore, these authors stated that all Late Triassic and many of the Late Jurassic forms illustrated in the literature are taxonomically different from *Lithocodium aggregatum* ELLIOTT. A group of Late Jurassic “*Lithocodium aggregatum*” characterized by large, subspherical to ovoid cavities/chambers (e.g., SCHMID & LEINFELDER, 1996) was recently re-interpreted as the traces of unicamerate excavating sponges (ichnogenus *Entobia*) by SCHLAGINTWEIT (2010) (Text-Fig. 1; Pl. 1, Fig. f). A comparable conclusion was drawn also by CHERCHI & SCHROEDER (2010) for Late Triassic representatives. As will be argued later in the present paper, the assumption that “Problematicum A” represents a boring organism was already envisaged in 1959 by OHLEN. In the present study, this ichnotaxonomic concept is specified with new aspects added based on material from Late Rhaetian limestones (“Oberer Rhaet Limestone”) of the Northern Calcareous Alps of Austria.



Text-Fig. 1.
Entobia isp. (as = adult stage) boring into a stromatoporoid skeleton and canals radiating into oncolidal crusts. Small, juvenile stage (js) completely boring into the oncolid crust. Late Tithonian – Early Berriasian of Crimea Mountains, Ukraine (detail from KRAJEWSKI, 2010, Fig. 4.61.A). An overview is shown in Plate 1, Fig. f. Scale bar is 2 mm.

Material

The thin-sections of the Oberrhaet Limestone studied are from Mt. Steinplatte ("Steinplatte reef") in Tyrol near the German-Austrian border (OHLEN, 1959; PILLER & LOBITZER, 1979; PILLER, 1981; STANTON & FLÜGEL, 1989; FLÜGEL & KOCH, 1995; KRISTYN et al., 2005; KAUFMANN, 2009) and Adnet, southeast of Salzburg (SCHÄFER, 1979; BERNECKER et al., 1999; REINHOLD & KAUFMANN, 2009). The present study is mainly based on the following thin-sections (size 10 x 14 cm and 10 x 8 cm):

- A/132/1: Brecciated bafflestone with scleractinian corals. The matrix between the corallites corresponds to fine-peloidal micrite. Some corals display microbial crusts, which exhibit entobian borings, occasionally affecting also the marginal zone of the coral skeletons.
- BG: In some parts, the thin-section shows a rudstone texture with isolated coral skeletons displaying thick (> 1 cm) microbial encrustations. Within the crust, tiny, branching filaments (assumed cyanobacteria), nubeculariid foraminifera and thaumatoporellacean algal thalli can be observed. The crusts are intensely bored by *Entobia* isp., affecting also the marginal zones of the coral skeletons, especially when these show crusts of reduced thicknesses. Within the matrix, benthic foraminifera such as duostominids, *Alpinophragmium perforatum* FLÜGEL, miliolids, some fragments of dasycladacean al-

gae and debris of echinoderms are present. Some bioclasts show worm borings.

- O 55: Bafflestone with scleractinian corals and some calcareous sponges. The matrix between the corals is a fine-grained packstone; large cement-filled vugs are also present. The corals display microbial encrustations heavily infected by entobian borings. These crusts in turn are partly encrusted by nubeculariids and *Alpinophragmium perforatum* FLÜGEL.
- B/G/2: Rudstone with corals, calcareous sponges showing thick microbial encrustations bored by *Entobia* isp. Other larger bioclasts include fragments of bivalves and gastropods, and solenoporacean algal thalli. These are accompanied by duostominid foraminifera, debris of echinoids and dasycladacean algae, and the microproblematicum *Coptocampylodon? rhaeticus* SCHLAGINTWEIT, GAWLICK & MISSONI.

Two additional samples are from the Chiemgau Alps of Germany (Mount Rauhe Nadel) and Mount Loser in the Austrian Salzkammergut.

Systematic Ichnology

According to the inferred interpretation of Late Triassic "*Lithocodium*" as sponge borings, the description uses the termini proposed by BROMLEY & D'ALESSANDRO (1984).

Ichnogenus *Entobia* BRONN, 1837

Entobia isp.

(Text-Fig. 2; Pls. 1–4; Pl. 5, Figs. a–f pars)

- 1959 Problematicum A – OHLEN, Pl. 10, Fig. 1; Pl. 17, Fig. 3, Late Rhaetian of Austria (Mount Steinplatte).
- 1969 Kavernöse Algenkrusten (Problematicum A OHLEN 1959) – ZANKL, Fig. 41, Norian–Rhaetian of Germany (Mount Hoher Göll).
- 1972 Problematicum A OHLEN – FLÜGEL, Pl. 5, Fig. 1, Late Rhaetian of Austria (Mount Steinplatte).
- 1979 Problematicum A OHLEN (probably belonging to the genus *Lithocodium* ELLIOTT) – SCHÄFER, Pl. 18, Figs. 9–10, Late Rhaetian of Austria.
- 1979 *Lithocodium* – SENOWBARI-DARYAN & SCHÄFER, Pl. 1, Fig. 8, Late Rhaetian of Austria.
- 1980 *Lithocodium* sp. – SENOWBARI-DARYAN, Pl. 21, Figs. 1–2, 4; Pl. 23, Figs. 1–2; Pl. 29, Fig. 3, Late Rhaetian of Austria.
- 1980 *Lithocodium* ELLIOTT – DULLO, Pl. 11, Fig. 7, Norian–Rhaetian of Austria.
- 1981 *Lithocodium* sp. – SCHÄFER & SENOWBARI-DARYAN, Fig. 3a, Late Rhaetian of Austria.
- 1981 *Lithocodium aggregatum* ELLIOTT – SADATI, Pl. 59/8, Norian–Rhaetian of Austria.
- 1981 Problematicum A OHLEN – *Lithocodium* – FLÜGEL, Fig. 9g, Fig. 17a, Late Triassic of Austria.
- 1982 *Lithocodium aggregatum* ELLIOTT – WURM, Pl. 29, Fig. 1; Pl. 37, Fig. 9; Pl. 38, Fig. 3, Norian–Rhaetian of Austria (Mount Gosaukamm).
- 1983 *Lithocodium-Bacinella* – KUSS, Pl. 14, Fig. 1; Pl. 17, Fig. 6 pars; Pl. 17, Fig. 7, Late Rhaetian of Austria.
- 1984 *Lithocodium aggregatum* ELLIOTT – SENOWBARI-DARYAN, Pl. 10, Fig. 7; Pl. 9, Fig. 2, Norian–Rhaetian of Sicily, Italy.
- 1986 *Lithocodium* sp. – MATZNER, Pl. 8, Figs. 4, 7, Norian–Rhaetian of Austria.
- 1988 *Lithocodium-Bacinella* – EHSES & LEINFELDER, Fig. 9, Late Rhaetian of Germany (Mts. Wallberg-Blankenstein).
- 1988 *Lithocodium* sp. – RIEDEL, Pl. 26, Fig. 12, Late Rhaetian of Austria.
- 1989 *Lithocodium-Bacinella* – STANTON & FLÜGEL, Pl. 25, Fig. 23 pars; Pl. 39, Fig. 7; Pl. 51, Fig. 11 ("multiple borings", not indicated!), Late Rhaetian of Austria (Mount Steinplatte).
- 1990 *Lithocodium* and *Bacinella* (encrusting a coral) – LAKEW, Pl. 47, Fig. 6; Pl. 50, Fig. 5, Rhaetian of Italy.
- 1991 *Lithocodium* ELLIOTT – REIJMER & EVERAARS, Pl. 66, Fig. 5, Norian–Rhaetian of Austria.
- 1994 *Bacinella/Lithocodium* – BORSATO et al., Pl. 1d, Late Triassic of Italy.
- ?1999 *Lithocodium* – SCHEIBNER & REIJMER, Pl. 15, Figs. 7–8, Sinemurian of Morocco.

- 2000 oncoid showing preserved microbial filament moulds – BOSENCE et al., Fig. 5e, Sinemurian of Gibraltar, Spain.
- ?2001 *Lithocodium* sp. – KORNGREEN & BENJAMINI, Pl. 2, Fig. 7, Norian of Israel.
- 2004 *Bacinella* sp., *Lithocodium* sp. – TOMAŠOVÝCH, Pl. 6, Fig. 5 pars; Pl. 6, Fig. 8, Late Triassic of Slovakia.
- 2004 “fenestral oncoids” ... formed by microbes (*Bacinella*) – FLÜGEL, Pl. 118, Fig. 2, Late Triassic of Austria.
- n.f. 2008 *Lithocodium* sp. – JADOUL & GALLI, p. 462 (Fig. 6d, not indicated), Early Hettangian of Italy.
- 2010 *Entobia* isp. 1 (illustrations!) – *Entobia* isp. A (text!) – CHERCHI & SCHROEDER, Fig. 1; Pl. 1, Fig. B; Pl. 2, Figs. A–B, F, Norian–Rhaetian of Iran, Late Rhaetian of Austria.

Description:

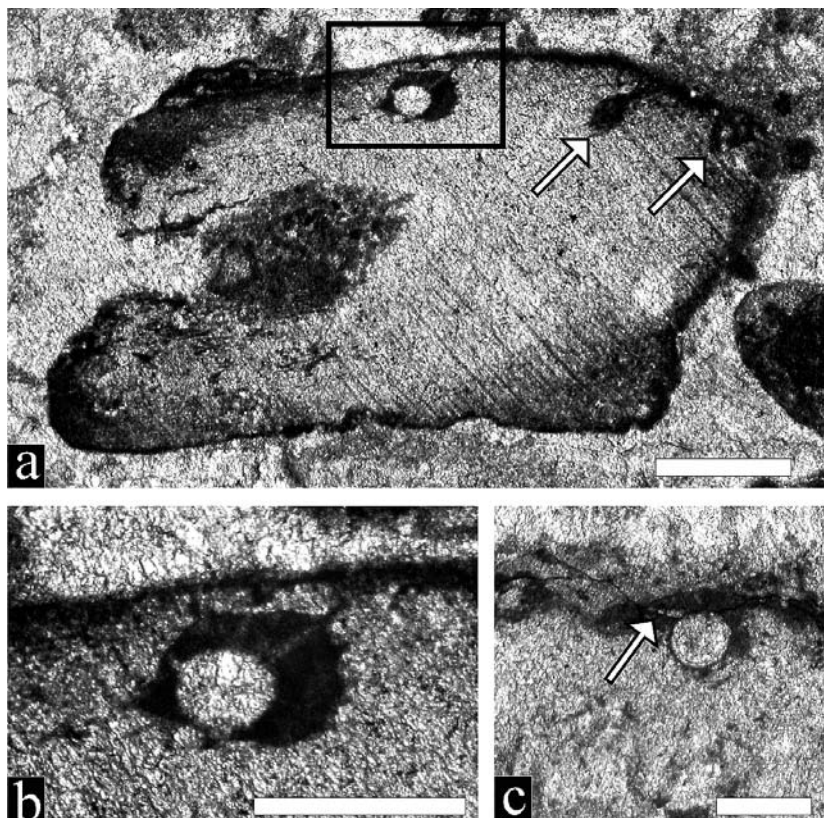
The network of *Entobia* isp. consists of a single subspherical, ovoidal to flattened chamber from which cylindrical, branching canals radiate. The chambers are bored into metazoan skeletons (e.g., corals) and their enveloping calcimicrobial crusts. The chambers may affect only the crusts (e.g., Pl. 2, Fig. e) or both (e.g., Pl. 1, Fig. b) (= supposed idiomorphs sensu BROMLEY & D’ALESSANDRO, 1984). With this respect, the thickness of the calcimicrobial crusts represents a crucial factor. In some cases, the chamber closely attaches the coral substrate with a flat base, not penetrating the skeleton (= stenomorph sensu BROMLEY & D’ALESSANDRO, 1984) (Pl. 5, Fig. a). The chambers vary in size (= diameter) from 0.15 mm up to 2.64 mm (see Tab. 1), the height ranges from 0.2 to 0.8 mm. Small juvenile chambers are almost spherical (Text-Fig. 2). With increasing size, mature chambers become flattened (high diameter/height ratio) (e.g., Pl. 1, Fig. b). One exception from this rule observed is represented by a form boring into highly concave substrate surfaces. In this case the dominating chamber growth is directed vertically into the substrate rather than laterally (Pl. 3, Fig. a). In transverse sections through the lower and middle part of the chambers, these exhibit a round outline (Pl. 3, Fig. h). Shallow transverse sections display a stellate outline by cut-

ting through the oblique radiating canals (Pl. 3, Fig. e). The substrate surface is commonly perforated by series of non-fused chambers, laterally clearly separated from each other (Pl. 2, Fig. d). In thin substrates that were bored from all sides (Pl. 2, Fig. b), chambers from opposite sides may become united (Pl. 2, Fig. a). Starting from the roof of the sparite-filled chambers, subparallel branching canals arise radiating upwards through the crust (thickness: 0.28 to 0.5 mm). However, these canals do not perforate the crust, ending blind shortly before the exterior surface (Pl. 4, Fig. e). The covering crust has a thickness of about 0.01 mm. The canals may branch up to 4 times, thus forming a system of up to 5 orders of canals. The branching may be simply bifurcate or multiple, successively decreasing in diameter toward the exterior (Pl. 4, Fig. e). Normally, the first order canals are rather thick, but in some cases, these are associated with thinner ones, e.g. having diameters of the second order canals of the former (Pl. 4, Fig. e). In tangential transverse sections, the canals form a dense, close-set arrangement. In the example shown on Plate 3, Fig. j, there are about 350 higher order canals per square millimeter. Rather often, chambers show an asymmetry in such a way that in vertical sections one side of the chamber is elongated exhibiting one comparably thick canal (up to 0.3 mm) that stretches obliquely through the crust

Text-Fig. 2.

Juvenile spherical chamber of *Entobia* isp. from the Upper Rhaetian limestone of the Northern Calcareous Alps.

- a Bioclast showing thin marginal micritization and several borings (arrows). Black rectangle marks the detail shown in b. Scale bar 0.5 mm, sample BG.
- b Detail from a, showing a subspherical chamber exhibiting some straight and unbranched canals within a micrite-filled boring. Scale bar 0.3 mm.
- c *Entobia* isp. boring into the marginal zone of a metazoan skeleton. Note the thick canal (arrow), presumably an apertural canal. Scale bar 0.5 mm, sample O 55.



(Fig. 2c; Pl. 1, Fig. d; Pl. 3, Fig. i; Pl. 4, Fig. a). This canal may be rather long (up to 2 mm) and in some cases open to the exterior (Pl. 2, Fig. b; Pl. 3, Fig. c).

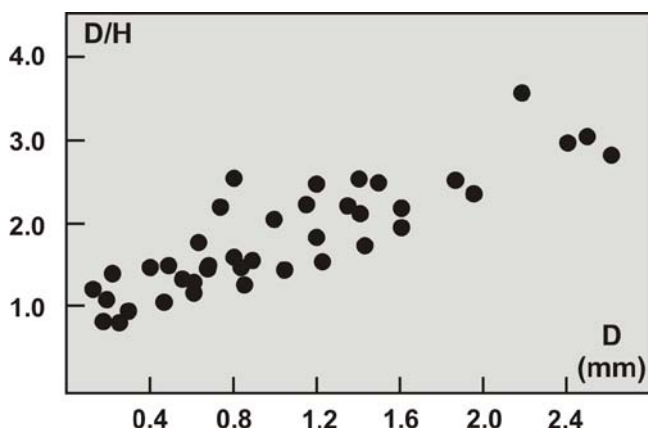
From the chamber base, a fine branching erosion mesh-work of boring filaments, marked by their micritized traces, penetrates the substrate vertically up to 1 mm (occasionally even more) (Pl. 4, Fig. a, c–d). The bored micritic canals have diameters between 0.01 and 0.06 mm. In some sections, these form some kind of a honey-comb pattern (Pl. 4, Fig. f). The micritic network can also be present in the interior of some chambers (Pl. 2, Fig. a; Pl. 3, Fig. f), obviously having invaded from adjacent or superimposed specimens.

Dimensions:

The measurements of chamber diameter (D), height (H) and ratio D/H of 40 specimens are compiled in Table 1. In accordance with SENOWBARI-DARYAN (1980, Tab. 10: 2.5 mm), the maximum chamber diameter observed is 2.64 mm; SCHÄFER (1979) reports a chamber diameter of up to 3 mm and OHLEN (1959) even up to 4 mm for “Problematicum A”. In Text-Fig. 3, the measured diameters of 40 specimens are plotted against the ratio chamber diameter/height. The first order canals have diameters (d1) of 0.03 to 0.15 mm (d2: 0.03 to 0.08 mm; d3: 0.025 to 0.05 mm; d4: 0.02 to 0.03 mm; d5: 0.015 to 0.025 mm). Other biometric data are given in the description.

Discussion:

In contrast to the Lower Cretaceous type-species *Lithocodium aggregatum*, the Late Triassic forms previously ascribed to this taxon are characterized above all by individual mm-sized cavities (SENOWBARI-DARYAN, 1980: Höhlungen, Hohlräume). Due to their contact to the underlying substrate or embedding, these were also termed basal cavities (CHERCHI & SCHROEDER, 2006), basin-like cavities (KOCH et al., 2002), interior central cavity (LEINFELDER et al., 1993, p. 203) or chambers according to the foraminiferan interpretation proposed by SCHMID & LEINFELDER (1996). In his description of Problematicum A, OHLEN (1959) described them as blister-like cavities. According to the calcimicrobial interpretation proposed by CHERCHI & SCHROEDER (2006), the taxon *Lithocodium aggregatum* comprises the dark



Text-Fig. 3. Dimensions of *Entobia* isp. from Late Rhaetian limestones of the Northern Calcareous Alps (data from Table 1). The chamber diameter D (in mm) is plotted against the ratio diameter (D) / height (H). The coefficient of correlation shows a rather high degree of correlation ($r = 0.86$).

Thin-section	D	H	D/H
O 55	0.8	0.3	2.66
	0.54	0.34	1.59
	0.72	0.48	1.5
	0.78	0.36	2.2
	1.6	0.8	2
	0.84	0.64	1.3
	0.82	0.54	1.5
	0.52	0.5	1.04
	1.15	0.52	2.21
	1.35	0.62	2.18
	1.4	0.66	2.12
	0.72	0.57	1.26
	0.32	0.32	1
	1.9	0.84	2.26
	0.87	0.54	1.61
	0.72	0.54	1.33
	1.2	0.48	2.5
	1.04	0.69	1.5
	1.38	0.52	2.65
	0.4	0.24	1.66
	0.72	0.4	1.8
	1.22	0.72	1.69
	0.8	0.48	1.66
	2.64	0.9	2.93
	0.6	0.48	1.25
	0.22	0.16	1.37
	0.19	0.2	0.95
	0.15	0.12	1.25
	0.33	0.3	0.91
A 132/1	2.4	0.8	3.0
	1.5	0.6	2.5
	1.88	0.72	2.6
	0.72	0.45	1.6
B/G/2	2.48	0.8	3.1
	1.44	0.8	1.8
	1.6	0.72	2.22
	1.2	0.63	1.9
	0.28	0.24	1.16
	1.0	0.48	2.08
	2.24	0.6	3.73
Number	40	40	40
Min.	0.15	0.2	0.91
Max.	2.64	0.8	3.73
Average	1.07	0.4	1.89

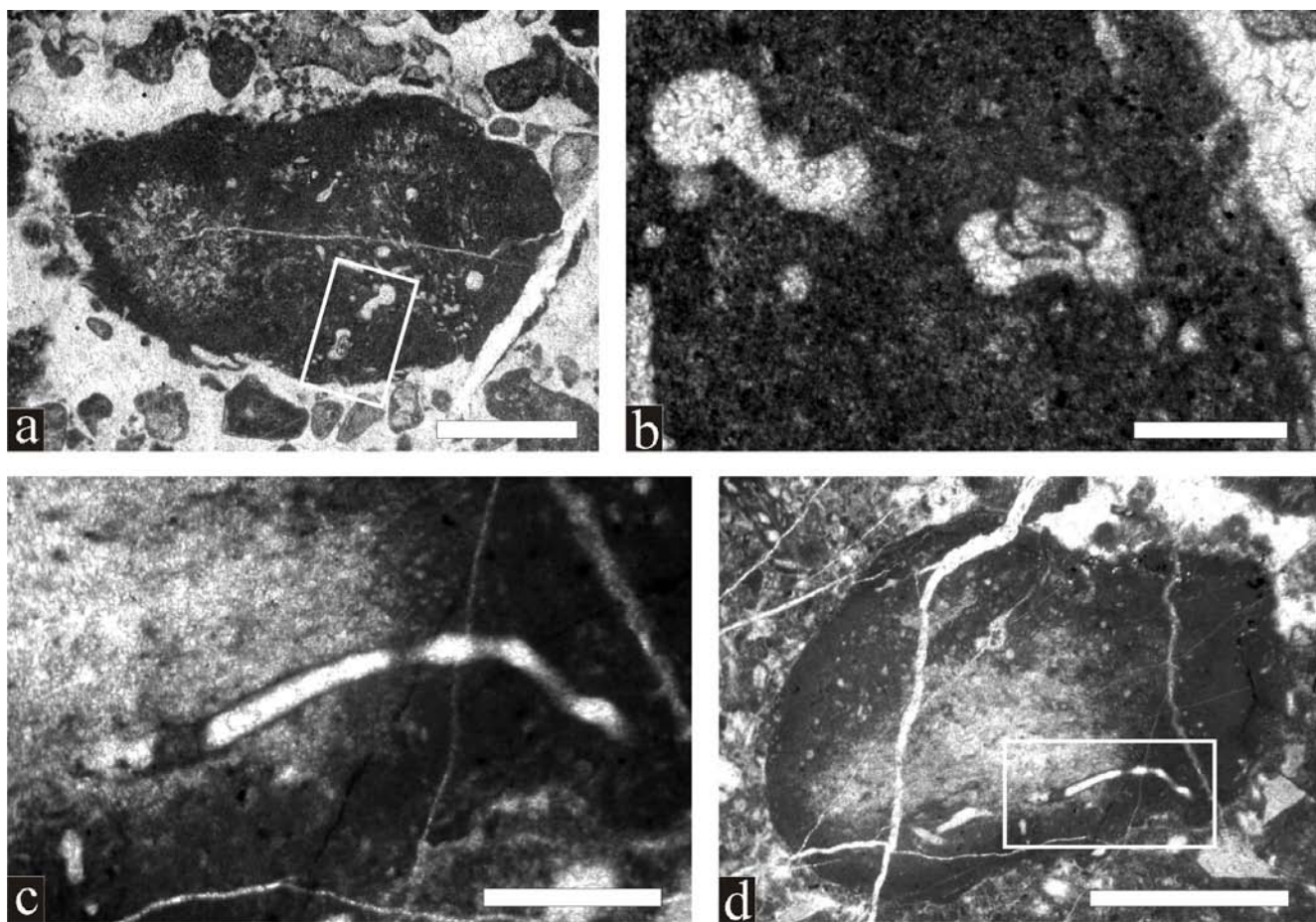
Table 1. Dimensions of *Entobia* isp. from the Late Triassic of the Northern Calcareous Alps. D = chamber diameter, H = chamber height (both in mm). See Text-Fig. 3 for the graphic illustration of the dimensions.

microcrystalline crust together with the cavities and the “alveolar system”. In a recent work of CHERCHI & SCHROEDER (2010), this view was modified with respect to the Late Triassic forms by interpreting the cavities “in calcimicrobial *Lithocodium* crusts” ichnotaxonically as chambers of boring sponges (ichnogenus *Entobia*). This view is accepted and followed here, too, although findings of sponge spicules as an ultimate proof of sponge origin are lacking. The “alveolar system” was interpreted by CHERCHI & SCHROEDER (2010) as branching apertural canals arising from these chambers, thus being part of the boring system.

For the Late Jurassic sponge borings, the entobians excavated into metazoan bioclats and their surrounding oncoidal-calcimicrobial crusts (SCHLAGINTWEIT, 2010). The crusts are therefore neither part of the boring system nor do they belong to “*Lithocodium aggregatum*”. In the surroundings of the chambers and the spaces between the radiating and branching canals, the original calcimicrobial microstructure is transformed into dense micrite. This transformation must

have been caused primarily by the etching process of the close-set system of the sponge excavating filaments transecting the crust roof of the chambers. SCHÄFER (1979, p. 80) assumed that the crust underlying the chambers was secondarily micritized (“*Krustenunterlage sekundär mikritisiert*”). As already remarked by OHLEN (1959, p. 73), “*individual cavities are separated by an irregular, somewhat porous structure*”. Within those parts of the crust that have not been affected by the sponge etching process, not micritized crust exhibiting fine-branching filaments of presumably cyanobacterial origin, nubeculariid foraminifera and thaumatoporellacean algal thalli can be observed. These crusts can be considered as calcimicrobial following CHERCHI & SCHROEDER (2010), or as porostromate since non-microbial taxa (foraminifera, algae) involved in the crusts are present as well.

Juvenile small subspherical chambers may be completely embedded in the substrate (Text-Fig. 2). During ontogeny, the substrate chamber roof may become removed by successive vertical and lateral chamber growth. All transi-



Text-Fig. 4.

Bioerosional structures in Upper Triassic limestones of the Northern Calcareous Alps.

- a Grain-to-rudstone with porostromate algal thallus exhibiting a calcimicrobial crust. In the lower part some boring galleries can be recognized. The white rectangle marks the detail shown in b.
Scale bar 1 mm, sample Los-11.
Norian–Rhaetian Dachstein Limestone of Mount Loser.
- b Detail from a, showing boring galleries with a cryptobiotic trochospiral foraminifer (right). Whether this form was actively boring or just dwelt in a cavity produced by another organism is unknown. This tiny form (test diameter 0.15 mm) resembles a juvenile *Tauchella endolithica* described from the Late Cretaceous by CHERCHI & SCHROEDER (2000).
Scale bar 0.2 mm.
- c Detail from d, showing a tubiform boring organism (polychaete or phoronid worm?).
Scale bar 0.5 mm, sample BG.
- d Bioclast (?algal thallus) exhibiting a boring of a tubiform organism (tube diameter up to 0.12 mm).
Scale bar 2 mm.

tions from small to large chambers (0.15 to several mm) occur; these small chambers are interpreted as belonging to *Entobia* isp. rather than representing another ichnospecies. From the chamber bases, numerous thin exploratory threads (sensu BROMLEY & D'ALLESANDRO, 1984) preserved as a micritic network, originated, etching downward into the calcareous substrate. Such an assumption was already envisaged by OHLEN (1959, p. 73): "The basal surface of each cavity is usually rather irregular and suggests that canals or pores perforated into the interior of the encrusted fragment. Rounded, 'porous' pockets within the fragments are probably the result of leaching or etching of the fragment by the organism" (> Problematicum A = *Entobia* isp.). The resulting pattern somehow resembles the polygonal pattern of chip formation (= erosion scars) in modern clonoid sponges, although these are smaller (15–85 µm) (e.g., COBB, 1969; RÜTZLER & RIEGER, 1973; FÜTTERER, 1974; CALCINAI et al., 2003). In any case, the sponge water-flow system remains unclear as the branching canals are closed towards the exterior. The single, thick canals on one side of the chamber might represent openings of such a system. Whether these were originally open to the exterior or secondary by erosion of the thin crust cover is unknown (e.g., Pl. 2, Fig. b; Pl. 3, Fig. c). In the example shown in Pl. 5, Fig. a–b, the covering crust obviously was removed by erosion marked by a concave depression on its surface and adjacent open canals. Another possibility for feeding could be that the sponge was directly consuming organic material dissolved from the calcimicrobial crusts or from the pore water. An indication for such an assumption could be the dense system of highly branching canals transecting the crusts observed in this group of Late Triassic to Late Cretaceous entobians affecting calcimicrobial crusts.

The Late Triassic entobians (previously referred to *Lithocodium aggregatum*) do not appear prior to the Norian (SENOWBARI-DARYAN, 1984) with most frequent records in the (Late) Rhaetian. Comparable to the Paleozoic forms (SCHÖNBERG & TAPANILA, 2006; TAPANILA, 2006), the Late Triassic entobians are unicamerate. Multicamerate forms seem to appear later during the Jurassic and seem to be the most common typus in the Paleogene (e.g., BROMLEY & D'ALESSANDRO, 1984; see compilation of VALLON, 2011). Single chambered or unicamerate forms include for instance the Paleozoic *Entobia devonica* (CLARKE) or the Late Cretaceous *Entobia cracoviensis* BROMLEY, KEDZIERSKI, KOŁODZIEJ & UCHMAN. Both ichnospecies, however, possess cm-sized subspherical chambers which differ from the Late Triassic (and also Late Jurassic) forms (BROMLEY et al., 2009; TAPANILA, 2006; SCHÖNBERG & TAPANILA, 2006). As a modern analogue trace-maker for cavities similar to the Paleozoic *Entobia devonica*, the unicamerate phloeodictyid sponge *Aka paratipyca* FROMONT is considered (SCHÖNBERG & TAPANILA, 2006).

In conclusion, the described Late Triassic *Entobia* isp. cannot be included in any of the so far established ichnospecies. On the other side, the introduction of a new ichnospecies is hindered by the fact that an exact 3-dimensional analysis is not possible based on the thin-sections studied.

Stratigraphic remarks:

This single-chambered entobians, preferentially boring into calcimicrobial-oncoidal crusts, are recorded so far from the Norian to Coniacian strata (SENOWBARI-DARYAN, 1984; own observations). It must be emphasized that the

lower range boundary seems to be better fixed than the upper one, as the rare Late Cretaceous occurrences of "*Lithocodium aggregatum*" (e.g., HÖFLING, 1985; CAMOIN, 1995) need to be re-studied again. The Late Triassic forms, often with one large and obliquely arranged canal (in addition to the close-set system of thinner branching canals) were also observed in Late Jurassic material where comparably large specimens with numerous canals radiating laterally in various directions occur, too. These differences might point to different ichnospecies, the establishment of a concrete ichnotaxonomic nomenclature, however, is hampered by the poor knowledge on the morphological variations of these forms.

Boring sponge gen. et sp. indet.

(Pl. 5a–f, pars)

Description:

Irregular ovoid to globular bodies (diameter 0.65–1.1 mm) inside the sparite-filled chambers of *Entobia* isp. are outlined by a thin, microcrystalline wall (thickness 0.08–0.015 mm). In general, it can be stated that the smaller the *Entobia* chamber is, the closer do these bodies occupy the available space both in diameter and height. In large chambers, the body diameter can be less than half of the chamber width. The wall surface may be smooth or may exhibit small protuberances. In some cases, it stretches into the basal part of the canals radiating from the chamber giving them a septate appearance. Some of the bodies show a composite appearance with smaller corpuscles inside.

Dimensions:

See Table 2. It must be stressed, that these remains are rather frequently observed in the studied thin-sections. However, only those data were used that enable the recognition of the full body size. In many cases, these are only dimly recognizable in the cement-filled cavities or cut tangentially.

Thin-section	D	H	Dc
O 55	0.82	0.3	-
	0.84	0.4	-
	0.75	0.36	0.92
	0.65	0.35	0.85
BG	1.04	0.47	1.1
	0.8	0.4	1.15
B/G/2	0.82	0.34	1.2
	1.1	0.4	1.75
	0.95	0.45	1.2
OW-12	0.8	0.6	1.7
A/132/1	0.86	0.48	0.95
Number	11	11	9
Min.	0.65	0.3	0.85
Max.	1.1	0.6	1.75
Average	0.86	0.41	1.20

Table 2.

Dimensions of boring sponge gen. et sp. indet.

From the Late Triassic of the Northern Calcareous Alps. D = sponge diameter, H = sponge height, Dc = diameter of chamber of *Entobia* isp. (all in mm).

Remarks:

Independently whether the described bodies are detectable or not inside the chambers, never has been observed an opening/entrance where other organisms (e.g., non-boring sponges, foraminifera) could have entered to live cryptically in abandoned cavities. Also, the chambers are all cement-filled with intact roofs and no traces of internal sediment that may have entered from the exterior. Therefore, it is assumed that the rather commonly observed thin-walled bodies represent remains of the former sponge that excavated the boring system addressed here as *Entobia* isp. They are interpreted as representing the outer surface of the sponge, an aspicular membrane (ectosome, dermis or cortex) (e.g., HOOPER, 2003). Similar forms were also observed within Late Jurassic entobians (SCHLAGINTWEIT, 2010). An equivalent body is also observable in Pl. 10, Fig. 7 (specimen on the right; Late Triassic of Sicily) of SENOWBARI-DARYAN (1984). The different and sometimes complex appearances do not permit to identify the original sponge morphology. Consequently, these appearances could correspond to collapsed body membranes, others seem to be fossilized more or less in life position. Some walls seem to line a single-chambered sponge, while others could belong to a multi-chambered form. Besides juvenile versus adult species, also intraspecific variability might be an additional factor of consideration. The occasionally observed cross partitions in the canals ("septation") are also interpreted as remains of the former body wall of the lateral appendages (filaments) that excavated the branching canals into the crusts.

Cryptoendolithic foraminifera, e.g., *Troglotella incrustans* WERNLI & FOOKES (SCHMID & LEINFELDER, 1996, for details) that in the Late Jurassic to Lower Cretaceous can rather frequently occur inside empty sponge chambers were not observed in the Late Triassic material studied. Only very rare specimens of nubeculariids attached to the chamber roof were observed (Pl. 5, Fig. b).

Remarks on Late Triassic Sponge Macrobioerosion

For practical reasons, the term reef is used here for the Late Triassic outer platform coral facies, subsuming also the mound facies applied by STANTON & FLÜGEL (1989) to Mount Steinplatte. The number of Triassic reef sites peaked during the Norian, then slightly declining in the Rhaetian followed by a marked reduction (about 50 %) in the Hettangian (KIESSLING et al., 2007). This trend is also reflected in a parallel manner by the diversity of corals in the mentioned interval and surpassing the Triassic-Jurassic boundary (RIEDEL, 1991; STANLEY, 2003; KIESSLING et al., 2007). Boring sponges appeared in the Lower Paleozoic (BROMLEY, 2004; SCHÖNBERG & TAPANILA, 2006; TAPANILA, 2006). However, they did not become abundant in reefal environments until the Late Triassic (VOGEL, 1993; PERRY & BERTLING, 2000). Concerning the impact of macrobioerosion on Late Triassic reefs, the scarce data available (e.g., STANTON & FLÜGEL, 1989, p. 118; BERTLING, 2000; PERRY & BERTLING, 2000) have to be supplemented with the occurrence of "Problematicum A" or "*Lithocodium aggregatum*", which are interpreted here as representing traces of excavating sponges.

The morphology of the Late Triassic and Late Jurassic sponge borings is generally comparable and both are associated with bioclastic substrates that exhibit enveloping crusts of calcimicrobial origin. For the Late Jurassic occurrences of the Northern Calcareous Alps, a lowering of the relative sea-level along with increased siliciclastic input was documented, obviously enhancing sponge bioerosion (SCHLAGINTWEIT, 2010); in Mount Steinplatte, a significant relative sea-level drop, accompanied with siliciclastic input, during the Late Rhaetian leading to exposure of parts of the platform was reported (STANTON & FLÜGEL, 1989; BERNECKER et al., 1999; KRZYSTYN et al., 2005). Several studies have documented that bioerosion rates of modern boring sponges (and other macroborer) increases with the elevation of the nutrient level and the resulting stress impact on coral reefs (ROSE & RISK, 1985; ZEA, 1994; HOLMES, 2000; WARD-PEIGE et al., 2005; HOLMES et al., 2009). The Late Triassic *Entobia* isp. is common in the reef core ("biolithite facies") being abundant in the oncoid facies (SENOWBARI-DARYAN, 1980, Fig. 9) or the crustose oncoid debris facies (WURM, 1982, p. 227). It can therefore be reasoned that the sponges preferentially bored into dead rubble substrates being in accordance with the observation of SENOWBARI-DARYAN (1980, p. 88) that "*Lithocodium*" is rarely observed upon corals in life-position. The construction of many boring chambers with the lower concave part dug into the substrate and the upper part positioned in the calcimicrobial-oncoid crusts highlights that crust formation occurred prior to the boring. In the biolithite facies, where entobian borings are less frequent than in the near-reef oncoid facies (SCHÄFER, 1979), in-vivo bioerosion is likely. In the Northern Calcareous Alps, the shallow-water platforms were drowned around the Triassic-Jurassic boundary, and thus also the facies suitable for boring sponges and their traces (*Entobia* isp.) disappeared. In his study, BERTLING (2000) also examined thin-section material from the Late Rhaetian of the Northern Calcareous Alps, stating that "*The pattern of coral reef macroboring ... remained essentially unchanged across the major end-Triassic extinction phase of corals*". In areas, where oncoid-bioclastic shallow-water facies was prevailing during the Lower Jurassic, e.g., rock of Gibraltar/Spain (BOSENCE et al., 2000), the same entobians as those recorded from the Late Triassic, may be present in the Lower Liassic showing that these became not extinct during the end-Triassic biological crisis but reduced in their abundances (see synonymy). The specimen detectable on Fig. 5e of BOSENCE et al. (2000) corresponds to a transverse section (see Pl. 3, Fig. h, this work) and was noted internally as possibly belonging to *Lithocodium* (pers. comm. D. BOSENCE). Summarizing, the increased abundance of boring sponges during Late Triassic times obviously was not the causal reason for the decline of corals, but can be considered as an expression of changing physical-chemical parameters causing these impacts.

Besides boring sponges, also other macroborings (> 0.1 mm) are recorded from the Upper Triassic platform carbonates of the Northern Calcareous Alps. Small trochospiral foraminiferans comparable to the Late Cretaceous *Tauchella endolithica* (see CHERCHI & SCHROEDER, 2000, for details), were observed inside cement-filled borings (Text-Figs. 4a-b). Whether the foraminiferans were actively boring these galleries or just non-boring cavity-dwellers, however, is unknown. Slightly bended, bored tubes within the calcareous substrates may be the product of boring

polychaete or phoronid worms (e.g., VOIGT, 1975; HUTCHINGS, 2008; EMIG, 2010) (Text-Figs. 4c–d). These borings were detected in reefal debris facies together with *Entobia* isp. Borings of lithophagid bivalves were described by CARTER & STANLEY (2004) from the Norian–Rhaetian Zlambach Beds and Norian Dachstein Reef Limestone. Quantitative and qualitative data on Late Triassic bioerosion are scanty (BERTLING, 2000; PERRY & BERTLING, 2000), allowing only a first estimation and comparison with other time slices. An interesting topic of future investigations would be the compilation of the macroboring assemblages (semiquantitative frequencies, composition, intensity, substrate type, etc.) in the different parts of the Late Triassic platforms and the comparison and integration with the characteristic associations of other organism groups (e.g., SCHÄFER & SENOWBARI-DARYAN, 1981; SENOWBARI-DARYAN & SCHÄFER, 1978, 1979). It is worth mentioning, that microborings of selected Triassic facies realms of the Northern Calcareous Alps were studied by SCHMIDT (1990, 1992).

Conclusions

The Late Triassic structures ascribed to *Lithocodium aggregatum* ELLIOTT by many authors are interpreted as representing borings of unicameral sponges following CHERCHI & SCHROEDER (2010) and SCHLAGINTWEIT (2010). This interpretation resulted from morphological analogies (e.g., chambers, canals, boring network) of representatives of the ichnogenus *Entobia* BRONN although a real proof, such as detection of sponge spicules inside the chambers, is still lacking. *Entobia* isp. cannot be included in any of the so far established ichnospecies. On the other side, the creation of a new ichnospecies is not possible with the

thin-sections studies, given that an exact 3-dimensional analysis is needed. Therefore, an open nomenclature is used for the description of these forms. Thin-walled bodies/structures inside the cement-filled chambers are interpreted as preserved body walls (membranes) of the former sponge. These unicameral entobians with their characteristic system of branching canals arising from the chamber roofs and boring preferentially into calcimicrobial-oncoidal crusts and/or corals are reported from the Norian–Coniacian with peak records in the Late Triassic and the Late Jurassic and more rare records in the Early and Late Cretaceous. The enhanced and widespread appearance of these boring sponges in the Norian–Rhaetian might be linked to the same oceanic physico-chemical disturbances such as change of trophic conditions that led to the end-Triassic biological crisis. As they bored into dead coral substrates, they cannot be considered the primary cause for the decline of Late Triassic coral reefs. In any case, future semi-quantitative tempo-spatial assessment of macrobioerosion must bear in mind this peak occurrence of boring sponges in the Late Triassic, so far unconsidered as previously referred to the incertae sedis "*Lithocodium aggregatum*".

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Plate 1

Entobia isp. from the Late Triassic (Late Rhaetian) of the Northern Calcareous Alps (a–e) and the Late Jurassic (?Late Tithonian) of the Crimea Mountains, Ukraine (f).

Scale bars 2 mm.

- a Coral with thin calcimicrobial crust and two entobians.
Sample BG.
- b Coral with thin crust of calcimicrobes and foraminifera exhibiting one chamber of *Entobia* (width 1.5 mm, height 0.7 mm).
Sample O 55.
- c Numerous entobians boring into a coral skeleton enveloped by a calcimicrobial crust which in turn are encrusted by foraminifera. Note the micritized traces of the excavating filaments between individual chambers.
Sample O 55.
- d Coral bored by *entobians*. The central part shows a network of anastomizing boring filaments (= "*Bacinella* threads" of some authors). On the right, only the micritized zone around the chamber is cut (white arrows). Note the thick oblique canal (opening?) on the left side of the chamber (black arrow).
Sample O 55.
- e Coral bored by entobians.
Sample O 55.
- f Two large specimens of *Entobia* boring into a stromatoporoid skeleton and canals radiating into oncoidal crusts. Late Tithonian – Early Berriasian of the Crimea Mountains, Ukraine (detail from KRAJEWSKI, 2010, Fig. 4.61.A). A detailed view is shown in Text-Fig. 1.

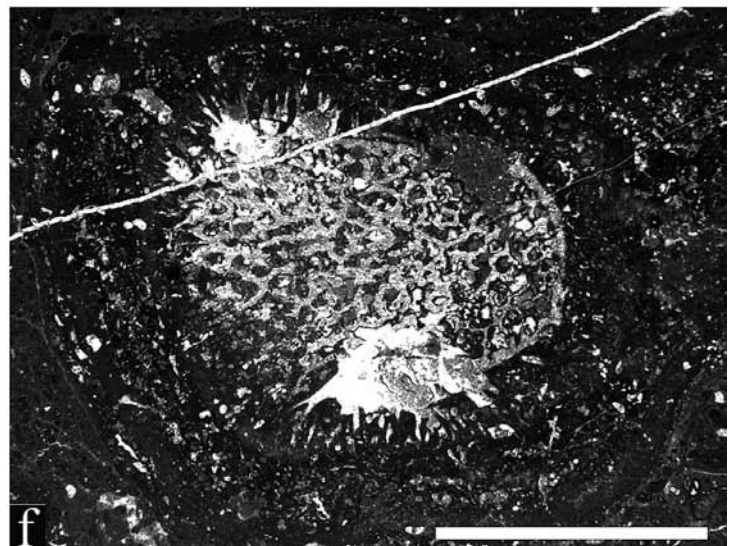
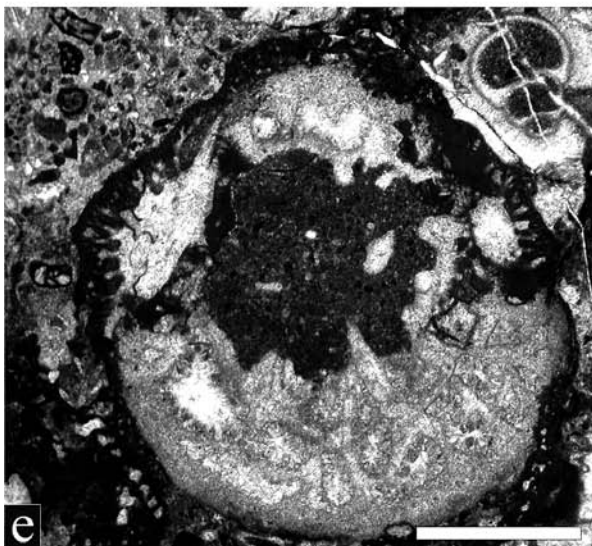
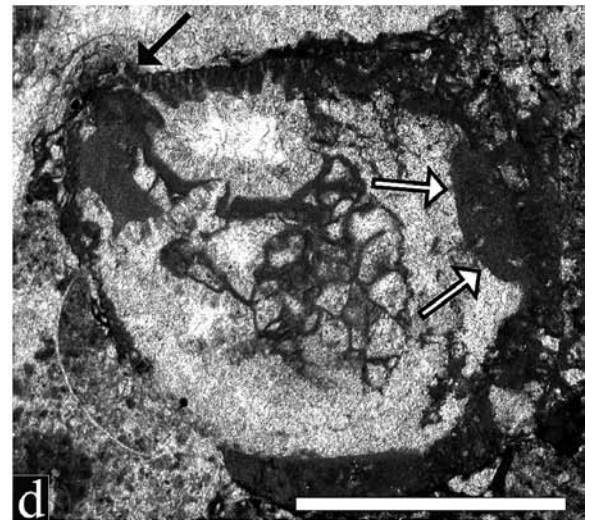
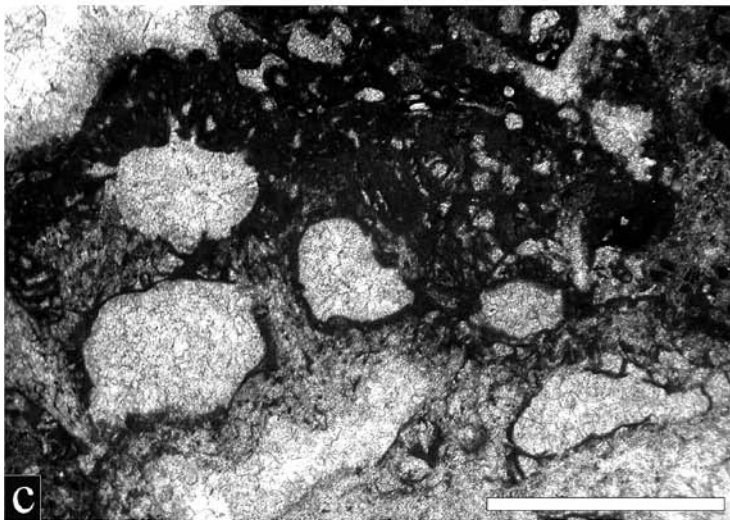
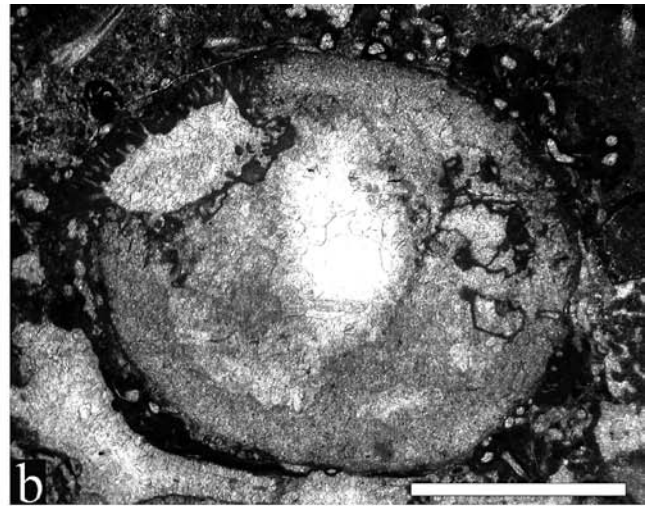
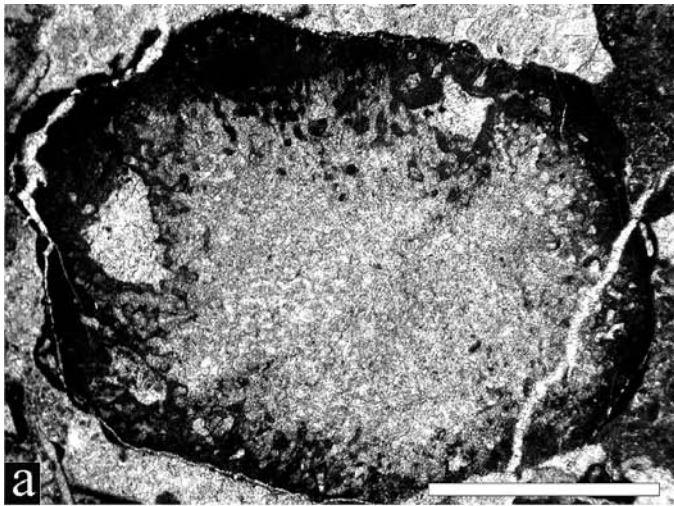


Plate 2

Entobia isp. from the Late Triassic (Late Rhaetian) of the Northern Calcareous Alps.

Scale bars 1 mm.

- a Two large chambers fuse in the centre of a substrate excavating the latter from two opposite sides.
Note the micritized boring network inside the chambers. Two smaller chambers are present in the substrate enveloping crusts (above).
Sample B/G/2.
 - b Several specimens boring the substrate from all sides, in contrast to the example shown in a, not penetrating deep enough to fuse.
Note the thicker canal open to the exterior (above).
Sample BG.
 - c Two specimens boring into calcimicrobial crusts.
Note the preserved sponge remains inside the chambers (detail see Pl. 5, Fig. c).
Sample B/G/2.
 - d Three boring chambers, clearly separated from each other, excavating into a coral skeleton and oncoidal crust.
The substrate between the two chambers on the right was removed by the boring/etching process of the two specimens.
Sample A/132/1.
 - e Several specimens boring into the outer zone of a thick calcimicrobial crust enveloping coral rubble.
Sample A/132/1.
 - f Rather large chamber within calcimicrobial crusts resulting from lateral growth.
Sample BG/2.
-

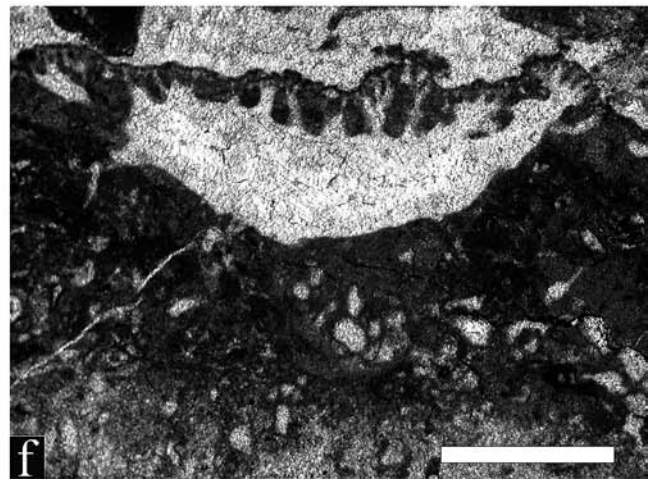
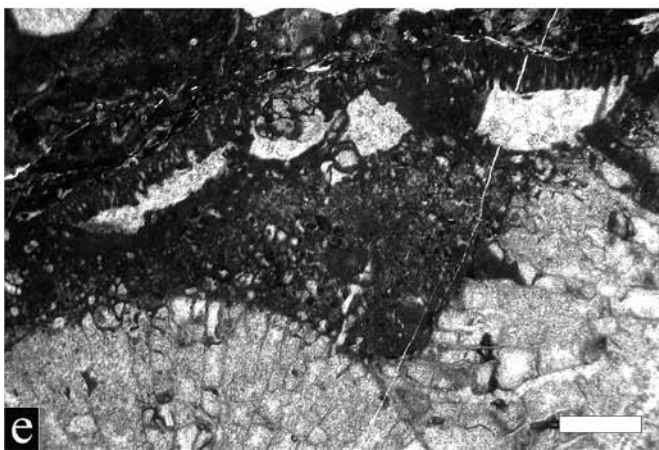
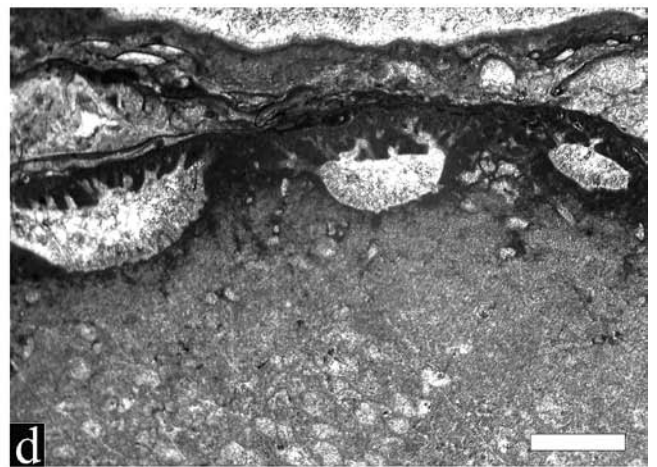
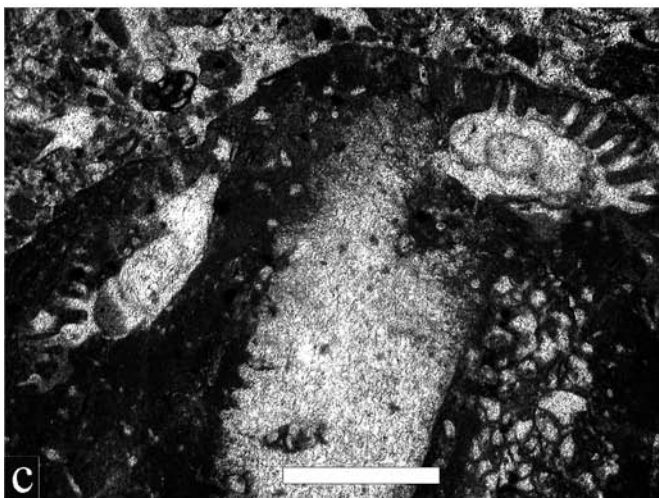
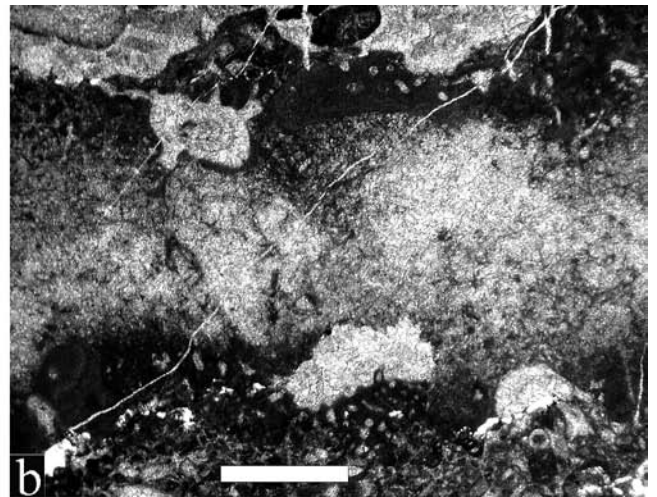
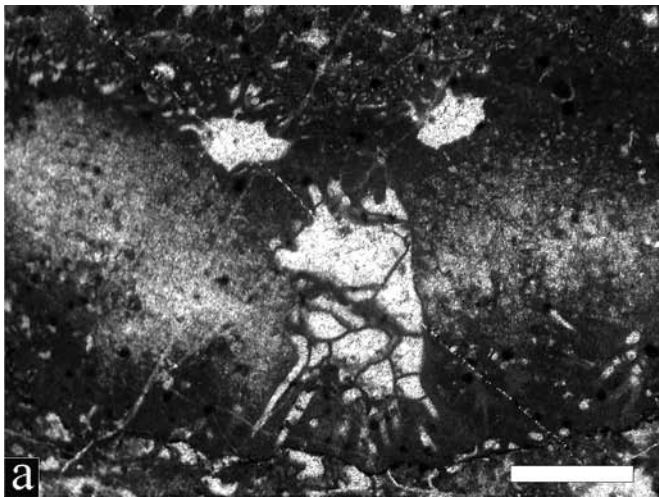


Plate 3

Entobia isp. from the Late Triassic (Late Rhaetian) of the Northern Calcareous Alps.

Scale bars 1 mm.

- a *Entobia* boring into a pelecypod shell. Note the sack-like shape of the boring and the micritized traces of the radiating excavating filaments.
Sample O 55.
- b Irregular-ovoid boring within a coral.
Sample O 55.
- c Two entobians bored into a calcimicrobial crust. The arrow points to a possible aperture.
Sample BG.
- d Numerous entobians within a coral and the enveloping calcimicrobial crust, which in turn is overgrown by encrusting foraminifera.
Sample O 55.
- e Transverse section of a boring chamber within a calcimicrobial crust.
Sample BG.
- f Boring chamber within a calcimicrobial crust filled by an irregular meshwork interpreted as the micritized traces of excavating filaments from adjacent and/or superimposed entobians.
Sample BG.
- g Oblique section of a boring chamber within a calcimicrobial crust.
Sample BG.
- h Round transverse section of a boring chamber within a calcimicrobial crust.
Sample BG.
- i Boring chamber within a coral. Note the micritization around the chamber and the rather long canal on the left side. It is overlain by an encrusting foraminifer.
Sample O 55.
- j Tangential section through the close-set, honey-comb-like pattern of the canal system.
Sample O 55.

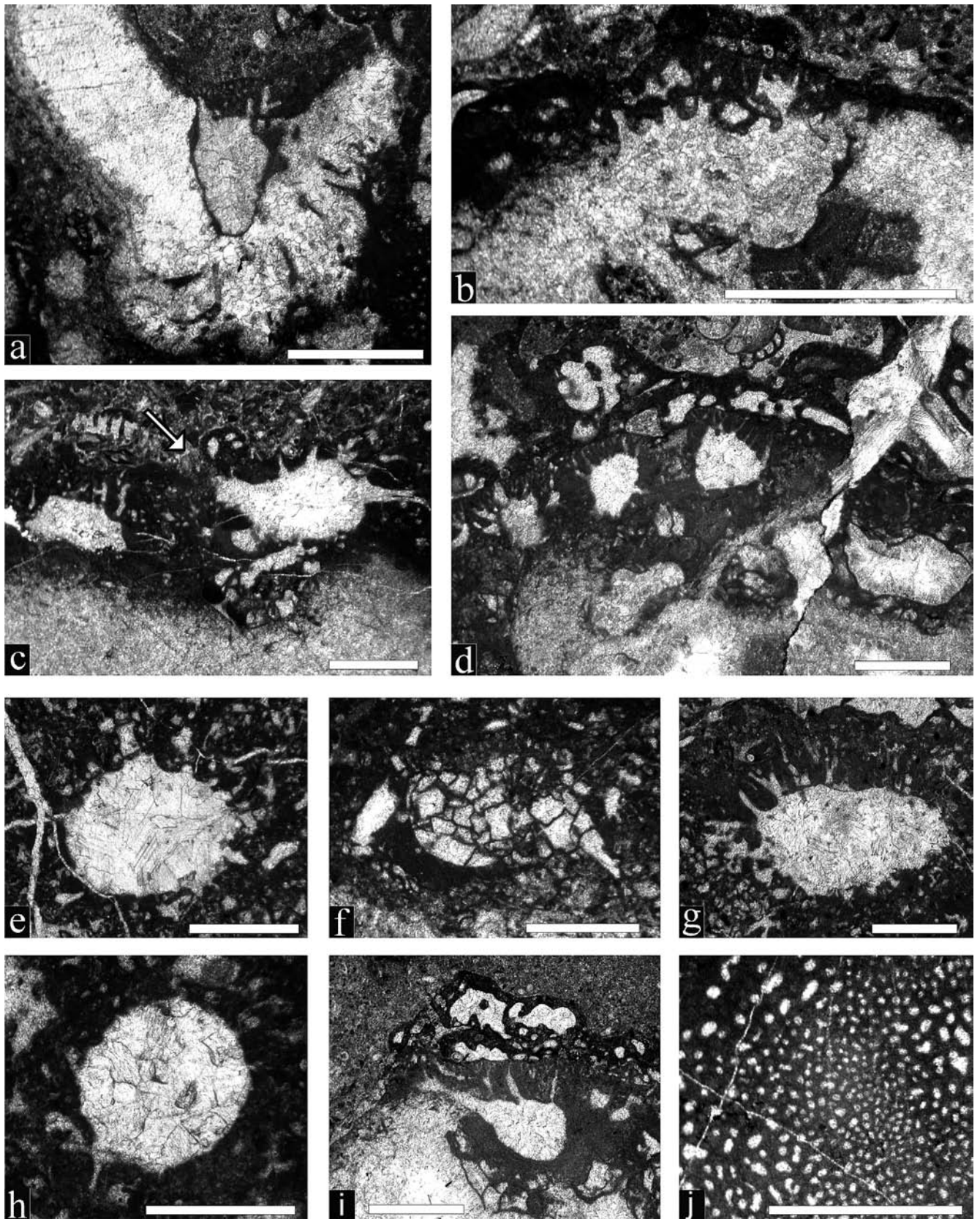


Plate 4

Entobia isp. from the Late Triassic (Late Rhaetian) of the Northern Calcareous Alps.

- a Specimen with ovoid chamber from which numerous thin and one larger (arrows) branching canals arise. The latter is rather long and transects the crusts in an oblique manner. The crust surrounding the chamber, and its base toward the substrate, is transformed to dense micrite (white dashed line). The upper zone of the substrate is pervaded by micritized traces of boring filaments.
Scale bar 1 mm, sample O 55.
- b Two entobians boring into a coral.
At the base of the right specimen, two thick branching canals arise (white arrows), one filled with sparite the other with micrite. The specimen on the left shows one thicker canal (black arrow) obliquely transecting the crust.
Scale bar 1 mm, sample O 55.
- c–d Detailed views of the micritized network of excavating filaments within the coral skeleton arising from the chamber base.
Scale bar 0.3 mm, sample O 55.
- e Detail of the branching canal system arising from the chamber roof.
Scale bar 0.3 mm, sample O 55.
- f Erosion meshwork (erosion scars?) within the substrate below the chamber.
Scale bar 0.3 mm, sample O 55.

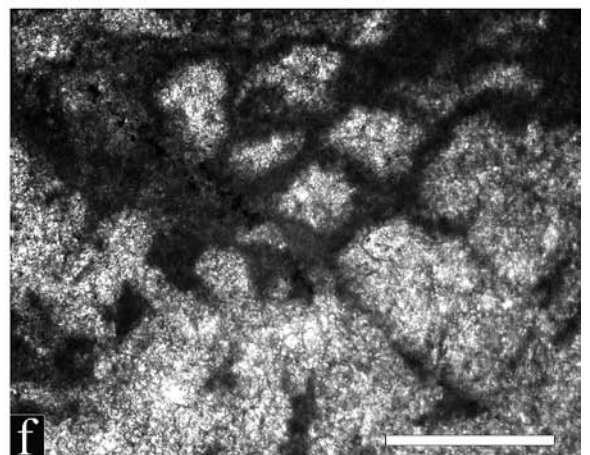
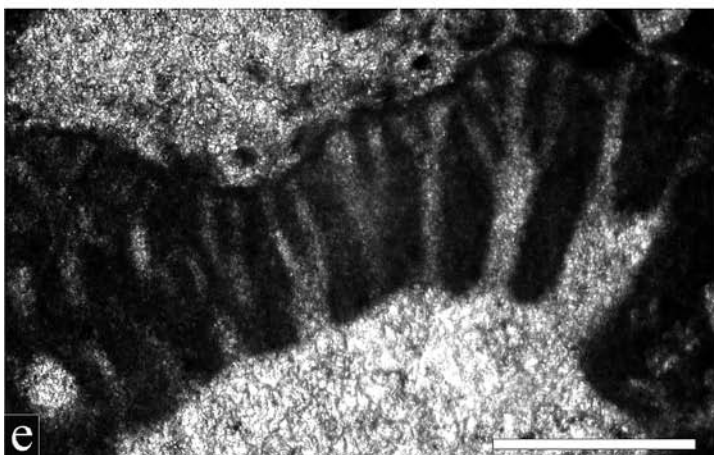
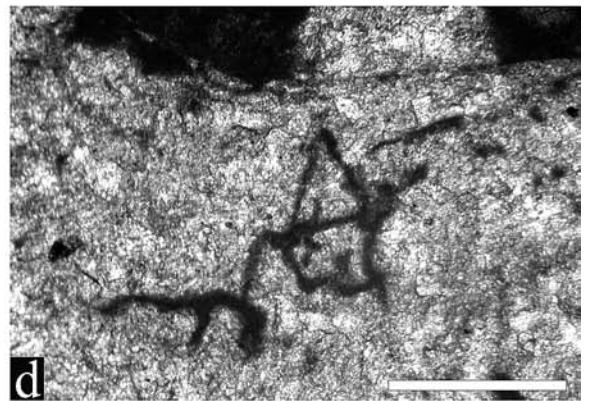
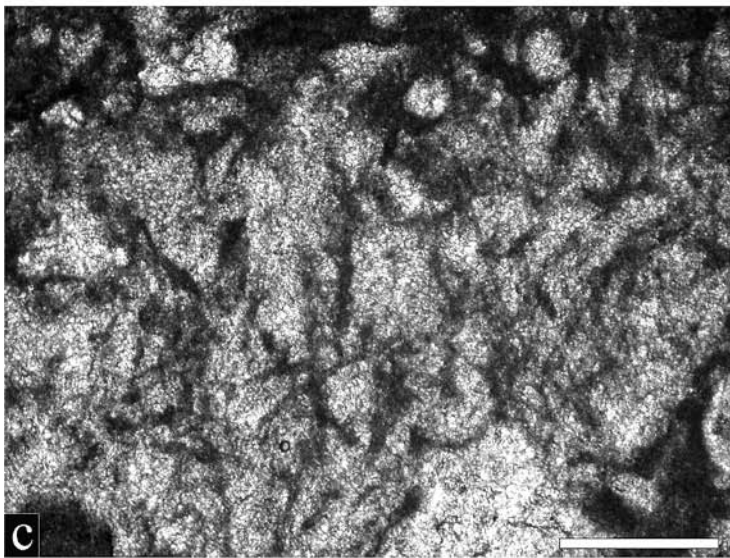
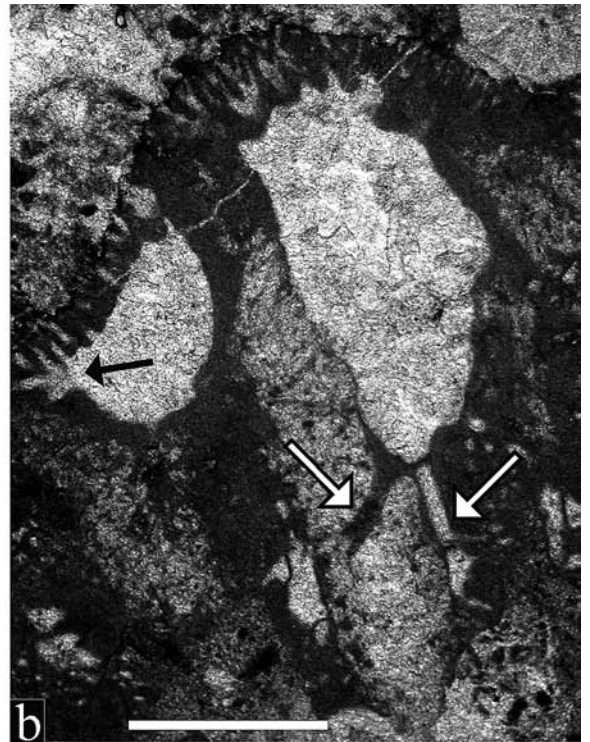
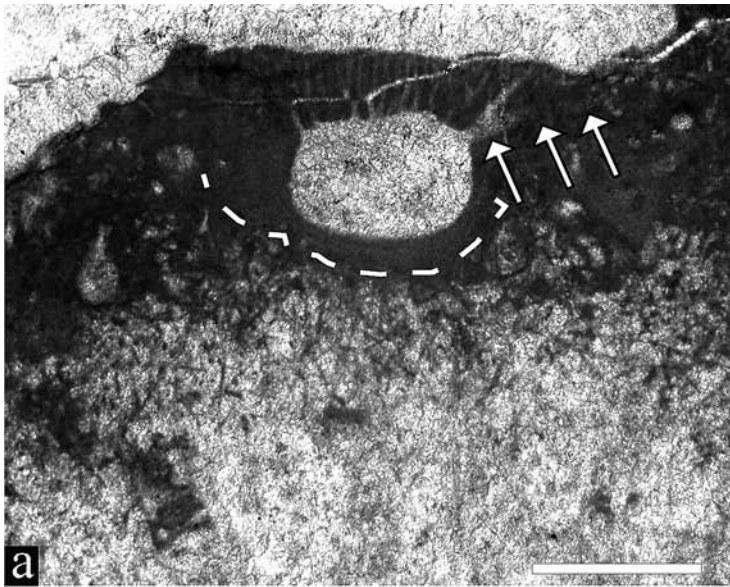
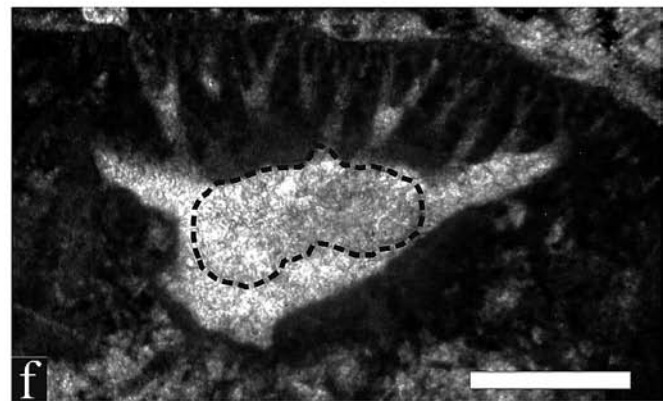
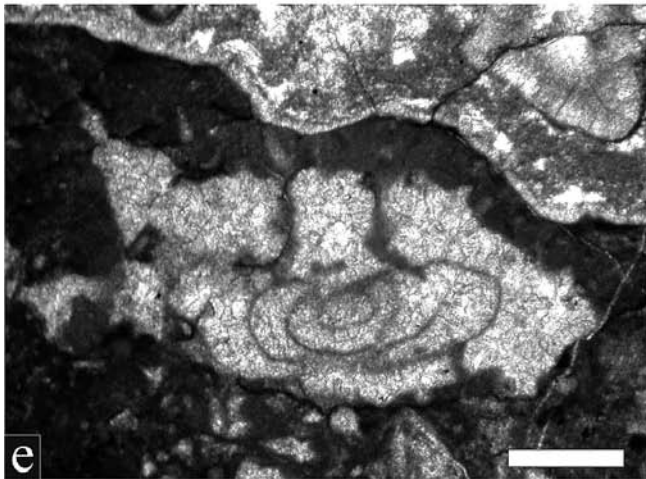
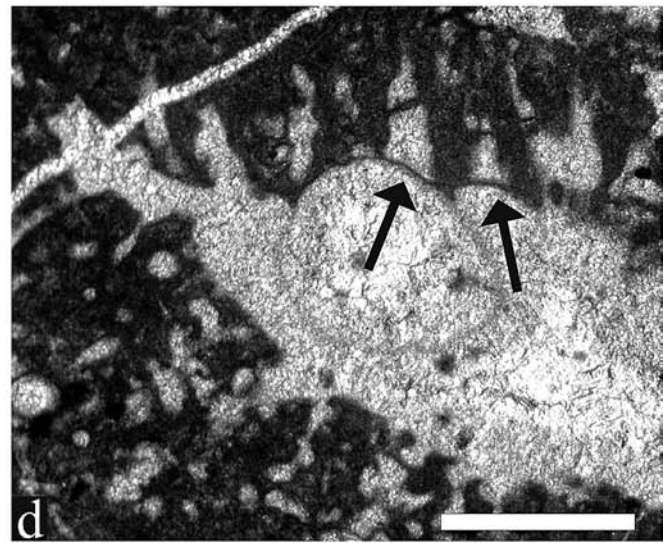
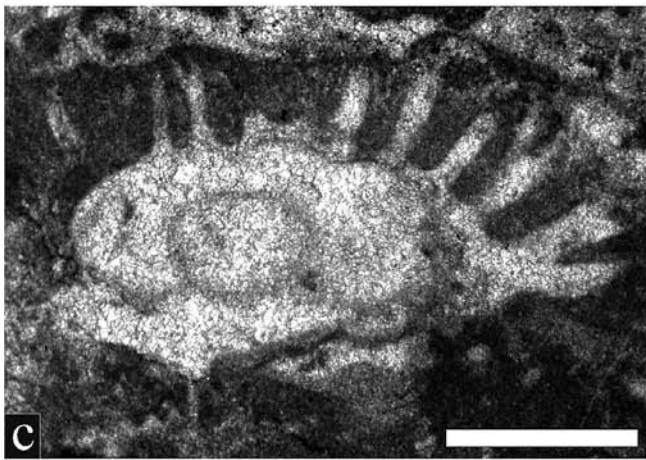
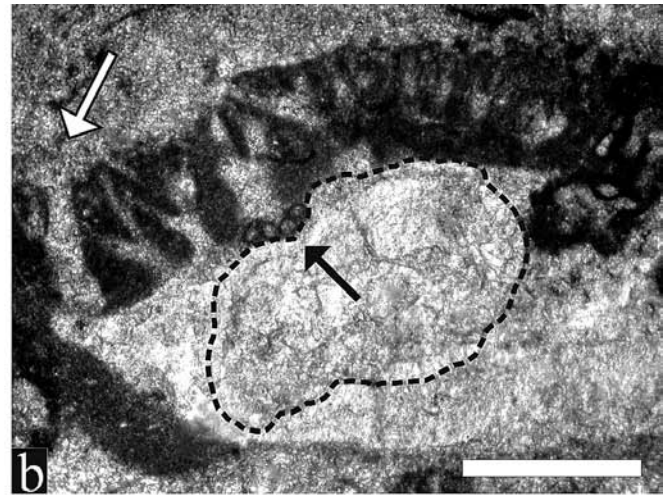
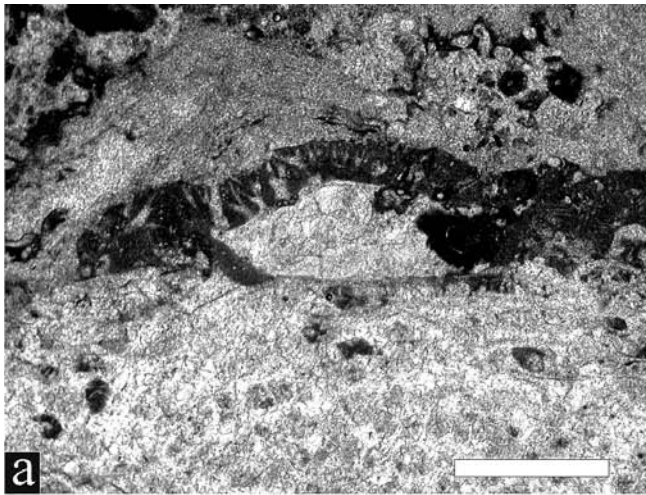


Plate 5

Boring sponge gen. et sp. indet., assumed producer of *Entobia* isp., from the Upper Rhaetian of the Northern Calcareous Alps.

- a *Entobia* isp. boring into a microbial crust enveloping a coral skeleton.
Scale bar 1 mm, sample OW-12, Late Rhaetian of Oberwössen, Chiemgau Alps.
- b Detail from a, showing a thin-walled globular body (size: 0.8 mm x 0.6 mm), outline marked by the black dashed line, inside the sparite-filled cavity of *Entobia* isp. (size: 1.7 mm x 0.7 mm), as assumed remnant (body wall) of the boring sponge. Note the globular to ovoid cryptobionts of unknown affinity inside the boring (arrow).
Scale bar 0.5 mm.
- c Detail from Plate 2, Fig. c showing a globular sponge (size: 1.05 mm x ~ 0.5 mm) largely occupying *Entobia* isp.
Scale bar 0.5 mm, sample B/G/2.
- d Part of one *Entobia* chamber with assumed sponge body wall (arrows) stretching into the proximal parts of the canals, thus, pretending a septation of the latter.
Scale bar 0.5 mm, sample B/G/2.
- e Multi-chambered? boring sponge inside *Entobia* sp.
Scale bar 0.5 mm, sample BG.
- f Globular boring sponge (size: 0.75 mm x 0.35 mm) inside *Entobia* isp.
Scale bar 0.5 mm, sample O 55.



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