

**Taxonomic Revision of Late Jurassic “*Lithocodium aggregatum* Elliott”  
 sensu Schmid & Leinfelder, 1996**

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10 Text-Figures

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Northern Calcareous Alps  
 Late Jurassic  
 Bioerosion  
 Ichnology  
 Boring sponges  
 Entobia  
*Lithocodium*  
*Bacinella*

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**Taxonomische Revision oberjurassischer „*Lithocodium aggregatum* Elliott“ sensu Schmid & Leinfelder, 1996**

**Zusammenfassung**

Basierend auf oberjurassischem Material aus Portugal, wurde die aus der Unterkreide ursprünglich als Kalkalge beschriebene Art *Lithocodium aggregatum* Elliott von Schmid & Leinfelder (1996) als loftusiide Foraminifere neu interpretiert. Vor kurzem wurde die Notwendigkeit einer taxonomischen Revision der Formen aus der Obertrias und dem Oberjura von Schlagintweit et al. (2010), die Unterkreide-Formen von *Lithocodium aggregatum* Elliott als heterotrichale Grünalge beschrieben, hervorgehoben. Reichhaltiges Material aus dem Oberjura der österreichischen Nördlichen Kalkalpen zeigt, dass diese hingegen ichnologische Strukturen (ichnogenus *Entobia*) darstellen, erzeugt von bohrenden Schwämmen, die ihre Gänge in kalkigen Substraten (Kalziummikroben-Onkoide und Metazoenskelette) anlegten. Im Bereich um die Bohrkammern und im Raum zwischen den sich verzweigenden Kanälen sind die mikrobiellen Mikrostrukturen nicht mehr erkennbar und in dichten Mikrit transformiert. Dünnwandige mikrokristalline Körper mit oder ohne laterale Anhänge innerhalb der Bohrungen werden als Reste (imprägnierte Wand?) der diese erzeugenden Schwämme interpretiert. Im Kernbereich von allseitig angebohrten Onkoiden zeigt sich häufig ein irregulär ausgebildetes „bacinellides“ Maschenwerk, das auf sogenannte pionierende Bohrfilamente zurückgeht und in dieser Ausbildung auch von modernen clonaiden Schwämmen bekannt ist. Spicula wurden in den Bohrkammern nicht festgestellt, aber gelegentlich zu beobachtende partielle Verkieselungen von Onkoiden weisen auf ein früheres Vorhandensein hin. Auf der anderen Seite werden die leeren Bohrkammern oft von der Foraminifere *Troglotella incrustans* Wernli & Fookes besiedelt. Dies stellt ein weiteres Beispiel für die Assoziation von cryptoendolithischen Foraminiferen und Schwämmen dar.

**Abstract**

Based on Late Jurassic material from Portugal, *Lithocodium aggregatum* Elliott, originally described as a calcareous alga from the Lower Cretaceous, was reinterpreted as a loftusiid foraminifer by Schmid & Leinfelder (1996). Recently, the necessity of a taxonomic revision of the Late Triassic and Late Jurassic forms has been stressed by Schlagintweit et al. (2010) who redescribed the Lower Cretaceous *Lithocodium aggregatum* Elliott as a heterotrichale calcareous green alga. Abundant specimens occurring in the Late Jurassic of the Northern Calcareous Alps of Austria show that these in contrast are ichnological structures (ichnogenus *Entobia*) produced by excavating sponges that bored their galleries into calcareous substrates (calcimicrobial oncoids and metazoan skeletons). Around the bored chambers and between the branching canals, the originally microbial microstructures are no more discernible and transformed into dense micrite. Thin-walled microcrystalline bodies with or without lateral appendages inside the borings are interpreted as remains (impregnated body wall?) of the sponges. The core zone of all-side bored oncoids may show an irregular “bacinellid” meshwork that is interpreted as the traces of so called pioneering excavating filaments, which are known from modern clonaid sponges. Spicules were never observed inside the empty chambers, but occasional silicification of oncoids point to their former presence. The empty chambers are often colonized by the foraminifer *Troglotella incrustans* Wernli & Fookes representing a further example of the common association of cryptoendolithical foraminiferans and sponges.

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## Introduction

*Lithocodium aggregatum* Elliott (1956) and *Bacinella irregularis* Radoičić (1959) are two enigmatic taxa of the Late Jurassic – Early Cretaceous epeiric sedimentary record which have aroused more than 50 years of controversy concerning their biogenic nature, possible relationship or synonymies. *Lithocodium aggregatum* was originally described by Elliott as a siphonal (= non-septate filaments) codiacean (= udoteacean) alga from the Lower Cretaceous of Iraq; other interpretations include a sponge, red algal, foraminiferal and cyanobacterial (calcimicrobial) origin. New material of *Lithocodium aggregatum* from the Lower Aptian of the western Maestrat Basin (E Iberian Chain, Spain), together with detailed illustrations of Elliott's original material housed at the Natural History Museum in London, yielded new insights into its biogenic nature and morphological interpretation (Schlagintweit et al., 2010). *Lithocodium* was re-interpreted as a heterotrichale filamentous-septate green alga (order Ulotrichales?). The crusts were described as consisting of a basal prostrate and an erect filament system replacing “medullary” and “cortical” filaments in the previous udoteacean algal terminology of Elliott (1956).

Several Late Jurassic references cannot be included in the emended diagnosis of *Lithocodium* as they are morphologically different; the same accounts for all Late Triassic reports. The paper of Schmid & Leinfelder (1996), where Late Jurassic “*Lithocodium aggregatum*” from Portugal is re-described as a Loftusiid foraminifer, attracted much attention from the scientific community. On the one hand this interpretation was integrated in standard books (Scholle & Ulmer-Scholle, 2003), but then was also declined. For example, Cherchi & Schroeder (2006) rejected the foraminiferan interpretation and proposed a calcimicrobial nature of *Lithocodium aggregatum* Elliott. That study, however, was based on Aptian material which is different from the Late Jurassic material reported in Schmid & Leinfelder

(1996). Abundant material from the Late Tithonian (?Earliest Berriasian) of the Northern Calcareous Alps of Austria allows a revision of these forms.

## Sample Locations and Material

The thin-sections used in the present study come from the uppermost parts of the Lärchberg Carbonate Platform of Mount Dietrichshorn and Mount Lofer Kalvarienberg (see Ferneck, 1962; Darga & Schlagintweit, 1991; Dya, 1992; Schlagintweit, 2005; Sanders et al., 2007) (Text-Fig. 1). Two additional illustrated specimens come from Mount Höherstein (Gawlick et al., 2007) and Mount Zwerchwand (Gawlick et al., 2010).

From a microfacies point of view, the investigated marly limestones of the Lärchberg Carbonate Platform are oncoidal-dominated float-/rudstones exhibiting a fine-clastic terrigenous input (Text-Fig. 2). Beside scattered extraclasts and debris of terrestrial land plants, larger bioclasts are represented by pelecypod shells, e.g., diceratids (see Sanders et al., 2007), gastropods and skeletons of stromatoporoids (e.g., *Milleporidium remesi* Steinmann) and corals. Amongst the benthic foraminifera, the presence of *Anchispirocyclina lusitanica* (Egger) and *Kastamonina abanica* Sirel is worth mentioning. Calcareous algae include *Pinnatiporidium* div. sp. (common), *Marinella lugeoni* Pfender and the Dasycladales *Clypeina loferensis* Schlagintweit, Dieni & Radoičić, *Salpingoporella annulata* Carozzi, *Neogyroporella? gawlicki* Schlagintweit, and *Delofrella quercifoliipora* Granier & Michaud. Microencruster include omnipresent calcimicrobes, either as thick crusts or irregular domal bodies, and occasionally *Koskinobullina socialis* Cherchi & Schroeder.

## Taxonomic Part

Ichnogenus *Entobia* Bronn, 1838, emended Bromley et al. 2009

**Diagnosis:** “Boring in carbonate substrate comprising a single chamber or networks or boxworks of chambers or noncamerate galleries, connected to the substrate surface by several or numerous apertures. The galleries show increase in size during growth; in some forms, inflation at more or less regular distances produces a system of closely interconnected chambers; in other forms chambers lie distant from one other; in still other forms no cameration develops. The boring surface of most forms bears a cusped microsculpture. Fine pioneer (exploratory) threads are usually present, arising from all or some surfaces of the system. Apertural canals lead to the apertures (in- and exhalent pores).” (Bromley et al., 2009, 151).

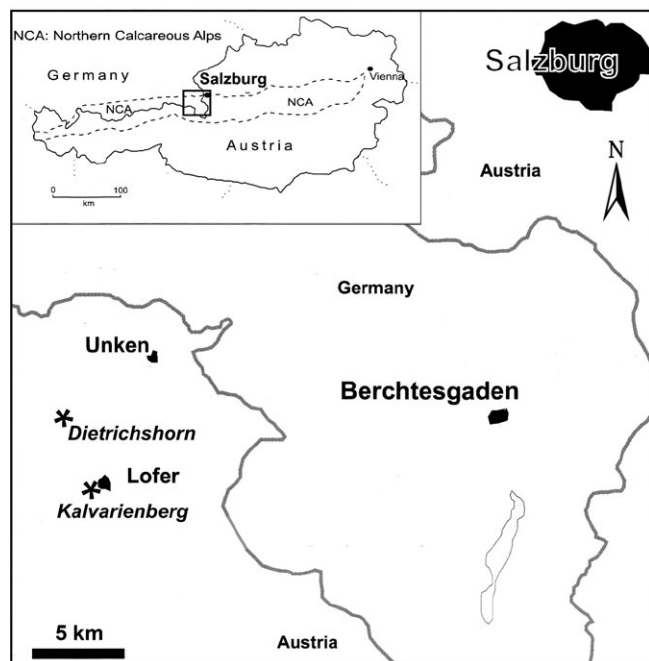
Type ichnospecies: *Entobia cretacea* Portlock, 1843.

### *Entobia* isp. 1

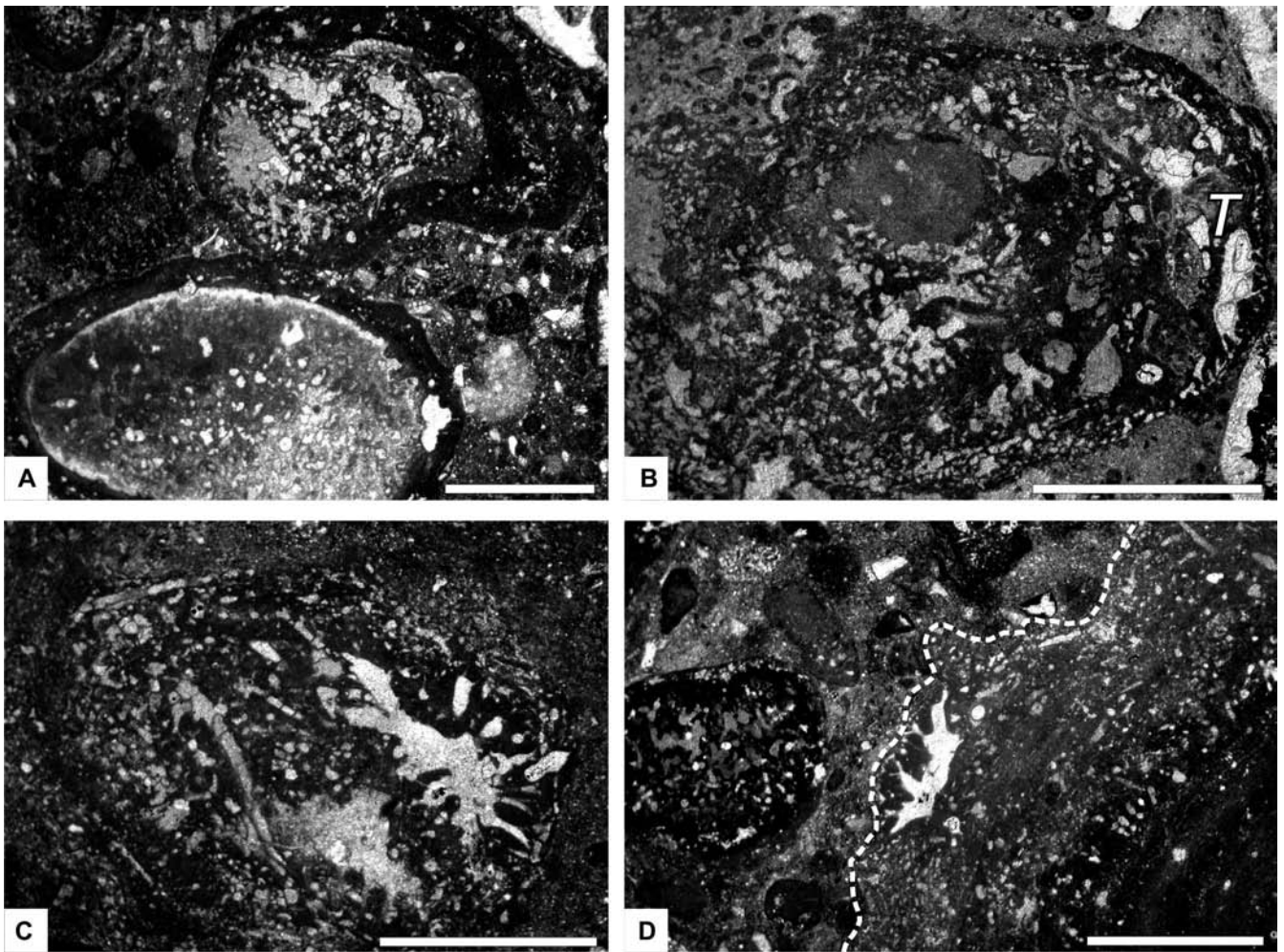
(Text-Figs. 2A pars, B–C, D pars, Text-Figs. 3A–H, Text-Figs. 4A–C, E–F, Text-Figs. 5C, D–E pars, Text-Figs. 6A–B pars, D–F pars, Text-Figs. 7A–F, Text-Fig. 8, Text-Fig. 10A)

Selected synonymy:

1968 *Lithocodium morikawai* Endo – Barthel, Pl. 1, Fig. 1, Late Jurassic of S-Germany.



Text-Fig. 1. Generalized geographic sketch map with the location of Mount Dietrichshorn and Mount Lofer Kalvarienberg in the Salzburg Calcareous Alps near the German-Austrian border.



Text-Fig. 2A–D.

Oncoidal float-/rudstones with rounded and encrusted coral debris (below in A), and extraclasts within a micritic matrix exhibiting fine-grained terrigenous input. Note the cryptoendolithic foraminifer *Troglotella incrustans* Wernli & Fookes (T) in B. “*Lithocodium aggregatum* Elliott” sensu Schmid & Leinfelder (1996) is omnipresent in the oncooids (“*Lithocodium* oncooids”). In D, one specimen of “*Lithocodium aggregatum*” occurs within the outermost oncooid layer (white dashed line). Mount Dietrichshorn, sample Die 170f and 170m, scale bars 2 mm.

1977 *Bacinella* in growth position (within oncooids) – Dahanyake, Figs. 6–8, Late Jurassic of France.

1992 *Bacinella irregularis* Radoičić, *Lithocodium* sp. – Dya, Pl. 5, Figs. 5–6, Late Jurassic of Austria.

1993 *Lithocodium* sp. – Leinfelder et al., Pl. 42, Figs. 1–7 (pars), Late Jurassic of Portugal.

1995 *Lithocodium* sp., *Bacinella irregularis* Radoičić – Nose, Figs. 95–98, 103, Late Jurassic of Portugal.

1996 *Lithocodium aggregatum* Elliott – Schmid & Leinfelder, Pl. 1, Figs. 1–2, 5, Pl. 2, Figs. 1–5, Late Jurassic of Portugal.

1996 *Lithocodium aggregatum* upon “*Bacinella* meshwork” – Herrmann, Pl. 2, Fig. 4, Late Jurassic of Romania.

1998 *Bacinella* nodule with *Lithocodium aggregatum* – Helm & Schülke, Pl. 16, Fig. 7, Late Jurassic of NW Germany.

1999 *Lithocodium aggregatum* – Dupraz, Pl. 6, Figs. 8–9, 10–15 (pars), Late Jurassic of Switzerland.

2002 *Lithocodium aggregatum* Elliott – Scherze & Höfling, Pl. 2, Fig. 4, Late Jurassic of Spain.

2003 Oncooid type 2–4 (not mentioned!), *Bacinella irregularis*, *Lithocodium aggregatum* – Hug, Pl. 2, Figs. 6–8, Pl. 3, Figs. 1, 6–7, Late Jurassic of Switzerland.

2003 algal nodule with *Bacinella* core covered by crusts of *Lithocodium* – Dragastan & Richter, Pl. 5, Fig. 1, Neocomian of Greece.

2005 *Lithocodium aggregatum* Elliott – Helm, Pl. 10, Fig. 3, Late Jurassic of NW Germany.

2007 *Lithocodium-Bacinella* – Védérine et al., Pl. 10a–f, Late Jurassic of Switzerland.

2007 *Bacinella irregularis* Radoičić – *Lithocodium aggregatum* Elliott – Bucur et al., Pl. 3, Fig. 4, Pl. 7, Fig. 3, Late Jurassic of Romania.

2007 not indicated – Gawlick et al., Fig. 15/14, Late Jurassic of Austria.

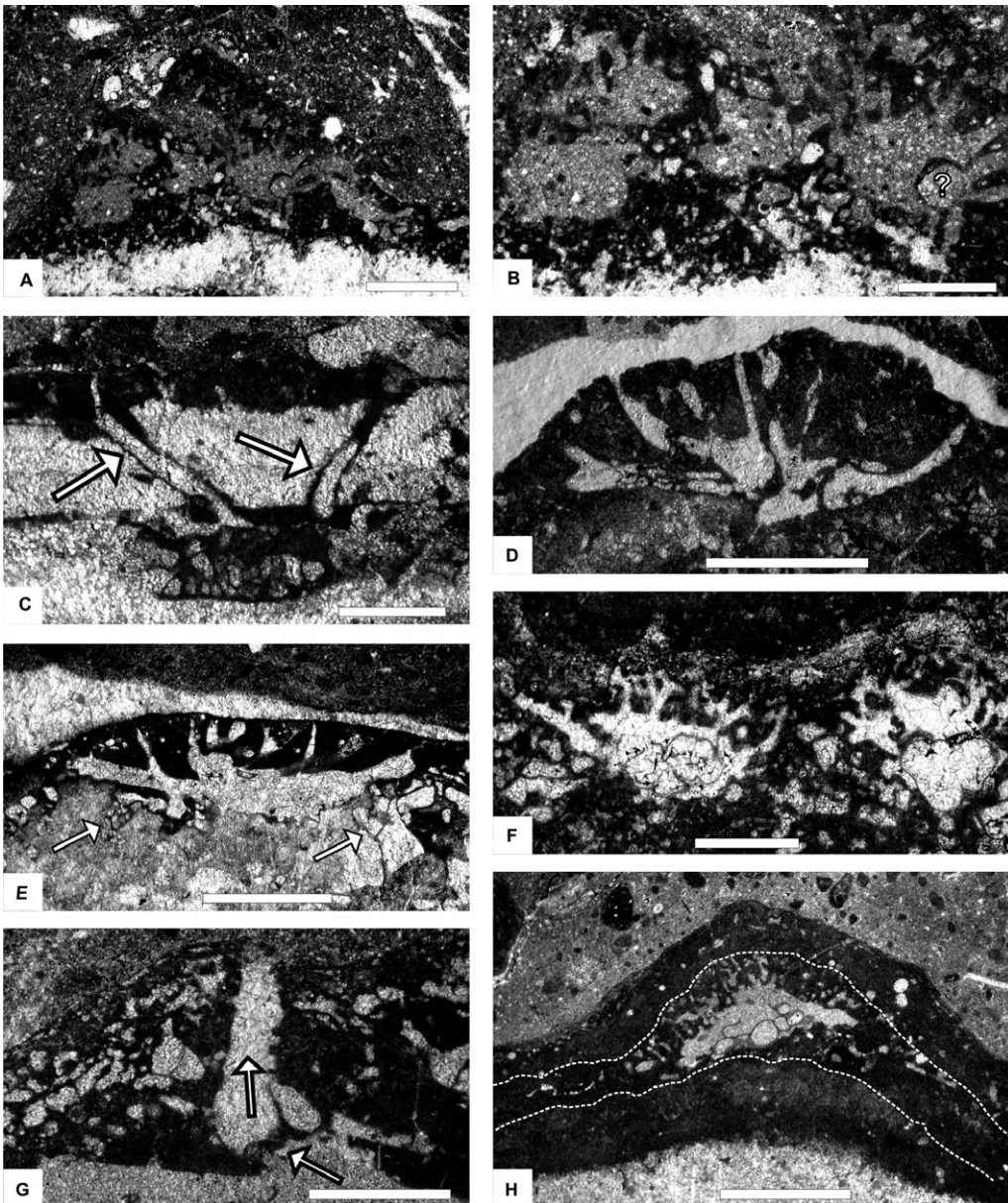
2007 *Lithocodium* – Sanders et al., Fig. 4e, Late Jurassic of Austria.

2008 *Bacinella-Lithocodium* oncooid – Védérine, Pl. 1, Fig. 14, Late Jurassic of Switzerland.

2008 Oncooid of *Bacinella irregularis* Radoičić and *Lithocodium aggregatum* Elliott – Hosseini & Conrad, Pl. 4C, Valanginian of Iran.

2008 *Lithocodium* – Krajewski, Fig. 7g, Late Jurassic of Ukraine.

2009 *Lithocodium-Bacinella* – Védérine & Strasser, Fig. 7d, Late Jurassic of Switzerland.



Text-Fig. 3.

Boring galleries of *Entobia* isp. 1 within calcimicrobial crusts, pelecypod shells and stromatoporoids/corals.

Late Tithonian – ?Earliest Berriasian of the Northern Calcareous Alps, Austria.

A–B Mound-shaped, finely agglutinating calcimicrobial crust with several bored chambers of *Entobia* isp. 1 and almost touching canals.

Note an attaching arenaceous foraminifer at the top of the crust (A) and the filling of the empty boring chambers with sediment. Note the rounded body (?) inside the chamber on the right (B).

Mount Lofer Kalvarienberg, sample Lof 6-3-5, scale bar 1 mm for A, 0.5 mm for B.

C Chamber excavated in a two-layered pelecypod shell (diceratid, compare Sanders et al., 2007) with two canals (arrows) obliquely transecting the outer layer and reaching into the overlying calcimicrobial crust. Within the latter, the canals are branching.

Note the patchily distributed micrite within the chamber and filamentous meshwork as well as the micritic lining of the bored canal.

Mount Dietrichshorn, sample Die 170a, scale bar 0.5 mm.

D Boring within layered calcimicrobial crusts. Chamber with radiating and partly curved canals and meshwork of apophyses (= excavating filaments) reaching downwards into the older crust layer.

The total width of the boring (chamber + canals) is 2.6 mm.

Mount Dietrichshorn, sample Die 39, scale bar 1 mm.

E Oblique section bored in a calcimicrobial crust covering a stromatoporoid skeleton (*Milleporidium*). At the chamber base, micritic branching threads (= produced by excavating filaments), partly forming a meshwork, extend downwards into the skeleton (arrows). Total diameter of boring is ~ 3.5 mm.

Mount Dietrichshorn, sample Die 170h, scale bar 1 mm.

F *Entobia* isp. 1, two specimens boring into a calcimicrobial crust.

Note the short branching canals arising from the chamber roof and the long and thicker, oblique radiating canal on the left side. The thin-walled, irregular inflated bodies at the chamber bases either belong to the cryptoendolithic foraminifer *Troglotella incrustans* Wernli & Fookes or represent remains of the former boring organism (see Text-Fig. 9E–H).

Mount Dietrichshorn, sample Die 170c, scale bar 0.5 mm.

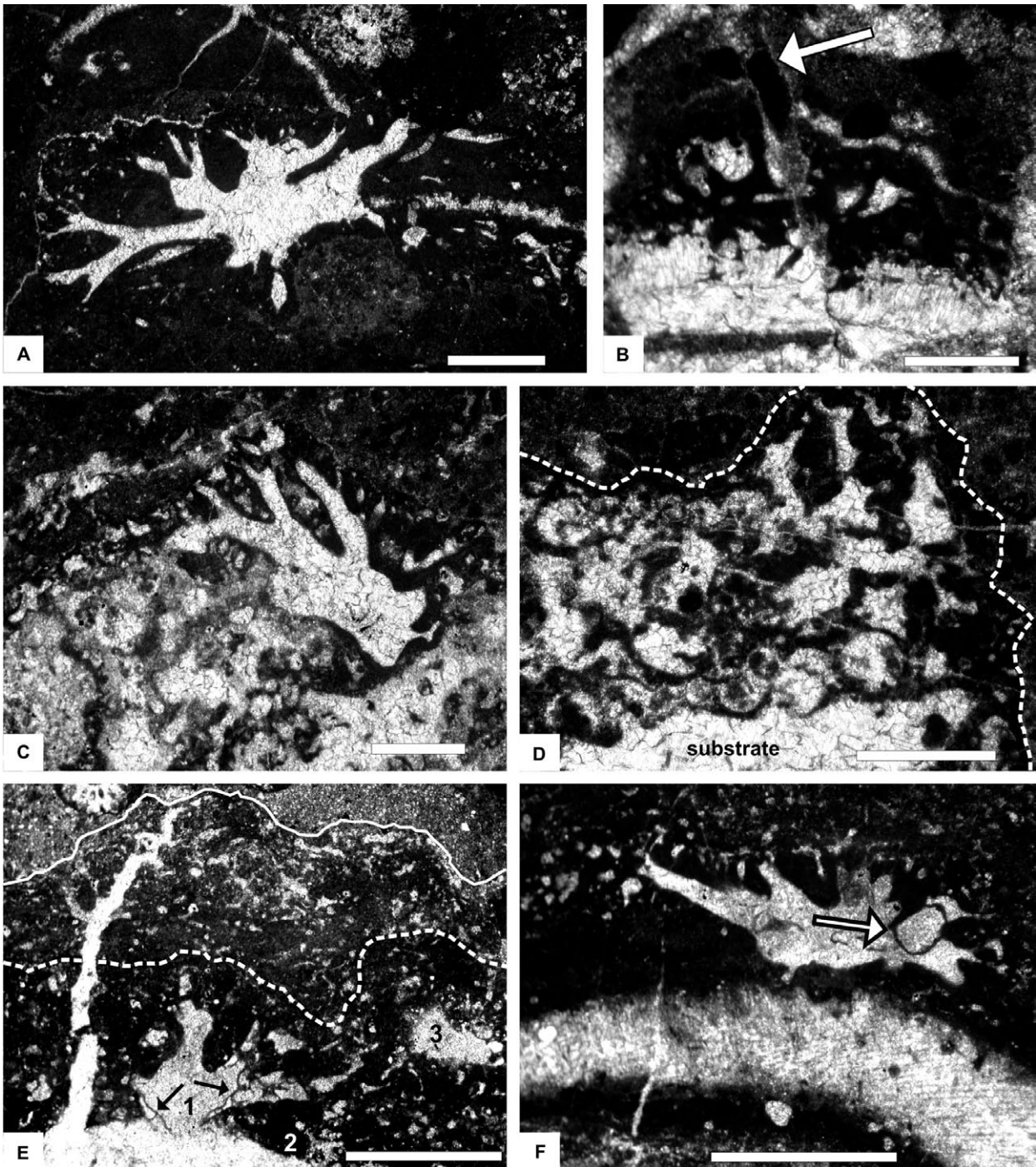
G Specimen with possible aperture of the former sponge (osculum) splitting off from an oblique radiating canal (arrows).

Mount Dietrichshorn, sample Die 170m, scale bar 0.5 mm.

H Oblique section of a single chamber bored into a calcimicrobial crust sandwiched between two unborings (white dashed lines).

The irregular pattern results from the oblique sectioning of the fine branching canals. Note that laterally, the middle crust also does not show further evidence of borings. Inside the empty chamber, the cryptoendolithic foraminifer *Troglotella incrustans* Wernli & Fookes is visible.

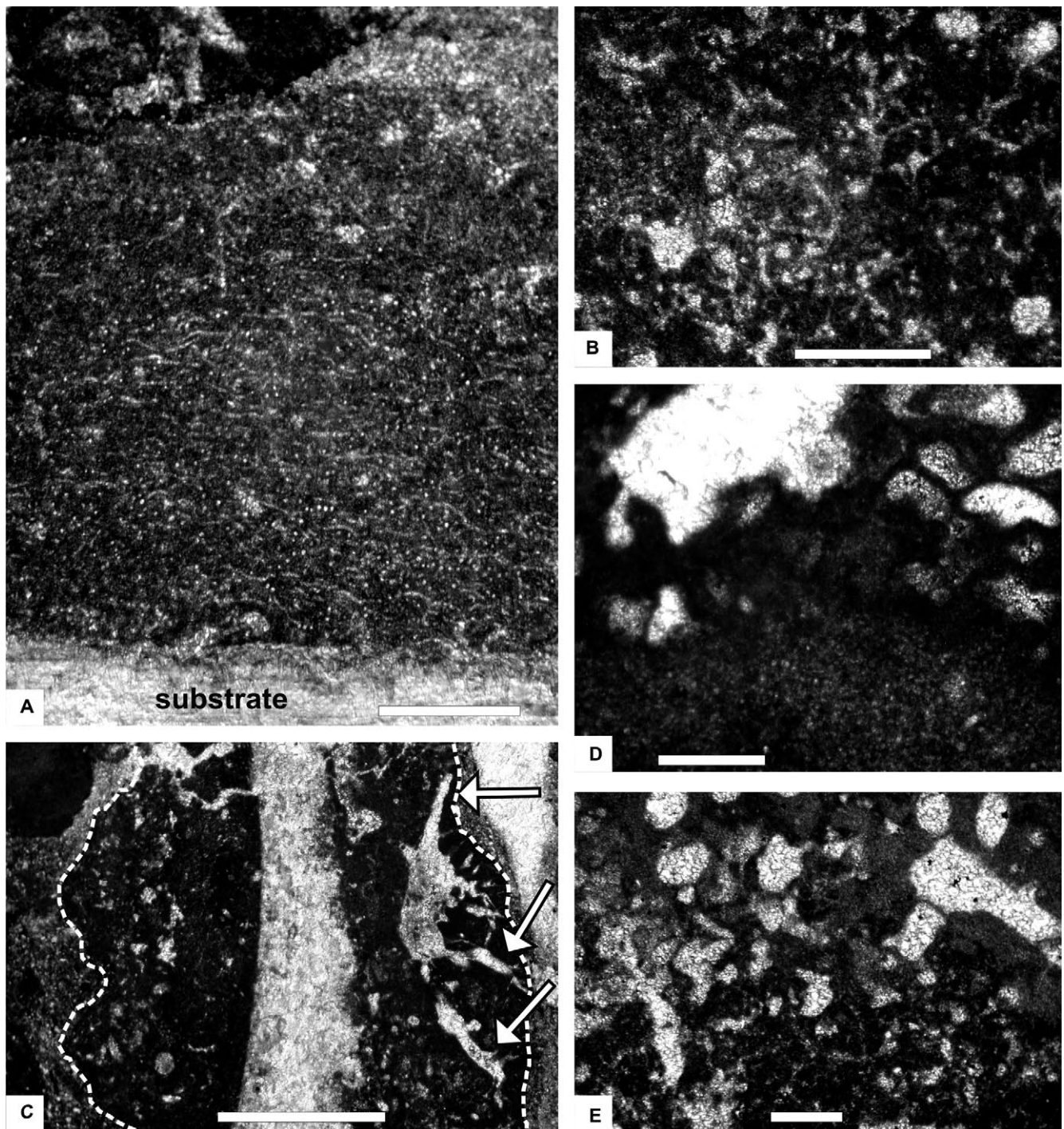
Mount Dietrichshorn, sample Die 170f, scale bar 1 mm.



Text-Fig. 4.

Boring galleries of *Entobia* isp. 1 (A–C, E–F) and *Entobia* isp. 2 (D) within calcimicrobial crusts, pelecypod shells, and stromatoporoids/corals. Late Tithonian – ?Earliest Berriasian of the Northern Calcareous Alps, Austria.

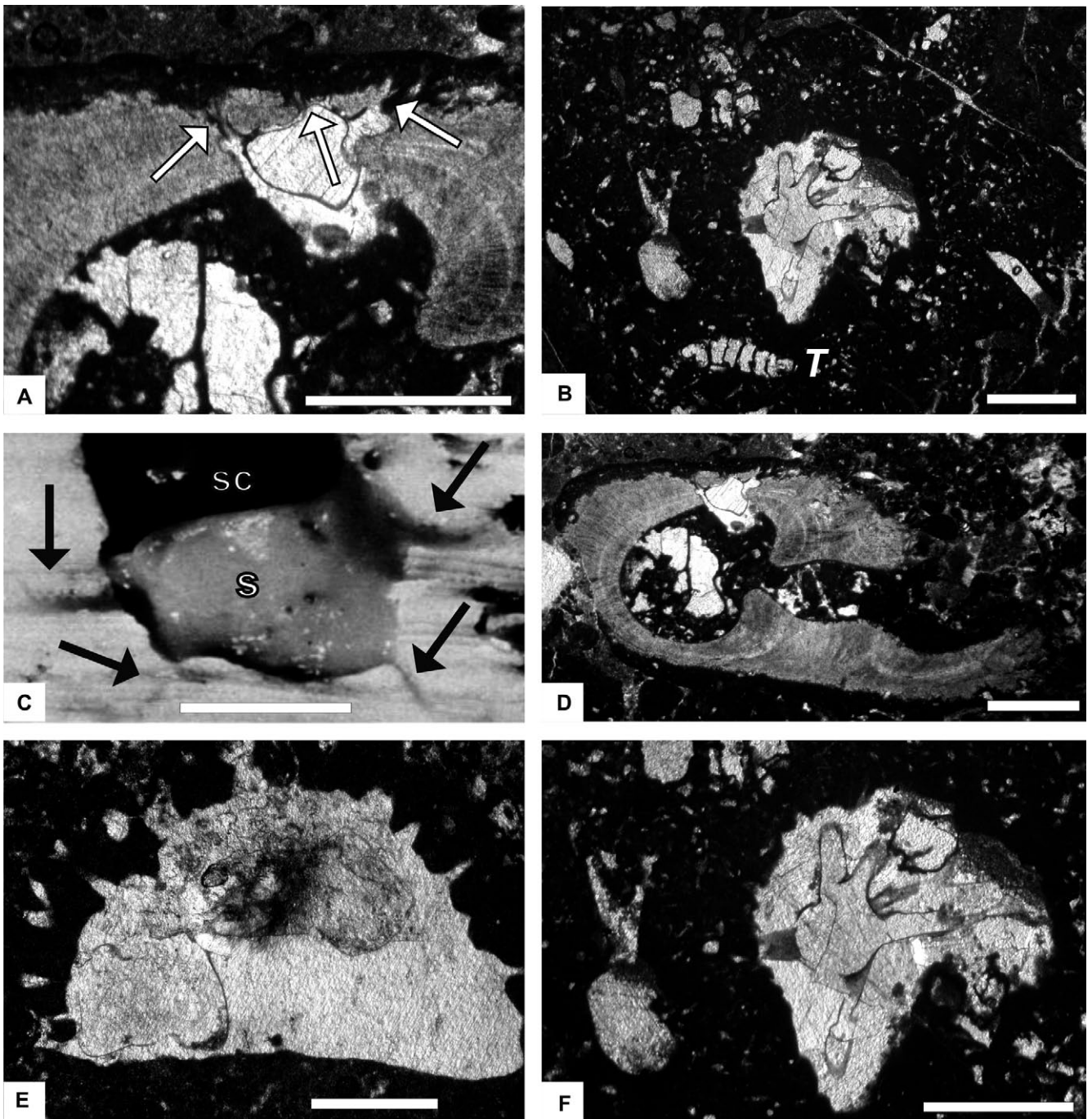
- A Oblique section showing the up to four times branching of the canals (left side) along with decreasing diameters. This section is comparable to Schmid & Leinfelder (1996, Pl. 2, Fig. 3).  
Mount Dietrichshorn, sample Die 169b, scale bar 1 mm.
- B Broken shell fragment with bored microbial crust. Arrow points to a possible preserved aperture (diameter: about 0.15 mm) projecting above the crust surface.  
Mount Dietrichshorn, sample Die 170a, scale bar 0.5 mm.
- C *Entobia* isp. 1 boring into a calcimicrobial crust upon a stromatoporoid skeleton.  
Mount Dietrichshorn, sample Die 31, scale bar 0.5 mm.
- D Oblique section through a camerate entobian (*Entobia* ichnosp. 2) boring into a calcimicrobial crust (outer boundary marked by the white dashed line) encrusting a calcareous bioclast (substrate). The close set chambers (greatest diameters: 0.2 to 0.35 mm) are connected by thin canals and form an anastomosing gallery.  
Mount Dietrichshorn, sample Die 8, scale bar 0.5 mm.
- E Oblique section of a bioclast enveloped by calcimicrobial crusts. Entobians of different sizes (1–3) are restricted to the inner crust (irregular boundary marked by the white dashed line) affecting also the bioclastic core. Inside the largest specimen (1), possible remains of the former sponge can be recognized lining the boring (chamber + canals). Note the boring of an unknown producer on the left, transjecting both crust layers.  
Mount Dietrichshorn, sample Die 170m, scale bar 1 mm.
- F Specimen bored into a calcimicrobial crust enveloping a pelecypod shell.  
Note the oblique radiating canal on the left side and an egg-shaped body (arrow) inside the chamber (see explanations in the text).  
Mount Dietrichshorn, sample Die 170m, scale bar 1 mm.



Text-Fig. 5.

Calcimicrobial crusts and traces of excavating sponges (*Entobia* isp. 1).  
Late Tithonian – ?Earliest Berriasian of the Northern Calcareous Alps, Austria.

- A Calcimicrobial crust (thickness about 0.8 mm) enveloping a pelecypod shell as host substrate. The tiny tubiferous calcimicrobes belong to the genus *Girvanella* Nicholson, exhibiting outer tube diameters of ~ 6 to 8  $\mu\text{m}$ .  
Mount Dietrichshorn, sample Die 170m, scale bar 0.2 mm.
- B Calcimicrobial crust with branching porostromate filaments.  
Mount Dietrichshorn, sample Die 170m, scale bar 0.2 mm.
- C Pelecypod shell envelopped by a calcimicrobial crust (outer boundary marked by the white dashed line). On the right side the chamber of *Entobia* isp. 1 within the crust shows larger canals (arrows) radiating obliquely upwards to the crust surface (arrows).  
Mount Dietrichshorn, sample Die 170m, scale bar 1 mm.
- D Part of an empty sponge chamber (*Entobia* isp. 1) with a filamentous meshwork (= traces of excavating filaments) within a girvanellid calcimicrobial crust.  
Mount Dietrichshorn, sample Die 170f, scale bar 0.2 mm.
- E Boring gallery of *Entobia* isp. 1 inside a calcimicrobial crust.  
Note, that in the intensely bored zone (above), the original crust structure is almost completely lost and replaced by dense micrite. The transition between both zones is gradual.  
Mount Dietrichshorn, sample Die 170m, scale bar 0.2 mm.



Text-Fig. 6.

*Entobia* isp. 1 with internal bodies, interpreted as remnants of the former sponge.

Late Tithonian – ?Earliest Berriasian of the Northern Calcareous Alps, Austria.

A, D *Entobia* isp. 1 boring into a tube of *Carpathocancer? plassenensis* Schlagintweit & Gawlick as host substrate (D). The tube obviously was already filled with microbial carbonate. In this case, the “bacinellid” meshwork fabric inside may be either the product of microbes or traces of the fine excavating filaments. From the chamber roof, three canals transect the host tube (arrows), reaching into the overlying microbial crust (A). Within the cement-filled chamber, an irregular rounded body with a thin microcrystalline wall occurs interpreted as relics of the former sponge.

Mount Höherstein Plateau, sample A 3182, scale bars 1 mm.

B Large oncid intensely bored by *Entobia* sp. 1.

The central part is shown in detail view in F. Note the foraminifer *Troglotella incrustans* Wernli & Fookes (T), here presumably as active borer.

Mount Zwerchwand, sample B 84, scale bar 1 mm.

C Modern sponge *Aka coralliphagum* (Rützler), Bermudas, boring into a coral, modified from Rützler (1971, Plate 4g).

S = sponge body, sc = substrate chamber, arrows = pioneering filaments (e.g., Ward & Risk, 1977). Scale bar 1 cm.

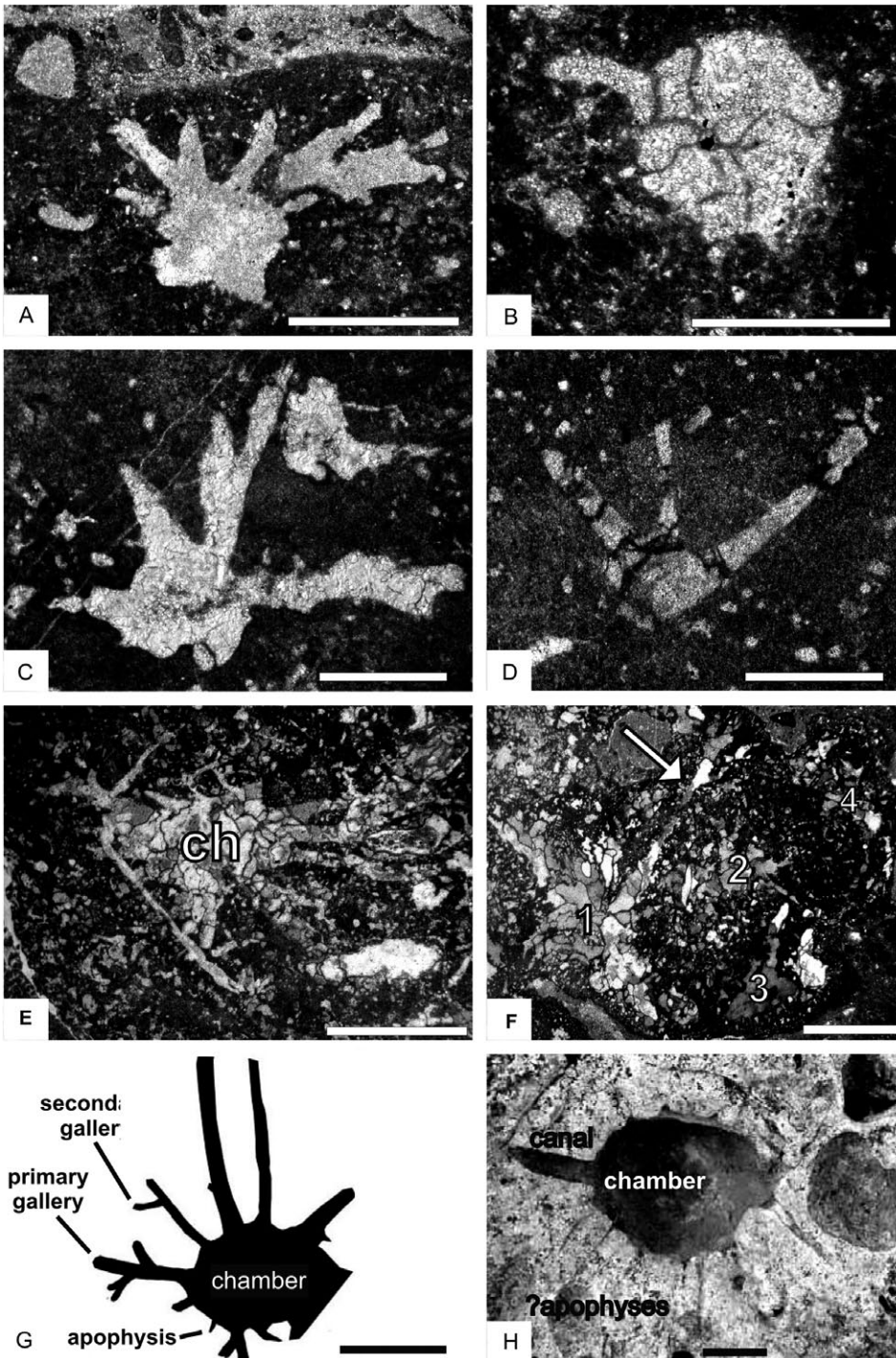
E Vertical section through a hemispherical boring with short, bifurcating canals on the upper side. Inside the sparite-filled boring, thin-walled bodies occur with protrusions on its upper side having more or less the same outline as the excavated chamber but of smaller dimensions (compare Text-Fig. 8H).

Mount Zwerchwand, sample B 84, scale bar 1 mm.

F Detail of Text-Fig. 6B showing two borings.

Inside the right boring a subspherical body bearing radial appendages can be recognized. Interpreted as remnant of the former sponge, this taxon obviously was the producer of the borings shown in Figure 7A–D (especially 7A). Here, the substrate between the individual canals was removed with continuing sponge growth.

Scale bar 1 mm.



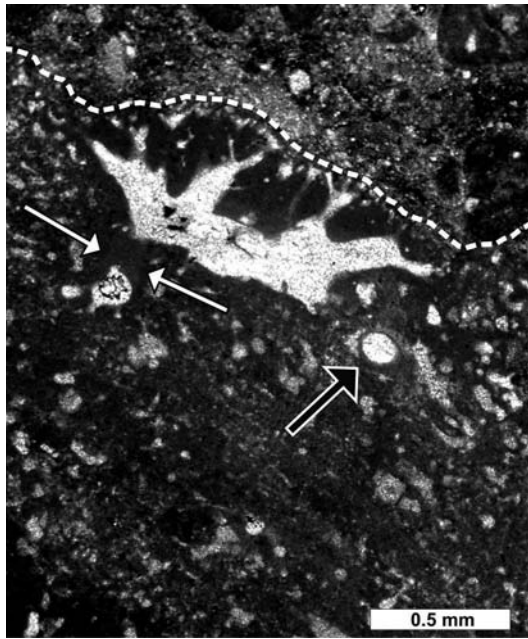
Text-Fig. 7.  
*Entobia* isp. 1 within calcimicrobial crusts from the Late Tithonian – ?Earliest Berriasian of the Northern Calcareous Alps (A–F), and comparison with other entobians (G–H).

- A Oblique section through a chamber showing several radiating canals. Note the finely agglutinated crust. Mount Dietrichshorn, sample Die 170f, scale bar 1 mm.
- B Transverse section through a chamber with one canal and meshwork interpreted as traces of excavating filaments having entered the chamber from a neighbouring one. Mount Dietrichshorn, sample Die 170m, scale bar 0.5 mm.
- C Oblique section of a chamber with radiating canals. Mount Lofer Kalvarienberg, sample Lof 1, scale bar 0.5 mm.
- D Slightly oblique transverse section through a chamber with radiating canals. Note the micritic filaments inside the chamber and canals. Mount Lofer Kalvarienberg, sample KOWG, scale bar 0.5 mm.
- E Oblique transverse section through a large chamber (ch) with numerous branching canals. Almost the whole calcimicrobial oncoïd is occupied by the boring. The irregular meshwork inside the gallery is interpreted as representing the traces of the excavating filaments of adjoining specimens. The greatest observed diameter of the boring (chamber + canals) is ~ 6.5 mm. Mount Dietrichshorn, sample Die 39, scale bar 2 mm.
- F Oblique transverse section of a large chamber (1) with long radiating canals reaching to the other side of the oncoïd (arrow). Other smaller specimens (2–4) with their spreading apophyses presumably account for the irregular meshwork inside the large boring. Greatest observed diameter ~ 6.8 mm. For comparison see also Schmid & Leinfelder (1996, Pl. 1, Fig. 5). Mount Dietrichshorn, sample Die 170f, scale bar 2 mm.
- G Chamber terminology of *Entobia devonica* (Clarke), redrawn from Tapanila (2006).
- H *Entobia cracoviensis*, modified from Bromley et al. (2009, Text-Fig. 4d). Late Cretaceous of Poland.

**Description:** A single, ovoid chamber ranging in size from 0.5–2.0 mm (mostly between 0.5–0.8 mm), bearing numerous radiating canals. Substrate either exhibiting single chambers (e.g., Text-Fig. 4C) or intensely bored from all sides with close set chambers and almost touching canals reveal a camerate entobian (Text-Figs. 3A–B). The bored substratum corresponds to calcimicrobial (oncoïdal or domal upon bioclasts) crusts, pelecypod shells (e.g., oysters, diceratids), corals or stromatoporoids. The straight or bending canals have variable diameters. The thickest diameters are observable at the connection to the chamber, successively decreasing in growth direction after branching. The observed range is from ~0.6 mm (proximal) to 0.02 mm (distal). The length of the canals is also variable,

depending on the chamber size. The maximum observed canal length is up to 4.5 mm in the specimen shown in Text-Fig. 7F. Branching occurs several times (= primary, secondary etc. galleries *sensu* Tapanila, 2006) (e.g., Text-Fig. 4A). The maximum width/diameter observed of the boring (chamber + canals) is about 6.8 mm (Text-Fig. 7F). Due to oblique sectioning, the full size is not visible but may reach up to 1 cm. In vertical sections, small chambers are subspherical, with increasing size they become compressed-ovoid. Chamber base is mostly convex, more rarely planar. Radiating canals are arising from the chamber roof and the slightly elongated ends. Chambers bored inside skeletal material show individual canals transecting the substrate roof and extending into the overlying calci-

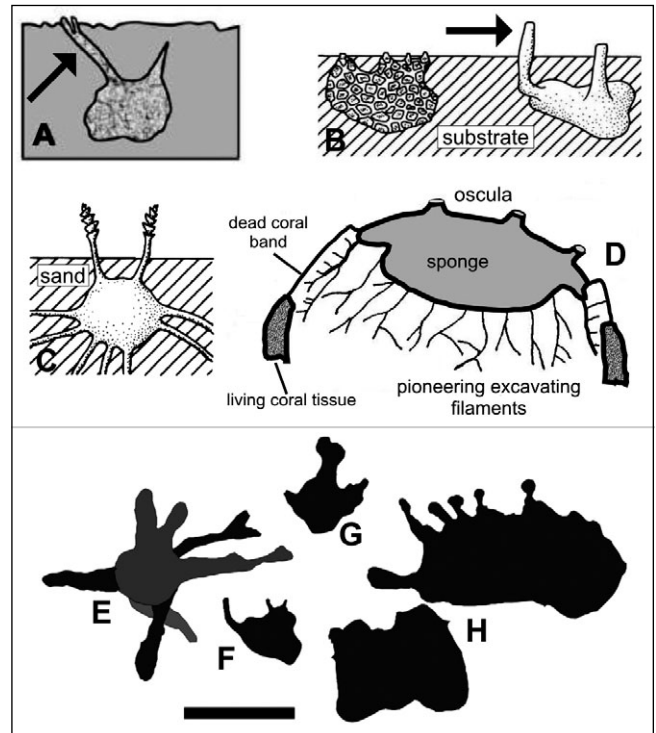




Text-Fig. 8. Oblique section of *Entobia* isp. 1 boring into the outer zone of a calcimicrobial oncoid (Detail from Text-Fig. 2D). Around the boring chamber and the spaces between the upward directed, branching canals, the original calcimicrobial structures are lost, transformed into dense micrite. This phenomenon can be also observed around individual canals stretching into the calcimicrobial crusts (white arrows). The black arrow indicates an oblique transverse section of a canal. Mount Dietrichshorn, sample Die 170m.

microbial crusts (Text-Fig. 3C). In other cases the roof is completely destroyed (etched?) and the chambers seem to fill a small concave hollow inside the substrate. The canals of the elongated endings may be straight or bending upwards. Almost all canals are ending blind, extremely rare are indistinct tubiferous structures elevated above the substrate to form a possible aperture (Text-Figs. 3G, 4B). In transverse sections (~ parallel to the substrate surface), chambers are spherical exhibiting up to six canals radiating in all directions (e.g., Text-Fig. 7D). No spicules were observed inside the mostly sparite-filled chambers.

**Comparisons:** Reliable ichnospecific determination requires the complete knowledge of the three-dimensional morphology, e.g., by means of epoxy casts or micro-computed tomography (Schönberg & Shields, 2008), therefore, our specimens are described with open nomenclature. The morphological characteristics of the Late Jurassic material fit the diagnosis of the ichnotaxon *Entobia* Bronn, which is the result of boring sponges (Text-Figs. 9A–B, D), namely their empty chambers or galleries (e.g., Bromley & D'Alessandro, 1984; Schönberg & Tapanila, 2006). The general shape of the Late Jurassic ichnotaxon can be compared with other non-camerate entobians exhibiting radiating canals such as the Palaeozoic *Entobia devonica* (Clarke) (Text-Fig. 7G) or Late Cretaceous *Entobia cracoviensis* Bromley, Kedzierski, Kolodziej & Uchman (Text-Fig. 7H). Both ichnospecies, however, possess cm-sized subspherical chambers which differ from the Late Jurassic forms (Bromley et al., 2009; Tapanila, 2006; Schönberg & Tapanila, 2006). Moreover, *E. cracoviensis* is assumed to represent an endopsammic sponge with the upper part being buried by sand (see Text-Fig. 9C). Concerning the comparable small chamber size of the Late Ju-

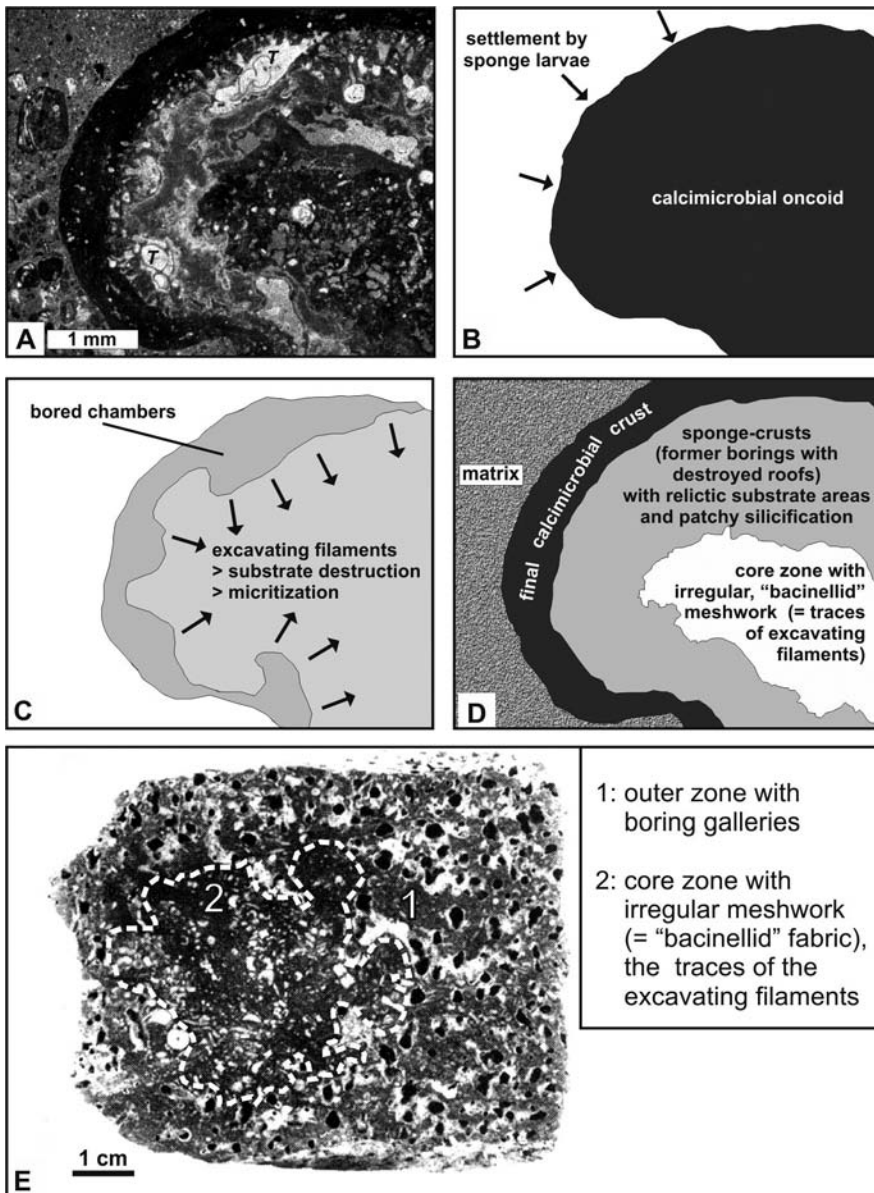


Text-Fig. 9. Modern carbonate substrate excavating (A–B, D) and endopsammic (C) sponges compared with thin-walled bodies inside Late Jurassic *Entobia* isp. 1 (E–H), interpreted as remnants of the former sponge body wall,

- A Boring stage of *Aka coralliphagum* (Rützler) within the substrate (redrawn from Rützler, 1971). Arrow: inclined papillary tunnel/canal leading to the substrate surface.
  - B Schematic drawing of single-chambered boring sponges (modified from Boury-Esnault & Rützler, 1997). Arrow: Fistule protruding above the substrate.
  - C Endopsammic sponge, living buried in sand with fistules reaching, and extending beyond the substrate surface (modified from Boury-Esnault & Rützler, 1997).
  - D Schematic drawing of a vertical section of a clionoid sponge digging into a massive coral with a band of dead skeleton around the sponge, redrawn after Zea et al. (2007). Note the basal traces of excavating filaments penetrating anastomosingly downwards into the substrate.
  - E–H Possible preserved sponge body walls. E: see thin-section picture Text-Figs. 6B and F; F: Text-Figs. 6A and D; G: see thin-section picture Text-Fig. 4E, specimen 1; H: see thin-section picture Text-Fig. 6E.
- Scale bar 1 mm.

assic representatives (mostly less than 1 mm), it must be stressed that the chambers of excavating sponges can be even smaller, e.g., 0.06 mm to 0.335 mm in *Entobia mikra* or 0.102 to 0.756 mm in *Entobia nana*, both from the Pleistocene of Greece (Wisshak, 2008). The chambers of most modern clionoids measure 2–4 mm (K. Rützler, pers. comm.).

**Discussion:** According to the diagnosis of Bromley et al. (2009), fine pioneer (exploratory) threads or filaments (e.g., Ward & Risk, 1977) should arise from the surface of the boring gallery. Thin-section material or cut rock pieces, however, show that supposed traces of the latter also originate from the chamber bases reaching downwards into the substrate. All-side bored, cut and polished limestone boulders from the Dutch coast show an outer zone with the empty boring galleries and a core zone without bored chambers exhibiting an irregular meshwork (Hoeksema, 1983) (Text-Fig. 10E). The latter might be interpreted as the micritized traces of excavating pioneering filaments arising



Text-Fig. 10. Interpretation of the genesis of the Late Jurassic oncoidal ichnofabric (A–D) and comparison with bored limestone boulder from the coast of the Netherlands (modified after Hoeksema, 1983, Pl. 1, Fig. 4) (E).

- A All-side bored superimposed oncoidal crusts showing partial silicification. In some chambers, the cryptoendolithic foraminifer *Troglotella incrustans* Wernli & Fookes (7) can be observed. Note the filamentous “bacinellid” meshwork in the centre. Mount Dietrichshorn, sample Die 170f.
- B–D Schematic reconstruction of the genesis of the ichnofabric shown in A. Further details in the text.
- E Cross-section through a boulder from the coast of the Netherlands showing intense borings by *Cliona celata* (modified from Hoeksema, 1983, Pl. 1, Fig. 4). Note the filamentous meshwork in the core produced by excavating filaments (1, boundary marked by white dashed line) and the boring chambers (black) in the outer zone (2).

from the chamber bases (Text-Fig. 9D). In the Late Jurassic material, equivalent irregular meshworks can be also found in the core zone of the host substrates, e.g., oncoids (Text-Fig. 10A). These meshworks have been classically referred to *Bacinella irregularis* Radoičić or bacinellid fabrics (Schlagintweit et al., 2010, for details). For instance, Herrmann (1996, Pl. 2, Fig. 4) showed a microbial crust with “*Lithocodium aggregatum*” (= *Entobia* isp. 1) upon a solenoporacean thallus with “*Bacinella filaments decompose and intersperse*” the latter. In the core zones of the studied oncoids, the meshwork is “filled” with micrite or microsparite (see also Fig. 98 in Nose, 1995). These meshworks (but without micritic fillings), addressed as *Bacinella irregularis* or “*phrenoteca-like bacinellimorph structures*” by Schmid & Leinfelder (1996, Pl. 1, Fig. 5), were also observed within the sparite-filled entobian chambers (e.g., Text-Figs. 7E–F). Here they are interpreted as remnants or traces of excavating filaments that entered the chambers from laterally neighbouring individuals or others occurring in superimposed crust layers. Therefore, isolated chambers or chambers within outermost oncoid layers and lacking laterally associated specimens are devoid of such meshworks (e.g., Text-Figs.

4A, C). It is noteworthy, however, that not all “bacinellid” fabrics, e.g., micritic threads connecting carbonate-clastic particles are the product of excavating sponges (e.g., Hillgärtner et al., 2001: microbial filaments). These meshworks, however, are dominantly sparite-filled.

The development of different boring (micro)fabrics seems to depend on the microstructure (e.g., dense, porous, presence of stylolites in bored boulders) and mineralogy (e.g., calcite, aragonite) of the bored substrate (e.g., Ward & Risk, 1977; Hoeksema, 1983). The anastomosing filamentous meshwork (= network of tiny tunnels) was observed in the core zone of oncoids, whereas in pelecypod shells individual micritic branch-like tunnels reaching some millimetres into the substrate were detected, an observation also reported by Sanders et al. (2007). In the same manner, Hoeksema (1983, p. 64) mentioned that the bored boulders (like the one refigured here in Text-Fig. 10E) are “very porous”, thus, obviously accounting for the easy proliferation of the excavating filaments, filling the complete core zone. The specific substrate-boring fabric relationships, however, need further investigations.

Another detail observable in thin-sections is the micrite between the bored canals or chambers and the surrounding host sediment. For the problem of the taxonomic *versus* ichnotaxonomic treatment of micritic linings within borings (e.g., Text-Fig. 3C) see Bertling et al. (2006). They can be either the product of a fine-scale dissolution-precipitation process or the infilling of microbial carbonate from the overlying crust. The occurrence of the micrite also between the chamber base and the substrate speaks for the first of the two possibilities.

From the observations made, it is evident that "*Lithocodium aggregatum*" as described by Schmid & Leinfelder (1996) neither belongs to Elliott's taxon (Schlagintweit et al., 2010) nor represents a loftusiid foraminifer. The agglutinating/trapping of detritic siliciclastics by the calcimicrobial crusts as evidenced from the Alpine material, was interpreted as representing the agglutinated foraminiferan wall of "*Lithocodium aggregatum*". Both the fine-clotted, agglutinating/trapping as well as the girvanellid microtexture of the calcimicrobial crusts are clearly discernible between the boring structures indicating their role as host substrates (e.g., Text-Fig. 4E, Text-Fig. 5, Text-Figs. 7A–B, Text-Fig. 8). In the oncoid zone with the bored gallery (chamber + canals), the originally microbial microstructure is mostly not more discernible and replaced by more or less dense micrite (e.g., Text-Fig. 8). Irregular patches of the former between the canals and a gradual transition to oncoidal parts not influenced by the physico-chemical boring process show that the micritization obviously was causally linked to the bioerosional processes (dissolution/precipitation) (Text-Figs. 5B, D–E). This connection is also clearly evidenced in the specimen shown in Text-Fig. 2D, respectively the detailed view of Text-Fig. 8. Here, the dense micrite surrounds the single chamber and the branching canals. The individual radiating canal shows a micritic envelope clearly distinguishable from the clotted microbial fabric of the host crust.

The canals of the entobians are visible, for example, in Pl. 2, Fig. 3 of Schmid & Leinfelder (1996); an oblique transverse section with the bases of the canals and the irregular filamentous meshwork inside the chamber (protrusion from laterally associated entobians?) is visible in Pl. 1, Fig. 5 of the same work.

Still insufficiently known and needing further investigations, are the details of the water-flow system of the former boring sponges producing the Late Jurassic entobians. In specimens that bored into oncoids that were still growing, apertures became overgrown at least after the death of the sponge. Anyway, non-branching canals with open ends, arranged perpendicular to the substrate and sometimes displaying protrusion from the crust surface (Text-Figs. 3G, 4B), might represent parts of the former water-flow system of these sponges.

It is most likely that the sponges were directly consuming the organic material of the calcimicrobes. Fitting the observed mass-occurrences of Late Jurassic calcimicrobial oncoids affected by sponge borings, Bertling (1999, p. 174) asserted that "*Jurassic boring sponges could only thrive in limited environments and were triggered especially by presence of their main source of nutrition, i.e. bacteria suspended from microbial mats*".

The occurrence of *Troglotella incrustans* Wernli & Fookes within the borings (chamber + canals) represents a further example of cryptoendolithic foraminifera associated

with sponges (e.g., Feifel, 1930; Frentzen, 1944; Oesterle, 1968; Kazmierczak, 1973; Munk, 1994; Guilbault et al., 2005). In the case of *Troglotella incrustans*, its branching chambers (see Schlagintweit et al., 2005; Schlagintweit, 2008) facilitated the colonization of the branching ichnofabric. Beside the common *Troglotella incrustans*, also rare other cryptoendolithic foraminifera (e.g., with hyaline wall) were observed inside the borings.

Occasionally, ovoid bodies can be observed inside the chambers (Text-Figs. 3G, 4F). Whether these are transverse or oblique sections of *Troglotella* or perhaps represent parts of the former sponge such as internally produced, asexual buds or gemmules (e.g., Fell, 1974; Manconi & Pronzato, 2007) is unclear. Other thin-walled bodies (wall thickness ~ 10 to 15 µm) of similar shape as the outline of the bored chamber but smaller, are interpreted as representing remnants of the sponges (impregnated former body wall?) (Text-Figs. 6A–B, E–H, Text-Figs. 9E–H). Morphologically, these are similar to modern boring or clionid sponges (compare Text-Fig. 9A–B). Others with elongated radiating appendages (Text-Fig. 6F) are interpreted as the sponge producing the borings with the stellate outline (= boring canals) in transverse sections (e.g., Text-Fig. 7A). Morphologically this type is similar to some modern endopsammic sponges (Text-Fig. 9C). During continuing sponge growth, the substrate between the individual canals was obviously removed resulting in a large, more rounded chamber outline. In any case, the shape of these bodies makes it very probable that these were remnants of the producer of the borings: bioeroding sponges. Such details observable in thin-section material, however, are not available from the general method to study ichnofabrics by means of epoxy casts. To my knowledge, they have so far not been reported from fossil material. Interpreted as remains of the former sponge, they were therefore not included in the ichnological description.

It is difficult to judge whether morphological differences of the bored chambers can be interpreted as variability (growth stages, e.g., Bromley & D'Alessandro, 1984) or in terms of different ichnospecies. These details need further investigations.

**Palaeoenvironment:** The terrigenous-influenced palaeoenvironment of the investigated Alpine material is referred to a gravely near-shore environment interfingering with a clastic-influenced lagoon (see Sanders et al., 2007). With borings of lithophagid bivalves (ichnogenus *Gastrochaenolites*), occurring in the stromatoporoid skeletons, this palaeoenvironment fits the so-called *Entobia* ichnofacies (Bromley & Asgaard, 1993; Gibert et al., 1998, 2007). The overall presence of calcimicrobial encrustations and oncoids with *Girvanella*-porostromate algae, boring bivalves (*Gastrochaenolites*) and "*Lithocodium-Bacinella*" (= *Entobia* ichnosp. 1, as described in the present paper) is also reported from the Portuguese Late Jurassic material that is referred to a near-shore shallow ramp facies (e.g., Leinfelder et al., 1993; Nose, 1995, Fig. 126). The discovered oncoid-building and destroying taxa can be referred to the *Girvanella* and "*Bacinella-Lithocodium*" association of Schmid & Leinfelder (1996) is excluded here from the binder guild and instead transferred to the destroyer guild (Fagerstrom, 1987; Grötsch et al., 1994).

Contrasting the described Late Jurassic findings, modern excavating sponges have been recorded mainly from coral reefs (e.g., Zea, 1994; Schönberg, 2000; Carballo et al., 2008). As a common aspect, however, the obvious relation of enhanced nutrient levels and intensification of bioerosion is also reported from present-day studies (e.g., Hallock, 1988; Holmes, 2000; Fabricius, 2005; Ward-Paige et al., 2005).

**Stratigraphy:** Oxfordian to Albian. It must be stressed, that this indication only has a provisional character. In any case, a longer stratigraphic range of *Entobia* isp. 1 must be verified by the study of younger and older occurrences of "*Lithocodium aggregatum*" reported in the literature.

### ***Entobia* isp. 2**

(Text-Fig. 4D)

**Remarks:** In the studied thin-sections there are also camerate entobians with small chambers (diameter in growth direction 0.2 to 0.35 mm) and thin intercameral canals producing an anastomosing gallery. These borings are rarer than *Entobia* isp. 1, but both may co-occur. *Entobia* isp. 2 also bores into calcimicrobial crusts. The poor material precludes any further details.

### **Conclusions**

Specimens of Late Jurassic "*Lithocodium aggregatum* Elliott", as described by Schmid & Leinfelder (1996) are transferred to the ichnogenus *Entobia* Bronn, representing the boring traces of carbonate excavating sponges. Given that the morphological variability (e.g., growth stages) is difficult to assess from the fossil material, it can therefore not be excluded that the material described by the authors might belong to different entobians. Besides, these medium-sized non-camerate entobians were preferentially boring into calcimicrobial crusts (oncooids) with cores represented mainly by pelecypods and stromatoporoids. Oncooid-boring entobians referred to *Bacinella-Lithocodium* are rather common in the Late Jurassic (e.g., Dahanayake, 1977; Védrine, 2008). Thin-walled bodies with lateral appendages inside the borings are interpreted as remains of the former sponge (impregnated body wall?) whereas spicules were never observed.

In the top parts of the Lärchberg Formation of the Northern Calcareous Alps, *Entobia* typically occur within a near-shore *Entobia-Gastrochaenolites* ichnofacies. These results give further evidence, that the taxon "*Lithocodium aggregatum*" is a mix-up of different taxa/ichnotaxa in the literature. Interpreting the Lower Cretaceous type-species as an encrust-

ing green alga (Schlagintweit et al., 2010) and some Late Jurassic specimens as sponge borings, also the Late Triassic forms, often resting in borings (e.g., Pl. 38, Fig. 3 of Wurm, 1982), need taxonomic revision as well as the Late Cretaceous occurrences. What has been stated for "*Lithocodium aggregatum*", accounts for "*Bacinella irregularis* Radoičić". The Lower Cretaceous type-species of *Bacinella* has been interpreted recently as a green alga boring into crusts of *Lithocodium aggregatum* Elliott (Schlagintweit et al., 2010). The present study shows that the assumed traces of the excavating filaments (micritic tunnels or branches) can produce an anastomosing "bacinellid fabric" inside the core zone of bored oncooids. Originating from the boring chambers (= many previous references of *Lithocodium aggregatum*), this vertical arrangement/zonation obviously accounted for the interpretation of "*Bacinella*" as the older part of "*Lithocodium*" in some cases. Equivalent zonations and ichnofabrics are also reported from modern *Cliona* species. Other bacinellid fabrics of general homeomorphic appearance, however, might represent filamentous calcimicrobes. Both examples (*Lithocodium* and *Bacinella*) clearly demonstrate that each case has to be carefully studied and that many illustrations in the literature, especially when representing detailed views, do not allow a transfer to certain taxa/ichnotaxa.

The new results evidencing the wide distribution of entobians (see selected synonymy) boring into calcimicrobial crusts (or oncooids) in Late Jurassic times confirm the statement made by Bertling (1999, p. 173), though preferentially referring to reefal facies, that "*boring sponges ... became more important in more southerly regions (remark: compared to northern Germany or France) during the Tithonian. This is likely to be linked to a falling sea-level whose increased nutrient input triggered microbial growth in shallow water. With sponges feeding on microbes, the Late Jurassic was the time of a change to modern borer associations in reefs*". The present results give evidence that future quantitative data sets should differentiate between different palaeoenvironments, not only focusing on bioerosion in reefs (Bertling, 1999; Kiessling, 2002, Fig. 24).

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