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BORING SPONGES (ICHNOGENUS *ENTOBIA*) IN MESOZOIC *LITHOCODIUM* CALCIMICROBIAL CRUSTS

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Abstract. Globular cavities in calcimicrobial *Lithocodium* crusts are interpreted as trace fossils of boring sponges belonging to the ichnogenus *Entobia*. Two informal groups can be differentiated: a Norian-Rhaetian group from Tabas area (NE Iran) and Adnet (near Salzburg, Austria), characterized by large chambers and broad bifurcating apertural canals, and a second group from the Aptian of central Italy presenting smaller chambers and canals. The distal ends of these canals are closed by alveolar structures, preventing water circulation and leading to the death of the sponge.

Riassunto. Cavità globulari presenti nelle croste microbialitiche di *Lithocodium* vengone interpretate come tracce fossili di spugne perforanti appartenenti all'icnogenere *Entobia*. Si possono differenziare due gruppi morfologici. Un gruppo, del Norico-Retico, proveniente dall'area di Tabas (Iran nord-orientale) e da Adnet (Salisburgo, Austria), è caratterizzato da grandi camere e larghi canali aperturali biforcati; un secondo gruppo, proveniente dall' Aptiano dell'Abruzzo (Italia centrale), presenta camere e canali di dimensioni inferiori. Le estremità distali di questi canali in entrambi i gruppi sono chiuse da strutture alveolari, che, impedendo la circolazione dell'acqua, hanno causato la morte della spugna.

Introduction

The taxonomic position of the enigmatic genus *Lithocodium* (type-species: *L. aggregatum*), first described by Elliott (1956) in Lower Cretaceous limestones from Iraq, was highly controversial during the last decades. This microproblematicum, widespread in Late Triassic - Middle Cretaceous shallow marine carbonates of the Tethys realm, encrusts bio- or lithoclasts, forming flat or nodular bodies of single or superimposed dark, micritic units. Each unit presents numerous cavities of different size and shape; its external part is developed as a layer of thin-walled alveoli, which are open towards the underlying cavities, but closed outwards. These alveoli are subdivided in their distal part by short plates of different length and thickness forming a reticulate pattern.

Elliott (1956) interpreted *Lithocodium* in the original description as a codiacean alga. For the first time, Camoin & Maurin (1988) suggested that this genus and the frequently associated microproblematicum *Bacinella* Radoicic may be microbial in origin. However, Schmid & Leinfelder (1996) regarded *Lithocodium* as a loftusiacean foraminifer, basing (1) on the allegedly planispiral coiling of the test, (2) the presence of cribrate apertures connecting neighbouring "chambers", (3) the presence of agglutinated detrital quartz grains in the wall, and (4) a complex alveolar layer in the outer part of the "chambers". Referring to these arguments, we pointed out (Cherchi & Schroeder 2006) that a planispiral coiling of the test, as well as cribrate apertures cannot be proved and that the detrital material suspended in the surrounding water was trapped in mucilagenous sheaths. We followed the interpretation of *Lithocodium* as calcimicrobial crusts. This interpretation was supported by the observation of Conrad & Clavel (2008) that the dark *Lithocodium* crusts have a high organic content.

There is still a number of problems regarding the interpretation of the different cavities within the calcimicrobial crusts. A study of Upper Triassic and Aptian material proved that some cavities must be regarded as trace fossils of boring sponges, which are the subject of this paper.

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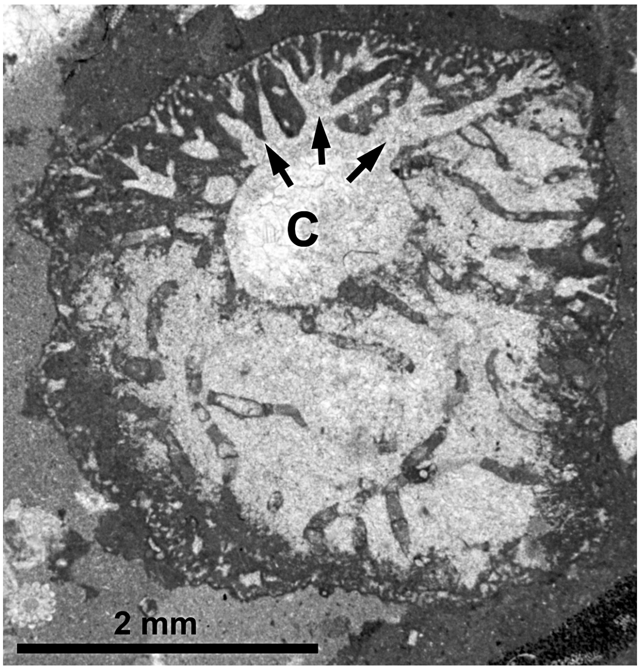

Fig. 1 - Strongly recrystallized bioclast surrounded by a calcimicrobial crust and showing a single *Entobia* isp. 1. C: chamber. The arrows point to some radiating and bifurcating canals. Tabas area (NE Iran). Norian-Rhaetian.

After a recent re-study of the Lower Cretaceous type-material of *Lithocodium aggregatum*, Schlagintweit et al. (2010) proposed that this taxon is a ulvophycean alga, whose epilithic gametophytic stage is differentiated into a ramified system of prostrate filaments from which a system of erected septate branching filaments arise. This latter system is comparable with the "alveolar layer" described by former authors, being present also in our Triassic and Aptian specimens. However, a system of relatively large prostrate filaments is completely lacking in our material. A detailed discussion of the recent interpretation by Schlagintweit et al. is not the aim of this paper.

Material

The present study is based on thin sections of ten specimens from Upper Triassic and Aptian samples, just as on a re-examination of sections already published by other authors. In the following, localities and stratigraphical indications are given for the illustrated material.

1. Tabas (NE Iran). Nayband Formation, Norian-Rhaetian (Fig. 1; Pl. 2, fig. F). For further information see Senowbari-Daryan (2005). Depository: Senowbari-Daryan collection, Institute of Palaeontology, Erlangen University (Germany).
2. Adnet (south of Salzburg, Austria). Upper Rhaetian (Pl. 1, fig. B; Pl. 2, figs. A-B). For further information see Schäfer (1979) and Bernecker et al. (1999). Depository: Institute of Palaeontology, Erlangen University (Germany).
3. Campo Gelato, south of Colle Marzo (sheat 348 Antrodoco, Abruzzo, central Italy). Aptian (Pl. 1, fig. A; Pl. 2, figs. C-E). Depository: Cherchi-Schroeder collection, Forschungsinstitut Senckenberg, Frankfurt am Main (Germany).

Description

The figures of the present paper (Fig. 1; Pl. 1, figs. A, B) show sections of more or less recrystallized coral bioclasts which are surrounded by a dark micritic calcimicrobial crust. These crusts exhibit irregularly distributed cavities of different size and shape, partly extending into the bioclast (Pl. 1, fig. B; Pl. 2, figs. A, E). The outer part of the crusts is developed as a thin layer of alveoli (e. g. Pl. 1, fig. A; Pl. 2, fig. F). These are open to the underlying cavities, but closed outwards and subdivided in their distal part by short plates, forming a reticulate pattern (upper part of Pl. 1, fig. B; Pl. 2, figs. B, F).

We interpret the cavities within the calcimicrobial crusts of our material as fossilised borings of endolithic sponges. Spicules of boring sponges are composed of opaline silica, which is in general readily soluble in seawater, but under special taphonomic conditions they may be replaced by calcite (see examples in Reitner & Keupp 1991 and Bromley & Schönberg 2008). In our thin sections, spicules as well as scalloped sponge scars along the section walls of erosion chambers, providing evidence for sponge bioerosion (e. g. Bromley & Schönberg 2008, fig. 5 B-D), were not observed. The moulds, which are filled with sparry calcite, are trace fossils and must be designated as ichnotaxa.

We ascribe the borings, figured in the present paper, to the ichnogenus *Entobia* Bronn, 1837, whose emended diagnosis, given by Bromley & D'Alessandro (1984, p. 238), runs as follows: "Boring in carbonate substrates comprising a single chamber or networks or boxworks of galleries connected to the surface by several or numerous apertures. Morphology changes markedly with ontogeny. The galleries show progressive increase in diameter during growth; in some forms, inflation at more or less regular distances produces a system of closely interconnected chambers; in other forms, chamber development is restricted to only a brief ontogenetic stage; in still other forms, no cameration is developed. The surface of the boring bears a cuspate microsculpture that may be lost in gerontic specimens. Fine apophyses arise from all or most surfaces of the system".

An ichnospecies identification of our sections is not possible, because (1) the material being to our disposal is too small, and (2) the necessary embedding-casting technique, developed by Golubic et al. (1970), is not applicable. However, we can differentiate two informal groups (A and B), which will be described in the following.

The relatively large chambers of the two groups are irregularly ellipsoidal, globular or dome-shaped, and correspond to the cavities interpreted by Schmid & Leinfelder (1966, e. g. Fig. 1; Pl. 1, fig. 4; Pl. 2, fig. 2) as chambers of loftusiacean foraminifers. The single chambers of both groups are not connected by intercameral canals.

Entobia isp. A

A strongly recrystallized bioclast from the Norian-Rhaetian Nayband Fm. of Tabas area (Fig. 1) shows a somewhat oblique section of a single *Entobia* chamber with a maximal diameter of 1.25 mm. Three apertural canals (arrows), 0.15-0.25 mm in diameter at their proximal end, radiate from the upper part of the chamber outwards, bifurcating in branches with a diameter of approx. 0.1 mm. These branches are closed at their distal end, where they are subdivided by tiny plates, forming in their entirety an alveolar network (Pl. 2, fig. F).

A bioclast from the Upper Rhaetian of Adnet (Pl. 1, fig. B) displays two vertical sections of chambers (V) with a diameter of 2 mm, and a transversal section (T) near the base of a third chamber. The vertical sections show that the chambers are connected with the surface of the calcimicrobial crust by numerous radiating and bifurcating canals (arrows), 0.04-0.06 mm in diameter at their proximal end. As in the Tabas specimens, the branches are closed at their distal end, showing an alveolar network composed of short plates of different length.

Entobia isp. B

A sponge bioclast from the Aptian of Campo Gelato (Pl. 1, fig. A; Pl. 2, figs. C-E) shows within the calcimicrobial crust a single tiers of partially closely packed entobians, which are nevertheless not connected by intercameral canals. Sections of chambers are mainly elliptic (broader than high) or irregularly rounded (0.3-0.6 mm in diameter) and obviously smaller than those of *Entobia* isp. A. At the left margin of the figure, the arrow points to a large cavity produced by the fusion of three neighbouring chambers. The very small radiating canals digitate only exceptionally. The canals are generally subdivided by only one short plate, forming in their entirety a very thin alveoler layer (Pl. 2, figs. C-E).

Remarks

In living bioeroding sponges, water currents provide food passing through the apertural canals into the internal cavities of the sponge body. When these canals become closed, e. g. by covering of microencrusters or other deposits, the system of water circulation is interrupted, leading to the death of the sponge.

This could also be the case in the entobians described in this paper, where the externally closed alveolar layer covers the distal end of the apertural canals. Several authors (see references in Cherchi & Schroeder 2006, p. 439) took the view that the outer wall of the alveoli is perforated. However, this opinion cannot be confirmed. We suppose that a locally damaged surface of the alveolar layer, caused e. g. by mechanical factors or by grazing organisms, led to such conclusions.

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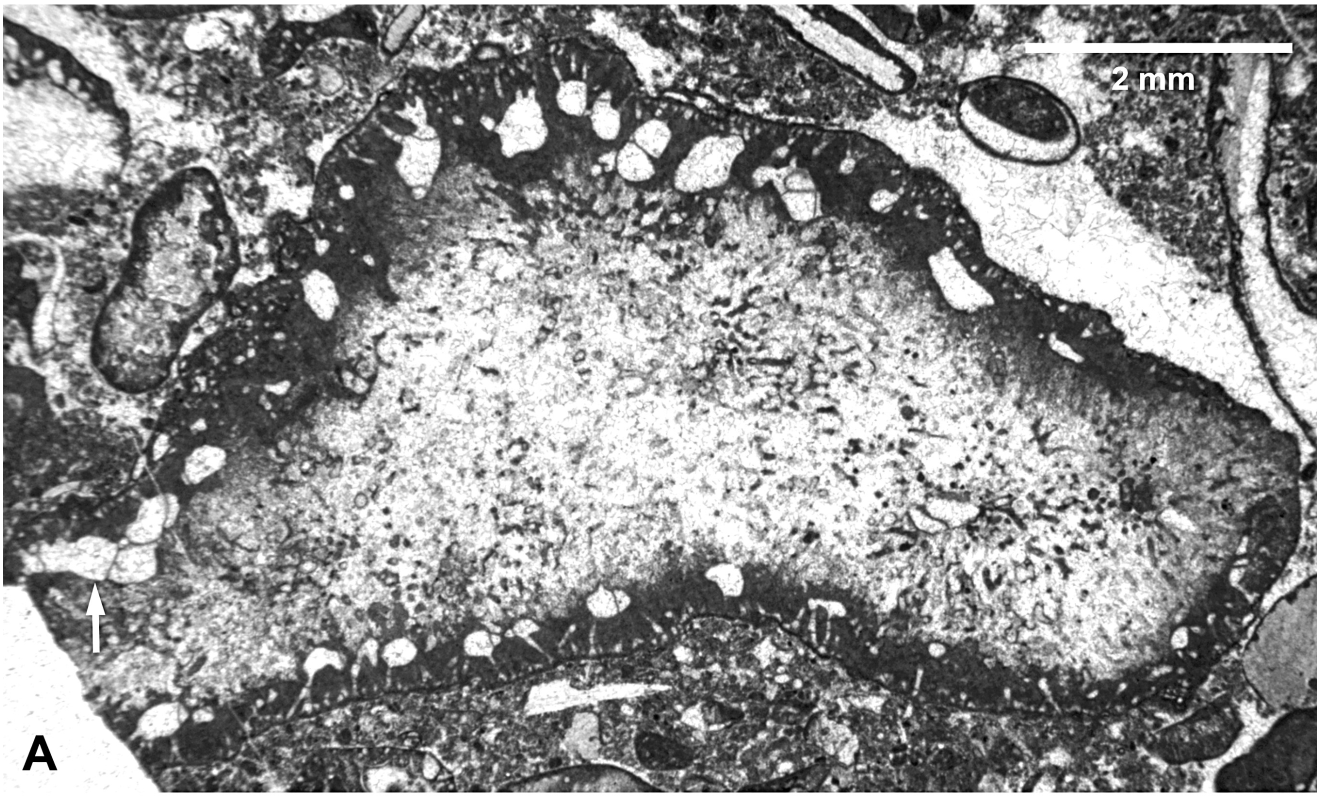
PLATE 1

Fig. A	- Coral bioclast surrounded by a calcimicrobial crust which shows numerous borings of *Entobia* isp. 2. The arrow points to a large cavity produced by the fusion of three neighbouring chambers. Campo Gelato (Italy). Aptian. Enlarged details of this section are presented on Pl. 2, figs. C-E.
Fig. B	- *Entobia* isp. 1 (V: vertical sections; T: transversal section near the base of a chamber). The arrows point to some radiating canals. Adnet (near Salzburg, Austria). Upper Rhaetian. The enlarged upper half of this section is presented on Pl. 2, fig. F.

PLATE 2

Fig. A	- *Entobia* isp. 1, vertical section. The arrow points to a circular section of a cryptobiotic foraminifer. Adnet (near Salzburg, Austria). Upper Rhaetian. Scale bar: 1 mm.
Fig. B	- *Entobia* isp. 1, vertical sections. Adnet (near Salzburg, Austria). Upper Rhaetian. Scale bar: 0.5 mm.
Fig. C	- *Entobia* isp. 2. Detail of Pl. 1, fig. A (upper border). Campo Gelato (Italy). Aptian. Scale bar: 0.5 mm.
Fig. D	- *Entobia* isp. 2. Detail of Pl. 1, fig. A (upper border). Campo Gelato (Italy). Aptian. Scale bar: 0.5 mm.
Fig. E	- *Entobia* isp. 2. Detail of Pl. 1, fig. A (lower border). Campo Gelato (Italy). Aptian. Scale bar: 0.5 mm.
Fig. F	- *Entobia* isp. 1. Detail of Fig. 1 (upper half). Tabas area (NE Iran). Norian-Rhaetian. Scale bar: 1 mm.



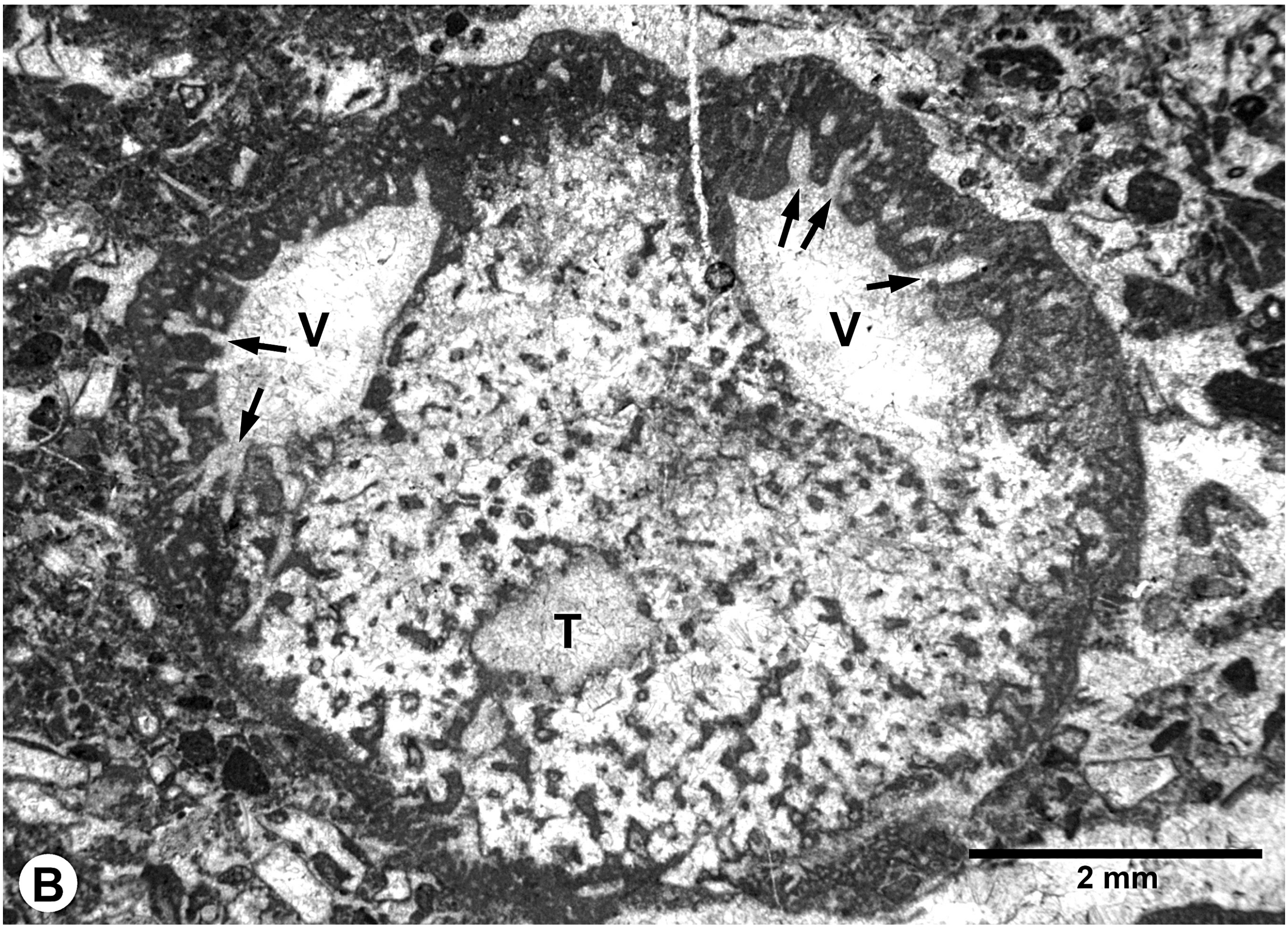


PLATE 1

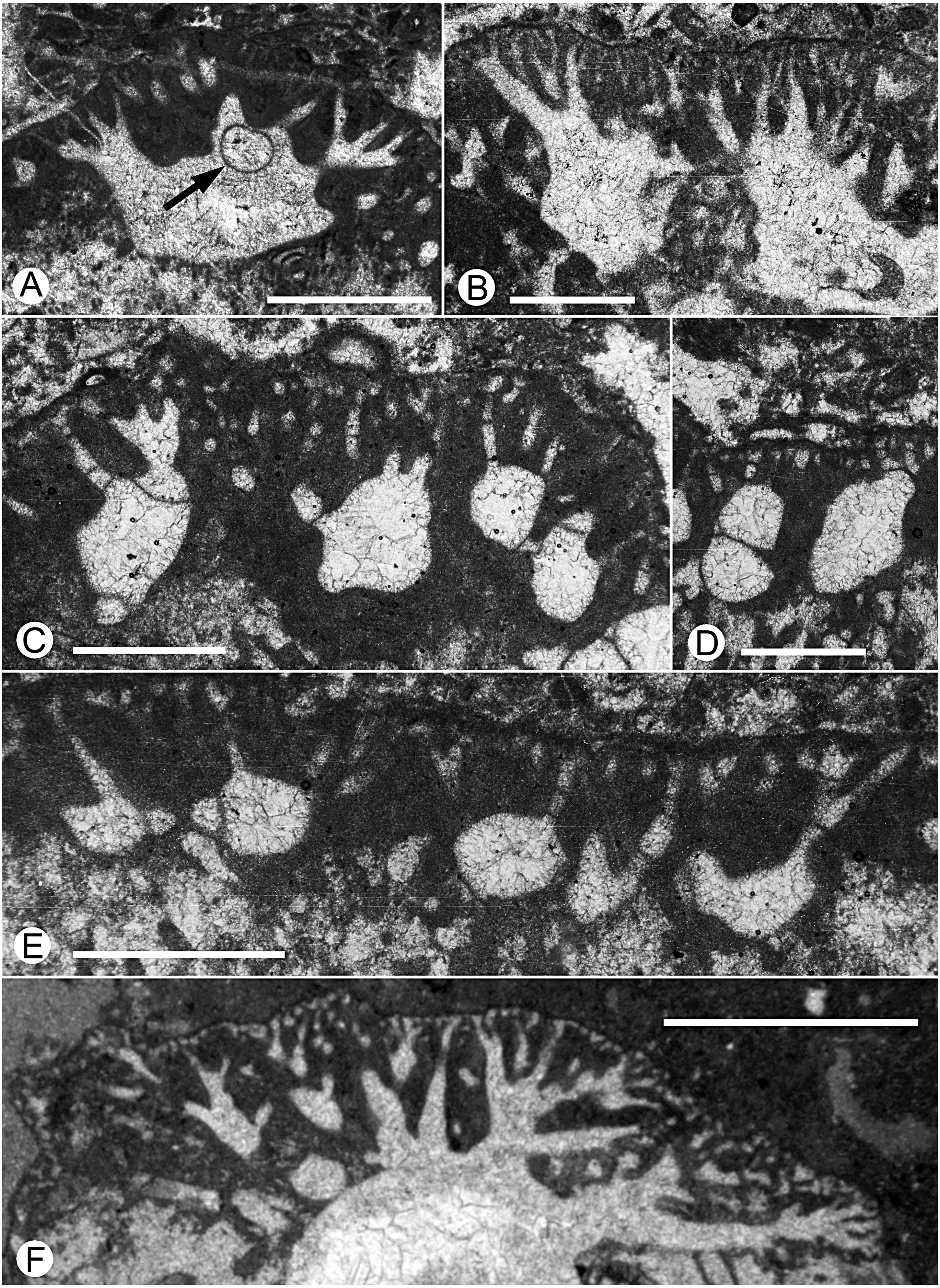


PLATE 2

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