

Remarks on the *Bačínella* Radoičić, 1959 (type species *B. irregularis*) and its representatives

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with 8 Figures and 1 Table

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Abstract: *Bačínella irregularis* was described by RADOIČIĆ (1959) as an alga incertae sedis. Based on material from the Lower Aptian of the western Maestrat Basin (Spain), the genus *Bačínella* with its various species is revised; an emended diagnosis is given as well as a detailed description. *Bačínella* is interpreted as an organism excavating complex branching galleries into biogenic hard substrates, e.g., the crusts of *Lithocodium aggregatum* ELLIOTT (such as in the holotype specimen of *B. irregularis*). Its morphology and boring pattern is comparable to that of modern filamentous-septate euendolithic green algae of the class Ulvophyceae. These forms, however, are microfilamentous (microborer) whereas *Bačínella* has larger filament diameter. Nearly all of the “*Bačínella irregularis*” occurrences reported in the literature do not belong to this taxon, but represent irregular vesicular crusts (“bacinellid” fabrics = *Bačínella irregularis* auct. non) that display some resemblances with modern microbial mats.

Keywords: Calcareous algae Chlorophyceae Taxonomy Bioerosion Lower Cretaceous Spain

Zusammenfassung: *Bačínella irregularis* wurde von RADOIČIĆ (1959) als eine Alge incertae sedis beschrieben. Basierend auf Material aus dem Unter-Aptium des westlichen Maestrat-

Beckens (Spanien) wird die Gattung *Bačínella* mit ihren verschiedenen Arten revidiert sowie eine emendierte Diagnose wie auch detaillierte Beschreibung gegeben. *Bačínella* wird als Organismus der komplexe, sich verzweigende Bohrgänge in biogene Hartsubstrate, zum Beispiel Krusten von *Lithocodium aggregatum* ELLIOTT (wie der Holotyp von *B. irregularis*), anlegt. Die Morphologie und das Bohrmuster ist vergleichbar mit modernen filamentös-septaten euendolithischen Grünalgen der Klasse Ulvophyceae. Beinahe alle Vorkommen von *B. irregularis* in der Literatur gehören nicht zu diesem Taxon sondern stellen irregulär vesiculäre Krusten („bacinellide Gefüge“ = *Bačínella irregularis* auct. non) dar, die gewisse Ähnlichkeiten zu modernen mikrobiellen Matten haben.

Introduction

Lithocodium aggregatum ELLIOTT (1956) and *Bačínella irregularis* RADOIČIĆ (1959) are two enigmatic taxa of the Late Jurassic to Early Cretaceous epeiric sedimentary record, which have aroused more than 50 years of controversy concerning their taxonomic position, possible relationship and synonymies. Several authors considered *Bačínella irregularis* and *Lithocodium aggregatum* as synonyms with *Lithocodium* having priority as described earlier (SEGONZAC & MARIN 1972; LUPERTO SINNI 1979; BANNER et al. 1990; KOCH et al. 2002), while others treated the two microproblematica as different taxa (ELLIOTT 1963; SCHMID 1996; SCHMID & LEINFELDER 1996; CHERCHI & SCHROEDER 2006). *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. Recently, *Lithocodium aggregatum* was re-interpreted as a heterotrichale filamentous-septate green alga (order Ulotrichales?) by SCHLAGINTWEIT et al. (2010). The crusts as described by these authors are formed by a basal prostrate and an erect filament system, which correspond to the

“medullary” and “cortical” filaments of the previous udoteacean algal terminology used by ELLIOTT (1956).

On the other hand, *Bačínella irregularis* was originally described by RADOIČIĆ (1959) as an alga incertae sedis. However, many authors have later assumed a cyanobacterial/microbial origin for this microproblematicum (SCHÄFER & SENOWBARI-DARYAN 1983; MAURIN et al. 1985; CAMOIN & MAURIN 1988; RIDING 1991a; SCHMID & LEINFELDER 1996; VACHARD et al. 2001; UȚA & BUCUR 2003). Alternatively, SCHLAGINTWEIT et al. (2010) re-interpreted *Bačínella irregularis* as a euendolithic chlorophycean alga, possibly belonging to the Ulotrichales. Given that the main goal of the last-mentioned work was the re-description of *Lithocodium aggregatum*, the present study deals exclusively with the genus *Bačínella* RADOIČIĆ. It critically discusses the species inventory, and provides a new generic diagnosis along with a detailed description of the type species. In addition, new microstructural details of “bacinellid fabrics” (= *Bačínella irregularis* RADOIČIĆ auctorum non) are presented.

Sample location and material

The specimens studied are from Lower Aptian sedimentary successions that crop out in the western Maestrat Basin of the eastern Iberian Chain (Fig. 1). The deposits studied lie within the marls of the Forcall Formation and constitute a sub-basin-wide horizon formed by several episodes of coral rubble encrusted by microorganisms, clearly dominated by *Lithocodium aggregatum* crusts (BOVER-ARNAL et al. 2010, 2011). The ammonite-biostratigraphic data (MORENO-BEDMAR et al. 2009, 2010) permit to ascribe this horizon to the upper part of the *Deshayesites forbesi* biozone (Lower Aptian).

The material studied comprises 73 thin-sections, which were sampled from nine different outcrop sections in the vicinity of the towns of Aliaga, Montoro de Mezquita, Camarillas and Miravete de la Sierra (Teruel province, Spain; Fig. 1).

Taxonomic part

Kingdom Plantae

Division Chlorophyta PASCHER, 1914

Class Ulvophyceae MATTOX & STEWART, 1984

? Order Ulotrichales BORZI, 1895

Family ?

Genus *Bačínella* RADOIČIĆ, 1959, emended herein

The following species of *Bačínella* (in alphabetical order) were described since its establishment by RADOIČIĆ in 1959:

Bačínella bicellularis SADATI, 1981 (Fig. 2/5-6), Late Triassic of Austria. From the Middle Jurassic of Egypt, *B. bicellularis* was reported by KUSS (1990) forming individual layers within oncoids. Internal structures with two types of cells, large basal cavities and smaller “distal” cells as in *B. bicellularis* are also known from thaumatoporellacean algae (DE CASTRO 1990) (Fig. 2/7) or *Pseudolithocodium carpathicum* MIŠIK, 1979. Affinities between the latter taxon and thaumatoporellaceans were remarked by CHERCHI & SCHROEDER (2005), distinguishing “an upper zone subdivided by small partitions” (= smaller distal cells of SADATI) and “a lower zone made up of large irregular cavities” (= large basal cavities of SADATI). The taxon described in open nomenclature by CHERCHI & SCHROEDER (2005) from the Liassic of the Southern Alps/Italy is formed by superimposed crust layers and shows striking similarities (if not identical) to *Bačínella bicellularis*. The transverse section of SADATI (1981: Pl. 1, Fig. 2) displays an identical mosaic-like pattern and fine perforations (much smaller than the “dermal” cells) in the walls as in *Bačínella ordinata* PANTIĆ, 1972 (see below). Bearing in mind the wide morphological variability usually exhibited by

thaumatoporellacean algae (DE CASTRO 1990), “*Bačínella bicellularis*” is here interpreted as belonging to this group. Status: not a representative of *Bačínella*. It has been interpreted as a thaumatoporellacean alga (SCHLAGINTWEIT 2011).

Bačínella crispa ELIÁŠOVÁ, 1981, Late Jurassic of Czech Republic. *B. crispa* was defined as a “*Bacinella* with a central tissue consisting of lobate elements”. According to SCHMID (1996), the description of *B. crispa* was inadequate and corresponds to a consortium of the cryptobiotic foraminifer *Troglotella incrustans* WERNLI & FOOKES, 1992 inside “*Lithocodium*”. This view was also accepted by SCHLAGINTWEIT (2008) demonstrating the irregular branching habitus of the epilithic, non-boring adult stage of *Troglotella* (= lobate elements of ELIÁŠOVÁ, 1981). Status: not a representative of *Bačínella*.

Bačínella elongata FOIS, 1981, Late Ladinian of Southern Alps, N-Italy. This species is represented by crusts or encrusting masses exhibiting a vertical growth. The inner structure consists of cells with an elongate tubular pattern “arranged in vertical series” and with “irregularly spaced, thin micritic transverse partitions”. This structure strongly recalls a solenoporacean alga. Status: this taxon must be removed from the genus *Bačínella*. It is unknown, and should be checked whether it corresponds to an individual taxon or belongs to an already existing solenoporacean alga.

Bačínella irregularis RADOIČIĆ, 1959 (type-species), Barremian-Aptian of Bosnia and Herzegovina. As can be inferred from the original diagnosis and description, the specific name refers to the irregularity of cells with respect to size and form. According to R. RADOIČIĆ (pers. comm.), the genus name refers to the region of the Bačina lakes, northwest of the delta of the river Neretva/Croatia where the taxon was observed for the first time in blocks of a megabreccia. The generic diagnosis of *Bačínella* was given as follows: “Nodular and incrustated algae whose interior is constructed by unregular cells of different size and form, which are filled with crystalline calcite (Remark: = sparitic), whereas the intercellular mass is cryptocrystalline (Remark: = micritic). The subdermal structure is differentiated” (RADOIČIĆ,

1959: 92). In the species description the “cells” of *Bačínella irregularis* were further specified by Radoičić as being “arranged into association or into some sort of unregular series which are intermingled”. The thin microcrystalline cross-partitions within the sparite-filled “cells” were not mentioned by Radoičić, but it can be inferred that the author was aware of this as otherwise the term “cell” would most likely have been replaced by “filament” or “siphon”. The holotype specimen shows that the “cells” are not really disorganised, but are radiating and successively branching, forming a network (Fig. 3/1). The description of these cells as being arranged in series, the mentioning of their intermingled character (= branching-radiating pattern) and the micritic intercellular mass make it clear, that RADOIČIĆ’s description directly refers to the holotype specimen and not the sparitic vesicular meshworks (= bacinellid fabrics) that are treated later in the paper. In the original description only two figures were provided: the holotype specimen and one paratype. The paratype also clearly shows the micritic intercellular mass but the arrangement of the cells is more irregular than in the holotype. The holotype is interpreted as representing a section subparallel to the plane of filament growth direction. The paratype seems to cut the filaments obliquely in a supposedly more adult part of the thallus where successive branching and anastomization results in a more complex and irregular cell pattern. Following article 7.2 of the International Code of Botanical Nomenclature (ICBN) (McNEILL et al. 2006), the nomenclatural type (here: holotype) “is not necessarily the most typical or representative element of a taxon”. In fact, the holotype specimen of RADOIČIĆ and the specimen from the Early Aptian of Spain showing the boring character of *Bačínella irregularis* are untypical (as being very rare) for the thin-section material as these are cutting in the plane where the branching-radiating filamentous cell pattern of the alga is well recognizable.

The specimens from the Lower Aptian of the western Maestrat Basin correspond to the taxon described by RADOIČIĆ (1959). In the Iberian material, it is evident that *Bačínella irregularis* represents an organism boring into micritic crusts of *Lithocodium aggregatum* (=

micritic “intercellular mass”). The original diagnosis of *Bačínella* is therefore interpreted as representing a mixture that refers to two different taxa (*Bačínella* and *Lithocodium*) and moreover does not include an adequate description of all morphological characteristics. An emended diagnosis is presented below. Status: valid.

Bačínella ordinata PANTIĆ, 1972 (Fig. 2/1), Ladinian of Montenegro: Its occurrence has been documented throughout the Late Triassic (SENOWBARI-DARYAN, 1984) and the Liassic (SCHEIBNER & REIJMER 1999). The thin external micritic wall usually appears homogeneously micritic. In some specimens, however, the wall exhibits a fine perforation (Fig. 2/2-4). On the basis of this external micritic alveolar wall, *Bačínella ordinata* is interpreted as a thaumatoporellacean alga *sensu* DE CASTRO (1990). It must be stated, that no holotype was designated by PANTIĆ (1972) in the original description. Status: not a representative of *Bačínella*. It has been interpreted as a thaumatoporellacean alga (SCHLAGINTWEIT 2011).

Bačínella? sterna RADOIČIĆ, 1972: The Cenomanian age of the Serbian type-strata of *Bačínella? sterna* was later revised as belonging to the Albian (BANJAC et al. 2007). The species was removed from *Bačínella* by BANNER et al. (1990), making it the type-species of the newly erected genus *Radoicicinellopsis*. The latter genus was established as a siphonous green alga (family Codiaceae). The nodular-shaped, indistinctly laminated thalli, however, do not show a siphonal architecture differentiated into a medulla and cortex, and can therefore not be included in this algal group. Status: *Radoicicinellopsis sterna* (RADOIČIĆ, 1972) is here considered a valid taxon (in any case not a representative of *Bačínella*), but the suprageneric position (udoteacean green alga according to BANNER et al. 1990) is unclear. An indefinite microbial origin is favoured.

In conclusion, no other *Bačínella* species diagnosed after the description of the type-species *B. irregularis* belongs to this genus (Tab. 1). Thus, *Bačínella* is interpreted as a monotypic taxon.

Emended diagnosis: Life-cycle is assumed to be heteromorphous, including a free-living (gametophytic) and a euendolithic (sporophytic) stage. The multicellular thallus of the euendolithic stage consists of irregular branching and anastomizing filaments with cross-walls forming a complex network that accommodates in a plane parallel to the substrate surface. The upwards-directed branching with successive reduction of diameter results in a close-set layer of fine terminal branches that end shortly before the substrate surface. The filaments consist of uniseriate barrel-shaped, cylindrical to irregularly swollen cells. Rare hairs (setae) occur, one to a cell.

Bačínella irregularis RADOIČIĆ, 1959

Fig. 3/1-2, Fig. 4/1-5, Fig. 5/1-5 (pars), Fig. 6/1-2

Synonymy: There are plenty of illustrations of “*Bačínella irregularis*” published since its description in 1959. Their listing would fill several pages. According to our emendation, only the figuration of REITNER (1987) from the Albian of Spain is included. For the interpretation of most illustrations in the literature see the chapter *Discussion*.

1959. *Bačínella irregularis* nov. gen., nov. sp. - RADOIČIĆ, Pl. 3, Figs.1-2.

1987. *Bačínella irregularis* RADOIČIĆ - REITNER, Pl. 21, Fig. 1.

2010. *Bačínella irregularis* RADOIČIĆ - SCHLAGINTWEIT et al., Figs. 11a-h, 12e-g.

Diagnosis: see generic diagnosis. According to our interpretation, the genus is monospecific so far. Diagnostic criteria for species differentiation might be cell dimensions and/or morphological criteria (e.g., branching pattern).

Description: The supposed heteromorphous life-cycle includes a free gametophytic generation of unknown shape and an euendolithic sporophytic phase to which the following description refers exclusively. The multicellular thallus is composed of branching septate filaments, euendolithic typically in crusts of *Lithocodium aggregatum* ELLIOTT, 1956, but also in thalli of other calcareous algae or metazoan skeletons. Cells that make up the filaments are arranged in linear rows (= septate filaments). Mostly, these are barrel-shaped to cylindrical (diameter 50-150 μm ; 70-220 μm measured from the holotype specimen). In the central part, large irregularly swollen cells occur (diameter up to 500 μm). Cells are separated by thin microcrystalline cross-walls (thickness ~6-35 μm) occurring at distances of 0.15 to 0.5 mm. Thick walls may have an indistinct lamellate appearance. The large irregularly shaped cells are mostly deeply lobed and interdigitated with adjacent cells in a puzzle-like manner. The marginal final cells are comparably thin (diameter 25-40 μm) forming a pseudoalveolar layer (= differentiated subdermal structure of RADOIČIĆ) towards the substrate surface without penetrating it (Fig. 4/5). Starting from the substrate entrance point, the alga may bore with a single straight to slightly undulating filament before they irregularly branch in all directions (Fig. 3/2). This network of branching and anastomizing filaments accommodates in a plane parallel manner to the substrate surface; the greatest observed thallus width is up to 5 mm (specimen shown in Fig. 3/2). Three different types of branching patterns occur: dichotomous, a Y-shaped bifurcating cell, branching by bisection of a cell during radial division resulting partitions that form a “T” (Fig. 6/1) (e.g., GRAHAM 1982 for details), and opposite, rectangular branching with the so-called “four-armed central cell” (NIELSEN, 1987) (Fig. 6/2).

Within the central part, rare hairs (or setae) one to a cell occur. They have a length of up to 0.5 mm with a basal diameter of 24-35 μm and are tapering distally (Figs. 4/2, 4/6). A basal septum towards the attaching cell is not detectable. As three-dimensional specimens are not available, it is unclear whether roundly terminating lateral appendages are rhizoidal processes or oblique sections of branches.

Within the studied material, there are all transitions from sparite-filled specimens with preserved cell cross-walls (e.g., Fig. 4/2) to specimens with microsparitic (e.g., Fig. 4/7) to micritic fillings without preserved cross-walls. In the latter case, only the empty boring trace is present.

Discussion: First of all, it must be noted that from the living alga, only the cross-walls of the cells of the filaments are preserved as a thin microcrystalline structure. An outer cell wall is not evident within the dark crusts of *Lithocodium* but it is detectable in the boring affecting a solenoporacean thallus (Fig. 5a). In another case, *Bačínella irregularis* was observed boring into a Liassic spongiomorphid skeleton (LE MAITRE 1935) (Fig. 5b-e). According to our knowledge, this finding represents the oldest record of *Bačínella irregularis*. With these two examples, the long-lasting discussion about a synonymy of *Bačínella irregularis* with *Lithocodium aggregatum* becomes obsolete, since in both cases the micritic “intercellular mass” *sensu* RADOIČIĆ (1959) (= *Lithocodium* crusts) is lacking.

As the description of *Bačínella irregularis* does not refer to a trace (here: boring gallery), it is treated taxonomically rather than ichnotaxonomically. Normally, fossil euendolithic chlorophytes are usually known from their borings. Mention should be made that the boring galleries of *Bačínella* resemble to some extent those produced by boring sponges: non-camerate (or open-camerate) representatives of the ichnogenus *Entobia* (e.g., Fig. 4/7). An example comprises the ichnospecies *E. cateniformis* consisting of a branching and anastomizing boring system (BROMLEY & D’ALESSANDRO 1984). These galleries, however, are continuous, whereas *Bačínella irregularis* displays transverse walls and thus cannot be transferred to the activity of boring sponges. Instead, from its morphology and boring pattern, *Bačínella* can be compared with modern chlorophycean algae (SCHLAGINTWEIT et al. 2010). The current classification of the Chlorophyta is based on a combination of morphological and ultrastructural features (e.g., COCQUYT 2009). Hence, since many structural and reproductive

features of *Bačínella* are unknown, the genus cannot reliably be accommodated in any of the existing orders and families of the Ulvophyceae. Concerning the supposed heteromorphous life-cycle, a free-living gametophytic generation can be inferred from the infection of the *Lithocodium* crusts via the hollow borings of lithophagine bivalves (Fig. 3/2). Furthermore, it can be stated, that the modern euendolithic genera comparable to *Bačínella*, such as *Endocladia* (= *Ectochaete*) AGARDH, 1841 or *Eugomontia* KORNMAN, 1960, belong to the orders Ulotrichales or with *Phaeophila* HAUCK, 1876, to the Ulvales (O'KELLY et al. 2004; GUIRY & GUIRY 2011) (Fig. 7). Both Ulotrichales and Ulvales belong to the class Ulvophyceae (GUIRY & GUIRY 2011). All the afore-mentioned taxa are filamentous, septate (with transverse walls) forms as *Bačínella*, but distinctly smaller. For example, filament (or cell) diameters are ~3-20 µm in *Endocladia* (THIVY 1943), ~6-9 µm in *Eugomontia* (KORNMAN 1960; NIELSEN 1987), ~5-25 µm in *Phaeophila* (THIVY 1943; NIELSEN 1987; KITAYAMA & GARRIGUE 1998), up to ~25 µm in the siphonaceous *Ostreobium* BORNET & FLAHAULT, 1889 (type-species *O. quekettii*) and even up to 140 µm in *O. duerdenii* (LUKAS 1974). Occasionally, euendolithic and/or cryptoendolithic calcitic *Ostreobium*-type siphonaceous tubes are preserved in Early Aptian *Lithocodium* crusts (SCHLAGINTWEIT et al. 2010). The general shape of the boring of *Bačínella*, however, does not allow a direct inference whether its trace-maker was siphonous or septate-filamentous. Boring networks of filamentous chlorophytes are known since the Ordovician (GLAUB & VOGEL 2004), e.g., the ichnotaxa *Reticulina* RADTKE, 1991 and *Rhopalia* RADTKE, 1991. Various examples are from the Early Jurassic-Late Cretaceous period (e.g., MÄGDEFRAU 1937; SCHINDEWOLF 1962; PUGACZEWSKA 1965). In any case, with filament or boring diameters > 100 µm, *Bačínella* must be considered a macroborer whereas modern euendolithic chlorophytes are typically microborer (e.g., SCHMIDT 1990; GLAUB 1994). Empty borings of *Bačínella* without preserved anatomical details such as walls or perforations must not be named by their producer. They rather constitute a discrete ichnotaxon, which remains to be named, however.

As already stated, the majority of references in the literature of *Bacinella irregularis* refer to “epibenthic meshwork crusts of noticeable thickness and extension” (SCHMID & LEINFELDER 1996: 31). These, however, are completely different to the taxon that RADOIČIĆ described in 1959, but identical to an illustration provided by the same author one year later that might be a reason for the following decades-lasting controversies (RADOIČIĆ 1960) (Fig. 3c). These structures have later been termed “bacinellid textures” (MAURIN et al. 1985) or “filamentous fabrics” (HILLGÄRTNER et al. 2001), and a cyanobacterial/calciomicrobial origin has been assumed by several authors (SCHÄFER & SENOWBARI-DARYAN 1983; MAURIN et al. 1985; CAMOIN & MAURIN 1988; RIDING 1991a; SCHMID & LEINFELDER 1996; VACHARD et al. 2001). Illustrated evidence for such an interpretation, however, was not provided. A more detailed interpretation/description of the micritic laminae that form these irregular vesicles was given by DUPRAZ (1999: 28) (Fig. 8/1). He remarked that they consist of many small dark (= micritic) dots that should represent calcification centers for light needles of possible primary aragonite, later transformed to a sparitic cement. The dark calcification centers could represent cyanobacteria that triggered calcification by photosynthesis upon or within a mucilageneous sheath (PENTECOST & RIDING 1986; RIDING 1991b) (Fig. 8/2).

In thin-sections of “bacinellid” vesicular fabrics from the Latest Jurassic-Earliest Cretaceous of the Getic Carbonate Platform (leg. O. Dragastan), individual small hollow tubes with a micritic envelope were detected forming the “walls” of many of the vesicles (Figs. 8/3-6). The outer diameter ranges from 9.5 to 50 μm , the width of the inner hollow tube is 5 to 25 μm . They can be compared with the so-called *Girvanella* group that is compared with calcified oscillatoriacean (cyanobacterial) sheaths. Although being rather common in the studied material, many of the micritic “laminae” appear solid without a detectable central tubiform hollow. Referring to the morphology and the size range, it seems likely that the observed tubes represent filaments of cyanobacteria. In fact, the fossil “bacinellid” crusts show morphological features that resemble those reported from modern microbial mats such

as pinnacles or reticulate surface patterns (NOFFKE et al. 2001; GERDES & KLENKE 2003; GERDES 2007; PORADA & BOUOUGRI 2007) (Fig. 9). It is worth to mention that already DRAGASTAN & RICHTER (2003: 87) mentioned a possible interpretation of “*Bačarella*” as an “algal mat resembling elephant skin texture”. The mat-character of these vesicular fabrics is furthermore evident in cases where they form bindstones that exhibit a high lateral extension in preferentially back-reefal or peritidal depositional settings and may show features of sub-aerial exposure (e.g., MASSE et al. 1998; BUCUR et al. 2010). Further studies for the understanding of these three-dimensional structures (mats), however, are needed.

Acknowledgements

Ovidiu Dragastan (Bucharest), Ivo Velić (Zagreb) and Adrian Immenhauser (Bochum) are thanked for providing thin-sections for this study. We are grateful to Ioan Bucur (Cluj-Napoca) for providing the figure from the Late Jurassic of Bulgaria, to Gisela Gerdes (Wilhelmshaven) for providing figures from modern microbial mats (including the permission for illustration), to Christophe Dupraz (Connecticut) for providing the figure from his Ph.D. thesis and to André Strasser (Fribourg) who helped to prepare a first version of this manuscript. The figurations from the original material of LeMaitre were kindly produced and provided by Hubert Benoit (Lille). With this respect we also acknowledge the intermediation of Daniel Vachard (Lille). Financial support by the Swiss National Science Foundation grant no. 20-121545.08, the I+D+I research project CGL2008-04916, the Consolider-Igenio 2010 programme, under CSD 2006-0004 “Topo-Iberia”, and the Grup Consolidat de Recerca “Geologia Sedimentària” (2009SGR-1451), is greatly appreciated. Last but not least, we thank the two reviewers....

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Figure Captions

Fig. 1. Geological map of the study area in the western Maestrat Basin (modified after CANÉROT et al. 1979 and GAUTIER 1980). The outcrop sections sampled are marked with a star and are the following (abbreviations of thin-section samples in brackets): Barranco de los Degollados (DE), Casa Cartujo (CC), Loma del Horcajo (PO), Las Cubetas (CUB), Cabezo de las Hoyas (HO), Camarillas (CA), Barranco de las Calzadas (CAL) and Barranco de la Serna (SE).

Fig. 2. *Bačínella ordinata* PANTIĆ, 1972 (1) and *Bačínella bicellularis* SADATI, 1981 (5-6), and their interpretation as thaumatoporellacean algae (2-4, 7). 1: From PANTIĆ (1972: Pl. 4/1), Ladinian of Montenegro. 2: Thaumtoporellacean alga from the Norian-Rhaetian Dachstein reefal limestone of the Northern Calcareous Alps of Austria. 3-4: Detailed views showing the finely perforated external wall. 5-6: From SADATI (1981: Pl. 1, Fig. 2 and Fig. 3), Norian-Rhaetian of Northern Calcareous Alps of Austria. Two types of cell sizes (a and b). Note the mosaic-like central part with homogeneous partitions comparable to *Bačínella ordinata* (Fig. 2/1); the external wall is finely alveolar/perforated (arrows in 5). 7: *Thaumtoporella parvovesiculifera* (RAINERI) from the Middle Jurassic of Croatia showing a finely perforated external wall and internal constrictions with two types of “cell” sizes (a and b).

Scale bars: 0.5 mm.

Fig. 3. *Bačínella irregularis* RADOIČIĆ, 1959. 1: Holotype specimen (from RADOIČIĆ 1959: Pl. 3, Fig. 1), Barremian-Aptian of Bosnia and Herzegovina (icm = micritic “intercellular mass” sensu RADOIČIĆ). 2: *Bačínella irregularis* specimen boring through superimposed and micritized crusts of *Lithocodium aggregatum* ELLIOTT, 1956 (= icm of RADOIČIĆ) starting from a *Gastrochaenolites* macroboring (G) where the gametophyte entered the hard substrate. The growth direction is marked by the white arrow. Lower Aptian of the western Maestrat

Basin, Spain. Thin-section DE-5H. 3: Irregular, foam-like meshwork (“bacinellid fabric”) figured as *Bačínella irregularis* by RADOIČIĆ (1960, Pl. 17, Fig. 1), Barremian-Aptian of Croatia. Note the completely different microstructure compared to the holotype specimen and not matching the original description, e.g., lacking of intercellular mass or cells arranged in series. 4: Same as 3. Note the completely encrusted coral (c) in the centre. Early Aptian of Oman (material leg. A. Immenhauser).

Scale bars: 0.5 mm.

Fig. 4. *Bačínella irregularis* RADOIČIĆ, 1959 boring into crusts of *Lithocodium aggregatum* ELLIOTT, 1956. Lower Aptian of the western Maestrat Basin, Spain. 1: Network of branching and anastomosing filaments of *Bačínella irregularis* which end with terminal fine branchlets (left above). Thin-section CAL-5V. 2: Detail from Fig. 2/2 showing cells each with one thin hair or seta (arrows). Thin-section DE-5H. 3-4: Network of *Bačínella irregularis* filaments exhibiting irregular swollen cells. Note the microsparitic filling in 3. Thin-sections HO-3V and HO-17V. 5: Branching filaments with terminal fine branchlets (above). Thin-section CAL-2V. 6-7: Boring galleries of *Bačínella irregularis* with microsparitic filling resembling to some extent those produced by non-camerate boring sponges (ichnogenus *Entobia*). Note the absence of preserved cell cross-walls. Note also the two thin tapering appendages (= setae) with upward growth towards the substrate surface in 6 (arrows). Thin-sections CA-3H and DE-3V.

Scale bars: 0.5 mm.

Fig. 5. a *Bačínella irregularis* RADOIČIĆ boring into the thallus of a solenoporacean alga. Note the visible filament cross-walls (arrows). Late Jurassic (most probably Late Tithonian) of Bulgaria (leg. Ioan Bucur). **b** *Bačínella irregularis* RADOIČIĆ (arrows) boring into a spongiomorphid skeleton. Pliensbachian of Morocco (slightly modified from LE MAITRE

1935, pl. 8/8). **c-e** Detailed views from a showing filament branchings and preserved transverse cell walls (arrows in **c**; **e**).

Fig. 6. Filament branching pattern in *Bačínella irregularis* RADOIČIĆ, 1959. 1: Detail from the holotype specimen of RADOIČIĆ, 1959 (see Fig. 3.1) showing dichotomous branching starting from a Y-shaped cell (black arrows) and the biseriate branching type with three cells separated by T-shaped cross-walls (white arrows). 2: Rectangular branching exhibiting the so-called “four-armed central cell” (NIELSEN, 1987). Thin-section HO-16V.

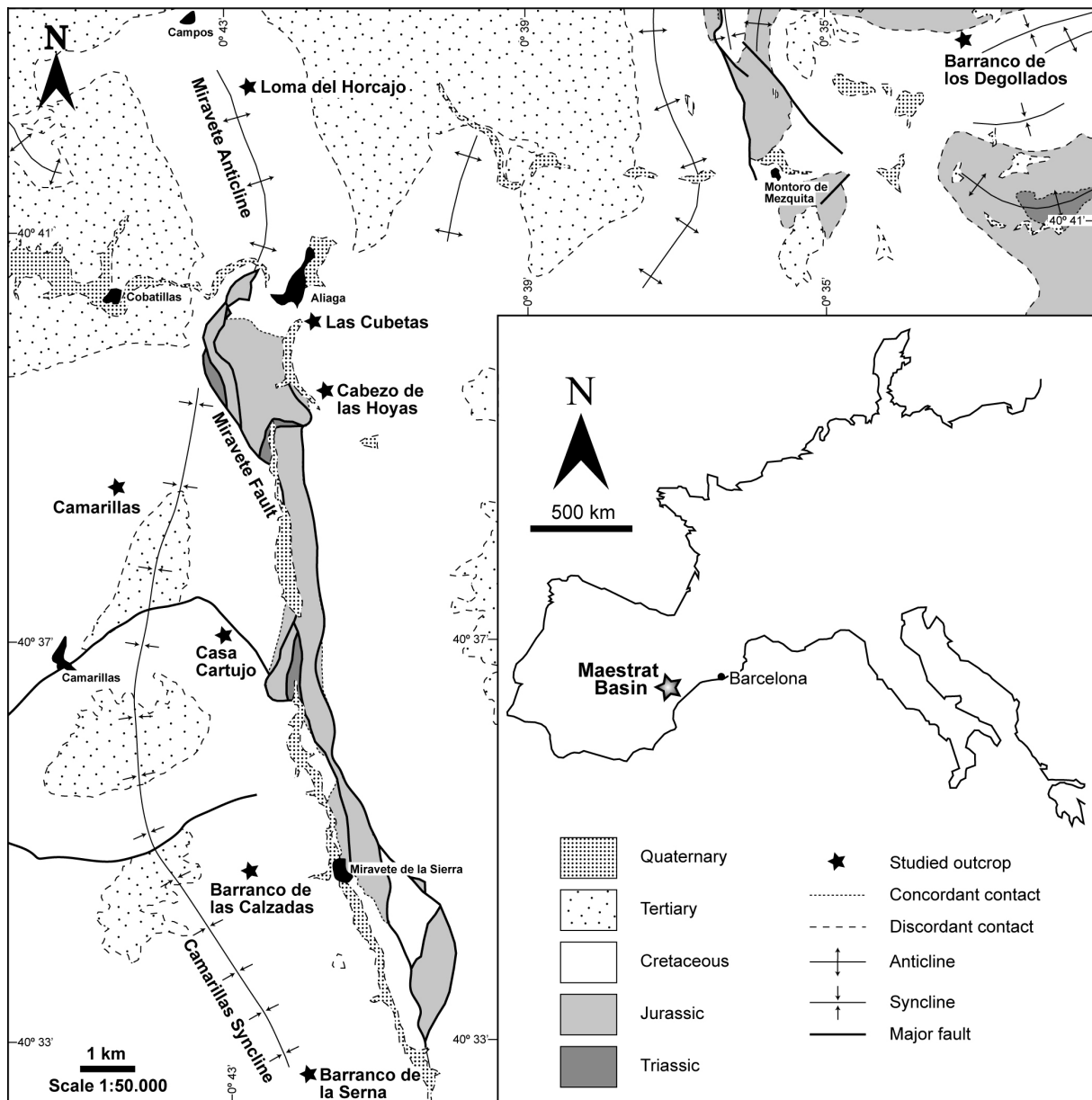
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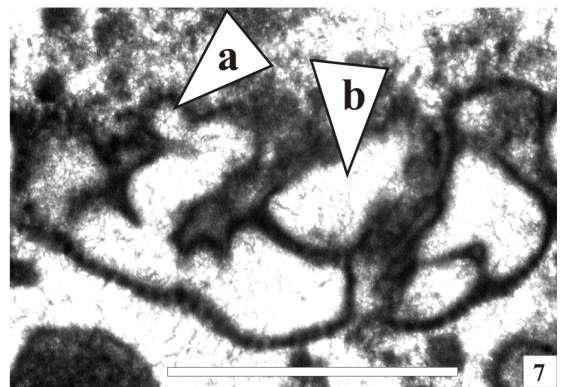
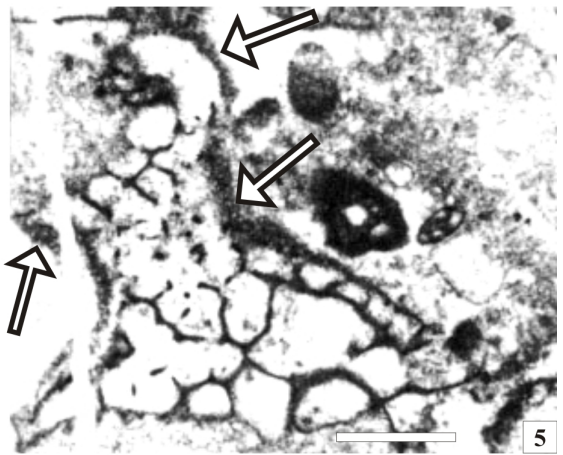
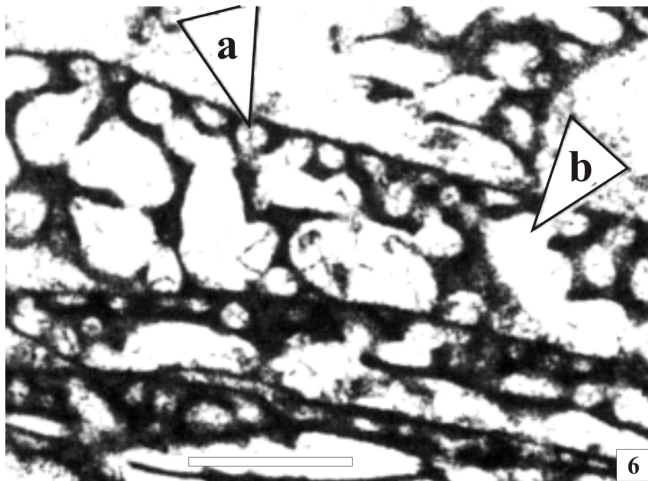
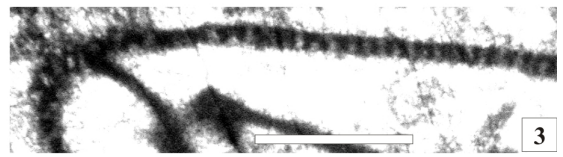
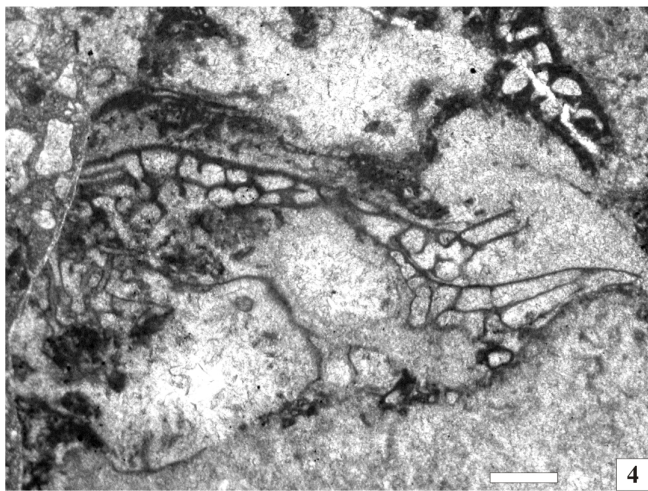
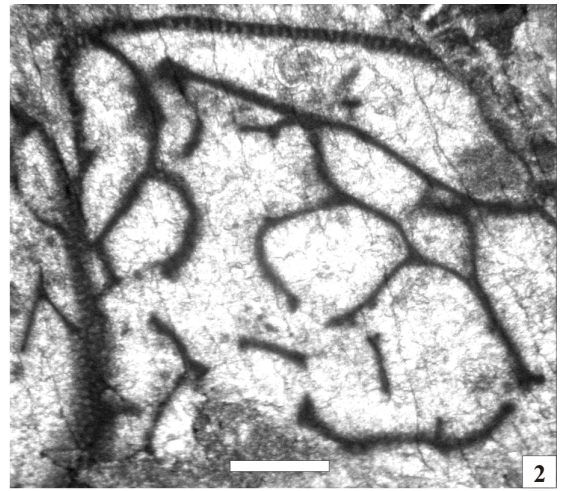
Fig. 7. Modern euendolithic chlorophytes that can be compared with the fossil genus *Bačínella* RADOIČIĆ, 1959. Note the indication of some of the morphological details used in the description 1, 3-4: *Phaeophila dendroides* (CROUAN & CROUAN) (1, 3 from THIVY 1943, Pl. 1/1 and 1/3; 4 from NIELSEN 1987). 2: *Eugomontia sacculata* Kornmann (from KORNMANN 1960, Fig. 5b).

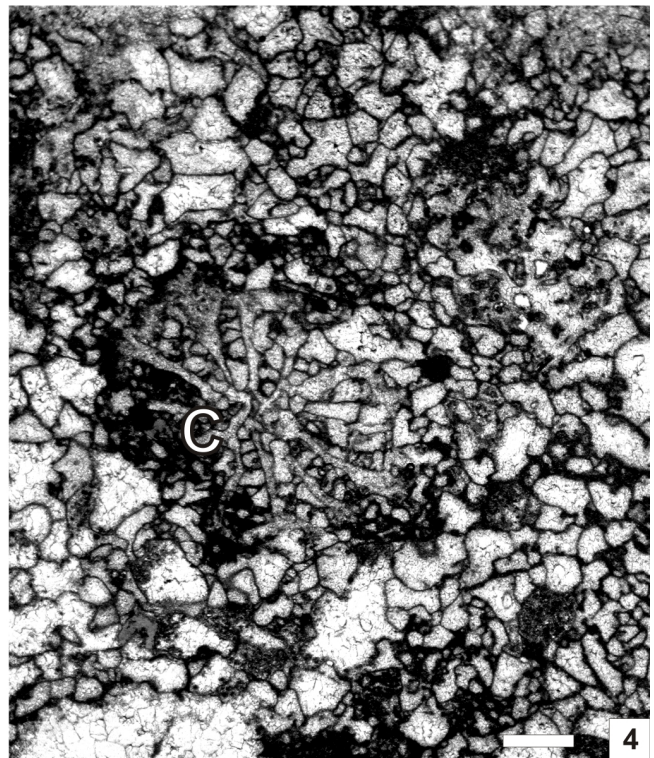
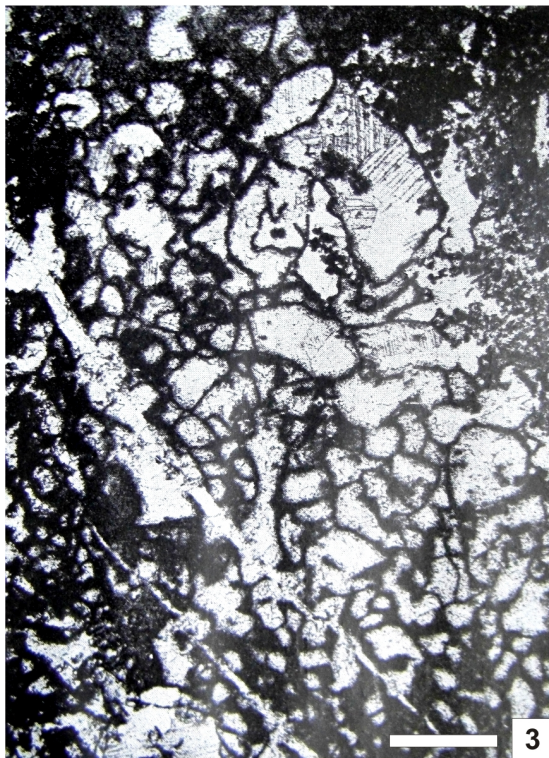
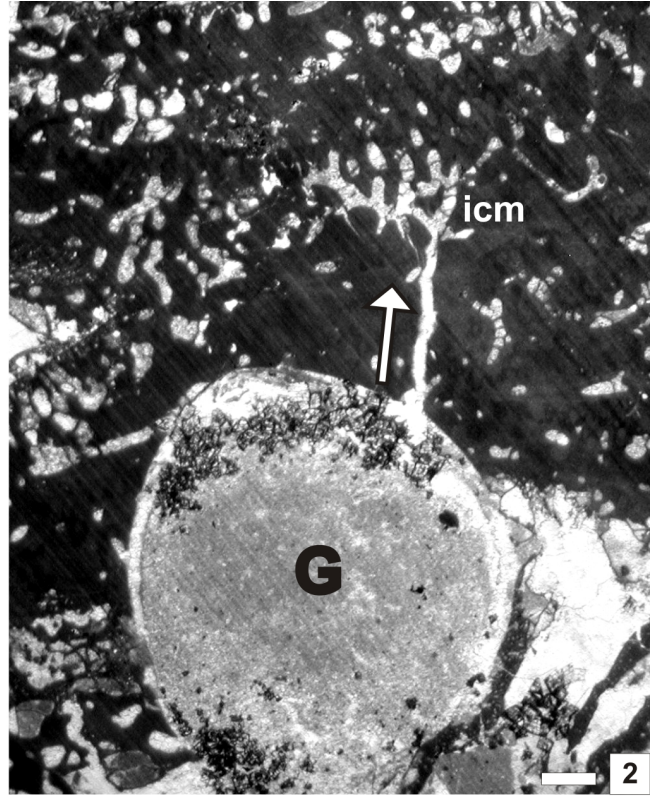
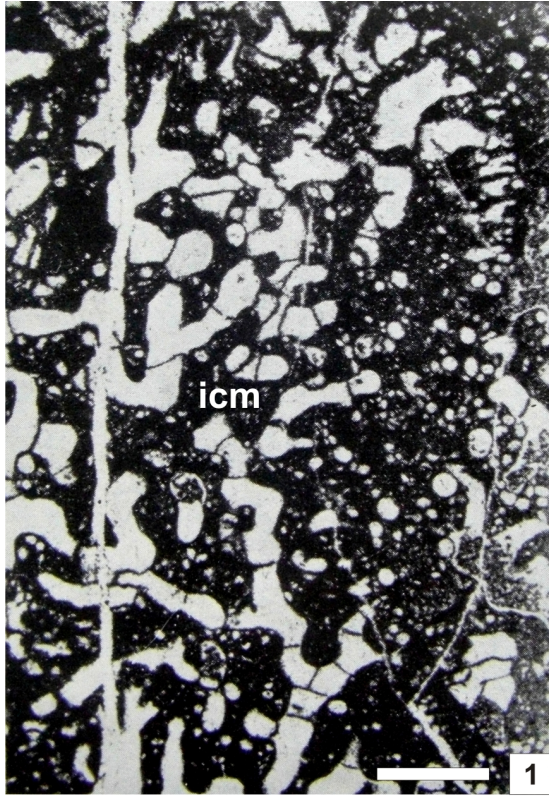
Fig. 8. Calcification processes in filamentous cyanobacteria and vesicular crusts (“bacinellid fabric” = *Bačínella irregularis* RADOIČIĆ, 1959 auct. non) of assumed calcimicrobial origin. 1: Microstructure of a Late Jurassic (Oxfordian) “bacinellid fabric”, Switzerland (modified from DUPRAZ 1999: Fig. 4.1). Without scale. 2: Calcification of a filamentous cyanobacterium during life-time. S = sheath, T = trichome (modified from RIDING 1991b: Fig. 2b-c). Without scale. 3: “Bacinellid fabric”, Tithonian-Berriasian of the Getic Carbonate Platform, Romania. Thin-section Ghimba 387-1. Scale bar 0.5 mm. 4-6: Detailed views showing tiny, bended hollow tubes interpreted as calcimicrobial filaments. Scale bars 0.5 mm.

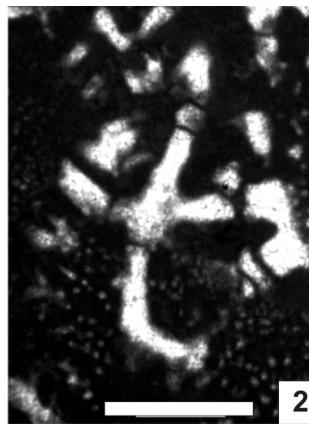
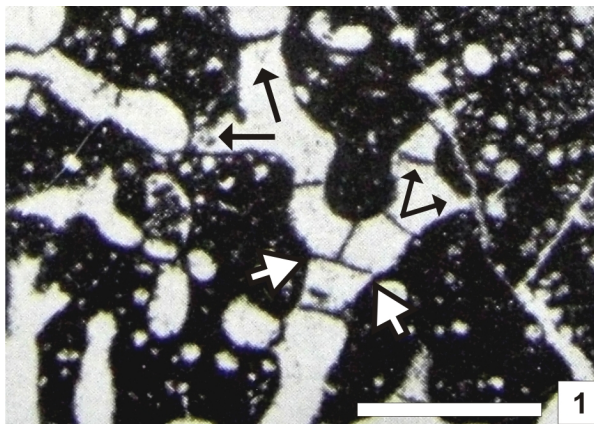
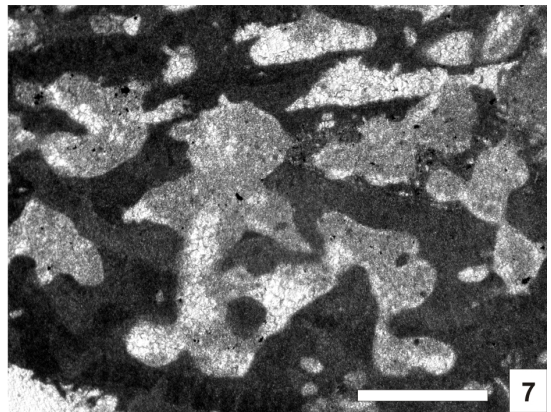
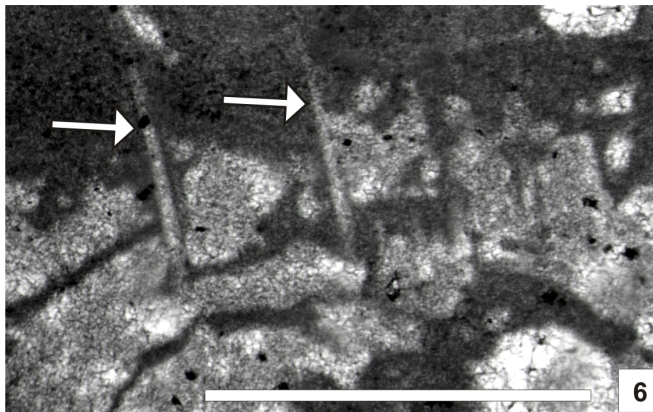
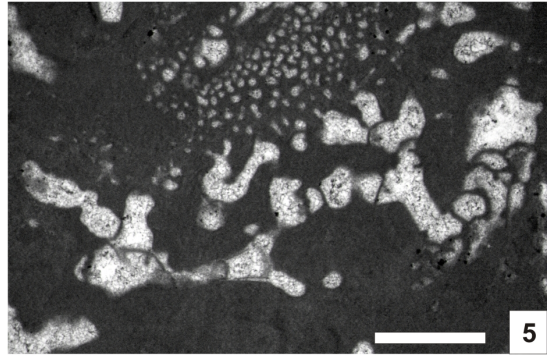
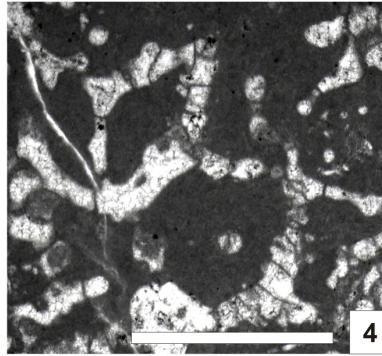
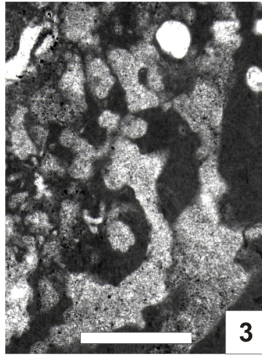
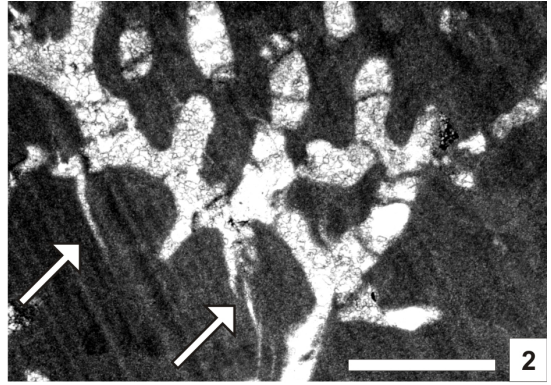
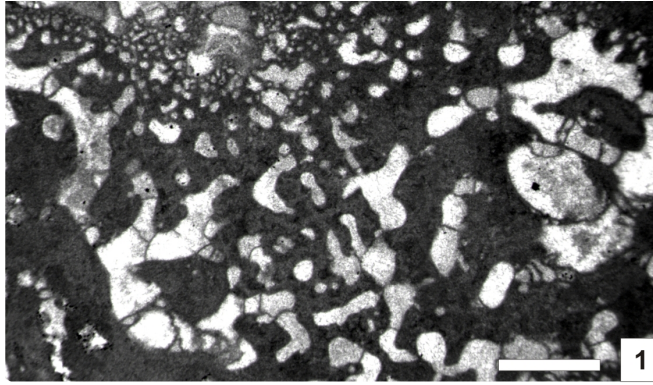
Fig. 9 Comparison of modern microbial mats (1, 3) with Early Cretaceous “bacinellid” fabrics (2, 4). 1: Microbial mat surface structure with pinnacles. Saline, southern Bretagne, France (from GERDES & KLENKE 2003: Fig. 8a). Scale bar 0.5 mm. 2: Structured top of a “bacinellid” crust. Early Aptian of Croatia. Scale bar 0.5 mm. 3: Polygonal reticulate surface pattern resembling “elephant skin” (from GERDES 2007: Fig. 2-1-5e). Scale bar 1cm. 4: Surface structure of a “bacinellid” crust. Early Aptian of Croatia. Note the differing dimensions compared to the modern example. Scale bar 0.5 mm.

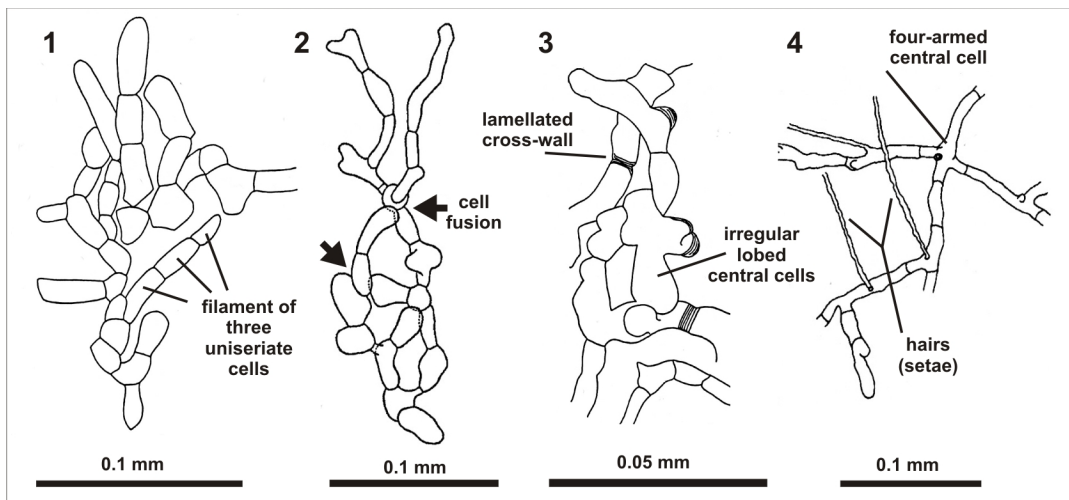
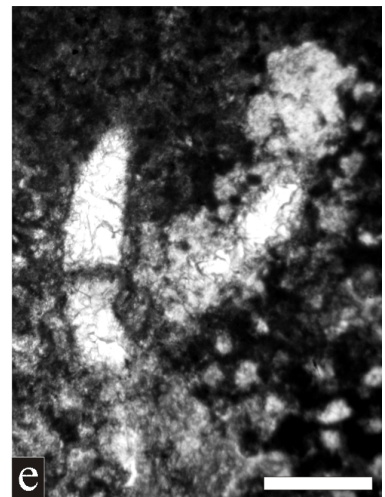
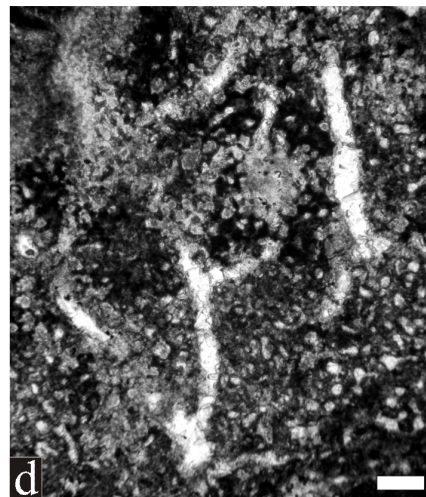
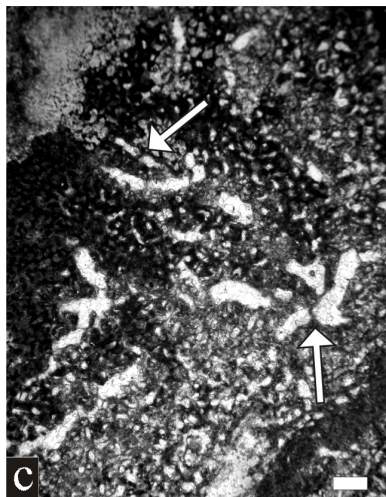
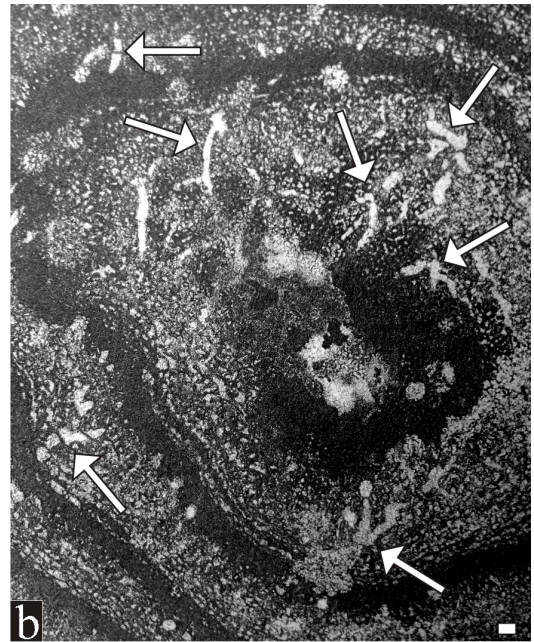
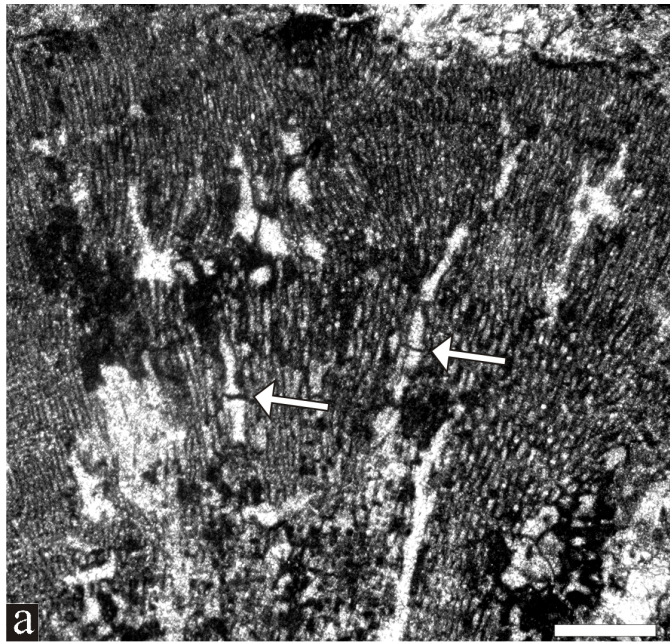
Tab. 1. Comparative table of *Bačínella* species and their interpretation. Details are given in the text.

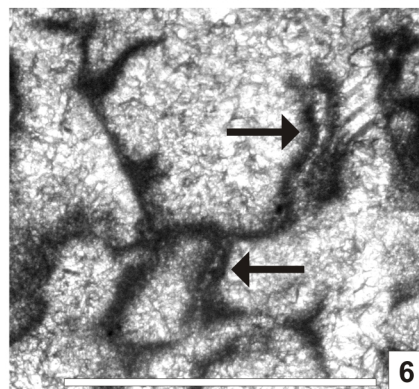
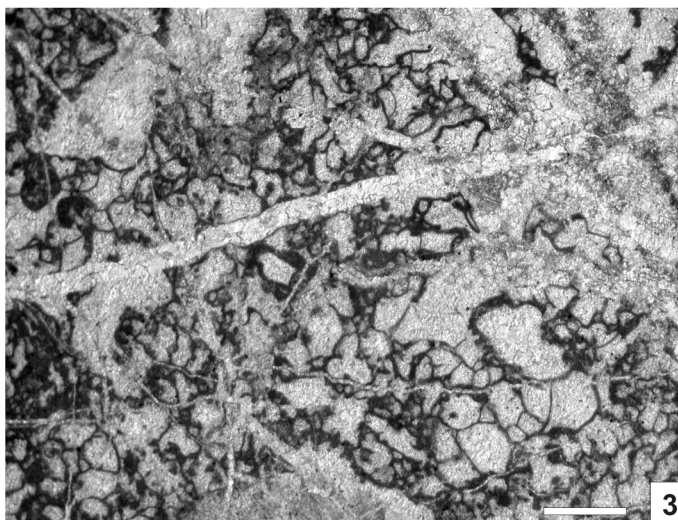
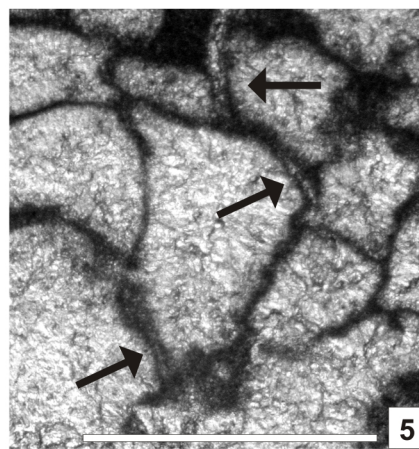
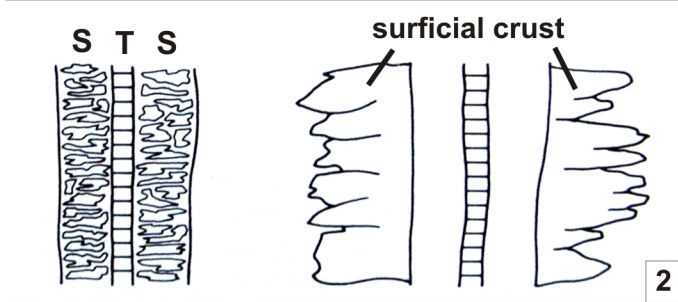
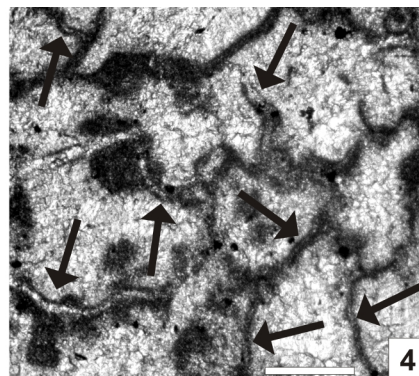
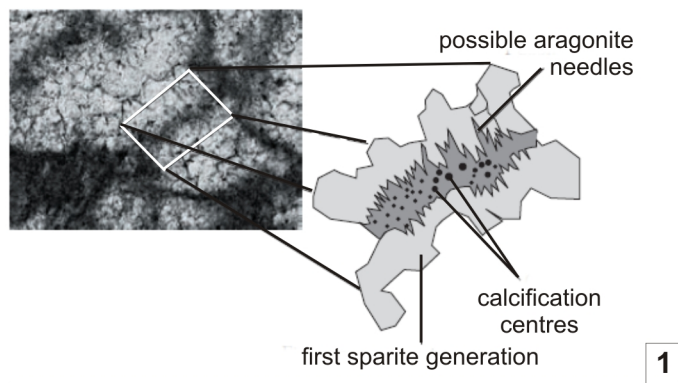


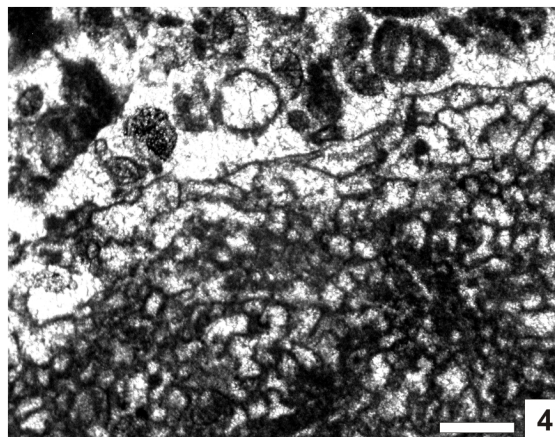
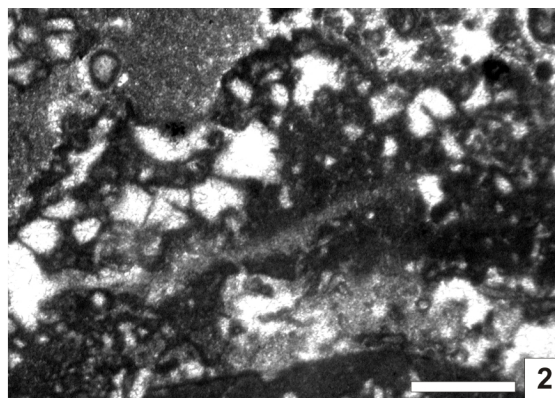
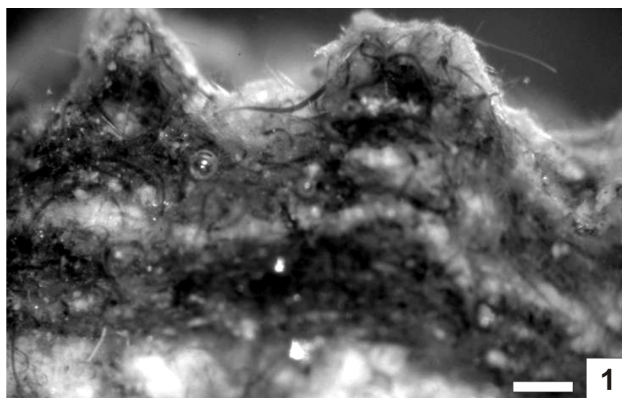












species	interpretation
<i>Bacinella irrregularis</i> RADOICIC, 1959 Barremian-Aptian of Montenegro	euendolithic chlorophyte alga
<i>Bacinella ordinata</i> PANTIC, 1972 Ladinian of Montenegro	thaumatoporellacean alga
<i>Bacinella? sterni</i> RADOICIC, 1972 Albian of Serbia	indefinite microbial origin
<i>Bacinella crispa</i> ELIASOVA, 1981 Late Jurassic of Czech Republic	irregular final part of the foraminifer <i>Troglotella incrustans</i>
<i>Bacinella elongata</i> FOIS, 1981 Ladinian of Italy	solenoporacean alga
<i>Bacinella bicellularis</i> SADATI, 1991 Rhaetian of Austria	thaumatoporellacean alga