

## Remarks on *Bacĭnella* Radoiĉić, 1959 (type species *B. irregularis*) and its representatives

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**Abstract** *Bacĭnella irregularis* was described by Radoiĉić (Bull Serv Géol Géophys Rep Serbie 17:87–92, 1959) as an alga incertae sedis. Based on material from the Lower Aptian of the western Maestrat Basin (Spain), the genus *Bacĭnella* with its various species is revised; an emended diagnosis is given as well as a detailed description. *Bacĭnella* is interpreted as an organism that excavated complex branching galleries into biogenic hard substrates, e.g., 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 (microborers) whereas *Bacĭnella* has a larger filament diameter. Nearly all of the “*B. irregularis*” occurrences reported in the literature do not belong to this taxon, but represent irregular vesicular crusts (“bacinellid” fabrics = *B. irregularis* auct. non) that display some resemblances with modern microbial mats.

**Keywords** Calcareous algae · Chlorophyceae · Taxonomy · Bioerosion · Lower Cretaceous · Spain

### Introduction

*Lithocodium aggregatum* Elliott (1956) and *Bacĭnella irregularis* Radoiĉić (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 *B. irregularis* and *L. aggregatum* as synonyms with *Lithocodium* having priority (Segonzac and Marin 1972; Luperto Sinni 1979; Banner et al. 1990; Koch et al. 2002), while others treated the two micropaleontological taxa as different taxa (Elliott 1963; Schmid 1996; Schmid and Leinfelder 1996; Cherchi and Schroeder 2006). *L. 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 alga, foraminiferal, and cyanobacterial (calci-microbial) origin. Recently, *L. 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).

In contrast, *B. irregularis* was originally described by Radoiĉić (1959) as an alga incertae sedis. However, many authors have later assumed a cyanobacterial/microbial origin for this micropaleontological taxon (Schäfer and Senowbari-Daryan 1983; Maurin et al. 1985; Camoin and Maurin 1988; Riding 1991a; Schmid and Leinfelder 1996; Vachard et al. 2001; Uřa and Bucur 2003). Alternatively, Schlagintweit et al. (2010) re-interpreted *B. irregularis* as a euendolithic chlorophycean alga, possibly belonging to the Ulotrichales. Given that the main goal of the

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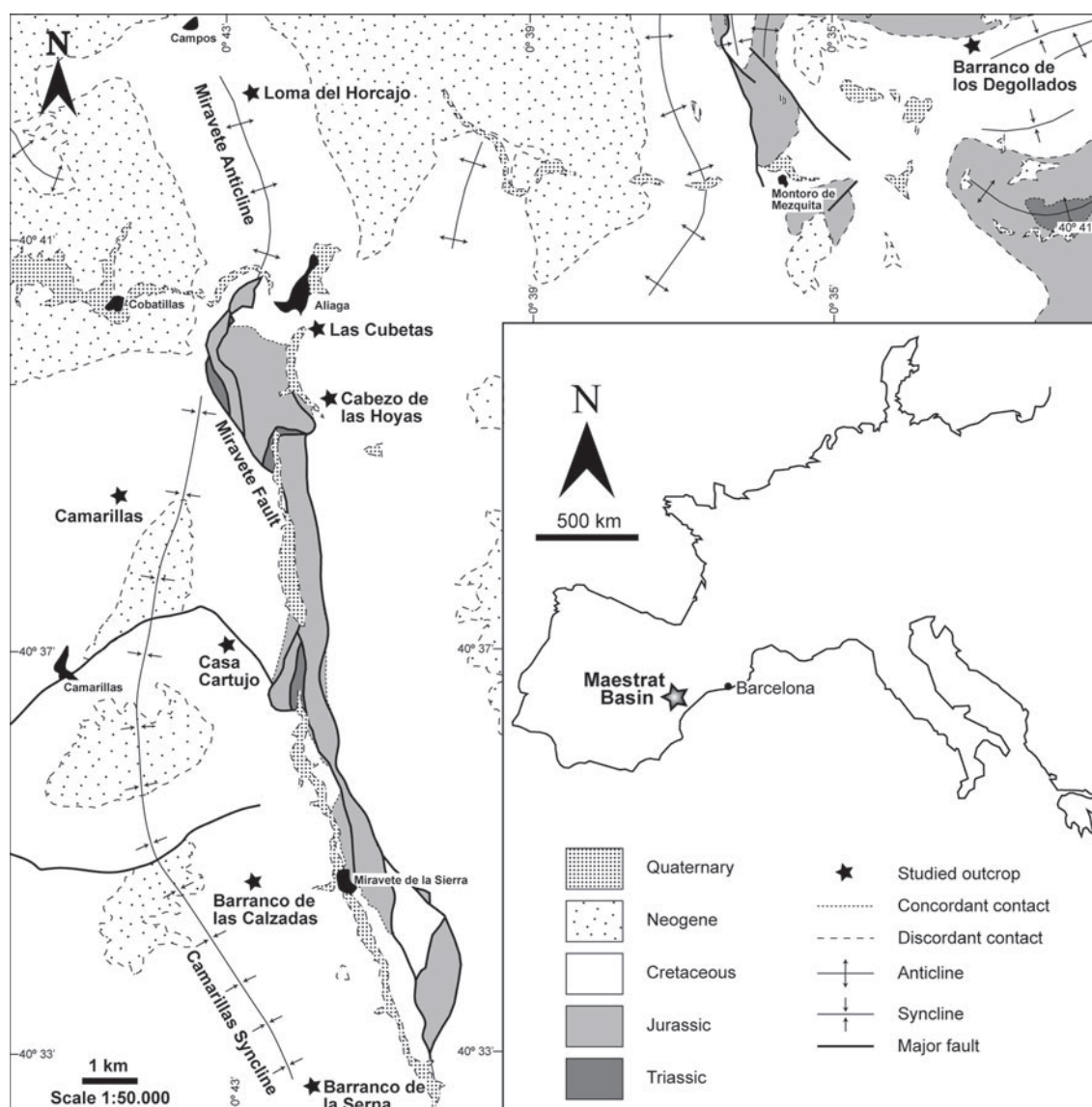
last-mentioned work was the re-description of *L. aggregatum*, the present study deals exclusively with the genus *Bacĭnella* Radoiĭć. It critically discusses the species inventory, and provides a new generic diagnosis along with a detailed description of the type species. In addition, new microstructural details of “bacinellid fabrics” (= *B. irregularis* Radoiĭć 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 levels of coral rubble encrusted by microorganisms, clearly dominated by *L. 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 comprises 73 thin-sections, which were sampled from nine outcrops in the vicinity of the towns of Aliaga, Montoro de Mezquita, Camarillas, and Miravete de la Sierra (Teruel province, Spain; Fig. 1).



**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 an asterisk and are as follows (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*)

## Taxonomic part

Kingdom Plantae

Division Chlorophyta Pascher, 1914

Class Ulvophyceae Mattox and Stewart, 1984

? Order Ulotrichales Borzi, 1895

Family ?

Genus *Bačinnella* Radoičić, 1959, emended herein

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

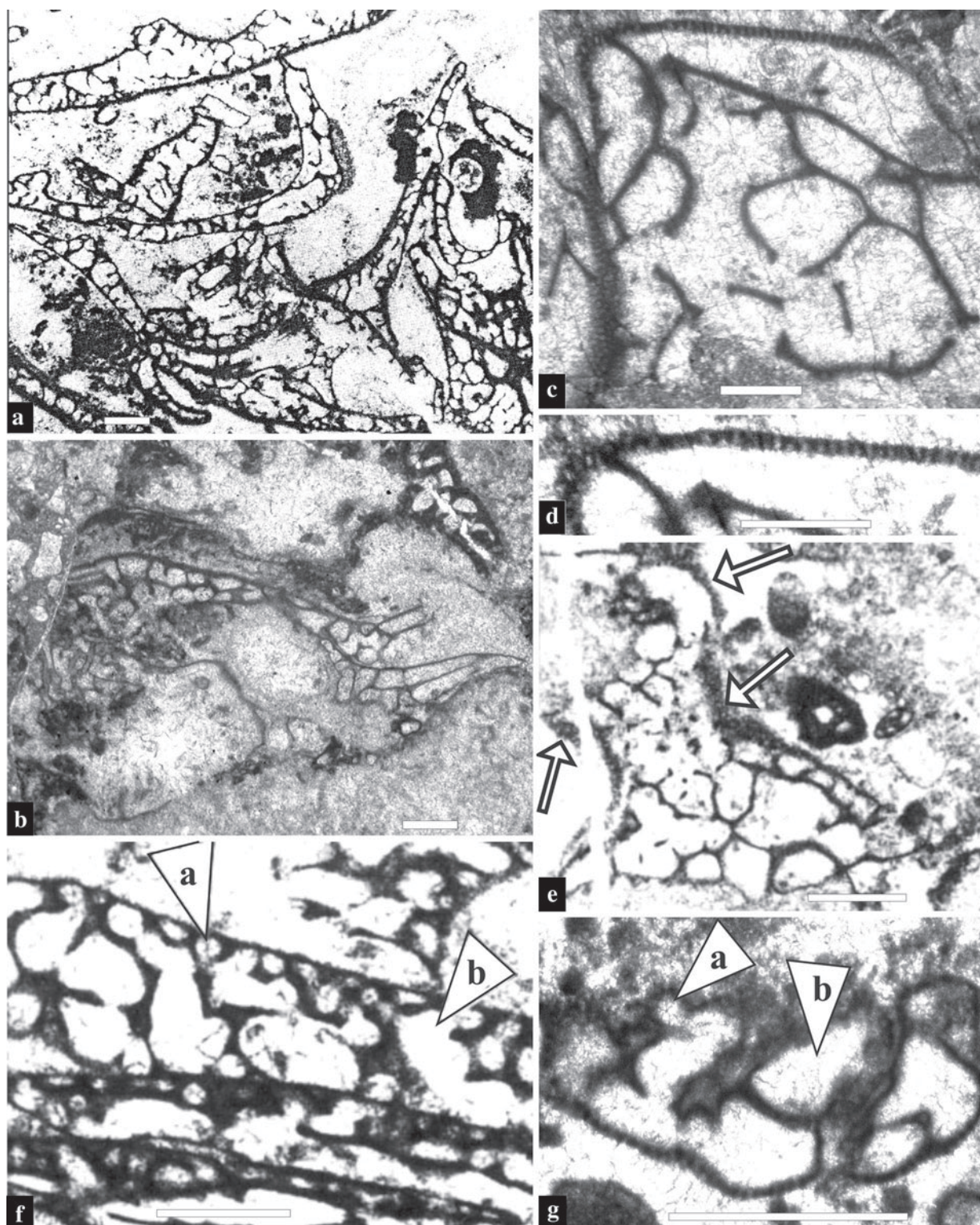
*Bačinnella bicellularis* Sadati, 1981 (Fig. 2e, f), Late Triassic of Austria. Kuss (1990) reported *B. bicellularis* from the Middle Jurassic of Egypt as forming individual layers within oncoids. Internal structures with two types of cells, large basal cavities and smaller “distal” cells as in *B. bicellularis* are also known from thaumatoporellacean algae (De Castro 1990) (Fig. 2g) or from *Pseudolithocodium carpathicum* Mišik, 1979. Affinities between the latter taxon and thaumatoporellaceans were discussed by Cherchi and Schroeder (2005), who distinguished “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 and Schroeder (2005) from the Liassic of the Southern Alps, Italy, is formed by superimposed crustose layers and shows striking similarities (if it is not identical) to *B. 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 *Bačinnella ordinata* Pantić, 1972 (see below). Bearing in mind the wide morphological variability usually exhibited by thaumatoporellacean algae (De Castro 1990), “*B. bicellularis*” is here interpreted as belonging to this group. Status: not a representative of *Bačinnella*. It has been interpreted as a thaumatoporellacean alga (Schlagintweit 2011).

*Bačinnella 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 and 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). In a recent paper, cavities containing *Troglotella* were interpreted as sponge borings excavated in Late Jurassic calcimicrobial crusts (Schlagintweit 2010). Status: not a representative of *Bačinnella*. Most likely a mixture/consortium of different (ichno)taxa.

*Bačinnella elongata* Fois, 1981, Late Ladinian of Southern Alps, northern 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 *Bačinnella*. It is unknown, and it should be checked whether it represents an individual taxon or belongs to an already existing solenoporacean alga.

*Bačinnella 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 *Bačinnella* was given as follows: “Nodular and incrusting 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, p. 92). In the species description the “cells” of *B. 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 them 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 disorganized, but are radiating and successively branching, forming a network (Fig. 3a). 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 (Fig. 3/a) and one paratype (Fig. 3c). 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 (compare Fig. 3d–e). With the partly closely attaching cells, the “intercellular mass” becomes reduced but is still visible in the paratype. Following article 7.2 of the International Code of Botanical





**Fig. 2** *Bačinella ordinata* Pantić, 1972 (a) and *B. bicellularis* Sadati, 1981 (e, f), and their interpretation as thaumatoporellacean algae (b–d, g). a From Pantić (1972, pl. 4/1), Ladinian of Montenegro. b Thaumatoporellacean alga from the Norian-Rhaetian Dachstein reefal limestone of the Northern Calcareous Alps of Austria. c, d Detailed views showing the finely perforated external wall. e, f From Sadati (1981, pl. 1/2–3), Norian-Rhaetian of the Northern Calcareous

Alps of Austria. Two types of cell sizes (a and b). Note the mosaic-like central part with homogeneous partitions in e comparable to *B. ordinata* (a); the external wall is finely alveolar/perforated (arrows in e). g *Thaumatoporella 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

**Table 1** *Bacĭnella* species and their interpretation

Species	Interpretation
<i>Bacĭnella irregularis</i> Radoiĉić, 1959 Barremian-Aptian of Montenegro	Euendolithic chlorophyte alga
<i>Bacĭnella ordinata</i> Pantić, 1972 Ladinian of Montenegro	Thaumatoporellacean alga
<i>Bacĭnella? sterni</i> Radoiĉić, 1972 Albian of Serbia	Indefinite microbial origin
<i>Bacĭnella crispa</i> Eliášová, 1981 Late Jurassic of Czech Republic	Consortium of the foraminifer <i>T. incrustans</i> and sponge borings in calcimicrobial crusts
<i>Bacĭnella elongata</i> Fois, 1981 Ladinian of Italy	Solenoporacean alga
<i>Bacĭnella bicellularis</i> Sadati, 1981 Rhaetian of Austria	Thaumatoporellacean alga

Details are given in the text

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 Radoiĉić and the specimen from the Early Aptian of Spain showing the boring character of *B. irregularis* are untypical (as being very rare) in thin-section material as these are cut 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 Radoiĉić (1959). In the Iberian material, it is evident that *B. irregularis* represents an organism boring into micritic crusts of *L. aggregatum* (=micritic “intercellular mass”). The original diagnosis of *Bacĭnella* is therefore interpreted as representing a mixture that refers to two different taxa (*Bacĭnella* and *Lithocodium*) and moreover does not include an adequate description of all morphological characteristics. An emended diagnosis is presented below. Status: valid.

*Bacĭnella ordinata* Pantić, 1972 (Fig. 2a), Ladinian of Montenegro: Its occurrence has been documented throughout the Late Triassic (Senowbari-Daryan 1984) and the Liassic (Scheibner and Reijmer 1999). The thin, external, micritic wall usually appears homogeneously micritic. In some specimens, however, the wall exhibits a fine perforation (Fig. 2c–d). On the basis of this external micritic alveolar wall, *B. 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 *Bacĭnella*. It has been interpreted as a thaumatoporellacean alga (Schlagintweit 2011).

*Bacĭnella? sterni* Radoiĉić, 1972. The Cenomanian age of the Serbian type stratum of *Bacĭnella? sterni* was later revised as belonging to the Albian (Banjac et al. 2007). The species was removed from *Bacĭnella* 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 sterni* (Radoiĉić, 1972) is here considered a valid taxon (in any case not a representative of *Bacĭnella*), but the suprageneric position (udoteacean green alga according to Banner et al. 1990) is unclear. An undefined microbial origin is favored.

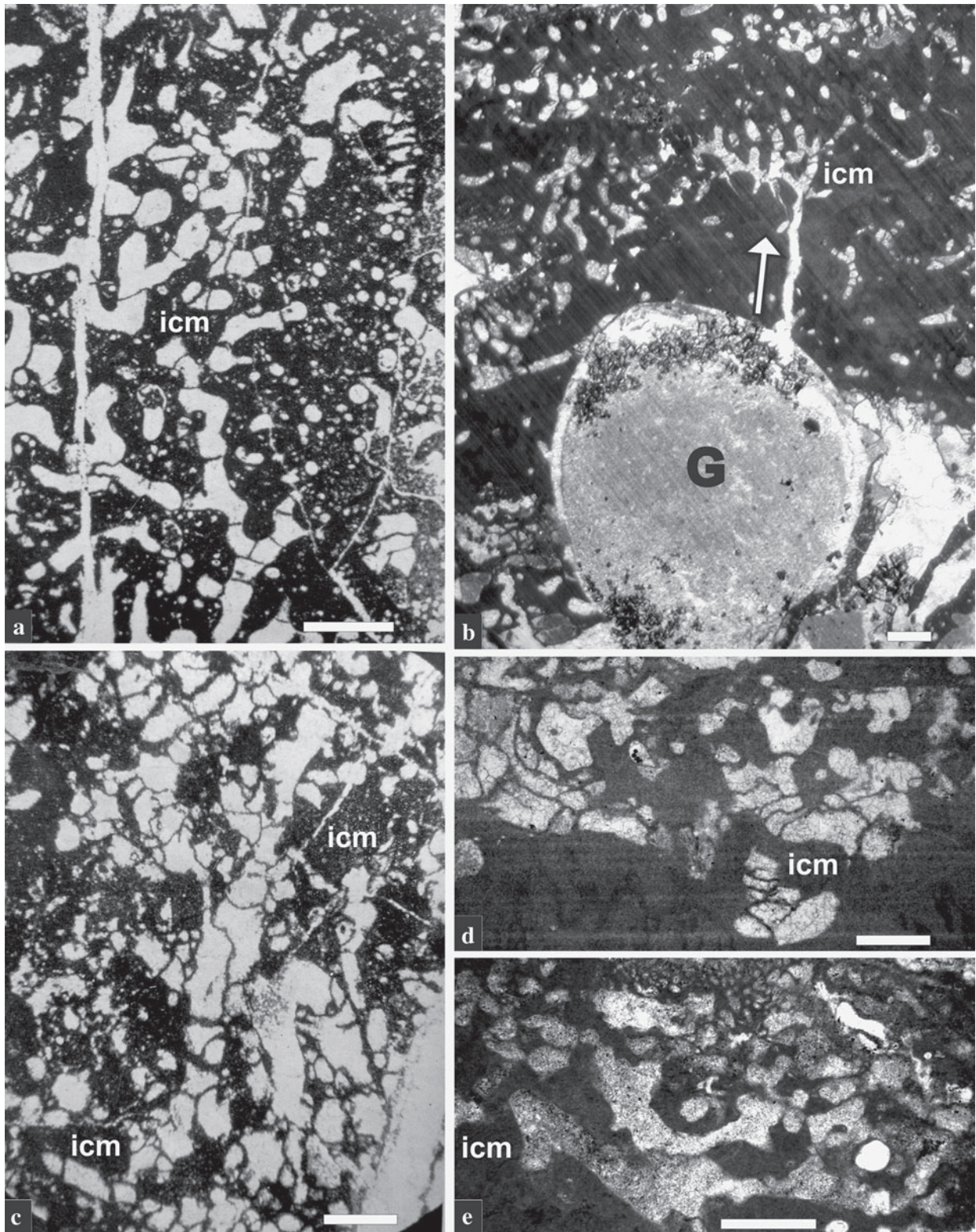
In conclusion, no other *Bacĭnella* species erected after the description of the type-species *B. irregularis* belongs to this genus (Table 1). Thus, *Bacĭnella* is interpreted as a monotypic taxon.

**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 anastomosing filaments with cross-partitions forming a complex network that is arranged 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. Hairs (setae) may be present.

*Bacĭnella irregularis* Radoiĉić, 1959  
Figs. 3a–e, 4a–e, 5a–e (pars), 6a, b

**Synonymy** There are plenty of illustrations of “*B. irregularis*” published since its description in 1959. Listing them would fill several pages. According to our emended diagnosis, only the figures of Reitner (1987) from the Albian of Spain is included. For the interpretation of most illustrations in the literature, see the chapter *Discussion*.





**Fig. 3** *Bacinella irregularis* Radoičić, 1959. **a** Holotype specimen (from Radoičić 1959, pl. 3/1), Barremian-Aptian of Bosnia and Herzegovina (icm = micritic “intercellular mass” sensu Radoičić). **b** *B. irregularis* specimen boring through superimposed and micritized crusts of *L. 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. **c** Paratype (from Radoičić 1959, pl. 3/2), Barremian-Aptian of Bosnia and Herzegovina. **d, e** Specimens from the Lower Aptian of the western Maestrat Basin comparable to the paratype. Thin-sections DE-5H and HO-3V. Scale bars 0.5 mm



\*1959 *B. irregularis* nov. gen., nov. sp.—Radoičić: 92, pl. 3/1-2

1987 *B. irregularis* Radoičić—Reitner: pl. 21/1

2010 *B. irregularis* Radoičić—Schlagintweit et al.: 531, 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 a euendolithic sporophytic phase to which the following description refers exclusively. The multicellular thallus is composed of branching septate filaments, euendolithic typically in crusts of *L. 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 in the holotype). In the central part, large irregularly swollen cells occur (diameter up to 500 µm). Cells are separated by thin microcrystalline transverse walls (thickness ~6–35 µm) occurring at distances of 0.15–0.5 mm. Thick walls may have an indistinct lamellar 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. 4e). Starting from the substrate entrance point, the algae may bore with a single straight to slightly undulating filament before they irregularly branch in all directions (Fig. 3b). This network of branching and anastomosing filaments extends in a plane parallel to the substrate surface. The greatest observed thallus width is 5 mm (specimen shown in Fig. 3b). Three different types of branching patterns occur: (1) dichotomous, a Y-shaped bifurcating cell, (2) branching by bisection of a cell during radial division resulting in partitions that form a “T” (Fig. 6a) (e.g., Graham 1982 for details), and (3) opposite, rectangular branching with the so-called “four-armed central cell” (Nielsen 1987) (Fig. 6b).

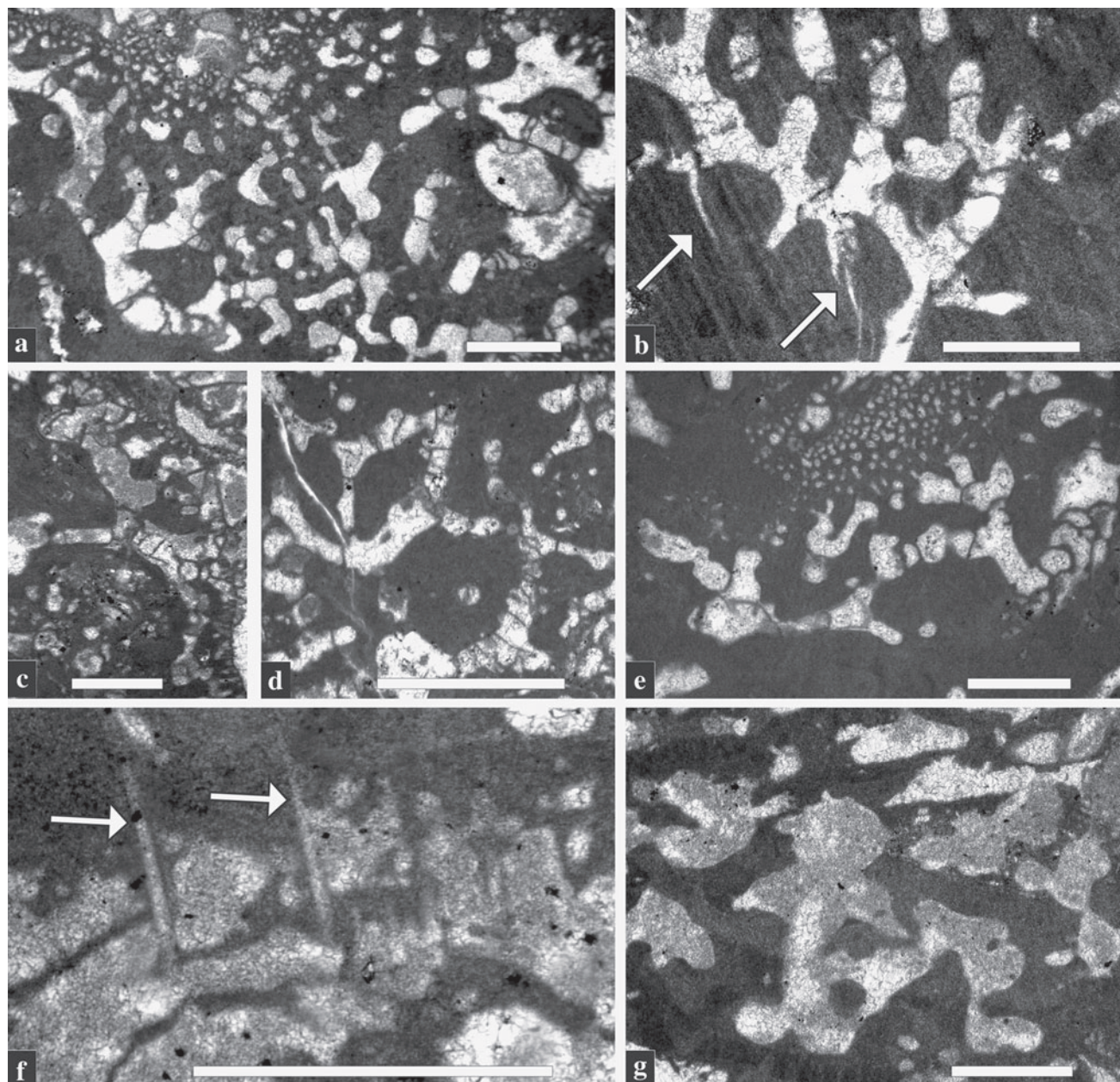
Within the central part, rare hairs (or setae) occur. They have a length of up to 500 µm with a basal diameter of 24–35 µm and are tapering distally (Fig. 4b, f). A basal septum towards the attaching cell is not detectable. As three-dimensional specimens are not available, it is unclear whether roundly 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 walls (e.g.,

Fig. 4b) to specimens with microsparitic (e.g., Fig. 4g) to micritic fillings without preserved walls. In the latter case, only the empty boring is present.

**Discussion** First of all, it must be noted that from the living alga, only the transverse 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, *B. 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 *B. irregularis*. With these two examples, the long-lasting discussion about a synonymy of *B. irregularis* with *L. aggregatum* becomes obsolete, since in both cases the micritic “intercellular mass” sensu Radoičić (1959) (= *Lithocodium* crusts) is lacking.

As the description of *B. 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 *Bacĭnella* resemble to some extent those produced by boring sponges: non-camerate (or open-camerate) representatives of the ichnogenus *Entobia* (e.g., Fig. 4g). An example comprises the ichnospecies *E. cateniformis* consisting of a branching and anastomosing boring system (Bromley and D’Alessandro 1984). These galleries, however, are continuous, whereas *B. irregularis* displays transverse walls and thus cannot be transferred to the activity of boring sponges. Instead, from its morphology and boring pattern, *Bacĭnella* 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 *Bacĭnella* 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. 3b). Furthermore, it can be stated that the modern euendolithic genera comparable to *Bacĭnella*, such as *Endocladia* (= *Ectochaete*) Agardh, 1841 or *Eugomontia* Kornmann, 1960, belong to the orders Ulotrichales or in the case of *Phaeophila* Hauck, 1876, to the Ulvales (O’Kelly et al. 2004; Guiry and Guiry 2011) (Fig. 7). Both Ulotrichales and Ulvales belong to the class Ulvophyceae (Guiry and Guiry 2011). All the aforementioned taxa are filamentous, septate (with transverse walls) forms as *Bacĭnella*, but distinctly smaller. For example,



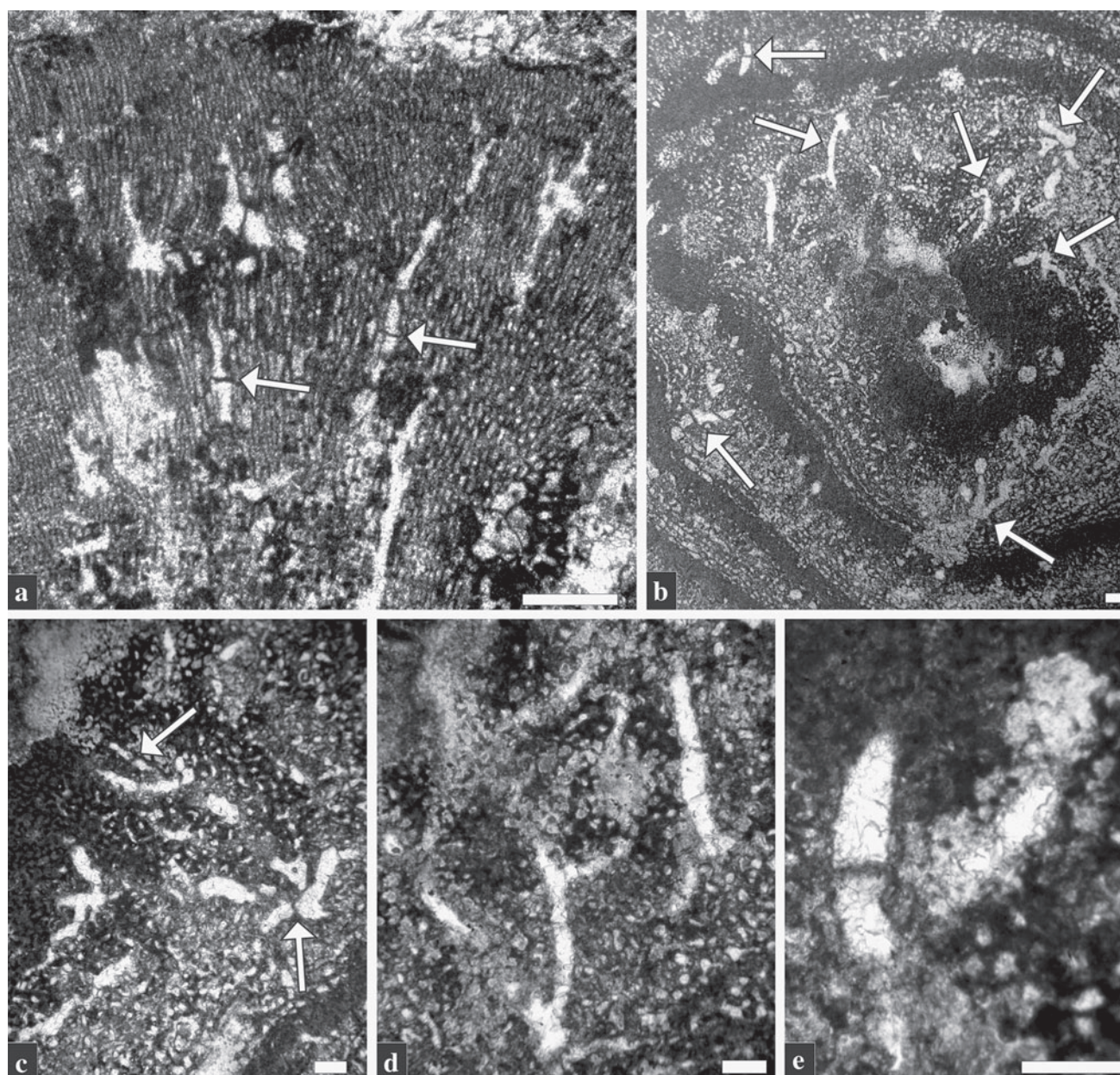
**Fig. 4** *Bačarella irregularis* Radoičić, 1959 boring into crusts of *L. aggregatum* Elliott, 1956. Lower Aptian of the western Maestrat Basin, Spain. **a** Network of branching and anastomosing filaments of *B. irregularis* which end with terminal fine branchlets (left above). Thin-section CAL-5V. **b** Detail from Fig. 3b showing cells each with one thin hair or seta (arrows). Thin-section DE-5H. **c, d** Network of *B. irregularis* filaments exhibiting irregular, swollen cells. Note the microsparitic filling in **c**. Thin-sections HO-3V and HO-17V.

**e** Branching filaments with terminal fine branchlets (above). Thin-section CAL-2V. **f, g** Boring galleries of *B. irregularis* with microsparitic filling resembling to some extent those produced by non-camerate boring sponges (ichnogenus *Entobia*). Note the absence of preserved transverse walls of cells. Note also the two thin tapering appendages (=setae) with upward growth towards the substrate surface in **f** (arrows). Thin-sections CA-3H and DE-3V. Scale bars 0.5 mm

filament (or cell) diameters are ~3–20  $\mu\text{m}$  in *Endocladia* (Thivy 1943), ~6–9  $\mu\text{m}$  in *Eugomontia* (Kornmann 1960; Nielsen 1987), ~5–25  $\mu\text{m}$  in *Phaeophila* (Thivy 1943; Nielsen 1987; Kitayama and Garrigue 1998), up to ~25  $\mu\text{m}$  in the siphonaceous *Ostreobium* Bornet and Flahault, 1889 (type species: *O. quekettii*) and even up to

140  $\mu\text{m}$  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 *Bačarella*, however, does not allow a direct inference whether its trace maker was siphonous or





**Fig. 5** **a** *Bačínella irregularis* Radoičić boring into the thallus of a solenoporacean alga. Note the visible transverse walls of the filaments (arrows). Late Jurassic (most probably Upper Tithonian) of Bulgaria (leg. Ioan Bucur). **b** *B. irregularis* Radoičić (arrows) boring into a

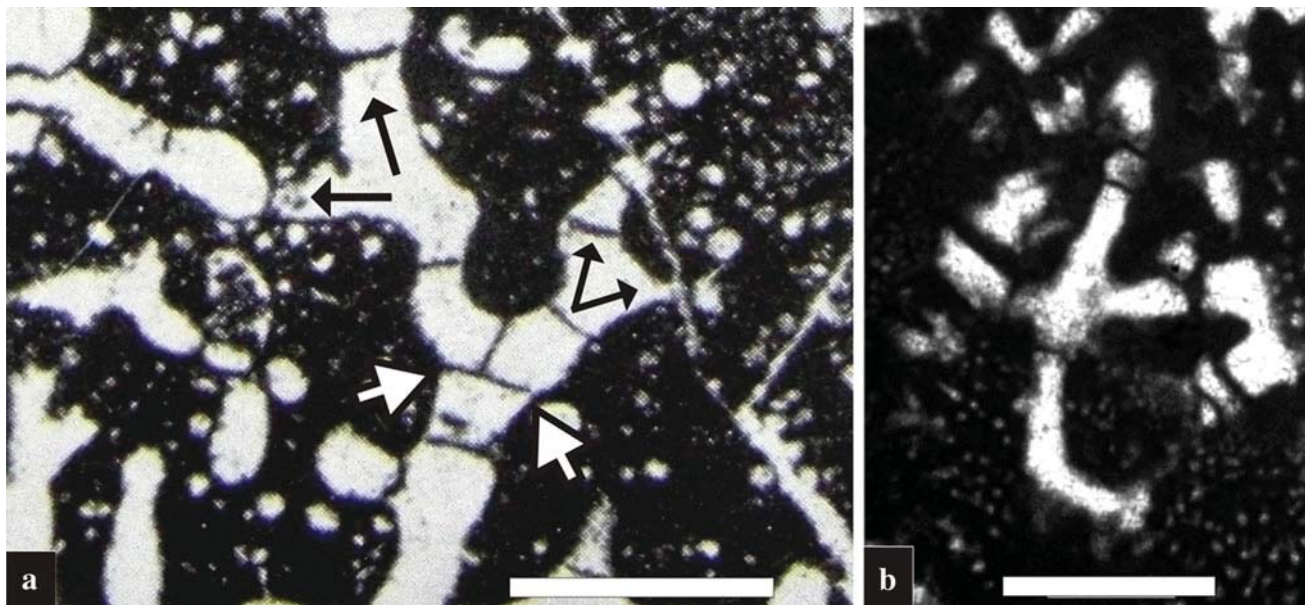
spongiomorphid skeleton. Pliensbachian of Morocco (slightly modified from Le Maitre 1935, pl. 8/8). **c–e** Detailed views from **b** showing filament branchings and preserved transverse cell walls (arrows in **b**; **c**)

septate-filamentous. Boring networks of filamentous chlorophytes are known since the Ordovician (Glaub and 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 eueuendolith 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 after their producer. They rather constitute a discrete ichnotaxon, which remains to be named, however.

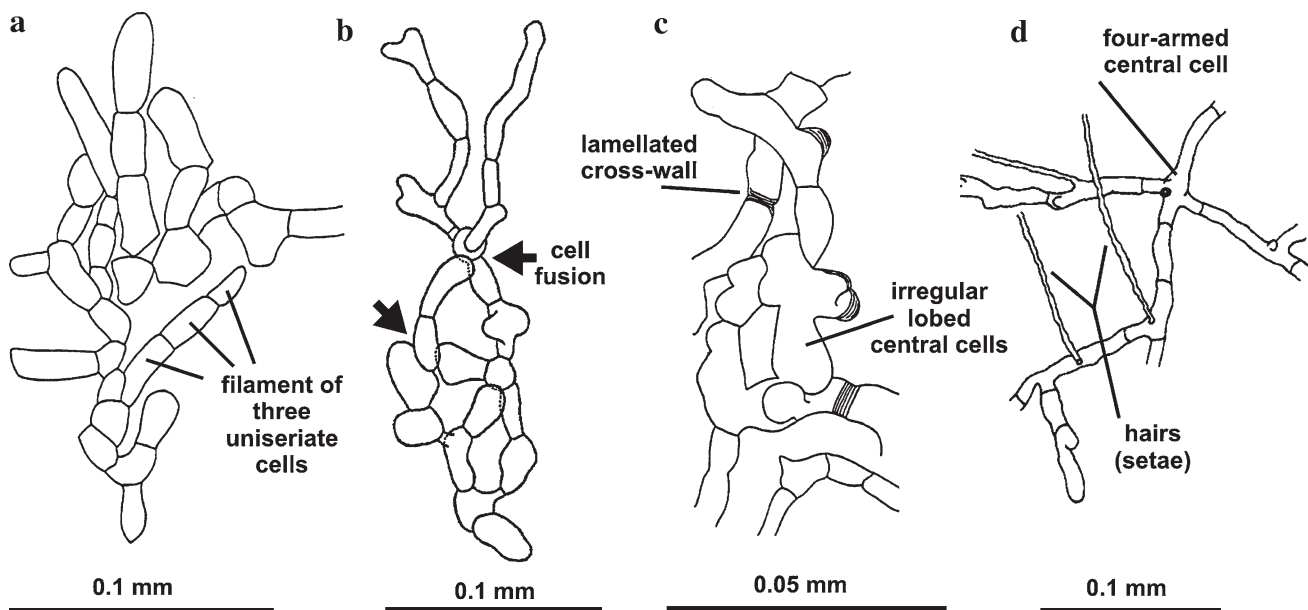
As already stated, the majority of references in the literature of *B. irregularis* refer to “epibenthic meshwork crusts of noticeable thickness and extension” (Schmid and Leinfelder 1996, p. 31). These, however, are completely different from the taxon that Radoičić described in 1959. These structures have later been termed “bacinellid





**Fig. 6** Filament branching pattern in *B. irregularis* Radoičić, 1959. **a** Detail from the holotype of Radoičić, 1959 (see Fig. 3a) showing dichotomous branching starting from a Y-shaped cell (black arrows) and the biseriate branching type with three cells separated by

T-shaped transverse walls (white arrows). **b** Rectangular branching exhibiting the so-called “four-armed central cell” (Nielsen 1987). Thin-section HO-16V. Scale bars 0.5 mm



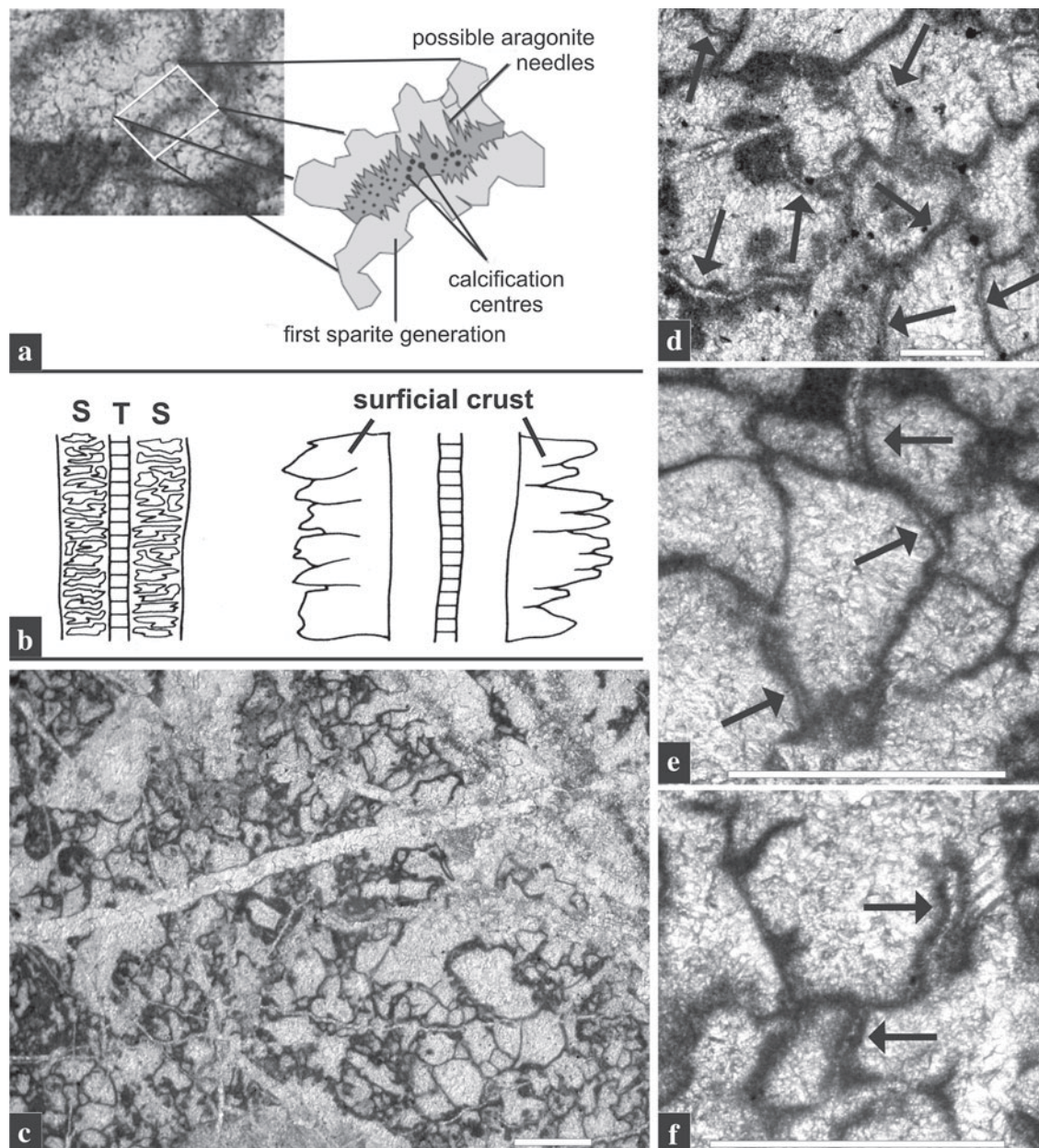
**Fig. 7** Modern euendolithic chlorophytes that can be compared with the fossil genus *B.* Radoičić, 1959. Note some of the morphological details used in the description. **a, c, d** *Phaeophila dendroides* (Crouan

and Crouan) (**a, c** from Thivy 1943, pl. 1/1 and 1/3; **d** from Nielsen 1987). **b** *Eugomontia sacculata* Kornmann (from Kornmann 1960, Fig. 5b)

textures” (Maurin et al. 1985) or “filamentous fabrics” (Hillgärtner et al. 2001), and a cyanobacterial/calcimicrobial origin has been assumed for them by several authors (Schäfer and Senowbari-Daryan 1983; Maurin et al. 1985; Camoin and Maurin 1988; Riding 1991a; Schmid and 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, p. 28) (Fig. 8a). 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





**Fig. 8** Calcification processes in filamentous cyanobacteria and vesicular crusts ("bacinellid fabric" = *B. irregularis* Radoičić, 1959 auct. non) of assumed calcimicrobial origin. **a** Microstructure of an Upper Jurassic (Oxfordian) "bacinellid fabric", Switzerland (modified from Dupraz 1999, Fig. 4.1). Without scale. **b** Calcification of a filamentous cyanobacterium during life-time. *S* Sheath,

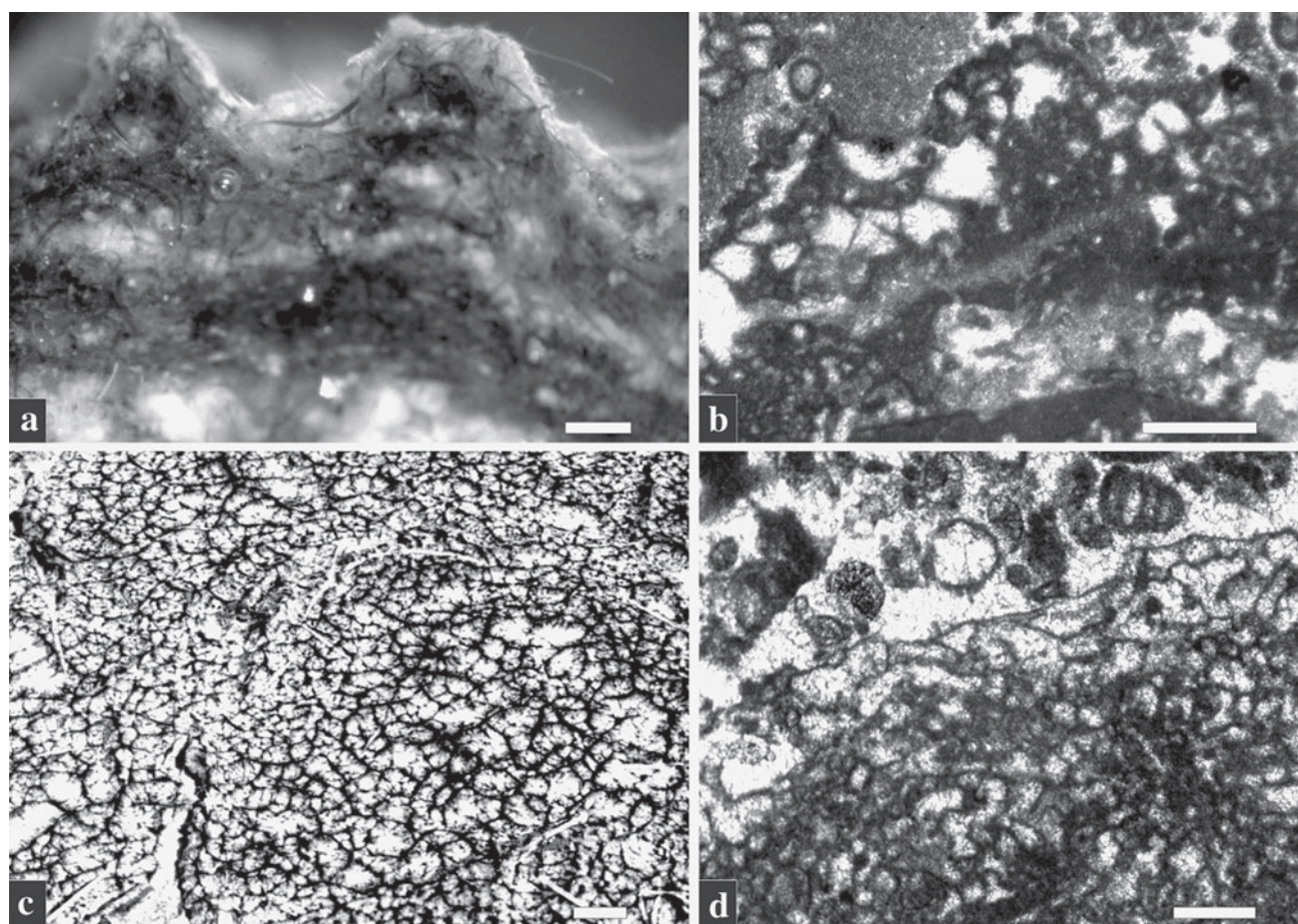
*T* trichome (modified from Riding 1991b, Fig. 2b, c). Without scale. **c** "Bacinellid fabric", Tithonian-Berriasian of the Getic Carbonate Platform, Romania. Thin-section Ghimba 387-1. Scale bar 0.5 mm. **d-f** Detailed views showing tiny, bended hollow tubes interpreted as calcimicrobial filaments. Scale bars 0.5 mm

cyanobacteria that triggered calcification by photosynthesis upon or within a mucilageneous sheath (Pentecost and Riding 1986; Riding 1991b) (Fig. 8b).

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 (Fig. 8c-f). The outer diameter ranges from 9.5 to 50  $\mu\text{m}$ , the width of the inner hollow tube is 5–25  $\mu\text{m}$ . They can be compared with the so-called *Girvanella* group that is compared with calcified oscillatoriacean (cyanobacteria) sheaths. Although being rather common in the studied material, many of the micritic "laminae" appear solid without a detectable central tubiform hollow.





**Fig. 9** Comparison of modern microbial mats (**a**, **c**) with Lower Cretaceous “bacinellid” fabrics (**b**, **d**). **a** Microbial mat surface structure with pinnacles. Saline, southern Bretagne, France (from Gerdes and Klenke 2003, Fig. 8a). *Scale bar* 0.5 mm. **b** Structured top of a “bacinellid” crust. Early Aptian of Croatia. *Scale bar*

0.5 mm. **c** Polygonal reticulate surface pattern resembling “elephant skin” (from Gerdes 2007, Fig. 2-1-5e). *Scale bar* 1 cm. **d** Surface structure of a “bacinellid” crust. Lower Aptian of Croatia. Note the differing dimensions compared to the modern example. *Scale bar* 0.5 mm

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 and Klenke 2003; Gerdes 2007; Porada and Bouougri 2007) (Fig. 9). It is worth to mention that already Dragastan and Richter (2003, p. 87) mentioned a possible interpretation of “*Bacĭnella*” 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 a better understanding of these three-dimensional structures (mats), however, are needed.

## Conclusions

The taxonomic re-interpretation of *Bacĭnella* and the critical assessment of its different “species” conclude that it represents a monotypic taxon. The type species *B. irregularis* Radoiĉić is considered a euendolithic chlorophyte. Microstructure and boring pattern compares *Bacĭnella* with modern representatives of the class Ulvophyceae.

Due to the new taxonomic concepts and interpretations, the organo-sedimentary, mostly crust-forming, pseudocellular meshworks can neither be referred to “*Lithocodium*” (=micritic layers) nor “*Bacĭnella*” (=sparitic vesicular zones). These “bacinellid” fabrics show some features that make them comparable to modern microbialites (e.g., microbial mats). However, further investigations on the microfabric characteristics and the microorganisms involved in their formation are still needed.



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