Erratum to: New insights into *Lithocodium aggregatum* Elliott 1956 and *Bacinella irregularis* Radoičić 1959 (Late Jurassic–Lower Cretaceous): two ulvophycean green algae (?Order Ulotrichales) with a heteromorphic life cycle (epilithic/euendolithic)

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Abstract The Late Jurassic–Lower Cretaceous microorganisms incertae sedis *Lithocodium aggregatum* Elliott and *Bacinella irregularis* Radoičić are taxonomically studied based on material from the Lower Aptian of the western Maestrat Basin (Spain). This study is supplemented with detailed photographs from Elliott's type-material. Given that the original description of *Lithocodium aggregatum* is ambiguous, a detail from the holotype is chosen as an epitype to serve as an interpretative type (article 9.7 ICBN). *Lithocodium* is re-interpreted as a filamentous-septate heterotrichale ulvophycean alga (?order Ulotrichales) exhibiting a heteromorphic life cycle consisting of two phases: an epilithic gametophytic and a euendolithic

sporophytic (*Gomontia* stage). *Bacinella irregularis* is interpreted and redescribed as a purely euendolithic ulvophycean alga which bores into either *Lithocodium aggregatum* or the substrate below *Lithocodium* crusts. A small microendolith boring into *Lithocodium* crusts capable of cryptobiotically stretching within its filamentous network is tentatively assigned to the siphonal chlorophyte *Ostreobium* Bornet and Flahault. Another associated microfilamentous boring chlorophyte with characteristic long thin hairs (setae) is described as *Phaeophila?* sp. The euendolithic community comprises a variety of micro- and macroborings that affect the thalli of *Lithocodium*. Finally, the filaments of the outer zone of the *Lithocodium* crust are infested by calcimicrobes (cyanobacteria, ?fungi). The description made by Elliott in his original work of the “inner layer” of *Lithocodium aggregatum* as “confused” is explained here as a complex multitaxon chlorophyte-calcimicrobial assemblage overprinted by multiple bioerosion ichnofabrics.

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Introduction

Microproblematica are microfossils with an unknown or uncertain systematic position, which were especially widespread within Upper Triassic–Cretaceous Tethyan platform carbonates (e.g., Senowbari-Daryan 1980, 1984; Schlagintweit 1991; Schmid 1996). Of all these enigmatic taxa, two of the best known are *Lithocodium aggregatum* Elliott (1956) and *Bacinella irregularis* Radoičić (1959). The taxonomic

nature of these two microproblematica, as well as their possible relationship or synonymies, has been the subject of much controversy over the last 50 years. *Lithocodium aggregatum* was originally described as a siphonal (= non-septate filaments) codiacean alga from the Lower Cretaceous subsurface (most probably Hauterivian according to Banner et al. 1990, p. 30; see also Ziegler 2001) from the Rumaila oil field near Basra, Iraq. Its codiacean nature was accepted by many subsequent authors (e.g., Johnson 1964; Poignant 1968; Höfling 1985; Banner et al. 1990; Radoičić 2005). Segonzac and Marin (1972) analyzed material with *Lithocodium aggregatum* from the Lower Aptian of Spain, including one locality (Barranco de Los Degollados) sampled in the present study (Fig. 1) and provided further details on its microstructure. They described two different types of thallial filaments: septate (with cross-partitions) basal ones and superimposed series of filaments lacking such cross-partitions. The former were compared to those present in ulochtrichalean green algae, for example genus *Gomontia* (op. cit., p. 333), whereas the non-septate filaments were compared to the filaments (or siphons) present in udoteacean/halimedacean green algae. Still maintaining

the algal interpretation, Segonzac and Marin (1972) concluded that this obviously aberrant structure could not be related to any known taxonomic group, neither fossil nor extant, and that therefore one may consider creating a new family (op. cit., p. 334, “*qu'on puisse faire un rapprochement sûr ou créer une nouvelle famille*”). Some years later, Elliott (1978, p. 438) still regarded *Lithocodium-Bacinella* “*a very doubtful structure not resolved by the re-study of Segonzac and Marin (1972)*”. Nearly two decades later, Banner et al. (1990) took up the idea of Segonzac and Marin (1972) and created the Lithocodoidea as a new subfamily within the Codiaceae (= Udoteaceae) including *Lithocodium aggregatum*. Although udoteacean green algae are siphonous, they redescribed the genus as possessing irregular septate subdermal (= medullar) filaments. Besides the assumed green algal nature, other authors proposed a sponge (Koch et al. 2002) or red alga origin (Wood 1999, p. 102), interpreted it as a litoiid foraminifera (Schmid and Leinfelder 1996) or assumed a microbial (= cyanobacterial) origin. This last view has experienced a wider acceptance, especially in recent times (e.g., Riding 1991a; Cherchi and Schroeder 2006; Conrad and Clavel

Fig. 1 Geological map of the western Maestrat Basin. The areas studied are marked with a star. Modified after Canérot et al. (1979) and Gautier (1980). The outcrop sections sampled 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), Casa Cartujo (CC), Barranco de las Calzadas (CAL) and Barranco de la Serna (SE)

Table 1 Comparison of different taxonomic interpretations (most important views) of *Lithocodium aggregatum* Elliott and *Bacinella irregularis* Radoičić

<i>Lithocodium aggregatum</i> Elliott			<i>Bacinella irregularis</i> Radoičić	
Author	Micritic crust	Internal structures	Author	Interpretation
Elliott (1956)	Codiacean green alga Thallus	Non-septate medullary + cortical filaments	Radoičić (1959)	Alga incertae sedis
Segonzac and Marin (1972), Banner et al. (1990)		Septate medullary + non-septate cortical filaments	Turnsek and Buser (1966), Beckmann and Beckmann (1966)	Hydrozoa
Leinfelder (1986), Koch et al. (2002)	Possible sponge nature		Segonzac and Marin (1972), Luperto Sinni (1979)	Older growth stage of <i>Lithocodium</i>
Schmid and Leinfelder (1996)	Lituolid foraminifera Test	Alveolar layer + chambers	Banner et al. (1990)	Codiacean green alga (assuming its synonymy with <i>Lithocodium</i>)
Riding (1991), Cherchi and Schroeder (2006), Conrad and Clavel (2008)	Calcimicrobial colony (= Cyanobacteria) Colony	Alveolar layer + cavities	Schäfer and Senowbari-Daryan (1983), Maurin et al. (1985), Camoin and Maurin (1988), Riding (1991), Schmid (1996), Vachard et al. (2001), Uta and Bucur (2003)	Cyanobacterian microbe
This work	Ulotrichalean green alga Thallus	Prostrate septate + erect septate filaments	This work	Euendolithic ulotrichalean green alga

2008). The possible foraminiferan nature of *Lithocodium aggregatum* proposed by Schmid and Leinfelder (1996) was discussed and rejected by Schlagintweit et al. (2005), Cherchi and Schroeder (2006) and Schlagintweit (2008). Nonetheless, other authors accepted the interpretation of Schmid and Leinfelder (e.g., Kolodziej 1997; Dupraz and Strasser 2002; Flügel 2004; Helm 2005). In the two paleobiological online databases (www.data.gbif.org, www.paleodb.org), *Lithocodium* is treated as a genus within the phylum Cyanobacteria. Table 1 shows an overview of the main taxonomic positions given to *Lithocodium aggregatum* Elliott and the new interpretation presented in this paper.

The taxonomy of *Bacinella irregularis* is not so controversial as many authors assume a cyanobacterian/microbial origin (Schäfer and Senowbari-Daryan 1983; Maurin et al. 1985; Camoin and Maurin 1988; Riding 1991a; Schmid and Leinfelder 1996; Vachard et al. 2001). Vachard et al. (2001) treated *Bacinella* as a cyanobacterian genus of the family Aphralysiaceae. One example of a completely different interpretation is that of Turnsek and Buser (1966, p. 545) who assumed *Bacinella* to be a stromatoporoid: “So far we do not know any alga with similar structure. The tubes at solenopores are parallel. We consider, that *Bacinella* belongs to the special group of hydrozoans, like *Cladocoropsis*. Different forms of “cells” with partings in *Bacinella* remind us of coenosteal tubes and interspaces

with tabulae in hydrozoans. Also the microstructure of skeletal elements of *Bacinella* we can obviously notice the medial dark line with radial fibrous”. Elliott (1963, p. 294) recognized *Bacinella* as an inner structure of some *Lithocodium* specimens, maintaining both as “doubtfully algal growths”. Elliott (1963, p. 295) also remarked that *Lithocodium* and *Bacinella* “may be constructed by the same organism”. Some authors were not as cautious as Elliott and directly assumed the synonymy between *Bacinella irregularis* and *Lithocodium aggregatum* with *Lithocodium* having priority as described earlier (e.g., Banner et al. 1990; Koch et al. 2002). Segonzac and Marin (1972), followed by several others (e.g., Luperto Sinni 1979) regarded *Bacinella* as corresponding to the basal part of *Lithocodium* while others treated the two as different taxa (e.g., Elliott 1963, Schmid and Leinfelder 1996; Cherchi and Schroeder 2006). A completely different conclusion was drawn by Fenninger (1972), who remarked that the description of *Bacinella* was more complete as it referred to a subdermal structure reminiscent of *Lithocodium*. Furthermore, Fenninger (1972) concluded that *Lithocodium* could represent the incomplete stage of *Bacinella*, referring only to its subdermal part. In this case, the morphogenus *Bacinella* should have priority.

In the framework of micropaleontological studies of Lower Aptian carbonates of the western Maestrat Basin (E Iberian Chain, Spain), abundant and well-preserved

material of *Lithocodium aggregatum* Elliott (1956) was analyzed. Together with detailed illustrations of Elliott's original material, it yielded new insights into its biogenic nature and morphological interpretation, allowing for an emended diagnosis.

Study area and geological overview

The specimens studied come from the Lower Aptian sedimentary succession cropping out in the western Maestrat Basin, in the eastern Iberian Chain (Fig. 1). This sedimen-

tary record can be divided into two long-term transgressive-regressive sequences (Bover-Arnal et al. 2010), which comprise four lithostratigraphic formations: Morella, Xert, Forcall, and Villarroya de los Pinares (Canérot et al. 1982; Salas et al. 2001; Bover-Arnal et al. 2009a, 2010). 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 (Fig. 2), clearly dominated by “*Lithocodium-Baccinella*-crusts” (Bover-Arnal 2010; Bover-Arnal et al. 2010). The taxa that compose the micropaleontological association and their relative abundances are summarized in Table 2.

Fig. 2 **a** Field view of the Barranco de las Calzadas area with the situation of the encrusted horizon with *Lithocodium aggregatum* Elliott within the marls of the Forcall Formation. **b** Outcrop view of the encrusted deposits with *Lithocodium aggregatum* Elliott exposed in the Barranco de las Calzadas section. **c** Schematic log of the Barranco de las Calzadas section with the situation of the rocks studied with *Lithocodium aggregatum* Elliott (modified from Bover-Arnal 2010)

Table 2 Microfossil inventory of the encrusted deposits of the western Maestrat Basin with relative abundances

Species	Semiquantitative abundance
Benthic foraminifera	
<i>Bdelloidina? urgonensis</i> Wernli and Schulte	***
<i>Charentia cuvillieri</i> Neumann	*
<i>Choffatella</i> cf. <i>decipiens</i> Schlumberger	***
<i>Daxia minima</i> Laug and Peybernes	***
<i>Everticyclammina</i> sp.	**
Lenticulinids	***
<i>Meandrospira</i> cf. <i>washitensis</i> Loeblich and Tappan	**
<i>Palorbitolina lenticularis</i> (Blumenbach)	****
<i>Praeorbitolina</i> gr. <i>cormyi-wienandsi</i> Schroeder	**
Textulariids	****
<i>Troglotella incrustans</i> Wernli and Fookes	*
<i>Neotrocholina</i> cf. <i>aptiensis</i> Iocheva	***
Pseudoostracods sensu Samuel et al. (1972)	**
Calcareous algae	
<i>Bacinella irregularis</i> Radoičić	***
<i>Lithocodium aggregatum</i> Elliott	****
<i>Neomeris?</i> sp.	*
<i>Terquemella</i> sp.	**
<i>Permocalculus?</i> sp.	**
<i>Polystrata alba</i> (Pfender)	**
Incertae sedis	
<i>Koskinobullina socialis</i> Cherchi and Schroeder	**
Others	
<i>Carpathocancer triangulatus</i> (Misik et al.)	**
“Berenicea”-type bryozoa	**
<i>Calcistella?</i> sp.	*
Echinoid remains	***
Gastropods (small forms)	**
Pharetronid sponges	**
Serpulids	***

* single specimen, ** rare, *** common, **** abundant

The ammonite biostratigraphic analysis carried out along the marls of the Forcall Formation by Moreno-Bedmar et al. (2009, 2010) permits us to ascribe this encrusted horizon to the upper part of the *Deshayesites forbesi* biozone (Lower Aptian) (Fig. 2). The occurring orbitolinids *Palorbitolina lenticularis* (Blumenbach) and *Praeorbitolina* gr. *cormyi-wienandsi* Schroeder confirm the Lower Aptian age of the deposits (Schroeder 1975).

Material

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). Besides the material from the Lower Aptian, detailed pictures from Elliott’s holotype and paratypes were kindly provided by the Natural History Museum in London (NHM). At the NHM, Elliott’s original thin sections are kept under the following numbers:

- holotype, original Reg. no. Ru 191 (pl. 1/5 of Elliott 1956) > NHM no. V41600
- paratype, original Reg. no. Ru 192 (pl. 1/2 of Elliott 1956) > NHM no. V41597
- paratype, original Reg. no. Ru 193 (pl. 1/4 of Elliott 1956) > NHM no. V41599.

The study was complemented by several figurations kindly provided by the following colleagues (the stratigraphy of the samples is given in brackets): Ioan Bucur and Emanoil Săsăran, Cluj-Napoca (Tithonian of Romania), Stefan Götz, Heidelberg (Hauterivian of the central Maestrat Basin, Spain), Bogusław Kolodziej, Kraków (Tithonian-Berriasian of Poland), Rajka Radoičić, Belgrade (Valanginian of Serbia).

Terminology

According to Golubić et al. (1981), the microorganisms capable of boring the substrate can be classified as follows: chasmoendoliths (inhabiting fissures in rocks open to the surface), euendoliths (actively boring into the substrate) and cryptoendoliths (settling in existing cavities). The general term for these three categories is endoliths, and epiliths for taxa that settle on the substrate surface. As stated by Wisshak (2006, p. 23) the boundaries are not always drawn precisely since epilithic organisms may have euendolithic stages. Algae that live inside other living algae, either actively boring into the tissue or just as cryptoendoliths inside existing internal structures, are called endophytes independently of the net impact of this association (i.e., beneficial or harming) (e.g., Correa 1994). For the observed boring structures, a maximum width of 0.1 mm is considered as the boundary between microborings and macroborings (e.g., Golubić et al. 1975; Glaub 1994; Wisshak 2006; Glaub et al. 2007). Empty boring structures are here treated ichnotaxonomically independently of whether it is known or unknown what produced them (e.g., Schmidt 1992; Glaub 1994; Bertling et al. 2006; Glaub et al. 2007). It should be noted that the ichnotaxonomic concept represents a pure morphological approach so that different ichnospecies

of the same ichnotaxon may be assigned to totally different biogenic groups as producers. These three-dimensional patterns are usually studied using resin borehole casts (cast embedding technique, Golubić 1983); thus, transferring two-dimensional characterizations obtained from thin-section studies to individual ichnogenus/-species is highly problematic, and usually impossible. When combining thin sections cut at different levels, at least a tentative assignment is possible.

When discussing the different taxonomic interpretations of *Lithocodium* found in the literature, the terms calcimicrobes and microbial carbonates (or microbialites) are used. For pragmatic reasons, these tiny filamentous-branching and tubiferous microorganisms (e.g., cyanobacteria) are here neutrally termed calcimicrobes (= microbes capable of triggering carbonate precipitation) (e.g., Riding 2000; Shen and Webb 2008) in a broader sense (e.g., Leinfelder et al. 1993) as the taxonomic status of these forms is still insufficiently known. One previous concept of fossil calcified cyanobacteria provided by Riding (1991a) included a variety of taxa of uncertain taxonomic status (microproblematica); some authors equate calcimicrobes with cyanobacteria, others also include problematic cyanophyta such as the porostromate algae (Shen and Qing 2008, “porostromate calcimicrobes”). The wide calcimicrobial approach used here permits the informal grouping of heterogeneous taxa of different suprageneric taxonomic positions and also of different morphologies. Microbial crust (or microbialite) has been defined in the literature as an organosedimentary deposit (here: microbial carbonates) of benthic microbial communities (Burne and Moore 1987; Riding 1991b, 2000; Schmid 1996; Browne et al. 2000).

Description of the crusts

A detailed description of the lithology and microfacies of the Lower Aptian *Lithocodium*-bearing coral rubble deposits is given by Bover-Arnal (2010) (see also Segonzac and Marin 1972). The following information essentially refers to the description and understanding of the *Lithocodium*-type micritic crusts; further details on the internal morphology are given in the paleontologic-systematic part of the paper.

The thin sections studied are composed mainly of three components: (I) coral rubble (~95% of the order Microsolenina) and more rarely rudistid fragments or oyster shells encrusted by (II) *Lithocodium aggregatum* Elliott (e.g., Fig. 3a) and surrounded by a (III) fine-grained matrix exhibiting terrigenous input. The matrix typically contains flat disk-shaped tests of *Palorbitolina lenticularis* (Blumenbach), which occasionally became encrusted (Fig. 3b). The thickness of the micritic *Lithocodium aggregatum*-crusts varies (Fig. 3a, c). Discordant layering indicates overturning

Fig. 3 Microfacies of *Lithocodium*-crusts from the Lower Aptian coral rubble deposits of the western Maestrat Basin. **a** Several (mostly comparable thin) crusts of *Lithocodium aggregatum* Elliott superimposed upon coral bioclasts infested by *Bacinella irregularis* Radoičić; note discordant growth of crust layers indicating erosion and overturning. **b** Thick crusts embedding recrystallized bioclast (bc) and the test of an orbitolinid foraminifera (dashed white line); note the various specimens of *Bacinella irregularis* Radoičić (arrows) boring inside the crusts. The orientation of the crust surfaces (white solid lines) in different directions (upwards/downwards) evidences multi-phase encrustations and overturning. **c** Rudistid shell with encrustation of *Lithocodium aggregatum* Elliott on both sides; note the comparably slight bioerosion of the shell and the reduced number of crust layers. **d** Encrustation succession of *Lithocodium aggregatum* Elliott and the arenaceous benthic foraminifer *Bdelloidina? urgonensis* Wernli and Schulte (B); note the absence of micritization of lower crust layers. **e** Several (presumably three) crust layers of *Lithocodium aggregatum* Elliott upon coral substrate infested by *Bacinella irregularis* Radoičić (B). The comparably thick crust results from oblique sectioning (compare a, c–d). **f** Detail from e showing micrite-filled filamental structures of *Lithocodium aggregatum* in the two lowermost crusts (white dashed lines) following the substrate and outer crust layer with sparite-filled filaments (cut transversely and obliquely). **g** Ichnogenus *Entobia* within coral bioclasts produced by boring sponges; note the channel to the surface (right side). **h** *Gastrochaenolites* ichnosp., macroboring produced by lithophagid bivalves affecting both substrate and crusts of *Lithocodium aggregatum* Elliott. Boring filled with stratified fine-grained sediment (geopetal filling); note the pyrite-stained boundary at the crust-boring boundary. Scale bars 1 mm, except f = 0.5 mm. Thin sections: a CA-3H, b SE-4V, c PO-1V, d CC-4V, e–f H0-16H, g CAL-2V, h SE-2H

(Fig. 3a). Accompanying crustose microbiota, switched between these crusts, include bryozoans, the red alga *Polysrata alba* (Pfender) and quite often the arenaceous foraminifera *Bdelloidina? urgonensis* Wernli and Schulte. None of these taxa occur as pioneer encrusters. Interestingly, within a crust succession of alternating layers of *Lithocodium aggregatum* Elliott and *Bdelloidina? urgonensis* Wernli and Schulte, siliciclastic particles only became incorporated into the foraminiferan test of the latter (Fig. 3d). Internally, the majority of the crusts seem to be completely structureless at first sight, however, several crust layers with micrite-filled internal structures are often dimly recognizable (Fig. 3e, f). Within the outermost crusts, which exhibit smooth surfaces, these structures are sparite-filled and well discernible. Thus, thick crusts are in fact composed of superimposed individual layers. Both *Lithocodium*-crusts and bioclasts display intense signs of bioerosion. Boring galleries made by endolithic sponges (*Entobia*) occur within the encrusted bioclasts (Fig. 3g). Borings of lithophagid bivalves (*Gastrochaenolites*) may affect both bioclasts and the surrounding micritic crusts, thus post-dating the crust-formation and indicating rapid lithification (Fig. 3h). Both ichnogenes *Entobia* and *Gastrochaenolites* were identified with approximately equal abundances in the thin sections studied. Moreover, the coral rubble shows intense bioerosion by chlorophyte algae, as described in the paleontological section of this work obvi-

ously infecting the coral skeletons even before the encrustation by *Lithocodium aggregatum* (Fig. 3e). It is assumed that the corals became encrusted after their death; in this

respect, corals in life position lacking *Lithocodium*-crusts or showing only minor encrustation were reported from other parts of the study area (Bover-Arnal 2010).

Interpretation of the crusts

The micrite enveloping the filaments of *Lithocodium* was assumed by Segonzac and Marin (1972) to be calcified mucilage produced during the lifetime of the organisms. Koch et al. (2002, p. 84) assumed that the crusts possess a primarily Mg-calcite mineralogy with crystals $< 1 \mu\text{m}$, which were slightly recrystallized to micrite ($< 4 \mu\text{m}$). In fact, in the smooth outer crust surface, the thin distal covering of the terminal filaments and the dense homogeneous microcrystalline texture where the filaments are completely embedded, correspond to calcified organic algal tissue (possibly in vivo micritization). A micritic thallus composition is also known in exceptional cases from some dasycladalean green algae such as the Late Jurassic *Salpingoporella? sellii* (Conrad and Varol 1990; De Castro 1997, p. 204, “pores...included in a...micritic, common collective sheath”). This common collective sheath is different from that of the group Rivulariaceae-Porostromata with individually sheathed filaments (e.g., Dragastan et al. 1996), indicating impregnation of the cyanobacterial sheaths with calcium carbonate (e.g., Riding 1977; Merz and Zankl 1993). SEM photographs of *Lithocodium* show “extreme equally granular, homogeneous micrite and minimicrite” (Neuweiler and Reitner 1992, p. 278, translated; see also SEM pictures in Banner et al. 1990). As inclusions, primary anhedral micrite is still recognizable, which, according to Neuweiler and Reitner (1992, p. 278) could correspond to biominerals produced within an organic medium. Following these authors, such observations are generally compared to calcified cyanobacteria where minimicrite is typically found (e.g., Flügel 2004, p. 75). Minimicrite may also be produced by multicyclic boring and concurrent filling of boreholes (Reid and Macintyre 2000). This possibility becomes important since the *Lithocodium*-crusts underwent intense macrobioerosion and microbioerosion with complete micritization of former boring galleries and algal filaments. In any case, an early or primary lithification is also evidenced by an initial boring of superimposed crusts into the lower one or the penetration by lithophagid bivalves (Fig. 3h).

The non-agglutination (actively to some extent) or trapping (passively) of the available silt-sized quartz grains by *Lithocodium* crusts is well documented, especially in the cases where the crusts occur in alternation with the encrusting foraminifer *Bdelloidina? urgonensis* Wernli and Schulte which incorporates the siliciclastics in its test wall (Fig. 3d). If *Lithocodium* should correspond to a microbial colony or microbial mat, trapping of the available foreign material deposited on the mat surface would be expected in our case (e.g., Riding 2000; Browne et al. 2000; Gall 2001; Noffke 2008), as also required in the definition of microbialite as an organosedimentary deposit (Burne and Moore

1987). Schmid and Leinfelder (1996, fig. 3) illustrated a “*Lithocodium*”-nodule together with the cryptobiotic foraminifer *Troglotella incrustans* Wernli and Fookes displaying incorporated (agglutinated) detrital quartz. The relationship of these Upper Jurassic forms and the Lower Cretaceous *Lithocodium aggregatum* Elliott are discussed later in the paper.

The dense dark micritic appearance and the smooth crust surface are also non-typical features of microbialites. Microbial crusts should, furthermore, show characteristic microfabrics (laminated, clotted, peloidal) (e.g., Keupp et al. 1993; Schmid 1996; Riding 1991b, 2000) and various microencruster intimately involved in crust formation (e.g., Leinfelder et al. 1993; Schmid 1996; Dupraz and Strasser 1999). Moreover, none of the authors who discuss the possible cyanobacterial nature of *Lithocodium aggregatum* take into further consideration the fact that filament diameters of cyanobacterians cover a range several orders smaller than those exhibited by the *Lithocodium aggregatum* (e.g., Le Campion-Alsumard 1979; Chafetz and Buczynski 1992; Stal 2007; Foster et al. 2009). As will be shown in the following chapter, the filamentous thallus architecture can convincingly be included in chlorophyte algae structure.

Systematic paleontology

In this chapter, the holotype figurations of both *Lithocodium aggregatum* and *Bacinella irregularis* supplemented by the paratype material and the original descriptions are critically commented on, bearing in mind our observations of the Lower Aptian specimens from the western Maestrat Basin that we studied. Detailed descriptions with emendations of both *Lithocodium aggregatum* Elliott and *Bacinella irregularis* Radoičić are then presented. Finally, other euendolithic/endophytic taxa, calcimicrobes, and ichnotaxa characteristically associated with the Lower Cretaceous *Lithocodium* crusts are also described.

Comments on the type-material of *Lithocodium aggregatum* Elliott

As already remarked, Elliott’s material is deposited at NHM. Details from the holotype and paratype “specimens” are illustrated in Fig. 4. The holotype (Elliott 1956, pl. 1/5) is represented by both large “nodular” masses and by thin crusts growing upon the skeleton(s) of the stromatoporoid *Burgundia* cf. *ramosa* Pfender (Fig. 4b, f). Not mentioned in the original description, Elliott (1963, p. 294) some years later remarked, that “*Lithocodium* is itself often intimately intergrown with the lamellar stromatoporoid *Burgundia*”. The apparent occurrence of two morphotypes accounted for the original genus characterization as “encrusting or

nodose” (Elliott 1956, p. 331). It is noteworthy that such a co-occurrence of two different morphotypes within the same sample is curious if not remarkable with respect to paleoenvironmental interpretation (see Rameil et al. 2010). Elliott (1956 p. 328), however, stressed that *Lithocodium* often “show(s) several superimposed thalles”, a character that obviously has been responsible for the species name: *aggregatum*. Our research has shown that apparently, the thick nodular thallus corresponds in fact to several superimposed thalli and, moreover, that greater individual crust thicknesses can result from oblique sectioning (Fig. 4b). Elliott’s “inner layer” of filaments was compared with the medullar zone of codiacean algae, which should be composed of a “confused inner layer” with “very irregularly disposed coarse filaments without definite orientation”. However, within the thin-crustose part of the holotype (Elliott 1956, pl. 1/5, lower right) this “inner layer” shows a very regular arrangement parallel to the crust and substrate surfaces (Fig. 4f). Only in the thicker “nodular” parts, irregular arrangements, often obliquely organized “coarse filaments” prevail and partly correspond to empty boring galleries (e.g., Fig. 4b, d): an ichnofabric produced by (micro-)bioeroding taxa. The overall presence of (micro-)borings within the *Lithocodium* tissue as a characteristic feature is well recorded in the material from the Lower Aptian of Spain, but is also present in the type-material of Elliott, the Lower Cretaceous of the Middle East (Banner et al. 1990) and the Hauterivian of Spain (Götz et al. 2005) though not mentioned in these works. Another type of microboring is represented by thin, slightly undulating channels with irregular distributed ovoid swellings. The supposedly irregular disposition of the inner (medullar) zone is furthermore given in oblique crust sections with the branching prostrate filaments as described in the present paper. This is clearly visible in the paratype shown by Elliott (1956, pl. 2/4) also with a boring obliquely transecting the algal crust (Fig. 4g).

Both the oblique-sectioned substrate-parallel branching filaments and the obliquely arranged borings were obviously intermingled by Elliott (1956) as filaments of a “medulla”. When reviewing the literature, it is evident that not only Elliott (1956) but most subsequent authors had problems with the assignment of the “medulla”. In the work of Banner et al. (1990) for example, “tubular filaments” parallel to the crust surface from which branching “cortical filaments” arise and also cellular structures occurring in borings of the basal substrate, were regarded as “medullary filaments” (Banner et al. 1990, p. 30, “medullary filaments....fill these borings”). In addition, the irregular “bacinellid” cellular structures that may trap bioclasts were assigned to the medulla (Banner et al. 1990, p. 30, “skeletal fragments may be...encapsuled during the growth of the medulla”). A trapping of foreign material within the medul-

lar zone of a “codiacean” alga is more than strange, and has not been observed in any other species in this group (e.g., Bassoulet et al. 1983).

In any case, neither more details in the description (e.g., dimensional data, etc.), nor detailed views (referring to the description), were provided by Elliott. Thus a definite and unequivocal interpretation of what Elliott understood as the taxon *Lithocodium* is not possible. Neither did Elliott describe the crusts as being composed of different taxa. Obviously, assuming that, besides the micritic crust/mass, all observable internal microstructures belong to *Lithocodium*.

In conclusion, the holotype cannot serve as a type, since the correct identification of the details of the internal structures of *Lithocodium aggregatum* is not possible. Also, the short original description, together with the low magnification of the three thin-section photographs, were difficult to interpret for subsequent authors, as indicated by the decades of controversy in the literature. Therefore, the designation of the crust-forming filamentous algae as *Lithocodium aggregatum* Elliott and the redescription of the genus *Lithocodium* Elliott is the way we have decided to choose not only to solve at least to some extent the existing taxonomic-ichnotaxonomic mixture but also to reinforce the validity of the genus *Lithocodium* Elliott. In our case, article 9.7 of the International Code of Botanical Nomenclature (ICBN) can be applied stating that “when the holotype, lectotype, or previously designated neotype, or all original material associated with a validly published name, is demonstrably ambiguous and cannot be critically identified for purposes of the precise application of the name of a taxon”....an epitype can be established as “a specimen or illustration selected to serve as an interpretive type”. When an epitype is designated, the holotype, lectotype, or neotype that the epitype supports must be explicitly cited” (Vienna Code) (McNeill et al. 2006; Hyde and Zhang 2008 for further discussion). Therefore, in order to permit a precise application of the name *Lithocodium aggregatum*, we here designate an epitype according to article 9.7 ICBN selected from Elliott’s holotype (1956, pl. 1/5, original number Ru.191) stored at NHM under the number V41600 and illustrated in the present paper in Fig. 4f. In addition, a part of the holotype showing a single-layered crust (or thallus) cut in a more or less perpendicular plane with respect to the substrate has been chosen as the epitype since Elliott (1956) already recognized that the nodular masses are composed of superimposed thalli which are clearly visible in one paratype of Elliott (1956, pl. 1/2). Besides the cross-walls in the “medullar” filaments sensu Elliott (Segonzac and Marin 1972; Banner et al. 1990) already mentioned, the “cortical filament(s)” are also septate (Fig. 4a, c). Due to the constrictions, the “medullary filaments” sometimes appear discontinuous in sections that do not pass directly along the

median plane (Figs. 3c, 4f). This feature is incompatible with a codiacean/udoteacean non-septate siphonous structure (see Bassoullet et al. 1983; Mu 1991), hence, the septate filaments are described in terms of a basal prostrate and an erect filament system. In addition, the material from the western Maestrat Basin provides morphological details that were not evidenced in the three illustrations of the original work, namely a euendolithic unicellular sporophytic stage, a chasmoendolithic basal part in the cases of sculptured or fissioned substrate surfaces, and an irregular vesicular final stage. The morphological details are furthermore supplemented by the description of euendolithic/cryptoendolithic taxa within *Lithocodium*, several ichnotaxa and associated calcimicrobes.

Emended description of *Lithocodium aggregatum* Elliott

Remarks The taxonomy used refers to the online database (AlgaeBase) from Guiry and Guiry (2009). The evidently cellular, septate (= with regular crosswalls) thallus structure of *Lithocodium aggregatum* Elliott excludes its inclusion in siphonous green algae, e.g., Udoteaceae (= former Codiaceae) (e.g., Bassoullet et al. 1983; Mu 1991) as stated previously. Banner et al. (1990) introduced the Lithocodoidea as a subfamily within the Codiaceae and curiously redescribed *Lithocodium* as possessing irregularly septate subdermal filaments. Within this subfamily, the two genera *Lithocodium* Elliott (assumed to be monospecific) and *Radoicinellopsis* Banner, Finch and Simmons (monospecific, based on *Bacinella sterna*) were included. It is, however, doubtful that *Radoicinellopsis sterna* belongs to siphonous green algae (e.g., Masse 1979; Leinfelder 1985). Therefore, the validity of the Lithocodoidea is challenged.

The suprageneric position (family) of *Lithocodium aggregatum* cannot be fixed precisely. Its belonging to the class Ulvophyceae is justified by the supposed occurrence of a “*Codiolum*” stage in the life cycle of *Lithocodium* (e.g., Pröschold and Leliaert 2007); taxa that can be compared with *Lithocodium* such as *Eugomontia* Kornmann or *Gomontia* Bornet and Flahault or those co-occurring such as *Phaeophila*-type or *Acrochaete*-type are included in the order Ulotrichales Wille (see Guiry and Guiry 2009). To the best of our knowledge, *Lithocodium* cannot be assigned to any extant taxa.

Division: Chlorophyta

Class: Ulvophyceae

Order: Ulotrichales?

Family: ?

Genus: *Lithocodium* Elliott 1956

Original diagnosis Encrusting or nodose Codiaceae with a subdermal structure similar to that of the segmented *Boueiina* (Elliott 1956, p. 331)

Fig. 4 Detailed views of *Lithocodium aggregatum* Elliott, holotype: d–f, h (Elliott 1956, pl. 1/5), paratype: a, c (Elliott 1956, pl. 1/2), paratype: b, g (Elliott 1956, pl. 1/4). a, c Detailed views showing the upright branching septate filaments rising from substrate-parallel prostrate septate filaments; crosswalls: of erect filaments in orange, of the prostrate filaments in red; note finger- to palisade-like appearance of filaments. b Oblique section of *Lithocodium aggregatum* Elliott fixed to the stromatoporeid *Burgundia* cf. *ramosa* Pfender (S); note the various borings (B, and white arrows; d–e: details in Fig. 17e–f). d Branching boring galleries within crust of *Lithocodium aggregatum*. e Oblique section of *Lithocodium aggregatum*; inside the crust parts of the skeleton of *Burgundia* cf. *ramosa* Pfender (arrows) are discernible. f Comparable flat crusts infested by *Lithocodium aggregatum* switched between encrusting stromatoporeid skeletons of *Burgundia* cf. *ramosa* Pfender; specimen showing the prostrate crust-parallel swollen septate filament from which branching filaments rise stretching towards the crust edge; this detail from the holotype is taken as interpretative epitope (article 9.7 ICBN). g Oblique section, detail from b. h Oblique section of *Lithocodium aggregatum* cutting the thick crust-parallel swollen filaments. Scale bars 1 mm for b, d, f, h; 0.5 mm for g; 0.3 mm for a, c. Thin sections: a, c V 41597, d–f, h V 41600, b, g V 41599. Copyright for a–h Natural History Museum, London

Emended diagnosis Encrusting epilithic alga with a possible heteromorphic life including a multicellular gametophyte and a unicellular sporophyte (*Gomontia* stage). Euendolithic sporophyte (*Gomontia* stage) bag-shaped with several branching or non-branching excrescences/appendages at its surface; special exit tubes for the release of the zoospores may be present. In cases of fissured or sculptured substrate surfaces, a basal vesiculiferous chasmoendolithic stage can be developed. Gametophyte thallus with heterotrichous organization differentiated into a ramified system of prostrate creeping septate filaments from which an erect system of septate branching filaments arise. Prostrate creeping filaments thick and with constrictions at irregular distances. Depending on the crust thickness, the erect filament system may be strongly reduced or well developed with successive branching in several layers; towards the smooth crust surface final filaments are covered with a thin sheet. The terminal stage may be constructed by large irregular cells directly arising from the prostrate filaments without preserved erect branching filaments; only their terminal part may be preserved as a zagged micritic rim. Thallus of dark microcrystalline calcite forms a common sheath where the filaments are embedded.

Lithocodium aggregatum Elliott 1956 (Figs. 3a, c, b–e pars, f, h pars, 4a–h, 5a–e, g, i, 6a–g, 7a–i, 8a–d, 14a pars, 15a–f pars, 17a–j, pars)

Synonymy The complex assemblage of euendolithic and endophytic chlorophytes accounts for the fact that in most cases, illustrations of *Lithocodium aggregatum* in the literature often also include other taxa that we have not tried to decipher in detail. In other cases, the low magnification does not allow a definitive identification. Furthermore,

Fig. 5 Euendolithic unicellular sporophytic *Gomontia* stage referred to *Lithocodium aggregatum* Elliott from the Lower Aptian of the western Maestrat Basin (**a–b, d–e, g**), the Upper Jurassic (Late Tithonian) of the Northern Calcareous Alps of Austria (**c**), Valanginian of Serbia (**i**) in comparison to modern Counterparts (**f, h**). **a** Two solitary large variable sack-like sporophytes with rhizoid-like branching appendages; note the micritic lining between the substrate and the sporophyte. The specimen on the left shows two large tubes which in turn exhibit finer appendages. **b** Two differently shaped sporophytes spreading with their upper appendages into a thin crust of *Lithocodium aggregatum* Elliott. **c** Ovoid sporophyte with two appendages. **d** Two specimens boring into a rudistid shell; right specimen with long tubes (possibly exit tubes) cutting across the crust and grading into large sparite-filled cells (compare Fig. 8). **e, g** Oblique sections of boring sporophytes of irregular star shapes. **f** Cultivated sporophytes of *Gomontia polyrhiza* (Lagerheim) within a bivalve shell; note the large morphological variability (thickness, height, appendages), combined from Kornmann (1959, figs. 7 and 9). **h** Same as **e** and **g**, cultivated sporophytes within bivalve shells (redrawn from Kornmann 1959, fig. 8e). **i** Several sporophyte stages within rudistid shell, Valanginian of Serbia (from Radoičić 2005, pl. 6/8). Scale bars 0.2 mm for all figurations. Thin sections: **a** CA-2H, **b** H0-6V, **c** Die-170, **d** P0-1V, **e** CAL-6V, **g** H0-4V

several (though not all) Late Jurassic references cannot be included as they are morphologically different; the same holds for all the Late Triassic reports that definitely cannot be included in the presented emendation of *Lithocodium aggregatum* Elliott. Therefore, only a small subjective choice of references is given including those discussed in the present paper, some poorly known or those from more recent publications.

*1956 *Lithocodium aggregatum* nov. gen., nov. sp. – Elliott, pl. 1/2, pl. 1/4-5
 1972 *Lithocodium aggregatum* Elliott – Segonzac and Marin, pl. 1/1-8
 1979 *Lithocodium aggregatum* Elliott – Luperto Sinni, pl. 41/1-2, 4-6
 1979 *Lithocodium morikawai* Endo – Mišák, pl. 2/1
 1982 *Dehornella* sp. – Jansa et al., pl. 6/1-3

Fig. 6 Chasmoendolithic (a, c–g) and pseudochasmoendolithic (b) filling stage of *Lithocodium* Elliott from the Lower Aptian of the western Maestrat Basin (a–e) and the Upper Jurassic of Poland (f) and Romania (g). **a** Chasmoendolithic fillings (arrow) within coral bioclasts. **b** Pseudochasmoendolithic filling structures within *Gastrochaenolites* ichnosp. The macroboring became encrusted by *Lithocodium aggregatum* Elliott at its base (arrows), then developed the irregular-vesicular final stage with cells filled with microsparite; later the clast with its completely filled macroboring became overlaid by various *Lithocodium* layers (with micritized filamental structures). **c**, **d** Chasmoendolithic fillings in interseptal space of corals; simple cross-partitions in voids of reduced width (e.g., **d** left) and house-of-cards

structures in broader voids (**c**, **d** right). **e** Several crust layers of *Lithocodium aggregatum* Elliott; note the development of prostrate and erect filament systems within the void. **f** Chasmoendolithic filling stages of *Lithocodium* sp. in sculptured coral surface; note the transition into large irregular basal cavities (from Kolodziej 1997; Tithonian–Lower Berriasian Stramberk-type limestone of the Polish Carpathians). **g** Chasmoendolithic fillings of *Lithocodium* sp. in interseptal spaces of a coral; note the thick micritic linings, Tithonian Sandulesti Limestone Formation, Trascau Mountains of Romania, see Săsăran et al. (2001). Scale bars 0.5 mm for a, c, d, f; 1.0 mm for b, e, g. Thin sections: a PO-1V, b CUB-4, c, d DE-4H, e H0-16V, f partly from Kolodziej (1997, fig. 2 g), g leg. Ioan Bucur

- 1985 *Lithocodium-Kruste, Bacinella irregularis* – Höfling, pl. 3/5–7
- 1987 *Lithocodium aggregatum* – Reitner, pl. 21/2, pl. 49/16
- 1990 *Lithocodium aggregatum* Elliott (pars) – Banner et al., pl. 1/1–4, pl. 2/1–4, pl. 3/1, pl. 4/1
- 1994 *Lithocodium aggregatum* Elliott – Grötsch et al., pl. 3/8
- 2004 *Lithocodium aggregatum* – Bucur et al., pl. 2/24
- 2005 *Lithocodium aggregatum* Elliott, microbialite aff. KL 18, Lithocodoidea – Radoičić, pl. 5/1–8, pl. 6/1–4, 8, pl. 7/1–2 (pars), pl. 8/3–6, 9
- 2005 *Lithocodium* crusts – Götz et al., figs. 6a–d
- 2006 *Lithocodium aggregatum* – Cherchi and Schroeder, figs. 1–3 (pars)
- 2008 *Lithocodium aggregatum* Elliott – Conrad and Clavel, figs. 5–7

Description The description takes into account the assumed heteromorphic life cycle and the optional occurrences of morphologically discrete basal and final stages. For clarity, remarks are given after each part of the description, which is divided up as follows:

- euendolithic *Gomontia* stage
- chasmoendolithic basal stage
- epilithic filamentous stage
- vesicular terminal stage.

Euendolithic *Gomontia* stage (Fig. 5a–e, g, i)

The euendolithic sporophyte stage (sporangia) is represented by differently shaped (e.g., ovoid, bag-, sack-like) swollen cells bored into the calcareous substrates, for instance rudistid shells (Fig. 5a–d, i). Morphologically variable, it includes forms that are wider than they are long and *vice versa*; forms widening upwards or becoming narrower. The base may be rounded, almost spherical or tapering. Occasionally, at the base or the transition to the appendages, micrite fills the space between the algal borings and the surrounding substrate; in other cases the bags fit closely inside the boring. The top is represented by branched or unbranched appendages spreading into the micritic crusts; some of them are distinctly larger (? exit tubes) touching the crust surface but not breaking through it (Fig. 5b, d). In oblique and transverse sections, irregular star-like micritic borings are discernible (Fig. 5e, g).

Remarks The Lower Cretaceous findings are directly comparable to the sporophyte stages of modern ulotrichalean algae (Fig. 5f, h), usually termed *Codiolum* stage (or *Gomontia* stage, e.g., Kornmann 1959; Nielsen 1987) referring to the species *Gomontia polyrhiza* (Lagerheim) (former *Codiolum polyrhizum*) and previously described as a separate taxon. A *Gomontia* stage may be present in spe-

Fig. 7 Epilithic stage of *Lithocodium aggregatum* Elliott from the Lower Aptian (a, b, d–i) and Hauterivian (c) of the Maestrat Basin. **a** Several superimposed crusts exhibiting discordant layering indicating movement/erosion; note the strongly reduced erect-branching system in the uppermost crusts (upper left). **b** Several superimposed crusts with boring in the uppermost layers (white arrows), the entrance point of the boring taxon (most probably a chlorophyte alga) is marked with (E). In the lower part, a sack-shaped euendolithic stage of *Lithocodium* is visible (contour marked by the solid white line) from which creeping prostrate filaments stretch in various directions. **c, d** Oblique sections showing the low-angle branching prostrate system (c from Götz et al. 2005). **e** Detailed view of the erect filament system with several layers of branchings easily recognizable by the dark pyritic fillings. **f** Oblique section, cutting two superimposed crusts on a coral substrate. **g** Detail from the multi-layered crusts shown in a (a different part of the thin section) almost perpendicular to the substrate showing both prostrate and erect filament systems with transverse partitions (arrows). **h** Oblique section of several superimposed crusts showing low-angle branching prostrate system (white arrows). **i** Several superimposed crusts (dashed white lines), in between arenaceous foraminifer *Bdelloidina? urgonensis* Wernli and Schulte (B) and boring gallery (Bo); S = substrate. Scale bars 0.5 mm for a, b, e, g, h; 1.0 mm for c, d, f, i. Thin sections: a CA-3H, b H0-16V, c H0-3VB, d SE-2V, e CUB-1, f DE-4V, g CA-3H, h CA-3H, i H0-3V

cies of several euendolithic genera such as *Collinsiella* Setchell and Gardner, *Eugomontia* Kornmann, *Gomontia* Bornet, and Flahault and *Monostroma* Thuret (e.g., Setchell and Gardner 1903, 1920; O’Kelly et al. 2004), but also in non-euendolithic taxa such as *Urospora* Areschuog or *Acrosiphonia* Agardh (Kornmann 1959, 1961, 1962; Sussmann and DeWreede 2001) and all of the order Ulotrichales (e.g., Guiry and Guiry 2009). The *Gomontia* stages of these genera are difficult to distinguish from each other in the field, which has created a lot of confusion in the past as well as taxonomic problems (e.g., Fan 1959; Wilkinson and Burrows 1972; Golubić et al. 1975; Pantazidou et al. 2006; Round 1981, p. 241). In some taxa (e.g., *Acrosiphonia grandis*), the *Gomontia* stage grows directly into a filamentous alga without formation of zoospores (Kornmann 1970). The identified Lower Cretaceous specimens are distinctly larger than their modern counterparts (e.g., Setchell and Gardner 1920, up to 150 µm in width and up to 240 µm in length). The larger elongated appendages might represent so-called exit tubes from which the zoospores are released (e.g., Kornmann 1959).

In most cases, the euendolithic sporophyte stage accompanies a non-boring epilithic gametophyte stage. In *Eugomontia*, however, both stages are euendolithic (Kornmann 1960). A further unique characteristic is that the *Gomontia* stage of *Eugomontia* is pluricellular; in all others it is unicellular. Therefore, the observed *Gomontia* stages could belong to the euendolithic *Bacinella irregularis* Radoičić. In this case, the observed large sporophyte dimensions would fit the cell diameters of the euendolithic *Bacinella* which are distinctly larger than, as for example the modern *Eugomontia* (Kornmann 1960, thickness about 6 µm).

Fig. 8 Irregular vesicular final stage of *Lithocodium aggregatum* Elliott from the Lower Aptian of the western Maestrat Basin. **a** Oblique section of two superimposed crusts; external upper crust with irregular vesicular final stage. **b** Detail from **a** showing development of large sparite- to microsparite-filled irregular vesicular pseudocells arising from tubular swollen prostrate filaments along with the successive reduction of the erect filament system. **c** Oblique section showing

several superimposed series of irregular final cells evolving from prostrate filaments (1–4). **d** Oblique crust section showing development of several irregular attached terminal pseudocell-systems rising from swollen tubular prostrate filaments. Arrows also indicate direction of growth/creeping. Scale bars 1.0 mm for **a–d**. Thin sections: **a–b** CAL-6V, **c** H0-8V, **d** H0-7V

Based on the branching appendages revealing conspicuous similarities to the erect filaments of *Lithocodium aggregatum*, the sporophyte stages are here tentatively ascribed to the genus *Lithocodium*. The illustrated *Gomontia* stages are from the Tithonian of Austria (Fig. 5c), the Valanginian of Serbia (Fig. 5i), and the Lower Aptian of the western Maestrat Basin of Spain (Fig. 5a, b, d, e, g).

The ichnotaxon *Cavernula* Radtke, which refers to the sporophyte stage of these euendolithic chlorophytes (Radtke 1991; Schmidt 1992; Glaub 1994), has been known since the Carboniferous (Wisshak et al. 2008, 20–35 µm in width, 30–70 µm in length). The complex boring pattern of *Eugomontia* Kornmann is related to the ichnotaxon *Rhopalia* Radtke (Radtke 1991; Golubić and Radtke 2008). In our case, the sack-like sporophytes are clearly delineated within the boring, sometimes with observable walls towards or inside the appendages, thus, excluding an ichnotaxonomical approach.

Chasmoendolithic basal stage (Fig. 6a–d, f–g)

In our material, these cellular structures completely fill existing cavities (e.g., *Gastrochaeonolites* ichnogenus, Fig. 6b) or the interseptal spaces of the corals (Fig. 6c, d, f, g); whether they also fill borings/etchings possibly produced by *Lithocodium* itself is unknown. It is noteworthy

that these structures are absent on smooth unsculptured substrate surfaces (e.g., rudistid shells, some stromatoporoids, Figs. 3c, 4f). This could be an indication of a no-boring ability. In the cases where the void is narrower, only horizontal to oblique transverse walls occur (Fig. 6d, left) and the substrate surface shows a thin micritic lining. In broader voids, a house-of-cards-like system composed of complete (from one side to the other) and incomplete (forming smaller cells within the void) partitions evolves (Fig. 6c, d, right). This character is a clear expression of the mechanical properties of these structures depending on the width of the spaces they occupy. In internally sculptured narrow spaces (e.g., interseptal spaces of microsolenids), the initial part of *Lithocodium* directly adjusts to the available space with a comparable thick micritic lining towards the sidewalls (Fig. 6g). In that manner, a comparably large penetration depth can be achieved. An exceptional case is what we here refer to as the pseudo-chasmoendolithic stage occurring in a boring of a lithophagid bivalve (Fig. 6b). Here, *Lithocodium* attached at one side of the boring at a time when this was horizontally oriented (geopetal attaching). The remaining available space was then completely filled with large vesicles of the aberrant final stage (see below). The bioclasts with borings completely filled by *Lithocodium* were totally encrusted afterwards by different *Lithocodium* crusts, and its older parts became totally

micritized. Within the whole encrusted crust-bioclasts complex, the filled borings appear as representing the chasmoendolithic basal stage described above.

Remarks This stage has already been commented on several times in the literature, for example:

- Banner et al. (1990, p. 30, pl. 5/2): “.....”*medullary filaments of encrusting Lithocodium may fill these borings so closely that the impressions may be gained, erroneously, that the encrusting alga had, itself, created the borings*”.
- Neuweiler and Reitner (1992, pl. 3/2): “*partly calcified single filament of Lithocodium. Cells arranged in rows as smallest structural element of Lithocodium*” (translated from German).
- Kolodziej (1997): “*In the places where it (remark: Lithocodium) has grown into the interseptal space of the coral skeleton it sometimes shows “bacinellimorph” structures*”.
- Daoud et al. (2004, pl. 2/4): “*Rudist skeleton perforated by Troglotella incrustans Wernli and Fookes hosted by Bacinella-Lithocodium*”.
- Matyszkiewicz and Slomka (2004, fig. 3/b, c): “*Bacinella partly fills voids between the septa in a scleractinian coral*”.
- Schlagintweit (2008, fig. 5): “*Infilling structures and microborings with Bacinella-Lithocodium*”.

These examples show that these cellular structures occurring in skeletal voids were ascribed to both *Lithocodium* and *Bacinella*. Segonzac and Marin (1972) and some other authors (e.g., Luperto Sinni 1979) regarded *Bacinella* as corresponding to the basal part of *Lithocodium*, here interpreted as a cellular filling stage of *Lithocodium aggregatum*. The prostrate filaments probably could not spread over sculptured surfaces, thus, first creating a plane surface for attachment by filling the substrate voids with a chasmoendolithic cellular meshwork. Only in cases where the voids are wide enough can the heterotrichale filaments be observed inside (Fig. 6e). The preservation of these vesicular basal structures can be considered as an indication for the rather rapid lithification of the crusts and comparable good mechanical properties; otherwise they might have been destroyed by compactional processes. It is noteworthy that in contrast to the irregular cellular final stage (see paragraph later in the text), no calcimicrobes were observed within the vesicles of the basal stage.

Epilithic filamentous stage (Figs. 3a–f, 4a, c, f, g, 7a–i, 14a pars)

The epilithic crustose thalli are seldom single-layered, for example in cases where these alternate with other crustose organisms such as encrusting foraminifera (Fig. 3d) or lam-

Table 3 Dimensional data of *Lithocodium aggregatum* Elliott from the Lower Aptian of the western Maestrat Basin (thicknesses in mm)

No.	Thickness of crust	Thickness prostrate system	Thickness erect system	<i>n</i>	Thin section
1.	0.08	0.032	0.036	1	PO-4V
2.	0.18	0.032	0.120	2	
3.	0.36	0.145	0.170	3	
4.	0.40	0.145	0.20	3	
5.	0.07	0.03	0.03	1	
6.	0.26	0.052	0.20	3	
7.	0.32	0.1	0.20	2	H0-6V
8.	0.25	0.05	0.19	3	
9.	0.16	0.066	0.07	1	PO-4V
10.	0.35	0.14	0.18	2	CAL-7H
11.	0.22	0.04	0.14	3	
12.	0.30	0.065	0.20	4	H0-16V
13.	0.36	0.12	0.20	3	
14.	0.36	0.09	0.25	5	CAL-3V
15.	0.45	0.08	0.26	3	DE-3H
16.	0.65	0.12	0.36	5	CUB-1
17.	0.26	0.09	0.16	3	SE-5H
18.	0.28	0.03	0.26	4	CAL-8V
19.	0.37	0.09	0.26	3	DE-5H
20.	0.42	0.14	0.22	3	CC-4V
Min.	0.08	0.03	0.03	1	
Max.	0.65	0.145	0.36	5	

n = max. number of filament layers/orders in the erect system

inar stromatoporoids (Fig. 4f). Mostly, there are several superimposed crust layers forming thick algal masses that can totally surround the bioclastic substrate (Fig. 3b, e). The image section shown in Fig. 7a, for instance, is a detail from a succession of up to 40 superimposed (mostly thin) crust layers. The thickness of individual crust layers is mostly between 0.2 and 0.4 mm (see Table 3). Segonzac and Marin (1972, p. 332) indicate thicknesses of 1 to 3 cm for the superimposed crusts, and a maximum of 0.45 mm for a single layer; Elliott (1956, p. 331) indicates “*commonly 0.25 mm*”. In cases of thick crust masses, the sparite-filled filaments can only be observed in the outermost layers (Fig. 3e); the older layers are completely micritized. The filamentous system is only recognizable in a slightly brighter color (dark grey instead of black) (Figs. 3f, 6a, 11e).

The thalli are differentiated into a prostrate basal part (or system) and an erect branching part (or system). The prostrate system is not directly attached to the basal substrate (e.g., coral skeleton, rudistid shell, or underlying *Lithocodium* crust) but separated from it by a thin micritic sheet (e.g., Fig. 7g). Transverse cell walls (septae) with thickness

of $\sim 8\text{--}15\text{ }\mu\text{m}$ occur at irregular distances forming uniseriate cells. Sometimes the filaments are constricted at the plane of septation giving rise to barrel-shaped uniseriate cells. These cells may also show a slight increase in diameter towards the growth direction, giving them the shape of a club. Especially comparable, thin prostrate filaments appear more or less without constrictions and without transverse septae (?lost as a result of recrystallization). This type was compared by Segonzac and Marin (1972, p. 335) with a garden hose (“tuyau d’arrosage”). In oblique sections, it can be seen that the prostrate filaments are branchings, often at acute angles (Figs. 4g, 7d, h) but also at right angles (Fig. 8a). With successive branching in the growth direction, the prostrate system radiates and spreads over the substrate. In sections transverse to the filament creeping direction, the individual prostrate filaments appear as irregular-ovoid spar-filled spaces separated from each other by a micritic tissue (Fig. 3e).

From the prostrate system, erect branching filaments rise upwards with several filaments originating from each cell. The erect filaments often start from short tapering protuberances of the prostrate filaments, whereas the lower part is more or less smooth. The shape of the filaments and their branching pattern is very variable, from swollen to cylindrical, parallel (pallade-like) or radiating. In oblique sections, the branching prostrate filaments can be misinterpreted as representing the first-order thick filaments of the erect system (Figs. 4g, 7d, f, h). However, even the first-order erect filaments are distinctly thinner than the prostrate filaments. They may bifurcate, trifurcate or quadrifurcate (Fig. 7a, e, g). Altogether, a maximum of five orders of filaments were observed (Fig. 7e). With successive branching, the diameters diminish slightly; the greatest difference in thickness is between the first- and second-order filaments. In very thin crusts, the erect system may become greatly reduced; in extreme cases to only one layer of erect filaments (Figs. 3a, 7a). The outermost filaments are closed to the exterior, terminating in a thin sheet (= terminal sheet of Banner et al. 1990, p. 28) (e.g., Fig. 3e). Septation is irregular and is often not so easily recognizable as in the prostrate filaments (possibly due to recrystallization processes) (e.g., Figs. 4a, c, 7g).

Remarks With the new interpretation, the couplet of medullary and cortical filaments is replaced by prostrate and erect filaments. The branching of the prostrate filaments (formerly medullary or subdermal filaments) was already recognized by Banner et al. (1990, p. 28, “they ramify diversely...”). In some recent works, the septate filaments have occasionally been interpreted as “*Bacinella*” threads within *Lithocodium*. The fact that not only the crust-parallel filaments (= medullary filaments of Elliott 1956; Banner et al. 1990; Segonzac and Marin 1972) but also the erect filaments are septate was not recognized by

Segonzac and Marin (1972), but in discussing affinities to ulotrichalean algae, and especially mentioning the genus *Gomontia*, they came very close to our interpretation.

The typical micritization of the older crusts was also noted by Elliott (1956, p. 331, “recrystallization has affected more inner layers than outer ones”) or later by Koch et al. (2002, p. 84, ... “the oldest parts of the organism became impregnated by micritic Mg-calcite”). The dimly recognizable microstructures of the micritized inner crusts were obviously overlooked by Banner et al. (1990, p. 24) or perhaps they were not recognizable in their material, as they stated that only “the terminal zone of growth developed cortical structures”.

Vesicular terminal stage (Fig. 8a–d)

Large, usually completely sparite-filled cells (vesicular textures of Maurin et al. 1985) occur in the outermost crust zones, evolving directly from the irregularly swollen cylindrical prostrate filaments (e.g., Fig. 8b). The giant cells can attain a length of up to 1.7 mm and a width or height of ~ 0.8 mm. These are different from the basal cellular fabrics as they possess larger sizes, lack the intermingling with micritic patches, and sometimes exhibit a rounded bent side facing upwards with short parallel protruding partitions/filaments. This last characteristic seems to correspond to the endings of the terminal filaments of a nearly completely reduced erect system. The continuous reduction of the erect system along with the irregular broadening of the prostrate filaments can be seen in the specimen shown in Fig. 8a, b. Furthermore, oblique sections show that each of the radiating prostrate filaments undergoes this evolution of giant terminal cells, forming a large irregular meshwork (Fig. 8c, d). In some cases, erect bushy or tubiferous filaments of assumed calcimicrobial origin are observable inside some vesicles (see Fig. 16). The same bushy calcimicrobes were occasionally also observed within thicker prostrate filaments of the outer crust zone (Fig. 16g).

Remarks As already remarked previously, we do not know of a modern algal taxon that shows the morphological features of *Lithocodium aggregatum* Elliott. Particularly, this is the case for the irregular giant terminal vesicular cell meshwork as the terminal development of the prostrate system along with the reduction of the erect system. It can be assumed that this vesicular stage was previously often recognized as *Bacinella irregularis* Radoičić. It is unknown whether the observed calcimicrobes inside these cells functioned as symbionts (cyanosymbionts) during the lifetime of *Lithocodium* or occupied them post-mortem. As this terminal stage was always observed at the outermost crust, a special morphological adaptation in order to host these probably phototrophic calcimicrobes can be hypothesized.

Comparisons Discussing the validity of other *Lithocodium* species, *L. regularis* Johnson (invalidly described as an alga, see Johnson 1969), *L. morikawai* Endo and *L. japonicum* Endo, Banner et al. (1990, p. 28) concluded that the genus “*may subjectively be monotypic*”, a view also accepted by Schmid and Leinfelder (1996). In these two works, both species established from the Upper Jurassic of Japan by Endo (1961) were considered to be identical to the Lower Cretaceous type-species *Lithocodium aggregatum*, and thus regarded as junior synonyms. The “*presence of well-marked sporangia*” in *Lithocodium japonicum* was accentuated by Endo (1961, p. 64) as a species character. In any case, it seems to be a strange procedure, if not taxonomically incorrect to create a new species for a fertile stage of another taxon, *L. aggregatum* + sporangia = *L. japonicum*. These sporangia, however, were correctly identified by Schmid and Leinfelder (1996) as the chambers of the cryptobiotic foraminifer *Troglotella incrustans* Wernli and Fookes, which can be arranged serially or irregularly within the so-called basal chambers just above the encrusted substrate (Fig. 9b, d, f). Therefore, the species *L. japonicum* is here interpreted as belonging to the “*Lithocodium aggregatum*”-*Troglotella incrustans* consortium as described by Schmid and Leinfelder (1996). It must be noted, however, that the chambers of *Troglotella incrustans* are not recognizable in all figurations of “*Lithocodium japonicum*”, only in pl. 5/3 and pl. 15/2 of Endo (1961). *Lithocodium morikawai*, the second species described by Endo (1961, p. 65) should be distinguished from *L. japonicum* and *L. aggregatum* by the “*presence of secondary and tertiary filaments*” although in the remarks for *L. japonicum*, the well-defined differentiation between the primary and secondary filaments was also stressed by Endo. Concerning *L. aggregatum*, Elliott (1956) did not explicitly remark on the order of the branchings, but his figurations, though displaying low magnification, allows us to recognize at least primary and secondary filaments. The material from the Lower Cretaceous of the Maestrat Basin allows the recognition of up to five orders of filament layers (cf. Banner et al. 1990, p. 28, “*usually three or more*”). Therefore, *L. morikawai* is here regarded as a junior synonym of *L. aggregatum*; the septate erect filaments are recognizable in plate 12, Fig. 4 of Endo (1961), the prostrate system for example in pl. 12, Figs. 1, 3.

The Late Jurassic specimens, illustrated by Schmid and Leinfelder (1996), do not allow recognition of a heterotrichal thallus morphology with septate prostrate and erect-branching filaments of *Lithocodium aggregatum* as redescribed here. The distinctly reduced or even non-branching aspect of the filaments, their obvious lack of septation and occurrence of roughly hemispherical basal cavities separated from each other (e.g., Schmid and Leinfelder 1996, pl. 1/4 or reconstructions text, figs. 7, 8) (e.g., Fig. 9c) are

totally different from the heterotrichal chlorophyte *Lithocodium aggregatum* Elliott as described in the present paper. Therefore, the Upper Jurassic representatives illustrated by Schmid and Leinfelder (1996) are considered as belonging to another (probably new) taxon, which could be identical to the forms reported from the Upper Triassic (Fig. 9a). In fact, besides the lack of epilithic septate filaments, the often mono-layered crusts reported from the Late Triassic to Late Jurassic are characterized by a more or less regular arrangement of spar-filled large basal cavities (e.g., Senowbari-Daryan 1980, 1984, pl. 10/7; Wurm 1982; Kuss 1983; Stanton and Flügel 1989, pl. 29/5a; Schmid and Leinfelder 1996). In most cases, these basal cavities are empty; Kuss (1983, pl. 17/7) figured microcrystalline irregular partitions inside; in the Upper Jurassic, as already emphasized, these cavities are often occupied with the tests of the cryptobiotic foraminifer *Troglotella incrustans* Wernli and Fookes. In addition, the Triassic crust layers are distinctly thicker, 0.95–1.75 mm according to Senowbari-Daryan (1980) (see Table 3 for comparison). Last but not least, the specimens described by Schmid and Leinfelder (1996) from the Upper Jurassic of Portugal may trap siliciclastic particles (Fig. 9e) and derive from shallow inner ramp settings, whereas our material from the Lower Aptian is interpreted to have flourished in deeper-water environments (see Bover-Arnal 2010).

Stratigraphy The stratigraphic range of *Lithocodium aggregatum* Elliott known so far is (Oxfordian?)Tithonian–Coniacian (see synonymy heading). Due to rare records of *Lithocodium aggregatum* Elliott in the Late Cretaceous (e.g., Höfling 1985; Steuber 2001: Middle Coniacian of Northern Calcareous Alps), this interval might not necessarily correspond to its total stratigraphic range. As already discussed, the Triassic illustrations of *Lithocodium aggregatum* (or *Bacinella irregularis*) in the literature (e.g., Senowbari-Daryan 1984; own data) cannot be ascribed to septate ulotrichalean algae; these organisms and structures need revision.

Comments on *Pseudolithocodium carpathicum* Mišík

The microencruster incertae sedis *Pseudolithocodium carpathicum* was described by Mišík (1979) from the Upper Jurassic of the Western Carpathians. It is characterized by “*two types of tissue*”, consisting of an older stage with larger irregular to oval cells and a younger part consisting of “*rarely bifurcating tiny tubes*” (or alveoles) more or less perpendicular to the thallus surface (Fig. 10a, e). In contrast to the genus *Lithocodium* Elliott, Mišík (1979, p. 709) stated that “*the tubes of the cortical layer are densely packed, not submerged in micrite*”. In the original diagnosis, *Pseudolithocodium* was characterized as an encrusting alga. Besides thalli fixed to hard substrates (e.g., corals,

Fig. 9 Enigmatic microencruster incertae sedis formerly ascribed to *Lithocodium aggregatum* Elliott from the Upper Triassic of Austria (**a**), the Upper Jurassic of Austria (**b–d, f**) and Portugal (**e**). **a** Specimen fixed to a substrate showing a large sparite-filled basal cavity/“chamber” (size: $\sim 1.4 \times 0.4$ mm), Norian-Rhaetian Dachstein Limestone, Mount Loser, Austria. **b** Specimen switched between microbial crusts; large basal cavity/chamber with cryptobiotic foraminifer *Troglotella incrustans* Wernli and Fookes, Upper Tithonian (?Lower Berriasian), Mount Dietrichshorn, Austria. **c** Specimen with large empty basal cavity/chamber (size: almost $3 \times \sim 1$ mm); below vesicular structures,

stromatoporoids), however, free irregular-shaped specimens may also be present within the surrounding matrix. In these forms, the differentiation of an older and younger part

Upper Tithonian (?Lower Berriasian), Mount Dietrichshorn, Austria. **d** Several separated chambers each with cryptobiotic foraminifer *Troglotella incrustans* Wernli and Fookes inside, Upper Tithonian, Mount Trisselwand, Austria. **e** Several superimposed crusts with trapped siliciclastics and *Troglotella incrustans* Wernli and Fookes (*T*), Kimmeridgian of Lusitanian Basin, Portugal. **f** Specimen fixed to a stromatoporoid skeleton with *Troglotella incrustans* Wernli and Fookes inside cavities/chambers, Upper Tithonian (?Lower Berriasian), Mount Dietrichshorn, Austria. Scale bars 1 mm for **a–f**. Thin sections: **a** Los-1, **b–c, f** Die-170, **e** AB-I-7 (leg. Martin Nose)

is not possible given that the “younger” alveolar layer surrounds the irregular ovoid cells of the “older” stage (Fig. 10c, d). In the Upper Jurassic of the Northern Calcareous

Alps of Austria, *Pseudolithocodium* occurs often associated with the alga incertae sedis *Thaumatoporella parvovesiculifera* (Raineri) (Schlagintweit and Ebli 1998, pl. 10/4) (Fig. 10a, b). In the cases where *Thaumatoporella* shows internal cell-like compartments, both have a similar appearance (see also Cherchi and Schroeder 2005). *Thaumatoporella* shows an outer wall of more or less constant diameter and strictly parallel and more or less isodiametric alveoles/pores (Fig. 10b); in *Pseudolithocodium* these are more irregular embedded in micrite which accounts for a distinctly darker appearance and may show branching in addition. It is worth to mention that *Thaumatoporella parvovesiculifera* was originally described with cylindrical thalli from the Upper Cretaceous of Italy (Raineri 1922; De Castro 2002); later a greater morphological variability (e.g., encrusting, nodular) was attributed to these thaumatoporellacean algae (De Castro 1990 for details).

Several authors have regarded *Pseudolithocodium* as a junior synonym of *Lithocodium* Elliott (Banner et al. 1990; Schmid 1996; Schmid and Leinfelder 1996; Koch et al. 2002). The assumption of such a synonymy has a direct consequence for the taxonomic interpretation of *Pseudolithocodium* (see Table 1). Senowbari-Daryan et al. (1994) remarked a possible difference at the species level, whereas others maintain the validity of both genera (Schlagintweit and Ebli 1999; Dragastan and Richter 2003). A differentiation into a prostrate basal part and an upper erect part with branching filaments giving rise to a heterotrichal thallus construction, as emended for *Lithocodium* Elliott, is not discernible on the original figurations. Hence, *Pseudolithocodium* Mišák is here regarded as a different taxon. Whether this taxon, however, can be included in the variability of those forms that we excluded from *Lithocodium aggregatum* Elliott, is beyond the scope of the present paper and needs further restudies of both Upper Triassic to Upper Jurassic representatives along with the original material of Mišák (1979).

Comments on the type-material of *Bacinella irregularis* Radoičić

First of all, it must be mentioned that the type-material of *Bacinella irregularis* is housed at the Geological Institute of Serbia in Belgrade, but not within a certain collection and at present unfortunately not available for re-study (pers. comm. Rajka Radoičić).

The holotype and one paratype of *Bacinella irregularis* are illustrated in Radoičić (1959, pl. 3/1–2). In the genus diagnosis, the interior of the crust is described as being “constructed by unregular cells of different size and form, which are filled with crystalline calcite (Remark: sparite) whereas the intercellular mass is cryptocrystalline (Remark: micrite)” (Radoičić 1959, p. 92) (Fig. 11a). In the

species description the “cells” of *Bacinella irregularis* are further specified as being “arranged into association or into some sort of unregular series which are intermingled”; the inner structure was interpreted by Radoičić as “unclear”; along the same line, we must remind that Elliott (1956) also characterized the inner part of *Lithocodium* as “confused”. Regarding the serial cell arrangement, detectable in the holotype specimen (Fig. 11a, c), we have to stress that the choice of the species name was somehow misleading. The thin microcrystalline cross-partitions within the sparite-filled “cells” were not explicitly mentioned; it can be assumed, however, that Radoičić was aware of this as otherwise the term “cell” would probably have been replaced by “filament” or “siphon”. In this regard, a general resemblance of the holotype of *B. irregularis* to *L. aggregatum* has been mentioned by Banner et al. (1990, p. 22), noting that the former “is distinguishable only by the more frequent occurrence...of thin walls separating the adjacent cells of particular filaments”. As Banner et al. (1990) were treating *Bacinella* as a junior synonym of *Lithocodium*, they must have considered these filaments with crosswalls as “medullary filaments” sensu Elliott as these authors were considering the “cortical filaments” to be non-septate. The differentiation of the “subdermal structure” of *Bacinella irregularis*, as remarked in the generic diagnosis, was compared by Radoičić with “that one of the species *Lithocodium aggregatum* Elliott”, but without further comments as to why it was obviously regarded to be different. The holotype specimen clearly allows us to recognize that the “cells” are not really disorganized, but are radiating (from right to left, Fig. 11a) and successively branching, forming a reticulate network. The direct continuity refers them to the typus of uniseriate septate branching filaments; their continuation into the final fine branching layer (“cortical zone” of Elliott) can be discerned on the left upper side of the holotype (Fig. 11a, c). The “small circular cells” described by Radoičić (1959, p. 92) within the “subdermal” “cryptocrystalline mass” are interpreted here as transverse sections of the uniseriate septate filaments. It is noteworthy that a “vague linear cell arrangement or a suggestion of septate tubes” was already remarked on by Beckmann and Beckmann (1966, p. 41). In the middle part of the holotype figuration (Fig. 11a), and also clearly visible in the studied Lower Aptian material from Spain (Fig. 11b, d), the forming of a network with anastomizing filaments can be observed. The diameter of the cells (= filament diameter) – as measured from the holotype figuration—is 0.07–0.22 mm (mostly around 0.15 mm). The septae occur at distances from 0.15 to 0.5 mm.

Much of the long-term confusion in the literature resulted from the fact that many authors were referring to the apparently more disorganized altered structure of the

Fig. 10 *Pseudolithocodium carpathicum* Mišák and *Thaumtoporella parvovesiculifera* (Raineri) from the Upper Jurassic of the Northern Calcareous Alps of Austria. **a** Succession of *Thaumtoporella parvovesiculifera* (Raineri) (Th) and *Pseudolithocodium carpathicum* Mišák (P) encrusting a stromatoporoid skeleton. **b** Encrusting thaumtoporellean alga with thin transverse walls forming closed and partly open

compartments/cells. **c–d, f** Free specimens of *Pseudolithocodium carpathicum* Mišák showing allside alveolar layer (arrows, **c**) and large cells with incomplete partitions (**f**). **e** Several layers of encrusting *Pseudolithocodium carpathicum* Mišák. Scale bars 1 mm for **a, e**; 0.5 mm for **b–d, f**

paratype specimen of *Bacinella irregularis*, considered here as an oblique section, and transferring it furthermore to any cellular-vesicular structures without taking a closer look at the original illustration of the holotype specimen.

? Order Ulotrichales
Genus *Bacinella* Radoičić

Original diagnosis Nodular and encrusted algae whose interior is constructed by unregular cells of different size and form, which are filled with crystalline calcite, whereas the intercellular mass is cryptocrystalline. The subdermal structure is differentiated (Radoičić 1959, p. 92)

Emended diagnosis Euendolithic, facultative cryptoendolithic alga boring into calcareous substrates. Thallus composed of uniseriate filaments basically cylindrical, barrel-shaped or irregular in shape exhibiting branching often in an opposite manner; hairs occasionally occur. Adult thalli form a complex anastomizing network inside the substrate within a zone parallel to the surface. Terminal cells with short branches (one or two layers) stretching close to the substrate surface without penetrating it. Cell- and cross-walls thin, of microcrystalline calcite.

Order: Ulotrichales

Family: ?

Genus: *Bacinella* Radoičić 1959

Bacinella irregularis Radoičić 1959

(Figures 11a–h, 12e–g)

Synonymy The cellular-vesicular structures associated with *Lithocodium aggregatum* Elliott or not, are different from the filamentous-septate and branching alga figured by Radoičić (1959) as the holotype specimen. Consequently, as interpreted herein, the synonymy list becomes drastically reduced.

*1959 *Bacinella irregularis* nov. gen., nov. sp. – Radoičić, pl. 3/1–2

1987 *Bacinella irregularis* Radoičić – Reitner, pl. 21/1

Description Euendolithic alga with a thallus consisting of septate uniseriate filaments. The alga bores into calcareous bioclasts (here: thalli of *Lithocodium aggregatum*, e.g., Fig. 11e) or stretches cryptobiotically into existing skeletal structures of corals or calcareous sponges (Fig. 12g). The boring activity of *Bacinella* penetrating crusts of *Lithocodium* is well discernible where embryos of the former were entering borings of lithophagid bivalves that were affecting both the bioclastic substrate and the superimposed crusts of *Lithocodium* (Fig. 11e). In this case, the juvenile part is more or less straight (nearly 2 mm long) with some short simple lateral branches penetrating several crust layers. In a zone parallel to the crust surface, the filament ramifies, stretching in various directions (about 5 mm in lateral extent). Branches may occur either upon two outgrowths of the mother cell or just juxtaposed at its rounded to flat tip. The filaments, however, not only show successive branching but also anastomization, forming bridges between the radiating filaments (Fig. 11b, d, e). Within the ramifying part, long thin hairs are sometimes observable (Fig. 11e). At their proximal parts, they are up to 40 µm in diameter, then taper in the direction of growth. The cross-walls delineating individual cells occur at irregular distances. Often, however, they are rather close-set (width equaling more or less the length) giving rise to a barrel-shaped appearance (Fig. 11g, h). Rarely, a cross-shaped branching pattern with a “four-armed central cell” sensu Nielsen (1987) can be

observed (Fig. 12e). More elongated cells may also show bending. A slight constriction is often present at the boundary between two adjacent cells.

Remarks First of all, it must be stressed that with its crust-parallel growth of branching uniseriate chambers from which short end branches emerge, *Bacinella* is close to *Lithocodium* which is epilithic crust-forming with a microcrystalline common thallus sheath enclosing the filaments. *Bacinella* instead is interpreted as a euendolithic taxon without an enclosing thallus sheath, best discernible when it appears as cryptoendolith within the interseptal spaces of microsolenids or calcareous sponges (Fig. 12f, g); within the dark micritic *Lithocodium* crusts this feature becomes masked. From those specimens that bore the substrate/crust from outside or inside (entrance being gained via borings produced by lithophagids post-dating the crust formation), it is evident that *Bacinella* bored through several superimposed thalli of *Lithocodium* before producing a ramifying and anastomizing network parallel to the surface. Obviously the specimens tried to reach the upper crust from the bored basal substrates in a direct way: a behavior possibly linked to phototaxis/geotaxis. In a very simplified way, one could characterize *Bacinella* as a more irregular and purely euendolithic stage of *Lithocodium*; we interpret these different features as characterizing two different genera, not indicating synonymy between *Bacinella* and *Lithocodium*.

In an unpublished PhD thesis, Scholz (1979, p. 26) drew the conclusion that *Lithocodium aggregatum* represents a crust produced by algae and *Bacinella irregularis* the boring pattern of the same alga: an interpretation close to our view. Some authors have already mentioned the “boring potential” of the *Bacinella/Lithocodium* organism (e.g., Maurin et al. 1985; Neuweiler and Reitner 1992); others deny such an ability (Banner et al. 1990). In the material we studied, the substrate (mostly coral rubble) was already intensely bored by endolithic sponges and *Bacinella irregularis* before becoming completely encrusted by *Lithocodium* crusts. In our interpretation, *Bacinella* can be well ascribed to the destroyer guild, whereas *Lithocodium aggregatum* Elliott can be included in the binder guild (Fagerstrom 1987; Grötsch et al. 1994).

As a consequence of our results, the microcrystalline cellular structures or meshworks from Triassic and younger strata, which have commonly been referred to as *Bacinella irregularis* by many previous authors (e.g., Senowbari-Daryan 1984; Schmid and Leinfelder 1996), need revision. These filamentous microfabrics often occur in well-sorted pack- to grainstone textures where they bind and trap small bioclasts and peloids, indicating shallow-water settings. Such microfabrics were formerly also termed “*bacinellid*”, “*bacinelloid*”, “*bacinellimorph*” structures or just “*Bacinella threads*” (Maurin et al. 1985; Neuweiler and Reitner

◀ **Fig. 11** *Bacinella irregularis* Radoičić from the Barremian-Aptian of Bosnia (a, c) and the Lower Aptian of the western Maestrat Basin (b, d–h). **a, c** Holotype specimen (from Radoičić 1959, pl. 3/1). In c, the euendolithic system of septate branching and also partly anastomizing filaments are colored to aid comprehension. Note the rather close set of cross-partitions giving rise to roughly cylindrical to barrel-shaped uniseriate cells. **b, d, f** System of branching and anastomizing uniseriate cellular filaments; note the different appearance of the terminal branching system towards the crust surface in comparison to *Lithocodium*. **e** Specimen boring through several superimposed and intensely micritized crusts of *Lithocodium aggregatum* Elliott (partly shown by the white dashed lines). Entry happened through a macroboring of *Gastrochaenolites* ichnosp. (G). Boring first straight, then in the upper part ramifying (branching, anastomizing, arrow 1) in a crust-parallel zone; note fine hair-like lateral protrusion (arrow 2). The branching part is directly comparable to the holotype specimen (a). **g, h** Detailed views showing the cylindrical to barrel-shaped uniseriate cells. Scale bars 1.0 mm for a–c, e–f; 0.5 mm for d, 0.3 mm for h–i. Thin sections: b CAL-5V, d H0-17V, e, g, h DE-5H, f H0-15V

1992; Schmid and Leinfelder 1996; Koch et al. 2002) (Fig. 13). Filamentous fabrics forming grain-to-grain bridges are also known from modern subtidal environments

where they were neutrally described as “filamentous fabrics”, but compared with *Bacinella* (Hillgärtner et al. 2001). They are most likely “microbial” in origin (Maurin et al. 1985; Camoin and Maurin 1988), i.e., microbial mats (see Riding 2000). Somehow similar structures are the so-called cusate and plumose microbialitic structures reported from Archean stromatolites (Sumner 1997). The bacinelloid fabrics, however, lack the vertical oriented supports of these structures.

These biosedimentary structures cannot be termed *Bacinella irregularis* any longer; they should rather be addressed simply as vesicular or cellular fabrics. The species *Bacinella bicellularis* Sadati and *Bacinella ordinata* Pantic cannot be referred to *Bacinella* or *Lithocodium* and hence are in need of taxonomical revision. The Cenomanian *Bacinella? sterni* Radoičić was already revised to *Radoicicinellopsis sterni* (Radoičić) by Banner et al. (1990). The factors accounting for the often observable co-occurrence of both micritic *Lithocodium*-type and vesicular *Bacinella*-type crusts on the one side and the “monotypic” dominance of only one type on the other side, is so far

Fig. 12 Modern euendolithic chlorophyte algae (a–d) that can be compared morphologically to *Bacinella irregularis* Radoičić (e–g). **a, c, d** *Phaeophila dendroides* (Crouan and Crouan) (a, c from Thivy 1943, pl. 1/1 and 1/3 figured as *Phaeophila engleri* Reinke; see Guiry and Guiry 2009, d from Nielsen 1987). **b** *Eugomontia sacculata* Kornmann (from Kornmann 1960, fig. 5b). **e** *Bacinella irregularis* Radoičić with opposite branching resulting in a characteristic “four-armed cen-

tral cell” (Nielsen 1987); note the boring into the fine-branching filaments of the erect system of *Lithocodium aggregatum* Elliott. **f** *Bacinella irregularis* Radoičić predominantly chasmoendolithic within interseptal spaces of coral. **g** *Bacinella irregularis* Radoičić chasmoendolithic within demosponge skeleton; note characteristic short barrel-shaped cells (compare holotype specimen, Fig. 11a). Scale bars 0.2 mm for a, g; 1.0 mm for f. Thin sections: e H0-16V, f CAL-1, g SE-2V

Fig. 13 Upper Jurassic–Upper Cretaceous “lithocodoid-bacinelloid” fabrics (sensu Neuweiler and Reitner 1992) from the Northern Calcareous Alps of Austria (**a–c**), Germany (**d**) and the Lower Cretaceous of Hungary (**e**). **a** Large masse of alternating fine-cellular “bacinelloid” and more micrite-rich “lithocodoid” fabric and large-vesicular sparite-filled bacinelloid fabric of unknown taxonomic position; reefal platform margin facies. Tithonian of Austria, Northern Calcareous Alps. **b** Bindstone with bacinelloid fabric consisting of differently sized and shaped sparitic vesicles binding bioclasts (e.g., foraminifera) and lithoclasts (e.g., peloids). Back-reefal to open lagoonal facies. Upper Kimmeridgian of Austria, Northern Calcareous Alps. **c** Detail from

b showing individual vesicles (possibly cells) that are partly connected to each other by means of small pores. **d** Filamentous fabric connecting different lithoclasts in a high-energy shore-zone depositional setting (so-called Untersberg Marmor). Upper Cretaceous (Late Turonian or Coniacian) of Germany, Northern Calcareous Alps. **e** Bacinelloid fabric (or *Bacinella*-bindstones in literature) binding bioclasts (mostly small benthic foraminifera) and lithoclasts (mostly peloids); back-reef to open lagoonal facies, Lower Cretaceous of Hungary. Scale bars 2 mm for **a–b**; 1.0 mm for **d**; 0.5 mm for **c**, **e**. Thin sections: **a** TK 8, **b**, **c** HW-1, **d** C-128, **e** Naghy-2

poorly understood. In these cases, however, it is necessary first to ascertain whether these micritic structures really belong to *Lithocodium* or not, see Fig. 13a, for example.

Order: Ulvales
 Family: Phaeophilaceae
 Genus: *Phaeophila* Hauck
Phaeophila? sp.
 (Figure 14a)

Description Creeping filaments (diameter 24–55 μm) with constrictions and several more or less parallel long hairs (setae) rising upwards and stretching into the erect filament system of *Lithocodium aggregatum*. The hairs stretch obliquely to the prostrate filament; they are 15–20 μm thick

and up to 700 μm long. The three-dimensional structure (e.g., possible branchings) is unknown. The sinuous appearance of the filaments with constrictions suggests a septate structure; septae, however, are not preserved.

Remarks The life cycle of *Phaeophila* and other endolithic chlorophytes is rather short (weeks to a month), so that normally only empty borings are found in substrates (Kiene et al. 1995). Other similar euendolithic ulvacean algae with thin upright hairs are *Acrochaete* Pringsheim or *Entocladia* Reinke (Fig. 14b–d) (e.g., Thivy 1943). These microfilamentous algae are typically endophytic, e.g., they live inside the thalli of brown algae (Srinivasan 1962; Correa et al. 1987, 1988; Kitayama and Garrigue 1998). Whether the Lower Cretaceous forms

Fig. 14 Euendolithic chlorophyte *Phaeophila*? sp. from the Lower Aptian of the western Maestrat Basin (**a**) compared to modern counterparts (**b–d**). **a** *Phaeophila*? sp., filament with irregular constrictions delineating uniseriate cells (cross-walls not preserved) from which thin, more or less isodiametric, bristle-like hairs (setae) arise; euendolithic within *Lithocodium* crusts. **b** *Entocladia vagans* (Börgensen) with one hair emerging from each cell (from Thivy 1943, pl. 4/4,

figured as *Ectochaete vagans*). **c** *Phaeophila dendroides* (Crouan and Crouan) showing uniseriate cell arrangement (from Thivy 1943, pl. 2/16 figured as *Phaeophila engleri*). **d** *Phaeophila dendroides* (Crouan and Crouan), detail showing several hairs (“setae”) emerging from each cell (from Thivy 1943, pl. 2/6 figured as *Phaeophila engleri*). Scale bar 0.3 mm for **a**. Thin section: **a** H0–4H

infested living or already dead *Lithocodium* thalli is unknown.

Class: Bryopsidophyceae

Order: Bryopsidales

Family: Ostreobiaceae

Genus: *Ostreobium* Bornet and Flahault

Ostreobium? sp.

(Figures 15a–f, 17h, i, pars)

Description Siphonous (non-septate) straight and unconstricted tubes, euendolithic within the micritic *Lithocodium* tissue and stretching cryptoendolithically in borings produced by other organisms or more often in the prostrate system of *Lithocodium aggregatum*. In the latter case, the tubes typically attach closely to the roof of the crypts of (mostly) larger diameters (Fig. 15b, c). The tubes have diameters of 40–145 μm , the wall thickness is ~ 8 –12 μm ; greatest observed tube length more than 5 mm (Fig. 15a); tube ends swollen (up to 200 μm). The straight crust-parallel tubes occur in a zone about 0.2 to 0.5 mm below the crust surface and show upward-branching with a slight terminal swelling stretching into the lower part of the erect filament system of *Lithocodium* (Fig. 15b, d–f). The thin tube wall appears dark when micritic; in random sections through the wall it appears translucent slightly yellowish to brownish.

Remarks The cryptoendolithic tubes were already recognized and illustrated by Banner et al. (1990, pl. 2/1, 3, p. 28) and incorrectly identified as, “distinctly tubular” medullary filaments. Our specimens, although a little larger, are very similar if not identical to the siphonaceous microendoliths within microsolenid corals from the Lower Aptian of Romania reported by Kolodziej et al. (2008). The long

straight and branching forms have diameters from 20 to 80 μm and were tentatively assigned to *Ostreobium*; their iron-impregnation gives the tubes a red-brownish color. It is noteworthy that the tube diameters of modern *Ostreobium* species are usually distinctly smaller, e.g., 3–6 μm for the widespread *O. quekettii* Bornet and Flahault (e.g., Lukas 1974; Tribollet 2008). The largest modern representative is *Ostreobium brabantium* Weber van Bosse with siphon diameters of 40–60 μm enlarging up to 150 μm at points of bifurcation (Budd and Perkins 1980, p. 885). *Ostreobium* represents a typical microeuendolith in modern hermatypic corals where it forms a typical green endolithic band or layer (e.g., Le Campion-Alsumard et al. 1995; Tribollet and Payri 2001; Försterra et al. 2005; Magnusson et al. 2007). *Ostreobium* was also observed as an endophyte within coralline algae (Ghirardelli 2002). The stretching that is often observed of the tubes at the roofs of empty borings or prostrate *Lithocodium* filaments can be interpreted as a phototactic growth. *Ostreobium* belongs to more than one category in the scheme of Golubić et al. (1981) as it can leave its boreholes (euendolith) and stretch into existing cavities/structures (cryptoendolith) of the substrate (Schroeder 1972; Golubić et al. 1975; Kobluk and Risk 1977); an observation also made in our material. This euendolithic chlorophyte has been reported from water depths ranging from 1.5 to 60 m (e.g., Lukas 1974).

Calcimicrobes

Epiphyton group

(Figure 16a–e, g)

Remarks The predominantly Paleozoic *Epiphyton* group *sensu* Riding (1991a) comprises micritic, dendritic filaments

Fig. 15 Cryptoendolithic and euendolithic chlorophyte *Ostreobium?* sp. from the Lower Aptian of the western Maestrat Basin. **a** Long straight tube within *Lithocodium* crusts; note the overprinting by the boring gallery (arrows). **b–c** *Lithocodium* crusts with cryptoendoliths attaching to the roof of a prostrate filament or bored gallery and branching upwards into the erect system. **d** Endolithic branching chlo-

rophyte tube boring into *Lithocodium* crusts. **e–f** Euendolithic chlorophyte tube, note the swelling at the branching areas; tube wall thin, greater thickness results from oblique cutting (**e**, right). Scale bars 1 mm for **a–d**; 0.5 mm for **e–f**. Thin sections: **a** CA-3H, **b** DE-5H, **c** H0-6V, **d–f** H0-11

of erect or pendant growth. Sometimes, also tufted masses of clotted micrite structures are observable referable to decayed *Epiphyton*-type filaments; another interpretation would explain them as microbial precipitates. These *Epiphyton*-type filaments were observed in the outermost crusts, preferentially inside the sparite-filled terminal megacells. Similar arborescent calcimicrobes are reported from modern stromatolites of Tonga as *Frutexitites*-type by Kazmierczak and Kempe (2006, fig. 3g).

It is unclear whether these calcimicrobes were dwelling in living (as cyanosymbionts) or dead *Lithocodium* tissue. Cyanobacteria as symbionts within Ulvovyceae/Chlorophyceae are known since the latest Proterozoic (Raven 2002). *Epiphyton* was illustrated by Masse (1979) from the Lower Cretaceous; according to Riding (1991a) this form, however, more closely resembles *Angulocellularia*. Comparable filamentous structures within Lower Cretaceous “*Bacinella*” pseudocells were already observed by Granier

Fig. 16 Calcimicrobes (cyanobacteria) associated with *Lithocodium aggregatum* Elliott from the Lower Aptian of the western Maestrat Basin. **a–c, g** *Epiphyton* group sensu Riding (1991a), with micritic erect to pendant dendritic filaments in aberrant terminal vesicles of *Lithocodium aggregatum* (**a, c, d**) and thick prostrate filaments (**g**). **d** Single erect branching filament. **e** Altered filaments (?*Epiphyton* group) geopetally filling within terminal vesicles of *Lithocodium*

aggregatum. **f** *Girvanella* group sensu Riding (1991a), with simple, loosely packed, flexuous, isodiametric, hollow tubes with microgranular walls inside terminal vesicle of *Lithocodium aggregatum*. **h** Filaments with swollen basal part and herringbone-like branching. Scale bar 0.5 mm for **a–h**. Thin sections: **a–c** CUB-41, **d** DE-2HB, **e** H0-11V, **f** DE-3H, **g** SE-2H, **h** H0-6V

(Granier 2003, fig. 6), who remarked that their degradation and decay may result in the commonly observed pseudosp- arite completely or partly (geopetally) filling these pseudocells. Equivalent observations were also made by Rameil et al. (2010, fig. 2a), interpreted as “collapsed walls” caused by “mechanical burial compaction”. They are here interpreted as decaying or collapsed filaments geopetally filling the basal parts of the pseudocells. It can be assumed that the filaments recorded within *Lithocodium-Bacinella* crusts by Maurin et al. (1985), unfortunately without illustration, also correspond to the “tiny *Epiphyton*-like bushes”.

Girvanella group (Figure 16f)

Remarks The *Girvanella* group sensu Riding (1991a) comprises thin-walled more or less isodiametric simple flexuous tubes (see also Riding 1977). Like the *Epiphyton* group, loosely packed *Girvanella*-type tubes were observed inside the large sparite-filled terminal cells of *Lithocodium aggregatum*. The external tube diameters are 50–65 µm; the thickness of the thin microgranular walls is ~8–14 µm. In the material studied, *Girvanella*-like tubes are distinctly

more rare than the bushy filaments of the *Epiphyton* group. It is noteworthy that Waite et al. (2007) also report the association of *Lithocodium* with *Girvanella* from Late Albian boundstones of Texas. Fenninger (1972, pl. 3/4) observed irregularly arranged filaments (diameter including the wall: 20 µm) reminiscent of *Girvanella* tubes inside “*Bacinella*” tissue, and considered a possible algal or fungal origin. Comparable filaments/tubes were also reported by Schott (Schott 1983, pl. 1/4) from Late Triassic intertidal algal laminites with bacinelloid texture.

Bioerosion features in Lower Cretaceous crusts of *Lithocodium aggregatum* Elliott

Macroborings

Indet 1

(Figures 4b, d, h, 17a, b pars, c, j)

Description Borings either perpendicular or oblique to the crust surface; rather long (several mm) passing through several crust layers and consisting of a thick main channel (width up to 0.4 mm) and occasionally long, though more often short, lateral branches. The latter are often formed at the boundaries between superimposed crust layers. In perpendicular borings, this branching leads to a rectangular pattern (Fig. 17j). The diameter of the main channel may undulate (Fig. 17b) or increase in the boring direction (Fig. 17a). This type may show irregular terminal branching with fine short branches stretching to the crust surface (Fig. 17a). In many cases where only smaller parts of the borings are observable in the thin sections, the boring direction cannot be determined reliably.

Remarks This macroboring type is common in the material from the Lower Aptian of the western Maestrat Basin. It also occurs in the type-material of Elliott (1956) (Fig. 4b, d, h). What produced this macroboring is unknown; the general pattern might point to a chlorophyte alga.

Indet 2

(Figure 17b pars, d–f, h, i pars)

Description It is characterized by tubular, slightly undulating, channels of variable diameter bearing spheroidal to ovoidal swellings, often slightly lateral in position. The swellings are distinctly larger (up to 200 µm thick, up to 300 µm long) than the channels. The distance between successive swellings ranges from 0.15 mm to more than 1 mm. The diameter of the channels is highly variable, often between 28 and 38 µm. In some cases, the diameter decreases in the boring direction by much as 150 µm. Rather long (up to 500 µm) hairs can be observed occasionally (Fig. 17h).

Remarks This macroboring is the most common form observed in the thalli of *Lithocodium aggregatum* from the

Fig. 17 Boring patterns within Lower Cretaceous crusts of *Lithocodium aggregatum* Elliott (Spain: a–d, h–j; Iraq: e–f; Abu Dhabi: g). **a** Boring within several superimposed crusts (dotted white lines, crust surface: solid line) showing terminal branchings comparable to the epilithic *Lithocodium* (*M* = matrix, *B* = foraminifer *Bdelloidina? urgonensis* Wernli and Schulte, *Go* = *Gomontia* stage within pelecypod shell). **b–c, j** Boring almost perpendicular to the crust surface with several short lateral branches on both sides (*M* = matrix). **d–f** Boring pattern characterized by thin, slightly undulating channels with round to ovoid swellings, often disposed laterally to the channels. **g** Thick crusts transected by several boring patterns. Below: same boring shown in **d–f** (arrow 1); above: system of thin straight channels with small angle or rectangular branchings, often with small rounded swellings at the branching points (arrows 2), and an indefinite macroboring (arrow 3). **h–i** Boring patterns similar to that shown in **d–f**; note the thin long lateral hairs (arrows in **h**) and crypto/euendolith chlorophyte *Ostreobium? (C)*. Scale bar 1.0 mm for **a, b, i**; 0.5 mm for **c–h**. Thin sections: **a** CA-3H, **b** H0-5V, **c** CAL-3V, **d** P0-4V, **e–f** V 41599, **g** from Banner (1990, pl. 1/2), **h** CAL-3vt, **i** H0-11V. Copyright for **e, f** Natural History Museum, London

Lower Aptian of the western Maestrat Basin but also the Hauterivian? type-material of Elliott (Fig. 17e, f). This bioerosional pattern bears some resemblance to the ichnogenus *Rhopalia* Radtke (Radtke 1991; Glaub 1994), which the chlorophyte *Phaeophila* is commonly considered to produce (e.g., Golubić and Radtke 2008; Heindel et al. 2008). It is noteworthy that the two known ichnospecies of *Rhopalia* have distinctly smaller dimensions (Radtke 1991; Golubić and Radtke 2008).

Microborings

Orthogonum-type

(Figure 17g pars)

Description This type of boring consists of a system of long (several mm) straight, supposedly cylindrical borings of rather uniform diameter (mostly 8–12 µm; occasionally up to 25 µm). Branching occurs obliquely or at right angles and may form a network. Moderate swellings (diameter 25–40 µm) occur at the branching points.

Remarks This microboring with its typical branching pattern was observed in the illustration of Banner et al. (1990, pl. 1/2) from the Lower Cretaceous of Abu Dhabi. It can be compared with the ichnogenus *Orthogonum* Radtke (e.g., Radtke 1991; Glaub 1994) known since the Ordovician (Glaub and Vogel 2004; Bromley 2004). *Orthogonum* is typically arranged parallel to the substrate surface, a feature that cannot be verified from the above-mentioned thin-section illustration. The different ichnospecies of *Orthogonum* are related to different producers of different biogenic groups (e.g., algae, fungi) (Glaub 1994); for example, *Orthogonum fusiferum* Radtke is referred to the fungus *Ostracoblabe implexa* Bornet and Flauhault (e.g., Perry and Macdonald 2002; Carreio-Silva et al. 2009).

A reconstruction of the described morphological stages of *Lithocodium aggregatum* Elliott and *Bacinella*

Fig. 18 Schematic drawing (not to scale) of the new taxonomic and morphological interpretation of *Lithocodium aggregatum* Elliott as a chlorophyte-calcimicrobial assemblage associated with cryptobiotic

and euendolithic taxa (ichnocommunity). *Bacinella irregularis* Radoičić is considered a euendolithic chlorophyte that may bore into the thalli of *Lithocodium aggregatum* Elliott

irregularis Radoičić together with the observed micro-/macroborings, the cryptobiotic chlorophyte taxon (*Ostreobium?* sp.) and the associated calcimicrobes is shown in Fig. 18. It must be stressed that in our reconstruction all these taxa and ichnotaxa co-occur; in fact, it represents a compilation obtained from various thin sections analyzed.

Comments on paleoecology and paleoenvironment of the *Lithocodium-Bacinella* chlorophyte microbial assemblage

The factors leading to or facilitating the proliferation of *Lithocodium-Bacinella* during certain periods, especially the Lower Cretaceous, have been addressed by several authors. Concerning the described Lower Aptian occurrences of the western Maestrat Basin, a deposition below the fair-weather base (= around 10–20 m, Tucker and Wright 1990) was assumed by Bover-Arnal et al. (2009b) and Bover-Arnal 2010). Certainly, a water depth greater than that usually assumed for shallower parts of the lower photic zone (e.g., Leinfelder et al. 1993, fig. 9) can be postulated. The rare and always very small debris of dasycladalean algae (Table 1) are not in contradiction with this as they are assumed as allochthonous. For the type-material of *Lithocodium aggregatum*, Elliott (1956) did not indicate microfacies or accompanying biota. The position of the type-locality Rumaila on the paleofacies map for the

Berriasian-Valanginian indicates “shallow-marine carbonates and clastics” (Ziegler 2001, fig. 12). At the type-locality of *Lithocodium aggregatum*, the occurrence of the stromatoporeoid *Burgundia* cf. *ramosa* in the type-material should be indicative of inner platform/ramp paleoenvironmental setting (see Leinfelder et al. 2005 for details). Banner et al. (1990, p. 32) concluded paleodepths of abundant in-situ specimens ranging from approximately 15 m to about 60 m. The associated fauna reported by the authors with neotrocholinids, lenticulinids, echinoderm debris, and rare planktonic foraminifera supports this assumption. From the Hauterivian of the central Maestrat Basin, Götz et al. (2005) described similar *Lithocodium* crusts associated with corals (e.g., microsolenids). The accompanying microbiota and the bioerosional features are similar to our Lower Aptian occurrence (compare Table 1). The morphological appearance of these crusts is also very similar. The paleoenvironment was interpreted by Götz et al. (2005) as a shallow-water depositional setting within the fair-weather base zone. In any case, there are several data from the Lower Cretaceous occurrences of *Lithocodium* where greater water depths than those indicated for the Late Jurassic were assumed (some to > 30 m according to Leinfelder 2001, fig. 11).

For mass occurrences of *Lithocodium*-type crusts from the Albian of Spain, Neuweiler and Reitner (1992) discussed

nutrient-rich conditions and/or a shift in seawater carbonate alkalinity. The latter factor was mainly considered because of the high primary production of calcium carbonate, a view recently adopted by Immenhauser et al. (2005) in assuming influx from weathering of emerged carbonatic areas. With respect to this, the partial pressure of atmospheric carbon dioxide should be also considered as another critical factor (Riding 2006 for details). Another important source of calcium carbonate, at least for the Lower Aptian occurrences in Spain, is the bioclasts themselves, which could have favored precipitation of microcrystalline calcite after bioerosive dissolution (e.g., Kobluk and Risk 1977; Chacón et al. 2006; Tribollet 2007 for discussion). Similarly, studies of modern stromatolites from the Bahamas have shown that “micritization is caused by extensive microboring and carbonate precipitation within boreholes concurrent with endolithic activity” (Macintyre et al. 2000, p. 915; Reid and Macintyre 2000). Of course it is not possible to estimate how much of the calcium carbonate preserved in the *Lithocodium aggregatum* crusts was derived from direct precipitation in the seawater or from dissolution processes of the calcareous substrates. However, as all bioclasts are commonly extensively affected by bioerosion, a considerable contribution of microcrystalline calcite of bioclastic origin to the crust masses seems likely. In recent times, attempts to correlate high trophic levels and rates of microbioerosion have been postulated but with no unambiguous final conclusions (Tribollet 2007 for details).

Some general considerations about the paleoenvironmental significance of the calcimicrobial community (Fig. 16) and the accompanying microfossils (Table 1) present in the thin sections analyzed can be provided. First of all, it is well known that modern microbes are adapted to low light intensities (e.g., Tribollet 2007); this statement should also be valid for fossil counterparts. This, however, does not necessarily mean that they were restricted to deep-water zones. The calcimicrobe *Girvanella* Nicholson and Etheridge (see Riding 1977, 1991a) shows a wide bathymetric range from shallow subtidal to slope settings; in the Paleozoic it is a characteristic constituent of deep-water mud-mounds (e.g., Pratt 1995). Chlorophytes showing an endolithic *Codiolum* stage such as *Gomontia* are reported from the upper photic zone down to the transition of the lower photic/aphotic zones (Le Campion-Alsumard 1979; Budd and Perkins 1980). As already mentioned, the rare and small debris of dasycladalean algae present in our thin sections are assumed to be allochthonous; the paleoecology of the encrusting peyssonneliacean alga *Polysratria alba* (Pfender), can be compared with the modern *Ethelia fosliei* Weber van Bosse, known from a depth range of 8–50 m (Massieux and Denizot 1964; Bassi 1997). These examples clearly demonstrate that an unequivocal paleobathymetric interpretation of the Lower Aptian *Lithocodium*-type crusts

cannot be deduced from the chlorophyte-calcimicrobial assemblage alone at the present state of knowledge.

Mass occurrences (bloom periods) of *Lithocodium aggregatum* crusts from the Late Hauterivian in southeast France (Conrad and Clavel 2008) and from some Lower Aptian occurrences were referred to as “microbial events” (Immenhauser et al. 2005). For the Lower Aptian *Lithocodium* blooms, a relation to the time-equivalent Oceanic Anoxic Event 1a (OAE1a; Selli level) was envisaged recently, however, with the triggering factors of these widespread blooms still poorly understood (Immenhauser et al. 2005, 2009; Bover-Arnal et al. 2009b; Bover-Arnal 2010; Rameil et al. 2010). It is noteworthy that the description as “microbial-foraminiferal” episode made by Immenhauser et al. (2005) referred to the interpretation of the micritic *Lithocodium*-type crust as representing a lituolid foraminifera following the model of Schmid and Leinfelder (1996). Discussing the possible driving factors for the initiation of the OAE1a coeval *Lithocodium*-episode, Immenhauser et al. (2005) also mentioned that, according to Erbacher et al. (1996), the OAE1 should coincide with a transgressive period. A comparable interpretation was also put forward by Waite et al. (2007). Those authors reported a characteristic widespread marker bed from the Upper Albian of Texas consisting of a dark-colored *Lithocodium* boundstone (up to 3.6 m thick) traceable over large distances, which interrupts normal shelf margin facies. Following the interpretation of the sequence stratigraphic framework provided by these authors, this marker bed characterizes “the maximum flooding interval of a single third-order depositional cycle” and records “an important environmental change across the platform”. However, further details of what kind of changes these actually were have not been given by Waite et al. (2007). Another example was published from the Late Oxfordian of the Swiss Jura Mountains by Védrine et al. (2007). These authors reported a patchy distribution of “*Bacinella*-*Lithocodium*” oncoids, concentrated around maximum-flooding periods and in highstand deposits “where low-energy conditions existed in relatively deep water but still in the photic zone”. For the Lower Aptian occurrences in the western Maestrat Basin, the levels with the encrusted coral rubble deposits with *Lithocodium aggregatum* should mark the start of the late Early Aptian Tethyan-wide regressive context that in the Galve sub-basin ended with subaerial exposure of platform carbonates at the uppermost Early Aptian (Bover-Arnal et al. 2009a, b). All the examples mentioned seem to indicate a relationship between the abundant occurrences of *Lithocodium aggregatum*-crusts and relative changes in sea level, as evidenced by sequence stratigraphic analyses and the paleoenvironmental disturbances involved.

In the aforementioned Lower Aptian case study from the western Maestrat Basin, an encrustation of dead coral

skeletons was assumed by Bover-Arnal et al. (2009b) and Bover-Arnal (2010). This view is in good accordance with observations from modern reefs, where living corals are mainly infested by passive endoliths (e.g., cryptoendoliths) whereas dead surfaces are actively bored (e.g., Scoffin and Bradshaw 2000). Analyzing Late Jurassic specimens, Bertling and Insalaco (1998, p. 156) made equivalent observations, assuming that living corals did not show equivalent boring densities “because of their protective cover of living tissue”. Also the overall presence of macroborings (*Gastrochaenolites*) is a typical post-mortem feature (e.g., Tapanila et al. 2004). The intense chlorophyte (micro-)bioerosion was obviously favored by an assumed low sedimentation rate. A possible link between high trophic levels and the mass-occurrence of the *Lithocodium-Bacinella*-type crusts described in the present paper was already envisaged by Bover-Arnal et al. (2009b) and Bover-Arnal (2010) in modern reefal environments, high rates of microbioerosion have been attributed to an increasing nutrient supply (e.g., Smith et al. 1981; Rose and Risk 1985; Holmes et al. 2000; Carreio-Silva et al. 2005). Rameil et al. (2010, fig. 10) presented the distribution of *Lithocodium*-crusts in dependence to trophic level, estimating a clear dominance in mesotrophic settings.

In conclusion, the paleoenvironmental significance of *Lithocodium aggregatum* occurrences must be carefully viewed in each case study. The scarce literature dealing with this topic, however, points to increased nutrient concentrations, which could have stimulated blooms of the chlorophyte *Lithocodium aggregatum* Elliott. Furthermore, the associated calcimicrobial paleocommunity and the micro-/macroendolithic community patterns should show differences depending on the water depth where these crusts were formed, as observed in modern taxa (e.g., Golubić et al. 1975; Le Campion-Alsumard 1979; Budd and Perkins 1980; Günther 1990; Glaub 1994; Perry 1998; Glaub 1994; Radtke and Golubić 2005; Gektidis et al. 2006; Glaub et al. 2007; Heindel et al. 2008). Concerning the Lower Aptian *Lithocodium*-crusts in the western Maestrat Basin, the uncertainty of the taxonomic calcimicrobial and ichnotaxonomical composition does not allow a clear conclusion concerning the paleodepth. The data in the literature show that *Lithocodium aggregatum* can occur in shallow-marine settings together with dasycladalean algae but also in deeper water areas (slope, outer shelf) together with planktonic foraminifera. The factors leading to mass-abundances of the *Lithocodium*-type crusts in certain levels/periods is so far poorly understood, but offers a wide area for future research combining geochemical, micropaleontological, biostratigraphical, and sedimentological approaches.

Conclusions

- If we refer to the internal thallus structure, none of the descriptions provided by Elliott (1956) or Radoičić (1959) are complete. *Lithocodium aggregatum* Elliott in its original description represents an ambiguous taxon that cannot reliably be determined as representing a mix-up or assemblage of epilithic-euendolithic chlorophytes and calcimicrobes with an overprint of ichnotaxonomical fabrics. In the Lower Cretaceous, this typical association can be characterized as *Lithocodium aggregatum*-chlorophyte-microbial assemblage. *Lithocodium aggregatum* Elliott is epitypified and redescribed as a filamentous-septate green alga that exhibits a heterotrichale thallus morphology. Also, with its irregular developed vesicular final stage, *Lithocodium* cannot be compared closer with any modern taxon.
- For the time being, *Bacinella* Radoičić is considered a separate genus, a boring filamentous-septate green alga with affinities to the modern ulvacean alga *Eugomontia* Kornmann. Details of the species-specific live histories of the two algae *Bacinella* and *Lithocodium* are still unknown. Therefore, a sporophyte *Gomontia*-phase typically associated with *Lithocodium*-crusts is only tentatively referred to *Lithocodium* Elliott. As the original material of *Bacinella* was not available for re-study, it cannot be ruled out that the holotype figuration of *Bacinella* represents a section through the prostrate branching system of *Lithocodium*, then representing its junior synonym.
- The maintenance of the Lithocodioidea Banner, Finch and Simmons as a subfamily of the Codiaceae or Udoteaceae is challenged as *Lithocodium* must be excluded, and it is rather doubtful that the other genus assigned to this subfamily, *Radoicicinellopsis*, belongs to the siphonous green algae.
- The Late Triassic and most of the Late Jurassic specimens that were referred to *Lithocodium aggregatum* Elliott are different and need taxonomic revision.
- Changes in trophic levels may have led to bloom periods of the epilithic alga *Lithocodium aggregatum* Elliott and its association of invasive chlorophytes and calcimicrobes in the Lower Cretaceous.

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