Diagnostic characters in fossil coralline algae (Corallinophycidae: Rhodophyta) from the Miocene of southern Moravia (Carpathian Foredeep, Czech Republic)

Juraj Hrabovský[a]*, Daniela Basso[b] and Nela Doláková[a]

[a]Department of Geological Sciences, Masaryk University, Kotl-a-rsk-a 2, 611 37 Brno, Czech Republic;
[b]Department of Earth and Environmental Sciences, University of Milano-Bicocca, Piazza della Scienza 4, 20126 Milano, Italy

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Fourteen coralline algal species (Corallinales, Sporolithales) from Early Langhian (Lower Badenian) red-algal limestones of the Carpathian Foredeep (Czech Republic) are described: *Sporolithon lvovicum* (Maslov) Bassi et al., *Lithothamnion roveretoi* Airoldi, *Lithothamnion moretii* Lemoine, ?*Lithothamnion* sp. 1, ?*Lithothamnion* sp. 2, *Mesophyllum alternans* (Foslie) Cabioch & Mendoza, *M.* cf. *erubescens* (Foslie) Lemoine, *M.* cf. *printzianum* Woelkerling & Harvey, *M. curtum* Lemoine, *Phymatolithon* sp., *Lithophyllum* sp. 1, *Lithophyllum* sp. 2, *Hydrolithon lemoinei* (Miranda) Aguirre et al. and *Spongites fruticulosa* Kützing. The characters used in coralline algal species description and identification are summarized and discussed. Five characters newly used in fossil material are associated with the structure and fate of presumed tetrasporangial, gametangial and carposporangial conceptacles, with the shape, size and organization of roof cells, and with the position of the asexuate conceptacles relative to the surrounding thallus surface. Gametangial conceptacles of *Phymatolithon* and gametangial and carposporangial plants of *Sporolithon lvovicum* are described for the first time.

Keywords: coralline algae; morphology; Carpathian Foredeep; Lower Badenian; Early Langhian; Central Paratethys

Introduction

Coralline algal limestones, also known as ‘Lithothamnium’ or Leitha limestones, of the Western Carpathian Foredeep (Czech Republic) have been investigated for general composition and genesis (Nov-ak 1975; Doláková et al. 2008; Zágoršek et al. 2009, 2012), as well as the taxonomy of the limestone-forming biotas (Zdra-z-ılkov-a 1988; Zágoršek 2010a, b). Many coralline species have been also reported from within the area and adjacent Paratethyan basins (Maslov 1956; Studencki 1988; Zdra-z-ılkov-a 1988; Pisera & Studencki 1989). However, according to modern taxonomic criteria (Piller 1994; Aguirre et al. 1996; Vannucci et al. 2009), their description is insufficient. New approaches in the study of the diagnostic characters of living coralline algal species, and reexaminations and redescriptions of living and fossil type species (e.g. Woelkerling 1983 (Philippi Collection); Basso et al. 1998 (Airoldi Collection); Aguirre & Braga 1998 and Aguirre et al. 2012 (Lemoine Collection); Bassi et al. 2007 and Braga et al. 2005 (Maslov Collection)) have supported an actuopalaeontological approach and profound reconsideration of fossil algal taxonomy (Braga et al. 1993; Basso 1994, 1995; Aguirre & Braga 1995). The taxonomy of fossil coralline algae is presently aiming to match biological nomenclature as closely as possible. Although the morphological taxonomy of modern coralline algae also includes characters seldom preserved or not yet reported in fossils, such as epithallial cells and the stages of formation of gametangial conceptacles (Penrose & Chamberlain 1993; Basso et al. 1996, 1997; Aguirre et al. 2012), most of the diagnostic characters applied by biologists are also useful to palaeophycologists (Bosence 1991; Basso et al 1996; Rasser & Piller 1999). Thus, many modern morphological species can be recognized and traced back to the Palaeogene (Basso et al. 1997) or Neogene (Aguirre & Braga 1995; Basso et al. 1996, 1997; Braga et al. 2009; Aguirre et al. 2012). Some new Recent species have been identified based solely on molecular taxonomy (Hina & Saunders 2013), but in other cases there has been a strong effort to use a combination of molecular and morphological characters in an integrated taxonomy (Boero 2010; Basso et al. 2015). Therefore, new characters are still being explored in the biological literature in a rather fluid taxonomic framework, but few of these characters are currently available for the identification of fossil species, such as the size, shape and organization of the vegetative cells (Basso et al. 1997; Aguirre & Braga 1998), and all of the features associated with the calcified chamber of asexuate compartments or conceptacles (Woelkerling & Harvey 1993; Basso 1995). Although some diagnostic characters at supraspecific rank are widely accepted in both the botanical and palaeontological literature (e.g. Braga et al. 1993; Harvey et al. 2005), an updated and comprehensive discussion of their use in combination with diagnostic characters for fossil species identification is presently lacking. The aim of the current study is to describe the fossil coralline algal assemblage of the Western Carpathian Foredeep, providing a critical discussion of the diagnostic criteria used for the circumscription of these fossil taxa.

Material and methods

Material

Samples were collected from outcrops in Kroužek, Podbřežice and -Židlochovice, and drill cores from -Židlochovice. We examined 32 thin sections, mostly cut from rhodoliths, which are stored at the Department of Geological Sciences, Masaryk University, Brno.

Terminology and taxonomy

The description of the growth forms follows Woelkerling et al. (1993), and the description of conceptacles type 1-4 follows Johansen (1981) (Fig. 1). In cases where the incomplete preservation of epithallial cells prevents genus attribution of melobesioid species with non-coaxial hypothallia, we use the notation ?Lithothamnion. Thickness of the ventral core is given in micrometres and also as the number of cells that reflects the number of adjacent filaments in hypothallia within sections of the thallus. The number represents cells of adjacent filaments that are superimposed on each other in the view of the section from the bottom to the top of the ventral core. Systematic positions at higher taxonomic ranks follow Woelkerling (1988), Braga et al. (1993), Harvey et al. (2003a), Le Gall et al. (2009) and Kato et al. (2011). The subfamily Mastophoroideae Setchell sensu Harvey et al. (2003a) is presently considered polyphyletic and is under revision (Kato et al. 2011). For this reason, Kato et al. (2011) split Mastophoroideae into three new subfamilies - Porolithoideae, Neogoniolithoideae and Hydrolithoideae - based on molecular data, and vegetative and reproductive anatomy of modern coralline algae, while leaving the taxonomic placement of Spongites unresolved. The two suprageneric taxonomic schemes (Harvey et al. 2003a; Kato et al. 2011) are not compatible as they use different diagnostic characters. However, Guiry & Guiry (2013) retained both systems, distinguishing the subfamilies Hydrolithoideae, Porolithoideae and Neogoniolithoideae according to Kato et al. (2011) while leaving Spongites and Pneophyllum in Mastophoroideae, following Braga et al. (1993) and Harvey et al. (2003a). We here follow Guiry & Guiry (2013), although we are aware that the systematic position of Spongites and Pneophyllum still needs to be verified (Kato et al. 2011).

Measurements

It should be noted that the measured parameters of vegetative and reproductive anatomy of each identified specimen were taken from a single plant. After the species were identified, we were able to apply a description to comparable species from other thin sections. Measurements of other plants of the same species are not included in the descriptions. For this reason, thin sections with the best preserved diagnostic characters are cited in the systematic account. Measured diagnostic characters are listed in Supplemental Table 1.

Abbreviations

LS, longitudinal section; VC, ventral core of basal filaments D hypothallium; PF, peripheral filaments D perithallium; EC, epithallial cells; D, diameter; L, length; H, height. The internal height of the columellate uniporate conceptacle chambers is given as H1 (from the central columella to the base of the pore canal) and H2 (the maximum height of the conceptacle chamber periphery) (following Basso et al. 1996). Measures in brackets indicate uncommonly observed minimum and maximum values.

Geological setting, age and lithology

The Carpathian Foredeep represents a system of Central Paratethyan peripheral basins connected by seaways to the other Paratethyan basins, the Mediterranean and Indo- Pacific (Kováč 2000; Kováč et al. 2007). The development of the Carpathian Foredeep was controlled by load from an accretionary wedge nappe pile as well as the deep subsurface load in front of the orogen in a compressive tectonic setting (Oszczypko 1998; Kováč et al. 2007). The sedimentary infill of its western sector (Southern Moravia, Czech Republic) consists of lower and middle Miocene mostly marine deposits, and Quaternary terrestrial sediments (Nehyba et al. 1997; Brzobohat-y et al. 2003; Kováč et al. 2007). The formation of red-algal limestone bodies at the studied localities occurred during the Early Badenian (D Early Langhian) within the Praeorbulina glomerosa and Orbulina suturalis planktonic foraminiferal biozones and nannoplankton zone NN5 (Fig. 2; Kováč et al. 2007; Doláková et al. 2008). The co-occurrence of the planktonic foraminifers Praeorbulina and Orbulina points to the second marine transgression during the ‘styrian’ or ‘intra-Badenian’ tectonic phase around 14.7 Ma (Kováč et al. 2007). This coincides with the acme of the Paratethyan carbonate factory and abundance of marine molluscs during the Early Badenian ‘build-up’ event (Harzhauser & Piller 2007; Piller et al. 2007). The Lower Badenian deposits represent the final stage of the marine depositional history of the western Carpathian Foredeep (Kováč et al. 1989). The studied sections are located on the eastern margin of the former sea (Fig. 3). The limestones represent a biological and lithological complex that forms blocks or lenses in calcareous ‘T-egel’ clays overlying basal coarsegrained deposits or directly on the pre-Badenian basement (Doláková et al. 2008). Occasionally they outcrop from surrounding sediments in small areas. The limestones are formed mostly by coralline red algae, bryozoans and molluscs, and, to a lessser extent, serpuliids, foraminifers and echinoids. They are sandy limestones due to a high content of lithoclasts or terrigenous material that may be locally dominant (Doláková et al. 2008). Generally, the composition of the algal limestones and the lithology of the eastern palaeocoast were controlled by tectonic activity and high-energy relief, in contrast to the western more or less gently deepening margin, with possible in situ formation (Doláková et al. 2008).

Systematic palaeontology

Division Rhodophyta Wettstein, 1901 Class Florideophyceae Cronquist, 1960

Subclass Corallinophycidae Le Gall & Saunders, 2007

Order Sporolithales Le Gall, Payri, Bittner & Saunders, 2009

Family Sporolithaceae Verheij, 1993

Genus *Sporolithon* Heydrich, 1897

Type species. *Sporolithon ptychoides* Heydrich, 1897, Recent, Sinai Peninsula, Egypt.

Sporolithon lvovicum (Maslov, 1956) Bassi et al., 2007

(Fig. 4A-H)

1956 Archaeolithothamnium keenanii var. lvovicum Maslov: 151, pl. 53, fig. 2, pls 54-55, text-fig. 75.

2007 Sporolithon lvovicum (Maslov); Bassi et al.: 121, fig. 4c-f. Basionym. Archaeolithothamnium keenanii var. lvovicum Maslov, 1956.

Material. Diagnostic characters best seen in thin sections 42139-111151 and 17311951. Age and locality. Lower Badenian (Early Langhian), Židlochovice, Kroužek, Carpathian Foredeep, Czech Republic.

Stratigraphical range. Badenian (Langhian-Early Serravallian).

Description. Growth form encrusting to warty protuberant, thallus 218-371 µm thick, protuberances L 0.9-2 µmx D 1.4-1.9 µm (Fig. 4A). Thallus monomerous with dorsiventral organization (Fig. 4B). VC non-coaxial, plumose, up to 10 cells thick (Fig. 4B). Cells rectangular, L 21-34 µm x D 9-16 µm (n D 25). PF zonation present (Fig. 4C). Zones consist of 3-6 long rectangular cells and 2-6 short rectangular to squarish cells. Cells L 14-17 (24) µm x D 9-14 µm (n D 20). Cell fusions present in VC and PF (Fig. 4B). Empty 6-15 calcified tetrasporangial compartments grouped in sori within the protuberances (Fig. 4A, D). Chambers H 91-120 µm x D 45-58 µm (n D 13), separated by 5-6-celled paraphyses that are as long as or longer and narrower than normal PF cells. Long cells of the paraphyses measure L 16-20 µm x D 6-8 µm (n D 8; Fig. 4E). No distinct layer of elongated cells below tetrasporangial compartments. Sori probably raised over the surrounding thallus surface at the time of maturity and later buried by new, subsequent thallus growth (Fig. 4A, D). Two carposporangial conceptacles observed. Carposporangial uniporate conceptacles are flask shaped, H 272-294 µm x D 368-419 µm, protrude markedly above the thallus surface in encrusting as well as in protuberant thalli (Fig. 4F). Roof 96-107 µm thick, 8-12-celled (Fig. 4F). Pore canal L 126 µm x D 83 µm. Gametangial uniporate conceptacle H 130 µm x D 510 µm (only one observed) protrudes on the thallus surface, apparently on the same thallus as the carposporangial plant. Roof type 1, consisting of 11 cells (Fig. 4G-H). We consider it a male conceptacle.

Remarks. Fusion of gametangial and sporangial plants was already described by Verheij (1993). Measured vegetative anatomy, conceptacles and growth form fit the type description (Bassi et al. 2007).

Order Corallinales Silva & Johansen 1986
Family Hapalidiaceae Grey, 1864
Subfamily Melobesioideae Bizzozero, 1885
Genus *Lithothamnion* Heydrich, 1897 nom. cons.
Type species. *Lithothamnion muelleri* Lenormand ex Rosanoff, 1866, recent, Western Port Bay, Victoria.

Lithothamnion roveretoi Airoldi, 1932
(Figs 5, 18A)
1932 Lithothamnion roveretoi Airoldi: 66, pl. 10, fig. 1a-c.
2010b Lithothamnion roveretoi Airoldi; Vannucci et al.: 224, pl. 1, figs 1-8.
Material. Diagnostic characters best seen in thin section 27611451.
Age and locality. Lower Badenian (Early Langhian), Podbřežice, Carpathian Foredeep, Czech Republic. Stratigraphical range. Thanetian to Serravallian (Vannucci et al. 2010b).
Description. Growth form encrusting, non-protuberant, thallus 610-784 µm thick, on other algae or on biogenic remains in multispecific rhodoliths (Fig. 5A). Thallus monomerous, with dorsiventral organization. VC up to 76 µm and eight cells thick. Cells rectangular to slightly trapezoidal, L 15-16 µm x D 7-8 µm (n D 10; Fig. 5B). PF zoned (Fig. 5B), with squarish to rectangular cells. Cells L 9-13 (15) µm x D 8-10 µm (n D 38). Longest PF cells occur at the base of zones or on lateral side of the conceptacles. Cell fusions present in VC and PF (Fig. 5B). Layer of flattened and probably flared EC, L 3-4 µm x D 4-5 µm (n D 7) observed above the conceptacles (Fig. 5C).
Multiporate asexuate conceptacles with flat roof and floor, markedly protruding about 65-76 µm above thallus surface (Figs 5A, 18A). Roof 5-6 cells (46-50 µm) thick, without rim. Roof cells L 7-12 µm x D 7-8 µm (n D 9), comparable to cells of the PF (Fig. 5D). Chambers 98-135 µm H and 327-498 µm D (n D 5). D/H is 2.7-3.3. Pore canals crossing the roof, about D 11 µm.
Remarks. Vannucci et al. (2010b) redescribed the type material of Lithothamnion roveretoi Airoldi, 1932. Measured vegetative anatomy, conceptacles and growth form fit their description.

Lithothamnion moretii Lemoine, 1928a
(Figs 6, 18B)

1928 Lithothamnium moretii Lemoine: 547, figs 2-3.

2012 Lithothamnion moretii Lemoine; Aguirre et al.: 300, figs 16-20.

Basionym. Lithothamnium moretii Lemoine, 1928a.

Material. Diagnostic characters were best seen in thin section 42139-111151.

Age and locality. Lower Badenian (Early Langhian),-Židlochovice, Carpathian Foredeep (Czech Republic).

Stratigraphical range. Priabonian-Early Serravallian.

Description. Growth form encrusting to protuberant (Fig. 6A) on other coralline algae. Protuberances up to L 3 μm x D 1.2 μm, crusts 392-567 μm thick. Thallus monomerous, dorsiventral. VC plumose, 8-11 cells thick, 69-109 μm thick. Cells rectangular, L 15-20 μm x D 7-9 μm (n D 15; Fig. 6B). PF zoned (Fig. 6B), formed by 2-5 rows of the rectangular cells L 15-17 μm x D 7-10 μm (n D 10) with large lumen and thin cell walls, and 1-4 rows of mostly squarish cells with small lumen and thick walls, L 9-13 μm (n D 17). Long cells grow abruptly on the short cells and became gradually shorter along the axis of the growth, towards the top. Zones are best developed in the protuberances. Cells of PF horizontally and vertically aligned. Cell fusions present in VC and PF (Fig. 6B). EC flattened and possibly flared, 4-5 μm long and 6-7 μm (n D 6) in diameter (Fig. 6C). Multiporate asexuate conceptacles developed mostly in protuberances (Figs 6A, 18B). Chambers H 128-143 μm x D 267-342 μm (n D 3), protrude 60-70 μm above the thallus surface. Chambers rectangular with flat floor and roof and rounded sides. D/H is 1.4-2.3. Poorly preserved roof 28-30 μm thick, consisting of 2-4 cells, lacking peripheral rim (Fig. 6D). Roof cells L 7-8 μm x D 6-8 μm (n D 15), different from the long cells at the sides of the conceptacles, comparable to the short squarish cells of the PF (Fig. 6D).

Remarks. Aguirre et al. (2012) redescribed the lectotype of Lithothamnion moretii Lemoine, 1928a. Measured parameters of vegetative anatomy, conceptacles and growth form fit their description.

?*Lithothamnion* sp. 1

(Figs 7, 18C)

Material. Diagnostic characters were best seen in the thin section 42139-11851.

Age and locality. Lower Badenian (Early Langhian), Židlochovice, Carpathian Foredeep, Czech Republic.

Description. Growth form encrusting. Thallus 261-654 μm thick. Superposed thalli up to 1.2 μm thick in the fertile portions with several conceptacles, where they appear warty-protuberant (Fig. 7A). Thallus monomerous, dorsiventral. The ventral core of the basal filaments plumose, 7-10 cells thick. Cells rectangular, L 14-20 μm x D 6-8 μm (n D 15). PF zonation irregular, not equally developed (Fig. 7B). Cells square to subrectangular, L 7-8 (17) µm x D 6-7 (9) (n D 15) µm, weak lateral and vertical alignment of cells. Cell fusions present in VC and PF (Fig. 7B). Multiporate asexuate conceptacles raised 112-142 µm above the thallus surface (Figs 7C, 18C). Chambers ellipsoidal, H 105-131 µm x D 349-545 µm (n D 5), with flat roof and floor. D/H is 2.3-3.3. Roof 38-48 µm thick, without rim, formed by 6-8 cells, L 5-6 µm x D 4-5 µm. Roof cells differ in size from vegetative PF (Fig 7D).

Remarks. ?Lithothamnion sp. 1 has some affinity with Lithothamnion obstrusum Airoldi as revised by Vannucci et al. (2010b); however, generic attribution is uncertain because we could not observe the shape of EC. Moreover, ?Lithothamnion sp. 1 has larger PF cells than L. obstrusum, and a characteristic gap left by overgrowth of the tetrasporangial conceptacles that is not known in L. obstrusum which, according to Vannucci et al. (2010b), is exclusively found in the Oligocene. Since many type species still need revision (Vannucci et al. 2009), we prefer to use open nomenclature and refer to our material as ?Lithothamnion sp. 1.

?*Lithothamnion* sp. 2

(Figs 8, 18D)

Material. Diagnostic characters were best seen in the thin section 17311951.

Age and locality. Lower Badenian (Early Langhian), Kroužek, Carpathian Foredeep, Czech Republic.

Description. Growth form fruticose, protuberances up to L 3.3 µm x D 1.5 µm (Fig. 8A). Thallus monomerous. Only secondary VC formed above the conceptacles was observed, 5 to 7 cells thick, non-coaxial. Cells L 17-19 µm x D 6-8 µm (n D 10; Fig. 8B). PF zoned (Fig. 8A), each filament consisting of 4-6 long cells, L 20-22 µm x D 8-11 µm, followed by 3-6 shorter cells, L 12-18 µm x D 8-12 µm (n D 23). Alternation of bands of long and short cells produce zonation. Cell fusions present in VC and PF (Fig. 8B). EC not observed. Multiporate asexuate conceptacles H 89-96 µm x D 236-327 µm (n D 4) with flat roof and floor (Fig. 8A-B, 18D). D/H is 2.6-3. Roofs 33-45 µm, 5-9 cells thick, without rim. Roof cells flattened to rectangular, L 4.5-8 µm x D 4.5-6 µm, thus different from cells of the PF (Fig. 8B).

Genus *Mesophyllum* Lemoine, 1928

Type species. *Mesophyllum lichenoides* Lemoine, 1928,
Recent, Cornwall, England.

Mesophyllum alternans (Foslie, 1907) Cabioch & Mendoza, 1998

(Figs 9, 18E)

1907 Lithothamnion philippi f. alternans Foslie: 17.

1998 Mesophyllum alternans (Foslie); Cabioch & Mendoza: 209, figs 1-20.

Basionym. Lithothamnion philippi f. alternans Foslie, 1907.

Material. Diagnostic characters best seen in the thin section 42139-111151.

Age and locality. Lower Badenian (Early Langhian), Židlochovice, Carpathian Foredeep, Czech Republic.

Stratigraphical range. Badenian (Early Langhian) to Recent.

Geographical distribution and habitat. Mediterranean and eastern Atlantic south of the Bay of Biscay. Species grow in the Atlantic intertidal zone, and to the depth of the dim light coralligène environment in the Mediterranean, at depths of 20-40 m (Cabioch & Mendoza 1998; Garrabou & Ballesteros 2000).

Description. Growth form encrusting non protuberant (Fig. 9A). Thallus 0.2-1.3 µm thick. Thallus monomerous, dorsiventral. VC plumose, non-coaxial to coaxial (Fig. 9A), 44-196 µm and 6-25 thick, consisting of rectangular cells, L 19-25 µm x D 10-13 µm (n D 20). PF weakly and irregularly zoned, formed by square to rectangular cells, L 8-11 (15) µm x 6-9 µm (n D 20), with weak lateral and vertical alignment. Cell fusions present in PF and VC (Fig. 9B). EC, L and D 4-5 µm (n D 7) x D 7 µm, flattened to rounded, in one layer (Fig. 9B). Meristematic cells as long as or longer than subtending cells (Fig. 9B). Multiporate asexuate conceptacles (Fig. 9C, D) slightly raised (up to 100 µm) above the surrounding thallus surface (Figs 9D, 18E), occasionally buried by subsequent thallus growth. Chambers H 131-216 µm x D 340-420 µm (n D 8), frequently filled by large, irregularly- shaped sterile cells (Fig. 9C, D). Adjacent fused conceptacles can reach D - 565 µm (Fig. 9A). D/H is 1.6-2.9. A layer of flat cells occurs at the base of the conceptacles (Fig. 9G). Roof 59-79 µm, 7-8 cells thick with weak peripheral rim (Fig. 9C). Roof cells L 8- 12 µm x D 7-9 µm (n D 30), thus comparable to the cells of the PF, becoming shorter towards the roof surface. Cells bordering pore canals somewhat narrower than adjacent cells (Fig. 9C). Pore canals L 61-79 µm x D 19 µm.

Remarks. Our material fits the description of Cabioch & Mendoza (1998).

Mesophyllum cf. *erubescens* (Foslie, 1900)

Lemoine, 1928

(Figs 10, 18F, G)

1900 Lithothamnion erubescens Foslie: 9.

1928 Mesophyllum erubescens (Foslie); Lemoine: 252.

Basionym. Lithothamnion erubescens Foslie, 1900.

Material. Diagnostic characters were best seen in the thin sections 42139-11551 and 42139-11951.

Age and locality. Lower Badenian (Early Langhian), Židlochovice, Carpathian Foredeep, Czech Republic.

Stratigraphical range. Lower Badenian (Early Langhian).

Geographical distribution and habitat. Mesophyllum erubescens is a cosmopolitan species (from New Zealand and South Australia, to Africa, South America and the Caribbean), growing down to about 25 m of water depth with variable growth forms (Farr et al. 2009; Horta et al. 2011).

Description. Growth form encrusting non-protuberant to layered to foliose. Thallus of relatively constant thickness 350-460 µm, superposed thalli up to 760 µm thick (Fig. 10A). Plant monomerous, dorsiventral (Fig. 10A, B). The VC coaxial to non-coaxial, 152-196 µm and 22-24 cells thick, formed by rectangular to trapezoidal cells, L 23-35 µm x D 9-12 µm (n D 15; Fig. 10B). PF 196-436 µm thick, zones irregular and wavy (Fig. 10B). Cells of PF rectangular to squarish, L 8-12 µm x D 7- 10 µm (n D 21). Cell fusions present in VC and PF (Fig. 10B). One layer of rounded to flattened EC, L 4-5 µm x D 5-7 µm (Fig. 10C). Cells of the meristem as long as or longer than cells subtending them. Multiporate asexuate conceptacles slightly protruding above the thallus surface (Figs 10D, 18F, G), and undergoing burial by subsequent thallus growth. Chambers in LS subrectangular with rounded sides, flat roof and floor, H 104-118µm x D 289-316 µm (n D 6). D/H is 1.8-3. Roof thin, about 30 µm and 3-4 cells thick, without peripheral rim. Squarish to slightly rectangular roof cells, L 5-7 µm (n D 7) x D up to 6 µm, thus different from cells of the vegetative PF.

Remarks. Our material is consistent with the comparative description of M. erubescens amongst other Mesophyllum species provided by Peña et al. (2011); however, the encrusting non-protuberant to layered growth form of the Badenian fossil differs from the knobby growth form of the living species. Moreover, we could not observe the shape of the pore canal cells, and therefore we consider the identification as uncertain.

Mesophyllum cf. *printzianum* Woelkerling & Harvey, 1993

(Figs 11, 18H)

1993 Mesophyllum printzianum Woelkerling & Harvey: 593, figs 24-29.

Material. Diagnostic characters were best seen in the thin section 17311951.

Age and locality. Lower Badenian (Early Langhian), Kroužek, Podb-ze-zice, -Židlochovice, Carpathian Foredeep,

Czech Republic.

Stratigraphical range. Lower Badenian (Early Langhian).

Description. Growth form encrusting, warty-protuberant in multispecific rhodoliths (Fig. 11A). Thallus 176- 730 µm thick. Maximum thickness reached by local superposition of the thalli. Protuberances L 5 µm x D 5 µm. Thallus monomerous, dorsiventral organization in the crustose portions. VC coaxial (Fig. 11B), 70-124 µm and (10) 16-20 thick, formed by trapezoidal cells, L 14-22 µm x D 5-7 µm (n D 15). PF irregularly and weakly zoned (Fig. 11A, B). Zones, when present, consist of long cells at the zone base that shorten towards the zone top along the axis of growth. Horizontal and vertical alignment of PF cells seldom observed in some spots. PF cells L 9-12 µm x D 6-8 µm (n D 28), squarish to rectangular. At the thallus surface and at the top of some conceptacles, two layers of the rounded to flattened but not flared EC, L 3-4 µm x D 7-8 µm (n D 8) occur (Fig. 11B). Cells of the meristem as long as or longer than cells subtending them (Fig. 11B). Multiporate asexuate conceptacles and uniporate carposporangial conceptacles were observed. Sporangial conceptacles in LS appear roundish to ellipsoidal with more or less rimmed roof and flat to slightly concave floor (Figs 11A, 18H). Chambers H 145-217 µm x D 275-403 µm (n D 9), rarely (three of tens observed) filled with large cells. D/H is 1.4-2.6. Roof, 45-54 µm thick, consisting of up to six squarish to slightly rectangular cells, L 4-9 µm x D 4-6 µm (n D 17), becoming shorter toward the roof surface. Cells of the roof are a little shorter than PF cells. In transverse section of the pore plate the pores appear bordered by about nine rosette cells (Fig. 11C). Conceptacles up to 100- 120 µm raised above the thallus surface. Carposporangial conceptacles uniporate, roundish, protruded above the thallus surface. Chambers H up to 280 µm x D up to 500 µm in diameter with pore canal L 100-160 µm x D 35 µm (Fig. 11D).

Remarks. All of the features described above fit the concept of Mesophyllum printzianum, as circumscribed by several authors (Woelkerling & Harvey 1993; Womersley 1996; Harvey et al. 2005; Farr et al. 2009). This is a living species not known outside Australasia, where it grows in intertidal and subtidal marine habitats to at least 25 m depth. Since we could not observe the diagnostic long cells bordering the base of the pore canals, and due to the present-day distribution of the species, we leave the identification uncertain.

Mesophyllum curtum Lemoine, 1939

(Figs 12, 18I)

1939 Mesophyllum curtum Lemoine: 92, pl. 2, fig. 13,text-fig. 61.

1998 Mesophyllum curtum Lemoine; Aguirre & Braga: 497, pl. 2, figs 5-7.

Material. Diagnostic characters were best seen in thin section 17311851.

Age and locality. Lower Badenian (Early Langhian), Židlochovice, Kroužek, Carpathian Foredeep, Czech Republic.

Stratigraphical range. Langhian (Early Badenian) to Tortonian.

Description. Growth form encrusting to warty protuberant, also as monospecific rhodolith (Fig. 12A). Thallus monomerous, dorsiventral organization in the encrusting portions. VC coaxial, up to about 200 µm and 13-22 cells thick, consisting of rectangular to slightly trapezoidal cells, L 11-27 µm x D 5-10 µm (n D 20; Fig. 12B). PF zoned (Fig. 12C, D). Each zone is 7-10 cells, 95-144 µm thick. Long cells at the base of the zone gradually shorten along the axis of growth towards the top. Transition of the short cells of one zone to the long cells of the next zone is abrupt.

Vertical and lateral alignment of cells usually evident. PF cells rectangular, L 8-16 µm x D 5-11 µm (n D 20). Cell fusions present in the PF and VC. Flattened, not flared EC L 3-6 µm x D 5-6 µm (n D 15) in one layer. Meristematic cells L 11-14 µm (n D 8) x D about 8 µm, as long as or longer than the cells subtending them (Fig. 12D). Asexuate multiporate conceptacles roundish to elliptical in sections, raised 100-180 µm above the thallus surface, abundantly borne in the crustose portions as well as in the protuberances (Figs 12A, 18I). Chambers H 128-226 x D 255-409 µm (n = 10). Roofs flat to slightly concave, 36-80 µm thick, consisting of 5-7 rectangular to mostly squarish cells, L 4-8 µm x D 3-5 µm (n D 17; Fig. 12B, E). D/H is 1-1.8. Roof cells became shorter toward the roof top. Pore canals L 41-80 µm x D 8-9 µm (Fig. 12E). In transverse section the pore is bordered by up to seven cells of the same dimensions as the other roof cells, but smaller than the vegetative PF cells (Fig. 12F).

Remarks. Aguirre & Braga (1998) redescribed the type material of Mesophyllum curtum Lemoine, 1939 from the Tortonian of Algeria. Measured parameters of vegetative anatomy, conceptacles and growth form in our material fit their description.

Genus *Phymatolithon* Foslie, 1898

Type species. Phymatolithon calcareum (Pallas, 1766)

Adey & McKibbin, 1970, Recent, Falmouth Harbour, England.

Phymatolithon sp.

(Fig. 13)

Material. Diagnostic characters were best seen in the thin section 42139-11951.

Age and locality. Lower Badenian (Early Langhian), Židlochovice, Carpathian Foredeep, Czech Republic.

Description. Growth form encrusting with undulate to knobby surface on biogenic remains or other coralline algae (Fig. 13A). Thallus monomerous with dorsiventral organization in the crustose portions. VC non-coaxial to locally apparently coaxial, 4-10 (20) cells thick (Fig. 13A). Cells rectangular in LS, L 12-20 µm x D 6-8 µm (n D 10). PF consist of zones 5-11 cells thick (Fig. 13B, C). Each zone defined by the gradual transition of long cells to short cells. Long cells of the new zone grow abruptly from the short cells along the axis of growth. Cells L 7-9 µm x D 5-7 µm (n D 24), rectangular with ovoid lumen (Fig. 13B, C). Cell fusions present in PF and VC. Rounded to flattened EC L 3-4 µm (n D 5) x D about 6 µm terminating the peripheral filaments at the thallus surface. Meristematic cells as long as or shorter than the cells subtending them (Fig. 13B). Asexuate multiporate conceptacles roundish with slightly concave to flat roof in LS, 3-5 cells thick, formed in knobby protuberances and slightly raised 20-45 µm above the thallus surface (Fig. 13C). Roof cells L 6 µm x D 5 µm (n D 10). Pores L up to 23 µm x D 8 µm. Chambers H 102-110 µm x D 157-223 µm (n D 6). D/H is 2.2-2.4. One gametangial plant with the same vegetative characters was observed adjacent to a tetrasporangial plant (Fig. 13A, D). Uniporate gametangial conceptacles borne on warty protuberances (Fig. 13D). Chambers H 70- 76 µm x D 184-189 µm (n D 2), protruding above thallus surface (Fig. 13D), with pores L 49 µm x D 16 µm. The floor of the conceptacles is flat to slightly convex. Mature conceptacles are not filled by vegetative cells.

Family Corallinaceae Lamouroux, 1812
Subfamily Lithophylloideae Setchell, 1943
Genus *Lithophyllum* Philippi, 1837
Type species. Lithophyllum incrustans Philippi, 1837,
Recent, near Sicily, Mediterranean Sea.

Lithophyllum sp. 1
(Fig. 14)
Material. Diagnostic characters were best seen in the thin section 17311951.
Age and locality. Lower Badenian (Early Langhian), -Židlochovice, Kroužek, Carpathian Foredeep, Czech Republic.
Description. Growth form encrusting on biogenic remains, frequently other coralline algae. Thallus up to 700 µm thick. Thallus dimerous with dorsiventral organization, locally showing a 'false coaxial' VC (Fig. 14A). VC consists of mostly squarish, rarely rectangular cells, L 12-17 µm x H 11-21 µm (n D 13). Cells of the PF squarish to rectangular, L 12-15 µm x D 8-12 µm (n D 20). The regular alignment of PF cells is evident (Fig. 14A, B). Cell fusions not observed. EC not preserved. Uniporate conceptacles presumed asexuate (Fig. 14B) appearing in LS as kidney-shaped, columellate. Chambers H 93-120 µm (H2) x D 193-246 µm (n D 9). After release of spores, they were sunken in the thallus by subsequent plant growth. Pores L 40-50 µm x D 27- 50 µm their base

(Fig. 14B). Roofs 47-52 µm thick, consist of cell filaments growing more or less perpendicular to the conceptacle chamber floor (Type 2), made of cells with the same size as those of the vegetative PF.

Lithophyllum sp. 2
(Fig. 15)
Material. Diagnostic characters were best seen in the thin section 17311851.
Age and locality. Lower Badenian (Early Langhian), Kroužek, Carpathian Foredeep, Czech Republic.

Description. Growth form encrusting to protuberant, thallus 0.6-0.7 µm thick on other coralline algae in the multispecific rhodoliths (Fig. 15A, B), unbranched, warty protuberances L up to 1.5 µm x D 1.5 µm (Fig. 15B).
Thallus dimerous to monomerous non-coaxial, with dorsiventral organization (Fig. 15C). Cells of the VC squarish to rectangular, L 11-29 µm x D 10-12 (14) µm (n D 20) in monomerous VC. PF consisting of rectangular to squarish cells with good vertical alignment of the cells. Cells of variable length, following a wavy, irregular zonation of the PF. Short cells are L 10-14 (18) µm x D 7-12 µm (n D 15), long cells L 18-25 µm x D 8-12 µm (n D 15). One to two layers of long cells are followed by one to two layers of short cells. Cell fusions not observed. Uniporate conceptacle with columella (Fig. 15A). Chambers buried in the thallus H 75-77 µm x D 163-191 µm (n D 5) (Fig. 15A, D). Pore canal cylindrical to bulbous, L 51-56 µm x D 31-39 µm, opening in a small depression below the surrounding thallus surface (Fig. 15D).

Subfamily Hydrolithoideae Kato & Baba in Kato et al. 2011
Genus *Hydrolithon* (Foslie) Foslie, 1909
Type species. Hydrolithon reinboldii (Weber-van Bosse & Foslie) Foslie, 1909, Recent, Muras Reef, East Kalimantan, Indonesia.

Hydrolithon lemoinei (Miranda, 1935) Aguirre et al., 2012
(Fig. 16)
1935 Melobesia lemoinei Miranda: 284, fig. 3A, B, pl. 38, fig. 1.
2011 Hydrolithon lemoinei (Miranda) comb. nov; Aguirre et al.: 282, fig. 6A-C.
Material. Diagnostic characters were best seen in the thin section 17311951.

Age and locality. Lower Badenian (Early Langhian), -Židlochovice, Kroužek, Carpathian Foredeep, Czech Republic.

Stratigraphical range. Oligocene to Lower Badenian (Early Langhian).

Description. Growth form: encrusting thallus 3-15 cells thick (Fig. 16A). In some portions of the rhodolith, only superposed VC occur. Thallus thicker in fertile portions (Fig. 16A). Specimens encrust substrate or biogenic remains, frequently other coralline algae. Thallus dimerous with dorsiventral organization (Fig. 16B). Cells of the VC squarish, rectangular or flattened, H 15-22 µm x L 14-24 µm (n D 10). PF consist of square to rectangular cells, L 13-26 µm x D 10-17 µm (n D 10). Since cells dimensions and shape abruptly change, both lateral and vertical alignment of the adjacent cells are weak or missing. Cell fusions present in VC and PF (Fig. 16B). Asexuate conceptacles H 131-143 µm x D 230-248 µm (n D 2), markedly protruding above thallus surface (Fig. 16A). Pore canals cylindrical, L 140-156 µm x D40-41 µm. Roof formed by shorter and narrower cells, 10-L 16.5 µm x D 9-13 µm. Cells surrounding pore canals perpendicular to the chamber roof (Type 2).

Remarks. Aguirre et al. (2012) redescribed the type material of Hydrolithon lemoinei (Miranda, 1935). Measured parameters of vegetative anatomy, conceptacles and growth form in our material fit their description.

Subfamily Mastophoroideae Setchell, 1943

Genus *Spongites* Kützing, 1841

Type species. Spongites fruticulosa Kützing, 1841, Recent, Mediterranean Sea.

Spongites fruticulosa Kützing 1841

(Fig. 17)

1841 Spongites fruticulosa Kützing: 33.

2006 Spongites fruticulosus Kützing; Basso & Rodondi:404, figs 1-34, tab. 1.

Heterotypic synonym. Spongites albanensis (Lemoine) Braga et al., 1993, p. 544, pl. 2, figs 1, 3, 4.

Material. Diagnostic characters were best seen in the thin section 42139-111051.

Age and locality. Lower Badenian (Early Langhian), Podbřežice, -Židlochovice, Carpathian Foredeep, Czech Republic.

Stratigraphic range. Oligocene to Recent.

Geographical distribution and habitat. Spongites fruticulosa is widespread within the Mediterranean Sea, where it occurs from 12 to 75 m depth. The species also inhabits the north-eastern Atlantic Ocean, the Indian Ocean and the Pacific Ocean (Basso & Rodondi 2006).

Description. Growth form encrusting, on bryozoans, coralline algae or serpulid tubes (Fig. 17A). Thallus monomerous or dimerous, organization dorsiventral (Fig. 17A). VC is 3-9 cells thick, consisting of rectangular cells, L 13- 26 µm x D 8-17 µm (n D 13). PF weakly zoned, made of rectangular, squarish to polygonal cells. Since shape of the cells change abruptly, weak or no lateral and vertical alignments of cells occur (Fig. 17A, B). PF cells L 9-23 µm x D 8-17 µm (n D 20). PF terminated by 1-2 flattened EC, L 6-8 µm x D 8-14 µm (n D 7) (Fig. 17B). Cell fusions occur both in the VC and the PF (Fig. 17B). Asexuate conceptacles empty and sunken in thalli by subsequent growth after release of spores (Fig. 17A, B). Chambers measure H 112-173 µm x D 306-370 µm (n D 6). Pore canal coneshaped, narrowing to the top, L 34.7-154.6 µm x D 57-92 at the base of pore. Roof consists of cells running more or less parallel to the chamber floor and bend toward the top to form the pore canal (Type 1).

Remarks. Our species fits the description of Basso & Rodondi (2006).

Discussion

Fourteen species of non-geniculate coralline algae were identified from the Lower Badenian (Early Langhian) redalgal limestones of the Carpathian Foredeep (Central Paratethys, Czech Republic). One species belongs to the order Sporolithales (genus Sporolithon) and the others to the order Corallinales, with nine species of the subfamily Melobesioideae (genera Lithothamnion, Mesophyllum, Phymatolithon), two species of Lithophylloideae (genus Lithophyllum), one species of Mastophoroideae (genus Spongites) and one species of Hydrolithoideae (genus Hydrolithon). The possibility of using the same diagnostic characters as used in biological material to separate fossil coralline species has already been discussed by many authors (Bosence 1991; Braga et al. 1993; Basso 1994, 1995; Rasser & Piller 1999). We have recognized observable diagnostic characters of fossil corallines (Supplemental Table 1) that provide the basis for species identification (key in Supplemental Table 2). We list the characters previously used in palaeontology by Bosence (1991), Braga et al. (1993), Aguirre & Braga (1995), Basso (1995), Basso et al. (1996, 1998), Aguirre & Braga (1998), Rasser & Piller (1999) and Vannucci et al. (2000, 2010a,b), and five characters recognized by phycologists but which are new to fossil coralline algal taxonomy. It should be noted that not all of these new characters were commonly observed in the studied samples, such as the epithallial cells, the gametangial conceptacles and the rosette cells. The newly applied characters are associated with the structure and fate of presumed tetrasporangial, gametangial and carposporangial conceptacles, with the shape, size and organization of roof cells and with the position of the asexuate conceptacles relative to the surrounding thallus surface. In Sporolithon lvovicum, we were able to include a number of cells in paraphyses. Since the examined anatomical characters have different diagnostic values, we discuss separately below those that are used for higher taxonomy and genera, and those that may be useful for the delimitation of fossil species.

Diagnostic characters at supraspecific ranks

Conceptacles. Johansen (1981) distinguished four types of tetra/bisporangial conceptacles based on the participation of the filaments in forming the conceptacle roof, and the way in which the chamber and the pore canal are formed. Conceptacles of Type 1 are uniporate (Fig. 1A). The roof is formed of filaments overarching from around the fertile area. The chambers are underneath the overarching roof and the pore-canal is surrounded by the ends of the roof filaments. Type 2 conceptacles are also uniporate; however, the roof is formed of filaments which have developed from within the fertile area (Fig. 1B). The chamber is formed by the breakdown of cavity cells amongst the reproductive cells. The canal and pore are formed by local tissue breakdown. Conceptacles of type 3 are multiporate and their roofs are formed of filaments which develop from within the fertile area (Fig. 1C). The chamber is formed by the breakdown of cavity cells amongst the reproductive cells; canal and pore are formed in the space occupied by a gelatinous plug. Each plug is formed above a tetrasporangium. Conceptacles of type 4 are uniporate (Fig. 1D). The roof is formed as in Type 3, except that the vegetative filaments amongst the sporangia do not break down, resulting in uniporate, monosporangial compartments (Johansen 1981). These types of asexuate conceptacles are diagnostic at higher taxonomic levels (orders, families and subfamilies; Harvey et al. 2003a,b; Kato et al. 2011). Sporangial compartments of Type 4 characterize the order Sporolithales, while types 1, 2 and 3 are present in the order Corallinales (Le Gall et al. 2009). Type 3 characterizes the family Hapalidiaceae (Harvey et al. 2003b). Types 1 and 2 are diagnostic of the family Corallinaceae, and in particular, Type 2 occurs in the subfamilies Lithophylloideae, Hydrolithoideae and Porolithoideae (Kato et al. 2011) while Type 1 is diagnostic of the subfamilies Mastophoroideae and Neogoniolithoideae (Kato et al. 2011). All gametangial conceptacles of any species are uniporate with the roof formed by centripetal growth of filaments around the fertile area (Johansen 1981). Only the male conceptacles of Clathromorphum and Melobesia differ in their roof formation (Lebednik 1978; Johansen 1981). The identification of the gametangial phase of fossil coralline species and its association with the corresponding asexuate phase is possible when the two plants, gametangial and tetra/bisporangial, possess the same growth form and vegetative anatomy and systematically co-occur at the same stratigraphical level or, better, in the same sample (Basso et al. 1996). The second condition is that the gametangial conceptacles have a shape and structure compatible with published accounts of the same species or of species of the same genus. The third condition is that no other species of the same genus co-occurs in the same material. As already noted (Verheij 1993; Townsend et al. 1995; Garrabou & Ballesteros 2000), two thalli may appear fused together, thus giving the appearance of a single thallus with both tetra/bisporangial and gametangial conceptacles, as in our material of Sporolithon lvovicum. Gametangial plants can be monoecious (male and female conceptacles on the same plant) as well as dioecious (male and female conceptacles on separate plants), and carposporangial conceptacles develop from the female conceptacle after fertilization. Separate male and carposporangial conceptacles are evidence for the dioecious nature of Sporolithon lvovicum.

Lateral anastomoses in vegetative cells. The type of connection between the cells of the adjacent cell filaments (cell fusions and secondary pit-connections) is well known by botanists to be a diagnostic criterion at the rank of the subfamily (Johansen 1969), although only Braga et al. (1993) have examined its identification as well as its use in systematic palaeontology. Most of the higher taxa possess cell fusions as an alternative to secondary pit connections, with the exception of Sporolithales which may have both on the same plant (Verheij 1992, 1993; Harvey et al. 2005). Combining the lateral anastomosis types (fusion or secondary pit) with the asexuate conceptacle type allows us to identify subfamilies. Based on this criterion, fossil algae belonging to the subfamily Lithophylloideae can be delimited from all other coralline taxa with uniporate asexuate conceptacles by the absence of cell fusions. Plants with cell fusion and multiporate asexuate conceptacles belong to the subfamily Melobesioideae. Excluding the parasitic species, corallines with cell fusions and uniporate asexuate conceptacles may belong to Neogoniolithoideae, Hydrolithoideae, Porolithoideae or Mastophoroideae (Harvey et al. 2003b; Kato et al. 2011). Caution must be taken to avoid misidentification of the gametangial plants that are always uniporate (discussed above) with the asexuate conceptacles of the Corallinaceae. It must be noted that cell fusions may also be evident under an optical microscope, whilst secondary pit-connections normally are not detected.

Epithallial cells and subepithallial initials. EC cover the outer surface of the coralline thalli and are produced by the upward division of the subepithallial initials or meristem. They are never connected by lateral anastomosis. The downward derivatives are cells of the PF (Johansen 1981; Irvine & Chamberlain 1994). The EC of Phymatolithon and Lithothamnion species differ in shape and calcification (Adey & McKibbin 1970; Irvine & Chamberlain 1994; Wegeberg & Pueschel 2002; Adey et al. 2005). Within Melobesioideae, only Lithohamnion possesses EC that are flattened and flared. The other genera may have more or less flattened or rounded EC (Adey 1966; Woelkerling 1988; Womersley 1996). The subepithallial initials differ in genera of melobesioid algae (Adey 1965, 1966). These cells are as long as, or longer than, cells subtending them in the genera Clathromorphum, Synarthrophyton, Lithothamnion and Mesophyllum. In contrast, subepithallial initials are as long as, or shorter than, subtending cells in the genus Phymatolithon (Adey & McKibbin 1970; Keats & Chamberlain 1997). The subepithallial initials and EC were not preserved in most of the studied material. Well-preserved EC in fossil corallines can also be identified by optical microscope, although better results are obtained using scanning electron microscopy (SEM; Braga et al. 1993; Aguirre & Braga 1998; Rasser & Piller 1999; Aguirre et al. 2012). We distinguished the genus Lithothamnion from Mesophyllum by the presence of flattened and flared EC that are only flattened in Mesophyllum. Lithothamnion and Phymatolithon were separated using the relative length of the subepithallial initials to the cells directly subtending them. It should be noted that EC are best observed around the conceptacle roof and where the subsequent overgrowth of thalli was fast enough to protect this layer from damage or sloughing. In some material, EC occurred partly intact just at the top of the thalli (i.e. Mesophyllum alternans and M. curtum), even without overgrowth. In the two unidentified melobesioid species with noncoaxial VC, we did not observe EC or subepithallial initials. According to the global distribution of present-day melobesioid algae, species of Clathromorphum can be excluded because of their restriction to the cool waters of subpolar-boreal regions (Adey 1965; Adey et al. 2005, 2010), incompatible with the warm-temperate to subtropical Middle Miocene climate of the Early Badenian in the studied region with warm water input from the Mediterranean (Kováč et al. 2005; Baldi 2006). The genus Synarthrophyton occurs only in the southern hemisphere, and is unknown in the fossil record (Keats & Chamberlain 1997; Aguirre & Braga 1998; Basso et al. 1998; Harvey et al. 2005). Its presence in our material is unlikely; thus, the two species probably belong to Lithothamnion or Phymatolithon. In the Recent Mediterranean, only P. calcareum, P. lenormandii and P. lamii occur (Basso et al. 1997; Bressan & Babbini 2003; Kaleb et al. 2012; Guiry & Guiry 2013). Likewise, in southern Australia, only two species have been recorded (Wilks & Woelkerling 1994). Only two representatives have been documented to date from the Central Paratethys. The first is widely documented in view of the conspecifity of Lithohamnium operculatum with P. calcareum (Basso et al. 1997) and the description of Phymatolithon sp. in the present work. We tentatively identify these species as ?Lithothamnion sp. 1 and ?Lithothamnion sp. 2, pending further research.

Thallus organization. Two types of thallus organization are observed: monomerous and dimerous (Woelkerling 1988). Hydrolithon lemoinei, Lithophyllum sp. 1 have dimerous organization, their thalli consisting of a VC (D ventral core or hypoyhallium) of filaments with PF (D perithallium) arising at right angles from them. The monomerous organization of thallus consists of the basal layers of filaments (D hypothallium) that run more or less parallel to the substrate and then curve upward or downward to form a peripheral thallus (perithallium; Rasser & Piller 1999). Lithophyllum sp. 2 shows monomerous to dimerous organization.

Arrangement of basal filaments. VC in monomerous thalli can be arranged coaxially or non-coaxially (Woelkerling 1988; Braga et al. 1993; Rasser & Piller 1999). The arrangement of VC is frequently used to delimit genera (Braga et al. 1993) or even, as an ancillary character, species within the genus Lithophyllum (Aguirre & Braga 1995; Basso et al. 1996). In the last few decades, this diagnostic character has often been discussed with regards to the genera Mesophyllum or Neogoniolithon, since the presence of a strictly coaxial arrangement along the whole ventral portion of thallus is not always constant (Woelkerling & Harvey 1992; Aguirre & Braga 1998; Cabioch & Mendoza 1998). Fossil representatives of the genus Mesophyllum can be separated from other melobesioid algae primarily on the basis of the coaxially arranged VC, which are always present at least for short distances (Basso et al. 1998; Aguirre & Braga 1998; Athanasiadis et al. 2004; Iryu et al. 2009; Peña et al. 2011; Aguirre et al. 2012). All studied species assigned to the genus Mesophyllum have a coaxial or non-coaxial to coaxial arrangement of VC, even in secondary growth over conceptacles, whereas species of Phymatolithon and Lithothamnion have a noncoaxial arrangement of VC.

Diagnostic characters at the rank of species. Many of the characters listed below have been recognized for approximately the last century as diagnostic (e.g. the shape and size of conceptacles). The recent use of basic descriptive statistics in reporting the size of anatomical structures has considerably improved our capacity to circumscribe the morphological species concept for fossil coralline algae, starting from the actuopalaeontological approach (Braga et al. 1993; Basso 1994, 1995). Other characters (like those of the conceptacle chamber roof shape and structure) started to be used only in recent decades, and their utility in palaeontology still needs to be explored fully. Commonly, a group of characters, rather than a single character, collectively circumscribe the fossil species from other congeneric species, as happens in botany. In this paper, only the characters observed in the Carpathian material are discussed.

Ventral core of basal filaments: structure. Within Mesophyllum and Neogoniolithon, different species may show a characteristic, rather constant thickness of the coaxial ventral core of basal filaments (VC) that, along with the mean size of its cells, may be used for separating fossil species, in association with other characters. Different organizations of VC are reported in different species of lithophylloid algae (Aguirre & Braga 1995). For example, Lithophyllum dentatum has both monomerous coaxial and dimerous organization, in contrast to L. nitorum and L. racemus which show only dimerous organization of the thallus (Aguirre & Braga 1995; Basso et al. 1996). The strictly dimerous VC construction was once used to identify the genus Pseudolithophyllum

Lemoine, presently merged into the genus Lithophyllum (Woelkerling 1988; Basso et al. 1996).

Peripheral filaments: organization and zonation. Many of the examined species cyclically produce bands of cells differing in length and wall thickness or lumen size. The calcification pattern has been attributed to several causes, including temperature associated with seasonal cycles (Basso 1994, 1995; Basso et al. 1997; Blake & Maggs 2003; Kamenos & Law 2010), lunar cycles (Freiwald & Henrich 1994; Blake & Maggs 2003) or both, with multiple-order cyclicity (Halfar et al. 2000). Species of Lithophyllum do not show distinct growth zones in PF (Aguirre & Braga 1995; Basso et al. 1996; Chamberlain et al. 1988), although zonation has been recently reported in a tropical Lithophyllum (Caragnano et al. 2014). In contrast, zonation (also reported as banding) is a common feature in living and fossil melobesioid algae (Basso 1994, 1995; Basso et al. 1997, 1998; Aguirre & Braga 1998; Halfar et al. 2000; Iryu et al. 2009; Aguirre et al. 2012), and can be useful amongst other characters to identify species (e.g. L. muelleri from other species of Lithothamnion; Maneveldt et al. 2008). Patterns of zonation can be diagnostic as well (Basso 1995; Basso et al. 1997). In our material, all species except for Lithophyllum sp. 1 and Hydrolithon lemoinei produce distinct growth zones. The best-developed growth zones were observed in species of Melobesioideae, in the genus Sporolithon, and infrequently in the mastophoroid species Spongites fruticulosa. It should be noted that zonation in these species can be evident in some portions of the thalli but almost undetectable or very weak in other parts of the same plant.

The alignment of perithallial cells. This is another ancillary character to be considered in the circumscription of fossil species (Aguirre & Braga 1995). Lithophyllum sp. 1 and Lithophyllum sp. 2 differ by showing a clear horizontal (i.e. adjacent cells of different filaments) and vertical (i.e. cells along the same filament) alignment of cells or only a vertical alignment, respectively. The alternation of weak with clear lateral and vertical alignment of cells is common in the studied species. In Spongites fruticulosa and Hydrolithon lemoinei, abrupt changes of cells dimensions prevent proper alignment of the cells.

Shape, size and fate of multiporate conceptacle chambers. These are the most obvious diagnostic features in species identification, provided that they are properly orientated in thin sections. Small variations in conceptacle diameter were once considered a sufficient reason to establish new species. The range of tetrasporangial conceptacle diameter reported for the living Mesophyllum macroblastum is 165-355 μm (Cabioch & Mendoza 2003; Harvey et al. 2005), but the fusion of adjacent conceptacle chambers may result in much larger apparent conceptacle size after their burial in the newly formed PF. The phenomenon of fused conceptacles is easy to identify in biological preparations and they are normally excluded from statistics (Woelkerling & Harvey 1993, p. 593, fig. 28C), but fusion is much more difficult to detect in fossil material, e.g. M. alternans (Fig. 9A).

The asexuate conceptacle chambers of some coralline species are rather constantly filled with large, sterile, irregularly shaped cells that persist in the conceptacle after burial in the PF (e.g. Mesophyllum printzianum, Woelkerling & Harvey 1993, fig. 26A; M. canariense, Peña et al. 2011, fig. 4e; Phymatolithon masonianum, Wilks & Woelkerling 1994, fig. 15; Synarthrophyton pseudosorus, Harvey et al. 2003b, fig. 30d, e). This character can be considered ancillary in identification of fossil species, as in our Mesophyllum alternans (Fig. 9A).

Shape and structure of asexuate conceptacle chamber roofs. These characters are widely accepted as diagnostic at species level. Roof morphology and the parameters of cells that border pore canals in asexuate conceptacles are diagnostic of species of Mesophyllum (Woelkerling & Harvey 1993; Womersley 1996; Harvey et al. 2005; Peña et al. 2011). The same characters have been used within the genera Lithothamnion and Phymatolithon (Irvine & Chamberlain 1994; Basso 1995; Womersley 1996; Harvey et al. 2005; Basso et al. 2011; Mariath et al. 2012). Two types of roof were observed in our species with multiporate conceptacles. A rimmed roof was observed in Mesophyllum alternans and M. cf. printzianum. Weakly concave roofs can be rarely seen in Phymatolithon sp. and M. curtum. Flat roofs without a peripheral rim were observed in the other melobesioid species, including the last two mentioned species. On rare occasions, M. cf. printzianum can even appear to be dome-shaped, with weakly raised conceptacles. The occurrence of a peripheral rim is a diagnostic character as easily detectable in fossil as it is amongst living melobesioids, which we used here in combination with other features to identify M. alternans and M. cf. printzianum. The imperfect preservation of our material precluded the possibility of systematically examining the dimensions and number of cells bordering the pore canals, which is considered diagnostic for melobesioid species (Irvine & Chamberlain 1994; Woelkerling & Harvey 1993). However, some sections show a surface view of pores bordered by rosette cells in Mesophyllum curtum (Fig. 12F) and M. cf. printzianum (Fig. 11C). Mature conceptacles of studied melobesioid species are usually raised above the thallus surface (Fig. 14). Since it is possible to measure the height of the conceptacle roof surface above the coeval thallus surface surrounding the conceptacle chamber, this diagnostic character has been used already in the description of corallines (Adey & Adey 1973), especially for species of Mesophyllum (Peña et al. 2011), and in the description of fossil Lithothamnion (Vannucci et al. 2010b). Markedly raised conceptacles were observed in L. roveretoi (Fig. 18A), Lithothamnion sp. 1 (Fig. 18C) and M. curtum (Fig. 18I), but seldom in M. cf. printzianum (Fig. 18H). In the studied material of Mesophyllum, the deepest sporangial conceptacles were observed in M. curtum, in contrast to M. alternans, M. cf. erubescens and M. cf. printzianum (Fig. 18I, E, F, H, respectively). However, the conceptacles of M. curtum can markedly protrude above the thallus surface, which is probably due to the spherical shape of the conceptacles and the thickness of the roof. As an additional diagnostic feature, Vannucci et al. (2010b) considered the relative size of roof cells in comparison to the surrounding vegetative PF cells to separate Lithothamnion roveretoi and L. obstrusum. In our material, only L. roveretoi and Phymatolithon sp. possess cells of the roof with the same parameters as the surrounding vegetative PF cells. In L. moretii, cells of the roof differ from the longest cells at the sides of the conceptacles; however, they are of the same dimension as the shorter cells of PF. In our material of Mesophyllum, the roof cells are different from the cells at the sides of the conceptacles and from cells of the PF. The observed differences are associated with asexuate roof development, described in detail by Woelkerling & Harvey (1993) in a southern Australian species of Mesophyllum. The cells above the new chamber become shorter in developing a pore plate during conceptacle development, in contrast to the cells of the peripheral rim and the sides of the conceptacles (Woelkerling & Harvey 1993). Wilks & Woelkerling (1995) noted that Phymatolithon repandum and P. masonianum from southern Australia can be separated according to other characters also based on roof thickness. Furthermore, Mesophyllum macroblastum and M. canariense differ from other representatives of the same genus by their roof thickness (Peña et al. 2011). Based on this character it is possible to separate Lithothamnion moretii and M. cf. erubescens from other species within their genera. The maximum thickness of the roofs in both species is less than the minimum values for the other species. Roof thicknesses in other representatives of the two genera overlap and thus are not of diagnostic value. However, we agree with Wilks & Woelkerling (1995) about treating this character with caution, possibly in combination with other diagnostic features. Roof thickness, and thus the number of cells composing the sporangial conceptacle roof, is also considered diagnostic of species within the genus Hydrolithon (Maneveldt 2005). Aguirre & Braga (1995) used the relative length of roof cells to separate Lithothamnion nitorum from other species of Lithophyllum (L. dentatum, L. incrustans, L. orbiculatum). This character was not considered here since both species of Carpathian Lithophyllum have roof cells that are apparently similar to the surrounding PF cells. In contrast, the positions of the pore openings differs in the two Lithophyllum species, that of Lithophyllum sp. 2 being in a small depression below the thallus surface, while the conceptacles of Lithophyllum sp. 1 were likely flush with the surrounding tallus surface. The shapes and positions of the cells bordering the pore canals are also diagnostic characters used to distinguish living species of Lithophyllum (Keats 1997; Riosmena-Rodriguez et al. 1999), although these have not yet been observed in fossil material. Pore canal parameters have been used in Lithophyllum species identification (Aguirre & Braga 1995; Basso et al. 1996). Pore canals of the asexuate conceptacles of Lithophyllum sp. 1 are conical and enlarged at the top, leaving an opening above the narrowed pore canal. In one conceptacle an apparently cylindrical pore was observed. Since a tetrasporangial conceptacle was not found in Lithophyllum sp. 2, we could not provide a comparison for this character.

Species identification in Sporolithon. The southern Australia Sporolithon species were examined by Townsend et al. (1995). They identified the following diagnostic characters for species identification: (1) the number of cells to which the sorus is raised above the surrounding plant surface; (2) the number of cells in paraphyses; (3) the occurrence of a basal layer of elongate cells at the base of the sporangial compartments; (4) the dimensions of tetrasporangial compartments; (5) the tetrasporangial pore diameter; (6) the fate of old sporangia (i.e. the possibility of finding sporangia buried in the thallus); and (7) the ratio of secondary pits to cell fusions. Harvey et al. (2002) rejected the diagnostic value of character (7). Within the fossil representatives of the genus Sporolithon, all the other characters may be observed, although we follow previous authors (Vannucci et al. 2000; Bassi et al. 2007) in identifying characters (3) and (4) as the most easily detectable in fossils. Although character (2), the number of cells in paraphyses, is sometimes neglected because it is not clear in thin sections (Aguirre & Braga 1998; Rasser & Piller 1999; Bassi et al. 2007), some palaeontologists have included it in species description (Vannucci et al. 2000). We were able to observe this diagnostic character in Sporolithon lvovicum, with 5-6 cells forming each paraphysis (Fig. 4E).

Growth form. Most examined samples are cuttings from larger multispecific rhodoliths. The thalli of species are superimposed on each other and all show an encrusting growth form, as most coralline algae are in their early stages of development (Johansen 1981). Some of them bear a kind of protuberance, and one (?Lithothamnion sp. 2) is described solely on the basis of its protuberances, or fragments of a fruticose rhodolith. The species of Sporolithon are both encrusting to warty protuberant, and those of Mesophyllum are encrusting or warty protuberant. An exception is M. cf. erubescens with an encrusting to layered growth form. There is a comparable situation in some species of Lithothamnion, where only ?Lithothamnion sp. 1 and ?Lithothamnion sp. 2 grow as warty protuberant or fruticose, respectively, while others are encrusting to layered. Furthermore, Lithophyllum sp. 2 forms short warty protuberances in contrast to the encrusting Lithophyllum sp. 1.We use growth form for species identification only in combination with other characters, since growth form may be highly variable in most species (Woelkerling et al. 1993; Wilks & Woelkerling 1994).

Conclusions

Most of the diagnostic criteria for the identification of Recent coralline algae can also be used for fossil species. Characters associated with the type of conceptacle formation, lateral anastomoses in vegetative cells, shape of EC, length of meristeme, thallus organization and arrangement of VC have been used for the separation of corallines at supraspecific level. Characters associated with the ventral core of basal filaments, growth zones and alignment of cells, sporangial chamber dimensions and fate, features of the roof, pore canals and growth form have enabled the identification of species in the order Corallinales. The occurrence of a layer of elongated cells at the base of the calcified compartments, the dimensions of calcified sporangial compartments, and the number of cells in paraphyses enabled us to describe a specimen of the order Sporolithales. In both Corallinales and Sporolithales gametangial plants were included, when possible, in species descriptions. Five newly used characters are associated with the structure and fate of presumed tetrasporangial, gametangial and carposporangial conceptacles, the shape, size and organization of roof cells, and the position of the asexuate conceptacles relative to the surrounding thallus surface. The Application of diagnostic characters on fossil corallines collected from the Badenian limestones of the Carpathian Foredeep enabled us to: 1. provide detailed descriptions of 14 fossil coralline species, with a key to their identification (Table 2); 2. document for the first time part of the life cycle of Sporolithon lvovicum, including male, carposporangial and tetrasporangial plants; we conclude that the gametangial plants of S. lvovicum were most likely dioecious; 3. describe for the first time the rosette cells in fossil Mesophyllum species; in our material, the number of rosette cells can be used collectively with other characters to separate M. curtum with up to seven rosette cells from M. cf. printzianum with up to nine rosette cells; 4. describe for the first time the gametangial conceptacles of a fossil Phymatolithon species.

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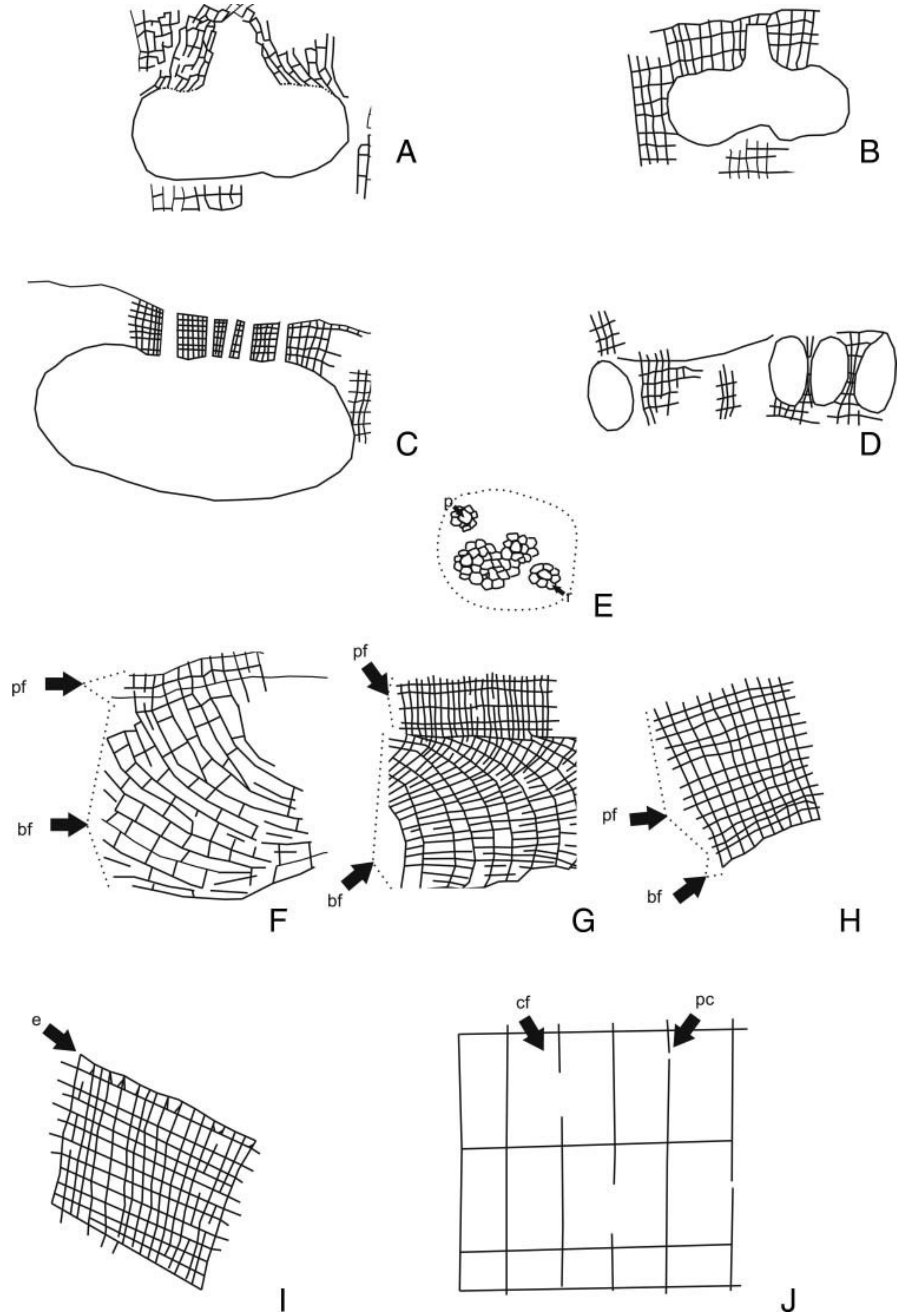


Figure 1. Diagnostic characters. A, uniporate tetra/bisporangial conceptacle type 1 according to Johansen (1981). B, uniporate tetra/bisporangial conceptacle type 2 of Johansen (1981). C, multiporate tetra/bisporangial conceptacle type 3 of Johansen (1981); conceptacle is sunken with developed peripheral rim and pore plate. D, calcified sporangial compartments type 4 of Johansen (1981). E, transverse section through pore plate with visible pores; p, bordering cells; r, roof cells. F, monomerous non-coaxial thalli, basal filaments (bf) and peripheral filaments (pf). G, monomerous coaxial thalli, basal filaments (bf) and peripheral filaments (pf). H, dimerous thalli, basal filaments (bf) and peripheral filaments (pf). I, peripheral filaments terminating with the meristem and one terminal epithallial cell; cells of the meristem are as long as or longer than cells subtending them. J, cell fusion (cf), and secondary pit connection (pc) co-occurring in the genus *Sporolithon*.

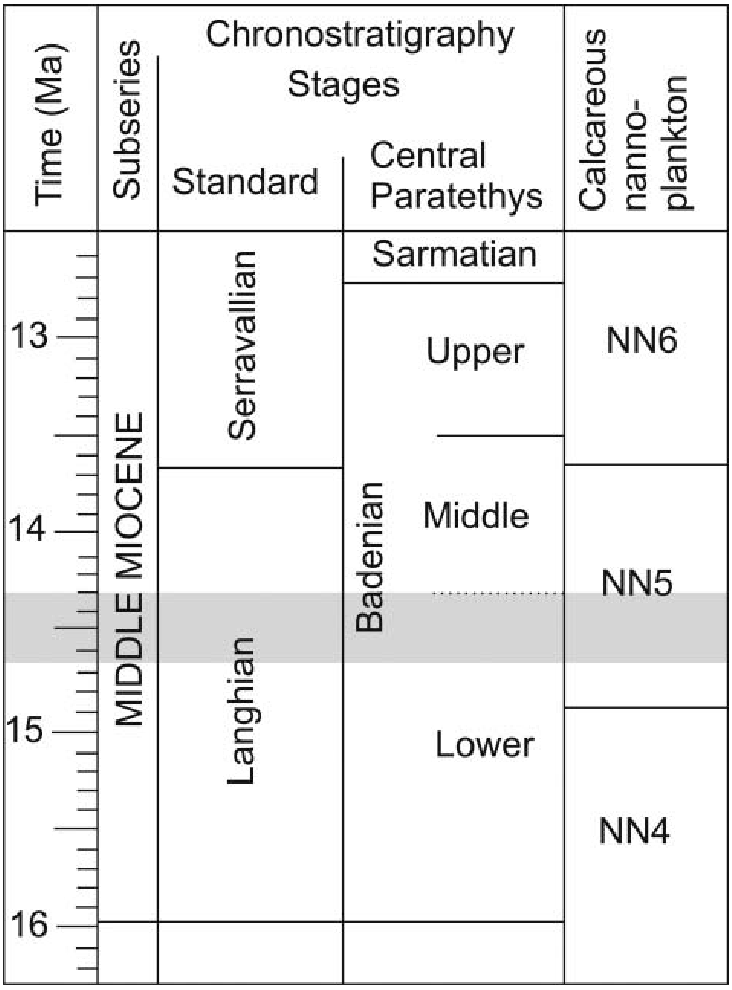


Figure 2. Stratigraphical position of studied coralline limestones according to Dol_akov_a et al. (2008). Calibrated using Gradstein et al. (2004).

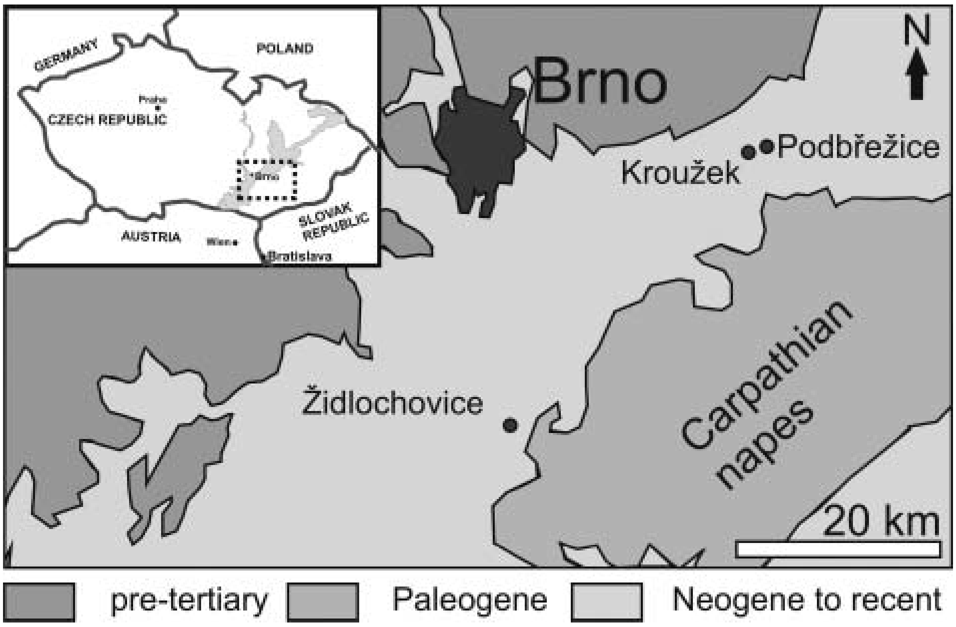


Figure 3. Location of the study area and distribution of Carpathian Foredeep Neogene deposits.

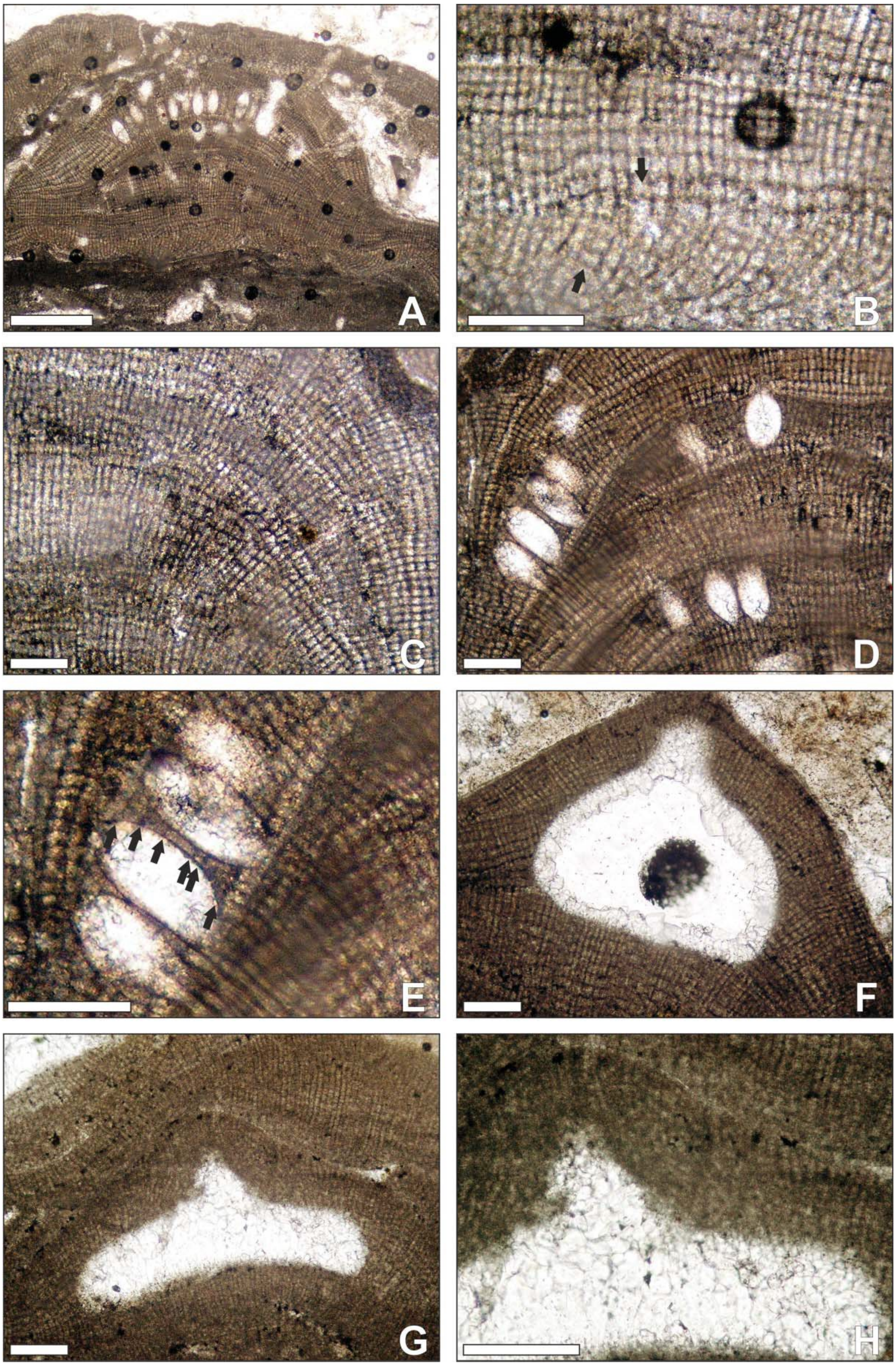


Figure 4. *Sporolithon lvovicum* (Maslov), thin section 17311951. A, encrusting thalli with warty protuberance; calcified sporangial compartments were overgrown by subsequent thallus growth. B, monomerous non-coaxial thalli; arrows mark cell fusions in VC and PF. C, weakly zoned PF; bands of shorter cells are marked by dark belt; D, calcified tetrasporangial compartments grouped in sori. E, detail of sporangial compartments from D; arrows mark presumed lower cell walls of cells of the paraphyses. F, detail of presumed carposporangial conceptacle of type 1. G, male conceptacle with one pore on encrusting thalli. H, detail of G showing conceptacle type 1. Scale bars: A = 500 µm; B_H = 100 µm.

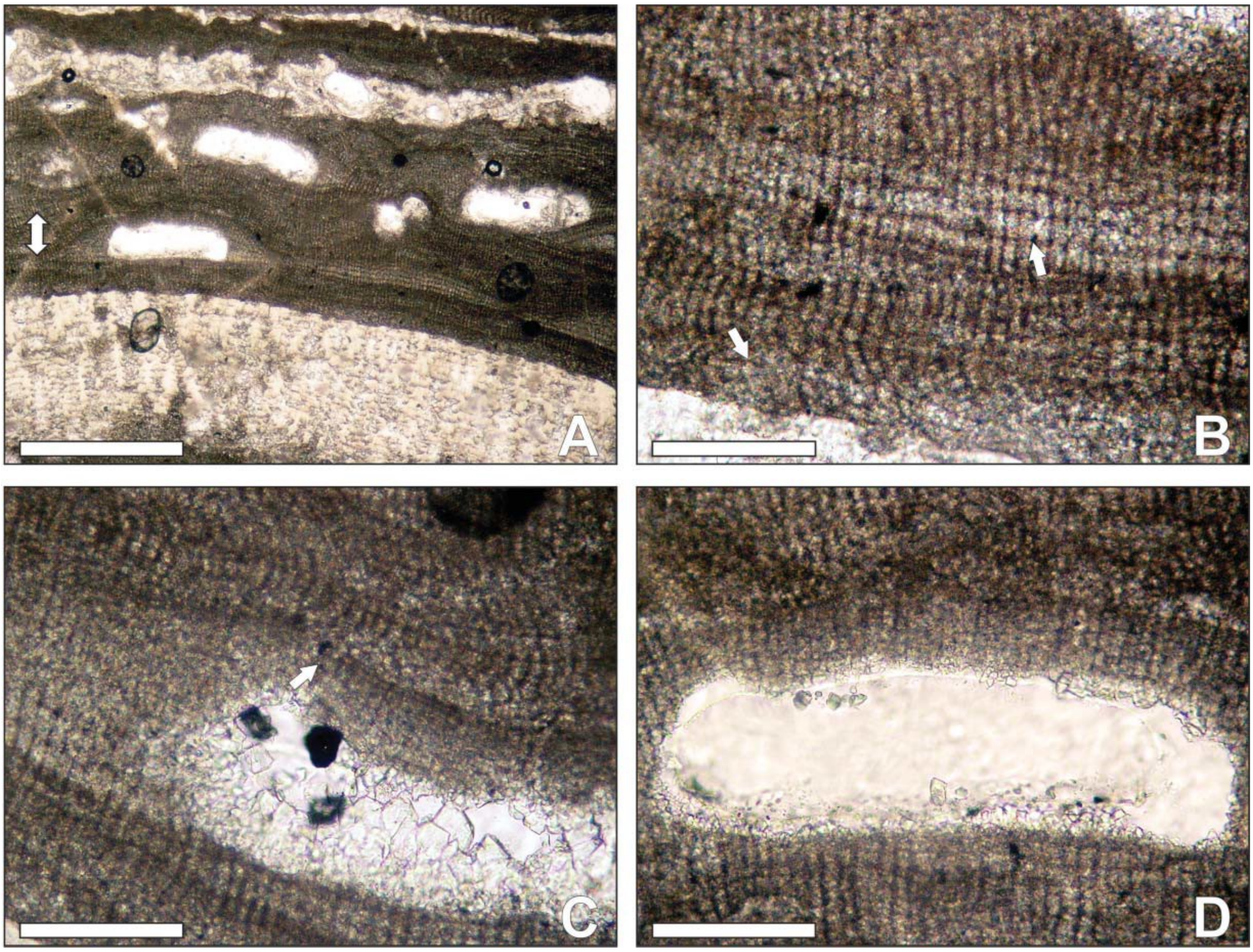


Figure 5. *Lithothamnion roveretoi* Airoldi, thin section 27611451. A, encrusting, monomerous non-protuberant thalli with dorsi-ventral organization; up_down arrows on the left margin point to the level that the conceptacle was raised above the thallus surface before burial by subsequent thallus growth. B, monomerous non-coaxial thalli; cell fusions present in PF and VC (arrows). C, multiporate tetra/bisporangial conceptacle with layer of epithallial cells at the top of the roof (arrow). D, detail of raised multiporate tetra/bisporangial conceptacle from A with flat roof and floor; cells of the roof are of same dimensions as other cells of PF. Scale bars: A = 500 µm; B_D =100 mm.

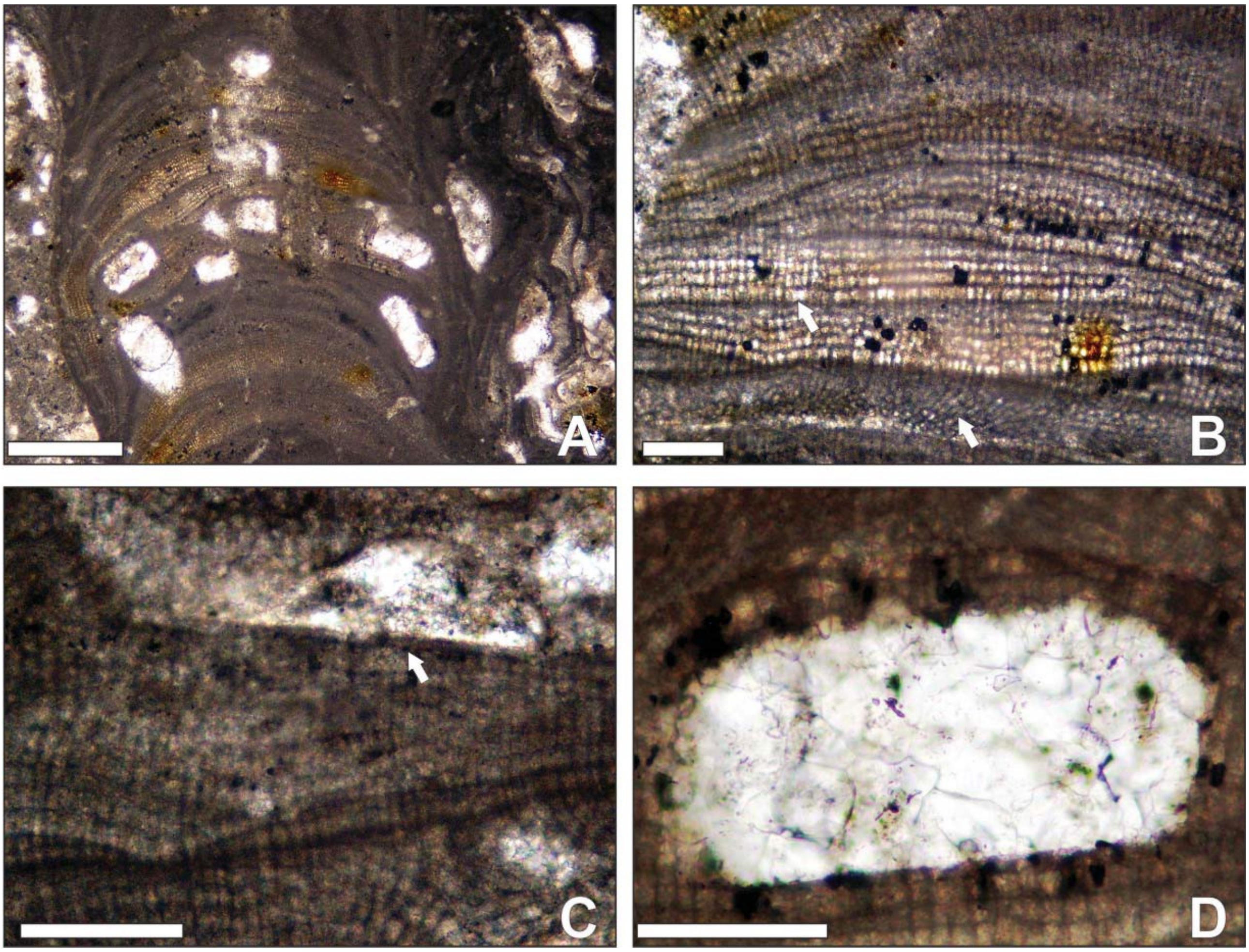


Figure 6. *Lithothamnion moretii* Lemoine, thin section 42139-111151. A, protuberant thalli with conceptacles slightly raised and buried by continuous growth of thalli. B, monomerous organization of thalli, non-coaxial VC and zoned PF; transition from short thickwalled cells to long cells with high lumen is abrupt; long cells are gradually shorter towards the top of the zone; arrows point to cell fusion in PF and VC. C, possible epithallial cells preserved below test of foraminifera (arrow). D, multiporate tetra/bisporangial conceptacle with markedly thin, poorly preserved roof; cells of the roof are comparable in dimensions to the shorter perithallial cells. Scale bars: A = 500 µm; B_D = 100 µm.

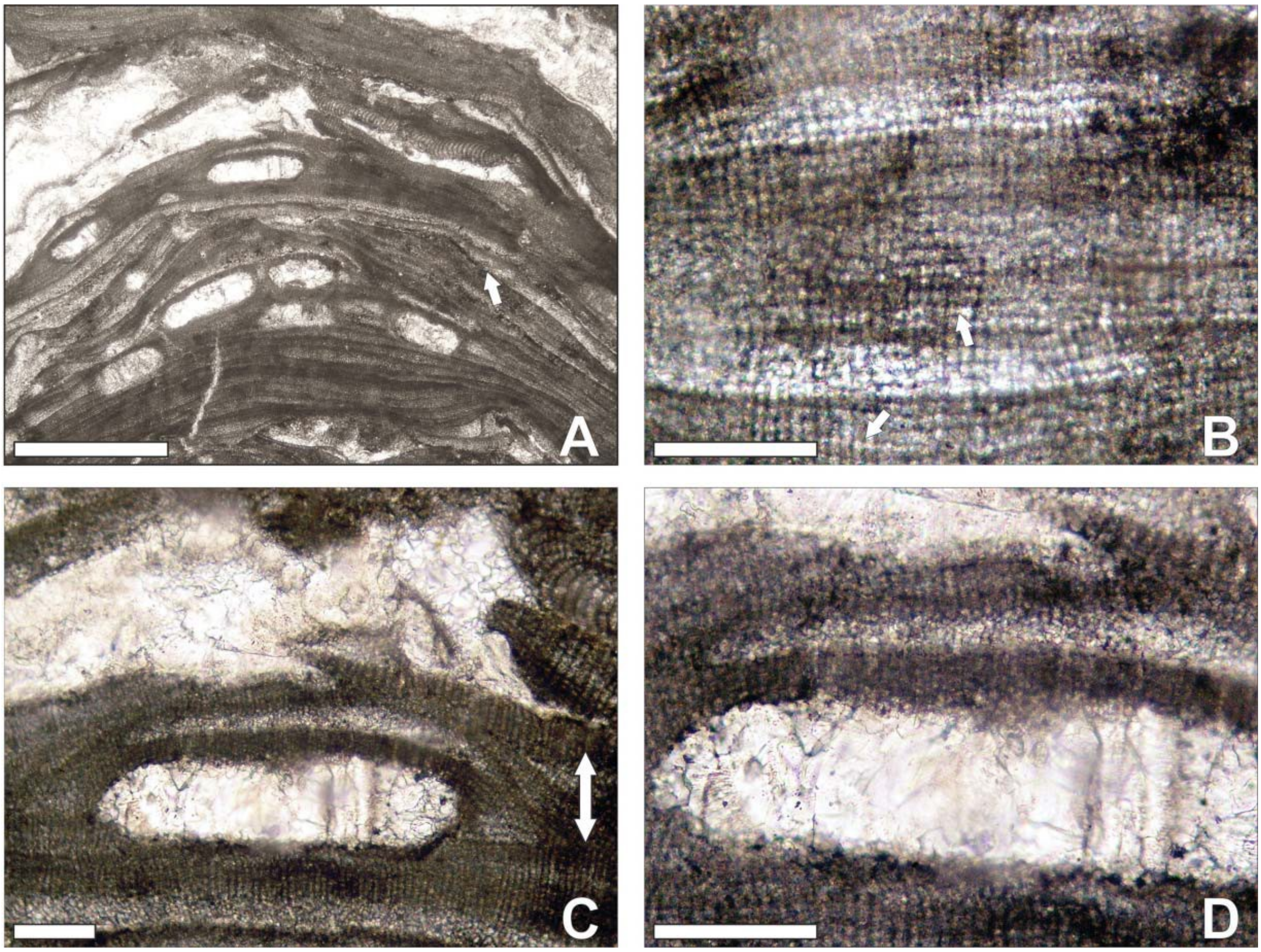


Figure 7. ?*Lithothamnion* sp. 1, thin section 42139_11851. A, encrusting monomerous superimposed thalli with multiporate tetra/bisporangial conceptacle; arrow points to non-coaxial VC. B, weakly zoned PF with cells connected by fusion (arrows). C, tetra/bisporangial conceptacle raised above thallus surface and overgrown by subsequent thallus growth; up_down arrows point to the level to which the conceptacle was raised above the thallus surface before burial by subsequent thallus growth. D, roof of the tetra/bisporangial conceptacle and secondary VC growing above the roof; cells of the roof differ in dimensions from other perithallial cells. Scale bars: A = 500 µm; B_D = 100 µm.

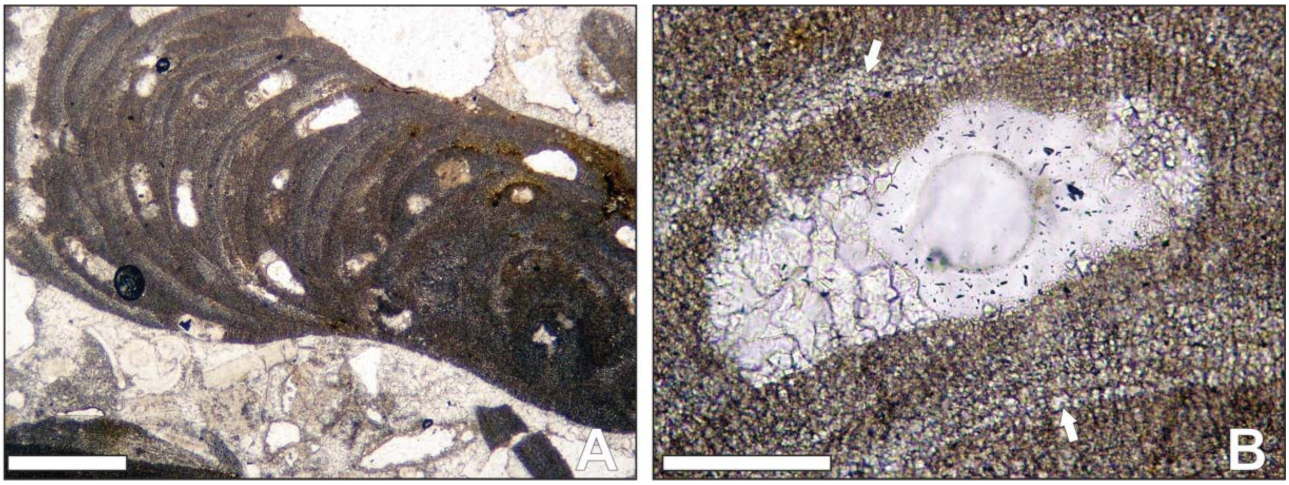


Figure 8. ?*Lithothamnion* sp. 2, thin section 17311951. A, section through protuberant portion of thalli with formerly raised conceptacles buried by continuous growth of the protuberance; conceptacles are formed at the tips and at the sides of the protuberance. B, detail of multiporate tetra/bisporangial conceptacle with cells of the roof of different dimensions from cells of the rest of the PF; cell fusions in secondary VC and PF are marked by arrows. Scale bars: A = 500 µm; B = 100 µm.

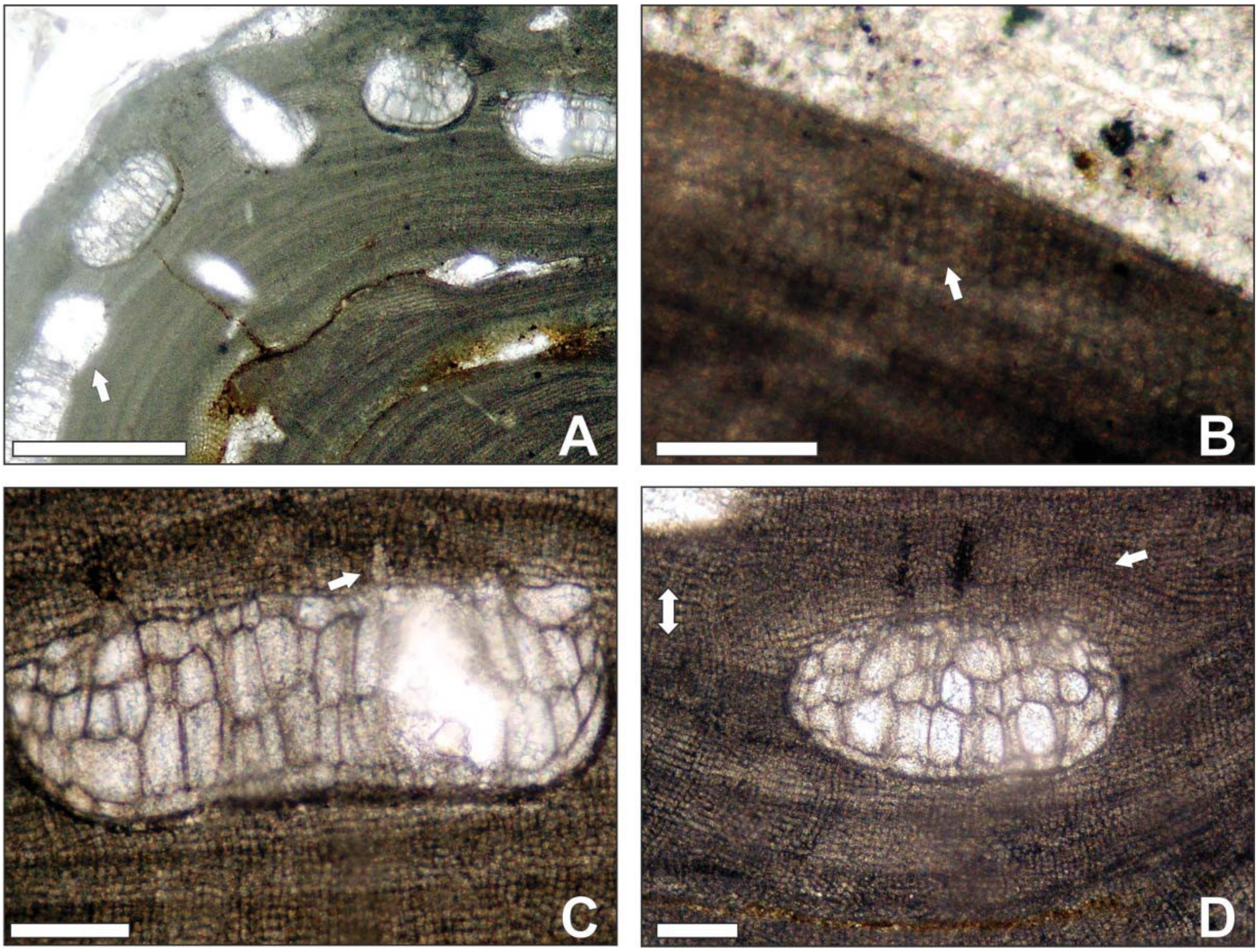


Figure 9. *Mesophyllum alternans* (Foslie), thin section 42139_111151. A, encrusting, monomerous, non-coaxial thalli with several tetra/bisporangial conceptacles; arrow points to fusion of tetra/bisporangial conceptacles. B, layer of flattened to rounded epithallial cells at the top of the thalli, above cells of the meristem that are as long or longer then cells subtending them; cell fusion is marked by arrow. C, multiporate tetra/bisporangial conceptacle, probably fusion of two conceptacles, with pore bordered by cells that are narrower than other roof cells (arrow). D, sunken multiporate tetra/bisporangial conceptacle with developed peripheral rim (arrow); up_down arrows point to the level to which the conceptacle was raised above the thallus surface, before burial by subsequent thallus growth. Scale bars: A = 500 µm; B_D = 100 µm.

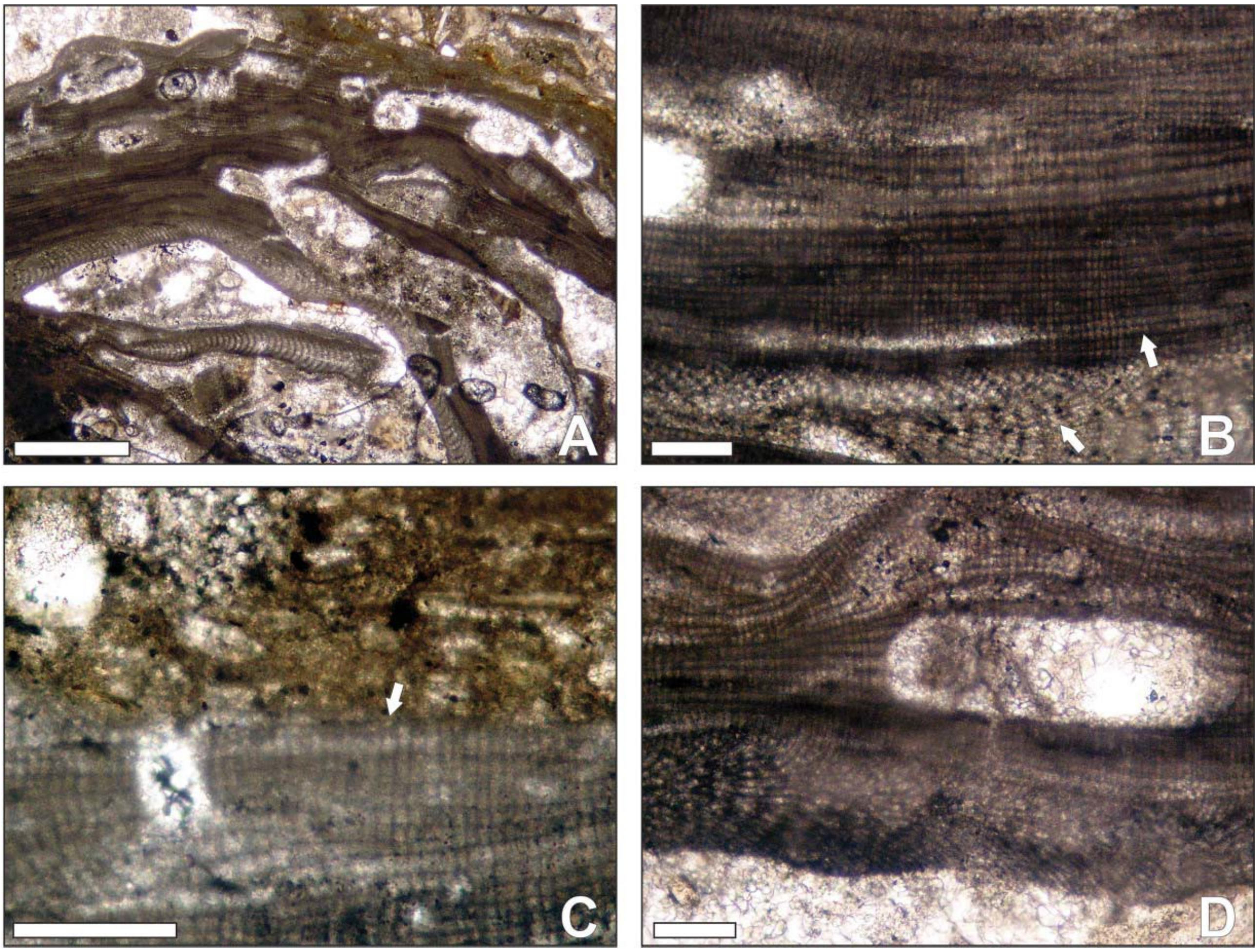


Figure 10. *Mesophyllum* cf. *erubescens* (Foslie), thin section 42139_11551. A, thick portion of thalli with encrusting, lamellate to layered growth form. B, detail of coaxial to non-coaxial thalli with cells of VC and PF connected with fusions (arrows); PF are weakly zoned. C, one layer of epithallial cells (arrow) above cells of the meristem that are as long or longer than cells subtending them. D, slightly raised tetra/bisporangial conceptacle with markedly thin roof without peripheral rim; conceptacle became buried by continuous growth of thalli. Scale bars A = 500 µm; B_D = 100 µm.

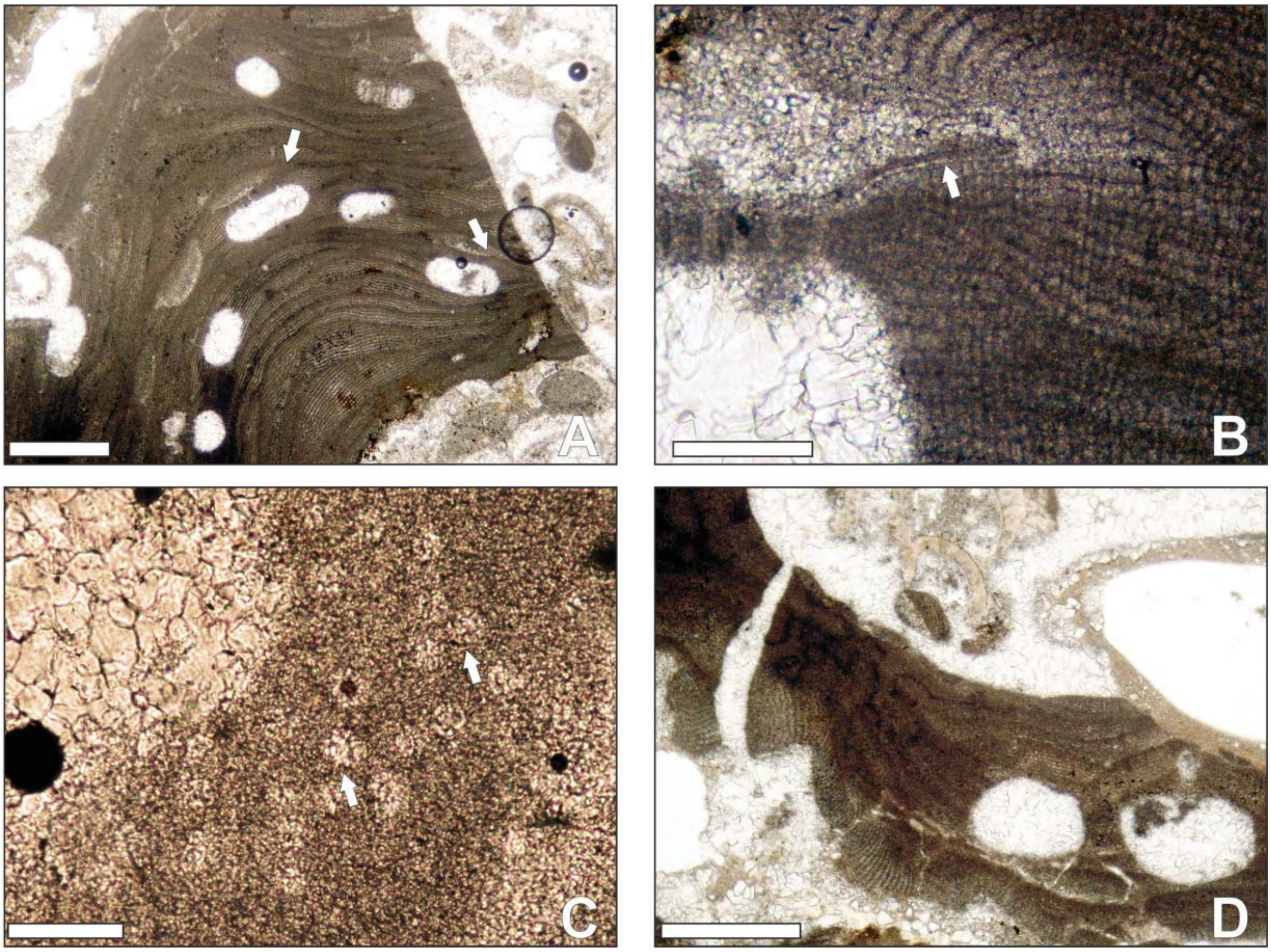


Figure 11. *Mesophyllum* cf. *printzianum* Woelkerling & Harvey, thin section 17311951. A, section through encrusting to protuberant thalli with multiporate tetra/bisporangial conceptacles; PF zonation is evident; arrows point to peripheral rims above conceptacles. B, detail of the multiporate tetra/bisporangial conceptacle; roof plate is formed by cells of different dimensions from the cells at the sides of the conceptacle; two layers of epithallial cells above cells of the meristem (arrow) that are as long or longer than cells subtending them; cell fusions present in VC and PF. C, transverse section through the pore plate with pores bordered by about nine rosette cells (arrows) that are of the same dimensions as or are a little flattened compared to adjacent pore plate cells. D, uniporate carposporangial conceptacles within monomerous coaxial thalli. Scale bars: A, D = 500 μm; B_C = 100 μm.

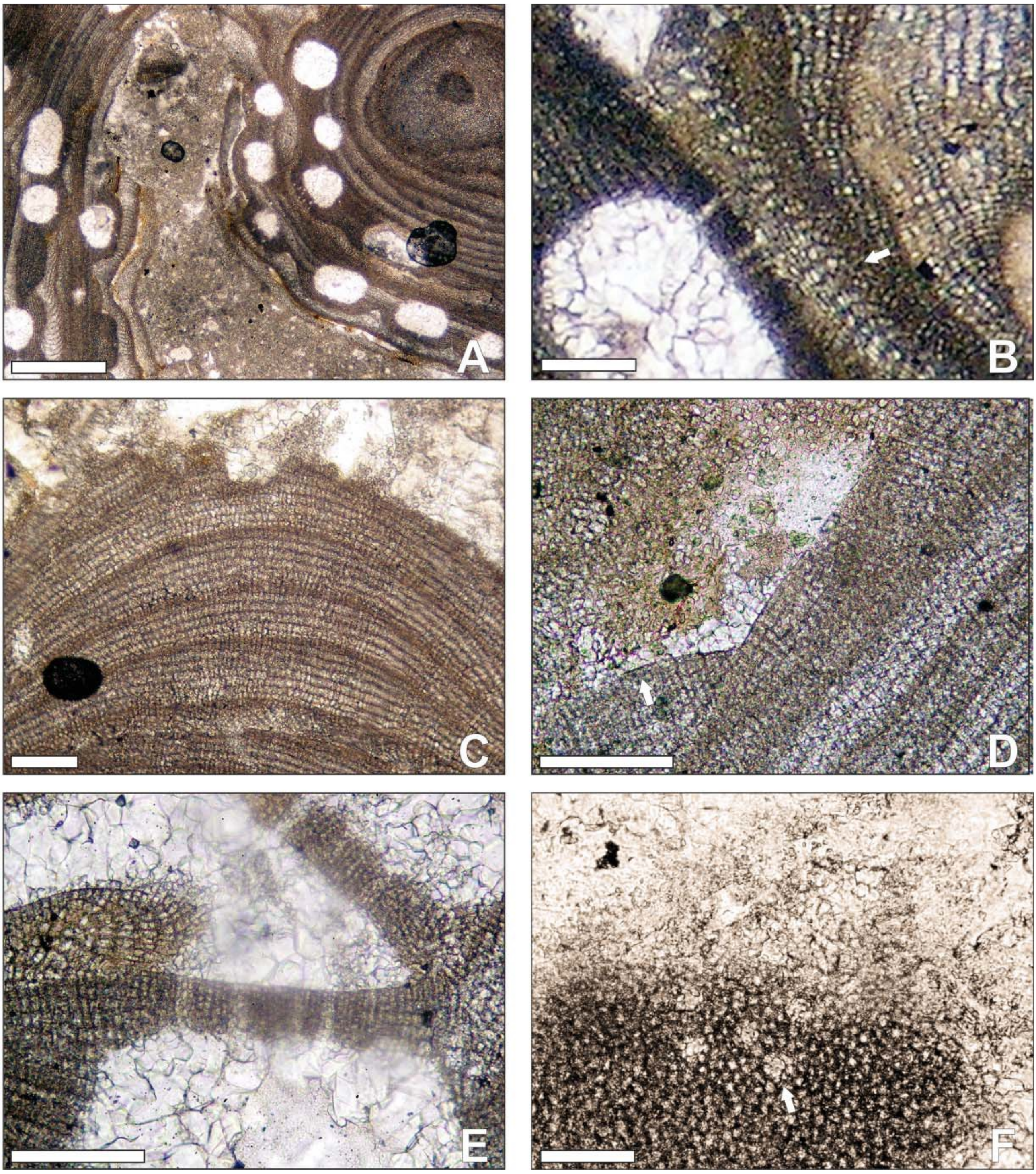


Figure 12. *Mesophyllum curtum* Lemoine, thin section 17311851. A, section from monospecific warty protuberant rhodolith with multiporate tetra/bisporangial conceptacles borne on protuberances. B, monomerous coaxial thalli (arrow). C, weakly zoned PF. D, layer of flattened cells of the epithallium above cells of the meristem (arrow) that are as long or longer than cells subtending them; cells of the peripheral filaments connected with fusion. E, detail of multiporate tetra/bisporangial conceptacle with flat roof; cells of the pore plate are of smaller dimensions than cells from the sides of conceptacle. F, transverse section through the roof showing pores bordered by about seven rosette cells that are of the same dimensions as adjacent pore plate cells. Scale bars: A = 500 µm; B_F = 100 µm.

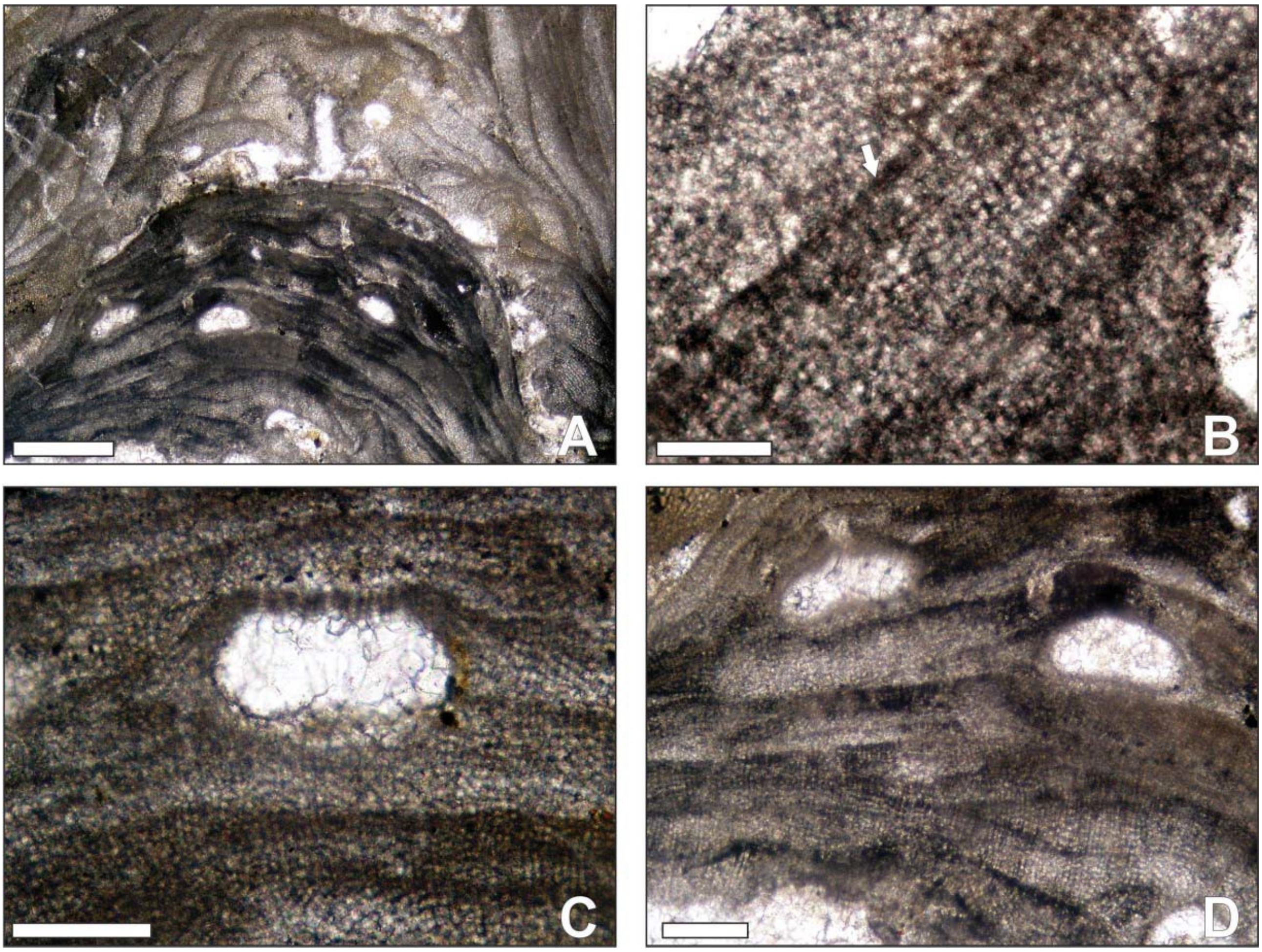


Figure 13. *Phymatolithon* sp., thin section 42139_11951. A, monomerous thalli with non-coaxial VC and zoned PF; gametangial warty protuberant plant is overgrown by tetra/bisporangial plant, and gametangial conceptacles are borne on warty protuberance. B, layer of epithallial cells above cells of the meristem (arrow) that are as long as or shorter than cells subtending them. C, multiporate tetra/bisporangial conceptacle with flat to slightly concave roof; partly raised conceptacle during maturity was buried by continuous growth of the thalli. D, growth zones and gametangial uniporate conceptacles. Scale bars A = 400 µm; B_D = 100 µm.

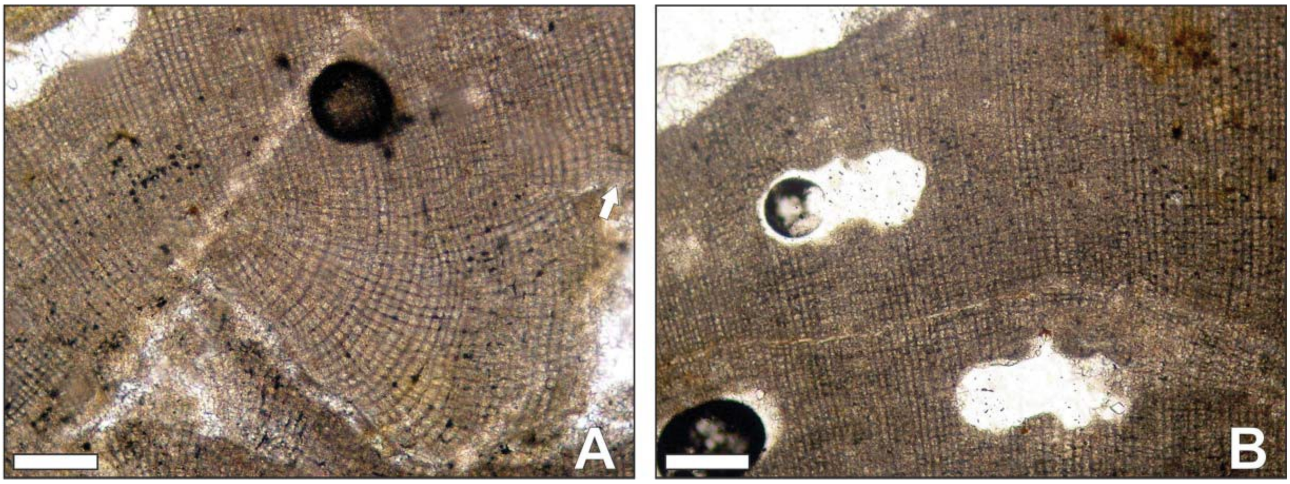


Figure 14. *Lithophyllum* sp. 1, thin section 17311951. A, encrusting portion of thalli with dimerous organization and false coaxial VC; one layer of rectangular to squared basal cells is marked by an arrow. B, uniporate tetra/bisporangial conceptacles with raised columella; cells of PF are not connected with fusions. Scale bars = 100 µm.

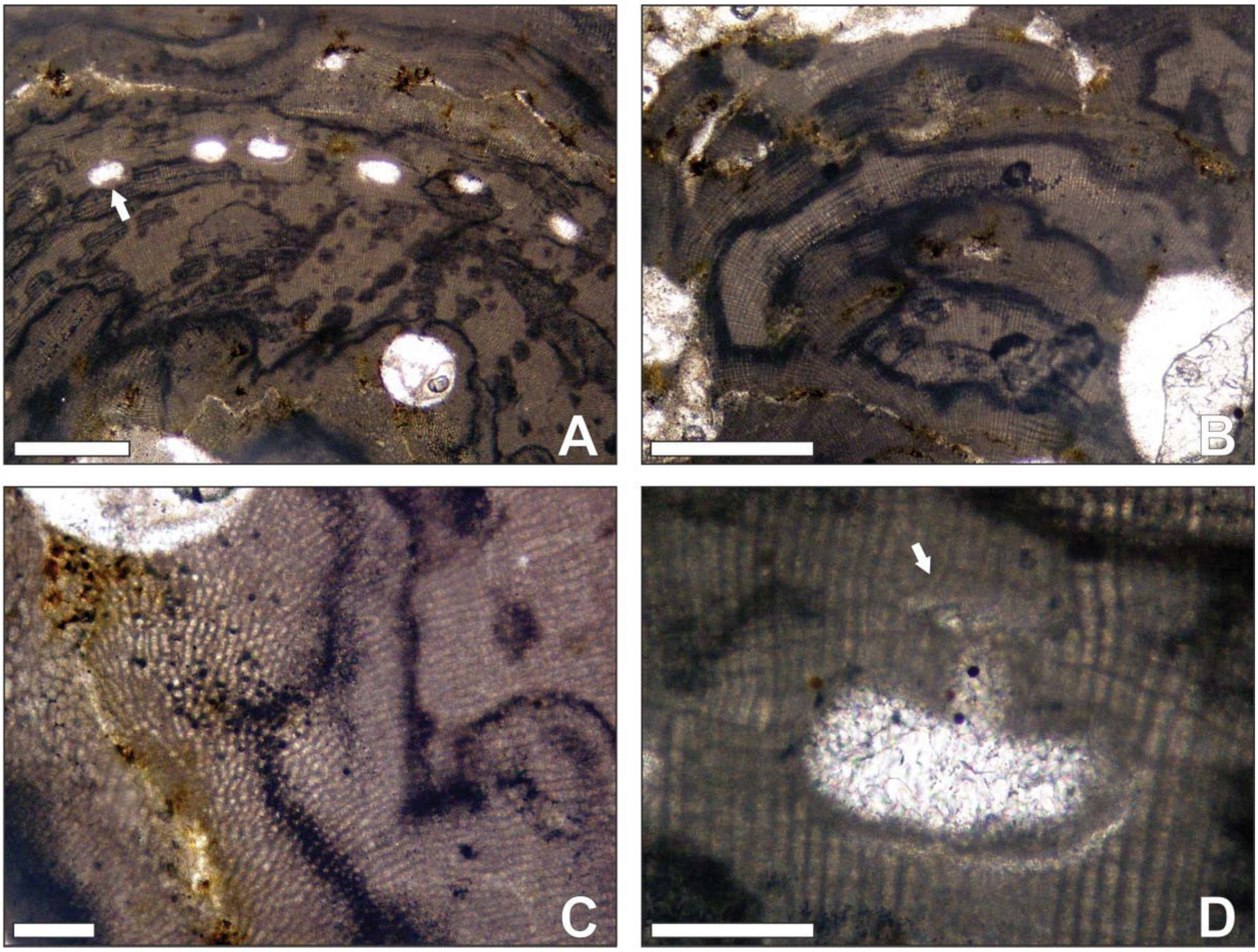


Figure 15. *Lithophyllum* sp. 2, thin section 17311851 A, encrusting thalli with aligned uniporate columellate conceptacles; columella is marked with an arrow. B, section through protuberant thalli with radial organization. C, monomerous non-coaxial portion of the thalli. D, detail of the conceptacle with bulbous pore canal; arrow marks depression within which pore opens. Scale bars: A, B = 500 µm; C, D = 100 µm.

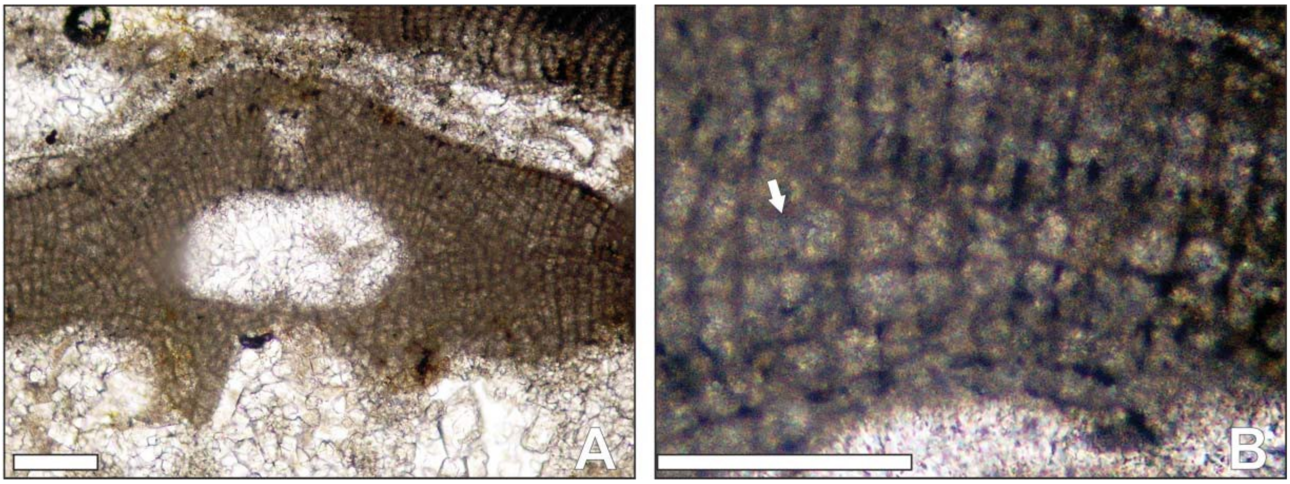


Figure 16. *Hydrolithon lemoinei* (Miranda), thin section 17311951. A, encrusting dimerous thalli with uniporate tetra/bisporangial conceptacle (type 2) raised above the thallus surface. B, dimerous thalli; cells connected with fusions (arrow). Scale bars = 100 µm.

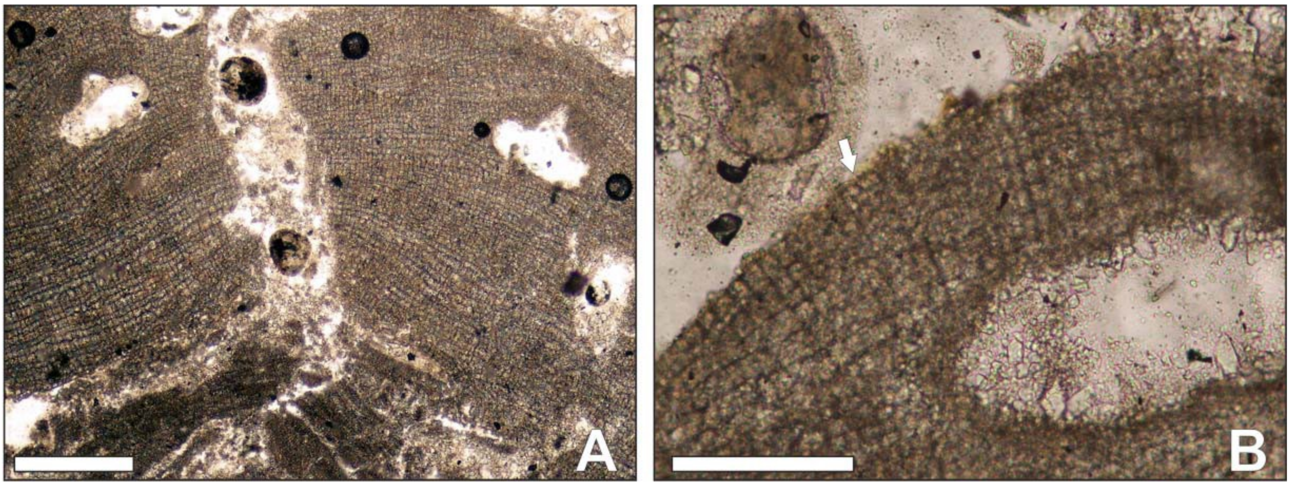


Figure 17. Spongites fruticulosus K€utzing, thin section 42139_111051. A, encrusting portion of the thalli with uniporate tetra/bisporangial conceptacles of type 1. B, two layers of epithallial cells at the top of the thalli (arrow); cells are connected with fusions. Scale bars: A = 400 μm; B = 100 μm.

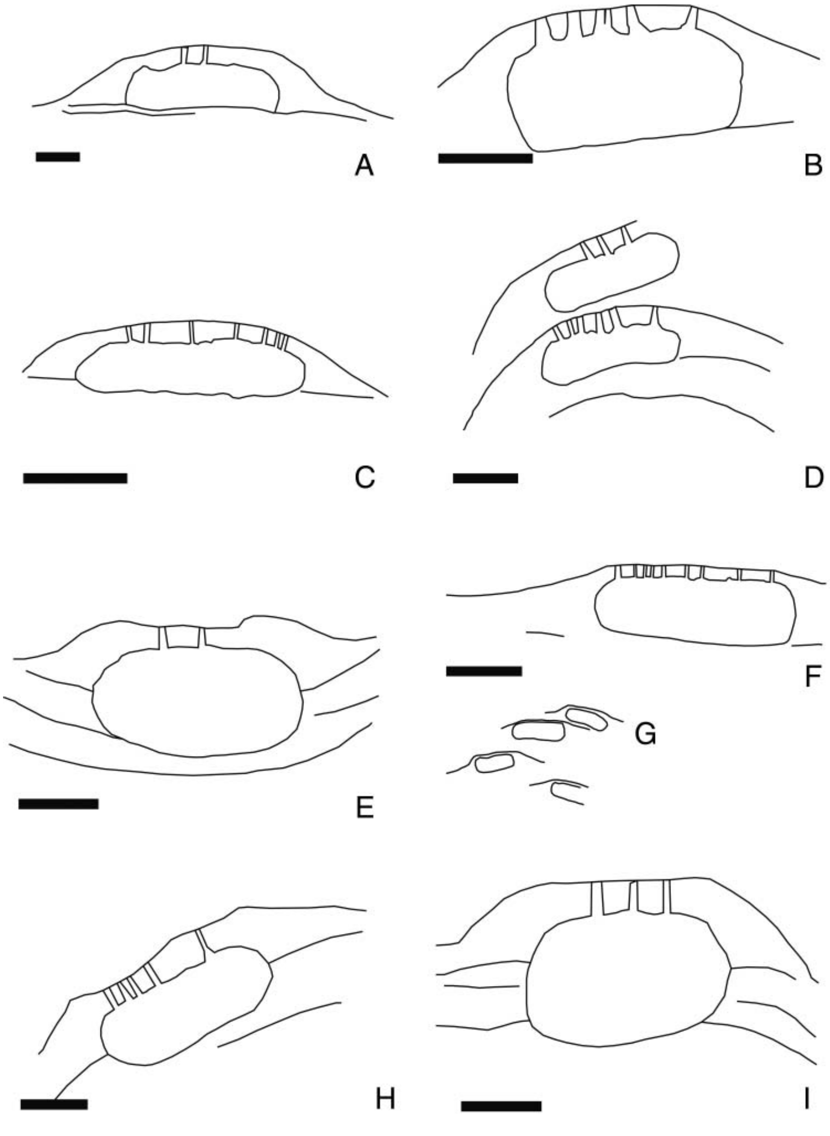
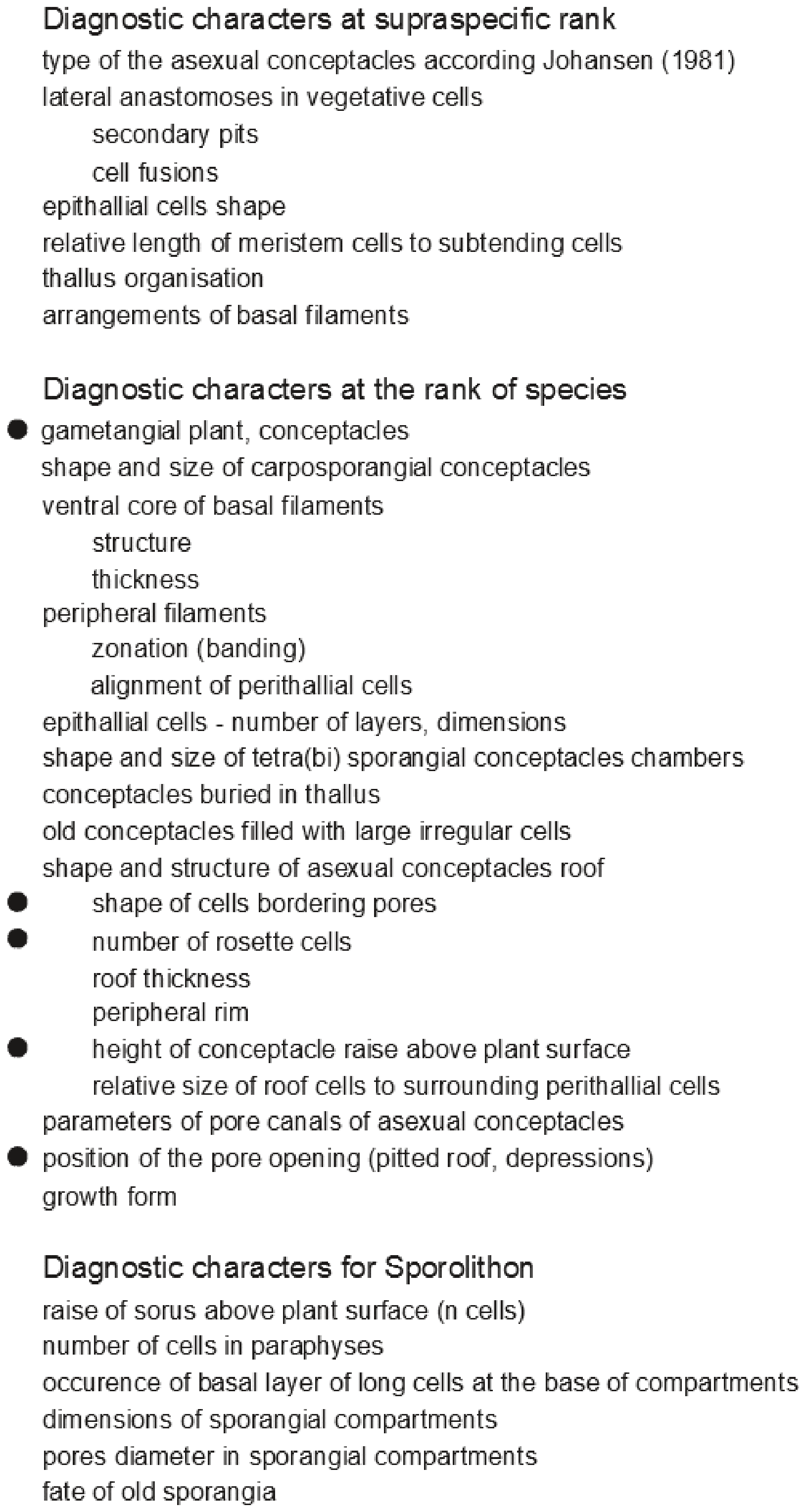


Figure 18. Drawings of distinctly raised/sunken tetra/bisporangial conceptacles of melobesioid algae. A, Lithothamnion roveretoi; B, Lithothamnion moretii; C, Lithothamnion sp. 1; D, Lithothamnion sp. 2; E, Mesophyllum alternans; F, G, Mesophyllum cf. erubescens; H, Mesophyllum cf. printzianum; I, Mesophyllum curtum. Scale bars = 100 μm.

Table 1. List of observed diagnostic characters (Bosence in Riding 1991, Braga *et al.* 1993, Basso 1995, Aguirre & Braga 1998, Basso *et al*. 1998, Rasser & Piller 1999, Vannucci *et al.* 2000, 2009, 2010). Black spots mark those diagnostic characters that were newly identified in fossil corallines in this work.



Diagnostic characters at supraspecific rank

- type of the asexual conceptacles according Johansen (1981)
- lateral anastomoses in vegetative cells
  - secondary pits
  - cell fusions
- epithallial cells shape
- relative length of meristem cells to subtending cells
- thallus organisation
- arrangements of basal filaments

Diagnostic characters at the rank of species

- ● gametangial plant, conceptacles
- shape and size of carposporangial conceptacles
- ventral core of basal filaments
  - structure
  - thickness
- peripheral filaments
  - zonation (banding)
  - alignment of perithallial cells
- epithallial cells - number of layers, dimensions
- shape and size of tetra(bi) sporangial conceptacles chambers
- conceptacles buried in thallus
- old conceptacles filled with large irregular cells
- shape and structure of asexual conceptacles roof
  - ● shape of cells bordering pores
  - ● number of rosette cells
  - roof thickness
  - peripheral rim
  - ● height of conceptacle raise above plant surface
  - relative size of roof cells to surrounding perithallial cells
- parameters of pore canals of asexual conceptacles
- ● position of the pore opening (pitted roof, depressions)
- growth form

Diagnostic characters for Sporolithon

- raise of sorus above plant surface (n cells)
- number of cells in paraphyses
- occurence of basal layer of long cells at the base of compartments
- dimensions of sporangial compartments
- pores diameter in sporangial compartments
- fate of old sporangia

Table 2. Identification key for the Lower Badenian (Early Langhian) coralline algae of the Carpathian Foredeep (Czech Republic).

Key for identification of non-geniculate coralline algae from Carpathian Foredeep

1. calcified compartments, sori	Sporolithaceae
1. conceptacles	2
2. sporangial conceptacles multiporate	Melobesioideae
2. sporangial conceptacles uniporate	Corallinaceae
Sporolithaceae	
1. thallus encrusting to warty-protuberant. Calcified compartments raised over surrounding thallus surface at the time of maturity, at least 5 cells in paraphyses, chambers 91-120µm / 42-58µm H/D, not formed on layer of elongated cells	Sporolithon lvovicum (Fig. 4A-H)
Melobesioideae	
1. basal filaments non-coaxial	2
1. basal filaments coaxial or coaxial to non-coaxial	3
2. epithallial cells flared and flattened, cells of the meristeme as long as or longer than cells subtending them	Lithothamnion
2. epithallial cells flattened or rounded, cells of the meristeme as long or shorter than cells subtending them	Phymatolithon
2. epithallial cells and cells of the meristeme not observed	?Lithothamnion
3. epithallial cells flattened or rounded, cells of the meristeme as long as or longer than cells subtending them	Mesophyllum
Lithothamnion	
1. peripheral rim not developed on the roof of sporangial conceptacles	2
2. roof of tetra/bisporangial conceptacles formed by cells of the same dimensions than the cells at the sides of the conceptacles and the cells of the peripheral filaments	3
2. roof of tetra/bisporangial conceptacles formed by cells of different dimensions than the cells at the sides of the conceptacles and the cells of the peripheral filaments	4
3. encrusting, non-protuberant, roof 5-6 cells and 46-50µm thick. Sporangial conceptacle chambers 98-135µm / 327-498µm H/D, markedly raised above thallus surface	Lithothamnion roveretoi (Fig. 5A-D)
4. roof of sporangial conceptacles less than 5 cells thick	5
4. roof of sporangial conceptacles more than 5 cells thick	6
5. encrusting to protuberant, roof 28-30 µm thick. Sporangial conceptacles chambers 129-143µm / 267-342µm H/D	Lithothamnion moretii (Fig. 6A-D)
6. encrusting to protuberant, warty protuberances formed by overgrowing crusts. Roof formed by 6-8 cells, 38-48 µm thick. Sporangial conceptacles chambers 105-131µm / 349-545µm H/D. Markedly raised above thallus surface	?Lithothamnion sp.1 (Fig. 7A-D)
6. protuberant, sporangial conceptacles formed in protuberances. Roof formed by 5-9 cells, 33-45µm thick. Sporangial conceptacle chambers 89-96 µm / 236-327µm H/D, raised above the thallus surface	?Lithothamnion sp.2 (Fig. 8A-B)
Mesophyllum	
1. peripheral rim and pore plate not developed on the roof of sporangial conceptacles	2
1. peripheral rim and pore plate developed on the roof of sporangial conceptacles	5
2. roof of sporangial conceptacles more than 5 cells thick	3
2. roof of sporangial conceptacles 3(4) cells thick	4
3. encrusting to protuberant, roof flat to slightly concave, formed by 5-7 cells, 36-80µm thick. Sporangial conceptacles raised, ellipsoidal to circular in section, chambers 128-226µm / 255-409µm H/D	Mesophyllum curtum (Fig. 12A-F)
4. encrusting to layered, roof of the sporangial conceptacles thin, formed by up to 3-4 cells, thin. Sporangial conceptacles slightly raised above thallus surface, chambers 104-118µm / 289-316µm H/D	Mesophyllum cf. erubescens (Fig. 10A-D
5. encrusting to layered, frequent multiple overgrowing. Roof of sporangial conceptacles up to 6 celled, pores bordered by up to 10 cells. Sporangial conceptacle chambers 145-217µm / 275-403µm H/D, rimmed, slightly to seldom markedly raised above thallus surface	Mesophyllum cf. printzianum (Fig. 11A-D)
5. encrusting to lamellate, roof 7-8 cells thick. Sporangial conceptacle chambers 131-216µm / 340-420µm H/D, slightly raised above thallus surface, rimmed	Mesophyllum alternans (Fig. 9A-D)
Phymatolithon	
1. encrusting to protuberant, peripheral filaments zoned. Gametangial and sporangial conceptacles born in protuberances. Sporangial conceptacle chambers 102-110µm / 157-223µm H/D, partly raised above thallus surface. Roof flat to slightly concave, 3-5 celled, up to 23µm thick	Phymatolithon sp. (Fig. 13A-D)
Corallinaceae	
1. sporangial conceptacles formed by initials peripheral to the fertile area (type 1 according Johansen)	Mastophoroideae
1. sporangial conceptacles formed by filaments interspersed among the fertile area (type 2 according Johansen)	2
2. cells of adjacent filaments connected with secondary pits	Lithophylloideae
2. cells of adjacent filaments connected with fusions	Hydrolithoideae
Mastophoroideae	
1. thallus monomerous, encrusting. No lateral and vertical alignment of cells. Chambers of sporangial conceptacles 112-173 µm / 306-370 µm H/D	Spongites fruticulosa (Fig. 17A-B)
Lithophylloideae	
1. thallus dimerous non-protuberant. Alignment of cells evident, conceptacles columellate, 93-120 µm / 193 – 246 µm H/D, cells of the roof do not differ in dimension from adjacent cells of peripheral filaments	Lithophyllum sp.1 (Fig. 14A-B)
1. thallus monomerous non-coaxial to dimerous, protuberant, presumed gametangial conceptacles columellate, 75-77µm / 163-191µm H/D, cylindrical-bulbous pore opened to small depression at the roof surface. Peripheral zoned.	Lithophyllum sp.2 (Fig.
Hydrolithoideae	
1. thallus dimerous, thin and non-protuberant. Sporangial conceptacles markedly protrude above thallus surface, chambers 131-143µm / 230-248µm H/D, cells are not aligned	Hydrolithon lemoinei (Fig. 16A-B)