

The first identification of fossil *Mesophyllum* in accordance to the modern taxonomic concepts in coralline algae

JURAJ HRABOVSKÝ, DANIELA BASSO, and GIOVANNI COLETTI



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Despite their common occurrence, the potential of coralline algae is not yet fully exploited in paleoecological reconstructions. The reasons are mainly grounded in the taxonomic inconsistency caused by poor preservation or insufficient knowledge of the type material of many species, and confusion derived from the difficult recognition of the coralline three-phased life cycle in the fossil record. Specimens of fossil coralline algae from newly collected samples, and historical Schaleková's collection of middle Miocene Paratethyan limestone were studied under optical and scanning electron microscopes, revealing the occurrence of the asexuate, male gametangial, and carposporangial conceptacles of *Mesophyllum crassiusculum* here documented for the first time. Based on the recent emendation of *Mesophyllum* and consequent circumscription of the genera *Mesophyllum* sensu stricto and *Melyvonnea*, this is the first and oldest finding of a fossil *Mesophyllum* sensu stricto. Moreover, we provide further evidence of the preservation potential of important diagnostic characters, such as the shape of epithallial and subepithallial cells, the shape of the conceptacle roofs, the number and shape of pore canals lining cells in the multiporate roof of the asexuate conceptacle chambers. The identification of *M. crassiusculum* in the middle Miocene of central Paratethys would deserve further biogeographic and paleoclimatic considerations that, however, are prevented by the incomplete exploration of the Paratethyan fossil record and the need of revision of other important type collections of closely related species.

Key words: Rhodophyta, Corallinophycidae, *Mesophyllum*, life cycle phases, taxonomy, Miocene, Slovakia.

Juraj Hrabovský [geoljuhr@savba.sk], Earth Science Institute of the Slovak Academy of Sciences, Dúbravská cesta 9, 840 05 Bratislava, Slovakia.

Daniela Basso [daniela.basso@unimib.it] and Giovanni Coletti [g.coletti@campus.unimib.it], Department of Earth and Environmental Sciences, University of Milano-Bicocca, P.zza della Scienza 4, 20126 Milano, Italy.

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Introduction

Coralline algae often dominate Miocene limestone beds from the central Paratethys. Corals, bryozoans, mollusks, polychaetes are less common but locally they can be the dominant components of the biofacies (Pisera 1985; Studencki 1988a; Riegl and Piller 2000; Doláková et al. 2008; Sremac et al. 2016). Skeletal assemblages and facies of these “Coralline Limestones” show similarities with both those of the modern Mediterranean and Red Sea (Seneš and Ondrejčíková 1991; Basso 1998; Riegl and Piller 2000; Basso et al. 2008) suggesting a complex depositional environment spanning potentially through different climatic zones (Seneš 1988, 1990; Seneš and Ondrejčíková 1991; Baráth 1992; Baráth et al. 1994; Pisera 1996; Riegl and Piller 2000). For the purpose of the paleoenvironmental analysis of these coralline-dominated limestone beds, the study of the algal assemblage (including its taxonomic com-

position at the lowest possible rank but also the distribution and the growth form of the different taxa) is fundamental (Basso 1998; Basso et al. 2008; Coletti et al. 2018).

Middle Miocene coralline algae from the central Paratethys were investigated mostly in the second half of the 20th century (Maslov 1956; Schaleková 1962, 1969, 1973, 1978; Schaleková and Čierna 1985; Golonka 1981; Pisera 1985; Studencki 1988b; Zdražilová 1988; Pisera and Studencki 1989). Since then, coralline taxonomy went through major changes and new diagnostic characters were introduced, affecting the taxonomy of some of the most common algae of these deposits with *Mesophyllum* as a good example (Studencki 1988a, 1999; Doláková et al. 2008; Sremac et al. 2016). Paleophycologists who first studied the corallines of the central Paratethys followed Lemoine's (1928) diagnosis for *Mesophyllum*, based on the occurrence of multiporate sporangial conceptacles and coaxially arranged ventral core filaments (= hypothallus). Presently, coaxial hypothallus

and multiporate asexual conceptacles are known to occur also in *Synarthrophyton patena* (Hooker and Harvey, 1849) Townsend, 1979 (Townsend 1979; Woelkerling and Harvey 1992), and may also occur uncommonly in some areas of the thallus of some species of *Lithothamnion* Heydrich, 1897, *Phymatolithon* Foslie, 1898 and *Clathromorphum* Foslie, 1898 (Keats et al. 2000; Basso et al. 2004; Merwe and Maneveldt 2014). Therefore, the definition of *Mesophyllum* was emended, incorporating reproductive characteristics of the male conceptacles (= *Mesophyllum* sensu lato; Adey 1970), thus allowing for a clear separation from *Synarthrophyton* (Lebednik 1978; Woelkerling and Harvey 1992). More recently, two new genera, *Capensia* Athanasiadis, 2017 and *Melyvonnea* Athanasiadis and Ballantine, 2014 were established upon the study and critical revision of a large number of type collections of modern *Mesophyllum* sensu lato species (Athanasiadis and Ballantine 2014; Athanasiadis 2017). The latter revision resulted in a profound further update of *Mesophyllum* diagnosis (= *Mesophyllum* sensu stricto; Athanasiadis and Ballantine 2014) that presently includes the morphology of the asexual conceptacle pore-canal lining cells (PCLC), the cystocarpic conceptacles morphology, dioecy, growth form and habitat (Athanasiadis 1999, 2001, 2007; Athanasiadis and Ballantine 2014; Athanasiadis 2017). The morphology of PCLC provides an important element to discriminate *Mesophyllum* sensu stricto from *Synarthrophyton* and *Melyvonnea* (Athanasiadis 2001; Athanasiadis and Ballantine 2014). *Capensia fucorum* (Esper 1796) Athanasiadis 2017 is the only species of the genus and contrary to *Mesophyllum*, is a hemiparasitic species (Athanasiadis 2017).

There are almost no data on either, gametangial conceptacles and PCLC of fossil *Mesophyllum*, with the exception of Mastrorilli (1968) and Coletti et al. (2018) for gametangial conceptacles and Hrabovský et al. (2015) for carposporangial conceptacles and pore lining cells. Therefore, the fossil records of *Mesophyllum* needs revision, in order to verify possible misidentifications of genus attribution after the recent diagnostic update (Athanasiadis 2017).

Recent researches proved that carposporangial and gametangial conceptacles are more common than previously believed, and features like the PCLC can be preserved in the fossil record (Basso et al. 1996; Braga et al. 2015; Hrabovský et al. 2015; Chelaru and Bucur 2016; Coletti et al. 2016). In this paper, we use for the first time the modern diagnosis of *Mesophyllum*, based on the above mentioned characters, for the identification of its middle Miocene representatives from the central Paratethys (Slovakia).

Institutional abbreviations.—AHFH, University of Southern California, Los Angeles, USA; NHM, Natural History Museum, Bratislava, Slovakia; TRH, Norwegian University of Science and Technology, Trondheim, Norway.

Other abbreviations.—D, diameter; H, height; L, length; PCLC, pore canal lining cells; SD, standard deviation; TS, thin section(s).

Material and methods

The following features, listed in the modern definition of *Mesophyllum* (Athanasiadis and Ballantine 2014) and possessing some fossilization potential, have been investigated: (i) predominantly coaxially arranged hypothallus (= ventral core filaments); (ii) single rectangular, generally flattened or rounded, but not flared epithallial cell; (iii) subepithallial meristematic cells mostly as long as or longer than cells immediately subtending them; (iv) multiporate sporangial conceptacles; (v) filaments lining the pore canals generally composed of more than 5 cells, similar, slightly elongated or smaller in length than other roof cells; (vi) sporangial pore canal lining cells thinner/wider than other roof cells; (vii) dioecious gametophytes; (viii) type of male conceptacle development (sensu Johansen 1981); (ix) carposporangial conceptacles with central pedestal; (x) predominantly encrusting growth form with simple and unbranched protuberances (Lebednik 1978; Woelkerling and Harvey 1992, 1993; Athanasiadis et al. 2004; Athanasiadis 2007; Athanasiadis and Ballantine 2014). Growth form description follows Woelkerling et al. (1993).

All studied specimens are stored in Natural History Museum. Specimens from two different collections were described. The first includes newly collected samples from Modrý Majer (nine thin sections, two acetate peels, and three polished cuts for SEM study). Bi/tetrasporophyte NHM B1857/1a and male gametophyte NHM B1857/1b were identified in TS 918-1 and a carpogonial-carposporangial plant NHM B1858 was identified in TS 918-7. The counterpart cut of TS 918-1, including tetrasporophyte NHM B1857/2a and gametophyte NHM B1857/2b, was observed under SEM. The Schaleková Collection includes tens of thin sections, twenty-seven of them come from Modrý Majer, but they do not contain *M. crassiusculum*. We found the species in TS IIIb455 collected in Kosihovce under the name *Mesophyllum gallettoi* Mastrorilli, 1968 (Schaleková 1978; Schaleková and Čierna 1985). Specimen from Schaleková collection (Schaleková and Čierna 1985) is labelled NHM B1859.

Light Microscope AXIOZEISS scope A1 was used in analyses of TS. Figures were provided by AXIOCAM 105 Color. Morphometry was done in AxioVision Microscopy Software. Counterparts were studied with Scanning Electron Microscope JEOL JSM-6390LV. Preparation of the counterparts followed a method modified from Braga et al. (1993). Differently from Braga et al. (1993) the best results were obtained with 1% HCl and 40–60 seconds of etching. Addition of 2% HCl caused net dissolution of the surfaces.

Geological settings

Limestone samples were collected from a site known as Modrý Majer (Schaleková 1978), which is located in Belá Hills, in the vicinity of the Belá village, about 4 km NW from Štúrovo town, 6 km SE from the Gbelce town, and south from

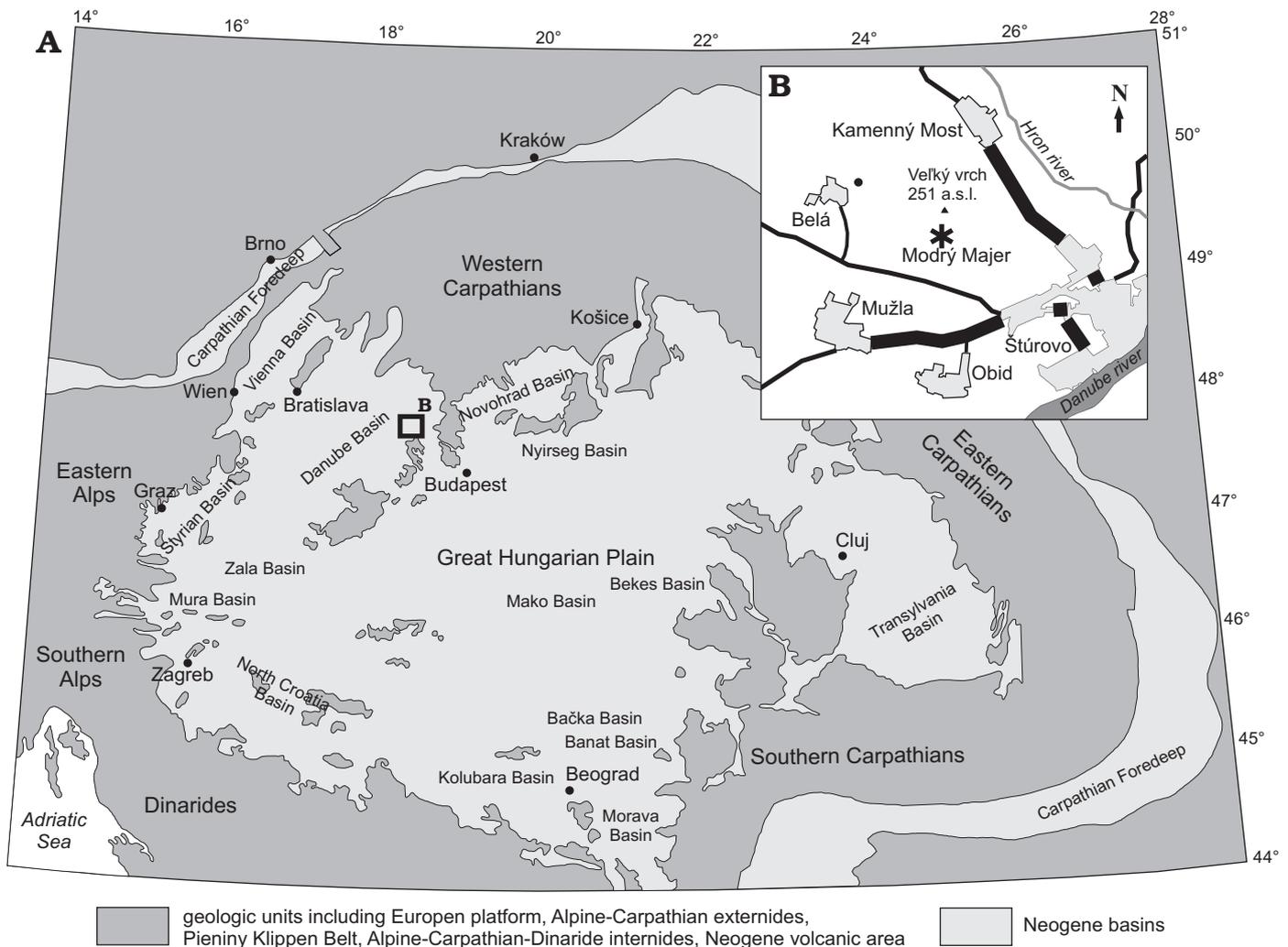


Fig. 1. The recent distribution of the central Paratethyan deposits with the location of the studied site. **A.** The central Paratethyan basins (modified from Kováč 2000). **B.** Map of the study area, asterisk indicates sampling site Modrý Majer.

the spot height Velký vrch (251 m a.s.l.) (Fig. 1). The site was previously studied by Seneš (1963) and Schaleková (1978) but it was already known from Matějka (1949). Belá Hills are located in the Southeastern Danubian Basin. The basin sedimentary record starts with the “Kiscellian” Formation deposited in the Želiezovce depression (Klučiar et al. 2016). The Bajtava, Špačince, and Pozba formations were deposited above the “Kiscellian” Formation during the Badenian (Klučiar et al. 2016). Upper Karpatian and lower Badenian terrestrial deposits locally lie directly on pre-Neogene basement (Kováč 2000). The hills are built by products of lower Badenian andesitic volcanoes above which algal reefs of the Špačince and Pozba formations developed (Schaleková 1978; Schaleková and Čierna 1985; Klučiar et al. 2016; Kováč et al. 2018). At the top there are clay, sand, conglomerate, organo-detrital limestone, and tuffaceous clay beds of the Sarmatian Vráble Formation. Slopes and low-lands are filled by the Pliocene Volkov Formation and by Quaternary deposits.

Algal limestone developed during both lower and upper Badenian, thus, stratigraphically, they cover the whole Badenian including Bajtava, Špačince, and Pozba forma-

tions (Hók et al. 1999; Vass 2002; Klučiar et al. 2016; Kováč et al. 2018). A more accurate stratigraphical positioning of studied limestone beds should require a detailed micropaleontological research that is out of the scope of this study. However, some additional considerations are necessary. Klučiar et al. (2016) documented algal reefs in the lower Badenian Špačince Formation of the Danubian Basin, and formerly placed in the now abandoned “middle” Badenian or Wielichian substage. Vass (2002) proposed that coralline algal bioconstructions developed on the Levice Horst elevations during the upper Badenian and included them into the Pozba Formation, which was previously considered as “middle” to “upper Badenian” by Hók et al. (1999). Limestone is not marked on the geological map of the scale 1:50 000 although they were known since Matějka (1949) fieldwork. Their stratigraphic relationship with volcanic and volcanoclastic units gives further information. Coral and coralline algal assemblages occur above lower Badenian andesites and are covered by upper Badenian (12.56 ± 0.1 Ma) volcanoclastics. Locally the limestone deposits are dated with nannoplankton to the upper Badenian. Therefore it seems to

be highly probable that studied limestone beds belong to the upper Badenian Pozba Formation (personal communication Samuel Rybár 2018).

Outcropping limestone bed is about 1 meter thick and covers an area of about 50 square meters. The bed lacks a siliciclastic fraction and is dominated by corals and coralline algae, gastropods are less common (Schaleková 1978). Schaleková (1978) described also the presence of encrusting foraminifers, benthic foraminifers, serpulids, and ostracods. In the thin sections, echinoid spines and bryozoan colonies were observed as well. Coralline algae are represented by discoid-shaped rhodoliths with warty-protuberant to wavy-laminar growth morphology as well as encrusting growth-forms developing over the small patches of corals and over corals fragments.

Systematic palaeontology

Phylum Rhodophyta Wettstein, 1901

Subphylum Eurhodophytina Saunders and Hommersand, 2004

Class Florideophyceae Cronquist, 1960

Table 1. Basic morpho-anatomical characteristics of fossil asexual, male and carposporangial plants of *Mesophyllum crassiusculum*. Measurements are in μm when not indicated otherwise. Abbreviations: D, diameter; L, length; n, number of filaments; “+” presence and “-” absence character; “±” intermediate.

	Bi/tetrasporophyte NHM B1857/1a	Male gametophyte NHM B1857/1b	Carposporangial conceptacles bearing gametophyte NHM B1858
Growth form	encrusting	encrusting	encrusting
	± appanate branches	± appanate branches	± appanate branches
	short unbranched protuberances	short unbranched protuberances	short unbranched protuberances
Thallus thickness	0.2–1.4 mm	0.4–1.5 mm	0.3–2 mm
Hypothallus			
thickness, filaments (n)	43–146, n = 8–22	45–185, n = 7–26	47–149, n = 6–27
arrangement of filaments	coaxial in patches	coaxial in patches	coaxial in patches
lateral fusion of cells	+	+	+
hypothallial cells: L, D	11–26, 5–11	10–29, 5–10	8–25, 4–8
hypothallial cells L/D ratio	2–4	2–4	2–4
Perithallus			
thickness	121–401	237–485	110–870
pattern of zonation	2–5 long vs. 1–2 short	2–5 long vs. 1–2 short	2–5 long vs. 1–2 short
cell fusions	+	+	+
perithallial cells: L, D	4–16, 4–11	5–15, 4–10	6–17, 4–10
perithallial cells L/D ratio	0.5–2	0.5–3	0.5–3
Meristemetic cells			
shape	elongated	elongated	elongated
meristemetic cells: L, D	8–12, 6–8	7–10, 6–7	8–10, 6
meristemetic cells L/D ratio	1–2	1–2	1–2
Epithallial cells			
cells (n)	1–2	1–2	1
epithallial cells: L, D	3–5, 5–7	4–5, 5–7	3, 4–6
epithallial cells L/D ratio	rounded, flattened	rounded, flattened	rounded
trichocytes	–	–	–

Subclass Corallinophycidae Le Gall and Saunders, 2007

Order Hapalidiales Nelson, Sutherland, Farr, and Yoon in Nelson et al., 2015

Family Mesophyllaceae Athanasiadis, 2016

Genus *Mesophyllum* Lemoine, 1928

Type species: Mesophyllum lichenoides (Ellis, 1768) Lemoine, 1928; Cornwall, England, Recent.

Mesophyllum crassiusculum (Foslie, 1902) Lebednik, 2004

Figs. 2–4.

1985 *Mesophyllum gallettoi* Mastroianni, 1968; Schaleková and Čierna 1985: 42.

Material.—Species was identified in the two thin sections NHM B1857/1a and NHM B1857/1b, and their counterparts studied on SEM NHM B1857/2a and NHM B1857/2b. One specimen was detected in Schaleková collection (Schaleková and Čierna 1985)—thin section NHM B1858.

Description.—The species develops non-protuberant rhodoliths or encrusts other coralline algae or corals (Fig. 2A). The core of the rhodoliths usually consists of corals but carposporangial-carpogonial plants also encrust other fruticose

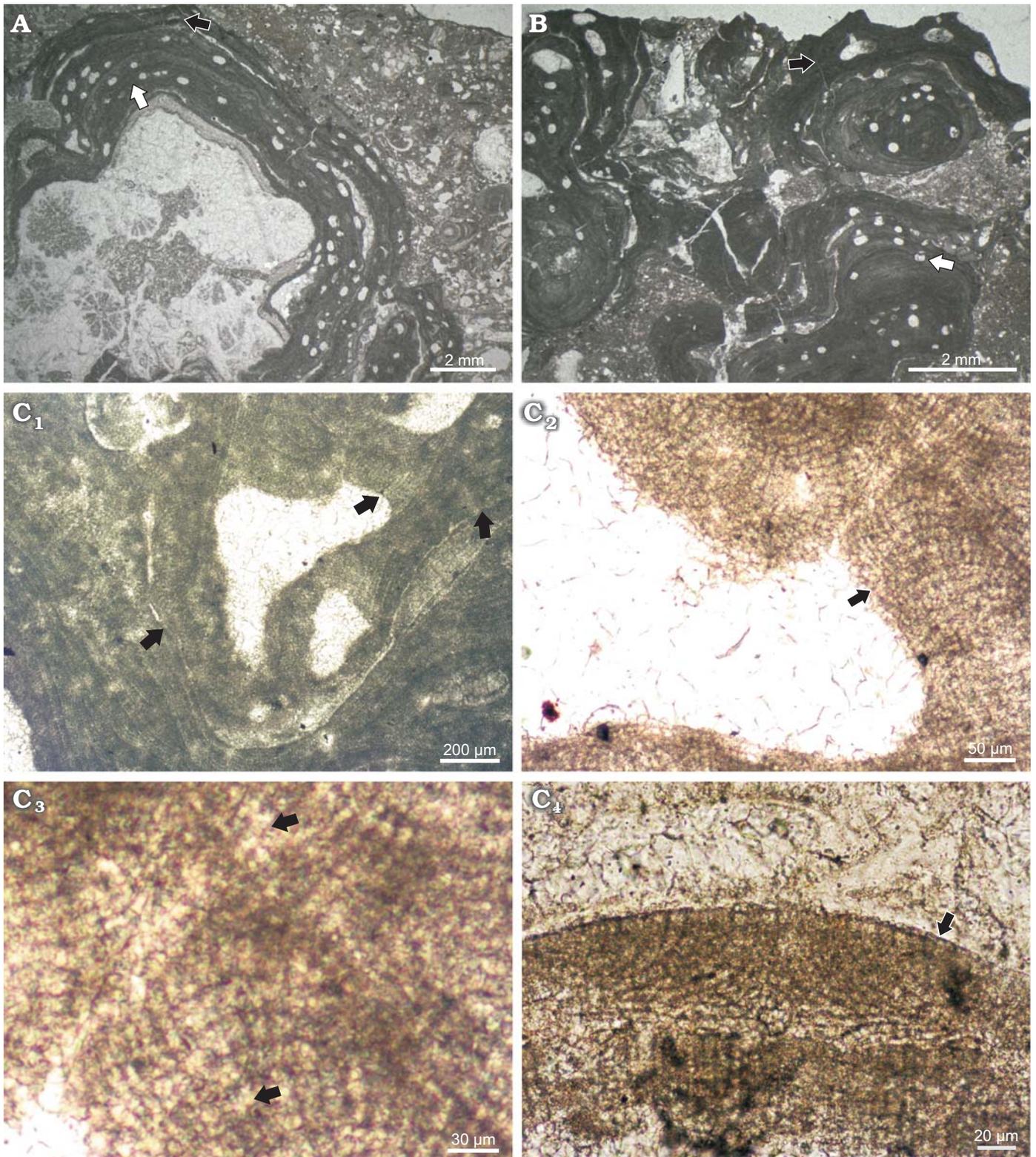


Fig. 2. Coralline alga *Mesophyllum crassiusculum* (Foslie, 1902) Lebednik, 2004 from early Serravallian, Miocene, Modrý Majer, Slovakia. **A.** Bi/tetrasporophyte and male gametophyte, NHM B1857/1a and NHM B1857/1b (TS 918-1), respectively. An asexual (tetra/bisporangial) plant (white arrow) overgrows a fragment of scleractinian coral colony. Growth form of coralline alga is encrusting. Male gametophyte overgrows tetrasporophyte (black arrow). **B.** Carposporophyte, NHM B1858 (TS 918-7). Carpoconial-carposporangial plant of *M. crassiusculum* (black arrow) overgrows a protuberant rhodolith of *Phymatolithon calcareum* (Pallas, 1766) (white arrow). Growth form of *M. crassiusculum* is encrusting and without protuberances. **C.** Bi/tetrasporophyte, NHM B1857/1a (TS 918-1). **C₁.** Applanately branching thallus (arrows). **C₂.** Pseudoparenchymatous thallus with coaxially to non-coaxially arranged hypothallus. Arrow points to the portion where coaxial hypothallus is best visible. **C₃.** Magnified portion of the thallus from **C₂**, arrows point to cell fusions in hypothallus and in the perithallus. **C₄.** Flattened epithallial cells above meristematic cells located at the top of the embedded conceptacle.

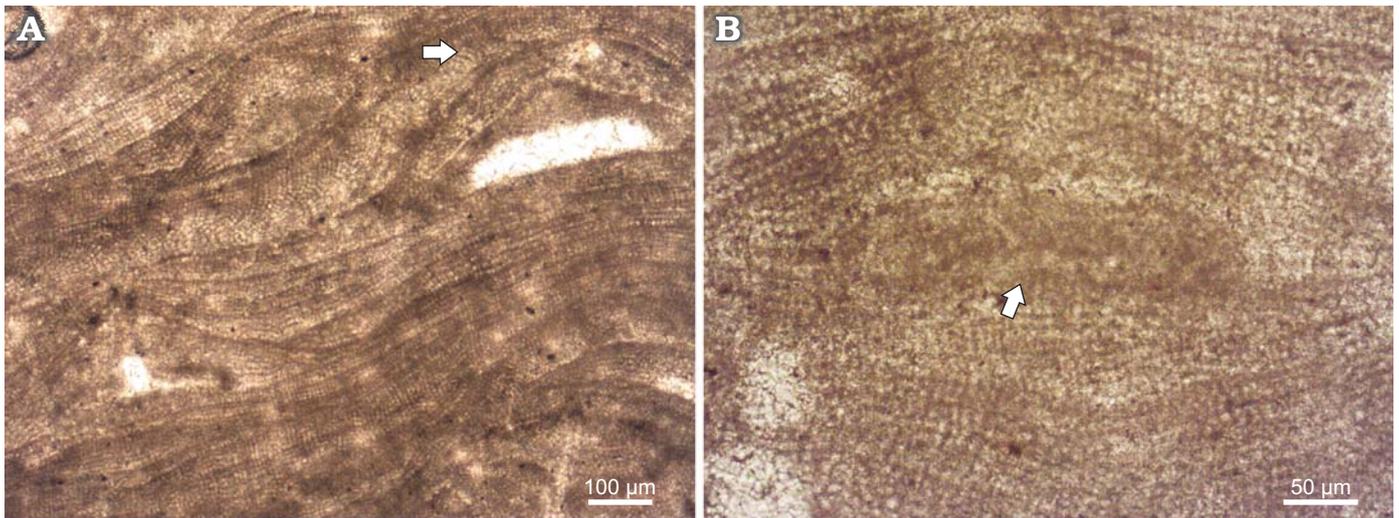


Fig. 3. Coralline alga *Mesophyllum crassiusculum* (Foslie, 1902) Lebednik, 2004 from early Serravallian, Miocene, Modrý Majer, Slovakia, male gametophyte, NHM B1857/1b (TS 918-1). **A.** Conceptacles of the type 1 (Johansen, 1981) were protruding above thallus surface during their maturity. Note the coaxial arrangement of the hypothallus; arrow points to the coaxial hypothallus. **B.** Conceptacle filled with material of unknown origin (arrow).

protuberant coralline algae (e.g., *Phymatolithon calcareum*; Fig. 2B). Growth form is encrusting without prominent or branched protuberances. Applanate branches locally develop (Fig. 2C₁). Two short warty protuberances 0.5×0.5 mm were also detected. Thickness of the superimposed thalli could reach few mm. Individual lamellae are 0.2–2 mm thick (Table 1).

Thallus is pseudoparenchymatous with dorsiventral organization, consisting of a single system of branching filaments (monomerous construction). Filaments of the hypothallus run in parallel with the substrate and can be arranged either coaxially or non-coaxially (Fig. 2C₂). In the asexual plants the hypothallus is 43–146 µm thick (Table 1). The hypothallial cells (n = 38) are 11–26 µm long (mean ± SD, 18±4 µm) and 5–11 µm in diameter (mean ± SD, 7±1.2 µm). Hypothallus filaments bend upward toward thallus surface and develop the peripheral portion of the thallus (perithallus). Cells (n = 180) are 4–16 µm long (mean ± SD, 9±2.3 µm) and 4–11 µm in diameter (mean ± SD, 7±1.5 µm) (Table 1). Cells within single filaments show cyclic variation in length. Sets of 2–5 long cells are alternated with 1–2 short cells. Such pattern results in irregular growth zones (Fig. 2C₁). Cells are laterally joined by cell fusions (Fig. 2C₃). Epithallial cells (n = 7) are rounded or flattened but not flared, measuring 3–4 µm in length (mean ± SD, 3±0.5 µm) and 5–7 µm in diameter (mean ± SD, 6±0.8 µm) (Fig. 2C₄). One or two cells are present above meristematic cells. Meristematic cells (n = 12) are as long or longer than cells immediately subtending them and measure 8–12 µm in length (mean ± SD, 10±1.5 µm) and 6–8 µm in diameter (mean ± SD, 7±0.6 µm) (Fig. 2C₄). The size of the vegetative characters observed in the sexual plants are largely overlapping with those of the asexual plants (Table 1).

Gametophyte encrusts tetrasporophyte. However, where margins of the two thalli meet, multiple overgrowths may occur. Presumed gametangial male conceptacle is of the

type 1 (Johansen 1981) and the mode of projection complies with those of *Mesophyllum* and *Lithothamnion* (according to Lebednik 1978) (Fig. 3A). In fact, in *Mesophyllum* and *Lithothamnion* the initiation of the male conceptacle development takes place just below the meristematic cells in contrary to *Phymatolithon* in which initiation takes place deep in the vegetative filaments, thus male conceptacle is not prominent in the latter (Lebednik 1978: 393, 394, text-figs. 8–9, 11). Male conceptacles (n = 7) measure 185–310 µm in diameter (mean ± SD, 254±63.7 µm) and 42–60 µm high (mean ± SD, 51±9.1 µm). Pore canal is 77–108 µm long (mean ± SD, 89±16.4 µm) and up to 54 µm broad (Table 1). Some conceptacles are filled with dark material of uncertain origin (Fig. 3B).

Carposporangial conceptacles are large and occur on other plant than male conceptacles (Fig. 4A). The presence of male and carposporangial conceptacles on distinct plants suggests that gametophytes are most likely dioecious. Chambers (n = 4) are dumbbell shaped, 519–689 µm in diameter (mean ± SD, 604±119.9 µm) and 155–229 µm in height (mean ± SD, 192±52.3 µm) measured aside of a well-developed central pedestal (H₂ according Basso et al. 1996) (Fig. 3A, Table 1). Pore length is 108–178 µm (mean ± SD, 143±49.6 µm) and its width is 112–143 µm (mean ± SD, 127±22.6 µm).

Multiporate sporangial conceptacles are rounded to oval (Fig. 4B₁). Conceptacles protrude above the thallus surface and are overgrown by thallus growth from the sides of the conceptacle. Chambers (n = 7) are 179–418 µm in diameter (mean ± SD, 326±59.2 µm) and 90–199 µm high (mean ± SD, 171±16.3 µm). D/H ratio is 1.6–2.4. The roofs are 42–69 µm thick and are formed by 6–9 cells that tend to be shorter towards the apex (Fig. 4B₂, C₁; Table 1). Pore canals are mostly lined by cells similar in size and shape to the other roof cells (Fig. 4B₂, C₂). Locally specialized thinner cells were observed (Fig. 4B₂, C₂). At least 6 cells lining each pore canal were observed under SEM (Fig. 4B₂). Pore canal cells thinner than those of the roof were observed also in the thin section

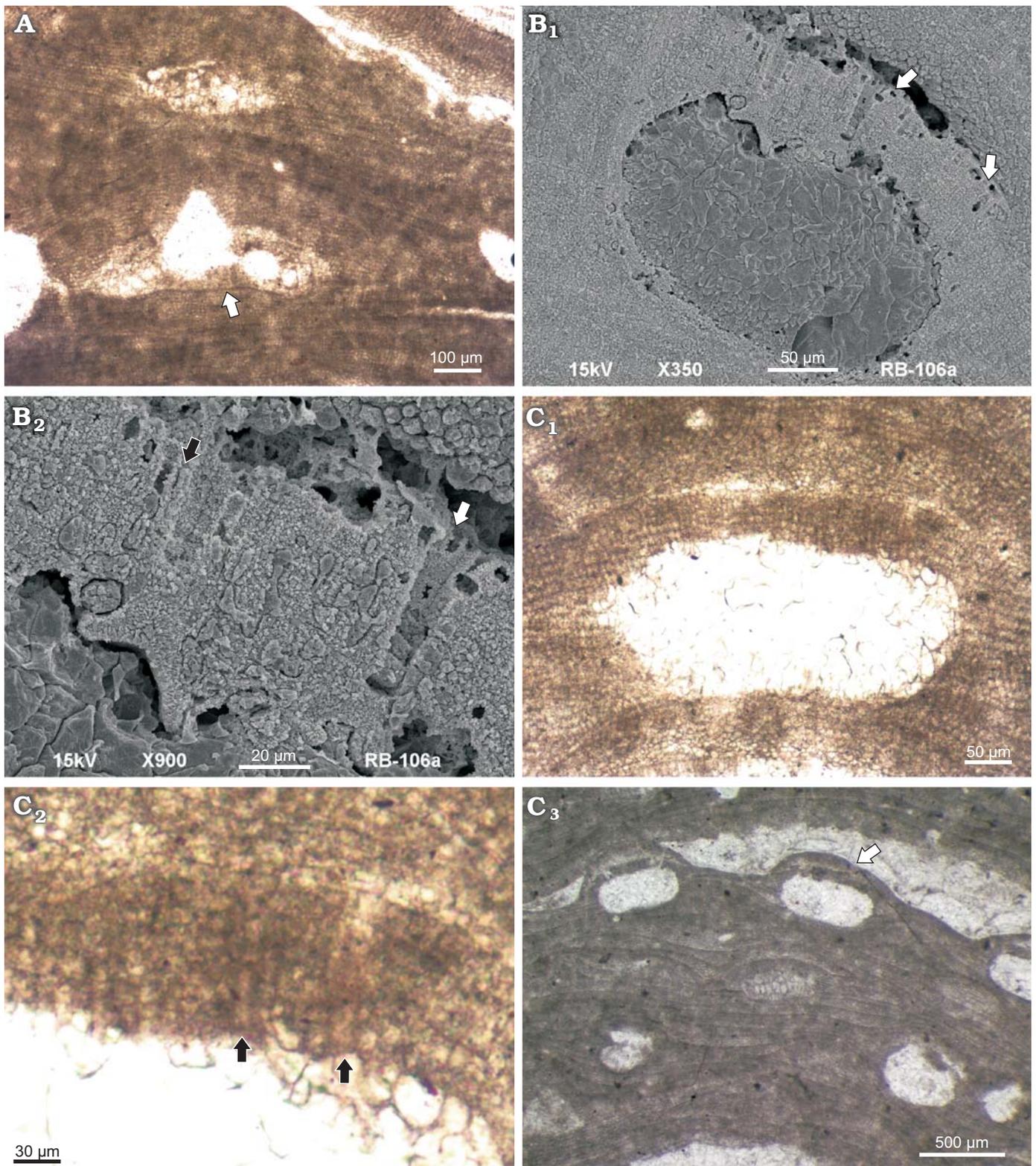


Fig. 4. Coralline alga *Mesophyllum crassiusculum* (Foslie, 1902) Lebednik, 2004 from early Serravallian, Miocene, Modrý Majer, Slovakia. **A.** Carposporophyte, NHM B1858 (TS 918-7), carposporangial conceptacle with central pedestal (arrow). **B.** Bi/tetrasporophyte, NHM B1857/2a (counterpart of the TS 918-1). **B₁.** Multiporate sporangial conceptacle, arrows point to the rounded epithelial cells located at the top of conceptacle roof. Rounded cell at the margin of the pore canal marks the surface of the roof. Adjacent pore canal cells are therefore considered as rosette cells. Note that rosette cells are not sunken. **B₂.** Asexual conceptacle with roof filaments and pore canal filaments consisting of at least 6 cells, arrows point to thinner (black arrow) and wider (white arrow) pore canal cells. **C.** Bi/tetrasporophyte, NHM B1857/1a (TS 918-1). **C₁.** Asexual multiporate conceptacle with roof filaments consisting of up to 7 cells. **C₂.** Detail of **C₁** with pore lining cells (arrows), the cells are same or wider (top of the pore canal) than adjacent roof cells. **C₃.** Embedded asexual conceptacles (arrow). Note chambers filled with adventitious cells. The roofs are convex to flat, lacking peripheral rim.

Table 2. *Mesophyllum crassiusculum* (Foslie, 1902) Lebednik, 2004 comparison from the Recent and middle Miocene. Measures are in μm when not indicated otherwise. Abbreviations: CP, central Paratethys; D, diameter; H, height; L, length; ND, no data; “+” presence, “-” absence, and “±” intermediate character.

Reference	Athanasiadis et al. 2004	Athanasiadis 2007	this work	this work	
Specimen	TRH #205	AHFH #70353	NHM B1857, B1858	NHM B1859	
Distribution	California, USA	California, USA	CP (Modrý Majer, Slovakia)	CP (Kosihovce, Slovakia)	
Habitat	littoral	littoral–sublittoral (49 m)	littoral	littoral	
Substratum	epilithic, rhodolith	epilithic	epilithic, rhodolith	epilithic, rhodolith	
Thallus growth form	encrusting	encrusting	encrusting	encrusting	
Thallus diameter	up to 7 cm	ND	ND	ND	
Ventral outgrowths	–	ND	ND	ND	
Peripheral protuberances	±	±	±	±	
Superimposing growth	+	+	+	+	
Lamella thickness	150–2500	ND	200–1400	150–2000	
Hypothallus thickness	52–300	ND	43–150	56–144	
Perithallus thickness	50–80	ND	121–401	up to 400	
Predominantly coaxial hypothallus	+	+	±	±	
Stratified perithallus	±	ND	±/–	±/–	
Elongated meristematic cells	+	ND	+	+	
Terminal trichocytes	–	ND	–	–	
Hypothallus cells: L, D	10–31, 5–13	15–30, 8–12	11–26, 5–11	12–20, 4–8	
Perithallus cells: L, D	4–23, 4–9	ND	4–16, 4–11	7–13, 5–11	
Epithallial cells	number of cells	1–3	ND	1	
	L, D	2–5, 3–9	ND	3–5, 5–7	
	shape	flattened	flattened	rounded, flattened	rounded, square
Asexuate (multiporate) conceptacles	external diameter	300–636	450–750	350–630	333–498
	external height	up to 160	120–250	75–120	75–100
	chamber D, H	250–410, 130–190	300–450, 180–240	275–418, 148–199	227–405, 135–202
	convex roof	+	+	+	+
	roof/pore plate thickness	40–70	42–60	42–69	44–70
	roof/pore plate cells	6–10	8–10	6–9	6–9
	pore plate diameter	170–300	260–470	ND	ND
	number of pores	36–50	ND	ND	ND
	conical canal	–	–	–	–
	pore canal diameter	10–14	c.10	10–13	10–16
	embedded conceptacles	+	ND	+	+
	conceptacles degenerate	–	ND	ND	ND
	peripheral rim	–	–	–	–
Pore canal lining cells	rosette cells	6–10	6–8	ND	ND
	rosette cells sunken	–	–	–	–
	cells per filament	6–8	8–10	6–9	6–9
	similar to contiguous	+	–	+	+
	smaller than contiguous	–	–	–	–
thinner and wider	–	+	+	+	
Bi/tetrasporangia: L, D	110–200, 25–70	120–175, 60–100	ND	ND	
Male conceptacles	external diameter	ND	ND	324–429	ND
	external height	ND	ND	87–115	ND
	chamber D, H	ND	ND	162–372, 42–90	ND
	roof thickness	ND	ND	27–45	ND
	pore canal diameter	ND	ND	57–69	ND
Carposporangial conceptacles	external diameter	ND	ND	ND	ND
	external height	ND	ND	ND	ND
	chamber D, H	ND	ND	470–689, 127–256	ND
	chamber shape	ND	ND	dumbbell	ND
	roof thickness	ND	ND	133–176	ND
	pore canal diameter	ND	ND	129–132	ND

(Fig. 4C₂). At the top of the pore canals epithallial cells and PCLC appear at the same level, indicating that rosette cells around the pore canal are not sunken (Fig. 4B₁). Conceptacles are embedded and locally filled with adventitious cells (Fig. 4C₃). Remains of these cells are present in some chambers (Fig. 4C₁). The roof is either flat or convex, with no peripheral rim and sunken pore plates. Old conceptacles become buried when covered by successive thallus growth (Fig. 4C₃).

Remarks.—We have identified *M. crassiusculum* from the newly collected middle Miocene material. The asexual (bi/tetrasporangial) specimens fully correspond with the type (Athanasiadis et al. 2004; Athanasiadis 2007). During the revision of the historical collection of Anna Schaleková we have identified one specimen of *M. crassiusculum* formerly described as *M. galettoi* (Schaleková and Čierna 1985). This specimen matches with both, Modrý Majer specimen and *M. crassiusculum* type (Fig. 5, Table 2).

Stratigraphic and geographic range.—Early Langhian of the central Paratethys (this work) to Recent of the Pacific Ocean (Athanasiadis et al. 2004; Athanasiadis and Ballantine 2014).

Discussion

The studied material corresponds to *Mesophyllum crassiusculum* as described by Athanasiadis et al. (2004) and Athanasiadis (2007) (Figs. 2, 3; Table 2). The pore canal cells shape, their number and the morphology of the roof of multiporate sporangial conceptacles fit within the description of the living plants of *M. crassiusculum*, although a complete comparison is prevented by the absence of data on gametophyte and carposporangial conceptacles in the Recent material (Athanasiadis et al. 2004; Athanasiadis 2007).

The specimen from the Schaleková's Collection published in Schaleková and Čierna (1985) was firstly identified as *Mesophyllum galettoi* Mastrorilli, 1968. However, our investigation revealed morpho-anatomical characteristics similar to the Recent *M. crassiusculum*.

Most of the morphoanatomical characteristics of the studied sporophyte and male gametophyte perfectly correspond to those of the specimens described by Coletti et al. (2018: supplementary material) as *Mesophyllum roveretoi* Conti, 1943, in the lower Miocene of the Sommières Basin (Southern France). Coletti et al. (2018) also describe a female gametophyte but in this case the comparison is more difficult because their specimen mainly reveals unfertilized conceptacles (Coletti et al. 2018: supplementary material). Because they do not present data on the epithallial cells or on the cells around the pore canal, a proper comparison is not possible. The similarity between *M. roveretoi*, *M. galettoi*, and *M. crassiusculum* suggests that a revisions of the original material of Conti (1943) and Mastrorilli (1968) is necessary.

Regarding the ecology of this species, according to Athanasiadis and Ballantine (2014) the genus *Mesophyllum*

generally inhabits Recent temperate seas, and its occurrence in the tropics, as is the case of *M. crassiusculum* reaching the coast of California south to the Pacific Mexico, is presently accompanied by the absence of all reproductive phases excluding the sporophyte. This in turn would suggest temperate climate during the late Badenian in the study area, a hypothesis supported by Studencki (1988a, 1999) after his studies of the coralline algae from Poland. To the contrary, tropical climate during the Badenian was commonly proved by the presence of colonial corals (e.g., Baráth 1992; Riegl and Piller 2000; Saint Martin et al. 2007; this paper), whose patches or small frameworks also presently co-occur with the modern *M. crassiusculum* (Glynn et al. 2017). Sub-tropical climate is documented in central Paratethys in the upper Badenian and even in the Sarmatian (Kováč et al. 2005, 2007; Harzhauser and Piller 2007). However, a broader discussion of paleoclimate based solely upon *Mesophyllum* occurrences would require the full revision of the fossil records and it is not yet possible because of insufficient data.

Identification of *Mesophyllum* sensu lato gametophytes and carposporophytes is problematic when dealing with the fossil record (Hrabovský et al. 2015). Other genera, such as *Neogoniolithon* Setchell and Mason, 1943, *Spongites* Kützing, 1841, *Pneophyllum* Kützing, 1843, and *Chamberlainium* Caragnano, Foetisch, Maneveldt, and Payri, 2018 possess both a coaxial hypothallus and uniporate spermatangial conceptacle chambers that could be confused with *Mesophyllum* carposporangial conceptacle chambers (Johansen 1981; Braga et al. 1993; Caragnano et al. 2018). However, the occurrence of a central pedestal associated to a coaxial hypothallus is a unique combination in *Mesophyllum* sensu stricto. This structure develops from the decalcification and dissolution of floor cells around the carpogonial branches (which make room for the carposporangia; Athanasiadis et al. 2004). This results in a distinct morphological elevation in the central part of the carposporangial chamber of *Mesophyllum* (Athanasiadis et al. 2004; Athanasiadis and Ballantine 2014). *Neogoniolithon* sporophytes from Atlantic coast of Mexico predominantly possess flat floors whereas the others have just an ill-defined inflexion of the chamber floor, differently from the distinctive “central pedestal” in *Mesophyllum* carposporangial conceptacles as well as from our samples (Athanasiadis et al. 2004; Quaranta et al. 2007; Mateo-Cid et al. 2014).

The absence of trichocytes in the studied material is another important evidence that supports their placement in *Mesophyllum* rather than *Neogoniolithon*. Recent molecular taxonomy suggests trichocytes importance in coralline algal systematic (Basso et al. 2014; Rösler et al. 2016; Caragnano et al. 2018). Trichocytes are commonly reported in modern and fossil *Neogoniolithon* species from temperate and tropical seas (Basso and Rodondi 2006; Kato et al. 2011; Mateo-Cid et al. 2014; Rösler et al. 2015, 2016; Villas-Boas et al. 2015; Caragnano et al. 2018) contrarily to *Mesophyllum* s.s. species that do not possess trichocytes (Athanasiadis and Ballantine 2014).

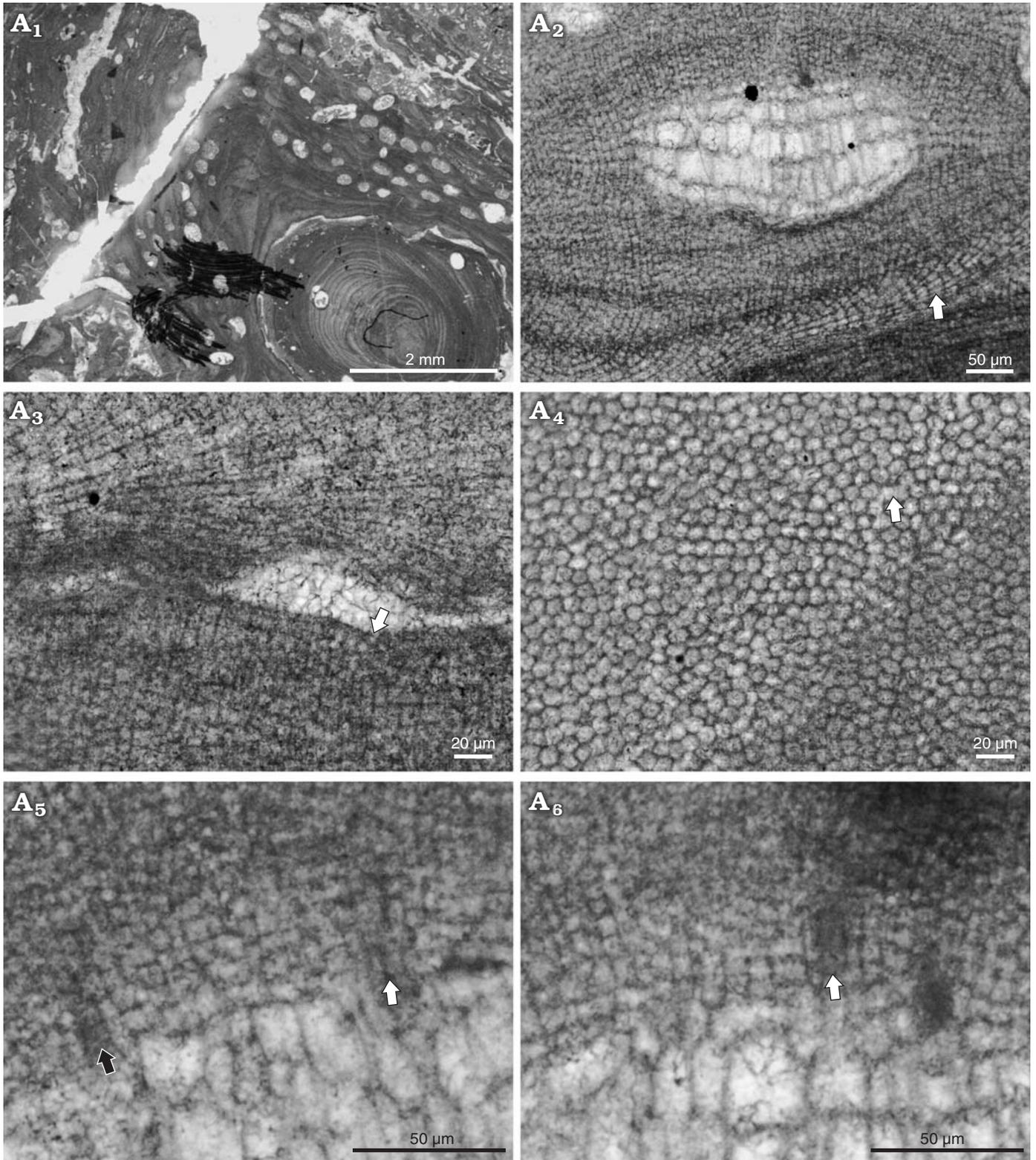


Fig. 5. Coralline alga *Mesophyllum crassiusculum* (Foslie, 1902) Lebednik, 2004 bi/tetrasporophyte, early Langhian, Miocene, Kosihovce, Slovakia. Schaleková's collection, NHM B1859 (TS IIIb455). A₁. Thallus morphology, growth form is encrusting with weak protuberances. A₂. Coaxial to non-coaxial hypothallus (arrow). A₃. Epithallial cells rounded or flattened (arrow). A₄. Lateral cell fusions of the cells in adjacent filaments (arrow). A₅. Pore canal anatomy, lining cells are same as adjacent roof cells (black arrow) or thinner near the base (white arrow). A₆. Pore canal anatomy, lining cells are thinner than adjacent roof cells in some portions of the pore canal filaments. Arrows point to the center of the pore canal.

There are no morphological characters allowing the distinction of fossil male plants of *Neogoniolithon* and

Mesophyllum. However, the following observations suggest that the specimens analyzed in this study are indeed

Mesophyllum gametophyte rather than *Neogoniolithon* plants: (i) overlapping vegetative morphoanatomical features with those of the sporophyte, (ii) co-occurrence of sporophyte and gametophyte of *Mesophyllum* in the same thin section, (iii) absence of trichocytes, (iv) absence of sporangial plants of *Neogoniolithon* in the same thin sections.

Actually, the observed carpogonial-carpogonangial, spermatangial and asexuate plants present the same: (i) growth form, (ii) thickness of the lamellate branches, (iii) perithallus zonation, (iv) ventral core thickness, (v) cells dimensions, (vi) lateral cells connections, (vii) meristematic cells elongation, (viii) epithallial cells shape, and (ix) absence of trichocytes (Table 1).

For these reasons, we tentatively describe the observed specimens as different life cycle phases of *Mesophyllum crassiusculum*. The discovery of *M. crassiusculum* gametophytes in modern plants will hopefully provide further evidence supporting our conclusions, but for the moment there is no other reports of specimens corresponding with our gametophyte from the Slovakian part of the central Paratethys (Schaleková 1962, 1969, 1973, and 1978; Schaleková and Čierna 1985; Hrabovský 2013).

This is not the first example of description of fossil gametangial plant and other examples are known from the literature e.g., in *Lithophyllum racemus* (Lamarck, 1816) Foslie, 1901 (Basso et al. 1996), *Phymatolithon calcareum* (Pallas, 1766) Adey and McKibbin, 1970 (Basso et al. 1997), *Mesophyllum roveretoi* Conti, 1943 (Mastrorilli 1968), *Mesophyllum* cf. *printzianum* (Hrabovský et al. 2015), *Lithothamnion ponzonense* Conti, 1943 (Conti 1943) or *Sporolithon preerythraeum* (Airoidi, 1932) Vannucci, Piazza, Fravega, and Basso, 2000 (Vannucci et al. 2000; Chelaru and Bucur 2016). Both, spermatangial and carpogonial plants were described in Chelaru and Bucur (2016) for *Spongites fruticulosus* and *Sporolithon* sp. 1. Chelaru and Bucur (2016) provided examples of gametophyte for two *Lithothamnion* species but did not specify whether male or female. Uncertain *Lithophyllum* sp. 2 gametophyte was documented in Hrabovský et al. (2015). Almost complete life cycle with tetrasporophyte, male gametophyte, and carpogonangial conceptacles were described for *Sporolithon lvovicum* (Maslov, 1956) Bassi, Braga, Zakrevskaya, and Petrovna Radionova, 2007 (Hrabovský et al. 2015) and *Hydrolithon braganum* Woelkerling, Bassi, and Iryu, 2012 (Woelkerling et al. 2012). *Neogoniolithon contii* (Mastrorilli, 1967) Quaranta, Vannucci, and Basso, 2007 has complete life cycle documented (Quaranta et al. 2007). However, further research in this direction is still necessary in order to fill one of the main gaps of knowledge in fossil coralline algae.

Conclusions

The gametophytic, carpogonophytic, and asexuate phases of *Mesophyllum crassiusculum* are documented from middle Miocene material collected in the central Paratethys. This is

the first report of this species in the fossil record, based on the complete matching with the morphology and anatomy of the modern asexuate counterpart. For the first time, the identification was based on the emended *Mesophyllum* diagnosis (Athanasiadis and Ballantine 2014) that includes sporophyte conceptacles pore canal anatomy, carpogonangial conceptacles floor morphology and dioecy. The number and shape of the pore canals lining cells in the multiporate conceptacle roof are shown to be a character with fossilization potential, very useful when preserved, for fossil coralline systematics. The carpogonangial *Mesophyllum* sensu stricto can be identified in the fossil on the basis of the unique combination of cell fusions, coaxial hypothallus, non-flared epithallial cells, and “central pedestal” at the center of the conceptacle floor. These results enrich the list of the fossil corallines for which the gametophyte/carpogonophyte have been described. Last but not least, our results highlight once more the necessity of further revisions of historical collections to improve the knowledge about the distribution, paleoecology and paleobiogeography of fossil coralline algae.

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