The taxonomy of middle Miocene red algae from the Gârbova de Sus Formation (Transylvanian Basin, Romania)

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Abstract: This study describes seventeen non-geniculate coralline algal species (orders Corallinales, Hapalidiales and Sporolithales) from the middle Miocene (lower-middle Badenian) red-algal limestones of the Transylvanian Basin, Gârbova de Sus Formation. For the description and identification at species level, we follow the common diagnostic features used for fossil species and some characters that are used as diagnostic for modern species (roof morphology for asexual conceptacles, the presence/absence of a layer of elongated cells below sporangial compartments and number of cells in paraphyses for *Sporolithon*, and measurements of gametangial and carposporangial conceptacles). Female conceptacles of *Spongites fruticulosus* KÜTZING are for the first time described in fossil material. We propose the attribution of *Lithophyllum platticarpum* MASLOV to *Spongites fruticulosus* KÜTZING as a gametangial thallus with male conceptacles.

Key Words: Central Paratethys; Badenian; rhodolith; gametangium; *Spongites fruticulosus*.

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Résumé : ***Systématique des algues rouges du Miocène moyen de la Formation Gârbova de Sus (Bassin Transylvanien, Roumanie).-*** Cette étude présente dix-sept espèces d'algues corallines non articulées (ordres des Corallinales, des Hapalidiales et des Sporolithales) provenant des calcaires à algues rouges du Miocène moyen (Badénien inférieur-moyen) de la Formation Gârbova de Sus du Bassin Transylvanien. Pour la description et l'identification au niveau spécifique, nous adoptons les caractéres diagnostiques habituellement utilisés chez les espèces fossiles et certaines caractéristiques qui sont considérées comme diagnostiques chez les espèces modernes (morphologie du toit pour les conceptacles asexués, la présence ou l'absence d'une couche de cellules allongées sous les compartiments sporangiaux et le nombre de cellules dans les paraphyses de *Sporolithon*, et les mesures des conceptacles gamétangiaux et carposporangiaux). Les conceptacles femelles de *Spongites fruticulosus* KÜTZING sont décrits pour la première fois chez des formes fossiles. Nous proposons le rattachement de *Lithophyllum platticarpum* MASLOV à *Spongites fruticulosus* KÜTZING pour un thalle gamétangial à conceptacles mâles.

Mots-clefs : Paratéthys centrale ; Badénien ; rhodolithe ; gamétange ; *Spongites fruticulosus*.

Introduction

The carbonate-siliciclastic succession of the Gârbova de Sus Formation cropping out at the western border of the Transylvanian Basin, mainly consists of coralline algae, larger benthic foraminifera and bryozoans. Although the importance of coralline algae as palaeoenvironmental indicators in Cenozoic carbonate deposits is very well documented elsewhere (among others: FRAVEGA *et al.*, 1994; NEBELSICK & BASSI, 2000; NEBELSICK *et al.*, 2000; RASSER, 2000; BRAGA & AGUIRRE, 2001; BASSO *et al.*, 2008; NEBELSICK *et al.*, 2013; COLETTI *et al.*, 2015), the coralline algae from the Transylvanian Basin are still insufficiently described.

Some early contributions (LÖRENTHEY, 1894a, 1894b; KOCH, 1900; PÁVAY-VAJNA, 1910; ŞURARU, 1992) mention "*Lithothamnium ramosissimum*", a species considered representative of Middle Miocene deposits, within the so called "Lithothamniumkalke". Later BUCUR & FILIPESCU (1994) studied the red algae from the western margin of the Transylvanian Basin and provided a detailed description and illustration of 13 species. A more recent study (BUCUR & FILIPESCU, 2011) of the Lopadea Veche section presents more illustrations of coralline algae, but the identification of specimens remains at genus level.

New samples were collected for the present study; hence, this is not the re-examination of species previously identified by other authors. Some of the species described here are recorded for the first time in the Transylvanian Basin or the Central Paratethys.

The re-evaluation of species and genera of coralline algae from the Transylvanian Basin is needed in the light of the recent revisions of some type collections containing species described in the 19th and 20th centuries (AGUIRRE *et al.*, 1996, 2011; BASSO *et al.*, 1998; BASSI *et al.*, 2005, 2007; VANNUCCI *et al.*, 2000, 2008; IRYU *et al.*, 2012), and the introduction of new diagnostic features for the identification of fossil species (HRABOVSKÝ *et al.*, 2015).

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An important purpose of the present study is to identify features that are used in descriptions of modern red algae. Gametangial and carposporangial conceptacles are identified following HRABOVSKÝ *et al.* (2015). We focused on the description of specimens bearing these features, because of their rare identification or misidentification in fossil material as mastophoroid/lithophylloid corallines, exclusively on the basis of their uniporate conceptacles.

Based on the latter features, the present study provides a detailed taxonomic description of Middle Miocene (Badenian) red algae (Corallinales, Hapalidiales, Sporolithales) from the Lopadea Veche section, Transylvanian Basin. This work aims to contribute to a better understanding of the palaeogeographic distribution of red algal assemblages in the Middle Miocene Central Paratethys and to improve our knowledge of the anatomy of fossil red algae.

Geological setting

The Transylvanian Basin is an intra-Carpathian sedimentary basin, part of the Central Paratethys. The basin had a back-arc type evolution, under regional compressional stress (CIULAVU, 1999). On the western border, the Neogene sedimentary formations developed on the Mesozoic structures of the Trascău Mountains (Eastern Apuseni Mountains) consisting of ophiolites and Tithonian - lowermost Cretaceous limestones of the Bedeleu Nappe or olistoliths of Stramberk-like limestones of the Upper Cretaceous Râmeți Formation (FILIPESCU, 1996).

The Middle Miocene from this area is represented by the sedimentary deposits of the Câmpie Group. The algal-bioclastic limestones with marly-argillaceous intercalations are characteristic of the Badenian Gârbova de Sus Formation, cropping out between Arieș and Ampoi Valleys. The Gârbova de Sus Formation corresponds in the north-western part of the Transylvanian Basin to the Badenian Dej Formation represented by the Dej Tuff, which was dated at 14.38 Ma in the Ciceu-Giurgești area (LEEUW *et al.*, 2013). The carbonate deposits formed in shallow-marine environments, along the Trascău Mountains, while deeper settings are characterized by the Dej Formation in the northern-central and eastern part of the Transylvanian Basin. The overlying Cheia Formation is represented by evaporites (salts and gypsum) that correspond to the earliest Late Badenian, Wielician stage (HOHENEGGER *et al.*, 2014). They are overlain by marls with radiolarians and *Spirialis* of the Upper Badenian Pietroasa Formation.

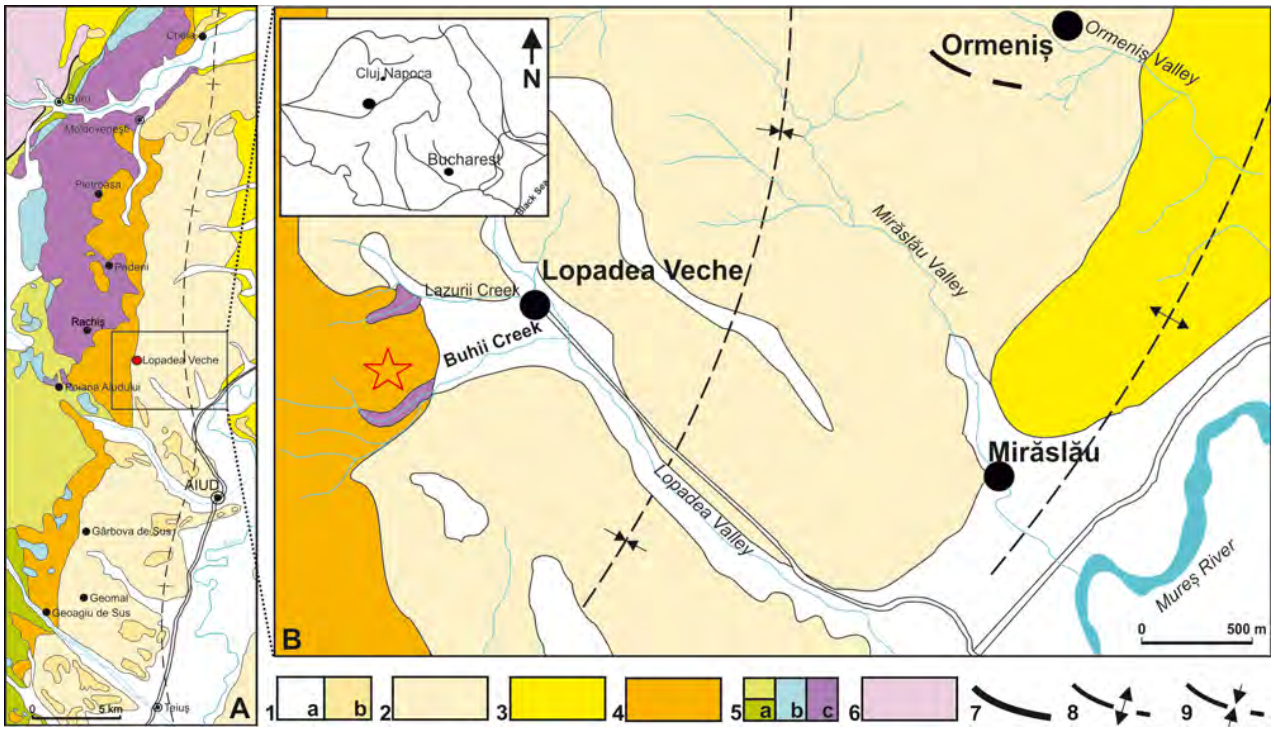

Figure 1: Location of the studied area. **A**, Geological map with the western border of the Transylvanian Basin (modified after LUPU *et al.*, 1967, and SĂNDULESCU *et al.*, 1978) showing the outcrops of Gârbova de Sus Formation; **B**, Detail of the Lopadea Veche area and location of the studied Lopadea Veche section on Buhii Valley; 1. Quaternary deposits (a, Holocene; b, Pleistocene); 2. Pannonian (Lopadea Formation); 3. Sarmatian (Măhăceni Formation); 4. Badenian (Gârbova de Sus Formation); 5. Mesozoic [(a, Cretaceous (Râmeți Formation); b, Jurassic (Bedeleu Nappe); c, Triassic-Jurassic volcanic arc)]; 6. Pre-Mesozoic basement units (metamorphites); 7. Thrust plane; 8. Anticline; 9. Syncline.

One of the most representative sections of Gârbova de Sus Formation is situated at Lopadea Veche (Fig. 1.A-B). The age of Gârbova de Sus Formation was initially considered to be Early Badenian, but studies of the foraminiferal fauna from the upper part of this section (FILIPESCU, 2001) extended it to the Wielician stage, which, according to HOHENEGGER *et al.* (2014), represents the earliest Late Badenian (earliest Serravallian). Other studies on this formation focused on the coral build-ups (SAINT-MARTIN *et al.*, 2007) and green algae (BUCUR *et al.*, 2011) from the Podeni section, bryozoans from Gârbova de Sus section (ZÁGORŠEK *et al.*, 2010) or calcareous nannoplankton and foraminiferal assemblages, used for biostratigraphic and paleoenvironmental interpretations (HOSU & FILIPESCU, 1995; FILIPESCU, 1996; FILIPESCU & GÎRBACEA, 1997).

The studied deposits of Lopadea Veche section are located in the Buhii Valley near the Lopadea Veche village on the western border of the Transylvanian Basin (Fig. 1.B). The succession consists of mixed carbonate-siliciclastic deposits about 30m thick that transgressively overlie the Mesozoic ophiolites of Trascău Mountains starting with a basal microconglomerate.

Material and methods

The Lopadea Veche section was sampled at intervals of 10 up to 30 cm. Coralline algae were examined in a total of 218 thin sections of various dimensions (6x6 cm up to 12x12 cm), obtained from 156 samples, including 16 rhodoliths extracted from the upper part of the succession.

Algal growth-form terminology follows WOELKERLING *et al.* (1993). We used the terminology proposed by WOELKERLING (1988) for the description of the structure of thalli of coralline red algae and the descriptions of JOHANSEN (1981). For species identification, accurate measurements were made using Image J-Software (ABRÀMOFF *et al.*, 2004) on photomicrographs made with Canon Powershot A640 mounted on a Zeiss microscope.

The abbreviations used in text and tables are the following: **VC**, ventral core of basal filaments; **PF**, peripheral filaments; **M**, mean value; **SD**, standard deviation; $\mathbf{H_1}$ and $\mathbf{H_2}$ for the internal heights in uniporate conceptacles and **n** for the number of measurements. The measured parameters of coralline algae cells and conceptacles follow BASSO *et al.* (1996) and RASSER & PILLER (1999). The measurements in the species descriptions belong either to a single specimen that shows as many features as possible or to multiple specimens identified as the same species. In tables, all dimensions are in µm.

Results

The studied coralline algal assemblages from Lopadea Veche show that melobesioids are abundant and the most diversified, especially *Lithothamnion* species. Mastophoroids, represented by dominant specimens of *Spongites fruticulosus*, and sporolithoids are common. However, lithophylloids and peyssonelliaceans are rare and geniculate corallines are very rare.

The corallines are represented by fragments, crusts, free branches (mäerl - type) or rhodoliths and characterize different facies types. The association of unattached branches of *Lithothamnion ramosissimum* and *Sporolithon* sp. 1 indicates mäerl - type facies, while the rhodolithic levels show a greater diversification of species.

In addition to the described species, the studied samples comprise mastophoroid and melobesioid taxa of uncertain generic placement, *Lithoporella melobesioides*, *Lithophyllum microsporum*, *Sporolithon Ivovicum* and *Peyssonellia antiqua*. The geniculate corallines are represented by undetermined specimens of *Corallina* and *Jania*, showing fragments of intergenicula lacking reproductive structures.

Systematic paleontology

In this study we describe non-geniculate coralline algal species of the orders Corallinales, Hapalidiales and Sporolithales. The systematic positions of genus and higher taxonomic ranks of red algae belonging to the Corallinophycidae follow WOELKERLING (1988), BRAGA *et al.* (1993), HARVEY *et al.* (2003), and KATO *et al.* (2011) who separated three new subfamilies (Porolithoideae, Neogoniolithoideae, Hydrolithoideae) from Mastophoroideae. Considering the uncertain systematic position of *Spongites* (KATO *et al.*, 2011), we follow M.D. GUIRY & G.M. GUIRY (2013) by taking into account the three new subfamilies (KATO *et al.*, 2011) and assigning *Spongites* to Mastophoroideae (HRABOVSKÝ *et al.*, 2015). The specimen showing uncertainties regarding the nature of conceptacles (asexual/ gametangial/ carposporangial) is noted ? *Neogoniolithon*, indicating the possibility of assignment to a gametangial thallus of *Mesophyllum*. When the shape of epithallial cells is unclear or not preserved, the melobesioids with non-coaxial ventral filaments are noted ? *Lithothamnion*.

Table 1: Comparison of biometric measurements of the identified species belonging to the family Corallinaceae.

Species		*Hydrolithon corculumis*				*Hydrolithon lemoinei*				*Spongites fruticulosus*				*Spongites* sp. 1				? *Neogoniolithon* sp.			
		n	Range	M	SD	n	Range	M	SD	n	Range	M	SD	n	Range	M	SD	n	Range	M	SD
VC cells	L					7	13-22	16.3	3.3	20	15-21	17.8	1.9	20	10-19	12.8	2.8	20	10-19	14.1	1.9
	D					7	15-24	19.4	2.8	20	11-16	13.3	1.6	20	6-9	7.5	0.6	20	7-11	9.4	1.3
PF cells	L	150	10-22	14.7	2.6	50	16-28	22.2	3.1	50	10-24	15.3	2.9	50	6-10	8.1	1	50	9-14	11.4	1.2
	L	30	23-21	25.9	2.7																
	D	150	6-14	10.8	1.2	50	10-19	14.3	2.6	50	8-16	11.7	1.6	50	5-10	6.8	1.1	50	5-8	6.6	0.7
Epithallial cells	L									15	4-7	5	0.9	2	3-5						
	D									15	7-14	9.1	2	2	5-8						
Conceptacles	D	11	185-311	262.7	41	2	163-250			33	240-484	387.2	55.6	22	363-715	541.6	116	9	552-642	603	33
	H	12	93-129	111.5	11.9	2	113-220			33	151-213	182.9	16.4	22	115-248	178.7	33	9	284-496	371	63.6
Pore canals	L	3	48-74			1	167			16	86-154	110.3	20.6	10	70-252	139.1	69.5	1	230		
	D	3	25-40			1	37			16	63-120	94.5	17.4	10	86-126	104.7	16.8	1	64-87		

Phylum Rhodophyta Wettstein, 1901

Class Florideophyceae Cronquist, 1960

Subclass Corallinophycidae Le Gall & Saunders, 2007

Order Corallinales Silva & Johansen, 1986

Family Corallinaceae Lamouroux, 1812

(Table 1)

Subfamily Hydrolithoideae Kato & Baba in Kato *et al.*, 2011

Genus *Hydrolithon* (Foslie, 1905) Foslie, 1909

Type species. *Hydrolithon reinboldii* (Weber-van Bosse & Foslie) Foslie, 1909, Recent, Muras Reef, East Kalimantan, Indonesia.

Hydrolithon corculumis (Maslov, 1962) Braga *et al.*, 2005

(Fig. 2.A-F)

Basionym. *Lithophyllum corculumis* Maslov, 1962, p. 80, Pl. 20, figs. 1-3.

Synonymy.

2005 *Hydrolithon corculumis* (Maslov) comb. nov.; Braga *et al.*, p. 211, Fig. 2.f-h.

Stratigraphical range. Badenian.

Description. Encrusting thallus (Fig. 2.A-B), 262-478 µm thick. Thallus shows dorsiventral dimerous organization (Fig. 2.C). Cells of the ventral core (VC) are similar to those in the peripheral filaments (PF) (Fig. 2.C). The cells are squarish to rectangular, 10-22 µm long and 6-14 µm wide. The roof cells and the cells at the sides of conceptacles become more elongated (Fig. 2.C-D & F), measuring 23-31 µm in length. Cell fusions are visible (Fig. 2.C-F).

The uniporate conceptacles measure 185-311 µm in diameter and 93-129 in height. The pore canals measure 48-74 µm in length and 25-40 µm in diameter and are bordered by 3-4 cells perpendicular to the conceptacle roof (Fig. 2.C & E).

Remarks. The investigated specimens fit the holotype description of Braga *et al.* (2005). *Lithophyllum corculumis* described and illustrated from the Badenian reefs of Poland (Pisera, 1985) shows higher conceptacles and the presence of cell fusions or secondary pit connections are unclear, suggesting that the specimen is not *H. corculumis*.

Studied thin sections. LVA 9, LVA 15, LVC 8x.

Hydrolithon lemoinei (Miranda, 1935) Aguirre *et al.*, 2011

(Fig. 3.A-D)

Basionym. *Melobesia lemoinei* Miranda, 1935, p. 284-285, Fig. 3A, B, Pl. 38, fig. 1.

Synonymy.

2011 *Hydrolithon lemoinei* (Miranda) comb. nov.; Aguirre *et al.*, p. 282, Figs. 5F & 6A-D.

2015 *Hydrolithon lemoinei* (Miranda) Aguirre *et al.*, 2011; Hrabovský *et al.*, p. 15-17, Fig. 16A-B.

Stratigraphical range. Oligocene - Badenian.

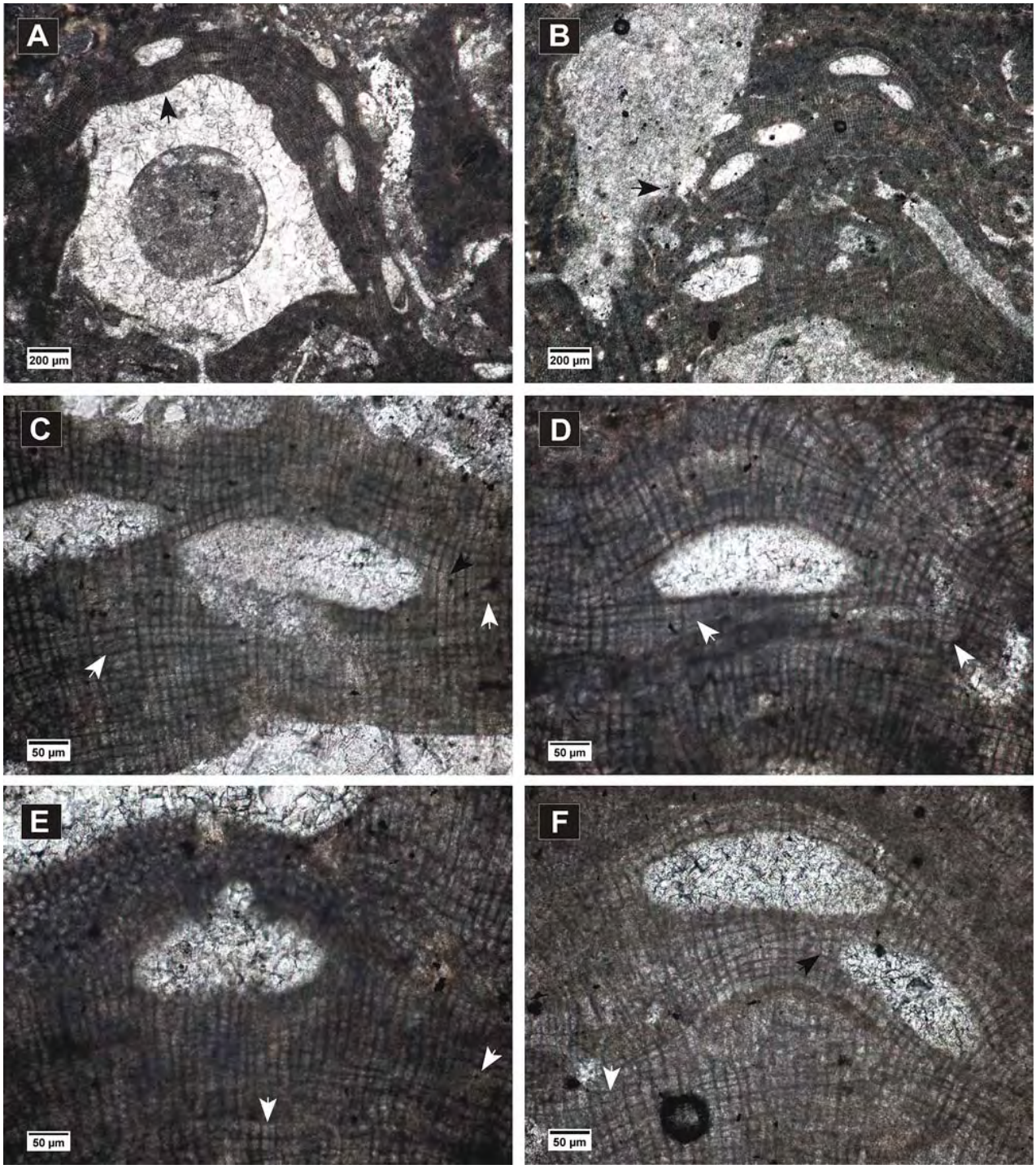

Figure 2: *Hydrolithon corculumis*. A-B, encrusting thalli showing uniporate conceptacles; C-F, peripheral filaments with cell fusions (white arrows) and cells elongated at the sides of the conceptacles and above them (black arrows); in C, E, slightly conical pore canals are visible.

Description. Encrusting thallus (Fig. 3.A), 90-384 µm thick. Thallus shows dorsiventral dimerous organization (Fig. 3.B). Cells of the VC are 13-22 µm long and 15-24 µm wide. Cells in the PF are predominantly rectangular, 16-28 µm long and 10-19 µm wide and do not show a particular alignment. The presence of cell fusions is noticeable in both VC and PF (Fig. 3.B).

The conceptacles are uniporate and protruding at the thallus surface (Fig. 3.C-D). They have flat floors and measure 163-250 µm in diameter and 113-220 µm in height. The pore canal is cylindrical, 167 µm long and 37 µm wide. The cells surrounding the pore canal are more or less perpendicular to the conceptacle roof (Fig. 3.C-D).

Remarks. The specimen fits the description of AGUIRRE *et al.* (2011) for the type material.

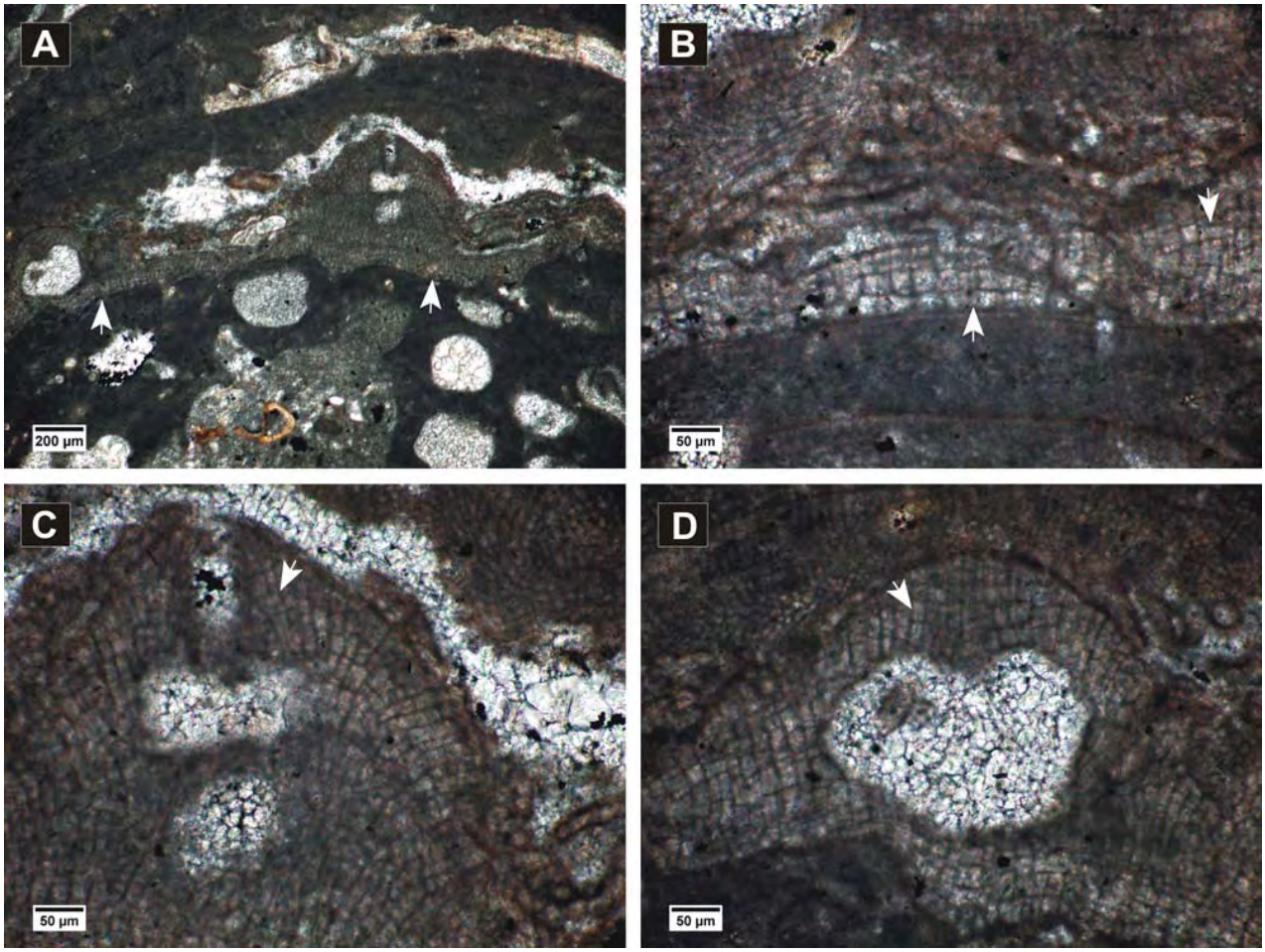

Figure 3: *Hydrolithon lemoinei*. A, encrusting dimerous thallus (arrows) showing uniporate conceptacles; B, dimerous thallus with VC cells similar to PF cells, cell fusions; C-D, uniporate conceptacles with flat floors showing roof cells more or less parallel with the pore canal (arrows).

Studied thin section. LVC 3.

Subfamily Mastophoroideae Setchell, 1943

Genus *Spongites* Kützing, 1841

Type species. *Spongites fruticulosus* Kützing, 1841, Recent, Mediterranean Sea.

Spongites fruticulosus Kützing, 1841

(Fig. 4.A-D - 5.A-F)

Synonymy.

1993 *Spongites albanensis* (Lemoine) comb. nov.; Braga *et al.*, p. 544, Pl. 2, figs. 1, 3-4.

2006 *Spongites fruticulosus* Kützing; Basso & Rodondi, p. 404, Figs. 1-34.

Stratigraphical range. Oligocene - Recent.

Description. Encrusting and protuberant thalli (Fig. 4.A) with monomerous dorsiventral organization. Non-coaxial VC (Fig. 4.B) consists of cells 15-21 µm long and 11-16 µm wide. Cells in PF vary in shape and their arrangement is irregular; however, weak horizontal rows can be observed. PF cells measure 10-24 µm in length and 8-16 µm in diameter. Epithallial cells are flattened or rounded (Fig. 4.C), 4-7 µm long and 7-14 µm wide. Cell fusions are frequent in PF and VC (Fig. 4.B & D).

Asexual conceptacles are buried in thalli and measure 240-484 µm in diameter and 151-213 µm in height. The pore canals are 86-154 µm long and 63-120 µm wide at the base. The cells lining the pore canal are oriented more or less parallel to the roof (Fig. 4.C-D).

Dioecious gametangial thalli are observed in fusion with the thallus bearing asexual conceptacles (Fig. 5.A-B), or encrusting other species (Fig. 5.C). Growth forms and vegetative structures are consistent with the thallus in asexual phase. VC is monomerous non-coaxial (Fig. 5.D), with cells 10-22 µm in length and 7-14 µm in diameter and PF cells measure 8-18 µm in length and 5-11 µm in diameter. Multiple cell fusions are observable (Fig. 5.E).

The small male conceptacles (Fig. 5.A-E) measure 137-202 µm in diameter and 32-58 µm in height. Pore canals are 27-106 µm long and 30-66 µm wide at the base.

Table 2: Biometric measurements of the fossil gametangial thalli of *S. fruticulosus* KÜTZING ([1] this study) in comparison with the biometry of recent specimens from the Mediterranean ([2] BASSO & RODONDI, 2006) and fossil specimens of *L. platticarpum* MASLOV described from Ukraine ([3] BRAGA *et al.*, 2005) and Poland ([4] STUDENCKI, 1989) and *Leptolithophyllum platticarpum* (MASLOV) POIGNANT from Corsica ([5] ORSZAG-SPERBER & POIGNANT, 1977).

Species		*Spongites fruticulosus* gametangial thallus				*Spongites fruticulosus* gametangial thallus	*Lithophyllum platticarpum*	*Lithophyllum platticarpum*	*Lepto. platticarpum*
Locality		(Romania)[1]				(Mediterranean)[2]	(Ukraine)[3]	(Poland)[4]	(Corsica)[5]
		n	Range	M	SD	Range	Range	Range	Range
VC cells	L	50	10-22	14	2.5	10-32	15-30		20
	D	50	7-14	10	1.5	5-17	10-14		10
PF cells	D	100	8-18	13	2.1	6-28	10-20	10-15	10-15
	D	100	5-11	8	1.2	5-22	10-15	9-12	10
Male conceptacles	D	30	137-202	170	18.6	190-230	210-230	120-150	200
	H	30	32-58	41	7.5	40-70	35-50	30-40	40
Pore canals	L	23	27-106	54	21.3	70-100	15		
	D	23	30-66	45	10	40-60			
Female conceptacles	D	2	122-171			125-345			
	H	2	42-55			170-308 (with pore canal)			
Pore canals	L	2	65-117						
	D	2	36-45						

Two female conceptacles are observed slightly protruding at the thallus surface (Fig. 5.F). Organic remains of carpogonial branches are observed in the conceptacle floors (Fig. 5.F). The chambers measure 122-171 µm in diameter and 42-55 µm in height, with pore canals 65-117 µm long and 36-45 µm wide.

Remarks. The identified gametangial specimens correspond to the ones collected from the Mediterranean and described by BASSO & RODONDI (2006). Gametangial thalli were identified in multiple thin sections, not only in fusion with the thalli bearing asexual conceptacles, but also encrusting other species in rhodoliths (Fig. 5.C) or as free nodules; nevertheless, they were always present in thin sections containing thalli in asexual phase. A close affinity of the identified gametangial male thalli with *Lithophyllum platticarpum* MASLOV is observed (Table 2). The type material of *L. platticarpum* was redescribed by BRAGA *et al.* (2005) and they concluded that *L. platticarpum* is the gametangial thallus of a mastophoroid species. Moreover, *Spongites albanensis* (LEMOINE) BRAGA, BOSENCE & STENECK, a heterotypic synonym of *Spongites fruticulosus* KÜTZING (BRAGA *et al.*, 2009), has been identified in association with *L. platticarpum* in Miocene rhodoliths from NW Italy (VANNUCCI *et al.*, 1994). Taking all the above in consideration, we consider that *Lithophyllum platticarpum* MASLOV, 1962, should be assigned to *Spongites fruticulosus* KÜTZING, as a gametangial thallus with male conceptacles.

Studied thin sections. The measurements for the thallus bearing tetrasporangial conceptacles were made for a specimen in LVA 11, where the features can be observed more clearly. Male thalli were studied in LVA 9, LVA 10 and LVB 6 and the female thallus was identified in LVB 5.

Spongites sp. 1

(Fig. 6.A-F)

Stratigraphical range. Late Eocene - Badenian.

Description. Encrusting thallus forming warty protuberances in the fertile parts (Fig. 6.A-B), with monomerous dorsiventral organization. VC appears non-coaxial (Fig. 6.C), 60-110 µm thick and consists of cells 10-19 µm long and 6-9 µm wide. PF zonated, with bands 78-150 µm thick. PF cells measure 6-10 µm in length and 5-10 µm in diameter. The epithallial cells seem flattened (Fig. 6.D), 3-5 µm long and 5-8 µm wide. Cell fusions are common in PF (Fig. 6.C).

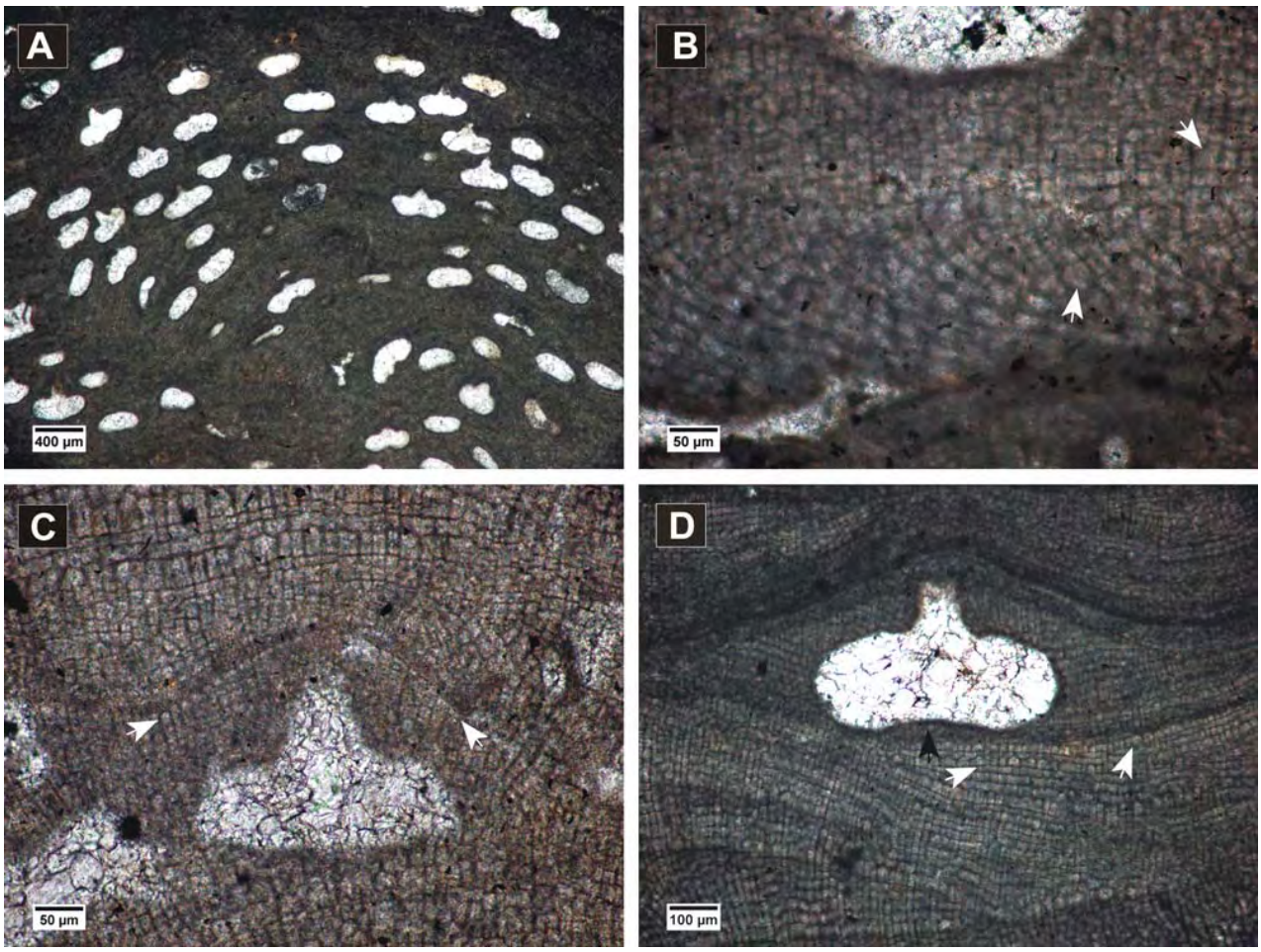

Figure 4: *Spongites fruticulosus*. A, thick encrusting thallus showing abundant uniporate conceptacles; B, non-coaxial ventral filaments, cell fusions present in both VC and PF (arrows); C-D, uniporate conceptacles with cells lining the pore canals more or less parallel to the roof (black arrow); C, layer of rounded and flattened epithallial cells (arrows); D, PF with multiple cell fusions (white arrow), uniporate conceptacle with slightly raised columella (black arrow).

Uniporate conceptacles (Fig. 6.A-B & E-F) have mostly flat floors, rounded sides and measure 363-715 µm in diameter and 115-248 µm in height. The pore canals are 70-252 µm long and their diameter at the base is 86-126 µm. They are lined by 1-14 cells.

Remarks. The growth form and biometric measurements of the studied specimen are similar to the ones of ? *Lithophyllum perrandoi* AIROLDI described by VANNUCCI *et al.* (2008); however, because of the presence of cell fusions in PF and the absence of evident secondary pit connections, we decided to attribute it to *Spongites*.

Studied thin section. LV 56.

Subfamily Neogoniolithoideae KATO & BABA in KATO *et al.*, 2011

Genus *Neogoniolithon* SETCHELL & MANSON, 1943

Type species. *Neogoniolithon fosliei* (HEYDRICH) SETCHELL & MANSON, 1943, Recent, El Tor, Sinai Peninsula, Egypt.

? *Neogoniolithon* sp. 1

(Fig. 7.A-D)

Description. Encrusting thallus, with dorsiventral organization and monomerous construction (Fig. 7.A-B). VC coaxial (Fig. 7.C), 100-180 µm thick with cells 10-19 µm long and 7-11 µm wide. PF cells measure 9-14 µm in length and 5-8 µm in diameter. A layer of mostly rounded epithallial cells is observed (Fig. 7.C). Cell fusions are frequent in VC and PF (Fig. 7.C).

Large uniporate conceptacles have rounded sides, mostly concave upward floors and are protruding at the thallus surface, mound-like (Fig. 7.A-B & D) They measure 552-642 µm in diameter and 284-496 µm in height. Pore canals are conical (Fig. 7.D) and measure 230 µm in height and in diameter, 87 µm at the base to 64 µm at the top. Roof cells are similar to the PF cells. The cells lining the pore canals are perpendicular to the conceptacle roof.

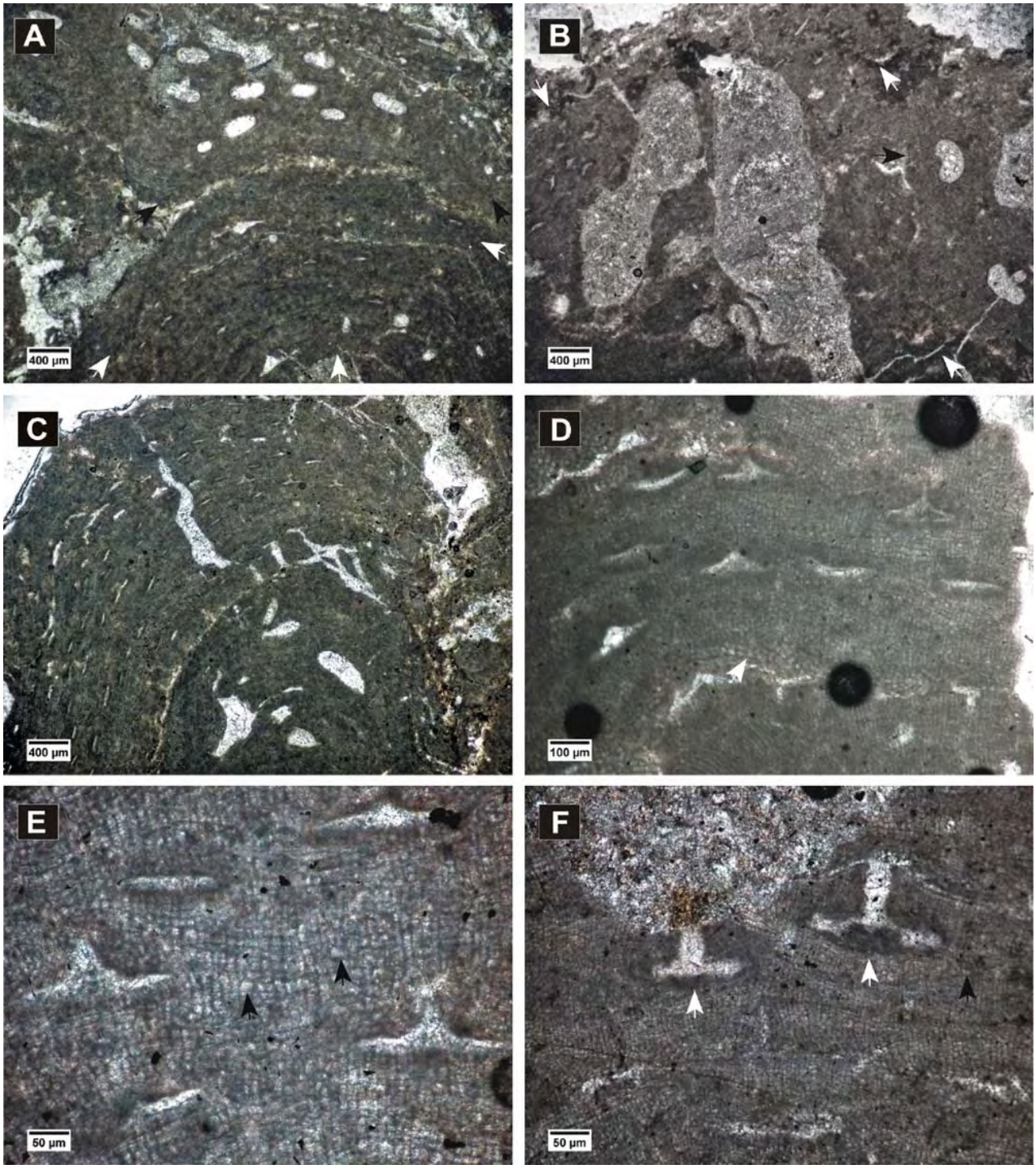

Figure 5: *Spongites fruticulosus*, gametangial thalli. A-B, encrusting male thallus (white arrows) fused with thallus bearing asexual conceptacles (black arrows); C, encrusting male thallus (arrow) bearing abundant conceptacles; D, male thallus showing non-coaxial VC (arrow); E, detail of male conceptacles, peripheral filaments with cell fusions (arrows); F, female thallus with peripheral filaments showing cell fusions (black arrow) and uniporate conceptacles protruding at the thallus surface, with conceptacle floors showing organic remains of carpogonial branches (white arrows).

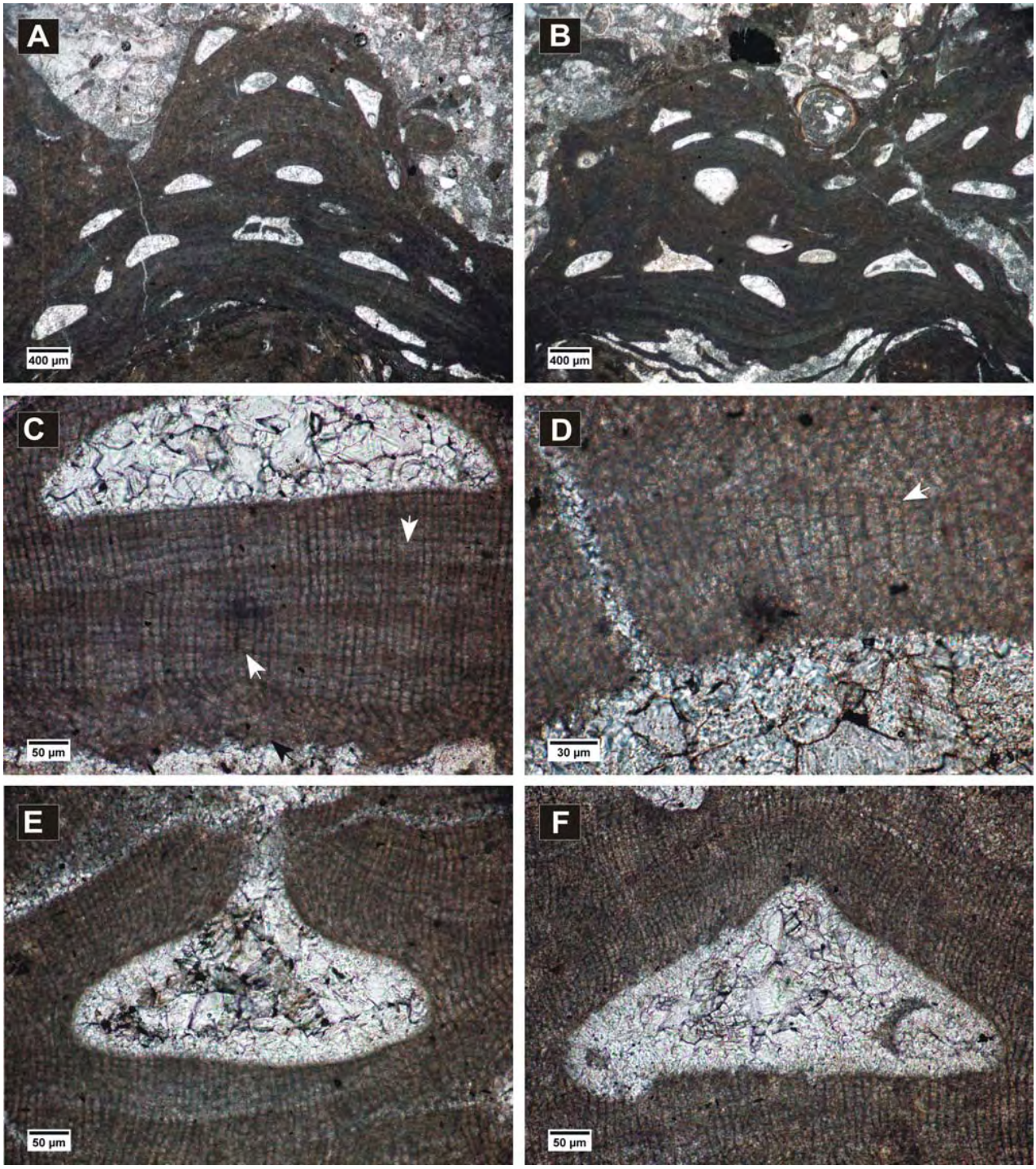

Figure 6: *Spongites* sp. 1. A-B, encrusting and protuberant thalli showing uniporate conceptacles; C, section of thallus showing thin non-coaxial VC (black arrow) and zoned PF with secondary pit connections (white arrows); D, flattened epithallial cells (arrow); E-F, detail of uniporate conceptacles.

Remarks. The specimen shows similarities with *Lithophyllum bassanense* MASTRORILLI (MASTRORILLI, 1973; PISERA & STUDENCKI, 1989). The coaxial VC shows evident cell fusions, therefore the specimen cannot be assigned to *Lithophyllum*. The presence of coaxial VC, cell fusions and uniporate conceptacles indicate *Neogoniolithon* species, but the uniporate conceptacles can also be gamentangial/ carposporangial; thereby, this specimen can be assigned to *Neogoniolithon* or to *Mesophyllum*, as a gametangial or carposporangial thallus. The studied sample includes also encrusting thalli of *M*. cf. *incisum* (description below), that resembles this specimen in biometric measu-rements and the protruding, mound-like nature of conceptacles. However, the gametangial and carposporangial thallus of *M. incisum* do not show similarities with this specimen; therefore we decided to attribute it to ? *Neogoniolithon*.

Table 3: Comparison of biometric measurements of the identified *Lithothamnion* species.

Species		*Lithothamnion crispatum*				*Lithothamnion ramosissimum*				*Lithothamnion roveretoi*				*Lithothamnion* sp. 1			
		n	Range	M	SD	n	Range	M	SD	n	Range	M	SD	n	Range	M	SD
VC cells	L	15	13-17	14.4	1.3	25	10-16	12.8	1.6	7	12-17	14.5	1.6				
	D	15	9-11	10.2	0.8	25	8-12	9.6	1.1	7	6-10	7.6	1.1				
PF cells	L	50	11-17	13.8	1.3	50	9-21	13.9	3.6	25	9-16	12.1	1.8	25	20-30	25.6	2.5
	L					50	18-27	22.9	3.0					25	13-18	15	1.4
	D	50	8-13	10.2	1.2	50	8-12	9.5	1.1	25	7-10	8.6	0.7	25	8-11	9.7	0.7
Epithallial cells	L	10	2-5	3.7	0.9									25	5-7	6.3	0.6
	D	10	7-11	8.9	1.1									25	6-12	8.8	1.3
Conceptacles	D	4	375-512	463.4	60.9	17	240-535	389.9	82.6	2	412-477			1	630		
	H	4	167-201	184.1	15.2	17	98-148	116.7	15.3	2	120-159			1	240		
Roof thickness			22-46				43-48				40-55				52-66		
Nr. of roof cells			2-4				3-4				4-6				4-6		
Roof cells	L	15	6-11	8.3	1.2					25	7-12	9.1	1.4	25	9-13	11.3	1.3
	D	15	5-8	6.3	0.9					25	5-8	6.6	0.8	25	7-11	8.5	1.2
Pore canals	L													2	20-24		
	D													2	30-32		

Species		*Lithothamnion* sp. 2				*Lithothamnion* sp. 3				? *Lithothamnion* sp. 4			
		n	Range	M	SD	n	Range	M	SD	n	Range	M	SD
VC cells	L	8	8-11	9.5	1.0	25	8-11	9.7	0.9	6	9-14	11.6	2.0
	D	8	6-8	6.9	0.6	25	7-10	9.1	0.8	7	8-11	9.1	1.1
PF cells	L	25	7-13	9.1	1.7	30	7-14	10.3	1.8	50	9-15	12	1.6
	L									25	14-26	20.1	2.8
	D	25	6-8	6.9	0.6	30	6-9	7.2	1.0	50	7-10	8.8	0.8
Epithallial cells	L					7	3-5	3.4	1.0				
	D					7	5-8	5.9	1.1				
Conceptacles	D	7	252-373	288.4	44.2	16	404-858	612.4	125.9	6	475-707	585.3	81.2
	H	7	133-165	148.2	12.1	16	208-356	295.8	47	7	289-384	331.6	35.1
Roof thickness			36-55				78-100				122-137		
Nr. of roof cells			3-4				6-9				6-9		
Roof cells	L	25	6-9	7.5	0.7	10	7-9	7.8	1.0	25	9-14	11.5	1.2
	D	25	5-7	5.5	0.5	10	5-7	6.4	0.7	25	5-7	6.1	0.5
Pore canals	L						20-46			8	13-42	22.1	9.3
	D						14-16			8	13-43	22.4	9.2

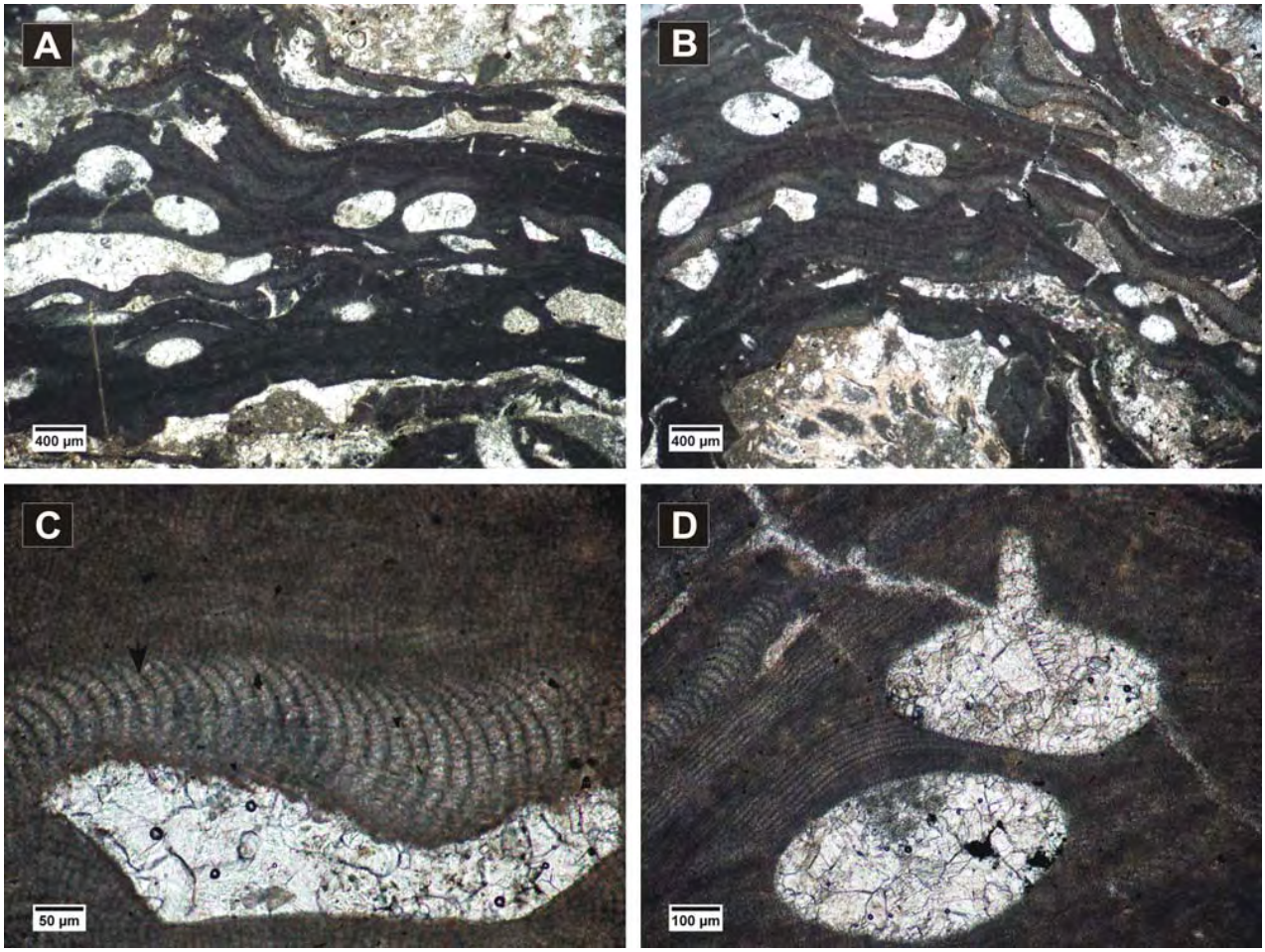

Figure 7: ? *Neogoniolithon* sp.1. A-B, encrusting fertile thalli showing uniporate conceptacles protruding at the thallus surface; C, coaxial ventral filaments, cell fusions present (arrow), layer of epithallial cells (arrowhead); D, detail of uniporate conceptacle with cylindrical-conical pore canal, regular arrangement of PF cells observed above the conceptacles.

Further investigations and reassessment of the *Lithophyllum bassanense* MASTRORILLI holotype may indicate a certain taxonomic position of this specimen.

Studied thin section. LV 39.

Order Hapalidiales NELSON, SUTHERLAND, FARR & YOON in NELSON *et al.*, 2015

Family Hapalidiaceae (GRAY, 1864) HARVEY *et al.*, 2003

Subfamily Melobesioideae BIZZOZERO, 1885

Genus *Lithothamnion* HEYDRICH, 1897

(Table 3)

Type species. *Lithothamnion muelleri* LENORMAND ex ROSANOFF, 1866, Recent, Western Port Bay, Victoria.

Lithothamnion crispatum HAUCK, 1878

(Fig. 8.A-D)

Synonymy.

2011 *Lithothamnion crispatum* HAUCK; BASSO *et al.*, p. 145, Figs. 1-30, tab. 1.

2016 *Lithothamnion crispatum* HAUCK; COLETTI *et al.*, p. 30-31, Figs. 1-8, tab. 2.

Stratigraphical range. Burdigalian - Recent.

Description. Encrusting and protuberant thallus showing a branch up to 5 mm thick (Fig. 8.A). Thallus monomerous, with dorsiventral organization. VC non-coaxial (Fig. 8.B), 125-158 µm thick, with cells 13-17 µm long and 9-11 µm wide. Zonation in PF is visible. Zones are 5-7 cells in maximum thickness. PF cells measure 11-17 µm in length and 8-13 µm in diameter. Epithallial cells are flattened and flared (Fig. 8.CD), 2-5 µm in length and 7-11 µm in diameter. Meristematic cells are as long as or longer than those subtending them. Cell fusions are observed in VC and PF (Fig. 8.B-C).

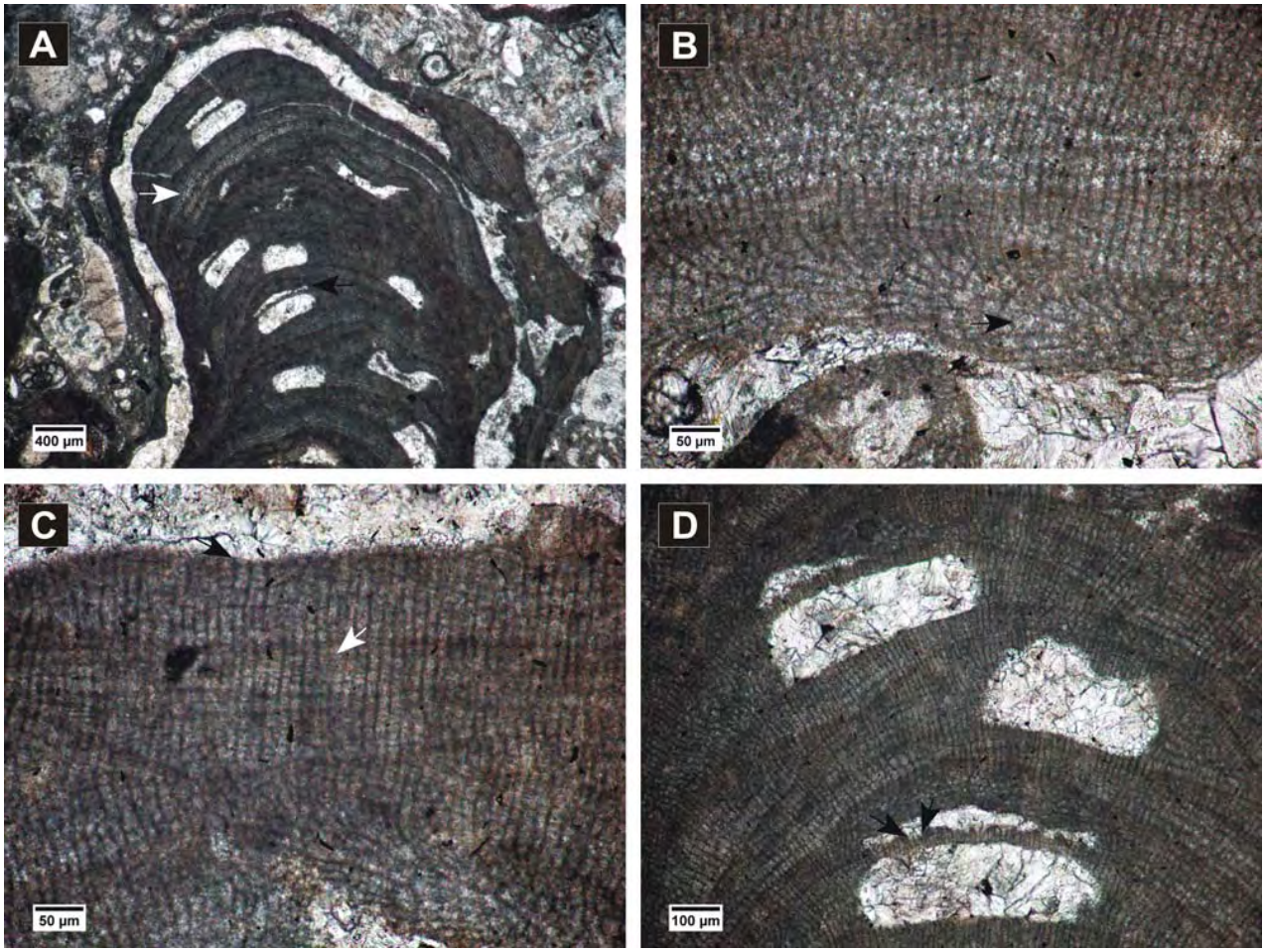

Figure 8: *Lithothamnion crispatum*. A, protuberant thallus showing zonation in PF (white arrow) and concavities above the conceptacle roofs (black arrow); B, cell fusion (arrow) in non-coaxial VC; C, cell fusion (white arrow) in PF, flared epithallial cell (black arrow); D, multiporate conceptacle showing depressions in the roof and wedge-shaped cells lining the pore canal (arrows).

Tetrasporangial conceptacles have rounded sides and flat floors, 375-512 µm in diameter and 167-201 µm in height. The conceptacle roofs are 22-46 µm thick and consist of 2-4 cell layers. Where some depressions are visible (Fig. 8.D), most probably connected with the pore canals, the roofs are thinner. The roof cells are 6-11 µm in length and 5-8 µm in diameter, smaller than other PF cells. Two wedged-shaped cells are observed lining a pore canal (Fig. 8.D).

Remarks. The depressions and wedge-shaped cells in the asexual conceptacle roofs, branched growth form, vegetative anatomy, and biometric measurements of the identified specimen are similar to the ones redescribed by BASSO *et al.* (2011) from the *Lithothamnion crispatum* HAUCK lectotype and the ones described by COLETTI *et al.* (2016) from fossil specimens.

Studied thin section. LV 49.

Lithothamnion ramosissimum (REUSS, 1847) PILLER, 1994

(Fig. 9.A-D)

Basionym. *Nullipora ramosissima* REUSS, 1847.

Synonymy.

1946 *Palaeothamnium archaeotypum* nov. sp.; CONTI, p. 42-46, Pl. III, fig. 3a-c; Pl. VIII, fig. 1a-c.

1996 *Lithothamnion ramosissimum* (REUSS); AGUIRRE *et al.*, p. 3-8, Pl. I, figs. 1-6; Pl. II, figs. 1-6.

Stratigraphical range. Middle Miocene.

Description. Encrusting and fruticose thallus, with protuberances up to 3 mm in diameter and 7 mm in length (Fig. 9.A-B). Thallus monomerous with dorsiventral organization. VC non-coaxial (Fig. 9.C), around 180 µm thick and consists of cells 10-16 µm long and 8-12 µm wide. PF shows zonation in protuberances (Fig. 9.A-B), zones extending from 70 µm to a maximum of 180 µm in thickness. PF cells measure 9-21 µm in length and 8-12 µm in diameter. Epithallial cells are not observed. Cell fusions are present in both VC and PF (Fig. 9.C).

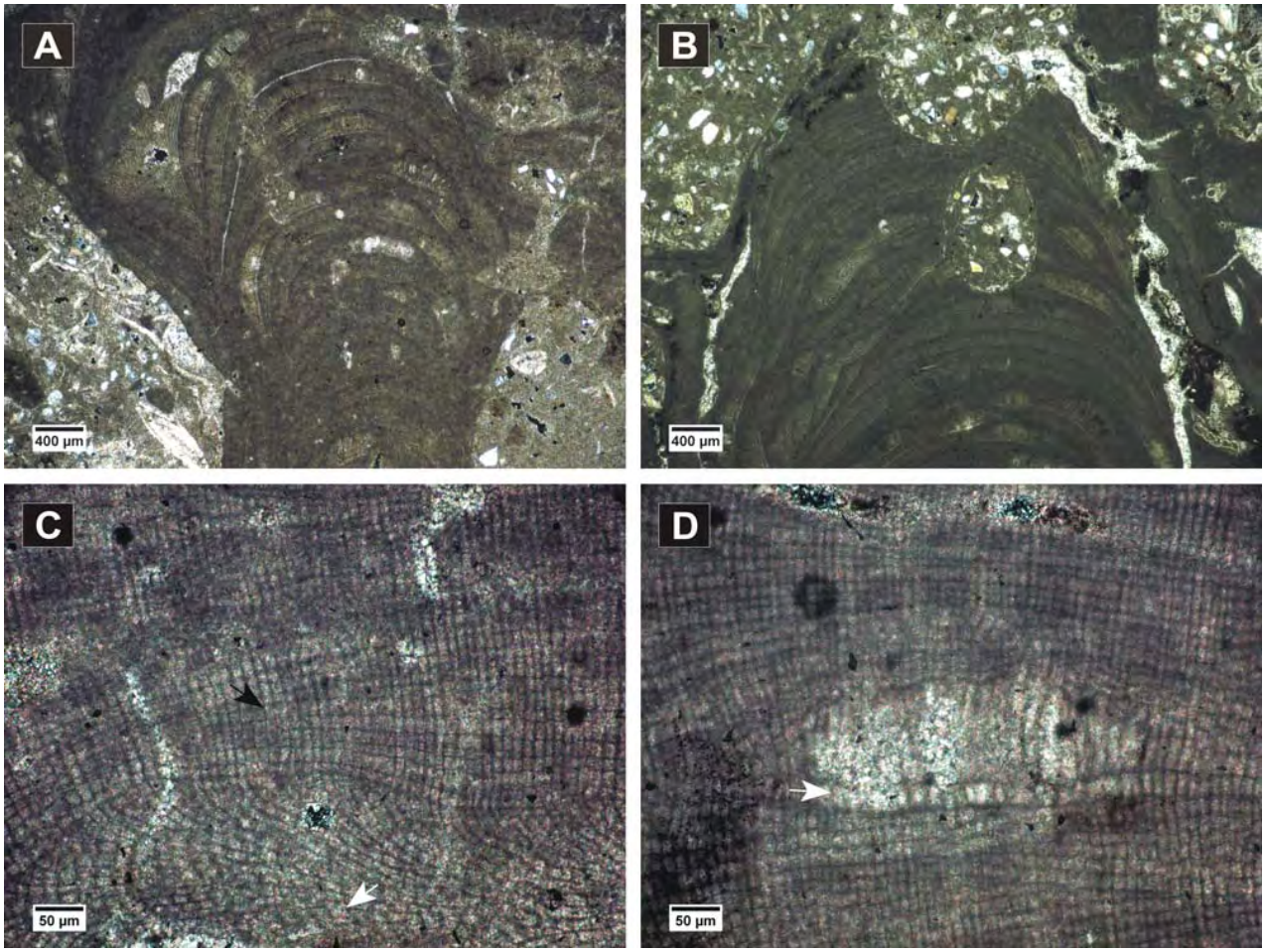

Figure 9: *Lithothamnium ramosissimum*. A-B, fertile fruticose protuberances showing zonation in peripheral filaments; C, non-coaxial ventral filaments showing cell fusions (white arrow), cell fusion in PF (black arrow); D, detail of multiporate conceptacle with layer of elongated cells (white arrow) and filling with longer cells (black arrow).

Multiporate conceptacles measure 240-535 µm in diameter and 98-148 µm in height. Almost all the chambers show early stages of development, being filled with large elongated cells (Fig. 9.D). Below the conceptacle floor is observed a layer of elongated cells (Fig. 9.D), 18-27 µm in length, similar to the cells from the sides of the chambers and smaller than those forming the chambers. The roofs are 43-48 µm thick, composed of 3-4 cells.

Remarks. AGUIRRE *et al.* (1996) described *Lithothamnion rammosissimum* (REUSS) from the type localities and BASSO *et al.* (1997) redescribed the lectotype material. The growth form, vegetative anatomy and biometric measurements of the identified specimen fit their descriptions.

Although the conceptacle heights of this species do not exceed 120 µm in the lectotype material (CONTI, 1946; BASSO *et al.*, 1997), we take into consideration the measurements of specimens studied from type localities (AGUIRRE *et al.*, 1996) as well.

Studied thin section. LV 2.

Lithothamnion roveretoi AIROLDI, 1932

(Fig. 10.A-B)

Synonymy.

2010 *Lithothamnion roveretoi* AIROLDI; VANNUCCI *et al.*, p. 224-226, Pl. 1, figs. 1-8, tab. 1.

2015 *Lithothamnion roveretoi* AIROLDI; HRABOVSKÝ *et al.*, p. 6-7, Fig. 5A-D.

Stratigraphical range. Middle-Late Eocene - Badenian.

Description. Growth form encrusting and slightly protuberant (Fig. 10.A). Thallus monomerous, with dorsiventral organization, 560-600 µm thick. VC is non-coaxial (Fig. 10.A-B) and 56-90 µm thick, with cells measuring 12-17 µm in length by 6-10 µm in diameter. PF slightly zoned, 312-496 µm thick with cells 9-16 µm in length and 7-10 µm in diameter. Cell fusion present in both ventral and peripheral filaments (Fig. 10.B). Flattened cells, presumed epithallial, are observed in conceptacle roofs (Fig. 10.B).

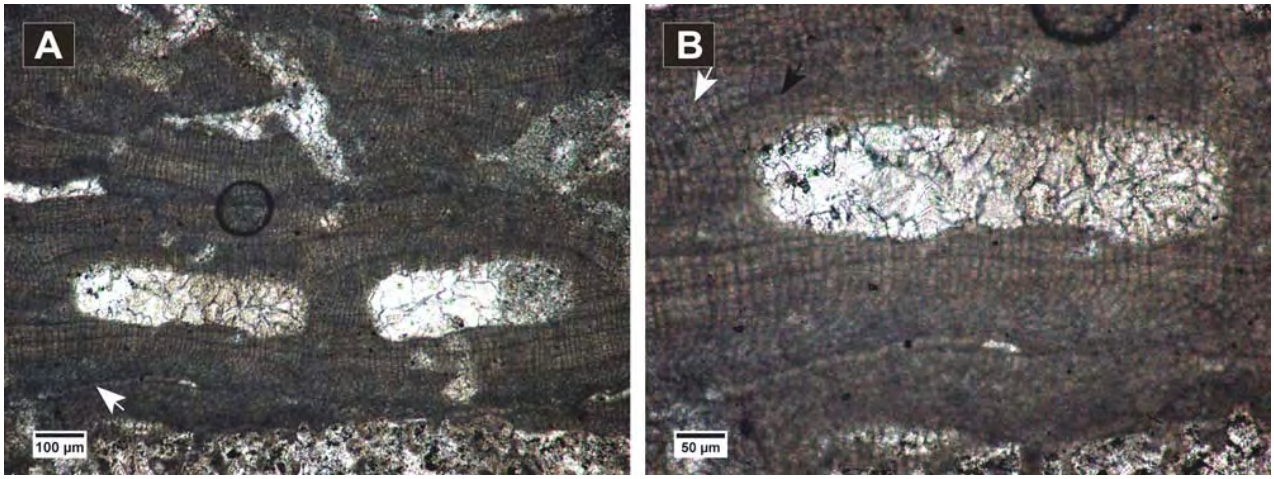

Figure 10: *Lithothamnion roveretoi.* A, encrusting and superposed thalli, non-coaxial VC (white arrow); B, cell fusions present in the peripheral filaments (white arrow), flattened and flared epithallial cell (black arrow).

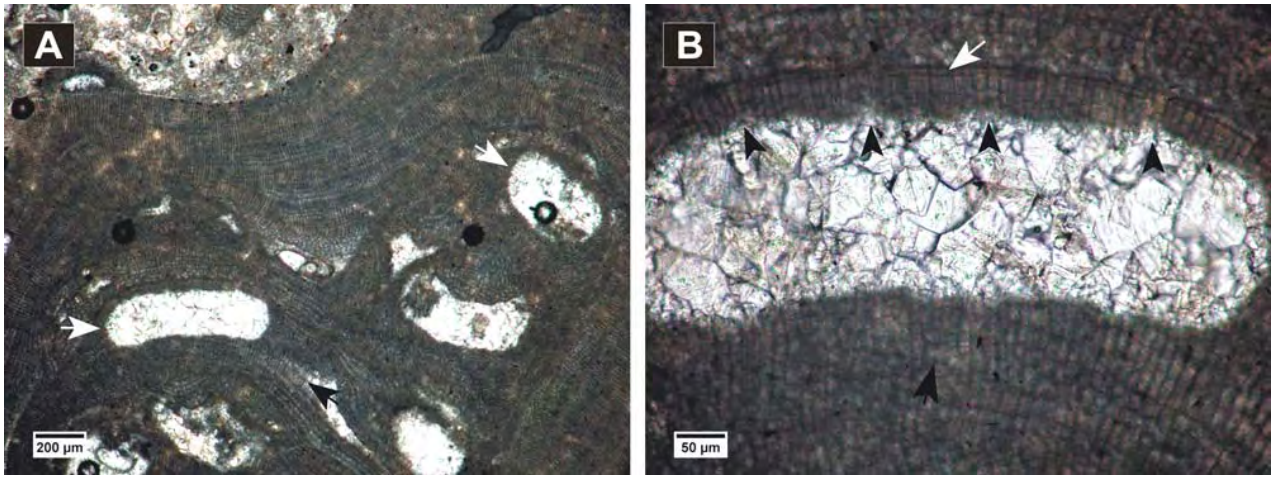

Figure 11: *Lithothamnion* sp. 1. A, encrusting thallus showing multiporate conceptacles (white arrows) and elongated cells in PF (black arrow); B, detail of a multiporate conceptacle, layer of flattened and flared epithallial cells (white arrow), cell fusion in PF (black arrow), conical pore canals (black arrowheads).

The conceptacles have flattened roofs and floors and were raised about 61-77 µm at the thallus surface. The chambers measure 412-477 µm in diameter and 120-159 µm in height. The roofs are 40-55 µm thick and composed of 4-6 cell layers. Roof cells measure 7-12 µm in length and 5-8 µm in diameter, conformable with the surrounding PF cells.

Remarks. The specimen fits the description of VANNUCCI *et al.* (2010) for the type material of *Lithothamnion roveretoi* AIROLDI; however, the conceptacles of the identified specimen are slightly higher. The occurrence of this species in the Upper Eocene of Romania (BUCUR *et al.*, 1987) is uncertain because it has different biometric measurements and no illustrations are provided. Therefore, we suggest that *Lithothamnion roveretoi* appeared in the Central Paratethys only during the middle Miocene.

Studied thin section. LV 7x.

Lithothamnion sp. 1

(Fig. 11.A-B)

Description. Unattached branched thallus (Fig. 11.A), with VC unrecognizable. PF zoned, 600-660 µm thick, with elongated cells 20-30 µm in length and 8-11 in diameter. The common cells are shorter, measuring 13-18 in length. Cell fusions frequent in PF (Fig. 11.B). Epithallial cells are flattened and flared (Fig. 11.B), 5-7 µm in length and 6-12 µm in diameter.

Only one conceptacle could be adequately measured, 630 µm in diameter and 240 µm in height, with roof and floor relatively flattened and rounded corners. The roof is 52-66 µm thick, formed by 4-6 cells, with peripheral rim. The roof cells are 9-13 µm in length and 7-11 µm in diameter, smaller than the surrounding PF cells. Pore canals seem conical (Fig. 11.B), 20-24 µm long and the basal part 30-32 µm wide.

Studied thin section. LV 60.

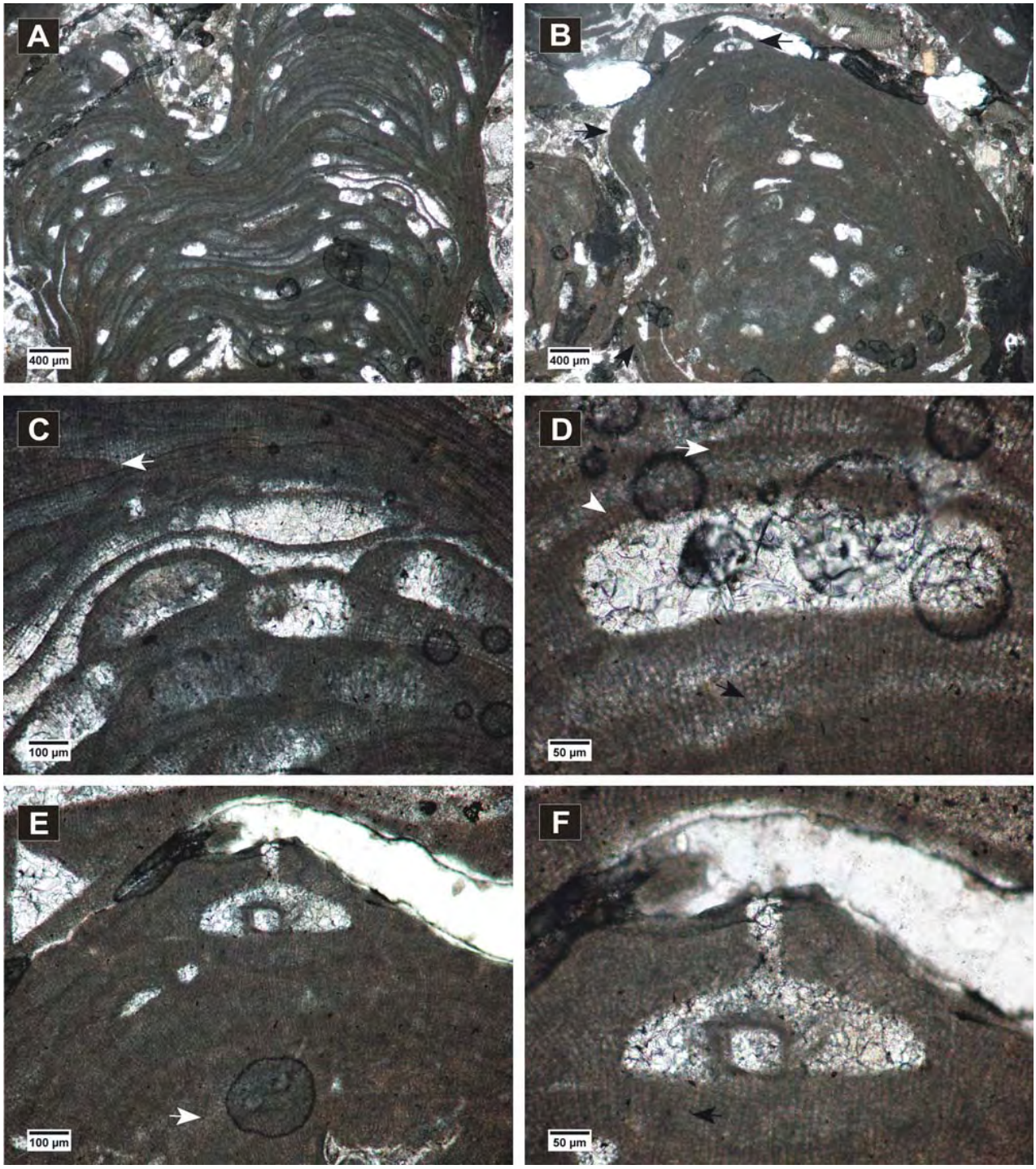

Figure 12: *Lithothamnion* sp. 2. A, fertile lumpy protuberance; B, gametangial thallus at the surface of a protuberance (arrows point to gametangial conceptacles); C, peripheral filaments showing irregular zonation (arrow) and multiporate conceptacles protruding and buried in thallus; D, detail of multiporate conceptacle with ventral filaments above the roof (white arrow), cell fusion (black arrow), layer of flattened and flared epithallial cells (white arrowhead); E, gametangial thallus showing uniporate conceptacle slightly raised at the thallus surface, non-coaxial ventral filaments (arrow); F, detail of gametangial conceptacle, cell fusion (arrow).

Lithothamnion sp. 2

(Fig. 12.A-F)

Description. Unattached branched thalli (Fig. 12.A-B), up to 8 mm in length and 5 mm in width. Ventral filaments are observed only above the conceptacles (Fig. 12.D). VC cells measure 8-11 µm in length and 6-8 µm in diameter. PF is irregularly zoned (Fig. 12.C), 2-3 or 5-6 cells long. PF cells are 7-13 µm long and 6-8 µm wide. Epithallial cells are flattened and flared (Fig. 12.D). Cell fusions are observed (Fig. 12.D).

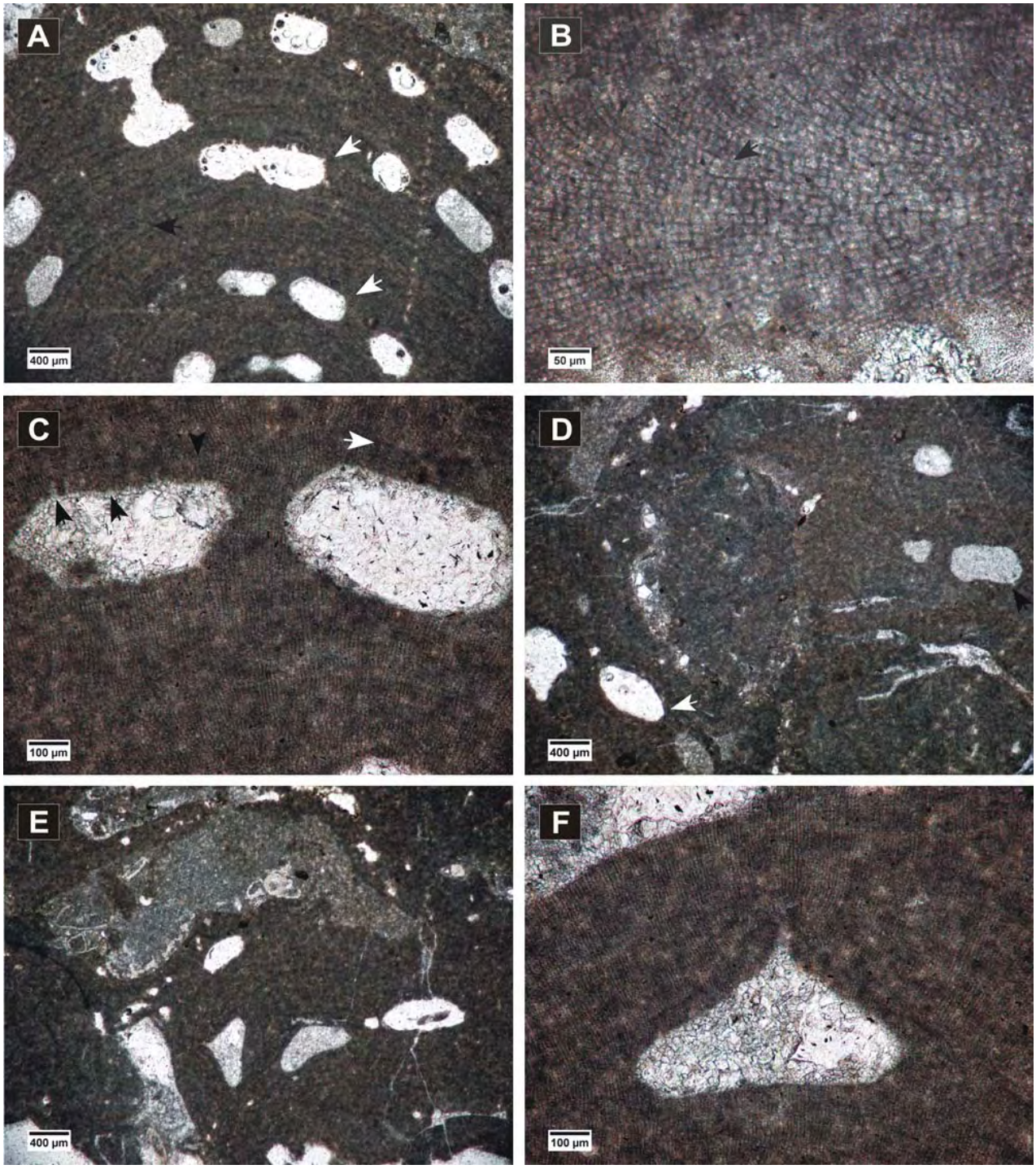

Figure 13: *Lithothamnion* sp. 3. A, encrusting protuberant thallus; B, non-coaxial ventral filaments with cell fusions (arrow); C, detail of multiporate conceptacles showing pore canals (black arrows), slightly sunken pore plate (white arrow), layer of flattened and flared epithallial cells (black arrowhead); D, presumed gametangial thallus (white arrow points to uniporate conceptacle) in fusion with the specimen in asexual phase (black arrow points to multiporate conceptacle); E. presumed gametangial thallus; F, detail of the uniporate conceptacle.

Asexual conceptacles were mostly raised above the thallus surface and then become buried due to continuous growing (Fig. 12.C). The chambers measure 252-373 µm in diameter and 133-165 µm in height and they commonly appear filled with large cells (Fig. 12.A-C). The roof is 36-55 µm thick, 3-4 cells long. The roof cells are 6-9 µm long and 5-7 µm wide, similar to the surrounding PF cells.

Presumed gametangial thallus is observed encrusting the thallus in asexual phase. VC is non-coaxial (Fig. 12.E), with cells 8-10 µm (M = 8.9; SD = 0.7) long and 4-8 µm (M = 6.1; SD = 1.2) wide (n = 20). PF is zoned with cells 7-11 µm (M = 8.8; SD = 0.6) long and 5-8 µm (M = 6.3; SD = 0.7) wide (n = 50). VC and PF

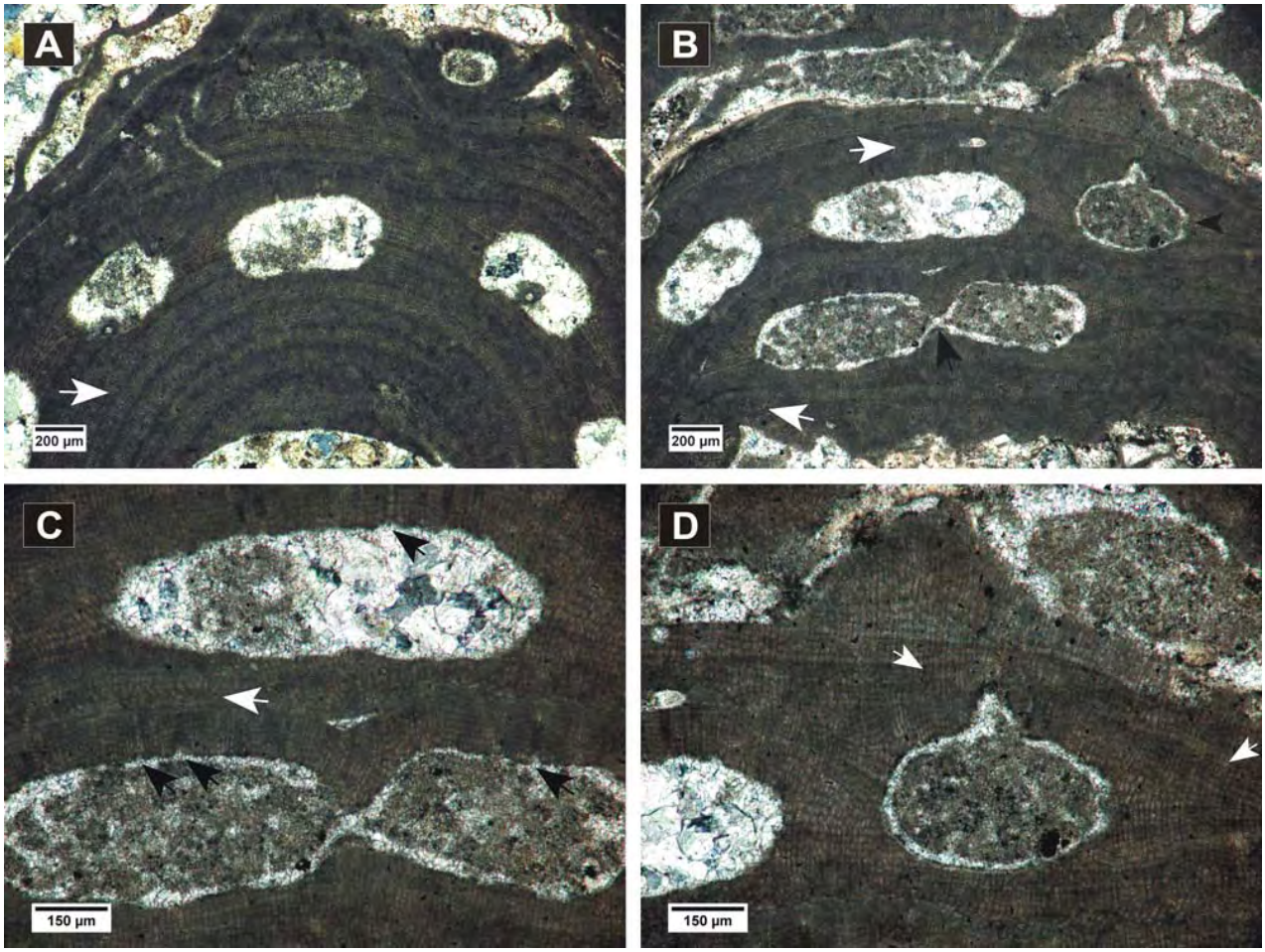

Figure 14: ? *Lithothamnion* sp. 4. A, encrusting, slightly protuberant thallus showing zonation in peripheral filaments (arrow); B, superposed thalli, two adjacent multiporate conceptacles (black arrow), non-coaxial ventral filaments (white arrows), presumed carposporangial conceptacle (black arrowhead); C, multiporate conceptacles with conical pore canals (black arrows), non-coaxial ventral filaments (white arrow); D, detail of presumed carposporangial conceptacle, cell fusions (white arrows).

cells are similar to the cells in the tetrasporangial thallus. Cell fusions are present (Fig. 12.F). Presumed gametangial conceptacles are observed slightly raised above the thallus (Fig. 12.B & E-F). The chamber with the visible pore canal measures 378 µm in diameter and 315 µm (H_1) / 92 µm (H_2) in height. The pore canal is 126 µm long and 41 µm wide.

Studied thin section. LV 74.

Lithothamnion sp. 3

(Fig. 13.A-F)

Description. Encrusting thallus with warty protuberances, up to 7 mm long and 5 mm wide. VC is non-coaxial (Fig. 13.B), 390-430 µm thick and consists of squarish to rectangular cells measuring 8-11 µm in length and 7-10 µm in diameter. PF irregularly zoned with cells 7-14 µm long and 6-9 µm wide. The epithallial cells are flat and flared (Fig. 13.C) and measure 3-5 µm in length and 5-8 µm in diameter.

Multiporate conceptacles are abundant, slightly raised and have flattened or slightly sunken pore plates (Fig. 13.A & C-D). The chambers have rounded sides and measure 404-858 µm in diameter and 208-356 µm in height. The conceptacle roofs are 78-100 µm thick, 6-9 cells long. Roof cells measure 7-9 µm in length and 5-7 µm in diameter, similar to the PF cells. The pore canals are 20-46 µm long and 14-16 µm wide at the base.

Two conceptacles, clearly uniporate and presumed gametangial, are observed in thallus apparently fused with the thallus bearing asexual conceptacles (Fig. 13.E-F). The chambers measure 520-660 µm in diameter, 370 µm (H_1) and 195 µm (H_2) in height, with pore canal 145 µm long and 77 µm wide.

Studied thin section. LV 11.

Table 4: Comparison of biometric measurements of the identified *Mesophyllum* and *Phymatolithon* species.

Species		*Mesophyllum* sp. 1				*Mesophyllum* sp. 2				*Phymatolithon calcareum*			
		n	Range	M	SD	n	Range	M	SD	n	Range	M	SD
VC cells	L	20	14-23	17	2.1	25	19-26	21.7	1.9	20	12-18	14.9	1.4
	D	20	11-15	13.1	1.3	25	5-12	8	1.9	20	7-12	9.7	1.1
PF cells	L	20	9-13	11.4	1.4	50	9-17	11.9	1.7	50	6-13	9.4	1.6
	D	20	6-9	7.6	0.8	50	6-9	7.8	0.8	50	5-8	6.3	0.7
Conceptacles	D	10	193-387	290.2	47.9	4	253-353	319.3	46.9	19	154-300	218.8	37.3
	H	10	159-274	216.5	35.7	4	223-305	259.7	40.4	19	89-160	128.7	19.8
Roof thickness			65-95				54-96				38-47		
Nr. of roof cells			6-7				5-7				3-5		
Roof cells	L	20	5-10	7.6	0.8	20	5-9	7.6	1.3	15	6-8	6.8	0.4
	D	20	5-7	5.9	0.4	20	4-7	5.5	1.0	15	5-6	5.7	0.3
Pore canals	L					2	52-61						
	D					2	7-12						

? *Lithothamnion* sp. 4

(Fig. 14.A-D)

Description. Encrusting and slightly protuberant thallus (Fig. 14.A-B). VC is 50-60 µm thick, non-coaxial, observed mainly above conceptacles (Fig. 14.B-C). Thallus monomerous with dorsiventral organization. Cells in VC measure 9-14 µm in length and 8-11 µm in diameter. PF zoned, showing bands 105-130 µm thick composed of 4-6 cells. PF cells are mostly rectangular, 9-15 µm in length and 7-10 µm in diameter. Elongated cells are present by the conceptacle sides, 14-26 µm long. Epithallial cells are hardly distinguished and their shape is uncertain, as well as the size of meristeme initials in comparison with cells subtending them. Cell fusion present.

Asexual conceptacles were raised above the thallus surface and then buried. The chambers have rounded sides, slightly convex-up floors and measure 475-707 µm in diameter and 289-384 µm in height. The roof is 122-137 µm thick and consists of filaments 6-9 cells long. Roof cells are 9-14 long and 5-7 µm wide, narrower than other PF cells. Pore canals are conical, 13-43 µm wide at the base and 13-42 µm long.

Presumed carposporongial conceptacle is found buried in the same thallus (Fig. 14.B & D). It measures 450 µm in diameter and 350 µm in height. The pore is 110 µm long and has a conical shape, 97 µm in diameter at the base and 35 µm in the top.

Studied thin section. LV 5.

Genus *Mesophyllum* Lemoine, 1928

(Table 4)

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

Mesophyllum sp. 1

(Fig. 15.A-D)

Description. Encrusting monomerous thallus with dorsiventral organization, usually superposed and forming short protuberances (Fig. 15.A). Coaxial to non-coaxial VC (Fig. 15.A-B), up to 218 µm thick. VC cells measure 14-23 µm in length and 11-15 µm in diameter. PF cells are 9-13 µm long and 6-9 µm wide. Epithallial cells are rounded (Fig. 15.C) and the meristeme initials are as long as or longer than cells subtending them. Cell fusions are present (Fig. 15.B-D).

Multiporate conceptacles are protruding at the thallus surface and then become buried in thallus. The chambers have rounded sides and flattened to concave floors (Fig. 15.A & C-D) and measure 193-387 µm in diameter and 159-274 µm in height. The roofs are convex, 65-95 µm thick and 6-7 celled, each cell 5-10 µm long and 5-7 µm wide. The roof cells are mostly rounded and smaller than the surrounding PF cells. A hardly observable narrower cell is observed lining a pore canal (Fig. 15.C).

Studied thin sections. LV 19, LV 51.

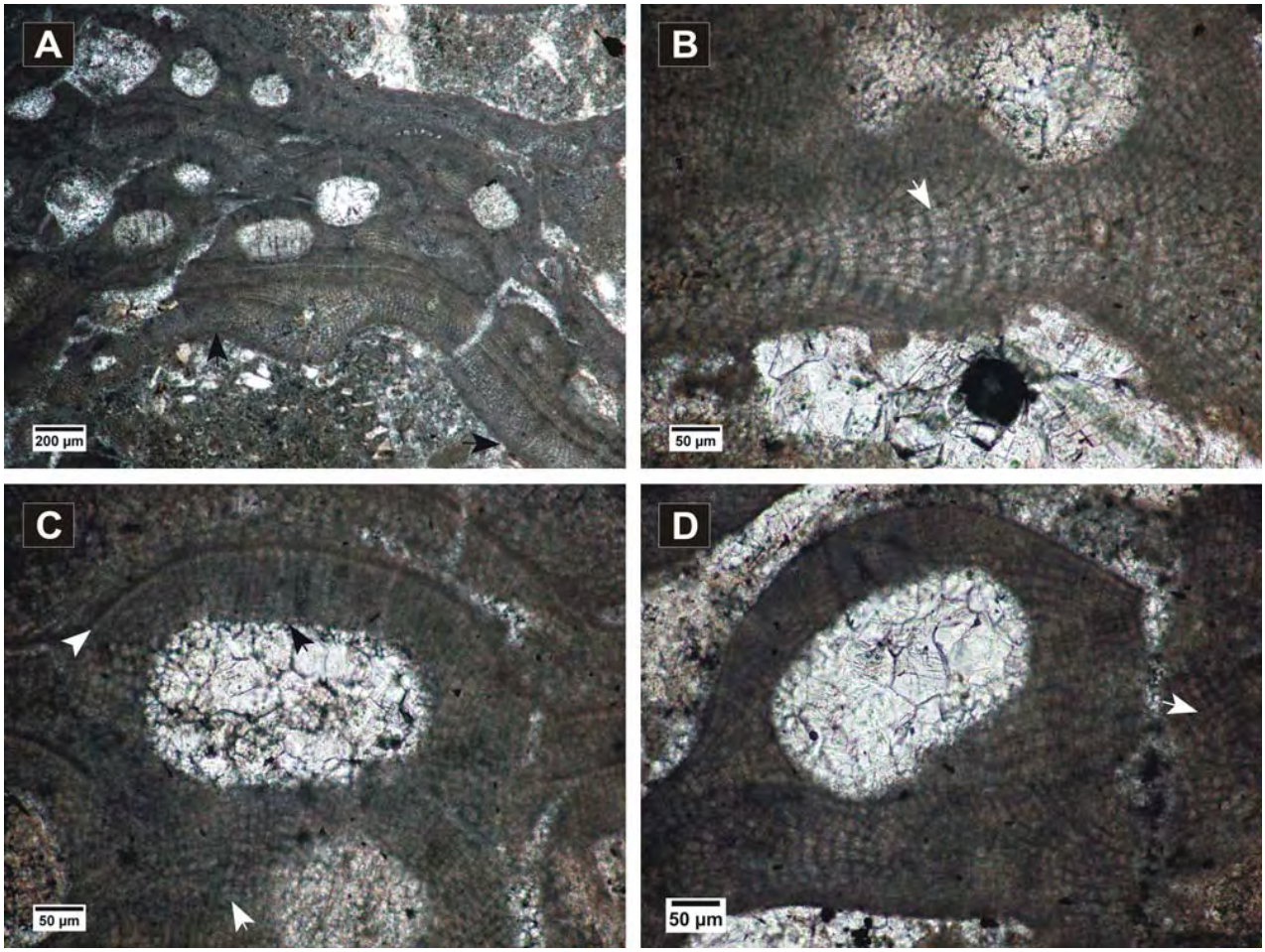

Figure 15: *Mesophyllum* sp.1. A, encrusting protuberant thalli with non-coaxial to coaxial ventral filaments (arrows); B, coaxial ventral filaments with cell fusions (arrow); C-D, multiporate conceptacles and peripheral filaments showing cell fusions (white arrows); C, layer of rounded epithallial cells (white arrowhead), narrow cell at the base of the pore canal (black arrow).

Mesophyllum sp. 2

(Fig. 16.A-D)

Description. Encrusting monomerous thallus with dorsiventral organization (Fig. 16.A). Coaxial VC (Fig. 16.A-B), 180-200 µm thick, consists of cells 18-26 µm long and 5-12 µm wide. Weak zonation is hardly observed in PF consisting of cells 9-17 µm long and 6-9 µm wide. Epithallial cells are flattened to round (Fig. 16.C). Cell fusions are frequent in both VC and PF (Fig. 16.B & D).

Multiporate conceptacles have different shapes, from elliptical to round or even trapezoidal (Fig. 16.A-B). The chambers become buried by the ventral filaments when thalli are superposed (Fig. 16.A). They measure 253-353 µm in diameter and 223-305 µm in height. The roofs have sunken pore plates and raised peripheral rim (Fig. 16.C), 54-96 µm thick and 5-7 cells long. Roof cells measure 5-9 µm in length and 4-7 µm in diameter, smaller than the surrounding PF cells. The pore canals are long (Fig. 16.C), 52-61 µm in length and 7-12 µm wide. The cells lining the pore canals seem similar to the rest of roof cells.

Remarks. The trapezoidal shape of the conceptacles and cell measurements of this specimen show similarities with *M. curtum* LEMOINE redescribed by AGUIRRE & BRAGA (1998), but the conceptacles are larger and the pore plates are sunken. The biometric measurements of this specimen does not fit any description of known species with sunken pore plates.

Studied thin section. LV 48.

Genus *Phymatolithon* FOSLIE, 1898

(Table 4)

Type species. *Phymatolithon calcareum* (PALLAS, 1766) ADEY & MCKIBBIN, 1970, Recent, Falmouth Harbour, England.

Phymatolithon calcareum (PALLAS, 1766) ADEY & MCKIBBIN, 1970

(Fig. 17.A-B)

Basionym. *Millepora calcarea* PALLAS, 1766.

Synonymy.

1986 *Phymatolithon calcareum* (PALLAS) ADEY & MCKIBBIN; WOELKERLING & IRVINE, Figs. 1-15.

1994 *Phymatolithon calcareum* (PALLAS) ADEY & MCKIBBIN; BASSO, p. 579, Pl. 1, figs. 1-4; Pl. 3, figs. 1-4.

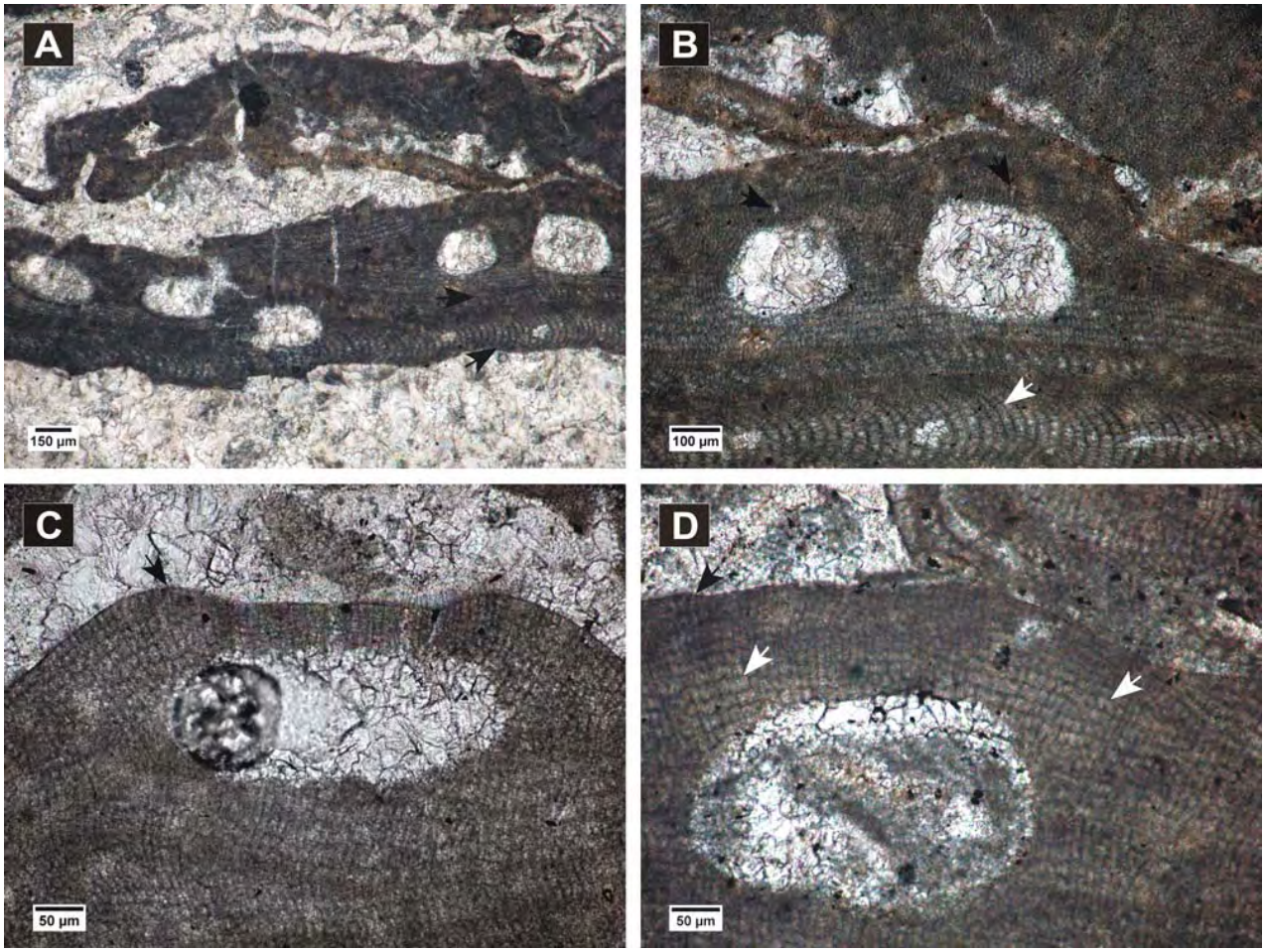

Figure 16: *Mesophyllum* sp. 2. A, encrusting thalli with coaxial VC (black arrows) and multiporate conceptacles; B, cell fusion in ventral filaments (white arrow), trapezoidal multiporate conceptacles with long pore canals and sunken pore plates (black arrows); C, detail of multiporate conceptacle showing clearly a sunken pore plate and rounded epithallial cell (arrow), cells lining the pore canals similar to the other roof cells; D, layer of flattened to round epithallial cells (black arrow), cell fusions in PF (white arrows).

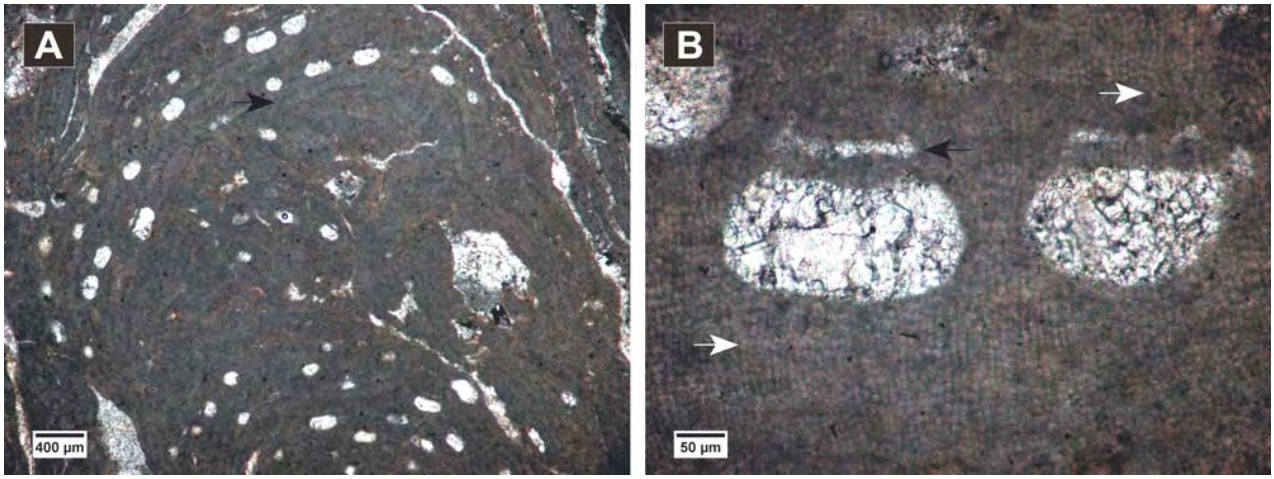

Figure 17: *Phymatolithon calcareum*. A, Protuberant fertile thalli showing weak zonation (arrow); B, multiporate conceptacles with calcified concavities (black arrow), ventral filaments above the chambers (upper white arrow), cell fusion (lower white arrow).

Table 5: Biometric measurements of the identified *Sporolithon* species.

Species		*Sporolithon praeerythraeum*								*Sporolithon* sp. 1							
		sporangial thallus				gametangial thallus				sporangial thallus				gametangial thallus			
		n	Range	M	SD	n	Range	M	SD	n	Range	M	SD	n	Range	M	SD
VC cells	L									20	12-20	16.9	2.4	15	14-20	16.8	1.8
	D									20	9-13	10.7	1.1	15	8-12	10	0.8
PF cells	L	50	12-27	20.6	3.3	50	14-30	20.2	4.1	50	11-16	13.2	1.2	50	13-19	16.6	1.5
	L									25	18-25	21.5	1.9				
	D	50	7-10	8.6	0.8	50	7-12	9.3	1.2	50	8-11	9.5	0.7	50	8-12	9.7	0.8
Sporangial compartments	D	16	45-78	58.1	8.4					52	41-67	54.2	5.3				
	H	16	88-118	103.6	7.5					52	102-158	129.8	11.8				
Elongated cells below sp. comp.	L	7	25-31	27.3	2.1												
	L	7	7-9	7.9	0.9												
Nr. of cells in paraphyses			3-6								3-6						
Longest cells in paraphyses	L									10	22-30	26.7	2.2				
	D									10	5-8	6.8	0.7				
Male conceptacles	D													2	210-240		
	H													2	39-44		
Female conceptacles	D													2	224-232		
	H													2	61-79		
Carposporangial conceptacles	D	1	164														
	H	1	190														

Stratigraphical range. Oligocene - Recent.

Description. Fruticose thallus (Fig. 17.A) showing a hardly distinguishable non-coaxial VC (Fig. 17.B). The cells in core filaments are 12-18 µm long and 7-12 µm wide. Zonation of the PF is observable (Fig. 17.A); each zone is made of 7-9 squarish to rectangular cells. Cells in PF are 6-13 µm in length and 5-8 µm in diameter. Hardly noticeable epithallial cells seem rounded. Cell fusions are present (Fig. 17.B).

Tetrasporangial conceptacles are abundant (Fig. 17.A) and have rounded sides and relatively flat roofs and floors. They measure 154-300 µm in diameter and 89-160 µm in height. The roofs are 38-47 µm thick and made of 3-5 small cell layers. The roof cells are 6-8 µm long and 5-6 µm wide. Distinct rims with a straight to concave shape are observed above the conceptacle roofs. (Fig. 17.B).

Remarks. The specimen fits the descriptions of BASSO (1994, 1997) for fossil and living species.

Studied thin section. LVC 9X.

Order Sporolithales
LE GALL, PAYRI, BITTNER & SAUNDERS, 2009

Family Sporolithaceae VERHEIJ, 1993

Subfamily Sporolithoideae SETCHELL, 1943

Genus *Sporolithon* HEYDRICH, 1897

(Table 5)

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

Sporolithon praeerythraeum (AIROLDI, 1932) VANNUCCI *et al.*, 2000

(Fig. 18.A-D)

Basionym. *Archaeolithothamnium praeerithraeum* AIROLDI, 1932.

Synonymy.

2000 *Sporolithon praeerythraeum* (AIROLDI, 1932) comb. nov.; VANNUCCI *et al.*, p. 193-197, Fig. 2, Pls. 1-2, tab. 2.

Stratigraphical range. Late Eocene - Badenian.

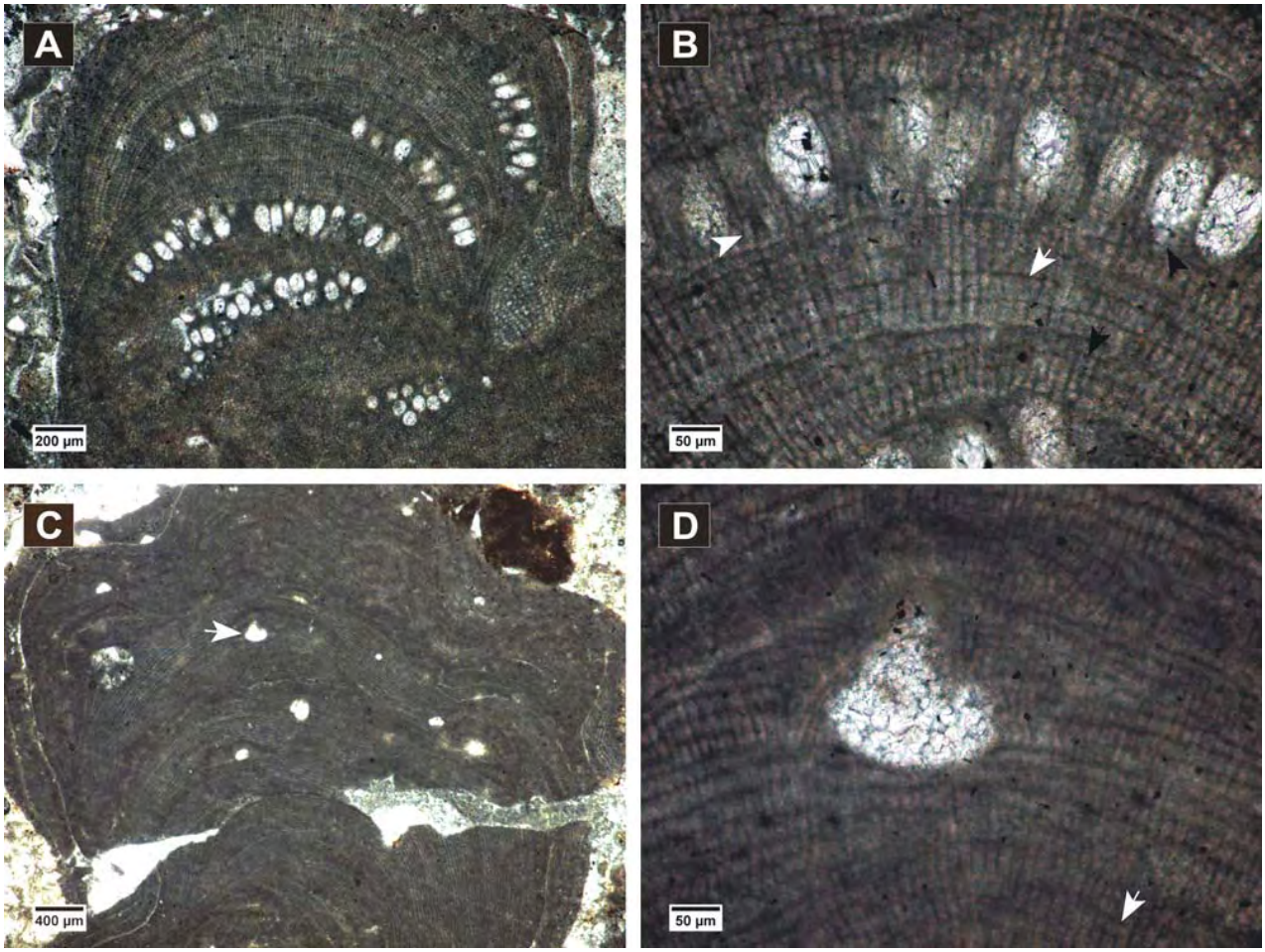

Figure 18: *Sporolithon praeerythraeum*. A, encrusting, lumpy thallus; B, detail of peripheral filaments showing cell fusion (white arrow) and secondary pit connection (black arrow), sporangial compartments form on elongated cells (white arrowhead), stalk cell (black arrowhead); C, presumed carposporangial thallus; D, detail of peripheral filaments showing the same cell arrangement with the thallus in asexual phase, presumed carposporangial conceptacle, cell fusion (white arrow), secondary pit connection (black arrow).

Description. Encrusting lumpy thallus with VC not visible (Fig. 18.A). The PF shows horizontal layers of rectangular to more elongated cells (Fig. 18.B). PF cells measure 12-27 µm in length and 7-10 µm in diameter. Both cell fusions and secondary pit connections are present (Fig. 18.B).

Sporangial compartments are buried in thallus and measure 88-118 µm in length and 45-78 µm in diameter. They are separated by 1-3 filaments in paraphyses, 3-6 cells long. A layer of elongated cells is present below the compartments (Fig. 18.B). These cells represent the longest cells in paraphyses and measure 25-31 µm in length and 7-9 µm in diameter. Stalk cells are rounded to trapezoidal (Fig. 18.B)

The presumed carposporangial thallus (Fig. 18.C) is represented by a lumpy protuberance. The VC is not observable. PF cells are 14-30 µm long and 7-12 µm wide. Cell fusions and secondary pit connections are present (Fig. 18.D). Within the thallus are observed a few structures resembling carposporangial conceptacles. The pear-shaped chamber showing a pore canal (Fig. 18.D) is 164 µm in diameter and 190 µm in height.

Remarks. Even though the ventral filaments are not observed, the presence of the presumed carposporangial thallus in the same sample with the specimen bearing sporangial compartments confirms the assignment to *S. praeerythraeum*, due to the resemblance of both thalli with the redescribed holotype (Vannucci *et al.*, 2000).

Studied thin section. LV 110.

Sporolithon sp. 1

(Figs. 19.A-F - 20.A-D)

Description. Large fruticose thallus up to 14 mm long with protuberances up to 3.5 mm wide (Fig. 19.A). VC non-coaxial (Fig. 19.B) with cells 12-20 µm long and 9-13 µm wide. Typical cells in PF are rectangular, 11-16 µm in length and 8-11 µm in diameter. Frequently, a distinct layer of flattened cells can be observed within the peripheral region, or exactly below the sporangial compartments (Fig. 19.C), 4-8 µm in length. Larger PF cells measure 18-25 µm in length. Epithallial cells not observed.

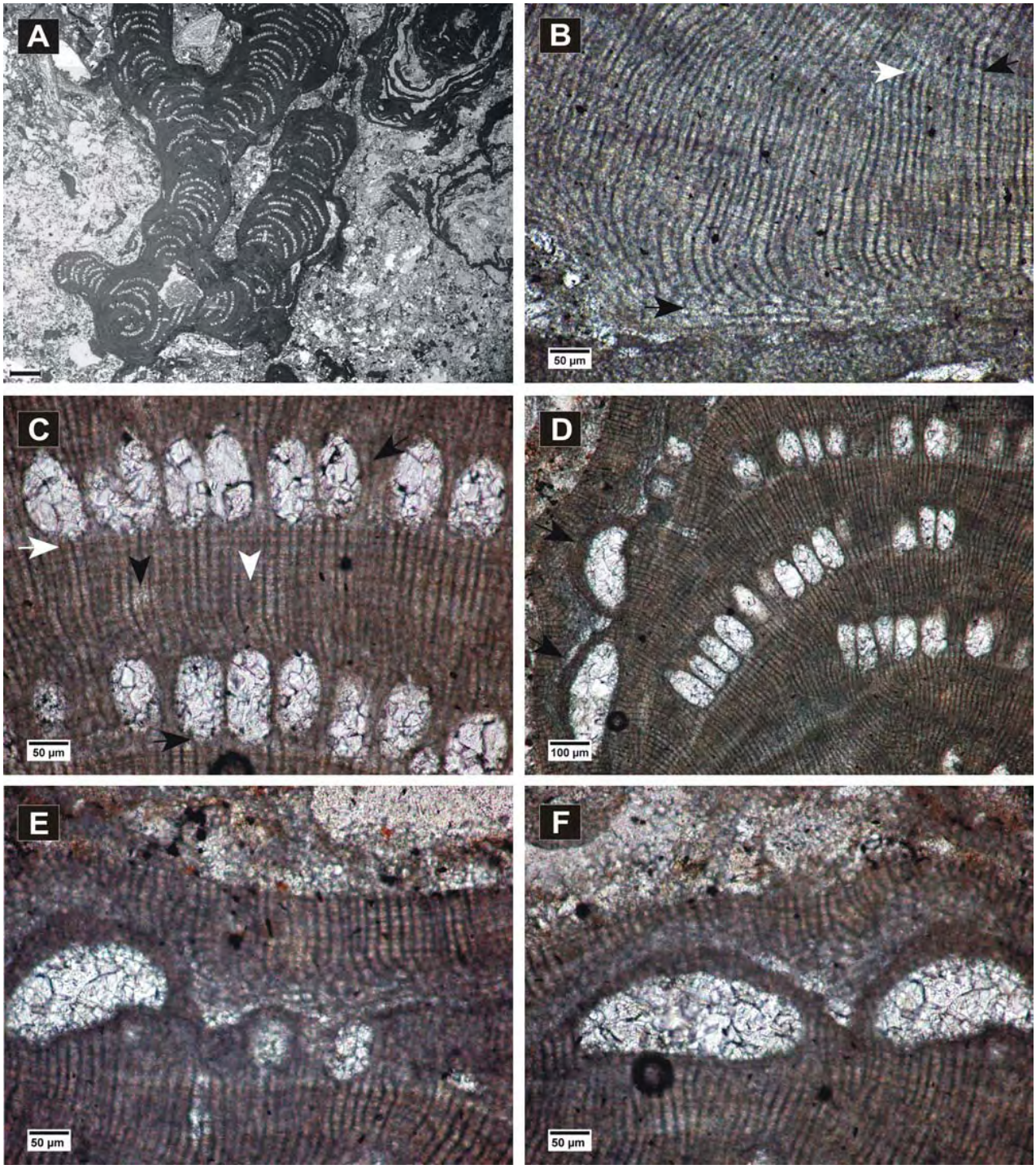

Figure 19: *Sporolithon* sp. 1. A, fertile fruticose branch; B, non-coaxial ventral filaments, cell fusions in VC (black arrow) and in peripheral filaments (white arrow); C, layer of flattened cells below sporangial compartments (white arrow), cells in paraphyses (upper black arrow), stalk cell (lower black arrow), peripheral filaments showing cell fusion (black arrowhead) and secondary pit connections (white arrowhead); D, gametangial conceptacles protruding at the thallus surface (arrows); E, detail of gametangial conceptacle and two small sporangial compartments raised at the thallus surface; F, detail of gametangial conceptacles.

Secondary pit connections are abundant in PF and cell fusions are also present (Fig. 19.B-C).

Sporangial compartments are cylindrical to ovoid (Fig. 19.C-D), up to 25 in a sorus and measure 102-158 µm in length and 41-67 µm in diameter. Layer of elongated cells below the sporangial compartments is absent. Paraphyses are 3-6 cells long (Fig. 19.C), the longest measuring 22-30 µm in length and 5-8 µm in diameter.

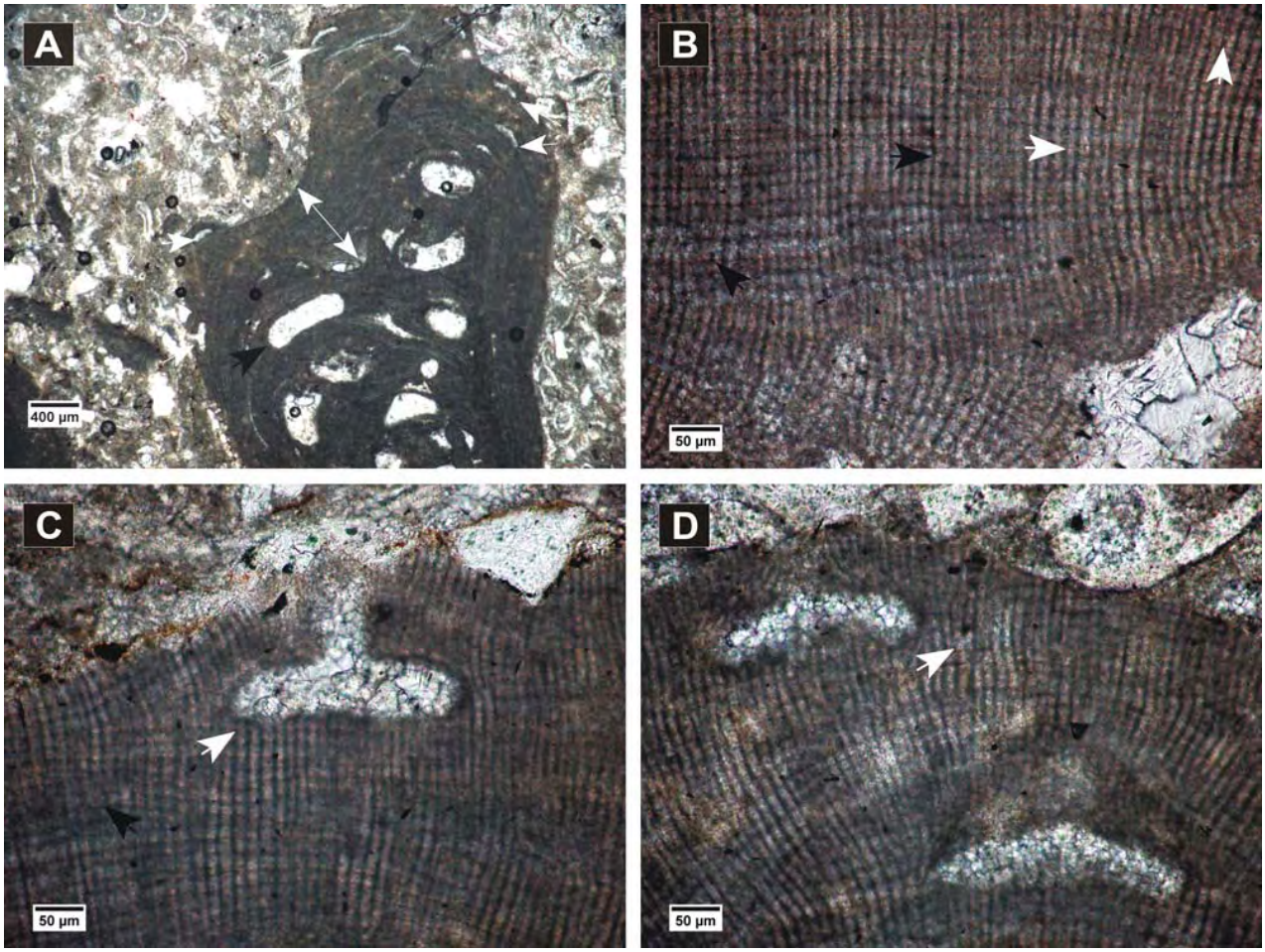

Figure 20: *Sporolithon* sp. 1, gametangial thallus. A, monoecious gametangial thallus (double-headed arrow) encrusting *Lithothamnion sp.1* and bearing uniporate conceptacles slightly raised at the thallus surface (white arrows); B-D, cell fusions (black arrows) and secondary pit connections (white arrows); B, peripheral filaments showing a PF cell arrangement similar to the one in thallus bearing sporangial compartments; C, presumed female gametangial conceptacle with cylindrical pore canal; D, presumed male conceptacles with a slightly convex floor.

Two smaller sporangial compartments measuring 77-95 µm in height and two gametangial conceptacles measuring 190-281 µm in diameter and 124-125 µm in height with pore canals not visible are observed raised at the thallus surface (Fig. 19.D-F).

Gametangial conceptacles are also observed slightly raised in monoecious thallus that encrusts *Lithothamnion* sp.1 (Figs. 11.A & 20.A), in the same thin section. VC hardly observable, with cells 14-20 µm in length and 8-12 µm in diameter. Cells in PF are 13-19 µm in length and 8-12 µm in diameter, similar to the ones in the thallus bearing sporangial compartments. Cell fusions and secondary pit connections are present (Fig. 20.B-D). The presumed female gametangial conceptacles (Fig. 20.C) measure 224-232 µm in diameter and 61-79 µm in height, with cylindrical pore canals 49-55 µm wide and 73-96 µm long. The presumed male conceptacles show a slightly convex floor (Fig. 20.D) and measure 210-240 µm in diameter and 39-44 µm in height.

Remarks. The identification of this species remains uncertain because of the presence of large sporangial compartments and the layer of flattened cells, which were not described from previous studies. *Archaeolithothamnium* sp. described from southern Poland (Pisera & Studencki, 1989) shows a similar growth form, biometric measurements of VC cells, PF cells and sporangial compartments. However, the number of cells in paraphyses cannot be observed in the illustrations.

Studied thin sections. LV 39, 60.

Discussion

The coralline algal assemblages from the Lopadea Veche section show a considerable diversification of species. Features that are used by phycologists to separate modern coralline species, have been identified in our material, and have proven to be effective for separating fossil species (Basso, 1994, 1995; Rasser & Piller, 1999; Iryu *et al.*, 2012; Rebelo *et al.*, 2014; Hrabovský *et al.*, 2015).

One of the most important goals in the taxonomic studies of fossil corallines is to provide a full and accurate description of species, therefore, the identification of asexual, gametangial and carposporangial phases of a species is critical. The gametangial and carposporangial conceptacles occur only in uniporate chambers and, unlike modern specimens, the fossil corallines do not show preserved male and female gametes or carposporophytes. Therefore, the uniporate conceptacles are commonly misidentified as tetrasporangial conceptacles of thalli in asexual phase.

The male conceptacles can be helpful in identifying coralline algal species if they are found in association with the tetrasporangial thalli (HARVEY *et al.*, 2005). Moreover, in case of fusion between the two types of thalli or when published accounts of the gametangial thalli of species or genera are available (VERHEIJ, 1993; HRABOVSKÝ *et al.*, 2015), the identification at species level is more feasible. In this study, the identification of the gametangial phase of species was the most accessible when taking notice of melobesioid thalli showing both multiporate and uniporate conceptacles (Figs. 12.B, 13.E & 14.B). The male and the female gametangial phase of mastophoroid species was obvious only for *Spongites fruticulosus*, because of the published accounts of modern gametangial thalli (BASSO & RODONDI, 2006). The gametangial/carposporangial thalli of *Sporolithon* sp. 1 (Figs. 19.D-F - 20.A-D) and *Sporolithon praeerythraeum* (Fig. 18.C-D) were identified because of the presence of both cell fusions and secondary pit connections and the resemblance to the thallus in asexual phase. Moreover, similar presumed carposporangial conceptacles of *S. praeerythraeum* are described from the paratype (VANNUCCI *et al.*, 2000) and gametangial conceptacles of *Sporolithon* sp. 1 are also found protruding in the same thallus bearing sporangial compartments.

Paleogeographic remarks

The red algal limestones from the Transylvanian Basin, Lopadea Veche section, show a great resemblance to the middle Miocene deposits of southern Poland. Nine of the identified species were also reported from the Korytnica Basin (PISERA & STUDENCKI, 1989) and the distinguished facies types from Pińczów limestones (STUDENCKI, 1988) were also recognized in the studied section. The coralline algal assemblages from the Badenian of Czech Republic were studied using similar taxonomic approaches (HRABOVSKÝ *et al.*, 2015). Nevertheless, the resemblance of these two accounts is relatively low, with only four common species. Further detailed analysis of other sections in the Transylvanian Basin (Pietroasa, Podeni, Gârbova de Sus) can indicate different paleoenvironmental conditions that may be important in the paleogeographic distribution of coralline species.

Taking into account the stratigraphical and paleogeographical distribution of *Lithothamnion crispatum* (COLETTI *et al.*, 2016), *Lithothamnion roveretoi* (VANNUCCI *et al.*, 2010; HRABOVSKÝ *et al.*, 2015), *Phymatolithon calcareum* (BASSO *et al.*, 1997) and *Sporolithon praeerythraeum* (VANNUCCI *et al.*, 2000), we conclude that during the middle Miocene, these species were distributed only in the Transylvanian Basin and other Central Paratethys basins. While *S. fruticulosus, L. crispatum* and *P. calcareum* are now common species in modern marine environments, *S. praeeryhraeum* apparently became extinct in the Mediterranean (Tethyan) domain by the end of the Paleogene (VANNUCCI *et al.*, 2000; see also VANNUCCI *et al.*, 2008, in respect to ? *Lithophyllum perrandoi*). However, this study indicates that the stratigraphical distribution of *S. praeeryhraeum* extended to the middle Miocene in the Transylvanian Basin.

Conclusions

Some diagnostic features commonly used for the identification and taxonomic description of modern coralline algae, were for the first time distinguished and used for describing middle Miocene specimens from the Transylvanian Basin, Romania.

This taxonomic study identified seventeen species belonging to Corallinales, Hapalidiales and Sporolithales. Gametangial/carposporangial thalli were identified and included in the description of six species (*Spongites fruticulosus*, *Lithothamnion* sp. 2, *Lithothamnion* sp. 3, ? *Lithothamnion.* sp. 4, *Sporolithon praeerythraeum*, *Sporolithon* sp. 1).

Female gametangial conceptacles of *Spongites fruticulosus* are for the first time identified and described in fossil material. We propose the assignment of *Lithophyllum platticarpum* MASLOV to *Spongites fruticulosus* KÜTZING, as a gametangial thallus with male conceptacles because of their revealed similarities (growth form, conceptacles and biometric measurements) and the fusion with the thallus in asexual phase.

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