Chamberlainium pentagonum (Conti) comb. nov. and *Spongites fruticulosus* (Corallinales, Rhodophyta) in the Miocene carbonates of the western Mediterranean

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Abstract: Molecular phylogenetic analyses discovered an unexpected biodiversity of coralline algae in modern oceans. This species richness is unlikely to be an exclusive characteristic of recent ecosystems. With the aim to investigate fossil coralline biodiversity, a large dataset of western Mediterranean Miocene specimens, previously identified as *Spongites fruticulosus* (and synonymized taxa), have been revised based on the current taxonomic framework. The analysis recognized two distinct groups. The first group includes the specimens fitting within the current description of *S. fruticulosus*. The second group consists of *Chamberlainium pentagonum* comb. nov., the first fossil representative of the genus. This species has been separated from *S. fruticulosus* on the basis of its smaller conceptacles and its thinner conceptacle roof. The very same characters have been highlighted by modern molecular phylogenetic analyses for separating *Chamberlainium* from *Spongites*. *Chamberlainium pentagonum*, similarly to the fossil specimens of *Spongites fruticulosus*, occurs in most of the investigated area and the two species coexist in several localities, indicating a similar and broad ecological tolerance for both taxa. These results suggest that Miocene coralline algal biodiversity is probably underestimated and prove the convenience of using large datasets for the study of fossil coralline algae.

Key-words:

* Mediterranean Sea;
* Neogoniolithoideae;
* Chamberlainoideae;
* Corallinales;
* calcareous algae;
* taxonomy;
* type collections

**Résumé : Chamberlainium pentagonum *(Conti) n.comb. et* Spongites fruticulosus *(Corallinales, Rhodophyta) dans les calcaires miocènes de Méditerranée occidentale.-* Des analyses phylogénétiques moléculaires ont révélé une biodiversité inattendue au sein des algues rouges calcaires des océans modernes. Il est peu probable que cette richesse des espèces soit une caractéristique exclusive des écosystèmes modernes. Afin d'étudier la biodiversité des algues rouges calcaires fossiles, un large ensemble de données issues d'échantillons du Miocène de la Méditerranée occidentale, auparavant identifiés comme *Spongites fruticulosus* (et ses synonymes juniors), a été révisé en s'appuyant sur le cadre taxinomique moderne. Cette analyse a identifié deux groupes distincts. Le premier groupe comporte les spécimens correspondant à la description actuelle de *S. fruticulosus*. Le second groupe est constitué par *Chamberlainium pentagonum* n.comb., premier fossile représentatif du genre. Cette espèce a été séparée de *Spongites fruticulosus* sur la base de la plus petite taille de ses conceptables et de l'épaisseur moindre du toit de ces derniers. Les mêmes caractéristiques ont été mises en évidence par les analyses phylogénétiques moléculaires modernes permettant de séparer *Chamberlainium* de *Spongites*. *Chamberlainium pentagonum*, tout comme les spécimens fossiles de *Spongites fruticulosus*,

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est présent dans la majeure partie de la zone étudiée et ces deux espèces cohabitent dans plusieurs localités, indiquant une tolérance écologique large et similaire pour les deux taxons. Ces résultats suggèrent que la biodiversité des algues rouges calcaires miocènes est probablement sous-estimée ; ils montrent l'intérêt d'utiliser des ensembles de données conséquents pour étudier les algues rouges calcaires fossiles.

Mots-clefs :

• Mer Méditerranée ;
• Neogoniolithoideae ;
• Chamberlainoideae ;
• Corallinales ;
• calcareous algae ;
• taxinomie ;
• collections de types

Introduction

In the last decades, molecular phylogenetic analysis has driven a new revolution in biological taxonomy, including the classification of coralline algae. The genetic approach resulted in significant changes and revisions at higher taxonomic ranks (*e.g.*, BAILEY & CHAPMAN, 1998; HARVEY *et al.*, 2003; LE GALL *et al.*, 2010; BITTNER *et al.*, 2011; KATO *et al.*, 2011; NELSON *et al.*, 2015; RÖSLER *et al.*, 2016; CARAGNANO *et al.*, 2018), and the discovery of a previously unknown species diversity (*e.g.*, PARDO *et al.*, 2014; SISSINI *et al.*, 2014; ADEY *et al.*, 2015; BAHIA *et al.*, 2015; BASSO *et al.*, 2015; HERNANDEZ-KANTUN *et al.*, 2015, 2016; NELSON *et al.*, 2015; MERWE *et al.*, 2015; RÖSLER *et al.*, 2016; LIU *et al.*, 2018; PEZZOLESI *et al.*, 2019). These studies also revealed remarkable genetic separation between biogeographic provinces, suggesting that many apparently cosmopolitan species were actually heterogeneous mixtures of geographically separated entities, nearly indistinguishable from the morphological point of view (*e.g.*, SISSINI *et al.*, 2014; MERWE *et al.*, 2015; RÖSLER *et al.*, 2016). In this context, the genus *Spongites* has changed its taxonomic position twice in the last years (KATO *et al.*, 2011; RÖSLER *et al.*, 2016). Molecular phylogenetic studies also proved that geographically separated populations, included in *Spongites* on a morpho-anatomical basis, actually belong to different subfamilies (MERWE *et al.*, 2015; CARAGNANO *et al.*, 2018). Furthermore, it has been suggested that even the Mediterranean population of the type species, *Spongites fruticulosus* KÜTZING (1841), could be formed from two separate entities (RÖSLER *et al.*, 2016; CARAGNANO *et al.*, 2018). While these results suggest that the cosmopolitan *S. fruticulosus* is likely a complex of different species, for coralline algal paleontology, from the Oligocene onward and all around the world, *S. fruticulosus* seems to be almost the only species of its genus (AGUIRRE & BRAGA, 2005). There are basically two reasons for this. First, paleontology can only rely on characteristics that can be preserved in the fossil record and many living species are based on characters that are either rarely preserved or not preservable at all. Second, until the type material of *Lithophyllum albanense* (LEMOINE, 1923) was rediscovered, reassessed, and synonymized with *S. fruticulosus* (BRAGA *et al.*, 1993; AGUIRRE *et al.*, 2012), paleontologists could rely only on the original description of the species, which was not sufficient for accurate taxonomic identifications. The original description of *Lithophyllum albanense* (LEMOINE, 1923: p. 281-282) did not have any illustrations of the microscopic anatomy of the specimen and presented only schematic drawings (LEMOINE, 1923: text-figs. 8-9). As a result, it is likely that over the years a number of similar species have been lumped together. The division of living coralline species is presently based on both DNA sequencing and morphology. While the former is obviously not possible with geological material, the latter gives results complying with DNA sequencing only when large and geographically extensive collections are analyzed (*e.g.*, BASSO *et al.*, 2015; ADEY *et al.*, 2018). This approach is also quite effective for fossil material (COLETTI *et al.*, 2016), since it allows for a better comprehension of intraspecific variability. Therefore, in order to establish whether or not the fossil population of *S. fruticulosus* represents a morphologically uniform entity, we investigated a large collection of fossil coralline algae morphologically close to *S. fruticulosus* and discussed their placement within the current taxonomic framework.

Material and methods

The analysis included twenty-five thalli from different formations of the western Mediterranean area, ranging in age from the Burdigalian to the early Messinian (Fig. 1; Table S1). Some of the examined specimens have already been published as *Spongites fruticulosus* (and synonyms), while other specimens are unpublished (Fig. 1; Table 1). The holotype of *Lithothamnion pentagonum* CONTI (1943), an ill-defined species stored in the collection of the DISTAV of the Genova University (VANNUCCI *et al.*, 2009), has been also re-examined. Although the examined thin sections of the specimens were prepared at different times (ranging from the 1940s to recently), the preparation technique is always the same. The specimen is embedded in epoxy resin and then cut with a rock saw. The resulting surface is polished with abrasive powder and then glued to a standard petrographic glass slide. The excess material is cut away with a rock saw and then the specimen is ground to a thickness of 30-40 μm. For anatomical observations, the fossil specimens were observed in thin section under a light micro-
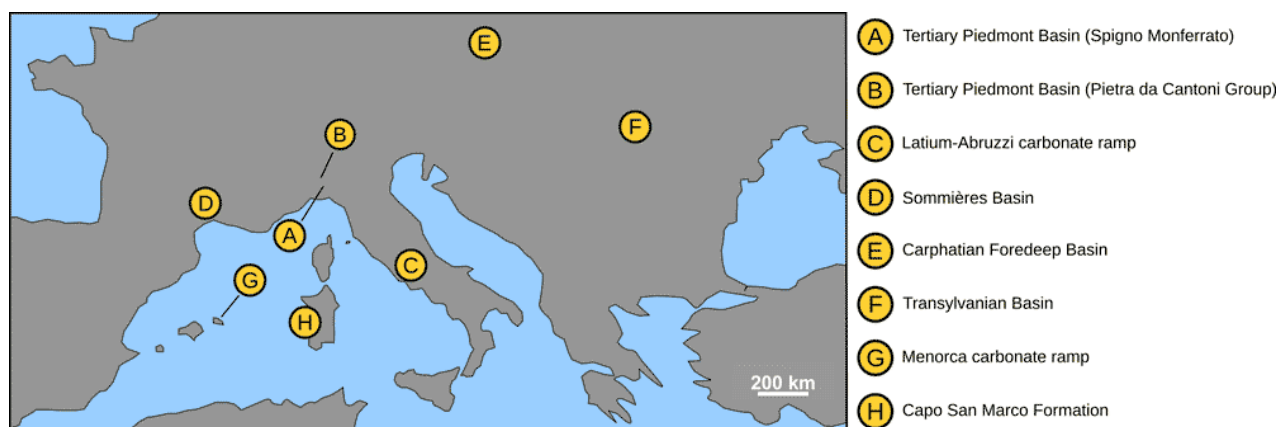
Figure 1: Geographic map of the studied localities.

scope. Growth-forms terminology follows WOEL-KERLING *et al.* (1993), while the terminology for the vegetative anatomy follows HRABOVSKÝ *et al.* (2016), using hypothallus and perithallus as synonyms for ventral core of basal filaments and peripheral zone respectively. The vegetative anatomy was studied along longitudinal radial sections (QUARANTA *et al.*, 2007; VANNUCCI *et al.*, 2008). The cell length was measured as the distance between two primary pit connections including the cell wall; the diameter of the cells was measured perpendicular to cell length and includes the cell wall (BASSO *et al.*, 1996). The reproductive anatomy was also investigated along radial sections. The conceptacles were measured along their axial sections (*i.e.*, the section that cuts the chamber in its central part, resulting in the pore canal being visible; AFONSO-CARILLO *et al.*, 1984; QUARANTA *et al.*, 2007; VANNUCCI *et al.*, 2008). The height of the conceptacle chamber was measured at the side of the columella (h2 *sensu* BASSO *et al.*, 1996). Male gamentangial thalli have been recognized based on the presen-ce of uniporate conceptacles with a small diameter and a very low (< 0.25) height/diameter ratio (H/D). Female gametangial thalli have been recognized based on the presence of uniporate conceptacles yielding a low H/D and the presence of large inflated cavities presumably corresponding to carposporangial conceptacles produced by development of a carposporophyte within the fertilized female conceptacle (BASSO & RODONDI, 2006). Asexual sporangial thalli have been recognized based on the presence of conceptacles of uniform size within each of the examined specimens, and a regular H/D in respect of the known proportions observed in the living species. Sporangial and gametangial thalli have been considered as different reproductive stages of the same species only when they were exhibiting the same vegetative anatomy and they were located close to each other (*e.g.*, same thin section or same stratigraphic layer) (BASSO *et al.*, 1996; HRABOVSKÝ *et al.*, 2016). The following abbreviations are used: D = diameter; H = height; L = length.

Table 1: Studied specimens, including localities, age and relevant literature; specimen numbers are in bold, the same identifying numbers are used throughout the paper.

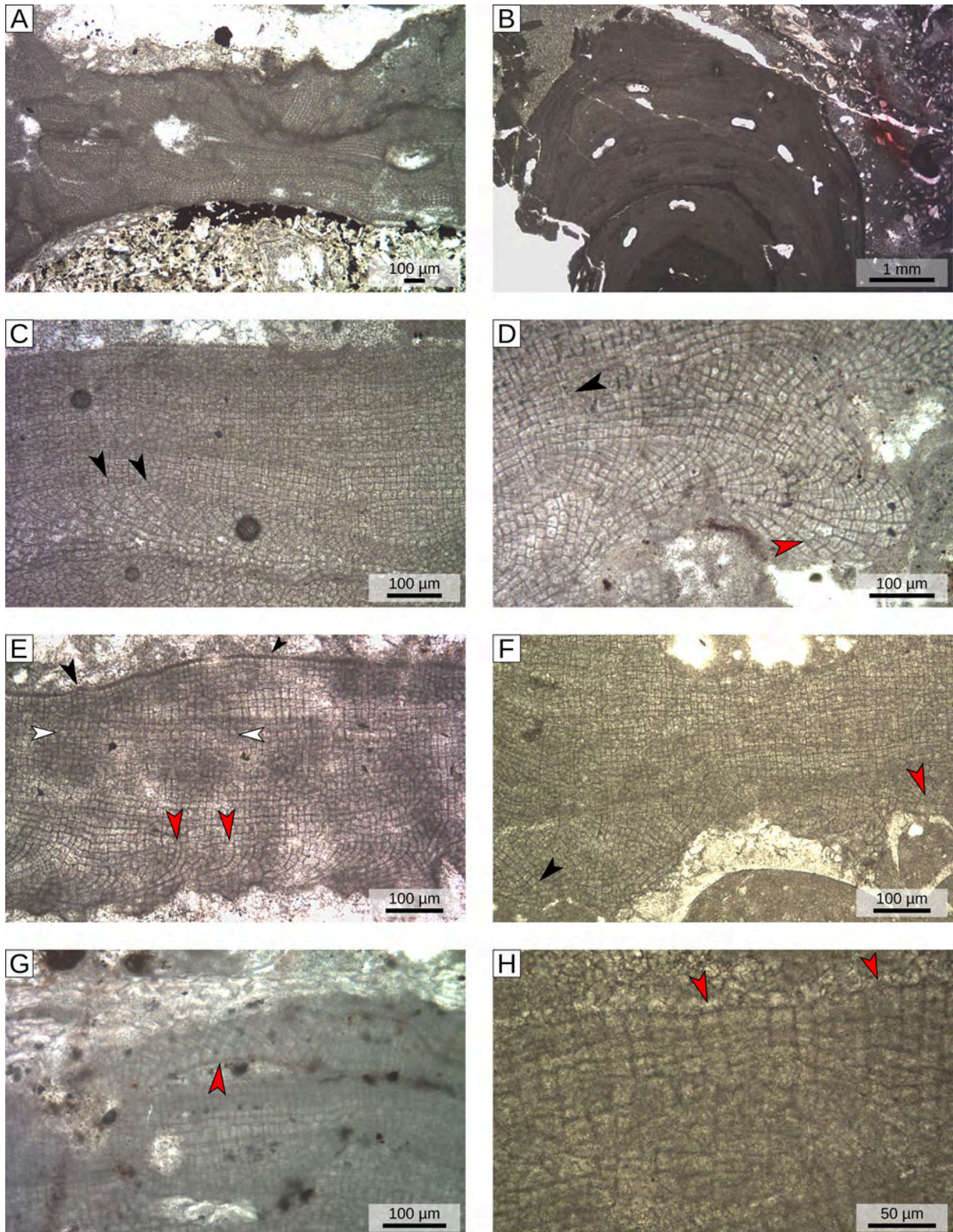|	Locality	Age	Specimens
A	Tertiary Piedmont Basin (Spigno Monferrato)	Burdigalian	Specimens published as: [**1**] *Lithothamnion pentagonum*, CONTI, 1943: Tav. VI.3a-e; Tav. VIII.4; [**18**, **19**, **20**] *Spongites albanensis*, VANNUCCI *et al.*, 1993; [**24**, **25**] *Lithophyllum platticarpum*, VANNUCCI *et al.*, 1993: Tav. I.a
B	Tertiary Piedmont Basin (Pietra da Cantoni Group)	Burdigalian	Unpublished specimens [**16**, **17**, **23**]
C	Latium-Abruzzi carbonate ramp	Burdigalian	Specimens [**3**, **4**, **5**] published as *Spongites* sp., BRANDANO *et al.*, 2007: text-fig. 5.b
	Sommières Basin	Burdigalian	Specimens [**21**, **22**] published as *Spongites fruticulosus*, COLETTI *al.*, 2018a: text-fig. 6.E; text-fig. S.3; table
E	Carpathian Foredeep Basin	Early Langhian	Specimen [**13**] published as *Spongites fruticulosus*, HRABOVSKÝ *et al.*, 2016: text-fig. 17.A; specimens [**14**, **15**] published as *Spongites* DO-LÁKOVÁ *et al.*, 2014.
F	Transylvanian Basin	Early Langhian	Unpublished specimens [**9**, **10**, **11**, **12**]
G	Menorca carbonate ramp	Early Tortonian	Specimens [**6**, **7**, **8**] published as *Spongites*, BRANDANO *et al.*, 2005: text-fig. 9
H	Capo San Marco Formation (Sardinia)	Messinian	Specimen [**2**] published as *Lithophyllum albanense*, FRAVEGA *et al.*, 1988
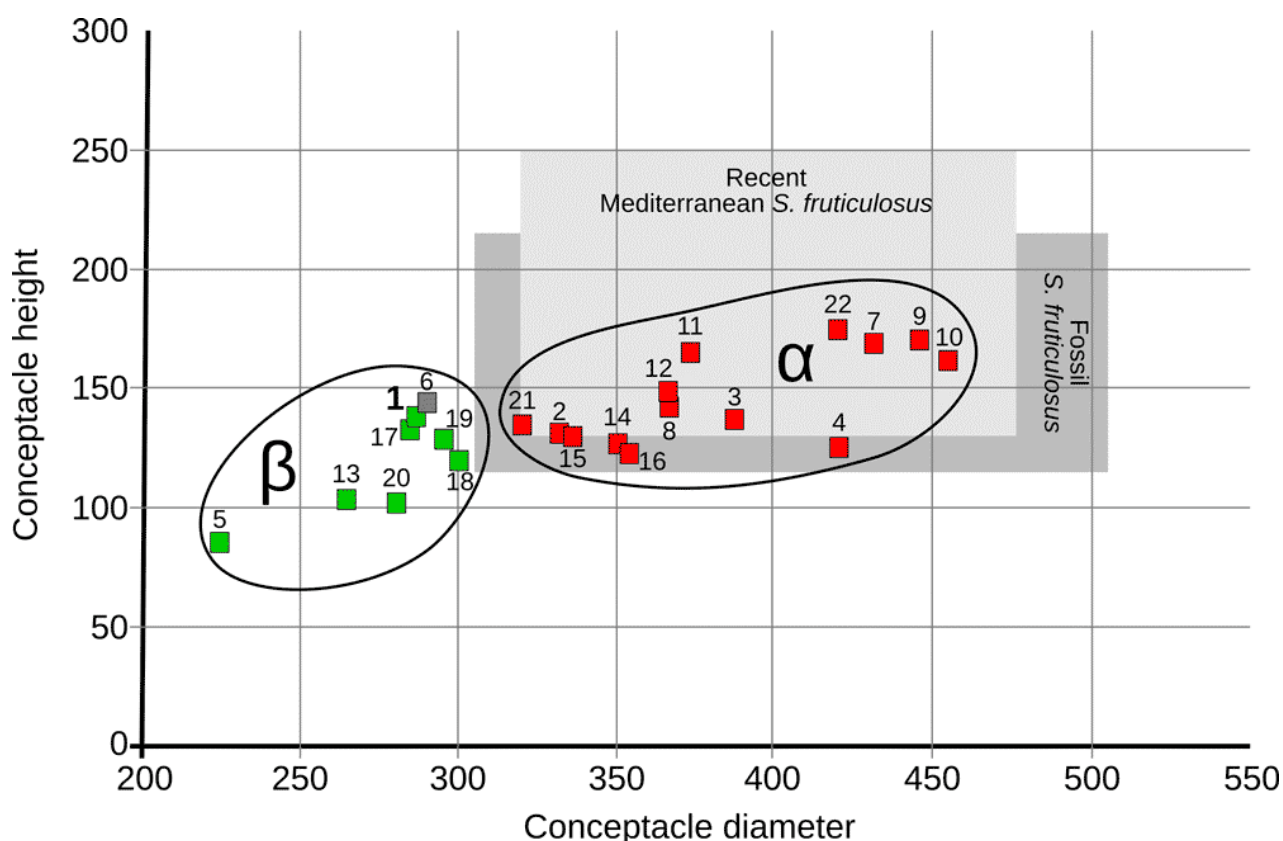
Figure 2: Scatter-plot including the values of conceptacle diameter (µm) and conceptacle height (µm) for all the examined sporangial thalli; green squares indicate dimerous specimens; red squares indicate monomerous specimens; specimen 6 is indicated by a gray square since the hypothallial portion of the thallus was not observed; the light grey field indicates the known variability of conceptacles size for the modern Mediterranean population of *Spongites fruticulosus*; the dark gray field indicates the known variability of LEMOINE's type material of *Lithophyllum albanense*, reassessed, and synonymized with *S. fruticulosus* by AGUIRRE *et al.* (2012).

Paleoecological setting

The Burdigalian specimens of the Latium-Abruzzi carbonate ramp (specimens 3, 4, 5), Tertiary Piedmont Basin (specimens 1, 16, 17, 18, 19, 20, 23, 24, 25) and Sommières Basin (specimens 21, 22) are related to similar environmental conditions. During the Burdigalian these areas were characterized by a tropical to sub-tropical climate and nutrient-rich waters, leading to the formation of carbonate facies dominated by coralline algae, large benthic foraminifera, barnacles, bryozoans and mollusks (VANNUCCI *et al.*, 1993; BRANDANO & CORDA, 2002; BRANDANO *et al.*, 2007, 2017; REYNAUD & JAMES, 2012; COLETTI *et al.*, 2015, 2017, 2018a, 2018b), with hermatypic corals occurring only locally (BRANDANO *et al.*, 2007). The paleoenvironment of the early Langhian specimens of the Carphatian Foredeep Basin (specimens 13, 14, 15) and of the Transylvanian Basin (specimens 9, 10, 11, 12), was also characterized by warm to subtropical conditions (SAINT-MARTIN *et al.*, 2007; DOLÁKOVÁ *et al.*, 2008, 2014; CHELARU *et al.*, 2019). The related skeletal assemblage was dominated by coralline algae, bryozoans and molluscs, associated with serpulids, benthic foraminifers, echinoids and hermatypic corals (the latter in the area of Lopadea Veche) (BUCUR & FILIPESCU, 1994; FILIPESCU & GÎRBACEA, 1997; SAINT-MARTIN *et al.*, 2007; DOLÁKOVÁ *et al.*, 2008, 2014). The early Tortonian specimens (specimens 6, 7, 8) from Menorca (Lower Bar Unit, POMAR *et al.*, 2002; BRANDANO *et al.*, 2005), are related to a high-energy, tropical, middle-ramp environment, where carbonate production was dominated by coralline algae, mollusks, echinoids, bryozoans and large benthic foraminifera (BRANDANO *et al.*, 2005). The early Messinian specimen of the Capo San Marco Formation (2) is associated with a skeletal assemblage dominated by mollusks, coralline algae, bryozoans and brachiopods (CHERCHI *et al.*, 1978; FRAVEGA *et al.*, 1988). This limestone testifies the last episode of marine deposition in the area before the Messinian Salinity Crisis and is related to a coastal, shallow-water environment (CHERCHI *et al.*, 1978; FRAVEGA *et al.*, 1988). Overall, all the examined specimens are related to warm-temperate to tropical shallow-water conditions.

▶ **Figure 3:** Vegetative anatomy of group α (*S. fruticulosus*). **A)** Encrusting growth form; specimen 9, locality F. **B)** Fruticose growth form; specimen 3, locality C. **C)** Monomerous organization with non-coaxial hypothallus; black arrowheads= hypothallial filaments bending upward and forming perithallus; specimen 9, locality F. **D)** Non-coaxial hy-

pothallus; red arrowhead= dichotomous branching of hypothallial filaments; black arrowheads= regularly organized perithallus; specimen 11, locality F. **E)** Monomerous organization with a non-coaxial hypothallus; red arrowheads= hypothallial filaments bending upward and forming perithallus; white arrowheads= poorly organized perithallus; black arrowheads= dome-shaped epithallial cells; specimen 7, locality G. **F)** Monomerous organization (black arrowhead) locally turning into dimerous organization (red arrowhead); specimen 16, locality B. **G)** Dimerous organization developing over a scar in the perithallus (red arrowhead); specimen 12, locality F. **H)** Dome-shaped epithallial cells (red arrowheads); specimen 16, locality B.
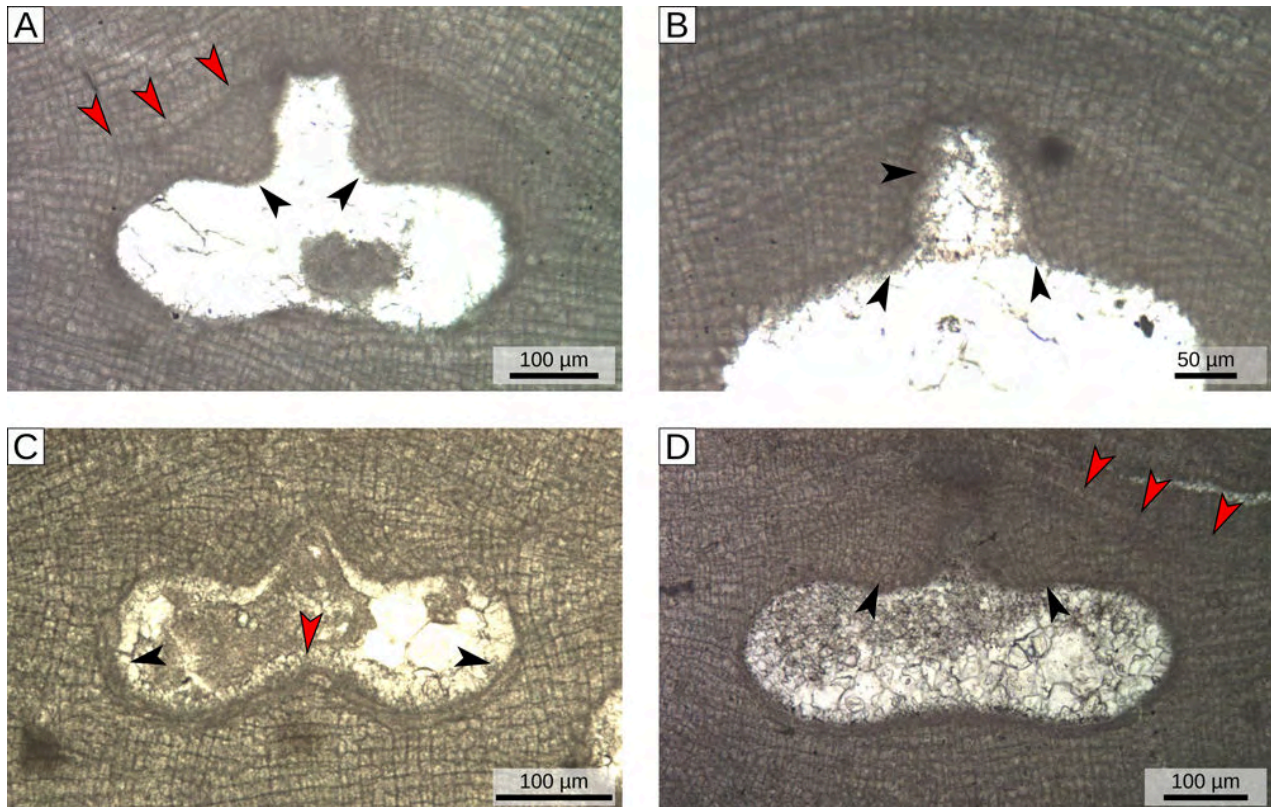
Figure 4: Asexual reproductive anatomy of group α (*S. fruticulosus*). **A)** Flask-shaped uniporate sporangial conceptacle lined by cells filaments that protrude into the pore canal (black arrowheads); red arrowheads= conceptacle roof originally protruding above the surrounding thallus surface; specimen 9, locality F. **B)** Magnified view of sporangial conceptacle roof with cell filaments protruding into pore canal (black arrowheads); specimen 9, locality F. **C)** Sporangial conceptacle lined by cell filaments (black arrowheads); red arrowhead= central columella; specimen 16, locality B. **D)** Magnified view of the roof that was clearly raised (red arrowheads) compared to the surrounding thallus surface; black arrowheads= filaments of small cells (with >8 cells) composing the roof of the conceptacle; specimen 10 locality F.

Results

The analyzed specimens can be broadly divided into two groups (Fig. 2): α) specimens that are morphologically and anatomically strictly corresponding to the modern concept of *Spongites fruticulosus* (BASSO & RODONDI, 2006); β) specimens that are not corresponding to the modern concept of *S. fruticulosus*. All the morphometric data of the investigated specimens are provided in the supplementary material (Table S1).

Group α: *Spongites fruticulosus*

This group includes 14 sporangial thalli (specimens: 2, 3, 4, 7-12, 14-16, 21, 22) from every studied locality, except Spigno Monferrato (locality A) (Figs. 1 - 2; Table 1). The thalli present encrusting (Fig. 3.A), warty or fruticose growth forms (Fig. 3.B) and are characterized by a mainly monomerous organization (Fig. 3.C-E). The hypothallus consists of several layers of rectangular cells (mean size: D 12.3 µm; L 19.1 µm) and lacks a coaxial organization (Fig. 3.D; Table S1). Each filament of hypothallial cells bends toward the thallus surface to form the perithallus (Fig. 3.C, 3.E). Locally the thallus may show a dimerous organization characterized by a basal layer of irregularly squared cells (Fig. 3.F-G) as observed in recent specimens of the species (BASSO & RODONDI, 2006). The perithallus is composed of rectangular cells with a mean D of 10.8 µm and a mean L of 12.8 µm (Table S1). The perithallus is locally grid-like (Fig. 3.D), while elsewhere, owing to the large number of wide cell fusions, the grid become less regular and the separation between cells of contiguous filaments appears less evident than the separation between cells of the same filament (Fig. 3.E). Epithallial cells are dome-shaped and much smaller than the average perithallial cells (Fig. 3.E, 3.H). Trichocytes were not observed.

Sporangial plants present flask-shaped uniporate conceptacles (Fig. 4.A), with conceptacle roof formed from cell filaments lining the outer border of the chamber and protruding into the pore canal (type 1 *sensu* JOHANSEN, 1981) (Fig. 4.B-C). The chamber has a mean size of 380 µm (D) x145 µm (H), while on average the pore-canal is 110 µm long and has a basal diameter of 100 µm (Fig. 4.A-B; Table S1). The central part of the floor of the conceptacle chamber is gene-
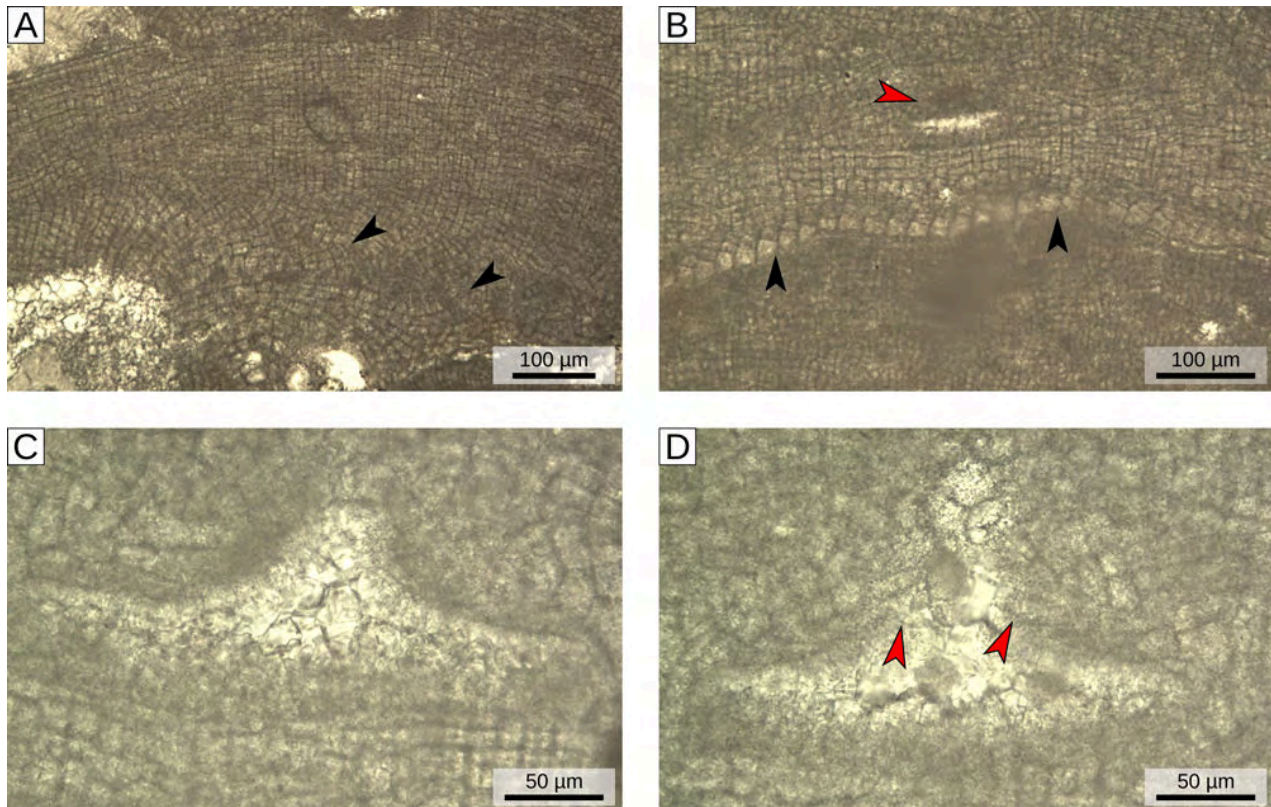
Figure 5: Vegetative and gametangial reproductive anatomy of group ɑ (*S. fruticulosus*) (specimen 23, locality B). **A)** Vertical section of vegetative thallus with a monomerous organization; black arrowheads= non-coaxial hypothallus. **B)** Portion of the thallus with dimerous organization; black arrowheads= basal layer of cells; red arrowhead= conceptacle. **C)** Magnified view of a gametangial conceptacle. **D)** Magnified view of a presumed gametangial conceptacle with conceptacle roof lined by cells filaments that protrude into the pore canal (red arrowheads).

rally raised forming a calcified columella (Fig. 4.C). The chamber has an average roof thickness of 90 µm and the roof is composed of cells (generally more than 8) slightly smaller and shorter than normal perithallial cells (Fig. 4.B, 4.D). The conceptacles slightly protrude above the surrounding thallus surface (Fig. 4.A, 4.D). Specimen 23 (Tertiary Piedmont Basin, locality B) has been considered as a gametangial plant, since it presents small and narrow conceptacles (mean size: D 145 µm x H 25 µm; H/D of 0.17; Table S1), and shares the same vegetative anatomy of the sporangial plant with which is associated (specimen 16, Tertiary Piedmont Basin, locality B) (Fig. 5; Table S1).

Group β: *Chamberlainium pentagonum*

This group includes 8 sporangial thalli (specimens: 1, 5, 6, 13, 17-20, from the localities A, C, E, G) (Figs. 1 - 2; Table 1), including the holotype of *Lithothamnion pentagonum* Conti (specimen 1, Tertiary Piedmont Basin, locality A). Differently from group ɑ, these algae mainly present an encrusting growth morphology (Fig. 6.A-B) characterized by a dimerous organization (Fig. 6.B-C). The basal layer of cells consists of irregularly squared to palisade-like large cells (mean size: D 19.9 µm; L 16.6 µm) (Fig. 6.C; Table S1).

The other vegetative characters do not differ from the first group (Table S1).

Sporangial plants have flask-shaped conceptacles with conceptacle roof formed from cell filaments lining the outer border of the chamber and protruding into the pore canal (type 1 *sensu* Johansen, 1981) (Fig. 6.D-F). The conceptacles are slightly protruding above the surrounding thallus surface (Fig. 6.E-F). The chamber is smaller than in group ɑ, with a mean size of 280 µm (D) x 120 µm (H) (Table S1). The central part of the floor of the conceptacle chamber is generally slightly raised forming a faint calcified columella (Fig. 6.E). Pore canals, on average, are 75 µm in length and 80 µm wide at the base (Fig. 6.E-F; Table S1). On average the roof is 55 µm thick and is composed of cells slightly smaller than the average perithallial cells (generally less than 8 cells) (Fig. 6.F). Specimens 24 and 25 (Tertiary Piedmont Basin, locality A) show very small and narrow conceptacles (mean size: D 120 µm; H 25 µm; average H/D = 0.2) (Fig. 6.H; Table S1). On the basis of their conceptacles shape and biometry, their vegetative anatomy, and their close association with specimens 18, 19 and 20 (Tertiary Piedmont Basin, locality A), they were considered male gametangial plants (Fig. 6.G-H).
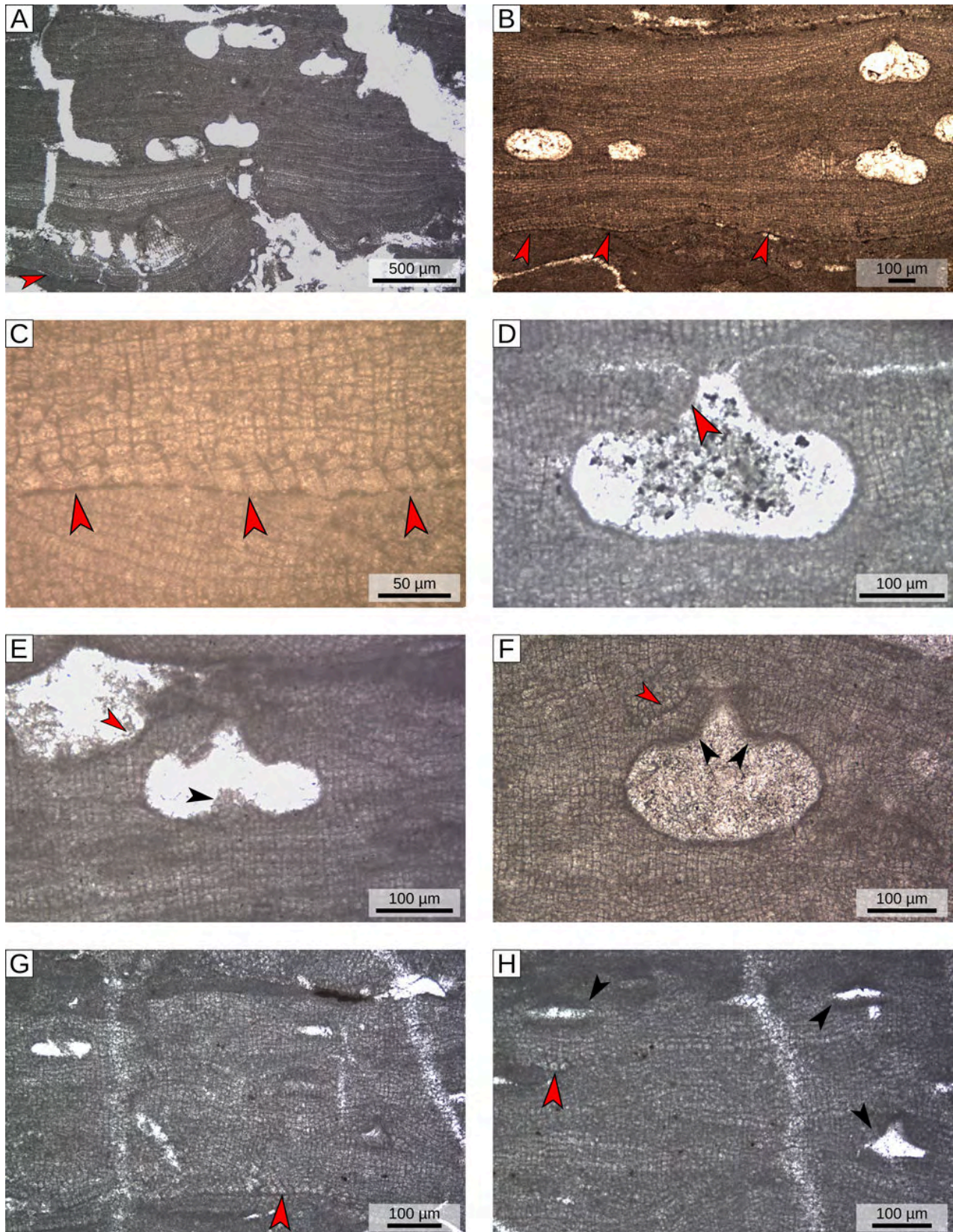
Figure 6: Vegetative and reproductive anatomy of group β (*C. pentagonum*). **A)** Encrusting growth-form characterized by dimerous organization (red arrowhead); specimen 18, locality A. **B)** Encrusting growth-form characterized by dimerous organization (red arrowheads); specimen 17, locality B. **C)** Magnified view of the basal layer of cells (red arrowheads), showing the dimerous hypothallus; specimen 17, locality B. **D)** Flask-shaped uniporate asexual conceptacles with conceptacle roof formed from cell filaments protruding into the pore canal (red arrowhead); specimen 18, locality A. **E)** Uniporate asexual conceptacle revealing a calcified columella (black arrowhead); red arrowhead=
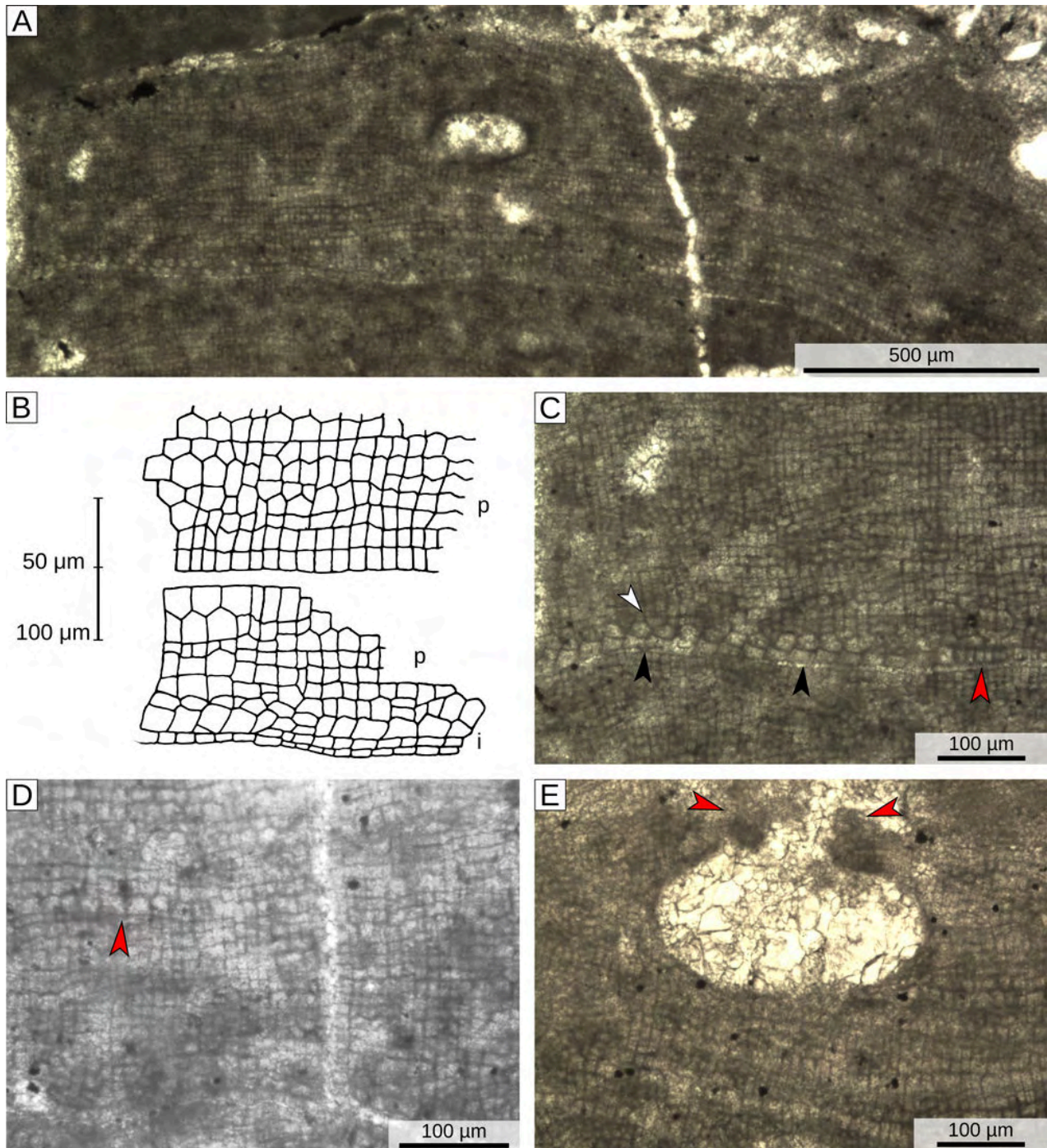
Figure 7: Holotype of *Chamberlainium pentagonum* (Conti, 1943), early Burdigalian, specimen 1, locality A. A) Vertical section of the thallus. B) Reproduction of Conti original sketches of vegetative anatomy, taken from Conti (1943); p= perithallus; i= hypothallus. C) Dimerous construction with the basal layer composed of irregularly squared (black arrowheads) to palisade-like cells (red arrowhead); white arrowhead= dichotomous division of the first cells that arise from the basal layer, producing two rows of erect filaments. D) Erect filaments with large and irregular cells (red arrowhead) created by the complete resorption of the wall separating the cells. E) Small ellipsoidal conceptacle with a thin roof (red arrowheads).

bending of the thallus surface indicating that the conceptacle was originally raised compared to the surrounding thallus surface; specimen 5, locality C. **F)** Uniporate asexual conceptacle with a thin roof composed of less than 8 cells (red arrowhead); black arrowheads= cell filaments protruding into the pore canal; specimen 6, locality G. **G)** Vertical section of vegetative thallus showing male conceptacles; red arrowhead= basal layer of cells revealing a dimerous hypothallus; specimen 24, locality A. **H)** Uniporate male conceptacles (black arrowheads), red arrowhead= secondary growth of a basal layer of cells, revealing a dimerous secondary hypothallus; specimen 24 locality A.

Overall, the specimens of this group fit with the description of the recently established genus *Chamberlainium* (Merwe *et al.*, 2015; Caragnano *et al.*, 2018). Since the holotype of *Lithothamnion pentagonum* (Conti, 1943), which has been re-examined and included in this analysis (specimen 1; Tertiary Piedmont Basin, locality B) (Figs. 1 - 2, 8), belong to this group, we propose for this species a new combination under the genus *Chamberlainium* and an emended description that includes all the examined specimens of group β.

Class Florideophyceae Cronquist, 1960

Subclass Corallinophycideae Le Gall & Saunders, 2007

Order Corallinales Silva & Johansen, 1986

Family Corallinaceae (Lamouroux, 1812) Harvey *et al.*, 2003

Subfamily Chamberlainoideae Caragnano *et al.*, 2018

Genus *Chamberlainium* Caragnano *et al.*, 2018

Type-species: *Chamberlainium tumidum* (Foslie, 1900) Caragnano *et al.*, 2018

Chamberlainium pentagonum (Conti, 1943) comb. nov.

Basionym: *Lithothamnium pentagonum* Conti, 1943, Tav. VI 3a-e; Tav. VIII 4.

Holotype description: The holotype of "*Lithothamnium pentagonum*" is the thin section labeled as 22 of the Conti Collection (1943-1946; Miocene, Ponzone - Alessandria, NW Italy; 2 km westward from Spigno Monferrato) stored at the DISTAV of the Genova University. It consists of a rhodolith composed of various and different coralline algal crusts, including the holotype of *L. pentagonum* (Fig. 7.A). In thin section 22 it is possible to recognize the portion of thallus illustrated in Conti's protologue (Fig. 7.B; Vannucci *et al.*, 2009). It should be noted that the cavity sketched in Conti's drawing (Tav. VI [II], fig. 3.e in Conti, 1943) is probably not a conceptacle. The holotype is an encrusting specimen 500 µm thick, which overgrows other coralline algae (Fig. 7.A). The thallus has a dimerous construction with the basal layer composed of irregularly squared to palisade-shaped large cells, 20 to 29 µm in diameter and 10.5 to 21 µm in length (mean size: D 25.5 µm; L 15.7 µm) (Fig. 7.C; Table S1). The first cells arising from the basal layer are often roughly pentagonal and divide dichotomously producing two rows of erect filaments that combined are more or less as wide as the cell from which they are derived (Fig. 7.C). The perithallus is composed of irregularly rectangular cells 8 to 18 µm long and with a diameter of 8 to 14 µm

(mean size: D 10.7 µm; L 13.4 µm) (Fig. 7.D; Table S1). Fusions between cells of contiguous filaments are abundant and frequently occupy most of the adjoining cell wall. The large and irregularly pentagonal cells described by Conti are produced by cell fusions (Fig. 7.D). Epithallial cells are small and dome-shaped. Trichocytes were not observed. The conceptacles are poorly preserved; they are uniporate and elliptical in shape, with internal chambers 230 to 300 µm in diameter and 125 to 160 µm in height (mean size: D 285 µm; H 140 µm) (Fig. 7.E; Table S1). The floor of the conceptacle chamber is raised centrally. The roof seems to be very thin and composed of cells smaller than those of the perithallus (Fig. 7.E).

Emended diagnosis: Encrusting growth form; dimerous construction; hypothallus composed of irregularly squared (in longitudinal radial section) to palisade-like cells in radial view (tangential section along the filaments); perithallus with common cell fusions; epithallial cells dome-shaped; sporangial conceptacles uniporate with the conceptacle chamber lined by cell filaments protruding into the pore canal; conceptacle chamber with an average diameter around 275 µm and always less than 300 µm; average roof thickness of less than 70 µm.

Discussion and conclusions

Based on the description of the modern Mediterranean population of *Spongites fruticulosus* provided by Basso and Rodondi (2006), the specimens of group α are conspecific with the Mediterranean *S. fruticulosus*. Their morphology also complies with the description of Lemoine's type material of *Spongites albanensis* (Aguirre *et al.*, 2012) (Fig. 2). Male gametangial plants similar to those of the Tertiary Piedmont Basin (specimen 23, locality B) are already known in the fossil record and are often identified as *Lithophyllum platticarpum* Maslov (1962) which has been recognized as a gametangial plant by Braga *et al.* (2005) and synonymized with *S. fruticulosus* by Chelaru and Bucur (2016). These results show that *S. fruticulosus* is indeed common in the Miocene carbonates of the western Mediterranean. Recent studies highlighted that the modern Mediterranean population of *S. fruticulosus* comprises at least two species, genetically different but morpho-anatomically very similar (Rösler *et al.*, 2016; Caragnano *et al.*, 2018). Among the specimens examined in this work and assigned to *S. fruticulous*, it is possible to recognize two different sub-groups, one characterized by smaller conceptacles (specimens 2, 3, 8, 11, 12, 14, 15, 16, 21) and one with larger conceptacles (specimens 4, 7, 9, 10, 22) (Figs. 2, 8). Although these two groups could actually represent two different species, the data available on both the modern population and the fossil record are not sufficient for a definitive conclusion to be drawn.
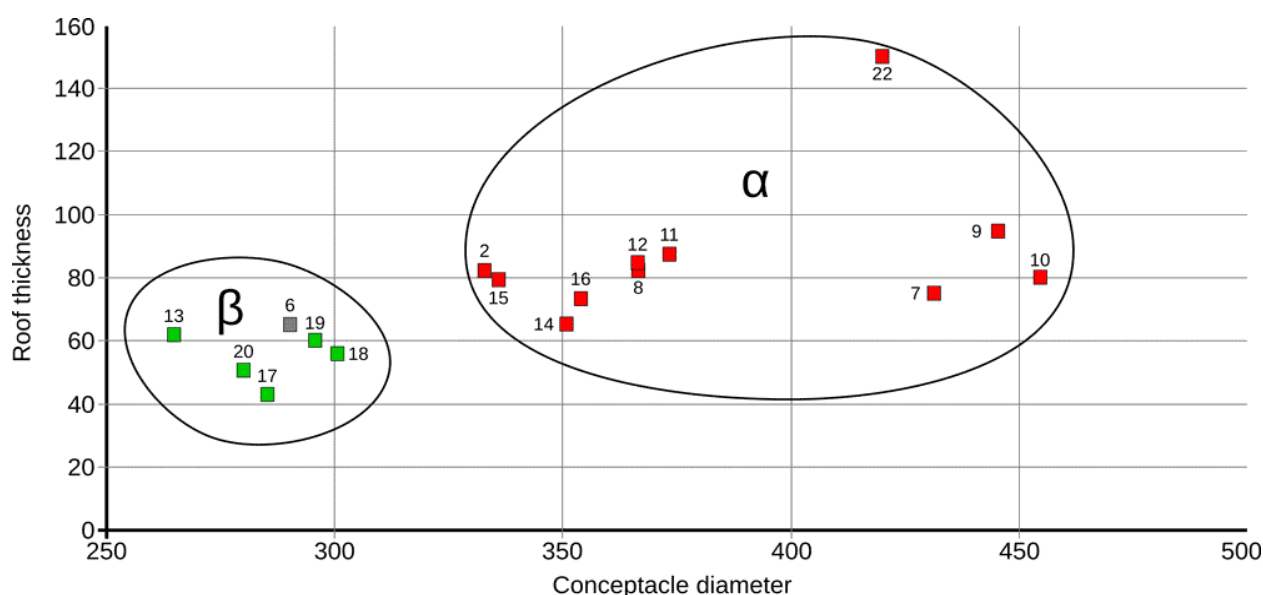
Figure 8: Scatter-plot including the values of conceptacle diameter (µm) and roof thickness (µm) for specimens of both groups (only the specimens with both measurements were included). Green squares indicate dimerous specimens; red squares indicate monomerous specimens; specimen 6 is indicated by a gray square since the hypothallial portion of the thallus was not observed.

The specimens of group β, are characterized by small conceptacles, thin roof and a dimerous construction and have been included in the genus *Chamberlainium* (Merwe *et al.*, 2015; Caragnano *et al.*, 2018). Although this genus belongs to the newly established Chamberlainoideae sub-family, it is very similar to *Spongites*, which belong to the Neogoniolithoideae sub-family (Caragnano *et al.*, 2018). Differently from *Spongites*, *Chamberlainium* is characterized by sporangial conceptacles with a diameter of less than 300 µm, a thin roof (less than 8 cells thick), and, in species with a dimerous organization, by a basal layer of palisade-like cells (in tangential sections) (Caragnano *et al.*, 2018). By using conceptacle diameter and roof thickness it is possible to clearly isolate *S. fruticulosus* (group α) from *C. pentagonum* (group β) (Fig. 8), indicating that the morphological characters recognized by Caragnano *et al.* (2018) in modern algae work very well also with fossil ones. Presently, *Chamberlainium* is reported to occur along the coasts of the Indo-Pacific Ocean (South Africa, Taiwan and California, while it is absent from the Mediterranean (Caragnano *et al.*, 2018). However, the presence of an Indo-Pacific species in the Mediterranean during the Miocene is not surprising since the two oceans were strongly connected during the early Miocene and limited connections existed also during the middle Miocene (Cornacchia *et al.*, 2018, and references therein).

During the Miocene, both *S. fruticulosus* and *C. pentagonum*, where widespread in the western Mediterranean region, occurring both in the northern and southern part of the investigated area (Fig. 1; Table 1). Furthermore, in several localities the two species occured together, indicating for both taxa a broad ecological tolerance. Based on the associated skeletal assemblage, both species apparently thrived in warm-temperate to tropical conditions, but further researches are necessary to fully resolve their ecological preferences during the Miocene. At now the genus *Chamberlainium* seems to be confined to geographical regions characterized by strong seasonal variability of sea surface temperatures, while *Spongites* occurs in both warm-temperate (Mediterranean Sea) and tropical conditions (Maldives, Indian Ocean) (Caragnano *et al.*, 2018). Therefore, similarly to their fossil counterparts, the living *Chamberlainium* and *Spongites* have a broad ecological tolerance and a preference toward warm water.

In accordance with the advancements in the study of living algae (Hernandez-Kantun *et al.*, 2015; De Jode *et al.*, 2019; Pezzolesi *et al.*, 2019; Rindi *et al.*, 2019), the results of this study indicate that Miocene coralline biodiversity in the western Mediterranean area was larger than expected, and that the best way to investigate this biodiversity is by using large data-sets of specimens and comparison with properly described type materials.

Acknowledgments

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Table S1: Morphometric data of the studied specimens; the identification numbers of the specimens are the same used in the main text.

Specimen			Cell diameter basal layer (dimerous construction)	Cell length basal layer (dimerous construction)	Hypothallial cell diameter (monomerous construction)	Hypothallial cell lenght (monomreous construction)	Perithallial cell diameter	Perithallial cell length	Conceptacle diameter	Conceptacle height	H/D	Columella	Pore canal diameter	Pore canal length	Roof thickness
1	*Lithothamnion pentagonum*	Mean	25.58	15.74			10.71	13.43	286.67	139.33	0.49	v	80.00		
		SD	2.36	3.22			1.23	2.45	25.17	18.34	0.03				
		Max	29.00	21.00			14.00	18.50	300.00	160.00	0.52				
		Min	20.28	10.50			8.17	8.67	230.00	125.00	0.46				
		n	33	33			90	90	3	3	3		1		
2	Capo San Marco	Mean			15.37	21.94	10.60	13.49	332.73	130.27	0.39	v	104.67	103.33	82.60
		SD			2.43	4.15	0.82	2.63	25.97	8.66	0.02		18.54	25.17	4.22
		Max			19.50	26.67	11.98	19.23	376.00	146.00	0.42		122.00	130.00	90.00
		Min			11.73	11.17	8.67	10.00	295.00	115.00	0.37		80.00	80.00	80.00
		n			42	42	70	70	11	11	11		6	3	4
3	Latium-abruzzi (CML 9)	Mean			10.76	16.31	9.82	12.52	387.00	137.67	0.36	v	95.00	100.00	
		SD			2.19	2.24	0.82	2.17	48.80	12.50	0.03				
		Max			13.75	19.05	11.20	17.25	450.00	153.00	0.41		95.00	100.00	
		Min			8.40	13.75	8.38	8.50	322.00	120.00	0.34		95.00	100.00	
		n			18	18	57	57	6	6	6		1	1	
4	Latium-abruzzi (CML 10)	Mean			10.19	18.04	9.57	12.39	420.00	125.50	0.30	v	100.00		
		SD			0.82	1.93	0.82	1.46	7.07	14.85	0.03				
		Max			11.67	20.40	10.65	14.17	425.00	136.00	0.32		100.00		
		Min			9.00	14.67	8.40	9.87	415.00	115.00	0.28		100.00		
		n			20	20	20	20	2	2	2		1		
5	Latium-abruzzi (MLS13)	Mean	v	v			9.28	11.19	224.75	86.50	0.39	v	68.50	50.00	
		SD					0.97	1.55	13.57	6.24	0.03				
		Max					11.18	14.00	235.00	95.00	0.42		72.00	45.00	
		Min					7.75	8.67	205.00	80.00	0.34		65.00	55.00	
		n					42	42	4	4	4		2	2	
6	Menorca (37)	Mean					10.17	12.95	290.00	144.00	0.48		72.40	82.50	65.00
		SD					1.04	1.56	19.72	11.01	0.02		14.79	12.58	9.13
		Max					12.53	16.40	310.00	160.00	0.51		90.00	100.00	75.00
		Min					8.12	10.50	260.00	129.00	0.45		50.00	70.00	55.00
		n					40	40	8	8	8		5	5	4
7	Menorca (40)	Mean			11.61	20.59	10.33	13.24	431.36	169.09	0.39	v	115.45	113.83	75.00
		SD			1.25	3.70	1.05	2.43	33.80	13.64	0.04		13.49	18.57	12.75
		Max			13.57	28.00	12.00	18.73	495.00	200.00	0.49		134.00	140.00	90.00
		Min			8.90	14.38	7.56	9.00	375.00	141.00	0.34		90.00	91.00	55.00
		n			60	60	60	60	22	22	22		11	11	5
8	Menorca (101)	Mean			v	v	12.97	14.44	366.63	143.63	0.39	v	110.83	118.83	82.46
		SD					2.17	1.76	21.78	7.87	0.03		23.54	22.41	17.96
		Max					17.73	16.80	410.00	160.00	0.47		135.00	140.00	110.00
		Min					9.73	11.73	343.00	135.00	0.36		75.00	80.00	60.00
		n					60	60	8	8	8		6	6	6
9	Lopadea Veche (1844-114451)	Mean			14.08	18.92	10.70	14.08	445.25	170.92	0.39	v	105.00	141.50	95.00
		SD			3.08	3.33	1.26	3.08	41.63	17.50	0.06		17.59	18.90	12.70
		Max			23.00	26.67	13.33	23.00	515.00	200.00	0.49		132.00	168.00	120.00
		Min			10.00	13.60	8.00	10.00	380.00	138.00	0.31		76.00	111.00	85.00
		n			36	36	90	90	12	12	12		10	10	10
10	Lopadea Veche (1844-114451 bis)	Mean			11.26	18.08	9.28	13.20	454.67	162.11	0.36	v	96.71	115.86	80.13
		SD			1.07	3.05	1.41	1.58	45.32	16.41	0.03		17.16	11.73	8.37
		Max			13.00	24.00	12.67	17.00	521.00	186.00	0.41		114.00	132.00	90.00
		Min			8.86	14.33	6.80	10.75	390.00	136.00	0.32		66.00	102.00	65.00
		n			60	60	60	60	9	9	9		8	8	8
11	Lopadea Veche (1849-111354)	Mean			14.55	17.63	10.86	14.55	373.20	165.80	0.44		93.20	107.80	87.50
		SD			1.84	3.56	1.49	1.84	11.65	12.34	0.04		12.15	16.21	10.41
		Max			18.25	24.00	13.75	18.25	382.00	174.00	0.48		102.00	125.00	100.00
		Min			12.07	12.67	8.38	12.07	355.00	145.00	0.38		72.00	81.00	75.00
		n			30	30	51	51	5	5	5		5	5	5

Specimen			Cell diameter basal layer (dimerous construction)	Cell length basal layer (dimerous construction)	Hypothallial cell diameter (monomerous construction)	Hypothallial cell lenght (monomreous construction)	Perithallial cell diameter	Perithallial cell length	Conceptacle diameter	Conceptacle height	H/D	Columella	Pore canal diameter	Pore canal length	Roof thickness
12	Lopadea Veche (1849-111451)	Mean			13.12	21.74	11.15	14.05	366.33	148.75	0.41	v	87.20	105.22	84.25
		SD			0.94	4.81	1.43	2.27	26.55	16.21	0.04		15.19	13.38	18.90
		Max			15.00	31.00	13.50	19.00	410.00	170.00	0.46		113.00	125.00	126.00
		Min			12.00	13.50	8.29	10.00	320.00	120.00	0.35		70.00	85.00	70.00
		n			60.00	60.00	75.00	75.00	11.00	11.00	11.00		11.00	11.00	11.00
13	Podbřežice	Mean	16.80	15.40			12.01	14.79	264.67	103.67	0.39		95.00	83.50	62.00
		SD	1.64	2.30			1.90	2.51	10.79	6.35	0.04				
		Max	19.00	19.00			16.67	20.86	277.00	111.00	0.43		100.00	111.00	62.00
		Min	15.00	13.00			9.75	12.33	257.00	100.00	0.36		90.00	56.00	62.00
		n	5	5			36	36	3	3	3		2	2	1
14	Židlochovice (42130-1050)	Mean			10.50	16.00	10.24	12.70	350.50	126.75	0.36	v	103.25	75.00	64.50
		SD			1.80	4.58	0.92	1.19	47.59	18.30	0.02		22.77	14.14	6.81
		Max			12.50	21.00	11.95	14.40	410.00	145.00	0.38		135.00	95.00	70.00
		Min			9.00	12.00	8.50	10.38	303.00	111.00	0.34		84.00	65.00	56.00
		n			9	9	40	40	4	4	4		4	4	4
15	Židlochovice (42134-11551)	Mean			11.35	18.12	9.98	12.22	335.80	129.80	0.39		86.60	107.20	79.33
		SD			2.52	3.01	1.19	0.79	28.55	12.34	0.02		9.61	15.61	17.47
		Max			14.00	21.00	12.67	13.67	374.00	142.00	0.42		103.00	125.00	94.00
		Min			9.00	14.33	9.00	11.50	300.00	114.00	0.38		78.00	87.00	60.00
		n			12	12	30	30	5	5	5		5	5	5
16	Tertiary Piedmont Basin (Torre Veglio)	Mean			13.13	22.65	10.81	13.20	353.85	123.56	0.35	v	85.00	86.80	73.17
		SD			2.94	6.80	1.16	2.44	33.92	15.86	0.05		11.70	25.89	6.52
		Max			24.00	47.00	13.77	19.00	433.00	160.00	0.46		100.00	138.00	80.00
		Min			8.40	10.75	8.75	8.50	308.00	94.00	0.27		66.00	56.00	65.00
		n			120	120	120	120	27	27	27		18	18	10
17	Tertiary Piedmont Basin (Treville)	Mean	16.50	17.00			10.00	12.70	285.13	134.63	0.47	v	80.75	52.00	43.00
		SD	4.20	2.80			1.20	2.70	14.38	6.21	0.03		7.63	8.00	6.98
		Max	21.00	19.00			13.00	24.00	307.00	147.00	0.51		88.00	60.00	52.00
		Min	10.00	15.00			8.00	9.00	260.00	127.00	0.43		70.00	44.00	35.00
		n	20	20			57	57	8	8	8		8	8	8
18	Tertiary Piedmont Basin (Spigno PVR2B)	Mean	21.02	19.48			10.24	13.03	300.29	119.43	0.39	v	84.33	62.17	56.00
		SD	3.27	1.24			1.15	2.09	29.89	18.50	0.04		13.62	11.30	12.07
		Max	26.50	21.00			12.80	18.00	350.00	142.00	0.47		107.00	80.00	73.00
		Min	16.30	17.50			8.08	10.97	270.00	91.00	0.34		66.00	50.00	42.00
		n	15	15			63	63	7	7	7		7	7	7
19	Tertiary Piedmont Basin (Spigno rcm3')	Mean	19.50	15.36			10.03	11.84	295.67	129.00	0.44	v			60.00
		SD	3.89	3.02			1.19	1.85	19.42	8.63	0.04				
		Max	25.00	19.00			13.00	14.53	320.00	140.00	0.50				60.00
		Min	13.50	11.50			8.45	7.50	270.00	120.00	0.39				60.00
		n	21	21			60	60	6	6	6				2
20	Tertiary Piedmont Basin (Spigno Monferrato Rc 9 0 s0)	Mean	v	v			11.74	9.35	280.00	102.50	0.36		71.50	120.00	51.00
		SD					1.73	1.10	29.62	14.64	0.05				5.70
		Max					15.50	11.68	310.00	118.00	0.41		78.00	120.00	55.00
		Min					8.20	7.40	250.00	90.00	0.30		65.00	120.00	45.00
		n					69	69	4	4	4		2	1	3
21	Sommières Basin (P6IV)	Mean			v	v	13.00	9.20	320.00	135.00	0.42	v	85.00	85.00	
		SD					1.80	1.80	15.00	10.00	0.02		15.00	5.00	
		Max					16.00	12.00	360.00	140.00	0.45		100.00	80.00	
		Min					9.00	6.00	300.00	110.00	0.38		65.00	90.00	
		n					43	43	7	7	7		4	4	
22	Sommières Basin (P6IV)	Mean			v	v	13.00	9.50	420.00	175.00	0.42	v	100.00	150.00	150.00
		SD					2.00	1.50	60.00	15.00	0.06				
		Max					17.00	11.00	500.00	190.00	0.50		100.00	150.00	150.00
		Min					10.00	7.00	365.00	160.00	0.37		100.00	150.00	150.00
		n					35	35	4	4	4		1	1	1
23 ♂	Tertiary Piedmont Basin (Torre Veglio)	Mean	21.07	16.79	12.10	18.06	11.36	10.36	143.86	24.73	0.17		46.15	38.82	
		SD	4.73	3.82	3.59	5.49	1.98	1.06	21.41	5.01	0.03		15.35	11.90	
		Max	25.63	21.97	22.70	32.00	18.20	13.00	195.00	38.00	0.24		77.00	66.00	
		Min	2.60	2.24	3.13	4.88	7.25	8.04	105.00	17.00	0.10		24.00	21.00	
		n	61	61	66	66	150	150	37	37	37		20	20	

Specimen			Cell diameter basal layer (dimerous construction)	Cell length basal layer (dimerous construction)	Hypothallial cell diameter (monomerous construction)	Hypothallial cell lenght (monomreous construction)	Perithallial cell diameter	Perithallial cell length	Conceptacle diameter	Conceptacle height	H/D	Columella	Pore canal diameter	Pore canal length	Roof thickness
24 ♂	Tertiary Piedmont Basin (Spigno Rc 9 0)	Mean	16.20	13.33			11.32	8.82	111.33	24.22	0.22		36.75	37.75	
		SD	1.54	2.59			1.96	1.04	10.91	5.38	0.05		11.79	4.86	
		Max	17.50	15.17			16.83	10.77	123.00	31.00	0.28		45.00	45.00	
		Min	14.50	11.50			8.67	6.30	94.00	17.00	0.14		20.00	35.00	
		n	10	10			58	58	9	9	9		5	5	
25 ♂	Tertiary Piedmont Basin (Spigno Rc 9 0)	Mean	v	v			11.94	10.13	130.00	22.00	0.17				
		SD					1.14	1.05							
		Max					14.07	12.08	140.00	24.00	0.20				
		Min					10.00	8.32	120.00	20.00	0.14				
		n					45	45	2	2	2				