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NEW OBSERVATIONS ON THE ANATOMY OF THE FOSSIL CALCAREOUS ALGA *SUBTERRANIPHYLLUM* ELLIOTT

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Riassunto. Una nuova collezione di esemplari di *Subterraniphyllum thomasii* Elliott raccolta presso Alessandria, in affioramenti della Formazione di Molare (Oligocene) e studiata in sezione sottile al microscopio ottico e al SEM ha mostrato per la prima volta l'esistenza di sinapsi primarie e fusioni cellulari, concettacoli unipori e intergenicoli calcarei articolati da presunte genicolazioni. Nell'insieme, questi caratteri confermano l'attribuzione di *S. thomasii* alle Corallinaceae genicolate. *Subterraniphyllum thomasii* presenta alcuni caratteri di affinità con le Corallinoideae, in particolare con la tribù Corallineae (posizione apicale dei concettacoli unipori, numero di strati cellulari nella medulla) e qualche similarità con le Metagoniolithoideae (graduale transizione tra medulla e cortex). Tuttavia, la mancanza di informazione sulla struttura genicolare - carattere diagnostico fondamentale nella sistematica delle corallinacee articolate - e i dettagli osservati nelle strutture di inserzione dei rami non permettono un più preciso inquadramento tassonomico di *S. thomasii*.

Abstract. New specimens of *Subterraniphyllum thomasii* Elliott collected from the Oligocene Molare Formation outcropping close to Alessandria (northern Italy) and studied in thin sections and by SEM showed that primary pit-connections, cell fusions, uniporate conceptacles and geniculate branches were present. These new observations collectively confirm the placement of *S. thomasii* within the geniculate Corallinaceae. Although *S. thomasii* share many diagnostic characters with the Corallinoideae, in particular with the tribe Corallineae (apical position of uniporate conceptacles, number of medullary cell layers) and some similarity with the Metagoniolithoideae (medullary cells gradually merging into the cortical cells) the lack of information on genicula and the observed details of insertion of branches do not allow to determine the suprageneric disposition of *S. thomasii*.

Introduction.

Subterraniphyllum thomasii Elliott 1957, the type species of *Subterraniphyllum*, was originally described with the original spelling *Subterraniphyllum thomasi*. On the base of ICBN articles 60C.1 and 60.11 (Greuter & al., 1994) this mispelling must be treated as an error to be corrected.

Elliott (1957) included the new monotypic genus in the family Corallinaceae, subfamily Corallinaea (at that time the only recognised subfamily of geniculate coralline algae) for the occurrence of segments, which he interpreted as intergenicula. Most authors accepted his view, with the exception of Lemoine (1977), who suggested an affinity of this genus with the Rhodymeniales (on the basis of the cortex features), while Tappan (1980) transferred *Subterraniphyllum* to the non-geniculate coralline subfamily Lithophylloideae without any explicit justification.

Some intergenicula showing incipient bifurcation were originally described (Elliott, 1957) in *S. thomasii.* The development of the bifurcation and the new intergenicula were not clarified. Moreover, no reproductive structures were observed. Mastrorilli (1968a, pl.102, figs 1-2) later reported an irregular cavity with a coarsely subtriangular profile, located on a small protuberance of the cortex characterised by very compact cells, and she interpreted it as a reproductive structure. However, the original thin section (Mastrorilli collection BTP Ponzone, section PO-V-2/293) containing the figured specimen showed that the reproductive structure belongs to a non geniculate epiphytic coralline alga. The aim of this note is the documentation of some newly observed anatomical features (vegetative and reproductive) that will hopefully allow a better definition of the genus *Subterraniphyllum*.

Material and methods.

Twenty-eight thin sections containing about 120 complete or fragmented intergenicula and basal segments have been obtained from samples collected in the Oligocene Molare Formation (Tertiary Piedmont Basin) outcropping at Costa d'Ovada (Alessandria, northern

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Italy). Samples belong to small coral reefs rich in calcareous algae. Some fragments have been prepared for SEM observations following the method described in Braga & al. (1993). In some instances, the negative SEM photo was used to give a better description of the algal microstructure.

Systematic palaeontology

Division **Rhodophyta** Wettstein 1901
Class Rhodophyceae Rabenhorst 1863
Order Corallinales Silva & Johansen 1986
Family *Corallinaceae* Lamouroux 1812

Genus *Subterraniphyllum* Elliott 1957, pag. 73

Type species: *Subterraniphyllum thomasii* Elliott 1957, pag. 73-75, pl. 13, figs. 1-9.

Synonyms.
Dendrophyllum cf. *gurgurdanensis* Thomas MS, Van Bellen 1956, pl. 2, figs. b, c (no description).
Subterraniphyllum ? sp. indet. A. Beckmann & Beckmann 1966, pag. 30, pl. 8, fig. 112.

Morphology.

Plant erect and branching, made of calcified, subcylindical segments (=intergenicula). Individual segments are up to 4 mm long and 0,6 to 1,1 mm in diameter (Pl. 1, Fig. 1, 5). The diameter of the intergenicula sometimes decreases in their median portion (Pl. 1, Fig. 2). The basal segment is club-shaped and shows a foot-like holdfast structure at its base (Pl. 1, Fig. 1). Some intergenicula show a possible bifurcation at their apices (Pl. 1, Fig. 3, 4). Other intergenicula show a lateral branching (Pl. 1, Fig. 1, 5); i.e., a "parent intergeniculum" connected with a "derivative intergeniculum". Joints between intergenicula show that the derivative intergeniculum is tapered at the insertion on the parent intergeniculum.

Vegetative anatomy.

The basal segment is corticated by small cells (L 10-20 x D 8-18 μm) that grow parallel to the substrate at the base, and then bend perpendicularly to the substrate, along the main axis of the segment (Pl. 1, Fig. 1).

The thallus organization is pseudoparenchymatous, composed of cells with calcified walls. In longitudinal thin sections the medullary cells are large, clear, subrectangular to polygonal (L 40-100 x D 20-75 μm). They are organised in apparent horizontal layers. Up to 28 cell layers (=tiers of medullary cells) have been counted in individual sterile segments. This feature points to a synchronous division and elongation of adjacent cells belonging to different longitudinal filaments (=coaxial growth). Adjacent cells are frequently fused together. Medullary cells are shorter toward the surface of intergenicula (Pl. 2, Fig. 1, 2). In oblique/transversal thin sections, cells are always irregularly polygonal and bevelled.

Small cavities (about 160 x 120-130 μm) in the medulla lined with thin, elongated cells protruding into the cavity (in longitudinal, subcortical section; Pl. 2, Fig. 3) are probably related with the insertion of derivative branches by means of a probable geniculum. The elongated thin cells lining these branch-insertion cavities appear squarish to very irregular in transversal section (Pl. 2, Fig. 4).

The transition from medulla to cortex is localized at a layer of polygonal cells (in thin section) which distally gives origin to a couple of cell filaments composed of small, squarish to subrectangular cells (squarish cells have 8-12 μm sides, subrectangular cells are L 10-25 x D 15-20 μm) (Pl. 3, Fig. 1-3). These small cells are also connected by cell fusions (Pl. 2, Fig. 1, Pl. 3, Figs. 4, 5) and collectively constitute the cortex.

A layer of cells showing variable length occurs within the cortex. Its cells are normally longer than the subtending cells. This is possibly a meristematic layer, which produces distally an epithallial layer of flat cells (L 8 x D12-15 μm). The epithallial layer is apparently missing at the apex of branches. In the meristematic layer frequent ovate heterocysts (trichocyte-like structures) can be observed (H 25-32 x D 18-20 μm) (Pl. 3, Figs. 4-6; Pl. 4, Fig. 1).

Overgrowths made of small cortex-type cells have been occasionally observed (Pl. 4, Fig. 1, 2). Possible primary pit-connections have been detected more frequently at the transition between medulla and cortex (Pl. 3, Figs. 1, 5, 6).

Reproductive structures.

Axial, pear-shaped uniporate cavities (D 280-380 x H 620-700 μm) have been observed in some intergenicula (Pl. 4, Fig. 3, 4). Both in longitudinal and transversal sections they appear lined with flattened cells (L 30-80 x D 8-15 μm) and are likely to represent the reproductive structures of *Subterraniphyllum* (Pl. 1, Fig. 3; Pl. 4, Fig. 3-6). They differ from the branch-insertion cavities by their apical position, their larger size, their shape and orientation of the lining cells (in L.S.) and their apical, ostiole-like opening (D about 40 μm).

Stratigraphy, palaeobiogeography and palaeoecology.

The genus *Subterraniphyllum* has a short stratigraphic range, occurring from Late Eocene to Early Miocene (Aquitanian) and more frequently in the Oligocene.

In the Late Eocene it occurs in Italy (Sicily, Elliott, 1957), in Greece (Karpathos, Auboin & al., 1976; Crete, Bonneau, 1970), in Macedonia (Lemoine, 1977), in Madagascar (Karche, 1972 *fide* Lemoine, 1977).

In the Oligocene it is reported from France (Aquitanie, Poignant, 1972 *fide* Poignant & Lorenz, 1985); Italy (Sicily, Blondeau & al., 1972; northern Italy, Tertiary Piedmont Basin, Ponzone area, Mastrorilli 1968a, 1968b and around Ovada, this paper); Greece (Crete, Bonneau, 1970; northern Peloponnesus, Dercourt, 1964 *fide* Poignant & Lorenz, 1985; Xanthe, Johnson, 1965; Mircou-Peripopoulou, 1974 *fide* Poignant & Lorenz, 1985), Macedonia (Lemoine, 1977), Slovenia (Bassi & Nebelsick, 1997, 2000), Iran (Elliott, 1957; Gollesstaneh, 1979; Sartorio & Venturi, 1988), Iraq (Van Bellen, 1956; Elliott 1957, 1960), Oman (Elliott, 1957, 1960), Madagascar (Karche, 1972 *fide* Lemoine, 1977), Borneo (Johnson, 1966) and Cuba (Beckmann & Beckmann, 1966).

In the Aquitanian it occurs in Italy (Sicily, Elliott, 1957), Iran (Elliott, 1957) and Madagascar (Karche, 1972 *fide* Lemoine, 1977).

Considering also the unpublished references included in Lemoine (1977) and Poignant & Lorenz

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PLATE 1

Subterraniphyllum thomasii Elliott. Transmitted llight optical microscope (OM) photographs.

Fig. 1 - Basal segment (parent) and articulation with the lateral (derivative) intergeniculum. Note small cells of cortication (white arrow). Thin section C.O.I.-S-3. Scale bar = 250 µm.
Fig. 2 - Longitudinal section (LS) of an intergeniculum showing decreasing diameter in its median portion. Thin section C.O.I.-F-4-1. Scale bar = 250 µm.
Fig. 3 - Intergeniculum with presumed bifurcation at its apex and oblique section of an uniporate conceptacle. Thin section C.O.I.-F-4-1. Scale bar = 300 µm.
Fig. 4 - Intergeniculum showing presumed apical bifurcation. Thin section C.O.I.-F-0-B-2. Scale bar = 250 µm.
Fig. 5 - Lateral branching with derivative intergeniculum tapered at the insertion on the parent intergeniculum. Thin section C.O.I.-F-0-B-1. Scale bar = 150 µm.

PLATE 2

Subterraniphyllum thomasii Elliott, OM photographs, except Fig. 1.

Fig. 1 - Medulla to cortex transition in an apical portion of an intergeniculum. Arrows indicate lateral fusions in the medulla and cortex. SEM photograph, stub B12-4/13697. Scale bar = 100 µm.
Fig. 2 - Medulla-cortex transition. Arrow indicates a lateral fusion in the medulla. Thin section C.O.I.-F-5. Scale bar = 150 µm.
Fig. 3 - Longitudinal subcortical section showing small cavities interpreted as trace of the insertion of lateral (derivative) branches. Note lining cells protruding into the cavities (arrow). Thin section C.O.I.-F-4-2. Scale bar = 150 µm.
Fig. 4 - Transversal section (TS) with a small cavity possibly related to the insertion of a derivative intergeniculum. Thin section C.O.I.-F-0-T-2. Scale bar = 150 µm.

PLATE 3

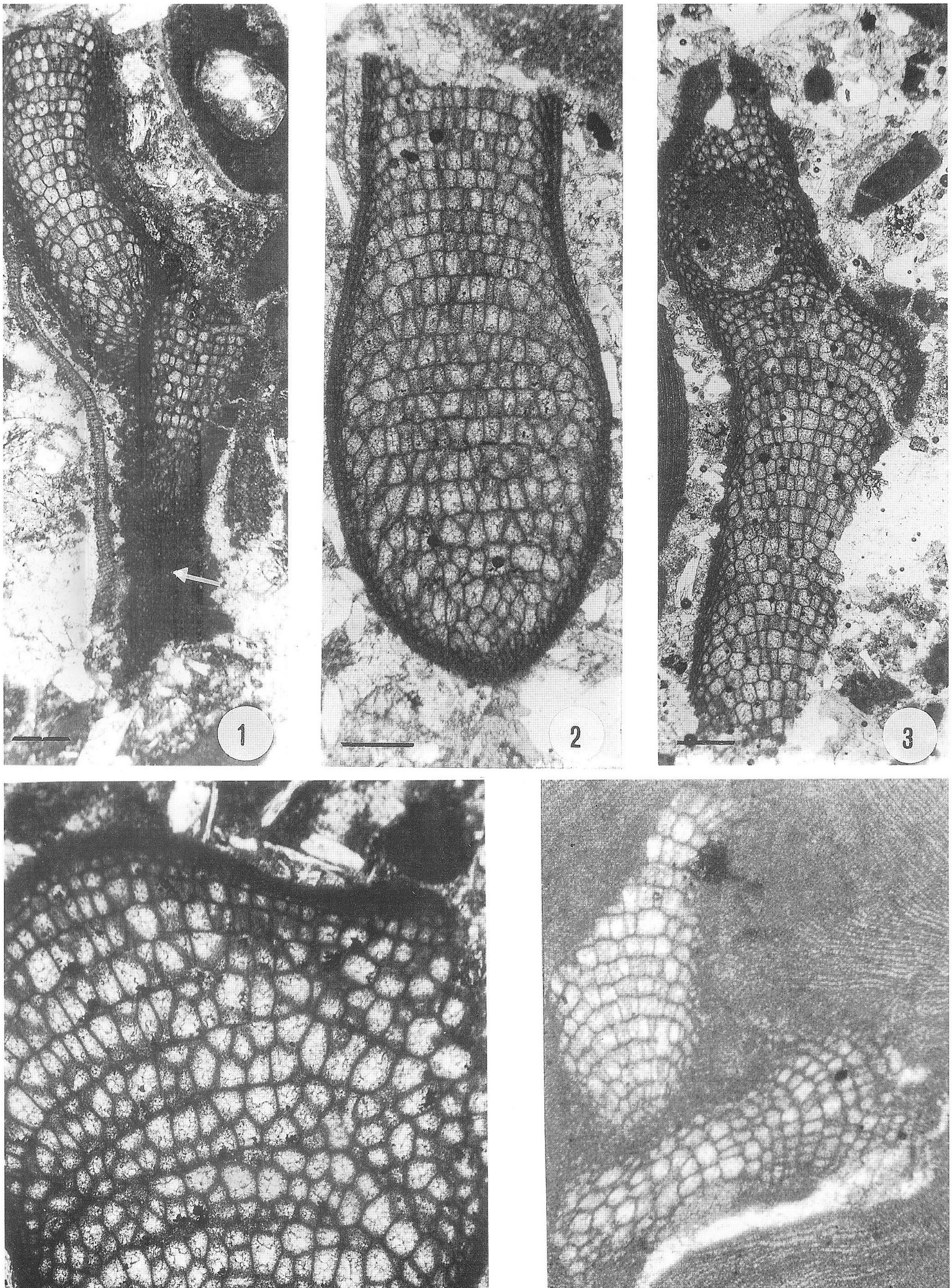
Subterraniphyllum thomasii Elliott, SEM photographs.

Fig. 1 - Transition from medulla to cortex: a layer of polygonal cells (P) which originate distally a couple of cell filaments (F). Arrows indicate primary pit connections. Negative photograph, stub B12-6/16797. Scale bar = 100 µm.
Fig. 2 - Same as in Fig. 1. Stub B11-11/16797. Scale bar = 100 µm.
Fig. 3 - Same as in Fig. 1, note medullary cells fusion (FM). Stub B12-10/16797. Scale bar = 100 µm.
Fig. 4 - Medulla-cortex transition. Note cell fusions in the cortex (arrow). Stub B12-5/13697. Scale bar = 100 µm.
Fig. 5 - Cortex lateral fusions (arrow). Arrowheads indicate primary pit-connections. Stub B9-5/16797. Scale bar = 100 µm.
Fig. 6 - Same as in Fig. 5. Note epithallial flat cells (black arrow) and presumed meristematic layer with ovate trichocytes (white arrow). Negative photograph, stub B9-4/16797.

PLATE 4

Subterraniphyllum thomasii Elliott, OM photographs except in Fig. 6.

Fig. 1 - Cortex with ovate trichocytes (arrow) within the presumed meristematic layer and overgrowth made of small cortex-type cells. Thin section C.O.I.-7. Scale bar = 25 µm.
Fig. 2 - Cortex with overgrowth made of small cells. Thin section C.O.I.-F-4-1. Scale bar = 150 µm.
Fig. 3 - An uniporate conceptacle; its pyriform cavity is lined with flattened cells. Thin section C.O.I.-7. Scale bar = 250 µm.
Fig. 4 - Detail of the conceptacle. Note flat lining cells (arrow). Same as in Fig. 3. Scale bar = 100 µm.
Fig. 5 - TS of a presumed conceptacle, lined with flattened cells (arrow). Thin section C.O.I.-F-3. Scale bar = 100 µm.
Fig. 6 - Same as in Fig. 5. SEM photograph, stub B17-5/4997. Scale bar = 100 µm.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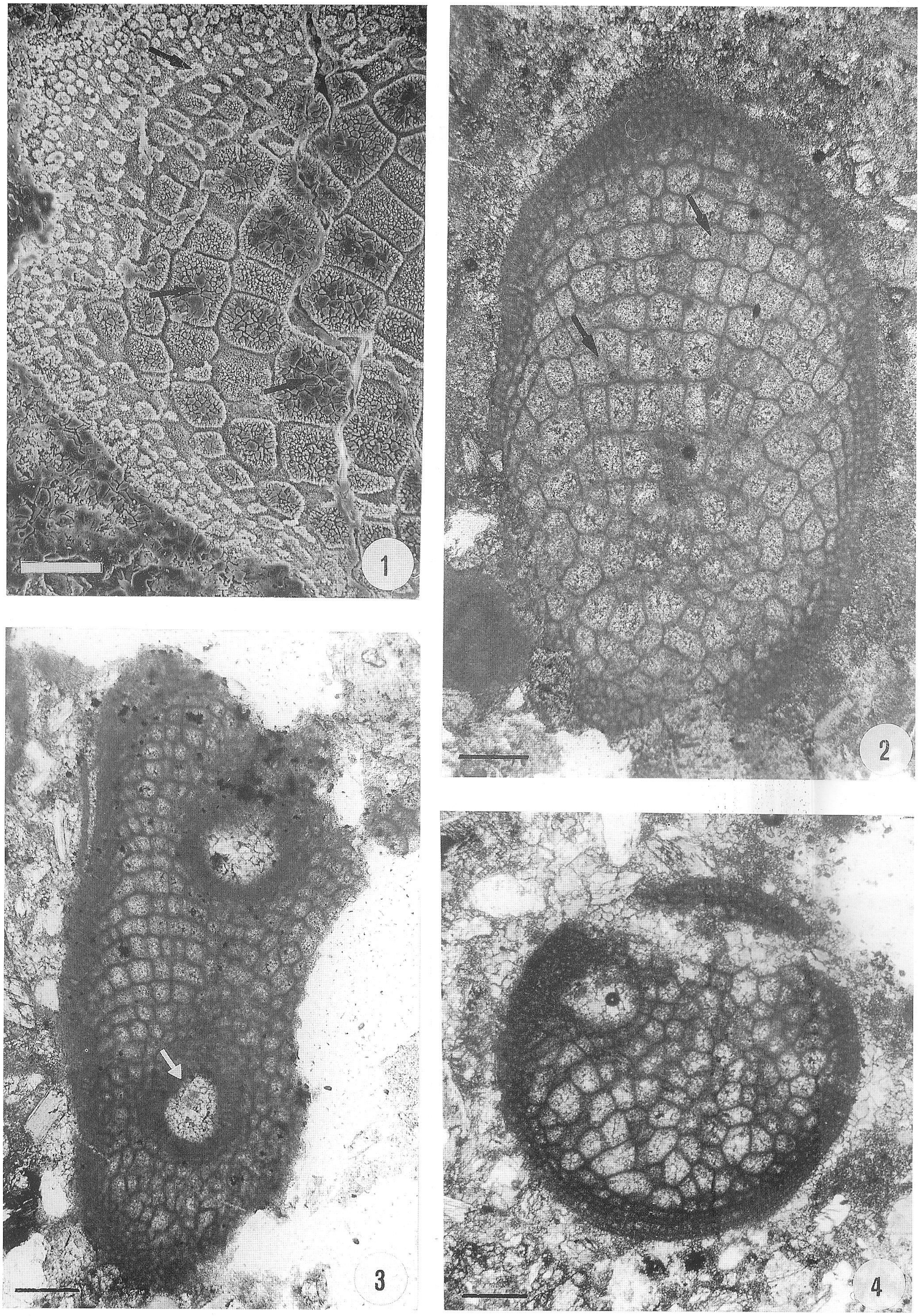
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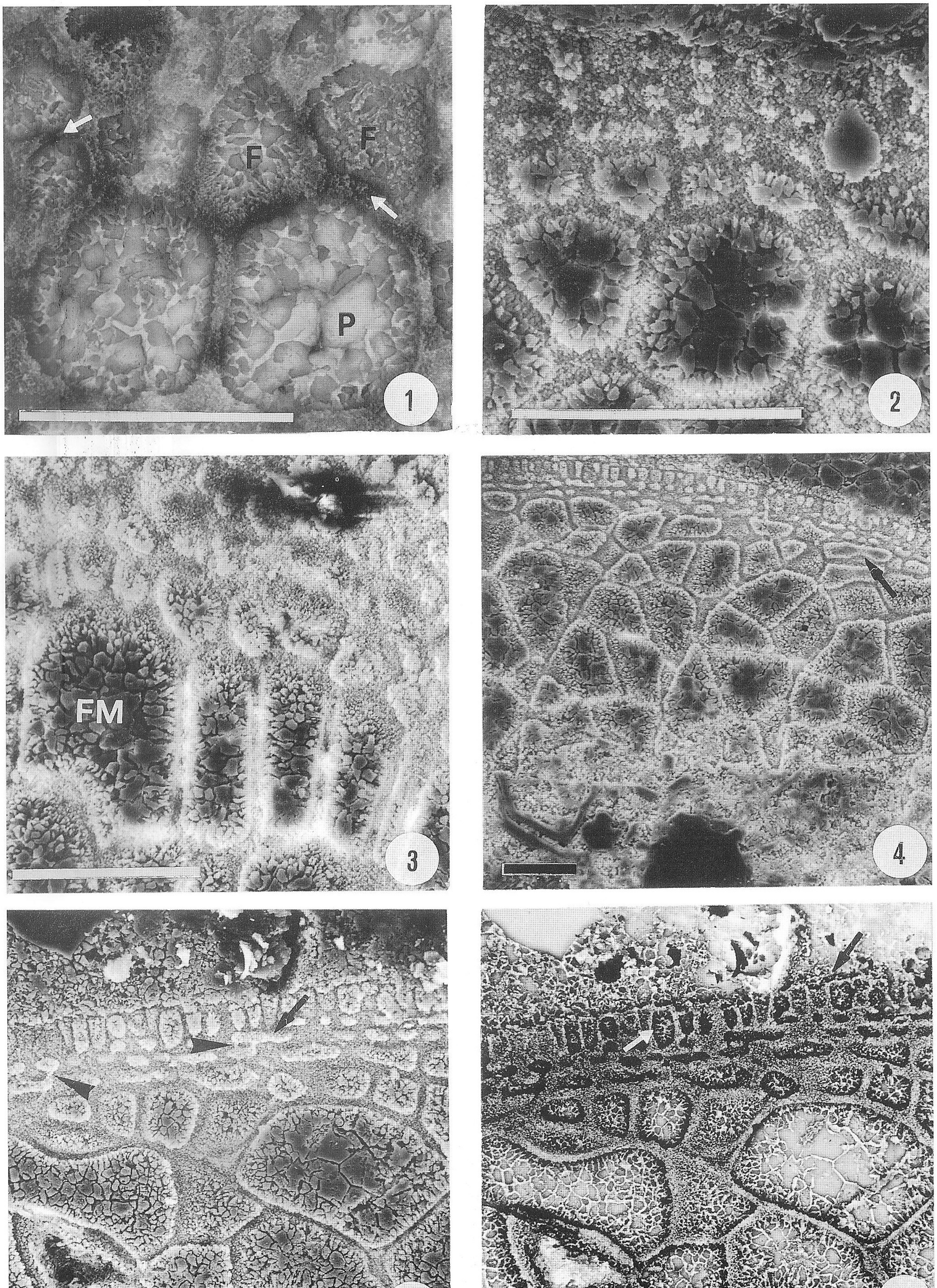
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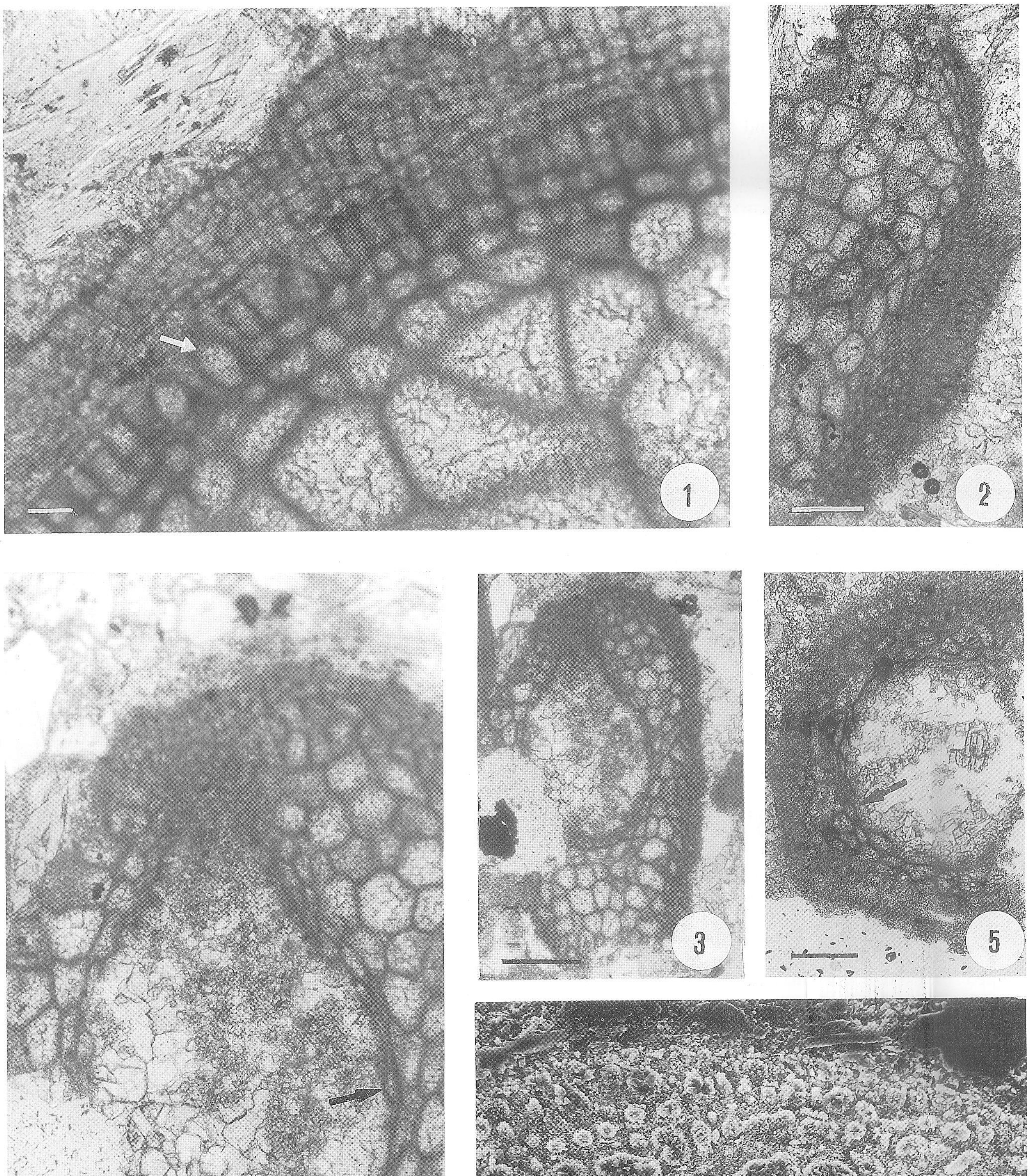

(1985), *S. thomasii* apparently was significant in the Oligocene Tethyan seaway; it is very rare in the eastern margin of the Atlantic ocean (Poignant, 1972 *fide* Poignant & Lorenz, 1985), in the Caribbean area (Beckmann & Beckmann, 1966) and in the Indo-Pacific area (Johnson, 1966; Karche, 1972 *fide* Lemoine, 1977).

Subterraniphyllum thomasii occurred in sublittoral, shallow reef environments of the Late Paleogene, sometimes in conditions of strong water energy (Van Bellen, 1956; Beckmann & Beckmann, 1966).

Discussion.

SEM observations on newly collected specimens of *Subterraniphyllum thomasii* give evidence of cell fusions between adjacent cells in the medulla and the cortex. At the periphery of branches cells divide to generate small, cortical cells at the thallus surface. Overgrowths might represent a secondary thickening of the cortex (Pl. 4, Fig. 1, 2). We recognize the presumed bifurcation at branch apices and the lateral branching in which a "derivative intergeniculum" originates from the "parent intergeniculum". These two features could represent different stages of the development of a lateral branch, that is to say before (stage of bifurcation at the branch apex; Pl. 1, Fig. 4) and after (stage of lateral branching; Pl. 1, Figs. 1, 5) genicular formation (Johansen, 1969a, b; 1981). Parent and derivative branches rarely conserve their articulation (geniculum not visible; Pl. 1, Figs. 1, 5). However, even after death and presumed disarticulation, the parent branch sometimes reveals traces of lateral geniculate branching in form of subcircular small cavities lined with thin, elongated and protruding cells.

The reproductive structures appear as axial, pear-shaped cavities lined with flattened cells. They are described here for the first time, since a revision of Mastrorilli's (1968a) original material showed that the reported conceptacle belongs to an epiphyte growing on *Subterraniphyllum*.

The calcification of the cell walls, the occurrence of presumed conceptacles, primary pit-connections and cell fusions justify the placement of *S. thomasii* within the order Corallinales Silva & Johanson 1986. The occurrence of cell fusions prevents from any comparison with the Lithophylloideae Setchell emend. Bailey 1999. The articulated branches, the uniform size of the medullary cells merging gradually into the cortical cells (Ducker, 1979) and the occurrence of cell fusions suggest an affinity of the fossil *Subterraniphyllum* with the subfamily Metagoniolithoideae Johansen (1969a). However, in *S. thomasii* new intergenicula appear to start from existing intergenicula, unlike *Metagoniolithon*, where new branches originate from meristematic genicula. Also the axial position of uniporate conceptacles points to maintain *Subterraniphyllum* separate from the Metagoniolithoideae.

Cell fusions, genicula and uniporate axial conceptacles are present in the subfamily Corallinoideae (Areschoug) Foslie. The two tribes of Corallinoideae - Corallineae Areschoug and Janieae Johansen & Silva - can be distinguished on the basis of the number of tiers of medullary cells (10-50 in Corallineae; 1-25 in Janieae) (Womersley & Johansen, 1996). These characters would suggest the inclusion of *Subterraniphyllum* in the subfamily Corallinoideae, tribe Corallineae (Athanasiadis, pers. comm.).

The suprageneric disposition of geniculate corallines is based on the morphology of genicula, which are not observable in our material. Moreover, the particular morphology of lining cells in cavities related to branch insertion is not documented in living Corallinoideae. Therefore, the suprageneric disposition of *S. thomasii* remains uncertain.

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