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Reassessment of Lemoine's newly discovered types of fossil corallines (Corallinales, Rhodophyta) preserved at the Muséum national d'histoire naturelle, Paris

Julio AGUIRRE [a], Juan C. BRAGA [a], Bruno de REVIERS [b] & William J. WOELKERLING [c]*

[a] *Departamento de Estratigrafía y Paleontología, Campus Fuentenueva s/n., Facultad de Ciencias, Universidad de Granada, 18071 Granada, Spain*

[b] *Département Systématique et évolution, UMR 7138 SAE, Muséum national d'histoire naturelle, CP 39, 57, rue Cuvier, 75231, Paris cedex 05, France*

[c] *Department of Botany, La Trobe University Bundoora, Victoria, 3083 Australia*

Abstract – Madame Marie Lemoine was one of the most prolific taxonomists on fossil coralline red algae (Corallinales, Rhodophyta) during the 20th Century. She described three non-geniculate genera and over 90 species. Samples from all over the world were sent to her, and she usually sent them back to the collectors. Thus, a significant number of her types are housed in different institutions or might be lost. Some, however, are housed in the herbarium at the Muséum national d'histoire naturelle in Paris (PC) where she worked for most of her life. We found the original material of nine fossil coralline species at PC: 1) three species from Haute-Savoie (France) [*Lithothamnium moretii*, *Lithophyllum simplex* and *Jania nummulitica*]; 2) five species from Albania [*Lithothamnium corallinæforme*, *Lithothamnium bourcartii*, *Lithophyllum koritzæ*, *Lithophyllum sphæroides* and *Lithophyllum (?) albanense*]; and 3) one species from SW France but originally described from the Carpathian Mountains [*Lithothamnium abrardii*]. The aim of this paper is to reassess the newly discovered original material in a modern taxonomic perspective and to typify the species for which Marie Lemoine did not establish a holotype.

Several of these species have been frequently reported by palaeophycologists. The species *albanensis*, either within *Lithophyllum* or *Spongites*, and *Lithothamnion moretii* are among the five most cited species of fossil corallines in the literature published during the XX century. *Lithophyllum simplex* is among the nine most cited fossil coralline species but its taxonomic circumscription cannot be confidently established because no reproductive structures can be identified in the type.

Fossil corallines / Lemoine / Muséum national d'histoire naturelle, Paris / type collections

Résumé – Madame Marie Lemoine fut l'une des taxinomistes du vingtième siècle les plus productives en matière de description de corallines fossiles. Elle décrivit trois genres et plus de 90 espèces de corallines non-articulées fossiles. Des échantillons du monde entier lui furent envoyés et, en règle générale, elle les réexpedia après leur étude. En conséquence, un nombre important de types des taxons qu'elle décrivit sont dispersés dans différentes institutions ou pourraient avoir été perdus. Certains sont malgré tout conservés dans l'herbier national du Muséum national d'histoire naturelle, à Paris (PC) où elle passa la plus grande partie de sa vie professionnelle. Nous avons pu localiser à PC le matériel

* Corresponding author: jaguirre@ugr.es

original de neuf corallines fossiles décrites par madame Lemoine : 1) trois espèces de Haute-Savoie : *Lithothamnium moretii*, *Lithophyllum simplex* et *Jania nummulitica*; 2) cinq espèces d'Albanie, *Lithothamnium corallinæforme*, *Lithothamnium bourcartii*, *Lithophyllum koritzæ*, *Lithophyllum sphæroides* et *Lithophyllum (?) albanense*; ainsi que 3) une espèce du sud-ouest de la France décrite originellement des Carpathes : *Lithothamnium abrardii*. L'objectif du présent article est de réétudier les espèces types du matériel original retrouvé à PC, dans un contexte taxinomique moderne and de typifier les espèces pour lesquelles Marie Lemoine n'avait pas désigné d'holotype.

Plusieurs de ces espèces ont été fréquemment rapportées par des paléophycologues. L'espèce *albanensis*, soit comme *Lithophyllum* soit comme *Spongites*, ainsi que *Lithothamnion moretii* sont parmi les cinq espèces de corallines fossiles les plus citées dans la littérature in du XX[e] siècle. *Lithophyllum simplex* est parmi les neuf espèces de corallines fossiles les plus citées mais son identité générique n'a pas pu être établie avec certitude car aucune structure reproductive n'a pu être mise en évidence dans le type.

Corallines fossiles / Lemoine / Muséum national d'histoire naturelle, Paris / collection type

INTRODUCTION

A number of taxonomic revisions of the type material of fossil coralline species has been carried out in the last decades (Piller, 1994; Rasser & Piller, 1994; Aguirre *et al.*, 1996; Basso *et al.*, 1997, 1998; Aguirre & Braga, 1998; Vannucci *et al.*, 2000; Bassi *et al.*, 2000, 2005, 2007; Woelkerling *et al.*, 2002; Braga *et al.*, 2005; Quaranta *et al.*, 2007; Vannucci *et al.*, 2008, 2009, 2010; Iryu *et al.*, 2009, 2012). However, many of the original collections of fossil species described by palaeophycologists during the last century are lost or as yet unstudied (Braga & Aguirre, 1995; Aguirre & Braga, 2005). This is the case for many types of fossil corallines described by Marie Flore Eugénie Lemoine (1887-1984), one of the most prolific taxonomists on fossil coralline algae during the 20th Century (Aguirre & Braga, 2005). Lemoine described 140 taxa of non-geniculate corallines (Lamy & Woelkerling, 1998: 141), of which three genera and over 90 species are based on fossil material (Aguirre and Braga, 2005). As indicated by Lamy and Woelkerling (1998: 140), samples from all over the world were sent to her and she usually sent them back to the collectors. Thus, a significant number of types are scattered in different institutions. This is the case of the samples preserved in the Julius Pia collection, at the Museum of Natural History of Vienna (Rasser & Piller, 1994) or the ones stored in the Emberger collection at the University of Nantes (Aguirre & Braga, 1998).

Lemoine worked at the Laboratoire de Cryptogamie in the Muséum national d'histoire naturelle (Paris) (PC hereafter), and part of the material she studied is housed in this institution (Lamy and Woelkerling, 1998). Woelkerling (1998, p. 394 and table 6) recorded 38 of Lemoine's types of corallines, including holotypes, lectotypes, isolectotypes, paratypes, and syntypes at PC.

Previously non-inventoried original material of nine species of fossil corallines has been re-discovered at PC. This material includes: 1) three species from Haute-Savoie; 2) five coralline species from Albania; and 3) one species from SW France but originally described from the Carpathian Mountains. The aim of this paper is to reassess these newly discovered Lemoine's original samples from a modern taxonomic perspective.

METHODS

The material studied includes thin sections and rock samples. Because some features needed for correct identification were not present in specimens in the original thin sections, new ultra thin sections were cut from the rock samples when possible. Original thin sections, samples and labels were photographed in order to correctly catalogue the newly discovered material.

Growth morphology of coralline algae is described according to the terminology proposed by Woelkerling *et al.* (1993) while the terminology of Woelkerling (1988), Woelkerling *et al.* (2008) and Chamberlain *et al.* (1988) is used for anatomical features, cell orientation and conceptacle dimensions. Morphological descriptions of cells and conceptacles, as well as measurements, are referred to longitudinal sections, except when indicated. Iryu *et al.* (2012: pp. 173, 175) provide further notes on terminology used in older papers on fossil algae.

The phylogenetic classification scheme of Le Gall *et al.* (2010) is followed for coralline orders, Sporolithales and Corallinales, and that of Harvey *et al.* (2003) and Harvey & Woelkerling (2007) for coralline families and subfamilies [but see the recent revisions of the subfamily Mastophoroideae by Kato *et al.* (2011) and Bittner *et al.* (2011) based on molecular data]. The taxonomic criteria for fossil corallines summarized by Braga (2003) are applied when particular diagnostic characters used for living corallines were not preserved.

Nomenclatural conventions and terminology are in accord with the Vienna edition (McNeill *et al.*, 2006) of the International Code of Botanical Nomenclature (ICBN) because the amended *Code*, which was approved in August 2011 at the XVIII International Botanical Congress (Melbourne) and is now in effect (McNeill *et al.*, 2011: 1511), was not available online or in final printed form at the time the present paper was submitted. Further information on the forthcoming Melbourne Code is provided in McNeill & Turland (2011) and McNeill *et al.* (2011).

MATERIAL

The Haute-Savoie (SE France) material

The Haute-Savoie collection includes samples from upper Eocene deposits of the environs of Lake Annecy sent to Lemoine by Dr Moret. Lemoine (1928a) described nine coralline species, five of them being new: *Lithothamnium moreti*, *Lithothamnium faurai*, *Lithophyllum simplex*, *Lithophyllum symetricum*, and *Jania nummulitica*. The material discovered at PC is stored in two boxes and includes samples from two localities: Montagne de Veyrier (north of Lake Annecy), and Mont Durand (close to St.-Jean-de-Sixt, east of Lake Annecy). Lemoine (1928a) also mentioned samples from two additional localities, Roc de Chère and Calvaire de Thônes, but they were not found at PC. In the preserved samples, we found the type material of *Lithothamnium moreti*, *Lithophyllum simplex*, and *Jania nummulitica* but the type material of *Lithophyllum symetricum* has not been located.

Lemoine (1928a, p. 548) stated that *Lithothamnium faurai* was going to be described in a future paper on the coralline algae from NE Spain collected by Bataller (Lemoine 1928b): "*Cette espèce m'a paru être la même qu'une espèce que je décrirai prochainement avec d'autres espèces du Nummulitique d'Espagne*". In the protologue, she stated that the Haute-Savoie specimen might belong to the Catalonian species: "*Un fragment observé dans le Priabonien de Haute-Savoie me parait appartenir à cette espèce*" (Lemoine 1928b, p. 98). The Catalonian material has not been found, thus the nomenclatural status of the name *Lithothamnium faurai* remains uncertain.

The Albania material

The Albania material includes samples collected by Dr Bourcart in Miocene deposits from two localities: 1) Koritza, early Miocene (Burdigalian) limestones with coralline algae; and, 2) Tirana, middle Miocene (Helvetian *sensu* Lemoine, 1924) limestones. Lemoine (1924) described five new species: *Lithothamnium corallinæforme*, *Lithothamnium bourcarti*, *Lithophyllum koritzæ*, *Lithophyllum sphæroides* and *Lithophyllum (?) albanense*. We have found the original material of all five taxa, individually preserved in five boxes stored at PC (see species descriptions below). When describing the new genus *Mesophyllum*, Lemoine (1928c) proposed the new combination *Mesophyllum koritzae* (Lemoine) Lemoine.

The Landes (SW France) material

Lithothamnium abrardi was described by Lemoine (1934) based on Lutetian (Middle Eocene) material gathered by Dimitrij Andrusov from the Orava Valley, Ostrá Skala (close to Dolní Kubín, western Carpathians), together with twelve other new species: *Lithothamnium andrusovi*, *Lithothamnium contraversum*, *Mesophyllum ramosum*, *Mesophyllum varians*, *Mesophyllum tropicale*, *Mesophyllum heteroclitum*, *Lithophyllum carpathicum*, *Lithophyllum continuum*, *Lithophyllum dubium*, *Lithophyllum densum*, *Amphiroa propria*, and *Corallina abundans*.

In the protologue of *Lithothamnium abrardi*, Lemoine (1934, pp. 274-275) mentioned that the species also occurs in Lutetian rocks from Donzaq (close to Bastennes; Landes, SW France). No type material coming from the western Carpathians was found at PC, but we discovered one sample identified as *Lithothamnium abrardi* from SW France in a box including a rock sample and a thin section.

SYSTEMATIC DESCRIPTIONS

Order Corallinales Silva *et* Johansen, 1986

Comments. The Order Corallinales comprises two families. The Hapalidiaceae is characterized, among other characters, by multiporate tetrasporangial/bisporangial conceptacles and uniporate male and female/carposporangial conceptacles. By contrast, the Corallinaceae is characterized by uniporate tetrasporangial/bisporangial conceptacles as well as uniporate male and female/carposporangial conceptacles. In the vast majority of fossil specimens with conceptacles, the contents are not preserved. Thus one can only be certain that empty conceptacles with multiporate roofs are tetrasporangial or bisporangial. Empty conceptacles with uniporate roofs might be male, female/carposporangial or tetrasporangial/ bisporangial.

None of the specimens dealt with in the present study have conceptacles with preserved contents. Consequently, the placement of specimens with empty uniporate conceptacles in the Hapalidiaceae or Corallinaceae is based on criteria such as the occurrence of flared epithallial cells, the occurrence of secondary pit-connections etc., which occur in some genera in one family but are lacking in all genera of the other family.

Family Hapalidiaceae Gray, 1864; emended by Harvey, Broadwater, Woelkerling *et* Mitrovski, 2003

Subfamily Melobesioideae Bizzozero, 1885

Genus *Lithothamnion* Heydrich, 1897

Lectotype species *Lithothamnion muelleri* Lenormand *ex* Rosanoff, 1866; designated by Woelkerling (1983a)

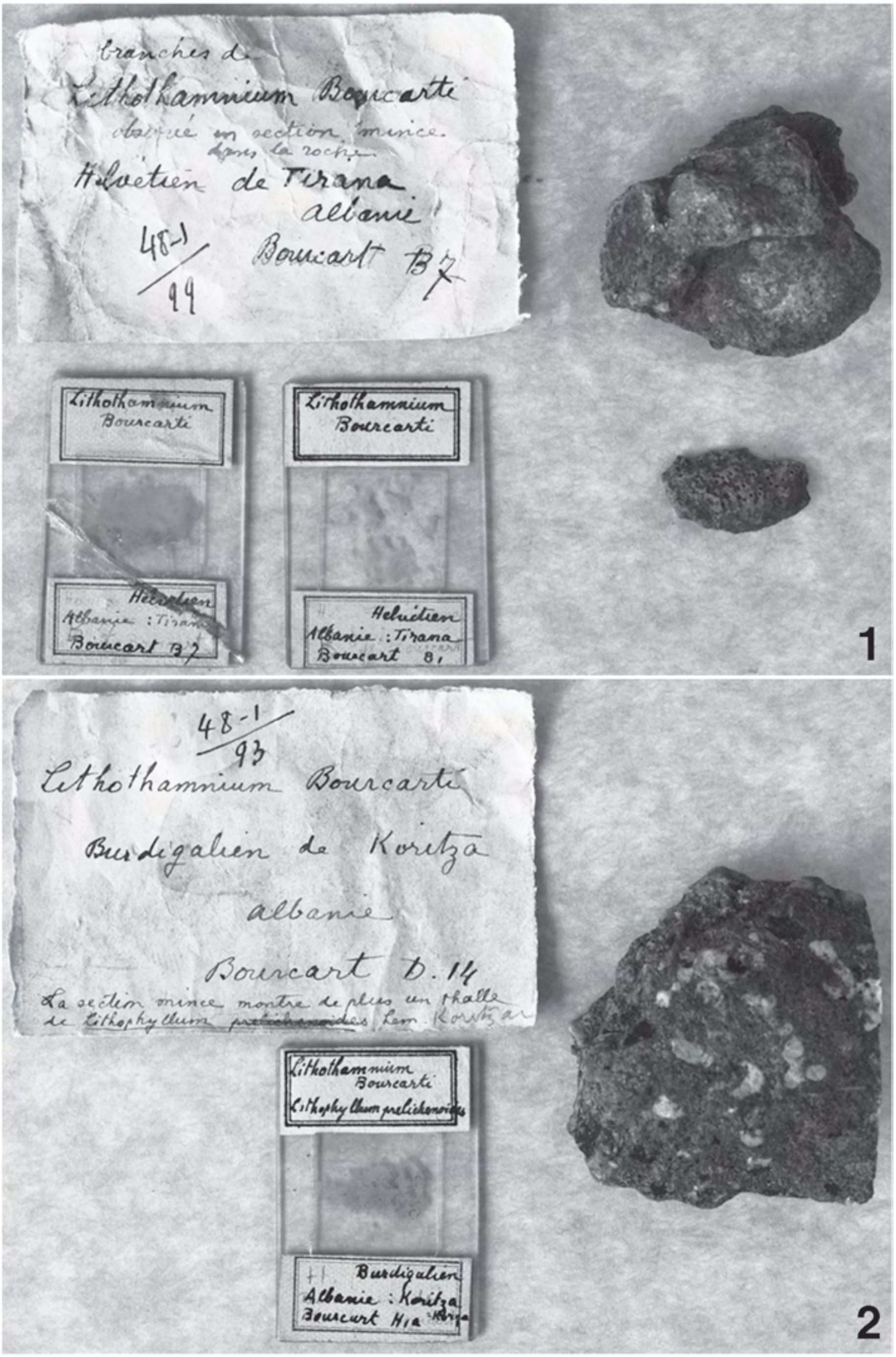
Lithothamnion bourcartii Lemoine, 1924 **Figs 1-9**

Lithothamnium bourcarti Lemoine (*Bulletin de la Société géologique de France*, 1924, pp. 277-279, fig. 3).

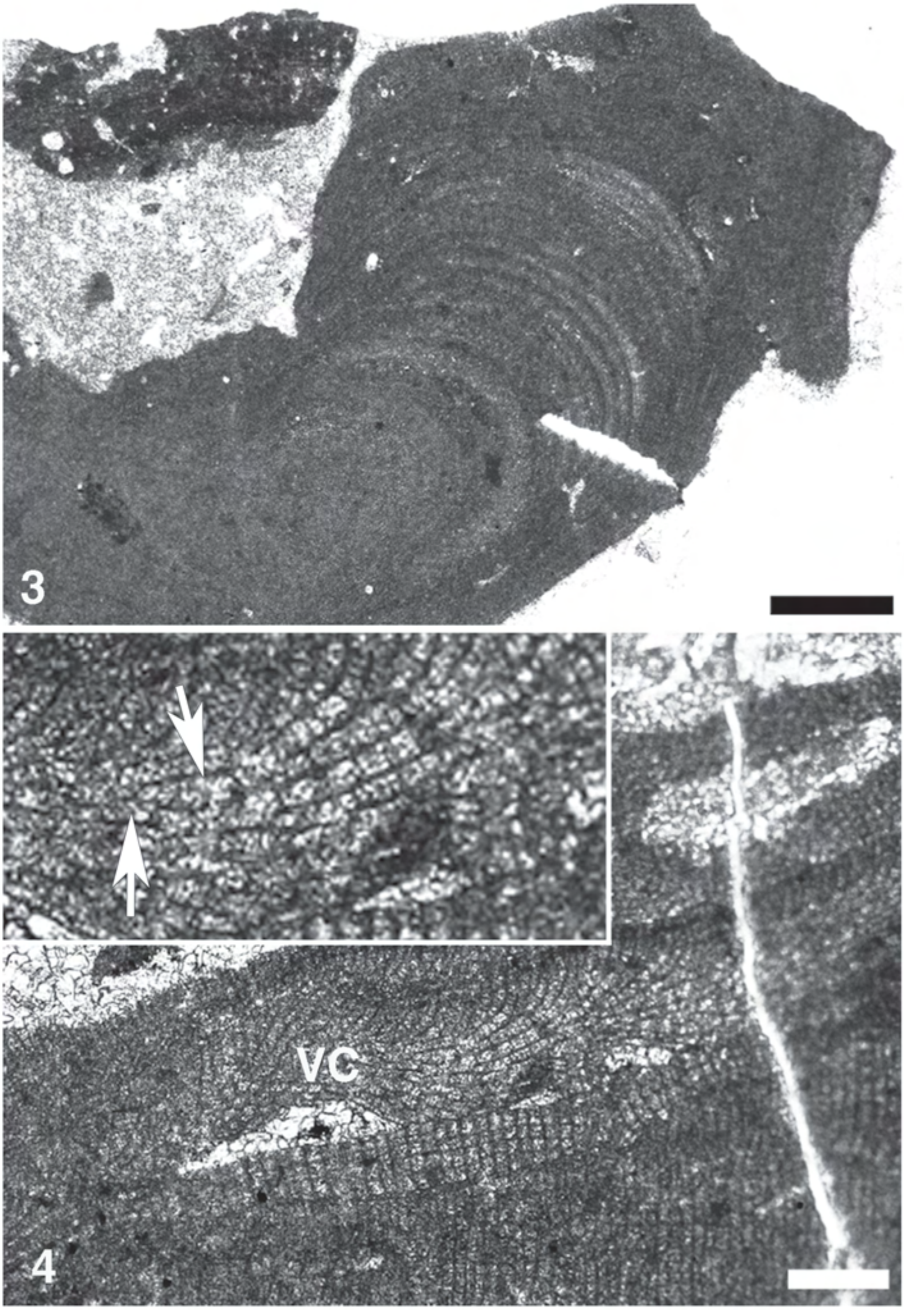
Original material. Lemoine (1924) based *Lithothamnion bourcartii* on material from two Albanian localities, Koritza and Tirana but did not designate a type. Both collections are preserved at PC in boxes numbered 48-1/99 and 48-1/93. Box 48-1/99 contains two rock samples, two thin sections and a note handwritten by Lemoine (Fig. 1). The note includes the species name ("*branches de* Lithothamnium Bourcarti *observé en section mince dans la roche*"), the age (Helvetian, mid-late Miocene), the locality (Tirana, Albania), and the numbering presumably used by Bourcart for the rock sample (Bourcart B7). Each of the two thin sections has two labels. One of them indicates the species name and the other records the age, the locality and the presumed Bourcart's numbers (Bourcart B7 and Bourcart B1) (Fig. 1).

Box 48-1/93 contains a label handwritten by Lemoine, one rock sample and one thin section (Fig. 2). On the label, Lemoine indicated the species name (*Lithothamnium bourcarti*), the age of the sample (Burdigalian), the locality (Koritza, Albania), the identification number probably used by Bourcart (Bourcart D.14) and an indication of the presence of a second species described in the same paper as *Lithophyllum koritzae* (Lemoine 1924: 279-280). This species was subsequently transferred into *Mesophyllum* (Lemoine 1928c: 253) and is dealt with separately below under *Mesophyllum*.

The rock sample, in box 48-1/93 and labelled as D.14, is a dark grey bioclastic packstone-grainstone, 4.7 cm in maximum length, in which coralline algal fragments stand out as white spots (Fig. 2). The thin section has two stickers, one containing the names of two species (*Lithothamnium bourcarti* and *Lithophyllum prelichenoides*) and the other indicating the age and the locality (Burdigalian; Albania: Koritza: Korça), as well as the identification code of Bourcart (Bourcart H_1a). Two additional thin sections, sections 7a and 7b, have been cut from the rock sample.



Figs 1-2. *Lithothamnion bourcartii* Lemoine. **1.** Lectotype from Tirana (Albania) stored in box 48-1/99. (Width of thin sections = 2.9 cm). **2**. Specimen of *Lithothamnion bourcartii* from Koritza (Albania) stored in box 48-1/93. (Width of thin section = 2.9 cm).



Figs 3-4. *Lithothamnion bourcartii.* **3.** Longitudinal section through fruticose branch of lectotype of *L. bourcartii* (scale bar = 500 µm). **4**. Plumose ventral core (VC) of lectotype of *L. bourcartii*. This microphotograph might be the basis of the sketch published by Lemoine (1924; fig. 3) (scale bar = 100 µm). Inset is an enlargement of the central part of the ventral core showing cell fusions (arrows).

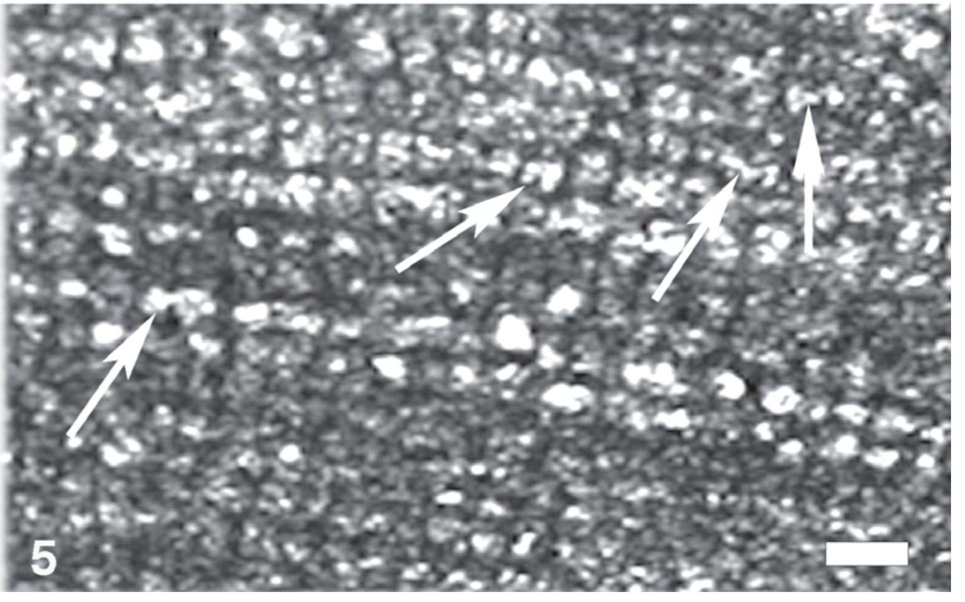


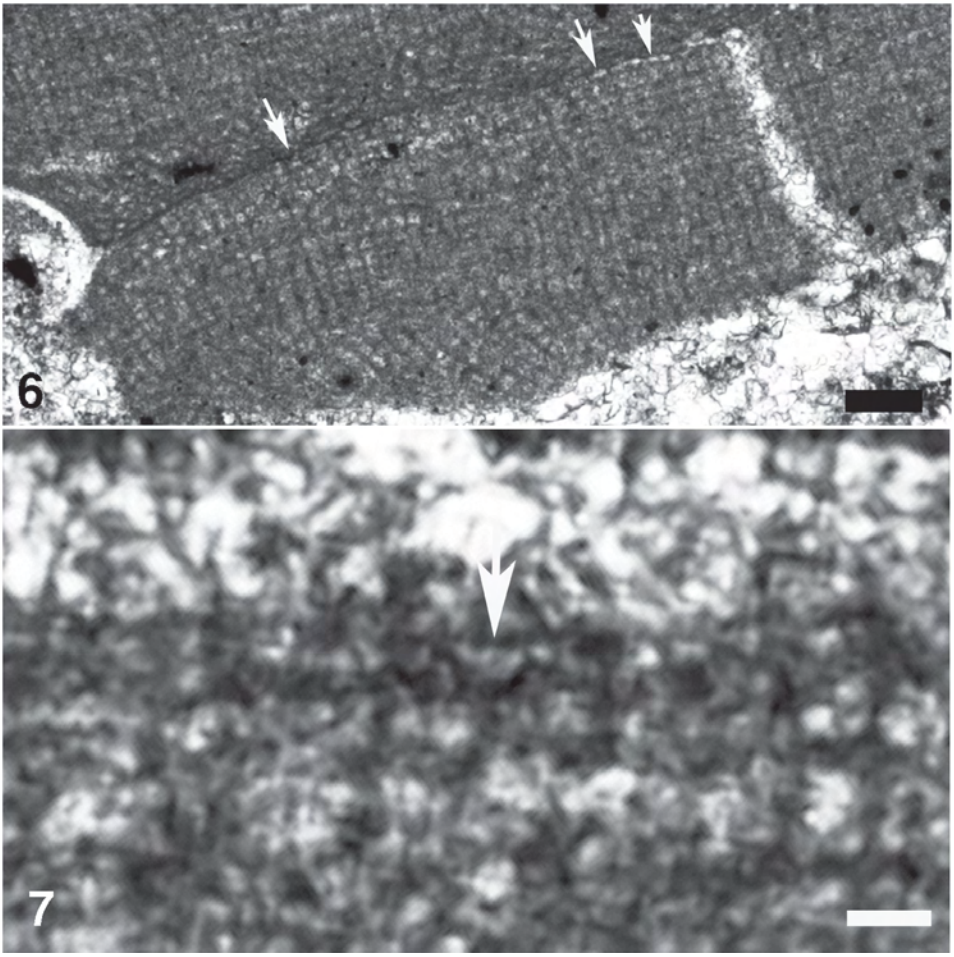
Fig. 5. Cell fusions (arrows) in the peripheral region of a branch of the lectotype of *L. bourcartii* (scale bar = 30 mm).

Lectotype designation. In the protologue, Lemoine (1924) referred to both the Koritza and the Tirana samples, but she did not designate holotype. We designate here the Tirana specimen, represented by the two thin sections and the two fragments included in the box 48-1/99, as the lectotype because it shows all known diagnostic features, including multiporate conceptacles.

Description of the lectotype. The lectotype includes warty to fruticose branches, with protuberances up to 4 mm in diameter (Fig. 3). Rarely, encrusting growth forms occur. The lectotype has a dorsiventral, monomerous organization. The ventral core is plumose, up to 160 µm thick (Fig. 4). Filaments run approximately parallel to the base of the thallus in the lower part of the ventral core and then curve upwards to the dorsal region. Cells are rectangular in section, measuring 16 to 36 µm (23.3 ± 5.3 µm; mean ± standard deviation) in length and 7 to 14 µm (10.4 ± 1.4 µm) in diameter. There are cell fusions (Fig. 4).

Protuberant branches are well developed, with regular growth zones in the inner part of the branches (Fig. 3). The thickness of these zones is very variable, ranging from about 96 µm to 673 µm, more frequently from 200 to 400 µm. Cells are rectangular in section. The cell size ranges from 16 to 23 µm (19.5 ± 2.3 µm) in length and 7 to 11 µm (9 ± 0.9 µm) in diameter. The great variability in cell size is due to a change in the cell length along filaments within the growth bands; from the base to the middle part cells are bigger, while in the upper part of the growth band, cells are smaller resulting in a more compact and dense grid. Cell fusions are conspicuous and there is no lateral cell alignment (Fig. 5).

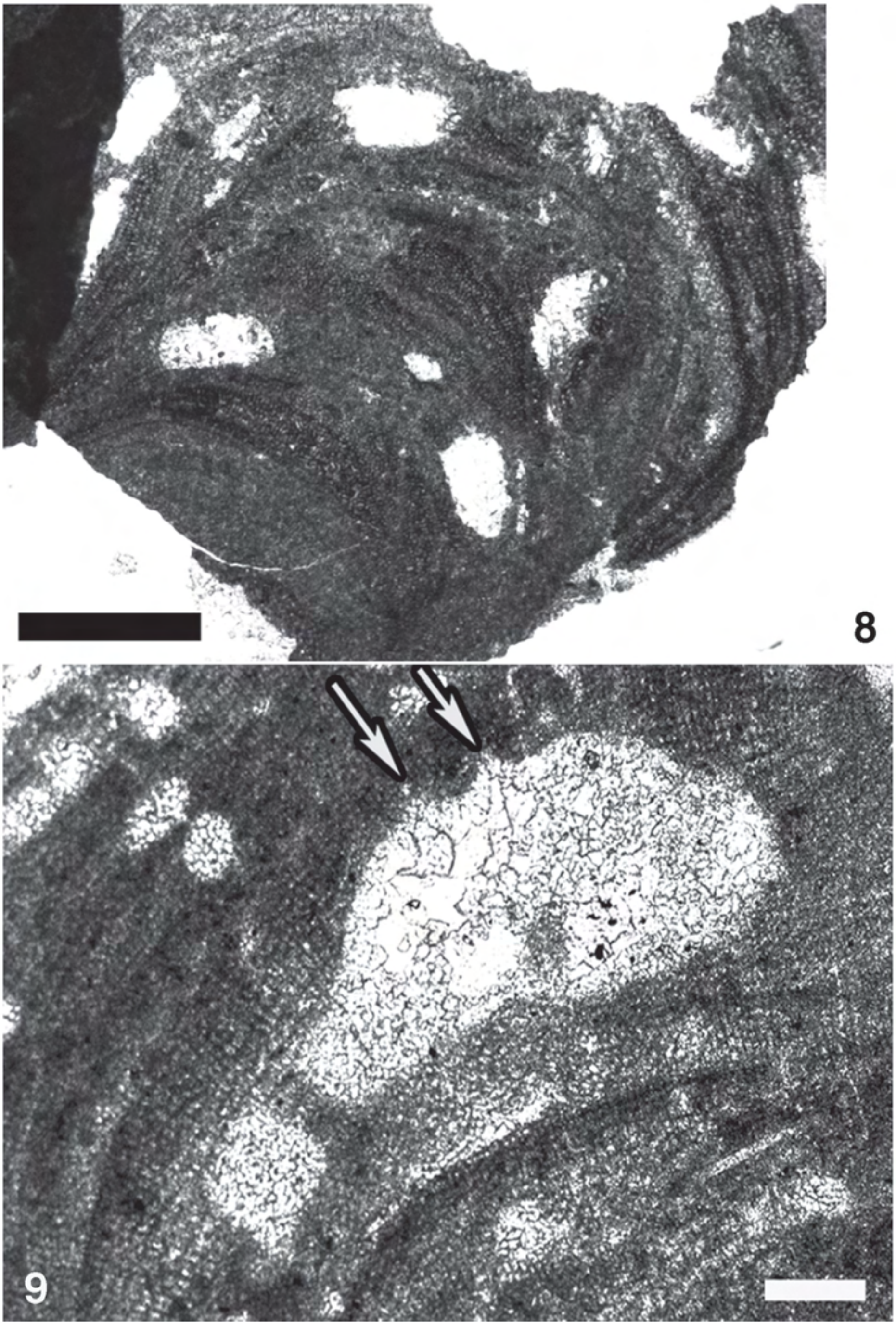
A row of flattened, rectangular cells can be occasionally seen at the surface of the plant that can be confidently interpreted as the epithallial cells (Fig. 6). The outer walls are flared (Fig. 7); cells measure 7 to 9 µm (8.3 ± 1.2 µm) in diameter and 2 to 5 µm (3 ± 1.2 µm) in length.



Figs 6-7. Epithallial cells of *Lithothamnion bourcartii*. **6.** Row of flat epithallial cells (arrows) in the outer margin of a thallus of the lectotype of *L. bourcartii* (scale bar = 50 μm). **7.** Enlarged view of epithallial cells of the lectotype of *L. bourcartii* with flared walls (arrow) characteristic of the genus *Lithothamnion*. The image is slightly out of focus because the thin section is thick and not well preserved (scale bar = 10 μm).

Several multiporate conceptacles occur buried in the thallus (Fig. 8). They are more or less oval in section and range in size from 298 to 327 μm (317.3 ± 16.7 μm) in diameter and from 154 to 173 μm (163.5 ± 9.6 μm) in height. This size range coincides with the measurements given by Lemoine (1924). Conceptacles, although buried, have slightly convex roofs, suggesting that they protruded somewhat above the thallus surface when first formed and the roofs have conical, small pore canals in the roof (Fig. 9). Conceptacle roofs are about five cells thick, very rarely up to eight cells. Cells of the conceptacle roof and cells around the pore canals do not differ in shape or size from other surrounding cells.

No male or female conceptacles have been observed.



Figs 8-9. Conceptacles of *Lithothamnion bourcartii*. **8.** Branch of lectotype of *L. bourcartii* with several buried multiporate conceptacles (scale bar = 500 μm). **9**. A multiporate conceptacle of lectotype of *L. bourcartii* with several pore canals in the roof (scale bar = 100 μm).

Remarks. The presence of multiporate conceptacles, cell fusions, and flared epithallial cells provide strong evidence that this species belongs to *Lithothamnion*, within the subfamily Melobesioideae (family Hapalidiaceae). Its status as a distinct species within *Lithothamnion* requires further assessment, a task beyond the scope of this study.

Lithothamnion corallinaeforme Lemoine, 1924 **Figs 10-15**

Lithothamnium corallinæforme Lemoine (*Bulletin de la Société géologique de France*, 1924, pp. 276-277, Figs 1-2).

Holotype. Lemoine (1924, p. 276) based *Lithothamnium corallinæforme* on a single specimen, which therefore constitutes the holotype (ICBN, Art 9.1). The rock sample matching the one illustrated by Lemoine (1924; Fig. 1) was found in a box labelled 48-1/95. The box also contains a note handwritten by Lemoine with the name of the species, the age (Burdigalian), the locality (Koritza, Albania), and the identification number probably used by Bourcart (D.15) (Fig. 10).

In the protologue, Lemoine (1924; p. 276 and Fig. 1) indicated that the species corresponded to the large fruticose alga preserved in the rock sample. Nonetheless, the anatomical features described in the paper were based on one branch isolated in the rock sample because Lemoine was afraid of destroying the beautiful large branching alga. The original thin section was not found in PC; consequently we made one thin section, section 2, from the large branching alga.

Description of the holotype. The holotype is fruticose with long and slender branches up to 2.5 cm in length and 0.2 cm in diameter (Figs 10-11). The thallus is monomerous with a dorsiventral organization, showing conspicuous concentric growth bands (Fig. 11).

The ventral core is plumose and up to 150 µm in thickness (Fig. 12). Cells are long and rectangular, measuring 18-36 µm (24.6 ± 5.5 µm) in length and 5-9 µm (7 ± 1.5 µm) in diameter. There are numerous cell fusions (Fig. 12).

In longitudinal section, the fruticose elongated branches look irregularly zonate (Fig. 11). Cell size decreases slightly along the filaments within each growth zone from the base to the top as well as from the centre to the periphery. Cells range from 9 to 18 µm (16.3 ± 2.3 µm) in length and from 4.5 to 9.1 µm (8.1 ± 1.3 µm) in diameter. Cell fusions are conspicuous and there is no alignment of cells of adjacent filaments (Fig. 12).

Flattened, flared-like epithallial cells can be occasionally observed at the thallus surface (Figs 13-14). They measure from 2 to 3 µm (2.7 ± 0.9 µm) in length.

Lemoine (1924) did not describe conceptacles in the original material but buried multiporate conceptacles occurred in the thin section we made (Fig. 15). They probably protruded slightly above the thallus surface before becoming buried, the roof being 4 to 6 cells thick. Cells lining the roof of the conceptacles are similar both in shape and size to those of the peripheral region (Fig. 15). Conceptacle chambers are 327-363 µm (345.5 ± 25.7 µm) in diameter and 120 µm in height.

Discussion. As commented above, Lemoine (1924) established the species *corallinaeforme* for a fruticose plant of slender branches, preserved in the rock sample found at PC. However, the microscopic description of the species was based on a branch fragment dispersed in the rock matrix and, in the protologue, she stated that the cells in the peripheral region of the branch are small and quadrangular-rounded in shape, measuring 5-10 µm (most likely 5-8 µm) in length and 5-10 µm in diameter (Lemoine, 1924, p. 277). Neither the vegetative features nor the cell dimensions in the branches observed in the ultrathin section cut from

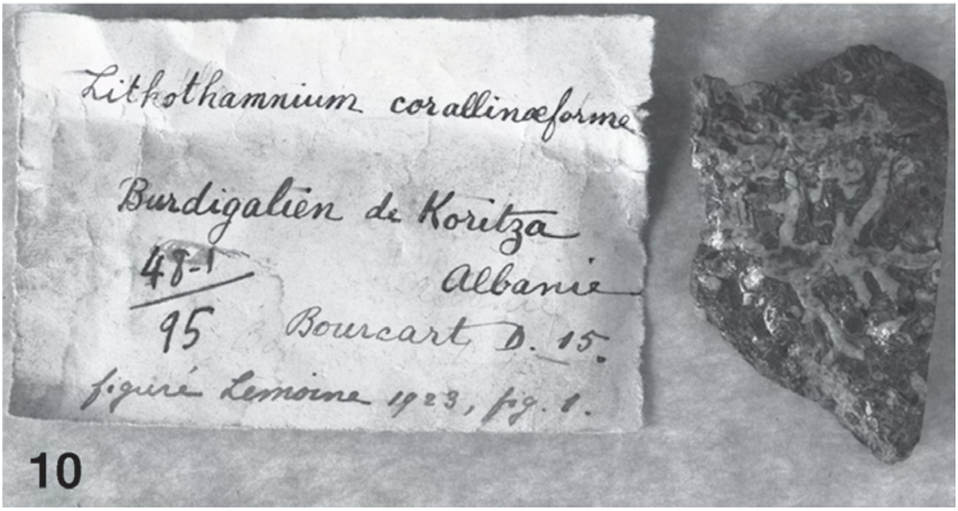


Fig. 10. Holotype of *Lithothamnion corallinaeforme* preserved at PC in the box numbered 48-1/95. The sample is the same one shown by Lemoine (1924; fig. 1). (Maximum length of the rock sample = 5 cm).

the holotype agree with those reported by Lemoine. It is most likely that her description was based on an oblique section of a branch or, alternatively, that she described the microscopic features of a taxon different from the holotype.

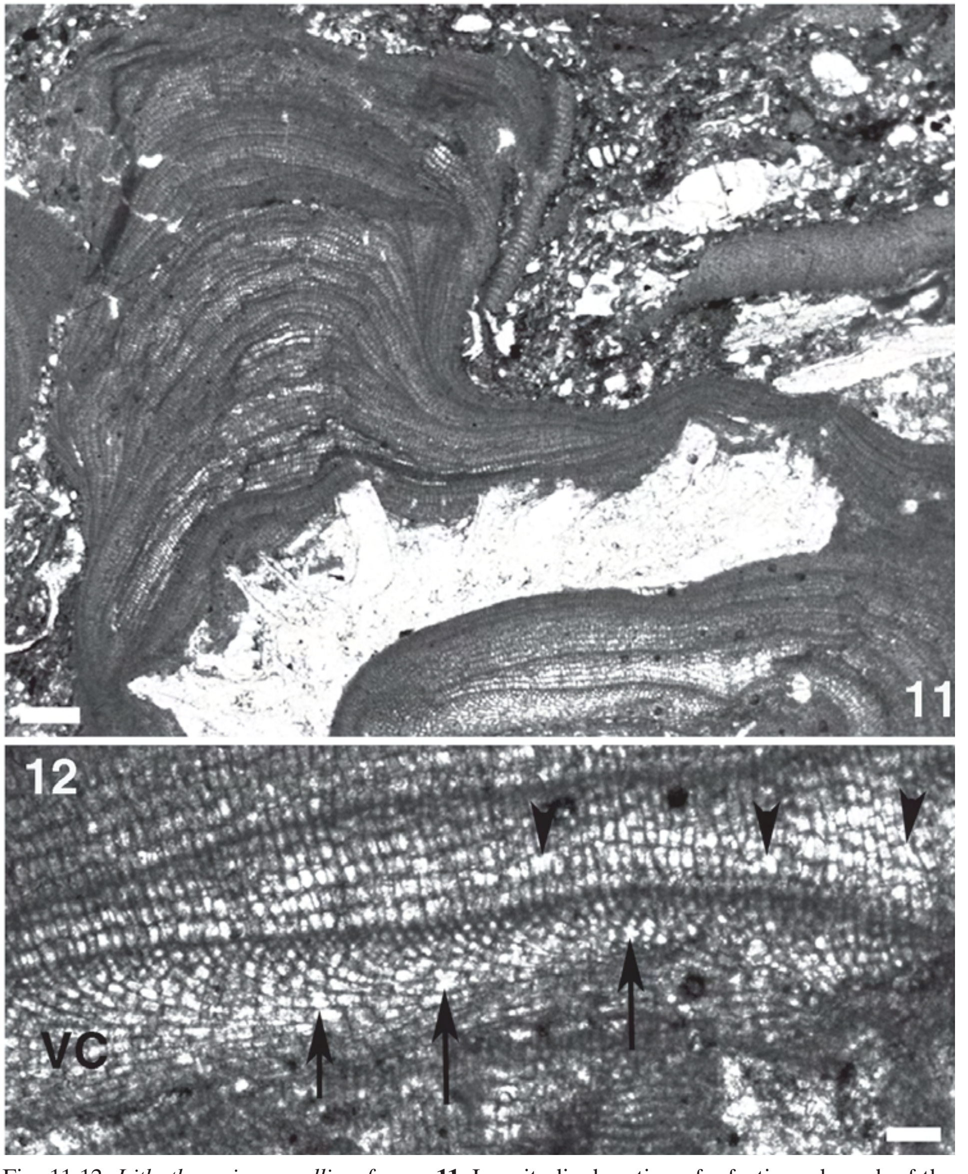
The occurrence of multiporate conceptacles and flattened, flared-like epithallial cells confirms the generic assignment originally made by Lemoine (1924). Its status as a distinct species within *Lithothamnion* requires further assessment, a task beyond the scope of this study.

Lithothamnion moretii Lemoine, 1928a **Figs 16-20**

Lithothamnium moreti (*Bulletin du Muséum d'Histoire naturelle*, 1928a, pp. 547-548, Figs 2-3).

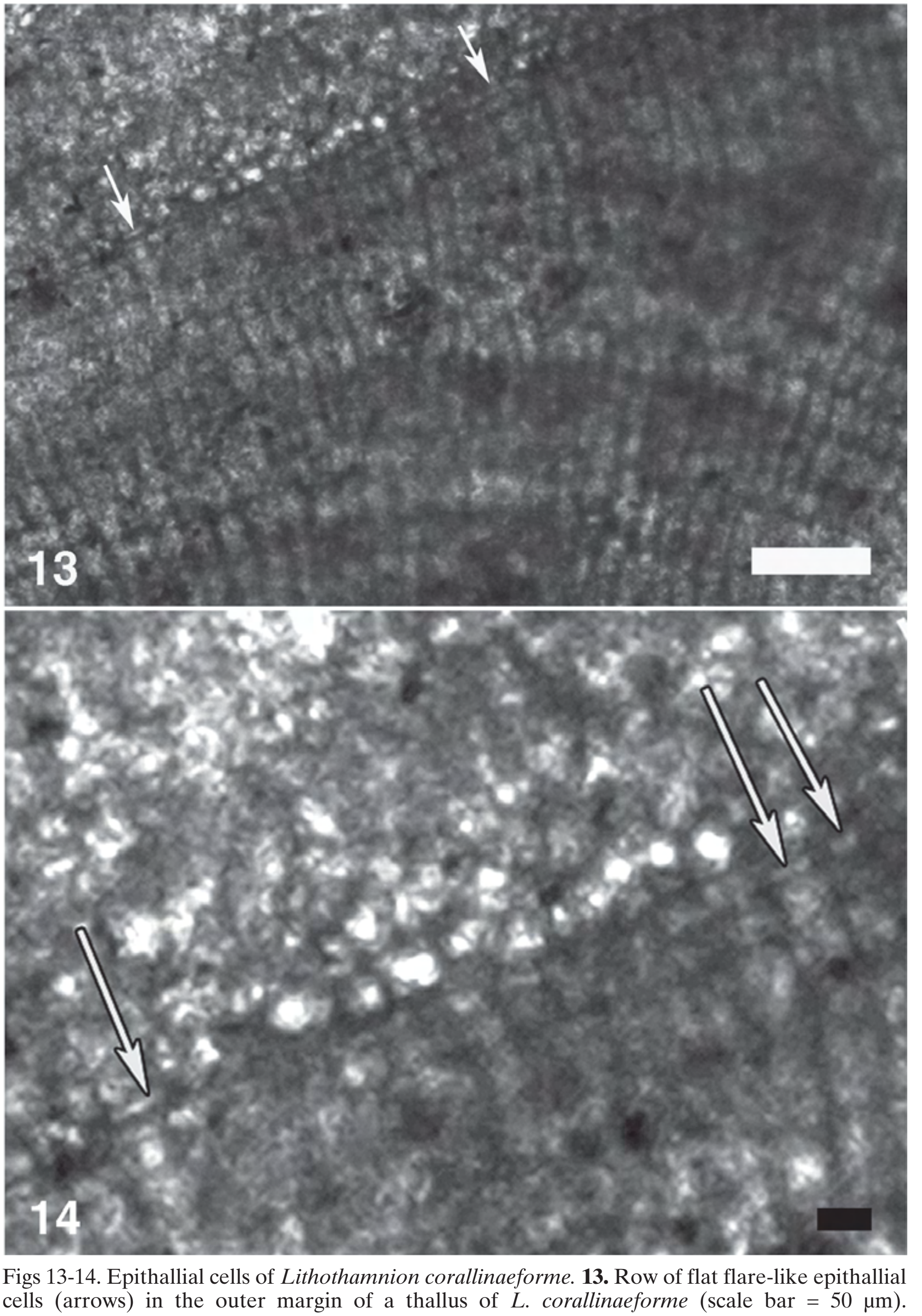
Original material. Lemoine (1928a) based the description of this species on Priabonian (Late Eocene) material collected from two localities: Roc de Chère (Annecy lake) and Mont Durand (close to Saint Jean de Sixt). The material preserved at PC is that of Mont Durand, stored in the box 48-1/117. The box contains a rock sample numbered as 5, one thin section labelled as 5 with a label indicating the locality ("*Mont Durand près St Jean de Sixt. H*^{te} *Savoie. Moret*"), and two notes (Fig. 16). One of the notes, handwritten by Lemoine, indicates the age and the locality of the sample, as well as a short description of other fossils present in the sample ("*couches à* Orthophragmina, Nummulites striatus, Ostrea gigantea") (Fig. 16). The typewriting of the other note, indicating the locality and the lithology, does not correspond with Lemoine's calligraphy (except for the name M. Moret in the last line of the note) (Fig. 16). The code number of the box is also added in this note but in a different calligraphy (Fig. 16).

The rock sample, 6.5 cm in maximum dimension, is a black bioclastic packstone with fragments of coralline algal branches. We have made an additional thin section from the rock sample (section 10).



Figs 11-12. *Lithothamnion corallinaeforme*. **11.** Longitudinal section of a fruticose branch of the holotype of *L. corallinaeforme* (scale bar = 200 μm). **12.** Plumose ventral core (VC) of crustose basal part of *L. corallinaeforme*. Note presence of numerous cell fusions, both in the ventral core (arrows) and in the peripheral region (arrowheads) (scale bar = 50 μm).

Lectotype designation. Lemoine (1928a; p. 457) did not designate a holotype and based the species description on two samples. We designate here the specimen from Mont Durand as lectotype since it is the only one found at PC. Additionally, both vegetative features and sporangial reproductive structures are preserved in the Mont Durand specimen.



Figs 13-14. Epithallial cells of *Lithothamnion corallinaeforme.* **13.** Row of flat flare-like epithallial cells (arrows) in the outer margin of a thallus of *L. corallinaeforme* (scale bar = 50 μm). **14.** Enlarged view of epithallial cells of *L. corallinaeforme* showing their characteristic flared shape (two arrows in the right). The picture is slightly out of focus because the thin section is thick and because of poor preservation (scale bar = 10 μm).

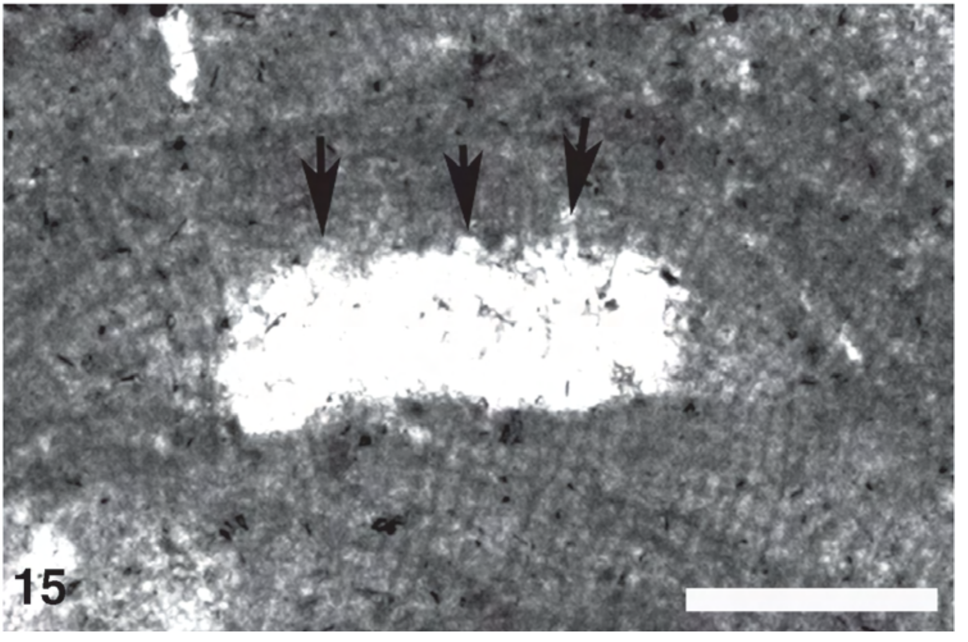


Fig. 15. Multiporate conceptacles of *L. corallinaeforme*. Arrows mark pore canals (scale bar = 100 µm).

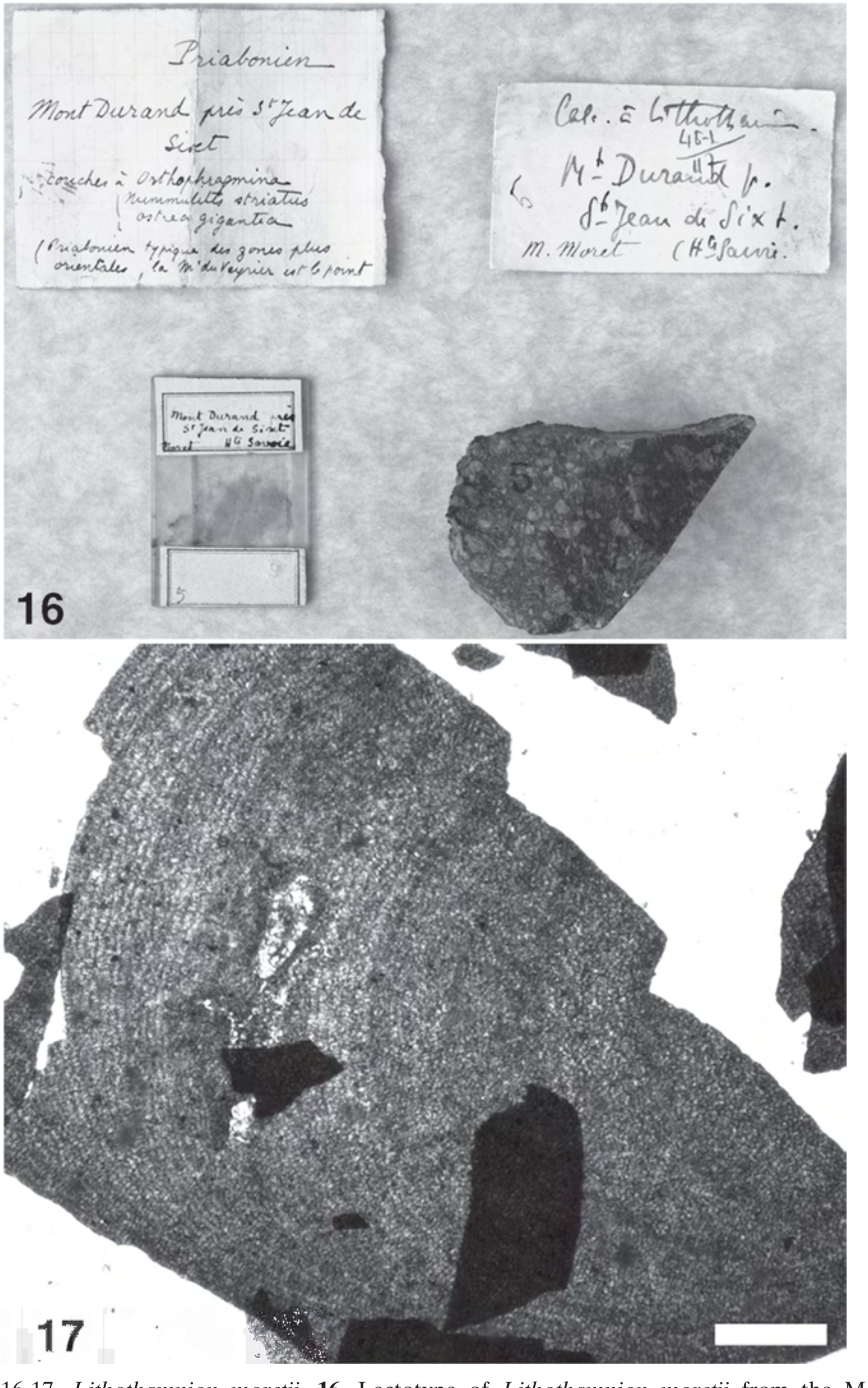
Description of the lectotype. The lectotype is warty to fruticose (Fig. 17), showing a dorsiventral monomerous organization with a plumose ventral core (Fig. 18). Filaments rise from the crustose base of the thallus and curve upward to the dorsal region. Cells in the ventral region are rectangular to quadrangular in section measuring 11-18 µm (15.2 ± 2.5 µm) in length and 5-9 µm (6.4 ± 1.2 µm) in diameter. Numerous cell fusions are present (Fig. 18).

In longitudinal section, the fruticose elongated branches consist of cells rectangular in section. They are 11-23 µm (15 ± 3 µm) in length and 5-11 µm (7.7 ± 1.7 µm) in diameter. In oblique sections, they are rounded. In the encrusting portions of the thallus, the peripheral region is massive, with no clear zonation, while in the branches a clear banding is observed (Fig. 17). There is no cell alignment of cells of adjacent filaments and cell fusions are conspicuous (Fig. 18).

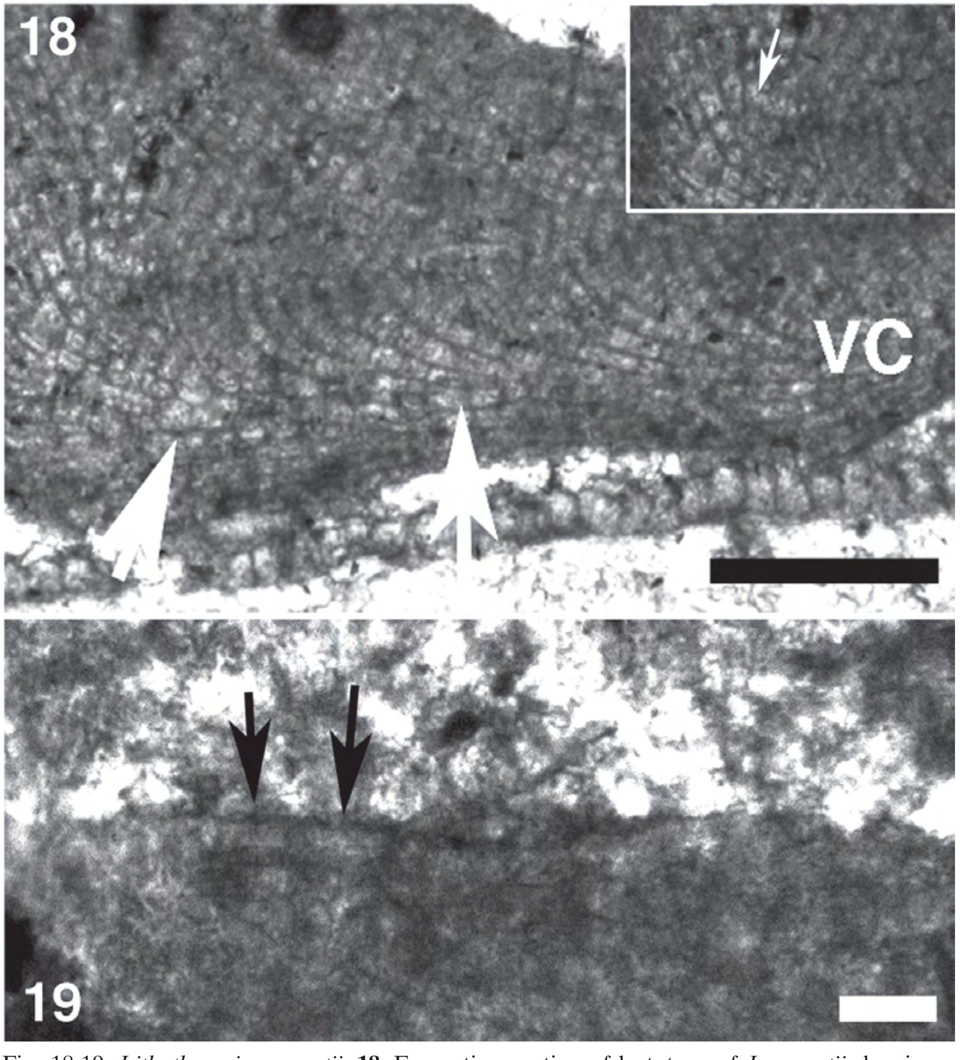
Flared epithallial cells occur at the thallus surface (Fig. 19).

Lemoine (1928a) referred to the presence of numerous multiporate conceptacles in the apices of the protuberances, measuring 300 to 525 µm in diameter and 75 to 150 µm in height. We have not identified these in the thin section preserved at PC; thus, the conceptacles described by Lemoine probably were in the sample from Roc de Chère, the other locality mentioned in the protologue. Multiporate conceptacles, however, occur in the Mont Durand lectotype. They are ovoid in section with numerous pore canals in the roof (Fig. 20). Conceptacles probably protruded above the thallus surface before becoming buried. The conceptacle roof is 4-5 cells in thickness (Fig. 20). Conceptacle chambers are 191 to 355 µm (273.4 ± 57.9 µm) in diameter and 91 to 146 µm (114 ± 16.9 µm) in height. Some conceptacles are secondarily infilled with large adventitious cells.

No male or female conceptacles were found.



Figs 16-17. *Lithothamnion moretii.* **16.** Lectotype of *Lithothamnion moretii* from the Mont Durand, close to St Jean de Sixt; housed at PC in box numbered 48-1/117. (Width of thin section = 2.9 cm). **17.** Section through lectotype *L. moretii* (scale bar = 200 μm).



Figs 18-19. *Lithothamnion moretii.* **18.** Encrusting portion of lectotype of *L. moretii* showing a plumose ventral core (VC). Note cell fusions both in the ventral core (arrows) and in the dorsal peripheral region (arrowheads in the insert) (scale bar = 100 µm). **19.** Flared epithallial cells (arrows) at the thallus surface of *L. moretii* (scale bar = 10 µm).

Discussion. Based on the vegetative anatomy, the presence of flared epithallial cells and the occurrence of multiporate conceptacles, the species belongs to *Lithothamnion* as stated by Lemoine. Its status as a distinct species within *Lithothamnion*, however, requires further assessment, a task beyond the scope of this study.

In the same sample from Mont Durand in which *Lithothamnion moretii* occurs, Lemoine (1928a) reported another new species as *Lithothamnium faurai*. She provided a very short description, indicating the growth morphology of the alga and the cell dimensions. Neither sketches nor pictures accompanied the

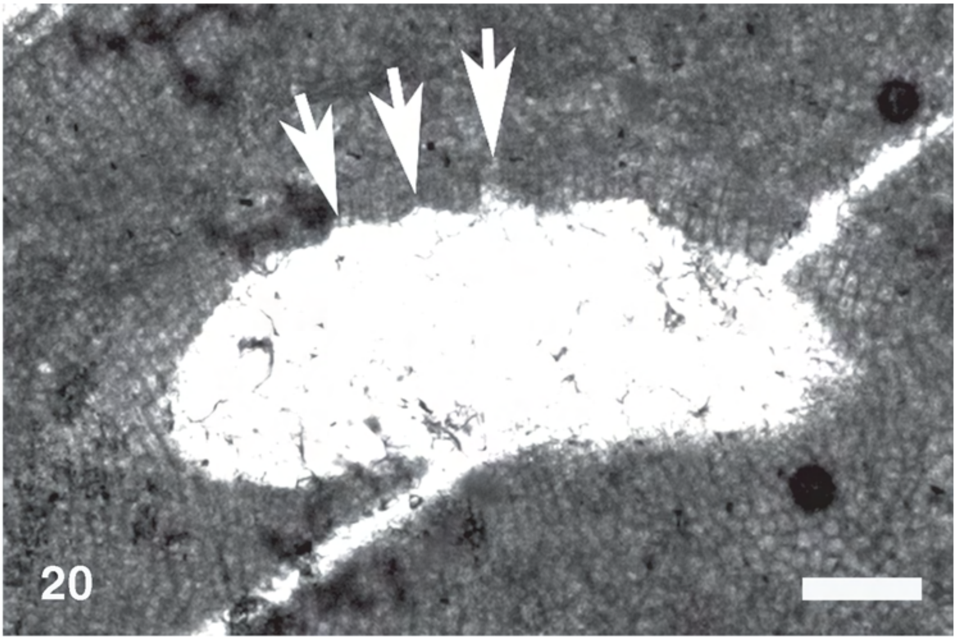


Fig. 20. Section through a multiporate conceptacle of *L. moretii.* Arrows point to three distinct pore canals in the roof of the conceptacle (scale bar = 100 µm).

description and, thus, the species name was not validly published (Art. 38.1 of the ICBN, McNeill *et al*., 2006). In the protologue, Lemoine (1928a; p. 548) stated that *L. faurai* also occurs in middle Eocene (Lutetian) rocks of Catalonia (NE Spain) and was formally described in another paper (Lemoine, 1928b, pp. 97-98). Unfortunately, the Catalonia material appears missing, and thus the status of *L. faurai* remains uncertain pending rediscovery of the Catalonian material or neotypification after reassessment of material from the type locality.

Genus *Mesophyllum* Lemoine, 1928c

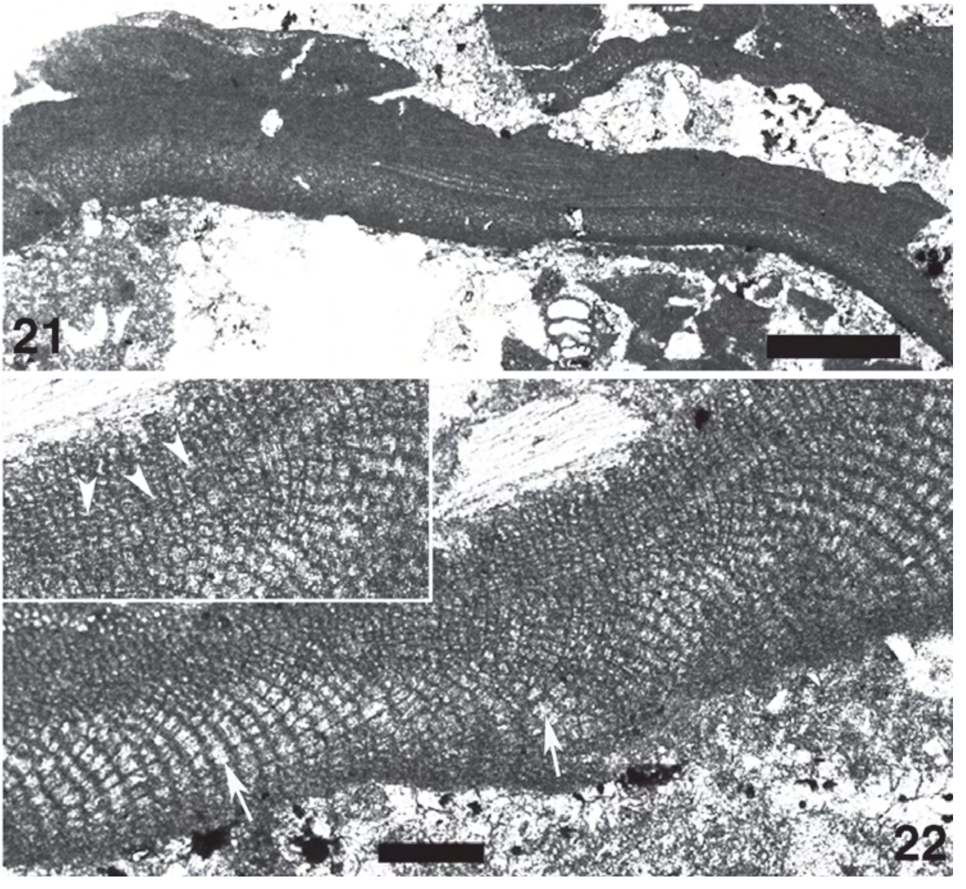
Lectotype species *Mesophyllum lichenoides* (Ellis) Lemoine, 1928c; designated by Ishijima (1942).

Mesophyllum koritzae (Lemoine) Lemoine, 1928c **Figs 2, 21-25**

Basionym. *Lithophyllum koritzæ* (*Bulletin de la Société géologique de France*, 1924, pp. 279-280, Figs 4-5).

Holotype. Lemoine (1924, p. 279) based *Lithophyllum koritzae* on a single specimen, which therefore constitutes the holotype (ICBN, Art. 9.1). In the protologue, Lemoine (1924, p. 279) referred to a specific thallus: "*A la base d'un massif de* L. Bourcarti *on observe une espèce crustacée à laquelle je donne ce nom nouveau; la section mince montre la presence de plusieurs thalles de cette spèce*..." (Lemoine, 1924, p. 279, fig. 4).

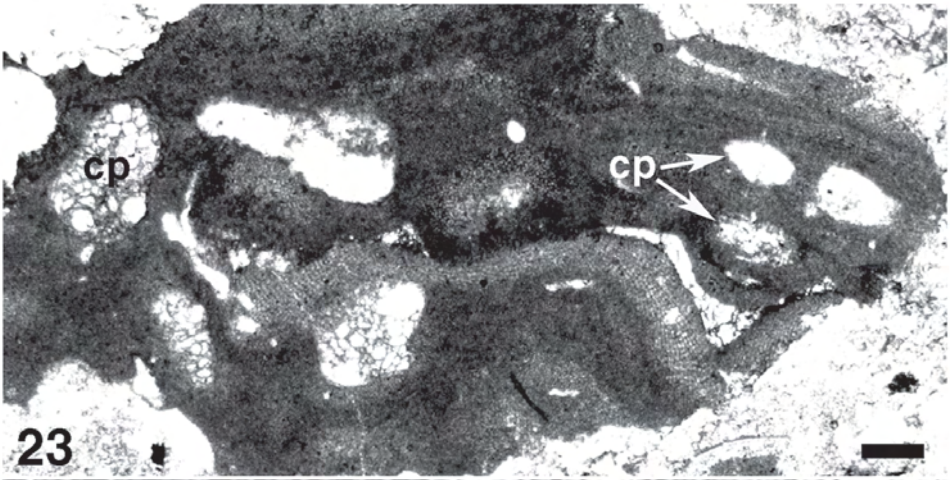
This thallus (Fig. 21), which forms part of the holotype, is easily identifiable in the thin section (Fig. 2) preserved at PC in box 48-1/93. That thin

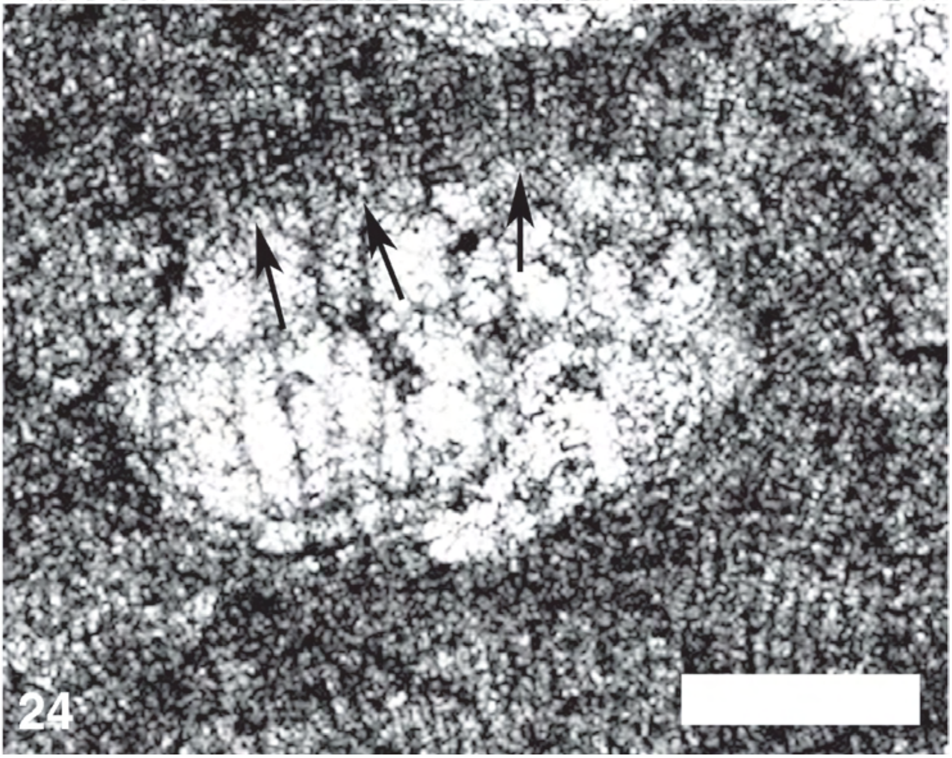


Figs 21-22. *Mesophyllum koritzae.* **21.** Thallus of holotype of *Mesophyllum koritzae* preserved on thin section at PC in box 48-1/93 (see Fig. 2). This image is of the specimen drawn by Lemoine (1924: fig. 4) (scale bar = 500 µm). **22.** Slightly oblique section showing monomerous organization of *M. koritzae*, with a thick coaxial ventral core and a thinner dorsal peripheral region. Arrows indicate cell fusions in the ventral core (scale bar = 100 µm). Insert shows an enlarged area of the thallus showing cell fusions in the peripheral region (arrowheads).

section also includes individuals of *Lithothamnion bourcartii* and individuals originally identified as '*Lithophyllum prelichenoides*'. In addition to the thin section, box 48-1/93 includes one rock sample, and a label handwritten by Lemoine, which in part reads "*La section mince montre de plus un thalle de* Lithophyllum prelichenoides *Lem.* Koritzae" (Fig. 2). The epithet *prelichenoides* is crossed out and the name *koritzae* is added at the end of the sentence in pencil by Lemoine (Fig. 2). This correction of the species name was not made on the label of the thin section.

Two additional thin sections (numbered 7a and 7b) containing conceptacle-bearing thalli of *M. koritzae* were prepared during the present study from the rock in box 48-1/93. Additional information on the rock and other material in box 48-1/93 is provided in the account of *Lithothamnion bourcartii* (see above) because the protologue of that species (Lemoine 1924, p. 277) is based





Figs 23-24. *Mesophyllum koritzae.* **23.** Multiporate conceptacles (cp) of *M. koritzae*, some of them secondarily filled by large cells (scale bar = 100 µm). **24.** Enlarged view of multiporate conceptacle of *M. koritzae* secondarily infilled with large cells. Arrows point to the base of three pore canals (scale bar = 100 µm).

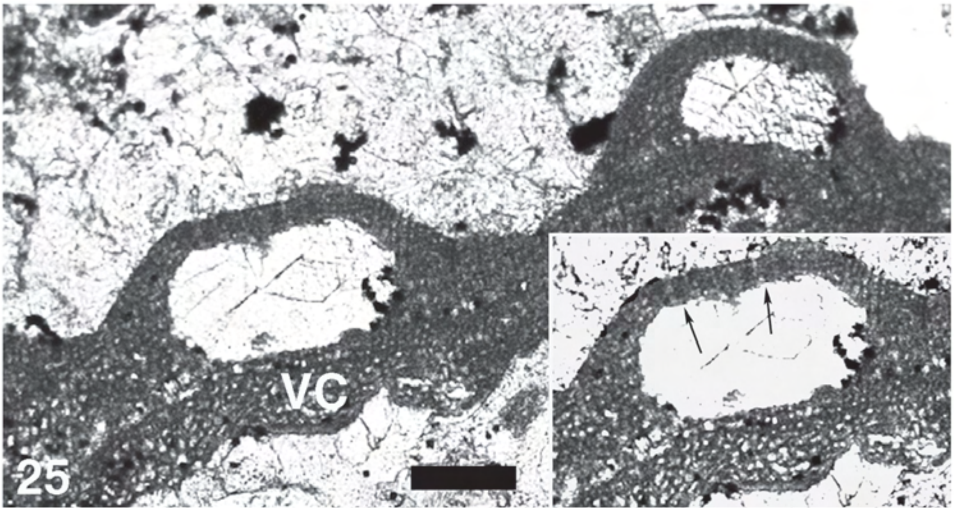


Fig. 25. Laminar coralline alga with a plumose ventral core (VC) and two protruding multiporate conceptacles preserved with the type material of *M. koritzae*. (scale bar = 100 µm). Inset is a slightly enlarged view of the conceptacle on the left side of the picture showing the base of two pore canals in the conceptacle roof (arrows).

in part on individuals on the same thin section that contains the thallus (Fig. 21) cited by Lemoine (1924, p. 279) in the protologue of *Mesophyllum koritzae*.

Description of the holotype. The holotype possesses a dorsiventral monomerous organization, with a thick ventral core (180-220 µm) with a coaxial arrangement of cells of adjacent filaments (Figs 21-22). The ventral core is approximately half of the thickness of the thallus and is formed by filaments growing parallel to the base of the thallus in the centre of the core and radiating downwards and upwards to the peripheral region. There are numerous cell fusions. Cells range from 18 to 27 µm (20.9 ± 2.5 µm) in length and from 5 to 11 µm (8.9 ± 1.5 µm) in diameter (Fig. 22).

Filaments in the peripheral region are more or less perpendicular to the surface of the thallus and consist of quadrangular cells measuring 7 to 14 µm (10.3 ± 2 µm) in length and 7 to 11 µm (8.7 ± 1.3 µm) in diameter. Cell fusions are conspicuous and cells are not laterally aligned.

In one of the newly prepared thin sections of the holotype, buried multiporate conceptacles occurred, some in-filled by adventitious cells (Figs 23-24). Conceptacle chambers are more or less ovoid in section, 260-350 µm in diameter and 150-160 µm high. Male or female conceptacles were not found.

Discussion. In the protologue of *Mesophyllum koritzae* (as *Lithophyllum*), Lemoine (1924) mentioned two conceptacles, 300-350 µm in diameter, with 4-5 pore canals in the roof. In the thin section preserved at PC, there is a thallus fragment with two conceptacles (Fig. 25), but this fragment is from thin laminar alga with a very thin plumose ventral core and a peripheral region consisting of large, quadrangular cells with no lateral alignment. Conceptacles are prominent on the thallus surface and ovoid in shape. Several pore canals are visible in one of the conceptacles (Fig. 25). None of these features fit with the holotype, and this thallus almost certainly belongs to a different (unidentified) species.

Lemoine (1928c) established *Mesophyllum* for species of nongeniculate corallines with multiporate conceptacles and with coaxial growth in the core region, and she transferred *Lithophylum kortizae* into *Mesophyllum*, as *M. koritzae* (Lemoine) Lemoine (1928c, p 253) because it has these characteristics. In the subsequent palaeontological literature, *Mesophyllum* traditionally has been delimited by the occurrence of these two features (e.g. Lemoine, 1928c; Braga *et al.*, 1993; Aguirre & Braga, 1998; Braga, 2003; Iryu *et al.*, 2009; Braga *et al.*, 2009a; Aguirre *et al.*, 2011).

As already noted (Basso *et al.*, 1998; Iryu *et al.*, 2009, pp. 412-413), however, some species of the related genus *Synarthrophyton* also show these features, and the character that distinguishes the two genera (unbranched spermatangial filaments in male conceptacles of *Mesophyllum*; branched spermatangial filaments in male conceptacles of *Synarthrophyton*) has never been observed in fossil material. Consequently, using the generic name *Mesophyllum* for fossil species with multiporate conceptacles and coaxial growth is a pragmatic solution to facilitate taxonomic accounts within paleontological publications, as stated by Iryu *et al.* (2009). Athanasiadis *et al.* (2004) indicated that a coaxial ventral core is characteristic in the vast majority of *Mesophyllum* species, and Peña *et al.* (2011), in describing the new species *Mesophyllum sphaericum* Peña *et al.*, have stressed that in the absence of knowledge of spermatangial conceptacles, coaxial growth is a central character in attributing species to *Mesophyllum*.

Family Corallinaceae Lamouroux, 1812

Subfamily Mastophoroideae Setchell, 1943

Genus *Spongites* Kützing, 1841

Lectotype species *Spongites fructiculosus* Kützing, 1841 (as *fruticulosa*); designated by Woelkerling (1985).

Spongites albanensis (Lemoine) Braga, Bosence *et* Steneck, 1993 **Figs 26-30**

Comments. This species is being treated under *Spongites* rather than *Lithophyllum* because available evidence from the type suggests that it is conspecific with *Spongites fruticulosus* as proposed by Braga *et al.* (2009b).

Basionym. *Lithophyllum (?) albanense* Lemoine (*Bulletin de la Société géologique de France*, 1924, pp. 281-282, Figs 8-9).

Type material. Lemoine (1924 p. 281) based *Lithophyllum albanense* on a single specimen, which therefore constitutes the holotype (ICBN, Art. 9.1). The holotype specimen includes in algal nodule (rhodolith) 6.5 cm in diameter – plus three small fragments clearly derived from the same sample – and two thin sections stored in a box numbered 48-1/97 (Fig. 26). The box also includes a note handwritten by Lemoine with the name of the species (*Lithophyllum (?) albanense*), the age of the sample (Burdigalian), the locality (Koritza, Albania) and the numbering probably used by Bourcart (Bourcart x22) (Fig. 26). The two thin sections, labelled as Bourcart x22[a] and Bourcart x22[b], have two labels written by Lemoine with the same information as that of the note in the box (Fig. 26). Lemoine added a question mark to the genus in the note but not in the two thin sections (Fig. 26). It seems that the addition of the question mark in the note was added later to highlight the doubtful attribution of the species to the genus *Lithophyllum*.

Description of the holotype. The holotype is warty to fruticose with robust branches, up to 9 mm in diameter (Fig. 26). It has a dorsiventral monomerous organization with a thin plumose ventral core consisting of filaments orientated

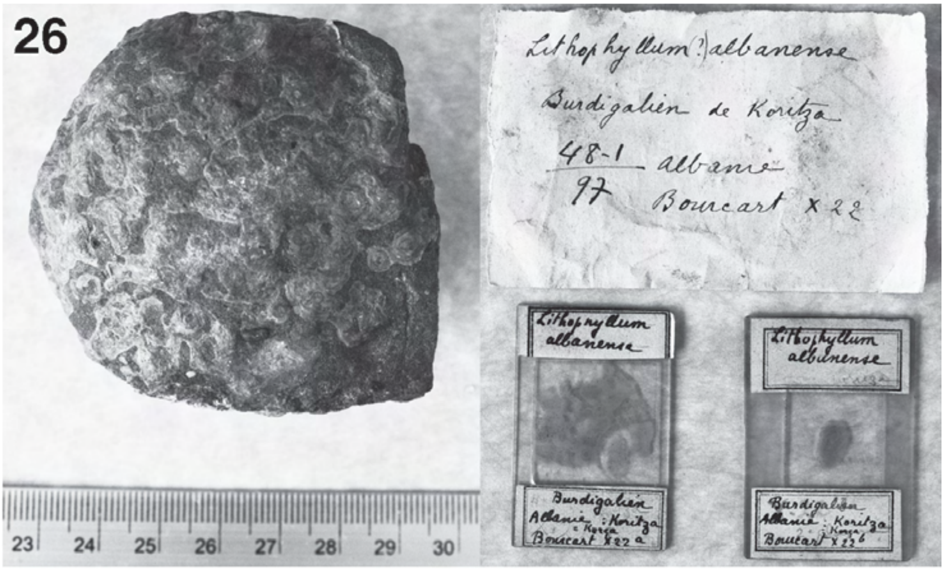


Fig. 26. Holotype of *Spongites albanensis* (Lemoine) Braga, Bosence & Steneck preserved at PC in a box numbered 48-1/97. (Width of thin sections = 2.9 cm).

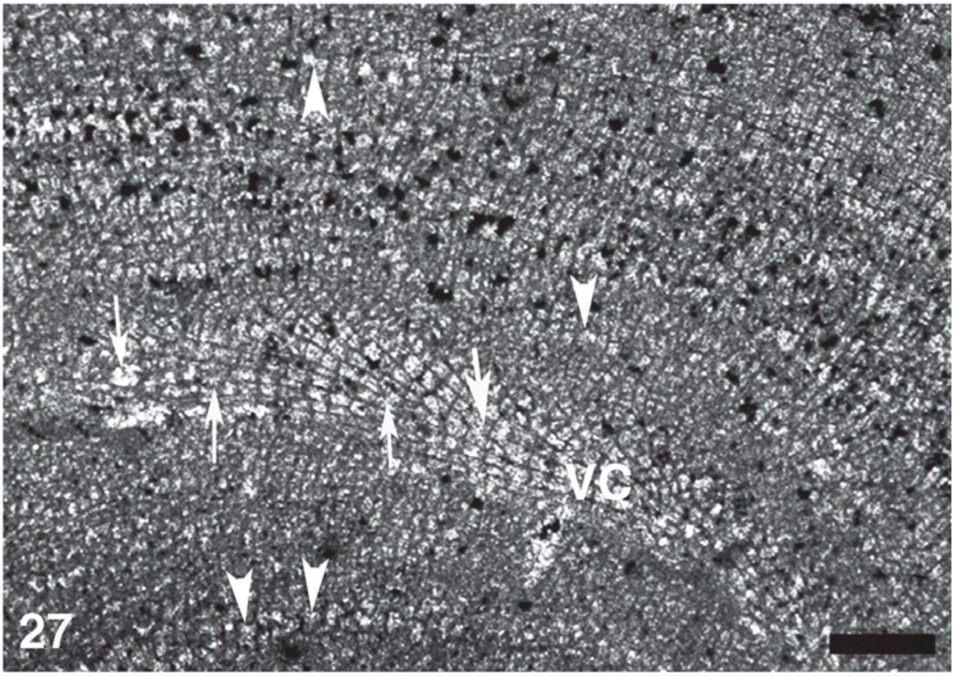
parallel to the base that curve upwards (Fig. 27). Cells are rectangular in section measuring 18 to 32 µm (24.3 ± 3.4 µm) in length and 7 to 14 µm (9.4 ± 1.3 µm) in diameter. Numerous cell fusions are visible (Fig. 27).

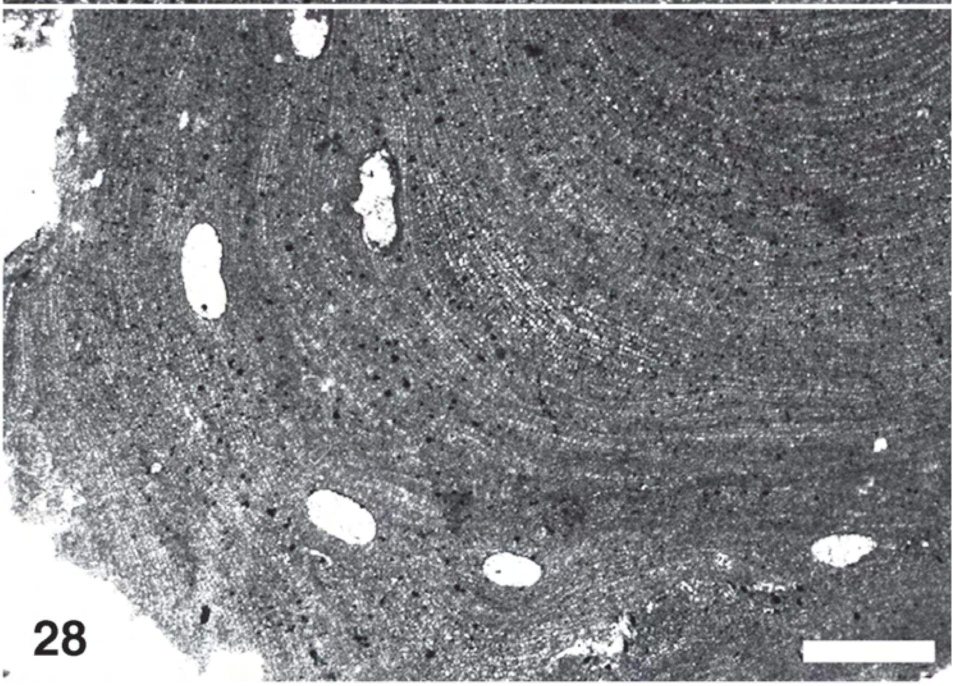
Upright branches are well developed (Fig. 28). Cells are rectangular and increase slightly their size in the centre of branches and columns. They are 11 to 23 µm (15.4 ± 2.5 µm) in length and 7 to 14 µm (9.3 ± 1.9 µm) in diameter. Branches are irregularly zonate (Fig. 28). There is no lateral cell alignment and cell fusions are conspicuous (Fig. 27).

Buried uniporate conceptacles are abundant (Fig. 28). They are ovoid to bean-shaped in section with a single conical pore canal in the roof (Figs 29 & 30). Conceptacles measure 308-510 µm (402.9 ± 70.4 µm) in diameter and 115-212 µm (162.1 ± 36.6 µm) in height. Pore canals can be up to 135 µm (111.4 ± 18.7 µm) in height and 150 µm (138.5 ± 7.7 µm) in diameter at their bases. The floor is occasionally slightly raised centrally; this feature can be interpreted as the possible remnants of a columella (Fig. 30), which, in turn, provides indirect evidence that the conceptacle was tetrasporangial (or possibly bisporangial). Lemoine (1924, p. 282, fig. 9) also illustrated conceptacles with slight central humps.

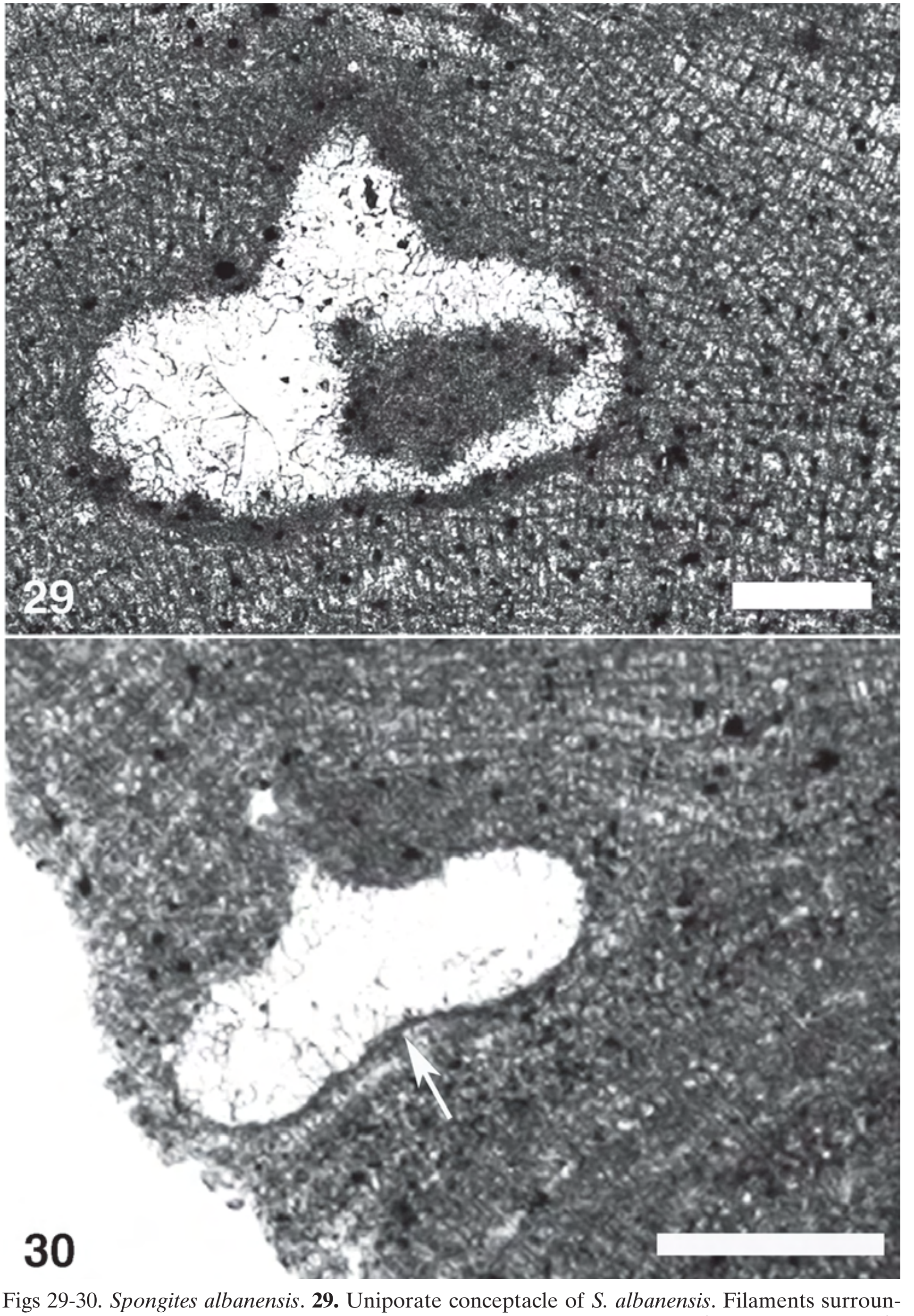
Prior to becoming buried, the conceptacles almost certainly protruded above the surrounding thallus surface. Filaments surrounding the pore canal are not perpendicular to the conceptacle roof, which is up to 9 cells in thickness (Fig. 29). The cell shape and size in the conceptacle roof and around the pore canal do not change in size and morphology with respect to the surrounding cells.

Discussion. Lemoine (1924) stated that this species does not show the typical features of the genus *Lithophyllum* and therefore she made the genus attribution with doubt. However, successive authors have considered this species as certainly belonging to *Lithophyllum*, eliminating the question mark of the original assignment. The species name has had a great impact in the literature of the last





Figs 27-28. *Spongites albanensis*. **27.** Detail of the plumose ventral core (VC) of *S. albanensis*. Numerous cell fusions are present both in the ventral core (arrows) and in the peripheral region (arrowheads) (scale bar = 100 µm). **28.** Section of a branch of *S. albanensis*. Note the presence of an irregularly zonated thallus and uniporate conceptacles (scale bar = 500 µm).



Figs 29-30. *Spongites albanensis*. **29.** Uniporate conceptacle of *S. albanensis*. Filaments surrounding the pore canal are oblique and nearly parallel to the pore-canal wall (scale bar = 100 µm). **30.** Uniporate conceptacle of *S. albanensis*. The floor is slightly raised (arrow) suggesting possible remnants of a columella (scale bar = 250 µm).

century since it is the second more cited species of fossil corallines (Aguirre & Braga, 2005). Braga *et al.* (1993), studying Late Miocene fossil plants from Malta and Spain, concluded that this species should be considered a member of the subfamily Mastophoroideae due to the presence of cell fusions, and uniporate conceptacles. They assigned the species to the genus *Spongites*, as *S. albanensis* (Lemoine) Braga, Bosence *et* Steneck, 1993. However, since the type material of this species has remained undiscovered until now, no comparison was carried out with the original specimens.

Among genera classically included in the subfamily Mastophoroideae, *sensu* Harvey *et al.* (2003) and Harvey & Woelkerling (2007), the species *albanensis* might be accommodated within *Pneophyllum*, *Spongites* or *Neogoniolithon* all of which are monomerous and have filaments orientated more or less obliquely to the walls of the uniporate conceptacle pore canal. The three genera are separated on differences in the distribution of the spermatangia within male conceptacles, the mode of tetrasporangial conceptacle formation and the mode of formation of gonimoblast filaments in female conceptacles (Penrose, 1991, 1992; Penrose & Woelkerling, 1992; Woelkerling, 1996). However, none of these reproductive features are readily preserved in the fossil record, thus making precise generic assignment of fossil species difficult. Braga (2003, p. 52) proposed a twofold alternative; either to consider the three genera as a genus complex in which species can be accommodated, or (assuming that *Pneophyllum* cannot be identified in the fossil record) to attribute those species with a predominantly coaxial organization to *Neogoniolithon* and those with a plumose ventral core to *Spongites*. This follows the original description of Setchell & Mason (1943) who considered filament arrangement in the ventral core a reliable vegetative character to differentiate *Neogoniolithon* and *Spongites*. Woelkerling (1988, pp. 141, 153) maintained this feature as a diagnostic character. Considering the palaeontological practical usage of the arrangement of the filaments at the base of the thallus as a criterion to separate *Neogoniolithon* and *Spongites*, the species *albanensis* can be placed within *Spongites* as emended by Braga *et al.* (1993).

S. albanensis is similar to *Spongites fruticulosus* in growth morphology, thallus organization, conceptacle size and shape, as well as cell dimensions (Woelkerling, 1985; Basso & Rodondi, 2006). Based on this, Braga *et al.* (2009b) concluded that Lemoine's species should be treated as a younger heterotypic synonym of *S. fruticulosus*. This treatment is supported by the present study of the type of *S. albanensis*.

Family Corallinaceae Lamouroux, 1812

Subfamily Corallinoideae (Areschoug) Foslie, 1908

Genus *Jania* Lamouroux, 1812

Lectotype species *Jania rubens* (Linnaeus) Lamouroux (1812), designated by Manza (1937)

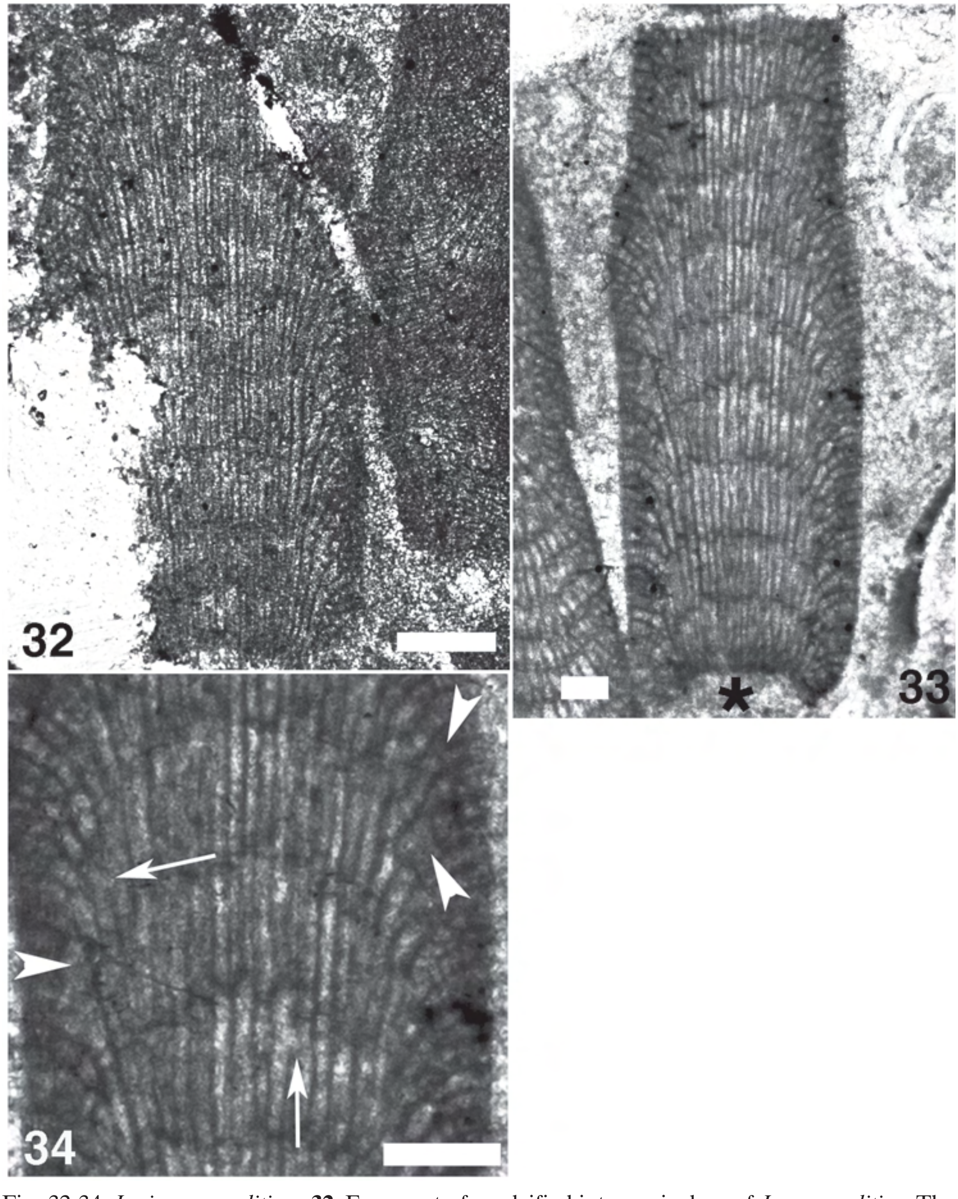
Jania nummulitica Lemoine, 1928a **Figs 31-34**

Jania nummulitica Lemoine (*Bulletin du Muséum d'Histoire naturelle***,** 1928a, pp. 550-551, Fig. 6).

Type material. Lemoine (1928a p. 550) based *Jania nummulitica* on a particular specimen, which therefore constitutes the holotype (ICBN, Art. 9.1). The type collection consists of one rock sample and one thin section within a box labelled

Fig. 31. Holotype of *Jania nummulitica* Lemoine stored at PC in the box numbered 48-1/116. This box also contains the lectotype of *Lithophyllum simplex* (see Fig. 34). (Width of thin section = 2.9 cm).

48-1/116 (Fig. 31). It also contains the lectotype of *Lithophyllum simplex* (see separate account below). The box also includes a note handwritten by Lemoine (Fig. 31), with the box number (48-1/116), the age of the sample (late Eocene), a description of the rock ("*grès calcarifères à Litho.*"), and the locality (Montagne de Veyrier). The thin section, identified as "*plaque 4*", has two labels, one listing the taxa identified in the thin section (*Jania nummulitica*, *Lithothamnium* sp., *Lithophyllum simplex*, *Lp. lichenoides*?) and the other giving details of the locality (Fig. 31). The first three species on the list are in ink whilst the last name, *Lithophyllum lichenoides*?, is in pencil and probably added afterwards. During the present study, three additional thin sections (sections 3a, 3b, 3c) were prepared from the rock sample.



Figs 32-34. *Jania nummulitica.* **32.** Fragment of a calcified intergeniculum of *J. nummulitica*. The protologue sketch (1928b; fig. 6) almost certainly is based on this fragment (scale bar = 100 μm). **33.** Intergeniculum of *J. nummulitica* showing the characteristic concave shape of the intergeniculum-geniculum interface (asterisk) (scale bar = 100 μm). **34.** Enlargement of the central part of the intergeniculum of Fig. 33 showing cell fusions in the core (arrows) and peripheral regions (arrowheads) (scale bar = 50 μm).

In the protologue, Lemoine (1928a, p. 551) states: "*Le fragment décrit ici provident des grès calcarifères de l'Eocène supérieur de la Montagne de Veyrier*". The fragment illustrated by Lemoine (1928a; Fig. 6) in the protologue occurs on the thin section at PC (Fig. 31) and is depicted here in Fig. 32. Further remains occur in the additional thin sections that we cut from the rock sample housed at PC in box 48-1/116.

Description of the holotype. The holotype includes calcified intergenicula of a geniculate coralline (Figs 32 & 33). Although no remains of geniculae have been preserved, the characteristic concave shape of the intergeniculum-geniculum interface indicates that genicula were present (Fig. 33).

Anatomically, intergenicula are monomerous, consisting of a single system of branched laterally coherent filaments that include a central core (medullary) region and a peripheral (cortical) region. Within each intergeniculum, the core region is composed of less than 10 tiers of cells. Cells of adjacent filaments are palisade-like and show poor lateral alignment. They measure 36-73 µm (50.3 ± 13.2 µm) in length (very rarely up to 100 µm) and 5-9 µm (6.8 ± 1.2 µm) in diameter. The filaments arch rapidly in the peripheral (cortical) region, close to the thallus surface, becoming perpendicular to it (Figs 32 & 33). In the peripheral region, the cells are smaller, 5-14 µm (8.1 ± 2.8 µm) in length and 5-9 µm (6.6 ± 1.5 µm) in diameter, and not laterally aligned. Cell fusions occur both in the core and peripheral regions (Fig. 34). No conceptacles have been found.

Discussion. Our observations confirm that this species is a geniculate coralline alga, as Lemoine (1928a) concluded. The presence of cell fusions places it in the subfamily Corallinoideae. Since the intergenicula have less than 10 tiers of medullary cells, the species belongs to the tribe Janieae (Womersley & Johansen, 1996). A molecular phylogenetic study of members of this group, *Jania*, *Cheilosporum* and *Haliptilon*, suggests that these three taxa might be co-generic; the name *Jania* has nomenclatorial priority (Kim *et al*., 2007). Thus, the generic assignment of the species made by Lemoine (1928a) remains correct. Its status as a distinct species within *Jania*, however, requires further assessment, a task beyond the scope of this study.

Taxa of uncertain family and genus placement

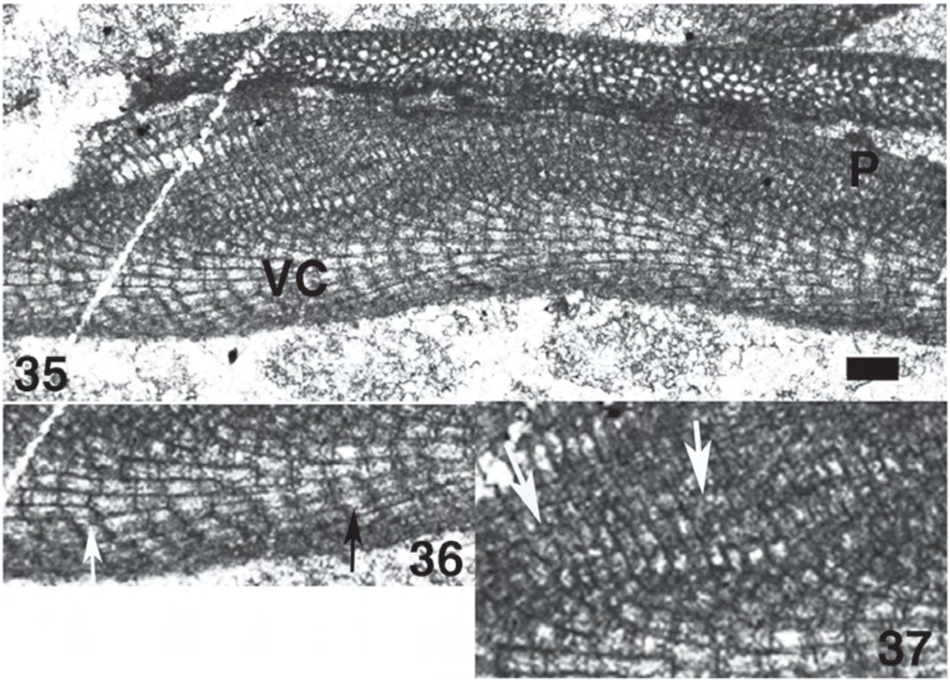
Lithophyllum simplex Lemoine, 1928a **Figs 31, 35-37**

Lithophyllum simplex Lemoine (*Bulletin du Muséum d'Histoire naturelle***,** 1928a, pp. 548-549, Fig. 4).

Original material and lectotypification. Lemoine (1828a) based *Lithophyllum simplex* on late Eocene material from Montagne de Veyrier and from Priabonian of Calvaire de Thônes but did not designate a holotype.

During the present study, the specimen from Montagne de Veyrier was found in PC, and it included the thin section containing the thallus upon which the sketch in the protologue (Lemoine, 1928a; fig. 4) is based. Consequently, we designate here as lectotype, the specimen from Montagne de Veyrier. We have not found the material from Priabonian of Calvaire de Thônes.

The designated lectotype specimen consists of one rock sample and one thin section within a box labelled 48-1/116 (Fig. 31). This collection also contains the holotype of *Jania nummulitica* (see separate account above). A note handwritten by Lemoine, indicating the label of the box (48-1/116), the age of the sample (late Eocene), a description of the rock ("*grès calcarifères à Litho.*"), and the locality (Montagne de Veyrier), is included in the box (Fig. 31). The thin



Figs 35-37. *Lithophyllum simplex*. **35.** Laminar thallus in the lectotype of *Lithophyllum simplex* showing a thick central plumose to coaxial core region (VC) and a thinner peripheral region (P) (scale bar = 50 µm). **36.** Cell fusions (arrows) in the ventral core of *L. simplex* in an enlarged area of the thalus of Fig. 35. **37.** Cell fusions (arrows) in the peripheral region of *L. simplex* in an enlarged area of the thalus of Fig. 35.

section, identified as "*plaque 4*", has two labels: one provides the details of the locality and the other lists the taxa identified in the thin section (*Jania nummulitica*, *Lithothamnium* sp., *Lithophyllum simplex*, *Lp. lichenoides*?). We cut three additional thin sections (sections 3a, 3b, and 3c) from the hand sample.

Description of the lectotype. The lectotype includes laminar thalli with dorsiventral, monomerous internal organization (Fig. 35). There is a thick coaxial to plumose ventral core (up to 170 µm in thickness) and a very thin peripheral region (sometimes absent or not preserved) (Fig. 35). Core region cells are 21 to 32 µm (24.5 ± 3.3 µm) in length and 7 to 14 µm (10 ± 2.2 µm) in diameter. Cell fusions are conspicuous (Fig. 36).

The peripheral region is very thin, 70-90 µm (only rarely reaching 110 µm). Cells of adjacent filaments are not aligned and there are cell fusions (Fig. 37). They are small and quadrangular in section, 5 to 9 µm (7.9 ± 1.5 µm) in length and 7 to 9 µm (8.2 ± 1.1 µm) in diameter.

Conceptacles have not been found, nor were they mentioned by Lemoine (1928a).

Discussion. Lemoine (1928a) based *Lithophyllum simplex* exclusively on vegetative features. She compared *L. simplex* with '*Lithophyllum lichenoides*' (presumably *L. lichenoides* (Ellis) Rosanoff *ex* Hauck, 1883, p. 268 and not *L. lichenoides* Philippi 1837, p. 389 – see Woelkerling 1983b, pp. 317-322 for details), and with *Lithophyllum prelichenoides* Lemoine, 1918, both species having similar vegetative anatomical characters than *L. simplex*. Lemoine added the species name *L. lichenoides* in pencil with a question mark to the label of the thin section "*plaque 4*" (Fig. 31), probably expressing doubt about the separation of this species from the new *L. simplex*.

The presence of numerous cell fusions excludes *L. simplex* from *Lithophyllum*, a genus characterized by the occurrence of secondary pit-connections rather than cell fusions. The lack of conceptacles in the lectotype, however, precludes any reliable generic or family assignment of the species and, consequently, the use of this species name should be avoided.

Lithophyllum sphaeroides Lemoine, 1924 **Figs 38-39**

Lithophyllum sphaeroides Lemoine (*Bulletin de la Société géologique de France*, 1924, p. 281, figs 6-7).

Type material. Lemoine (1924, p. 281) based *Lithophyllum sphaeroides* on a single specimen, which therefore constitutes the holotype (ICBN, Art. 9.1). The holotype specimen includes a note handwritten by Lemoine, one thin section and one rock sample (Fig. 38) stored in a box labelled 48-1/96. On the note, Lemoine wrote *Lithophyllum sphæricum* (see comments below), the age (Burdigalian), the locality (Koritza, Albania), the code of the Bourcart collection (Bourcart H_1b), and she referred to a figure in the paper ("*figuré Lemoine 1923 fig. 5"*) (see Fig. 38). The thin section has two labels, one with the name of the species and the other with the locality and the Bourcart code collection (Albania; Bourcart H_1b). The rock sample is a dark-grey calcarenite containing a small rhodolith with a nucleus made up of a fruticose alga coated by a thin encrusting one. This rock is the one illustrated in the protologue (Lemoine, 1924; Fig. 6). Because no reproductive structures are found in the thin section preserved at PC, we cut three extra thin sections from the sample; thin sections 6a, 6b, and 6c.

On the note and on the thin section label, Lemoine wrote the species name as *Lithophyllum sphæricum* (Fig. 38); however, the species name was published as *Lithophyllum sphæroides* (Lemoine, 1924). Thus, the name *Lithophyllum sphæricum* was a provisional name never published.

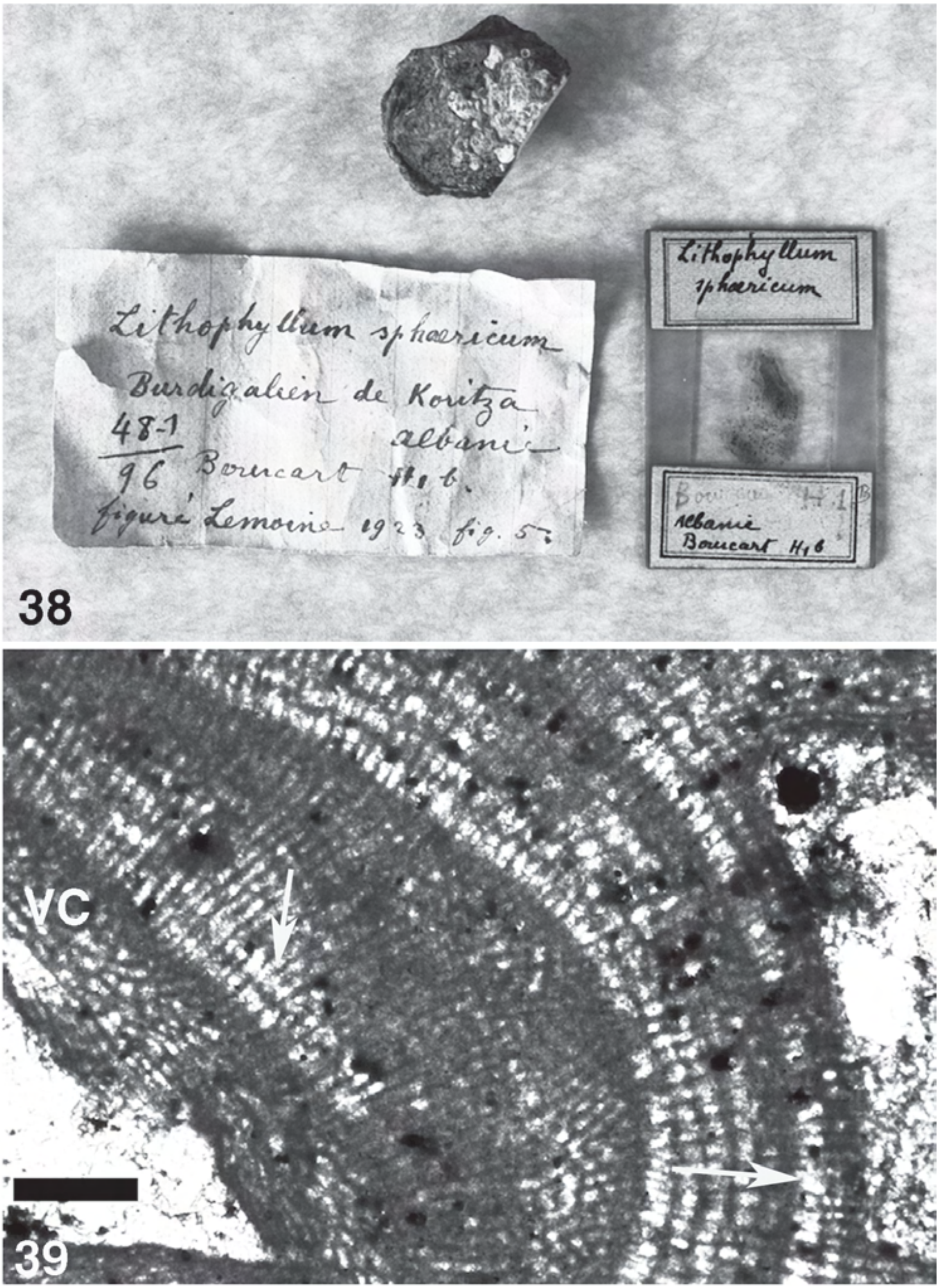
Although Lemoine indicated on the note that this species is shown in figure 5 in the paper (Fig. 38), *L. sphæroides* is actually illustrated in figure 6 (picture of the rock sample) and figure 7 (a sketch of the cells).

Description of the holotype. The holotype of *Lithophyllum sphaeroides* is a fruticose rhodolith. The thallus base is monomerous with a dorsiventral organization and a thin plumose ventral core up to 100 µm thick (Fig. 39). Filaments run approximately parallel to the base of the thallus in the lower part of the ventral core and then curve upwards. Cells are rectangular in section with thick walls, and measure 14 to 24 µm (18.6 ± 3.4 µm) in length and 5 to 10 µm (6.7 ± 1.8 µm) in diameter. Cell fusions are present (Fig. 39).

Fruticose branches arising from the dorsiventral basal region are regularly zonate (Fig. 39). Cells are rectangular or polygonal in section and cell size decreases from the base to the top in each band (Fig. 39). Cells are mostly 14 to 24 µm (19 ± 4 µm) in length and 5 to 10 µm (8.3 ± 1.7 µm) in diameter. Cell fusions are conspicuous, and only locally cells are laterally aligned (Fig. 39). As in the ventral core, cell walls are very thick.

No reproductive structures have been observed.

Discussion. Lemoine (1924) distinguished this species by having fruticose external growth morphology and thick cell walls: "*les cloisons séparant les rangées de cellules sont très épaisses, caractère assez rare dans les espèces fossiles*" (Lemoine, 1924;



Figs 38-39. *Lithophyllum sphaeroides.* **38.** Holotype of *Lithophyllum sphaeroides* Lemoine preserved at the PC in the box numbered 48-1/96. The rock sample is the one shown by Lemoine (1924; Fig. 6). (Width of thin section = 2.9 cm). **39.** Section through holotype of *L. sphaeroides*. Note the plumose ventral core (VC) and the large cells with thick cell walls. Numerous cell fusions occur (arrows) (scale bar = 100 µm).

p. 281 and Fig. 7). Cell-wall thickness, growth form, cell size both in ventral core and peripheral region, and general thallus organization are similar to those observed in *Lithothamnion corallinaeforme*. Cell fusions indicate that the species can not be attributed to the genus *Lithophyllum*. Nonetheless, the absence of reproductive structures in the holotype precludes any reliable family or generic adscription, and thus use of the name *Lithophyllum sphaeroides* should be avoided.

Lithothamniom abrardii Lemoine, 1934 **Figs 40-41**

Lithothamnium abrardi Lemoine (*Vestnik Státniho Geologického Ustavu Ceskoslovenské Republiiky*, 1934, pp. 274-275, fig. 3).
Syntype material at PC. Lemoine (934, p. 274-275) based the protologue primarily on material from the western Carpathian Mountains but also mentioned that the Carpathian material belonged to the same species as material found in Donzacq (Landes, SW France): "*Cet échantillon des Carpathes me paraît appartenir à la même espèce que des échantillons du Lutétien moyen du S. O. de la France, provenant de Donzacq près Bastennes (Landes), que j'ai etudiés il y a quelques annés, mais dont la description n'avait pas été publiée*". Lemoine, however, did not designate a holotype and thus, nomenclaturally, the Carpathian specimen and the Donzacq specimen are considered syntypes (ICBN, Art. 9.4).

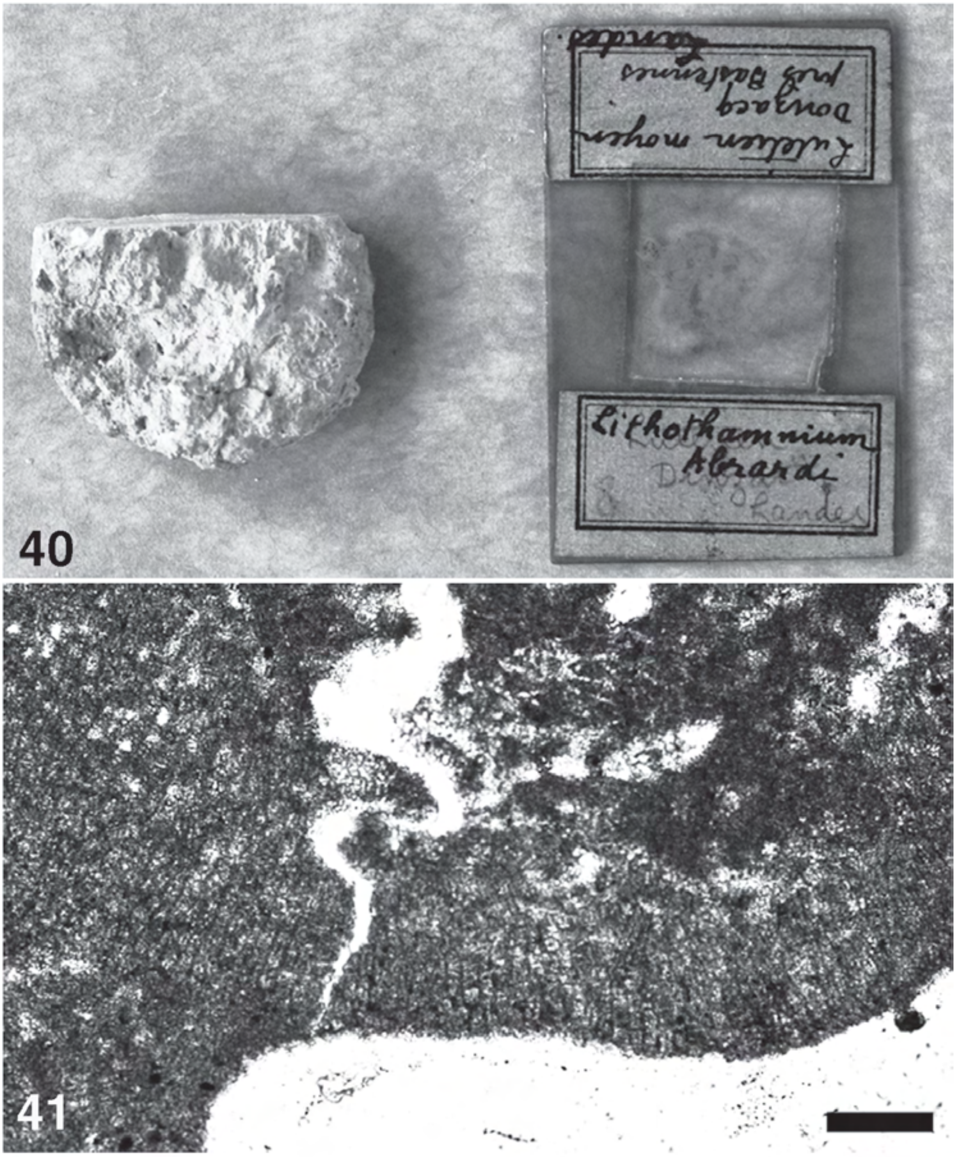
The Carpathian syntype has not been found in PC and its whereabouts is unknown. The French syntype, however, has been found in PC. We have decided not to designate a lectotype because the Carpathian specimen might still be found and the French specimen is very poorly preserved.

The French syntype consists of one rock sample and a thin section numbered 8 in pencil (Fig. 40). The thin section has two labels written by Lemoine: one with the name of the species (*Lithothamnium Abrardi*) and the other with the age of the sample ("*Lutetien moyen*") and the French locality (*Donzacq près Bastennes, Landes*) (Fig. 40). The sample is a *Nummulites* test, 2.7 cm in diameter, coated by a thin coralline crust. Two additional thin sections, sections 8a and 8b, have been prepared during the present study.

The alga both in the original thin section and in the newly prepared ones only shows obliquely cut filaments (Fig. 41). The poor preservation of the material precludes any detailed description of vegetative characters and no reproductive structures have been found. Consequently, the French syntype specimen cannot be assigned to a genus, subfamily or family, and use of the name *Lithothamnion abrardii* should be avoided.

CONCLUDING REMARKS

Original collections of nine fossil species described by the reputed phycologist Marie Lemoine have been found recently at PC. The material corresponds to species originally described as: *Lithothamnium corallinæforme*, *Lithothamnium bourcarti*, *Lithophyllum koritzae*, *Lithophyllum sphæroides* and *Lithophyllum? albanense*, from Albania (Lemoine 1924); *Lithothamnium moreti*, *Lithophyllum simplex* and *Jania nummulitica*, from Haute-Savoie (Lemoine, 1928a); and *Lithothamnium abrardi* originally described from the western Carpathians (Lemoine, 1934). In the protologues of these species, Lemoine emphasized the general vegetative morphology and cell size as the main taxonomic characters. The species are reassessed from a modern taxonomic perspective and typified in cases where Lemoine did not identify holotypes (Table 1).



Figs 40-41. *Lithothamnion abrardii* Lemoine. **40.** PC syntype of *Lithothamnion abrardii* Lemoine from Donzacq (Landes, SW France). (Width of thin section = 2.9 cm). **41.** Section of French syntype of *Lithothamnion abrardii*, showing obliquely cut filaments (scale bar = 100 µm).

Spongites albanensis, either included in *Lithophyllum* or in *Spongites* by different authors, and *Lithothamnion moretii* are species names of fossil corallines that have had a great impact among palaeophycologists during the last century as they are among the five most cited fossil coralline species in the literature (Aguirre and Braga, 2005). The species *Lithophyllum simplex* is among the nine most cited species (Aguirre and Braga, 2005). The generic assignment of *L. moretii* and

Table 1. Summary table of taxa studied indicating their original names, their taxonomic status as a result of this study, and the nature of the type material examined

Original names	*This study*	*Typification*
Lithothamnium bourcarti	*Lithothamnion bourcartii*	Lectotype (Tirana material)
Lithothamnium corallinæforme	*Lithothamnion corallinaeforme*	Holotype (Koritza material)
Lithothamnium moreti	*Lithothamnion moretii*	Lectotype (Mont Duran material)
Lithophyllum koritzæ	*Mesophyllum koritzae*	Holotype (Koritza material)
Lithophyllum ? albanense	*Spongites fruticulosus* (heterotypic synonym *Spongites albanensis* (Lemoine) Braga, Bosence *et* Steneck, 1993)	Holotype (Koritza material)
Jania nummulitica	*Jania nummulitica*	Holotype (Montagne de Veyrier material)
Lithophyllum simplex	Uncertain family and genus placement (presence of cell fusions)	Lectotype (Montagne de Veyrier material)
Lithophyllum sphaeroides	Uncertain family and genus placement (presence of cell fusions)	Holotype (Koritza material)
Lithothamnium abrardi	Uncertain family, subfamily and genus placement (poorly preserved material)	Syntype (Donzaq, Landes, material)

S. albanensis are well established. However, this is not the case for *L. simplex* taking into consideration the original material.

For three of these species we concluded that the taxonomic status and generic assignment, widely accepted as such by most scientists, are actually uncertain. Further, this reinforces the urgent necessity of reassessing original collections of fossil corallines in order to clarify their taxonomic status, and the on-going reassessment of fossil types also will contribute to the analyses of more far-reaching issues, such as palaeobiogeography, diversity changes through time, and evolutionary patterns.

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