

Taxonomic assessment of coralline algal species (Rhodophyta; Corallinales and Sporolithales) described by PFENDER, LEMOINE, and MIRANDA from northern Spain type localities

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(With 6 figures)

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Abstract

We have studied fossil coralline algal species described by PFENDER, MIRANDA, and LEMOINE from type localities in northern Spain. PFENDER (1926) described three new species from Camarasa (eastern Pyrenees, Lleida, NE Spain): *Archaeolithothamnium Oulianovi*, *Archaeolithothamnium Lugeoni*, and *Lithothamnium camarasae*. In the samples collected in this type locality, we have found specimens assignable to the last two species described herein as *Sporolithon lugeonii* (PFENDER) GHOSH & MAITHY, 1996, and *Lithothamnion camarasae* PFENDER, 1926. MIRANDA (1935) described two new species from Playa de Merón (NE San Vicente de la Barquera, Santander, N Spain): *Lithophyllum Royoi* (as well as *Lithophyllum Royoi* form *tenuis*) and *Melobesia Lemoinei*. We have recognized specimens attributable only to the latter species and we propose the new combination *Hydrolithon lemoinei* (MIRANDA) AGUIRRE, BRAGA & BASSI. Finally, LEMOINE (in LEMOINE & MENGAUDI 1934) studied samples from Roiz, Los Vía, and La Haya, three localities south of San Vicente de la Barquera, and described the species *Lithothamnium cantabricum*, *Lithophyllum quadrangulum*, *Lithophyllum Mengaudi*, and *Jania Mengaudi*. The only coralline algae recognized in the samples from Roiz, the type locality of *Lithothamnium cantabricum*, are plants of the genera *Sporolithon* and *Lithoporella*, as well as *Distochoplax biserialis* (DIETRICH) PIA, 1934, but no coralline algae attributable to the genus *Lithothamnion*. The description and illustration provided by LEMOINE (in LEMOINE & MENGAUD 1934) in the protologue are insufficient to associate any plants in the original localities with this name. Therefore, the circumscription of *Lithothamnium cantabricum* cannot be properly deciphered and the use of this name should be avoided. The examined specimens of *Lithophyllum quadrangulum* do not show enough taxonomic characters to be confidently placed in any coralline genus. In any case, the presence of cell fusions indicates that the species does not belong to *Lithophyllum*. The new combinations *Mesophyllum mengaudii*

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(LEMOINE) AGUIRRE, BRAGA & BASSI and *Arthrocardia mengaudii* (LEMOINE) AGUIRRE, BRAGA & BASSI are proposed for the remaining two species.

Keywords: Eocene, Oligocene, Cenozoic, Corallinae Algae, Systematics, Redescription, Neotype designation

Introduction

In the last century, most species names of fossil coralline algae were established using questionable taxonomic criteria such as cell dimensions and growth morphology (BOSENCE 1991; BRAGA & AGUIRRE 1995). The lack of well-defined diagnostic criteria together with relatively poor illustrations makes it difficult to understand the circumscription of a very large number of fossil coralline species. This was one of the reasons that led authors to introduce new species names instead of using the names already available for identifying newly collected examples, increasing the number of species names with no improvement in the methods of delimiting the new taxa (AGUIRRE & BRAGA 2005). As a consequence, it is very difficult to confidently assign specific names to fossil corallines in many cases.

One approach to solving this problem is to assess the type material of established species following new taxonomic criteria (e.g. PILLER 1994; RASSER & PILLER 1994; AGUIRRE et al. 1996; AGUIRRE & BRAGA 1998; VANNUCCI et al. 2000; BRAGA et al. 2005; BASSI et al. 2005; QUARANTA et al. 2008; IRYU et al. 2009; VANNUCCI et al. 2009, 2010). In many cases, however, the type collections cannot be found or are definitively lost. In those circumstances, re-sampling the type localities and studying their algal assemblages may contribute to improve our understanding of the original species (BASSI et al. 2002; AGUIRRE & BRAGA 2005). Accordingly, we have collected and examined samples of fossil corallines from Palaeogene rocks in Spanish localities belonging to the Pyrenean domain as well as to the Basque-Cantabrian region (Fig. 1), in which coralline species were described by Juliette PFENDER, M. Paul LEMOINE, and F. MIRANDA.

PFENDER (1926) described three coralline species as *Archaeolithothamnium Lugeoni*, *Archaeolithothamnium Oulianovi*, and *Lithothamnium camarasae* from the Eocene deposits of Camarasa (Catalonian Pyrenees) (Fig. 1A). LEMOINE (in LEMOINE & MENGAUD 1934) and MIRANDA (1935) identified new coralline species from Eocene and Oligocene rocks, respectively, from the environs of San Vicente de la Barquera (Cantabria, N Spain) (Fig. 1B). LEMOINE (in LEMOINE & MENGAUD 1934) described *Lithothamnium cantabricum*, *Lithophyllum Mengaudi*, *Lithophyllum quadrangulum*, and *Jania Mengaudi*, and MIRANDA (1935) described *Lithophyllum Royoi*, *Lithophyllum Royoi* forma *tenuis*, and *Melobesia Lemoinei*.

We sampled the original localities looking for specimens assignable to the species there established and we have re-described some of them following a modern approach. We have been able to confidently identify specimens attributable to all these species except

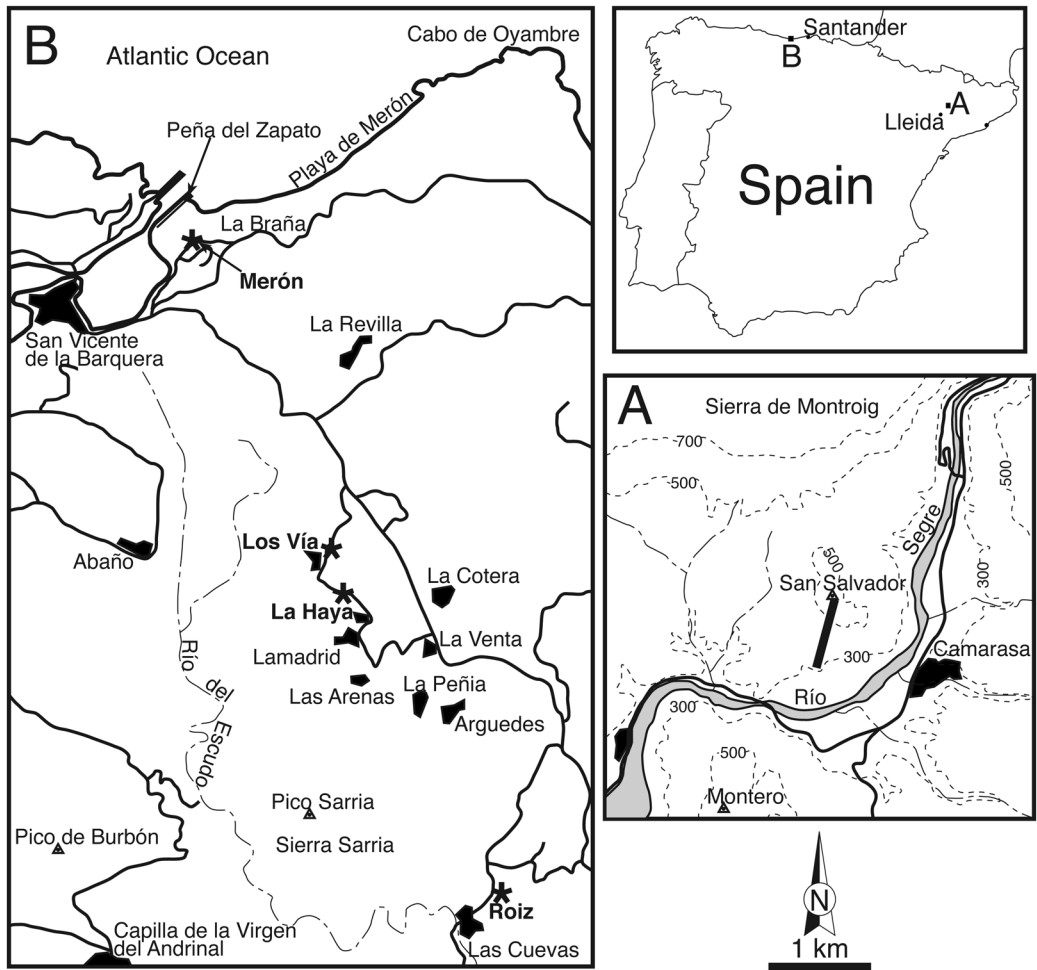


Fig. 1. A: Location map of Camarasa. The black bar indicates the studied section. B: Localities close to San Vicente de la Barquera. Asterisks indicate the sampling sites.

Archaeolithothamnium Oulianovi, *Lithophyllum Royoi* (as well as *Lithophyllum Royoi* forma *tenuis*), and *Lithothamnium cantabricum*. In the case of the former two species, no plants have been found showing the features of the taxa, which were relatively well described and illustrated in the protologue. In the case of *L. cantabricum*, the information provided by LEMOINE (in LEMOINE & MENGAUD 1934) in the protologue is insufficient to discern whether any plants in the original localities can be associated with this name. We designate neotypes according to Article 9.6 of the International Code of Botanical Nomenclature (McNEILL et al. 2006) for several species, as the original material seems to be lost.

Methods

Rock samples were collected from the original localities and cut into ultrathin sections: 50 from the Eocene algal limestones of Camarasa, 35 from the Eocene and 29 from the Oligocene rocks of San Vicente de la Barquera. All the material is housed at the Department of Stratigraphy and Palaeontology of the University of Granada. Since this work focusses only on the species first described in the studied localities, the total algal assemblages were not examined. According to the recent molecular phylogeny proposed by LE GALL et al. (2010), coralline algae are divided into two orders: Sporolithales and Corallinales. The former includes only one family, Sporolithaceae, whereas the latter consists of two families, Hapalidiaceae and Corallinaceae. The phylogenetic classification scheme of HARVEY et al. (2003) is followed for the subfamily and genus levels. Thallus orientation and nomenclature, and measured dimensions of cells and reproductive structures are those of WOELKERLING (1988), and terminology of growth forms is that of WOELKERLING et al. (1993).

Description of the localities

Type locality of PFENDER'S material

The original material is from San Salvador hill, immediately northwest of Camarasa (eastern Pyrenees, Lleida province, NE Spain) in the Sierra de Montroig on the right-hand bank of the Segre River (Fig. 1A). The locality belongs to the so-called Sierras Marginales, the externalmost part of the central zone of the Pyrenean mountain belt (ULLASTRE & MASRIERA 1995, 1996). The location of the section originally studied by PFENDER (1926) can be easily identified by the description in the text: "*Au Sud de ces lames cretaciques, l'Éocène forme des parois qui se terminent au sommet méridional de la colline. Au bas de ces escarpements se trouvent des terrasses cultivées, en gradin, chacune d'entre elles soutenue par un mur. Cet espace en gradins cultivés, qui s'étend sur l'éboulis, est limité au Sud par une nouvelle muraille, très redressée, toutefois moins en saillie que celle du Campanien.*" (PFENDER 1926: p. 322).

The studied section (Fig. 2A), about 250 m in thickness, can be divided into two distinct parts. The lower part consists of about 120 m of breccias and conglomerates with clasts of Jurassic and Cretaceous dolostones and limestones embedded in a carbonate matrix. The upper part is made up of an alternation of thin conglomerate beds with carbonate clasts and thick beds of bioclastic calcarenites (packstones and grainstones). Calcarenites in the lower 80 m are very rich in benthic foraminifers, mainly alveolinids. The presence of *Glomalveolina lepidula* HOTTINGER, 1960, *Alveolina trempina* HOTTINGER, 1960, *Alveolina* cf. *oblonga* D'ORBIGNY, 1826, and flusculinizzate alveolinids indicates an Ypresian age (early Eocene); uppermost SBZ-4-lowermost SBZ-10 according to the shallow benthic foraminifer zones of SERRA-KIEL et al. (1998). In the upper 50 m, calcareous



Fig. 2. **A:** Panoramic view of the Colina de San Salvador section (Camarasa), the type locality of *Sporolithon lugeonii* and *Lithothamnion camarasae*. Algae are especially abundant in the limestone beds at the upper part of the section. **B:** Partial view of the lower part of the Oligocene sequence at Playa Merón. This part of the section is close to La Braña, mentioned by MIRANDA (1935) as the type locality of *Hydrolithon lemoinei* (see Fig. 1B).

algae occur together with benthic foraminifers, fragments of bivalves, and corals. Here, corallines occur as fragments of branches loosely dispersed in the matrix, and very occasionally forming small fruticose rhodoliths with long branches. The rare occurrence of *Pellatispira madaraszi* (HANTKEN) BOUSSAC, 1906 suggests a middle–late Eocene age (latest SBZ-18 to SBZ-20). The section ends with thin beds of limestones intercalating thin beds of marls.

Type locality of MIRANDA'S material

The material studied by MIRANDA was collected by Royo-Gómez at a site precisely located by MIRANDA (1935: p. 279): “Según me comunica el Sr. Royo y Gómez, los ejemplares proceden de los conglomerados rojos de la parte inferior del Oligoceno de la playa de Merón, situados en el extremo occidental del escarpe de la Braña, frente a la llamada Peña del Zapato”. This locality is immediately northeast of San Vicente de la Barquera (Santander, N Spain), in the southernmost part of Playa Merón (Fig. 1B).

The rocks at Playa Merón are the only Oligocene marine deposits in the western Pyrenean domain and the Basque-Cantabrian region (PORTERO-GARCÍA & RAMÍREZ DEL POZO 1976; PUJALTE et al. 2002). The complete Oligocene sequence is ~300 m thick and includes reddish marls, limestones, and conglomerates and sands (PORTERO-GARCÍA & RAMÍREZ DEL POZO 1976). The coralline algae described by MIRANDA (1935) are from the reddish conglomerates and sands in the lower part of the Oligocene section (Fig. 2B). The clasts are from Eocene and Cretaceous limestone including corals. Coralline algae encrust some of the clasts, making up nodules with thin algal coatings. MIRANDA (1935) described the new species as *Lithophyllum Royoi* (*Lithophyllum Royoi* forma *tenuis*) and *Melobesia Lemoinei*.

Original localities of LEMOINE'S material

LEMOINE'S original samples come from three localities southeast of San Vicente de la Barquera (Cantabria, N Spain) (Fig. 1B): 1) Roiz, an area of a few small hamlets. The precise locality is an outcrop near the hamlet of Las Cuevas, south of Sierra Sarría (“Saria” in LEMOINE & MENGAUD 1934) (Fig. 3A); 2) A road-cut close to the hamlet of Los Vía (“Losbia” in LEMOINE & MENGAUD 1934) (Fig. 3B); 3) A road-cut near La Haya (“La Hoya” in LEMOINE & MENGAUD 1934) (Fig. 3C). All these sites are easily accessible and close to each other along the road from San Vicente de la Barquera to Treceño. In addition to the geographical locations, Mengaud provided descriptions of the rocks in which the algae were collected to facilitate the identification of the sites.

The original samples comprise lower Eocene (Roiz) and upper Eocene (Los Vía and La Haya) limestones belonging to the so-called San Vicente de la Barquera syncline (PORTERO-GARCÍA & RAMÍREZ DEL POZO 1976; PUJALTE et al. 2002). These rocks can be laterally followed along a W-E(SE) cartographic belt for several kilometres. The Roiz section includes a lower part consisting of ~70 m of whitish massive limestone (grainstone) with abundant alveolinids and miliolids (“*calcaire à Alvéolines*” of LEMOINE & MENGAUD 1934). The upper part, 20–30 m in thickness, is made up of thick algal packstone beds intercalating thin marly beds (“*calcaire à Algues*” of LEMOINE & MENGAUD 1934). The algal limestones are rich in benthic foraminifers, mostly alveolinids, small nummulitids and miliolids, fragments of bryozoans, and corals. Small rhodoliths and fragments of algal branches are scattered amongst these bioclasts. Lemoine described the species *Lithothamnium cantabricum* in samples from the upper limestones.

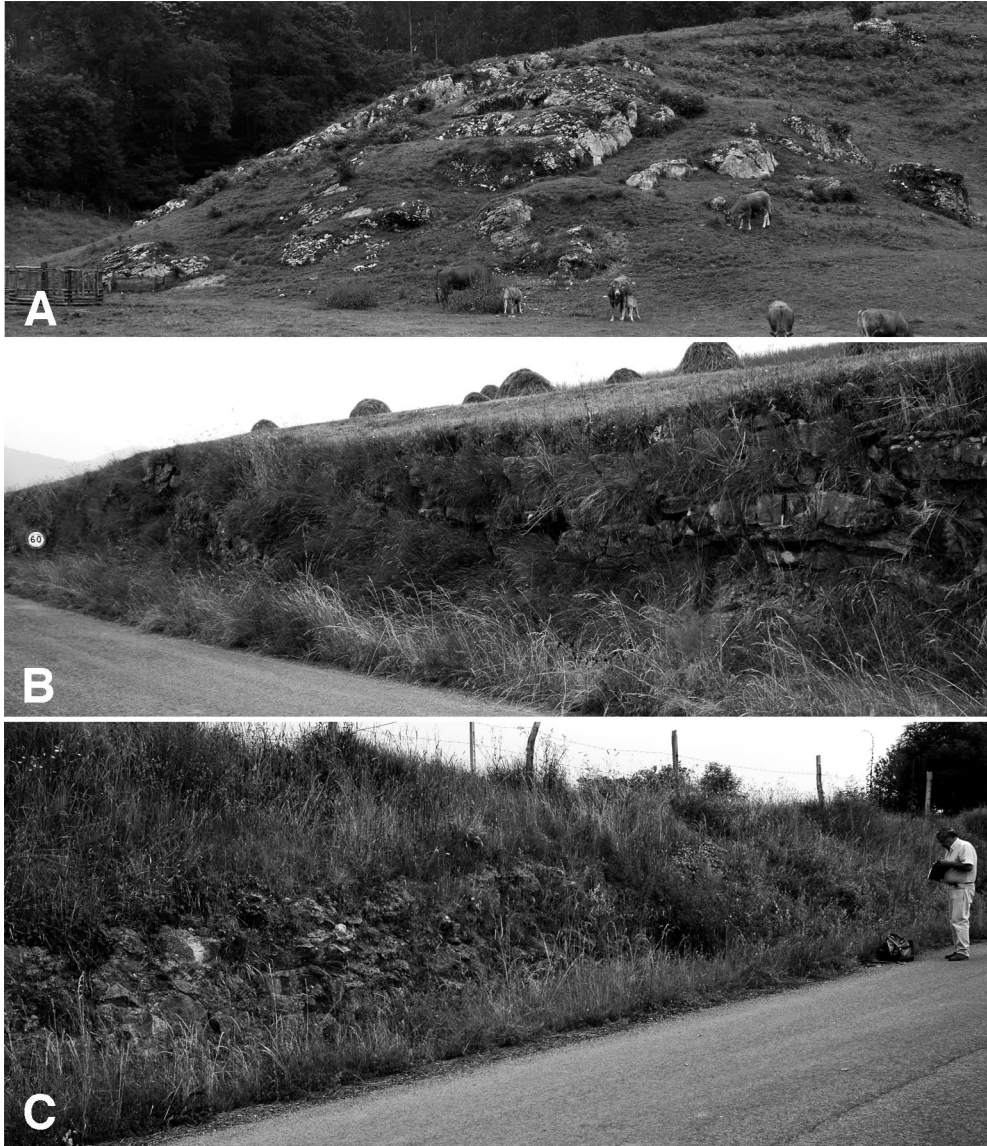


Fig. 3. **A:** Upper part of Roiz, where limestone beds intercalate with marly beds (“*calcaire à Algues*” of MENGAUD in LEMOINE & MENGAUD 1934). **B:** Los Vía type locality of *Mesophyllum mengaudii* and *Arthrocardia mengaudii*. Reddish limestones (“*calcaire rose à Polypiers*” of MENGAUD in LEMOINE & MENGAUD 1934) crop out at a small road cut. **C:** La Haya, original locality of *Arthrocardia mengaudii* and *Lithophyllum quadrangulum*, an outcrop of reddish limestone.

The upper Eocene deposits include pinkish-red, decimetre-scale bioclastic limestone beds alternating with centimetre-scale marl interbeds. The limestone beds are packstones-rudstones including channelized breccias and conglomerates of limestone clasts with boulders up to several decimetres in diameter. The limestone contains abundant corals, sponges, vermetid gastropods, benthic foraminifers, bivalves, and coralline algae (“*calcaire rose à Polypiers*” of LEMOINE & MENGAUD 1934). Dasycladaleans and halimedaleans, as well as the peyssonneliacean *Polystrata alba* (PFENDER) DENIZOT, 1968, are also present. In Los Vía, the red algal limestone is 12 m thick, whereas in La Haya only 2 m are exposed. Lemoine described three species from this limestone: *Lithophyllum Mengaudi*, *Lithophyllum quadrangulum*, and *Jania Mengaudi*.

Systematic palaeontology

Phylum Rhodophyta WETTSTEIN, 1901

Class Florideophyceae CRONQUISRT, 1960

Subclass Corallinophycidae LE GALL & SAUNDERS, 2007

Order Sporolithales LE GALL, PAYRI, BITTNER & SAUNDERS, 2010

Family Sporolithaceae VERHEIJ, 1993

Genus *Sporolithon* HEYDRICH, 1897a

***Sporolithon lugeonii* (PFENDER) GHOSH & MAITHY, 1996**

1926 *Archaeolithothamnium Lugeoni* PFENDER, p. 324, Pls 9, 12.

Neotype: PFENDER (1926) did not designate a holotype, but she did publish two pictures of a specimen. One is a general view (Pl. 9) and the other is a close-up of the thallus (Pl. 13). These illustrations and Pfender’s precise description of the diagnostic characters make it easy to unambiguously identify several specimens belonging to this species amongst the new samples. Since Pfender’s original material seems to be lost, we here designate as neotype (Art. 9.6 ICBN, McNEILL et al. 2006) sample PFCAM-3-2. The neotype material includes a hand sample, a whitish bioclastic limestone (packstone-grainstone), and two thin sections labelled PFCAM-3-2 and PFCAM-3-2’ (Figs 4A, C and D) cut from it. Plants of the species also occur in other samples from the type locality (for example, PFCAM-3-3B, Fig. 4B).

Type locality: The San Salvador hill in the Sierra de Montroig, immediately northwest of Camarasa, in the eastern Pyrenees (Lleida, Catalonia, NE Spain).

Age: Middle–Late Eocene (latest SBZ-18 to SBZ-20, in the biozonation of SERRA-KIEL et al. 1998).

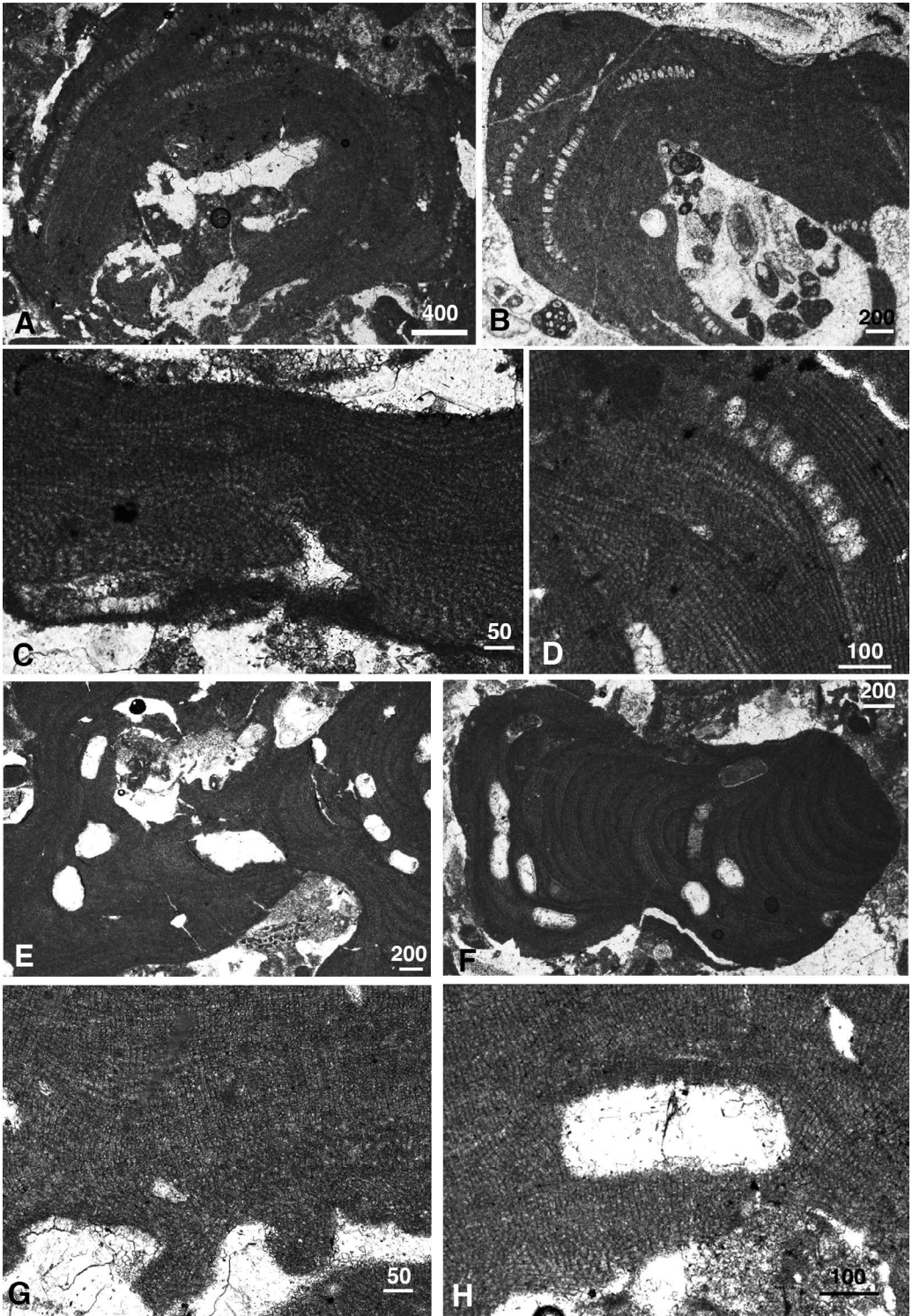
Description of the neotype: It includes encrusting to warty plants (Figs 4A and B) forming small nodules (rhodoliths). Encrusting portions of plants can be up to 1 mm thick. Protuberances (warts) are up to 2.5–3 mm long and 2 mm wide.

Thalli show a dorsiventral, monomerous organization with a thin (up to 100 μm), plumose ventral core (Fig. 4C). Cell filaments in the core curve upwards to give way to the peripheral region. Cells in the ventral core are rectangular in section, measuring 14–28 μm in height ($21.1 \mu\text{m} \pm 2.9$; mean \pm standard deviation) and 6–18 μm wide ($10.8 \mu\text{m} \pm 2.9$). Cell fusions are visible.

The peripheral region is well developed and homogeneous with no internal zonation (Figs 4A and B). Cells are rectangular in section and measure 8–20 μm in length ($12.5 \mu\text{m} \pm 3.1$) and 4–10 μm ($8.1 \mu\text{m} \pm 4$) in diameter. Cells of adjacent filaments are relatively well aligned and frequently fused.

Sporangial reproductive structures consist of sporangial compartments grouped into abundant sori flush with the thallus surface. As the alga grew, sori became buried in the thallus parallel to its surface (Figs 4A and B). A single sorus consists of up to 25 cavities. In vertical section, sporangial compartments are elongated and rectangular-ovoid in shape, whereas in oblique-transverse section they are round. They are 30–40 μm ($35.2 \mu\text{m} \pm 4.3$) in diameter and 65–95 μm ($76.2 \mu\text{m} \pm 8$) in height. Sporangial cavities developed on a layer of relatively elongated cells (up to 30 μm in length) (Fig. 4D). Possible remnants of a stalk cell can be observed at the base of some compartments. No sexual conceptacles have been found.

Remarks: The reproductive structures in the neotype are characteristic of sporangial plants of the order Sporolithales and the occurrence of single stalk cells is diagnostic of *Sporolithon* HEYDRICH, 1897a (WOELKERLING 1988, 1996; TOWNSEND et al. 1994). However, the preservation potential in fossil plants of features separating the other sporolithalean genus, *Heydrichia* TOWNSEND, CHAMBERLAIN & KEATS 1994, such as more than one stalk cell and filaments at the wall of each sporangial compartment, is unknown. PFENDER (1926) mentioned in the protologue of *Sporolithon lugeonii* that smaller cell and sporangial-cavity dimensions separate the species from *Sporolithon nummuliticum* (GÜMBEL) GHOSH & MAITHY, 1996 described by ROTHPLETZ (1891; as *Lithothamnium nummuliticum*). Examination of specimens attributable to *Sporolithon nummuliticum* from its type locality confirms Pfender's opinion.



Order Corallinales SILVA & JOHANSEN, 1986

Family Hapalidiaceae GRAY, 1864; emended by HARVEY,
BROADWATER, WOELKERLING & MITROVSKI, 2003

Subfamily Melobesioideae BIZZOZERO, 1885

Genus *Lithothamnion* HEYDRICH, 1897b***Lithothamnion camarasae* PFENDER, 1926**1926 *Lithothamnium camarasae* PFENDER, pp. 325-327, Pls 11, 14.

Neotype: PFENDER (1926) did not designate a holotype and the original material seems to be lost. Plants belonging to the species can be unequivocally identified following the illustrations and description of PFENDER (1926). The fruticose growth morphology, regular banding in the branches, and size of the sporangial conceptacles separate this species from others at the type locality. The best preserved plants occur in sample PFCM-3-2, which is designated here as neotype. This sample is also the neotype of *Sporolithon lugeonii* and includes a hand sample and two thin sections labelled PFCAM-3-2 (Figs 4E, G and H) and PFCAM-3-2'. Plants of *Lithothamnion camarasae* appear in other samples from the type locality as well (for example, PFCAM-3-3', Fig. 4F).

Type locality: The San Salvador hill in the Sierra de Montroig, just northwest of Camarasa, in the eastern Pyrenees (Lleida, Catalonia, NE Spain).

Age: Middle–Late Eocene (late SBZ-18 to SBZ-20 in the biozonation of SERRA-KIEL et al. 1998).

Description of the neotype: Plants occur as small algal nodules (rhodoliths) or as isolated branches. They are fruticose with long, slender branches (up to 6 mm long and 1 mm wide, exceptionally 2 mm in diameter) (Figs 4E and F) that show apical dichotomous divisions. Adjacent branches might coalesce and filaments of both branches can be fused together. Occasionally, encrusting growth forms appear as lateral flat expansions.

- ◀ Fig. 4. **A:** Encrusting plant in the *Sporolithon lugeonii* neotype. Thin section PFCAM-3-2. **B:** Thallus of *S. lugeonii* in thin section PFCAM-3-3B. **C:** Plumose arrangement of cell filaments in the ventral region of *S. lugeonii*. Neotype. Thin section PFCAM-3-2'. **D:** Detail of a sorus of *S. lugeonii*. Note well-defined lateral cell alignment in the peripheral region. Neotype. Thin section PFCAM-3-2'. **E:** General view of fruticose plants of *Lithothamnion camarasae* with sporangial conceptacles in the peripheral region. Neotype. Thin section PFCAM-3-2. **F:** Branch of *Lithothamnion camarasae* in thin section PFCAM-3-3'. Growth zones are well developed in the peripheral region. **G:** Plumose ventral region of *Lithothamnion camarasae*. Neotype. Thin section PFCAM-3-2. **H:** Slightly protruding multiporate sporangial conceptacle of *Lithothamnion camarasae*. Several small, conical pores are visible in the roof of the conceptacle. Neotype. Thin section PFCAM-3-2.

Thalli show dorsiventral monomerous organization with a plumose, thin (up to 90 μm) ventral core at the base of the branches (Fig. 4G). Cell filaments rise from the ventral side of the thallus curving upwards to the peripheral region. In encrusting portions of plants, the ventral core is thicker (up to 150 μm) than at the base of the branches. Cells are rectangular in section, measuring 10–25 μm (17.5 $\mu\text{m} \pm 3.8$) in height and 5–12 μm (6.8 $\mu\text{m} \pm 1.7$) in diameter. Cell fusions are present.

The peripheral region is well developed. In encrusting portions, it is thin (up to 50 μm) with neither growth zones nor lateral cell alignment. The inner part of the branches consists of a central or medullar core of arched tiers of cells showing growth zones (Figs 4E and F). Cell filaments run parallel to the axis of the branch in its centre and curve outwards to become perpendicular to the branch surface. Growth zones are thicker in the central part of the medulla and wedge out towards the periphery (Fig. 4F). In the medulla centre, zone thickness varies between 10 μm and 34 μm (21.6 μm on average). Cells are rectangular in section, measuring 8–23 μm (14.8 $\mu\text{m} \pm 3.8$) in height and 5–10 μm (7.8 $\mu\text{m} \pm 1.2$) in diameter. Cell fusions are conspicuous and generally there is no lateral cell alignment.

Flat cells, rectangular in section, at the thallus surface can be interpreted as epithallial cells.

Multiporate sporangial conceptacles, protruding slightly on the thallus surface, are abundant (Figs 4E and F). Conceptacle roof is flat and made up of filaments with 4–5 cells (Fig. 4H). Conceptacles are buried in the thallus and aligned in rows parallel to the growth zones. Their section is rectangular with rounded corners and their size varies depending on the sectioning; they are 175–480 μm (292.8 $\mu\text{m} \pm 71.8$) in diameter and 105–200 μm (133.9 $\mu\text{m} \pm 20.2$) in height (Fig. 4H). Pore canals are very thin and surrounded by cells similar in size and shape to those in the rest of the peripheral region. No sexual conceptacles can be observed.

Remarks: The flared character of the preserved epithallial cells is not completely obvious. However, as the preservation potential of the sharp corners of flared epithallial cells is very low due to very weak calcification at the top of their lateral walls, we assume that a flat rectangular section of preserved cells reflects its original flat, flared nature. Consequently, we propose that the species *L. camarasae* be retained in the genus *Lithothamnion*.

Genus *Mesophyllum* LEMOINE 1928

Mesophyllum mengaudii (LEMOINE) AGUIRRE, BRAGA & BASSI comb. nov.

Basionym: *Lithophyllum Mengaudi* LEMOINE, 1934 (in LEMOINE & MENGAUD 1934: Algues calcaires de l'Éocène de la province de Santander, Espagne). Bulletin de la Société de Histoire Naturelle de Toulouse; pp. 176–177, Figs. 2 and 3).

Neotype: LEMOINE (1934) did not designate a holotype and the original material seems to be lost. Figure 3 is intercalated in the protologue of *Lithophyllum Mengaudi* and, even if LEMOINE did not refer to it in the text, it likely represents a drawing of the species. The figure represents a portion of a coaxial core (hypothallium) and part of the peripheral region (perithallium). Plants belonging to this species can unequivocally be identified, according to this figure and the description of the species made by LEMOINE (1934), in samples from the localities mentioned in the protologue. We designate sample LOS VIA-2-1 as the neotype. This material includes one hand sample, a reddish bioclastic limestone (grainstone), and one thin section (LOS VIA-2-1) (Figs 5B and C). Sterile plant fragments have been observed in other samples from the type locality (LOS VIA-2-2 and LOS VIA-4', Fig. 5A).

Type locality: Los Vía, south of San Vicente de la Barquera (Santander, N Spain), erroneously written by Lemoine as Losbia (see above).

Age: Late Eocene.

Description of the neotype: They are unattached laminar plants consisting of constant thickness (up to 0.7 mm). Thalli show monomerous organization and conspicuous coaxial arrangement of the core, 250–300 μm in thickness (Fig. 5A). Cells in the core are rectangular in section, measuring 27–43 μm ($34.9 \mu\text{m} \pm 3.9$) in height and 7–17 μm ($10.8 \mu\text{m} \pm 3.1$) in diameter. Cell walls are thick and cell fusions, although present, are not abundant.

Coaxial core filaments curve upwards, and occasionally downwards as well, giving way to the peripheral region (Fig. 5A). In detail, the transition from one portion of the thallus to the other is as drawn by LEMOINE (in LEMOINE & MENGAUD 1934: Fig. 3). The peripheral region is thin (130–225 μm) with no obvious inner zonation or banding (Figs 5B and C). Cells are relatively big, measuring 8–21 μm ($13.7 \mu\text{m} \pm 3.6$) in length and 7–13 μm ($7.9 \mu\text{m} \pm 1.5$) in diameter. Numerous cell fusions are present. There is no lateral alignment of cells of adjacent filaments. Isolated trichocytes are observed.

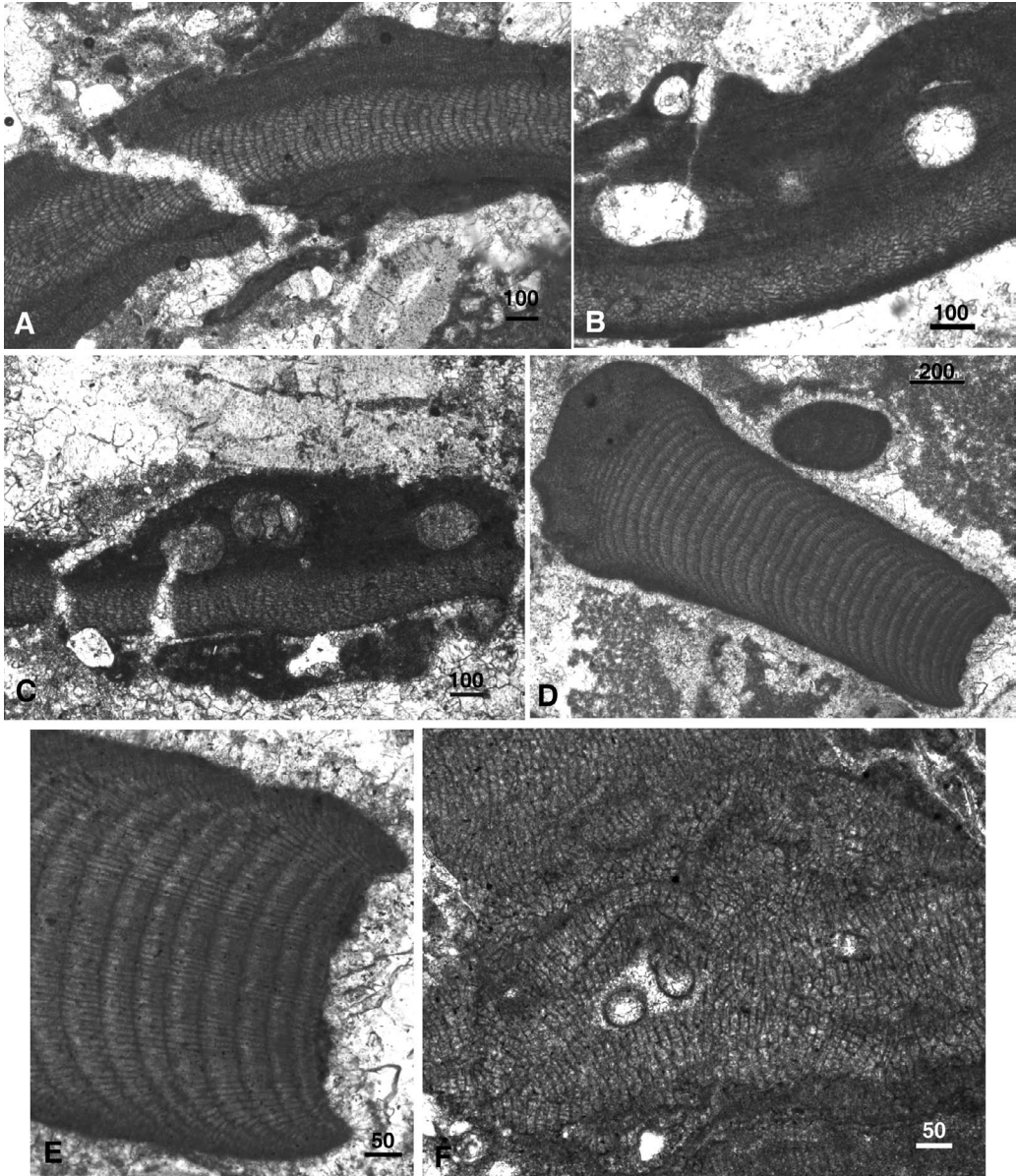
Multiporate sporangial conceptacles (Figs 5B and C) are rounded in section and protrude slightly on the thallus surface. Conceptacle size is 170–260 μm ($200 \mu\text{m} \pm 35.6$) in diameter by 130–150 μm ($136 \mu\text{m} \pm 7.6$) in height. Conceptacle roof is 7–8 cells thick. Pore canals are conical in shape, measuring up to 33 μm and are bordered by cells similar to the surrounding ones.

No sexual conceptacles have been observed.

Remarks: LEMOINE (in LEMOINE & MENGAUD 1934) described the presence in one plant of a conceptacle measuring 410 μm in diameter and 160 μm in height but she neither sketched it nor indicated the number of pores in the roof. In the material from the localities mentioned in the protologue, we have identified multiporate sporangial conceptacles in plants attributable to the species according to the rest of the anatomical features, such as growth form, thallus organization, as well as cell size. However, these conceptacles are clearly smaller than the one observed by Lemoine, the nature of which is uncertain

(perhaps sexual or cystocarpic). It is even unclear whether the plant bearing it belongs to the same species.

The presence of multiporate sporangial conceptacles and the coaxial arrangement of the core of the plant, allow for assignment of the species to *Mesophyllum* as delimited in its traditional palaeontological usage (e.g. LEMOINE 1928; BRAGA et al. 1993; BRAGA 2003; IRYU et al. 2009). Consequently, we propose the new combination *Mesophyllum mengaudii*.



Family Corallinaceae LAMOUROUX, 1812

Subfamily Corallinoideae (ARESCHOUG) FOSLIE, 1908

Tribe Corallineae ARESCHOUG, 1852

Genus *Arthrocardia* DECAISNE, 1842***Arthrocardia mengaudii* (LEMOINE) AGUIRRE, BRAGA & BASSI comb. nov.**

Basionym: *Jania Mengaudi* LEMOINE, 1934 (in LEMOINE & MENGAUD 1934: Algues calcaires de l'Éocène de la province de Santander (Espagne). Bulletin de la Société de Histoire Naturelle de Toulouse; pp. 178–179, Figs 5 and 6).

Neotype: LEMOINE (1934) did not designate a holotype and the original samples seem to be lost. The description and figures in the protologue of the species, however, allow for identification of plants assignable to the species both in Los Vía and La Haya localities. We designate here sample LOS VIA-1 from the former locality as the neotype. The neotype material includes twelve fragments from the large original piece of rock and seven thin sections cut from it (labelled LOS VIA-1-1 to LOS VIA-1-7) (Figs 5D and E).

Type locality: Los Vía, south of San Vicente de la Barquera (Santander, N Spain), erroneously written by LEMOINE as Losbia (see above).

Age: Late Eocene.

Description: The neotype includes geniculate coralline algae appearing as fragments of isolated intergenicula scattered in the sediment.

No complete genicula have been observed. The morphology of the apical parts of intergenicula suggests bifurcations (Fig. 5D) as well as pinnate branching.

Intergenicula are elongated, up to 1.7 mm long and 550 µm wide. They consist of more than 25 (up to 33) tiers of elongated, palisade-like medullary cells. These cells measure 30–57 µm (45.5 µm ± 8.5) in length and 5–10 µm (6.9 µm ± 1.5) in diameter. In transverse

- ◀ Fig. 5. **A:** Laminar plant of *Mesophyllum mengaudii* showing a central coaxial core with peripheral regions at both sides (thin section LOS VIA-4'). **B–C:** Two laminar thalli in the neotype of *Mesophyllum mengaudii* showing rounded multiporate sporangial conceptacles, which protrude slightly on the thallus surface. Thin section LOS VIA-2-1. **D:** Intergeniculum in the *Arthrocardia mengaudii* neotype with more than 25 tiers of elongated, palisade-like medullary cells. At the top of the intergeniculum (upper left corner of the picture), a bifurcation is observed. Thin section LOS VIA-1-1. **E:** Detail of the base of the intergeniculum in D showing very thin (two to three cell layers) cortex. Close to the margin, medullary filaments curve outwards being almost perpendicular to the plant surface. **F:** Encrusting plant of *Hydrolithon lemoinei*, tightly attached to another coralline alga with an uniporate sporangial conceptacle, protruding on the thallus surface. Neotype. Thin section MERON-1-17).

sections, medullar cells are rounded to polygonal in shape. Cell fusions are present and cells are laterally well aligned.

Medullar filaments are surrounded by 1–2 rows of cortical cells (Fig. 5E). They are rectangular in shape, measuring 10–30 μm ($18.8 \mu\text{m} \pm 5.3$) in length and 7–13 μm ($8.9 \mu\text{m} \pm 1.8$) in diameter. Cell fusions are present in the cortex.

Neither sporangial nor sexual conceptacles have been observed.

Remarks: Present-day tribes Corallineae and Janieae, in the subfamily Corallinoideae, can be separated by the number of tiers of medullary cells in the intergenicula, an anatomical feature preservable in the fossil record. Members of the former tribe have 10–25 (up to 50) tiers of medullary cells, whereas members of the latter have 3–6 (up to 25) (WOMERSLEY & JOHANSEN 1996). Since the examined fragments have more than 25 (up to 33) tiers of medullary cells, they can confidently be assigned to the tribe Corallineae. Within this tribe, the genus *Arthrocardia* is characterized by having more than 20 (up to 50) tiers of medullary cells (WOMERSLEY & JOHANSEN 1996). Therefore, the species can confidently be attributed to the genus *Arthrocardia* and the new combination *Arthrocardia mengaudii* is proposed.

Subfamily Mastophoroideae SETCHELL, 1943

Genus *Hydrolithon* (FOSLIE) FOSLIE, 1909

***Hydrolithon lemoinei* (MIRANDA) AGUIRRE, BRAGA & BASSI comb. nov.**

Basionym: *Melobesia Lemoinei* MIRANDA, 1935 (Algas coralináceas fósiles del Terciario de San Vicente de la Barquera (Santander); pp. 284–285; Figs 3A and 3B; Pls 38, Fig. 1).

Neotype: MIRANDA (1935) did not designate a holotype and the original samples of *Melobesia Lemoinei* seem to be lost. The drawings (Figs 3A and 3B) and the photo (Pl. 38, Fig. 1), together with the description provided by MIRANDA in the protologue, allow for confident identification of abundant plants belonging to the species in the type locality. Plants showing the diagnostic anatomical features and well-preserved sporangial conceptacles occur in the thin section MERON-1-17, which is designated as the neotype (Fig. 5F, and Figs 6A, C). No hand sample is associated to the neotype as no remains were left after preparing the thin section. Well preserved plants also occur in other samples from the type locality, such as MERON-1-20 (Fig. 6B).

Type locality: Playa de Merón, NE San Vicente de la Barquera (Santander, N Spain).

Age: Oligocene.

Description of the neotype: Thin encrusting plants tightly attached to hard substrates (Fig. 5F and Fig. 6A), mostly coral fragments but other coralline thalli as well.

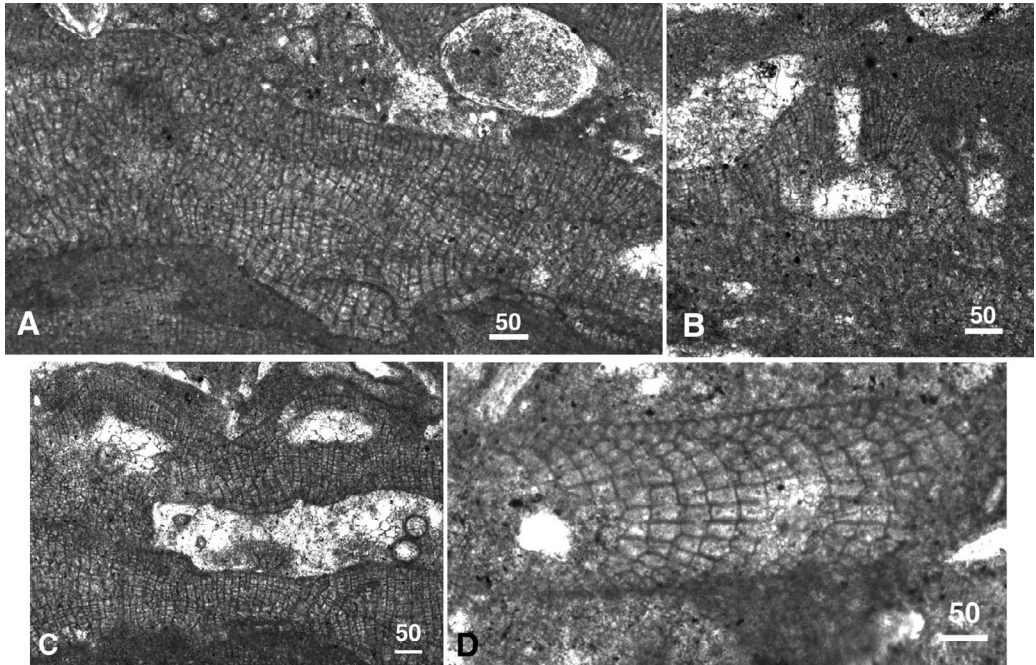


Fig. 6. **A:** Encrusting plant of *Hydrolithon lemoinei* showing a dimerous thallus organization. Primigenous filaments consist of polygonal cells attached to the substrate. Postigenous filaments arise perpendicularly from primigenous cells. Neotype. Thin section MERON-1-17. **B:** Detail of a sporangial conceptacle of *Hydrolithon lemoinei*. Note that the large, cylindrical pore canal is surrounded by cell filaments orientated approximately parallel to its wall. Thin section MERON-1-20. **C:** Detail of two sporangial conceptacles (one of them partially preserved) of *Hydrolithon lemoinei* neotype. Thin section MERON-1-17. **D:** Fragment of *Lithophyllum quadrangulum*. Thin section LA HAYA-3. This species is characterized by the large size of the cells, and the coaxial arrangement of the cell layers. The examined specimens have no anatomic traits for a proper assignment even at the subfamily level. Cell fusions, however, indicate that it does not belong to the subfamily Lithophylloideae.

Plant thickness is usually $\sim 75 \mu\text{m}$, except around the conceptacles, where it reaches up to $300 \mu\text{m}$.

Plants show dorsiventral dimerous organization. Primigenous filaments comprise non-palisade cells, polygonal in section and relatively large, measuring $10\text{--}25 \mu\text{m}$ ($17.7 \mu\text{m} \pm 3.7$) in height by $8\text{--}20 \mu\text{m}$ ($13.2 \mu\text{m} \pm 3.3$) in length (Fig. 6A). Cell size increases when the thallus adapts to substrate irregularities. Numerous cell fusions are visible.

Postigenous filaments arise perpendicularly from the primigenous ones (Fig. 6A). Cells of the postigenous filaments are also relatively large and quadrangular to rectangular in section with numerous cell fusions; they measure $10\text{--}27 \mu\text{m}$ ($16.6 \mu\text{m} \pm 4.3$) in height by $10\text{--}18 \mu\text{m}$ ($13.6 \mu\text{m} \pm 2.2$) in diameter. No lateral cell alignment is observed.

Sporangial conceptacles are triangular in section with a flat bottom and rounded corners (Fig. 5F). They measure 163–220 μm ($181.1 \mu\text{m} \pm 21.3$) in diameter by 67–110 μm ($87.2 \mu\text{m} \pm 19.4$) in height. They are very prominent on the thallus surface and have a single large pore canal in the roof (Fig. 5F, and Fig. 6B). Conceptacle roof is up to 6 cells in thickness and pore canals can be up to 113 μm ($63.3 \mu\text{m} \pm 39.6$) long. Pore canals are surrounded by cell filaments more or less perpendicular to the conceptacle roof (Fig. 6B). Three conceptacles are only visible in the thin section designated as the neotype. Therefore, measurements of conceptacle dimensions and pore canals are based on reproductive structures observed in the neotype and other additional thin sections.

No sexual conceptacles have been observed.

Remarks: The uniporate sporangial conceptacles and cell fusions indicate that the species should be included within the subfamily Mastophoroideae. Relevant anatomic features of the studied specimens are: 1) lack of palisade cells in the primigenous filaments, and 2) cell filaments surrounding the pore canals of the sporangial conceptacles approximately perpendicular to the conceptacle roof. These characters indicate that the species belongs to the genus *Hydrolithon* (FOSLIE) FOSLIE 1909 as circumscribed by PENROSE (1996) and, therefore, the new combination *Hydrolithon lemoinei* is proposed.

Species of uncertain affinity

Lithophyllum quadrangulum LEMOINE, 1934

Original localities: Los Vía and La Haya, south of San Vicente de la Barquera (Santander, N Spain), erroneously spelled by LEMOINE as Losbia and La Hoya (see above).

Age: Late Eocene.

LEMOINE (in LEMOINE & MENGAUD 1934) provided a very short description of this species based only on cell size. We have identified coralline remains confidently attributable to the species, but they always occur as small fragments (Fig. 6D). The large size of the cells in these fragments unequivocally suggests they correspond to the species schematically illustrated in the drawing of Text-Fig. 4 in LEMOINE & MENGAUD (1934). However, their preservation precludes even discerning whether they are geniculate or non-geniculate corallines. The observed fragments show a conspicuous core of monomerous coaxial organization (Fig. 6D). Cells are large, measuring 23–38 μm ($29.5 \mu\text{m} \pm 3.8$) in height by 10–20 μm ($14.9 \mu\text{m} \pm 2.7$) in diameter. Cell fusions are evident.

Cell filaments curve outwards, forming a one-cell thick cortex lining the coaxial core (Fig. 6D). Cells in the cortex are large and measure 7–17 μm ($11.2 \mu\text{m} \pm 3.2$) in diameter and 7–20 μm ($14.9 \mu\text{m} \pm 3.4$) in length.

No reproductive structures have been preserved.

Remarks: The fragmentary preservation of plants presumably belonging to "*Lithophyllum quadrangulum* LEMOINE, 1934" precludes any confident taxonomic adscription. Likewise, no specimen shows enough relevant features to be designated as neotype of the species name. In any case, the presence of cell fusions suggests that they do not belong to *Lithophyllum* or any other genus within the subfamily Lithophylloideae.

Concluding remarks

We have studied fossil coralline algae from localities in northern Spain, where new algal species were described in the 1920s and 1930s. The localities and species described are: 1) San Salvador hill (Camarasa, Catalanian Pyrenees), where PFENDER (1926) described three new species as *Archaeolithothamnium Lugeoni*, *Archaeolithothamnium Oulianovi*, and *Lithothamnium camarasae*; 2) Playa Merón (NW San Vicente de la Barquera, Cantabria), where MIRANDA (1935) described two new species as *Lithophyllum Royoi* (as well as the new form *L. Royoi* form *tenuis*) and *Melobesia Lemoinei*; and 3) Roiz, Los Vía, and La Haya (S San Vicente de la Barquera, Cantabria), where LEMOINE (in LEMOINE & MENGAUD 1934) described four new species as *Lithothamnium cantabricum*, *Lithophyllum Mengaudi*, *Lithophyllum quadrangulum*, and *Jania Mengaudi*. We were able to identify specimens attributable to all these species except *Archaeolithothamnium Oulianovi*, *Lithophyllum Royoi* (as well as the new form *Lithophyllum Royoi* forma *tenuis*), and *Lithothamnium cantabricum*. As all the original collections seem to be lost, we have designated neotypes according to Article 9.6 of the International Code of Botanical Nomenclature (ICBN, McNEILL et al. 2006) for the species that have been confidently recognized. We propose the following generic attributions and new combinations for the studied species: *Sporolithon lugeonii* (PFENDER) GHOSH & MAITHY, *Lithothamnium camarasae* (PFENDER), *Mesophyllum mengaudii* (LEMOINE) AGUIRRE, BRAGA & BASSI comb. nov., *Arthrocardia mengaudii* (LEMOINE) AGUIRRE, BRAGA & BASSI comb. nov., and *Hydrolithon lemoinei* (MIRANDA) AGUIRRE, BRAGA & BASSI comb. nov. Plants identifiable as *Lithophyllum quadrangulum* have been observed, but with not enough preserved features to confidently assign them to a genus. In any case, the presence of cell fusions precludes considering these fragmentary corallines as members of the subfamily Lithophylloideae.

Amongst the studied species, the names *Archaeolithothamnium lugeoni*, *Lithophyllum Mengaudi*, and *Lithophyllum quadrangulum* had a great impact in the literature of fossil corallines during the twentieth century, being cited 35 times, 19 times, and 14 times, respectively (Citation Index categories 3, 4, and 5 as defined by AGUIRRE & BRAGA 2005). These oft-described coralline algal species represent less than 10% of the total fossil species described in the last century (AGUIRRE & BRAGA 2005). Despite their relatively common use, uncertainty remained surrounding relevant taxonomic features and the generic and suprageneric adscription of two of the three species.

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References

- AGUIRRE, J. & BRAGA, J.C. (1998): Redescription of LEMOINE's (1939) types of coralline algal species from Algeria. – *Palaeontology*, **41**: 489–507.
- & — (2005): The citation of nongeniculate fossil coralline red algal species in the twentieth century literature: An analysis with implications. – *Revista Española de Micropaleontología*, **37**: 57–62.
- , — & PILLER, W. (1996): Reassessment of *Palaeothamnium* Conti, 1946 (Corallinales, Rhodophyta). – *Review of Palaeobotany and Palynology*, **94**: 1–9.
- ARESCHOU, J.E. (1852): Ordo XII. Corallineae. – In: AGARDH, J.G. (ed.): *Species, Genera et Ordines Algarum*. – Vol. 2, Part 2: 506–576, Lund (C.W.K. Gleerup).
- BASSI, D. (1995): Crustose coralline algal pavements from Late Eocene Colli Berici of northern Italy. – *Rivista Italiana di Paleontologia e Stratigrafia*, **101**: 81–92.
- , BRAGA, J.C., ZAKREVSAYA, E. & PETRONOVA-RADIONOVA, E. (2005): Re-assessment of the type collections of corallinean genera (Corallinales, Rhodophyta) described by V. P. MASLOV. – *Palaeontology*, **48**: 929–945.
- , ZAKREVSAYA, E. & FUGAGNOLI, A. (2002): A guide to the collections of Vladimir Petrovich Maslov (Rhodophyta, Corallinales). – In: BUCUR, I.I. & PHILIPESCU, S. (eds): *Research Advances in Calcareous Algae and Microbial Carbonates*. – pp. 71–81, Cluj-Napoca (Cluj University Press).
- BIZZOZERO, G. (1885): *Flora Veneta Crittogamica*. Part II. – pp. 255 Padova (Seminario).
- BOSENCE, D.W.J. (1991): Coralline algae: mineralisation, taxonomy, and palaeoecology. – In: RIDING, R. (ed.): *Calcareous algae and stromatolites*. – pp. 98–113, Berlin (Springer-Verlag).
- BOUSSAC, J. (1906): Développement et morphologie de quelques Foraminifères de Priabona. – *Bulletin de la Société Géologique de France*, **6**: 88–97.
- BRAGA, J.C. (2003): Application of botanical taxonomy to fossil coralline algae (Corallinales, Rhodophyta). – *Acta Micropalaenologica Sinica*, **20**: 47–56.
- & AGUIRRE, J. (1995): Taxonomy of fossil coralline algal species: Neogene Lithophylloideae (Rhodophyta, Corallinaceae) from southern Spain. – *Review of Palaeobotany and Palynology*, **86**: 265–286.
- , BOSENCE, D.W.J. & STENECK, R.S. (1993): New anatomical characters in fossil coralline algae and their taxonomic implications. – *Palaeontology*, **36**: 535–547.
- , BASSI, D., ZAKREVSAYA, E. & PETRONOVA-RADIONOVA, E. (2005): Reassessment of the type collections of Maslov's species of Corallinales (Rhodophyta). I. Species originally attributed to *Lithophyllum* and *Melobesia*. – *Revista Española de Paleontología*, **20**: 207–224.

- BRESSAN, G. & BABINI, L. (2003): Corallinales del Mar Mediterraneo: Guida Alla Determinazione. *Biologia Marina Mediterranea*, **10** (supplement 2): 1–237.
- CRONQUIST, A. (1960): The divisions and classes of plants. – *Botanical Review*, **26**: 425–482.
- DECAISNE, J. (1842): Essais sur une classification des algues et des polypiers calcifères de LAMOUROUX. – *Annales des Sciences Naturelles, Botanique, Seconde série*, **17**: 297–380.
- DENIZOT, M. (1968): Les Algues Floridées Encroûtantes (à l'Exclusion des Corallinacées). – 312 p., Paris (Muséum National d'Histoire Naturelle Paris).
- D'ORBIGNY, A.D. (1826): Tableau Méthodique de la Classe de Céphalopodes. – *Annales des Sciences naturelles, Paris, serie 1*, **7**: 245–314.
- FOSLIE, M. (1908): Algologiske notiser. VI. – *Det Kongelige Norske Videnskabers Selskab Museet*, **1908/7**: 1–20.
- (1909): Algologiske notiser. VI. – *Det Kongelige Norske Videnskabers Selskab Museet*, **1909/2**: 1–63.
- GHOSH, A.K. & MAITHY, P.K. (1996): On the present status of coralline red alga *Archaeolithothamnium* ROTH. from India. – *The Palaeobotanist*, **45**: 64–70.
- GRAY, J.E. (1864): *Handbook of British Water-Weeds or Algae*. – 123 p., London (R. Hardwicke).
- HARVEY, A.S., BROADWATER, S.T., WOELKERLING, W.J. & MITROVSKI, P.J. (2003): *Choreonema* (Corallinales, Rhodophyta): 18S rDNA phylogeny and resurrection of the Hapalidiaceae for the subfamilies Choreonematoideae, Austrolithoideae, and Melobesioideae. – *Journal of Phycology*, **39**: 988–998.
- HEYDRICH, F. (1897a): Corallinaceae, insbesondere Melobesieae. – *Berichte der Deutschen Botanischen Gesellschaft*, **15**: 34–71.
- (1897b): Melobesieae. – *Berichte der Deutschen Botanischen Gesellschaft*, **15**: 403–420.
- HOTTINGER, L. (1960): Recherches sur les Alvéolines du Paléocène et de l'Eocène. – *Schweizerische Paläontologische Abhandlungen*, **75/76**: 1–243.
- IRYU, Y., BASSI, D. & WOELKERLING, W.J. (2009): Re-assessment of the type collections of fourteen coralline species (Corallinales, Rhodophyta) described by W. ISHIJIMA (1942–1960). – *Palaeontology*, **52**: 401–427.
- KIM, J.H., GUIRY, M.D., OAK, J.H., CHOI, D.S., KANG, S.H., CHENG, H. & CHOI, H.G. (2007): Phylogenetic relationships within the tribe Janieae (Corallinales, Rhodophyta) based on molecular and morphological data: A reappraisal of *Jania*. – *Journal of Phycology*, **43**: 1310–1319.
- LAMOUROUX, J.V.F. (1812): Extrait d'un mémoire sur la classification des polypiers coralligènes non entièrement pierreux. – *Nouveau Bulletin des Sciences, par la Société philomatique de Paris*, **3**: 181–188.
- LE GALL, L. & SAUNDERS, G.W. (2007): A nuclear phylogeny of the Florideophyceae (Rhodophyta) inferred from combined EF2, small subunit and large subunit ribosomal DNA: Establishing the new red algal subclass Corallinophycidae. – *Molecular Phylogenetics and Evolution*, **43**: 1118–1130.
- , PAYRI, C.E., BITTNER, L. & SAUNDERS, G.W. (2010): Multigene phylogenetic analyses support recognition of the Sporolithales ord. nov. – *Molecular Phylogenetics and Evolution*, **54**: 302–305.

- LEMOINE, M.P. (1928): Un nouveau genre de Mélobésiées: *Mesophyllum*. – Bulletin de la Société Botanique de France, **75**: 251–254.
- & MENGAUD, L. (1934): Algues calcaires de l'Éocène de la province de Santander (Espagne). – Bulletin della Società Histoire Naturelle, Toulouse, **66**: 171–180.
- MCNEILL, J., BARRIE, F.R., BURDET, H.M., DEMOULIN, V., HAWKSWORTH, D.L., MARHOLD, K., NICOLSON, D.H., PRADO, J., SILVA, P.C., SKOG, J.E., WIERSEMAN, J.H. & TURLAND, N.J. (2006): International Code of Botanical Nomenclature (Vienna Code). – 474 p., Königstein (Koeltz Scientific Books).
- MIRANDA, F. (1935): Algas coralíneas fósiles del Terciario de San Vicente de la Barquera (Santander). – Boletín de la Sociedad Española de Historia Natural, **35**: 279–287.
- MISRA, P.K., JAUHRI, A.K., CHOWDHURY, A., & KISHORE, S. (2001): Palaeocene rhodophycean algae from the Ninnuyur Formation of the Cauvery Basin, southern India. – The Palaeobotanist, **50**: 311–339.
- PENROSE, D.L. (1996): The genus *Hydrolithon*. – In: WOMERSLEY, H.B.S. (ed.): The Marine Benthic Flora of Southern Australia. Rhodophyta – Part IIIB. Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales. – pp. 255–266, Canberra (Australian Biological Resources Study).
- PFENDER, J. (1926): Sur les organismes du Nummulitique de la colline de San Salvador près Camarasa. – Boletín de la Real Academia Española de Historia Natural, **26**: 321–330.
- PIA, J. (1934): Kalkalgen aus dem Eozän der Felsen von Hricovské Podhradie im Vaagtal. – Věstník Státního geologického Ústavu, Československé Republiky, **10**: 14–18.
- PILLER, W.E. (1994): *Nullipora ramosissima* REUSS, 1847 – a rediscovery. – Beiträge zur Paläontologie, **19**: 181–189.
- PORTERO-GARCÍA, J.M. & RAMÍREZ DEL POZO, J. (1976): Mapa Geológico de España E. 1:50.000. Comillas. – 46 p. Madrid (Servicio de Publicaciones del Ministerio de Industria).
- PUJALTE, V., BACETA, J.A. & PAYROS, A. (2002): Western Pyrenees and Basque-Cantabrian region. – In: GIBBONS, W. & MORENO, T. (eds): The Geology of Spain. – pp. 293–301, London (The Geological Society of London).
- QUARANTA, F., VANNUCCI, G. & BASSO, D. (2008): *Neogoniolithon contii* comb. nov. based on the taxonomic re-assessment of Mastrorilli's original collections from the Oligocene of NW Italy (Tertiary Piedmont Basin). – Rivista Italiana di Paleontologia e Stratigrafia, **113**: 43–55.
- RASSER, M. & PILLER, W. (1994): Re-documentation of Paleocene coralline algae of Austria, described by LEMOINE (1930). – Beiträge zur Paläontologie, **19**: 219–225.
- ROSANOFF, S. (1866): Recherches anatomiques sur les Mélobésiées. – Mémoire Société Impér. Science Naturelle Cherbourg, **12**: 5–112.
- ROTHPLETZ, A. (1891): Fossile Kalkagen aus den Familien der Codiaceen und der Corallineen. – Zeitschrift der Deutsche Geologische Gesellschaft, **43**: 295–332.
- SERRA-KIEL, J., HOTTINGER, L., DROBNE, K., FERRANDEZ, C., LESS, Gy., JAUHRI, A.K., PIGNATTI, J., SAMSO, J.M., SIREL, E., TAMBAREAU, Y., TOSQUELLA, J. & ZAKREVSAYA, E. (1998): Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. – Bulletin della Società Géologique de France, **169**: 281–299.

- SETCHELL, W.A. (1943): *Mastophora* and Mastophoreae: Genus and subfamily of Corallinaceae. – Proceedings National Academy Sciences, **29**: 127–135.
- SILVA, P.C. & JOHANSEN, H.W. (1986): A reappraisal of the order Corallinales (Rhodophyta). – British Phycological Journal, **21**: 245–254.
- STOCKAR, R. (2000): Fossil coralline algae from the Paleocene Montorfano Member type-section (Tabiago Formation, northern Italy). – Eclogae geologicae Helvetiae, **93**: 409–427.
- TOWNSEND, R.A., CHAMBERLAIN, Y.M. & KEATS, D.W. (1994): *Heydrichia woelkerlingii* gen. et sp. nov., a newly discovered non-geniculate red alga (Corallinales, Rhodophyta) from Cape province, South Africa. – Phycologia, **33**: 177–186.
- ULLASTRE, J. & MASRIERA, A. (1995): El Mesozoico de Artesa de Segre: precisiones estratigráficas y análisis tectónico-sedimentario del “frente” sudpirenaico entre Artesa y Camarasa (Pirineo Catalán, España). – Treballs Museo Geològic de Barcelona, **4**: 181–209.
- & — (1996): Evolución tectónica de las unidades sudpirenaicas al W y al E de la línea de accidentes del Segre (Pirineo Catalán, España). – Treballs Museo Geològic de Barcelona, **5**: 213–253.
- VANNUCCI, G., QUARANTA, F. & BASSO, D. (2009): Historical Type Collections of Fossil, Corallinales and Sporolithales (Rhodophyta) in the Dip. Te.Ris. – 65 p., Roma (Arace).
- , — & — (2010): Revision and re-documentation of M. AIROLDI’s species of *Lithothamnion* from the Tertiary Piedmont Basin (NW Italy). – Rivista Italiana di Paleontologia e Stratigrafia, **116**: 223–235.
- , PIAZZA, M., FRAVEGA, P. & BASSO, D. (2000): Revision and re-description of M. AIROLDI’s species of *Archaeolithothamnium* from the Tertiary Piedmont Basin (NW Italy). – Rivista Italiana di Paleontologia e Stratigrafia, **106**: 191–202.
- VERHEIJ, E. (1993): The genus *Sporolithon* (Sporolithaceae fam. nov., Corallinales, Rhodophyta) from the Spormonde Archipelago, Indonesia. – Phycologia, **32**: 184–196.
- WETTSTEIN, R.R. (1901): Handbuch der Systematischen Botanik Vol. 1. – 201 p., Leipzig (Deuticke).
- WOELKERLING, W.J. (1988): The Coralline Red Algae: An Analysis of the Genera and Subfamilies of Nongeniculate Corallinaceae. – 268 p. Oxford (Oxford University Press).
- (1996): Family Sporolithaceae. – In: WOMERSLEY, H.B.S. (ed.): The Marine Benthic Flora of Southern Australia. Rhodophyta – Part IIIB. Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales. – pp. 153–158, Canberra (Australian Biological Resources Study).
- , IRVINE, L.M. & HARVEY, A. (1993): Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). – Australian Systematic Botany, **6**: 277–293.
- WOMERSLEY, H.B.S. & JOHANSEN, H.W. (1996): Subfamily Corallinoideae. – In: WOMERSLEY, H.B.S. (ed.): The Marine Benthic Flora of Southern Australia. Rhodophyta – Part IIIB. Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales. – pp. 288–317, Canberra (Australian Biological Resources Study).