

REDESCRIPTION OF LEMOINE'S (1939) TYPES OF CORALLINE ALGAL SPECIES FROM ALGERIA

by J. AGUIRRE and J. C. BRAGA

ABSTRACT. The type material of eight coralline algal species of the 27 established by Lemoine (1939) from the Cretaceous and Cenozoic of Algeria is preserved in Emberger's Collection at the University of Nantes. This is one of the very few extant collections of the original fossil material of Mme Lemoine, probably the most influential and prolific author of coralline algal palaeontology in this century. The study of this collection highlights the importance of re-documentation of type material of fossil taxa defined decades ago with descriptions and illustrations focused on characters different from those considered diagnostic in modern taxonomy. We redescribe and illustrate the conserved types and revise their taxonomic adscription and nomenclature. *Archaeolithothamnium brevium*, *A. liberum* and *Lithophyllum Glangeaudi* are assigned to *Sporolithon*; *Mesophyllum Sancti Dionysii* and *M. curtum* are confirmed as belonging to *Mesophyllum*, and *Lithothamnium Betieri* to *Lithothamnion*; whilst the absence of relevant characters in the *M. Ehrmanni* and *Lithophyllum Sigi* types prevents any certain inclusion in the currently accepted coralline genera. These results illustrate the risks of using names of taxa established long ago without reassessing their precise circumscription and the necessity of avoiding the use of taxa with no preserved type material.

THE taxonomy of fossil coralline red algae is under revision as a consequence of new taxonomic criteria proposed both in the botanical and palaeontological literature (Braga *et al.* 1993; Braga and Aguirre 1995). The original diagnostic characters of many taxa are ambiguous or meaningless according to the modern criteria used for delimiting taxa from the species to family level (Bosence 1983; Braga and Aguirre 1995; Aguirre *et al.* 1996). Revision of the original collections has to be undertaken to redescribe the type material, pointing to the characters used in modern classifications, and to illustrate as much as possible of the relevant features of the types. However, the type material of many fossil coralline algal taxa is not conserved or cannot be located at present. This is probably the main difficulty in taxonomic studies of fossil coralline algae as the illustrations and original diagnoses for many fossil genera and species are inadequate for assessing their actual circumscription. In addition, interpretations of a particular species by later authors do not always coincide, which renders the selection of a neotype very subjective and arguable. All this makes the analysis of the few preserved original collections very important for coralline algal studies. Modern descriptions and illustrations of the taxa from these type collections should be the preferential basis for taxonomic assignments that must attempt to avoid specific and generic names devoid of precise meaning due to the lack of both adequate original descriptions and any type material to assess their actual nature.

Here we present a redescription of the types of eight nongeniculate coralline algal species established by Lemoine (1939) from Algeria, conserved in Emberger's Collection at the University of Nantes. Lemoine (1939) described 27 new species among the 61 she identified in the algal samples collected by Drs Ehrmann, Dalloni, Welsch, Glangeaud, Laffitte and Flandrin during production of the Geological Map of Algeria (first series). Emberger's Collection includes material collected by Ehrmann and Laffitte. As far as we know no other types of species established by Lemoine from fossil Algerian samples are preserved or can be located at the moment and none exists in Lemoine's own collection at the Musée Nationale d'Histoire Naturelle de Paris (M. Ardré, pers. comm. 1991).

Lemoine (1939) based her description of nongeniculate coralline species on the following attributes: (1) external morphology, (2) thallus dimensions and morphology, (3) size of the

'hypothallus' and 'perithallus' cells, and (4) conceptacle dimensions. The last character was impossible to apply in some species due to the lack of any reproductive structures. Photographs concentrated on the external appearance of the algal plants and text figures on the cell and conceptacle dimensions. These characters may be irrelevant or ancillary in the modern taxonomy of coralline species. We attempt to describe and illustrate the most relevant features in modern taxonomy of each group to which these species belong, thus completing the information already given by Lemoine (1939).

MATERIALS AND METHODS

We have examined the specimens and the thin sections from the collections of Ehrmann, Glangeaud and Laffitte from Algeria studied by Lemoine (1939). The samples from the original collections are labelled with Lemoine's hand script, except for sample 11 (corresponding to *A. brevium*). The samples and thin sections were subsequently renumbered, probably by Emberger, who cut some additional thin sections. We have also cut 17 thin sections from the original specimens to examine relevant characters in those species where they were not observable in the original thin sections.

In the taxonomic descriptions we follow Chamberlain *et al.* (1988) in orientation and nomenclature of cell and reproductive structure dimensions, and Woelkerling *et al.* (1993) in growth-form terminology.

SYSTEMATIC PALAEONTOLOGY

Division RHODOPHYTA Wettstein, 1901
 Class RHODOPHYCEAE Rabenhorst, 1863
 Order CORALLINALES Silva and Johansen, 1986
 Family SPOROLITHACEAE Verheij, 1993
 Genus SPOROLITHON Heydrich, 1897a

Type species. *Sporolithon ptychoides* Heydrich, 1897a, p. 67, pl. 3, figs 15–23; text-figs 2–3. Basionym: *Lithothamnium erythraeum* Rothpletz, 1893, p. 5.

Sporolithon brevium (Lemoine) Aguirre and Braga, comb. nov.

Plate 1, figures 1–3

Basionym. *Archaeolithothamnium brevium* Lemoine (Matériaux pour la Carte Géologique de L'Algérie. 1^{re} Série Paléontologie (1939), p. 43, pl. 1, fig. 4, text-figs 4–5).

Type material. Lemoine (1939), when describing the species, referred to several samples from the Turonian of Mansourah, Monts des Aurès, Algeria, collected by R. Laffitte. Of these, only two algal nodules (rhodoliths) are preserved, together with a thin section, in Emberger's Collection at Nantes.

Lectotype. Lemoine (1939, p. 43) did not designate a type and the example figured by Lemoine (1939, pl. 1, fig. 4; text-figs 4–5) does not seem to be preserved. According to Articles 9.2 and 9.9 of the ICBN (Greuter 1994) we designate here sample 11 (thin section no. 860) from Emberger's Collection as the lectotype from the original material. This is a piece (47 × 40 × 40 mm) cut from a fruticose plant with radial organization, which grew on shell fragments. Protuberances, sometimes branched and laterally coalescent, are up to 22 mm long and up to 5 mm wide. The other rhodolith of the type collection, measuring 45 × 42 × 21 mm, has a similar external appearance.

Vegetative anatomy. The lectotype plant has a dorsiventral and monomerous thallus organization with a plumose ventral core (Pl. 1, fig. 1) of constant thickness (42–72 μm). Cell filaments in the core run parallel to the substrate, and branch to produce new filaments that curve outwards in the peripheral region towards the thallus surface. In the protuberances the filaments become radially arranged (Pl. 1, fig. 2). Both in crustose portions of the thallus and in protuberances, new plumose cores arise from the peripheral filaments and facilitate

TABLE 1. Growth form, protuberance, cell and conceptacle dimensions, and other relevant characters in the species studied. *n* = number of measures; s.d. = standard deviation.

| | <i>S. brevium</i> | <i>S. liberum</i> | <i>S. glangeaudii</i> | <i>L. betieri</i> | <i>M. sancti-dionysii</i> | <i>M. curtum</i> | <i>M. Ehrmanni</i> | <i>L. Sigi</i> |
|---------------------------|----------------------------------|-----------------------------|-----------------------|------------------------------|------------------------------|-------------------------------------|---|-------------------------------------|
| Growth form | Fruticose | Encrusting to warty | Fruticose | Encrusting to lumpy | Encrusting laminar | Encrusting to warty | Encrusting | Fruticose |
| Protuberances | | | | | | | | |
| Length (maximum) | 22 mm | — | 28 mm | 5 mm | — | 8 mm | — | 6 mm |
| Diameter (maximum) | 5 mm | — | 9 mm | 8 mm | — | 2 mm | — | — |
| Ventral core cells | <i>n</i> = 50 | <i>n</i> = 30 | <i>n</i> = 8 | <i>n</i> = 50 | <i>n</i> = 50 | <i>n</i> = 50 | <i>n</i> = 30 | Not observable |
| Length range (μ m) | 7.1-28.4 | 10-32 | 14.2-28.4 | 7.1-21.3 | 14.2-39.1 | 17.8-28.4 | 7.1-14.2 | |
| Mean \pm s.d. | 11.9 \pm 5.1 | 17.5 \pm 5.6 | 21.3 \pm 5.4 | 12.8 \pm 3.3 | 25.9 \pm 4.8 | 20.9 \pm 2.4 | 11.6 \pm 2.3 | |
| Diameter range (μ m) | 3.6-14.2 | 3.6 \pm 10.7 | 3.6 \pm 10.7 | 3.6 \pm 10.7 | 3.6-14.2 | 3.6-10.7 | 3.6 \pm 10.7 | |
| Mean \pm s.d. | 8.9 \pm 2.5 | 8.5 \pm 2.1 | 7.1 \pm 1.9 | 7.5 \pm 2.2 | 7.9 \pm 2.4 | 8.1 \pm 2.3 | 7.9 \pm 1.8 | |
| Peripheral cells | <i>n</i> = 50 | <i>n</i> = 48 | <i>n</i> = 50 | <i>n</i> = 50 | <i>n</i> = 50 | <i>n</i> = 50 | <i>n</i> = 50 | |
| Length range (μ m) | 7.1-17.6 | 14.2-24.9 | 7.1-21.3 | 7.1-14.2 | 7.1-17.8 | 7.1-14.2 | 7.1-14.2 | |
| Mean \pm s.d. | 13.2 \pm 2.5 | 19.9 \pm 3 | 13.6 \pm 3.2 | 9.8 \pm 2.5 | 11.2 \pm 2.5 | 10.6 \pm 2.3 | 10.7 \pm 2.5 | 10.7 \pm 2.1 |
| Diameter range (μ m) | 5.3-14.2 | 3.6-14.2 | 3.6-10.7 | 3.6-10.7 | 3.6-10.7 | 3.6-10.7 | 3.6-10.7 | 3.6-7.1 |
| Mean \pm s.d. | 8.8 \pm 2 | 9 \pm 2.6 | 7.2 \pm 2.4 | 6.3 \pm 2.1 | 8.1 \pm 1.8 | 6.3 \pm 2.1 | 6 \pm 1.8 | 5.5 \pm 1.8 |
| Lateral cell alignment | Cells well aligned | Cells well aligned | Poorly defined | Poor | Cells well aligned | Poorly defined | Cells well aligned | Cells well aligned |
| Sporangial conceptacles | <i>n</i> = 50 | <i>n</i> = 3 | <i>n</i> = 2 | <i>n</i> = 8 | <i>n</i> = 16 | <i>n</i> = 42 | Not observable | <i>n</i> = 4 |
| Diameter range (μ m) | 21.3-46.2 | 32-35.5 | 28.4-32 | 431-647 | 240.3-627.5 | 186.9-427.2 | | 177.5-394.1 |
| Mean \pm s.d. | 36.6 \pm 4.8 | 34.3 \pm 2.1 | 30.2 \pm 2.5 | 501 \pm 102 | 471.4 \pm 114.8 | 279.7 \pm 48.8 | | 297.3 \pm 89.8 |
| Height range (μ m) | 35.5-85.2 | 56.8-71 | 56.8-71 | 216-277 | 160.2-267 | 133.5-253.7 | | 85.2-142 |
| Mean \pm s.d. | 65.5 \pm 8.2 | 61.5 \pm 8.2 | 63.9 \pm 10 | 231 \pm 31 | 219.4 \pm 30.4 | 204.4 \pm 24.4 | | 110.9 \pm 23.4 |
| Others | Weak zonation; Rare cell fusions | Rare (absent?) cell fusions | Rare cell fusions | Peripheral region well zoned | Peripheral region well zoned | Peripheral region irregularly zoned | Very weak zonation of peripheral region | Weak zonation; cell fusions present |

lateral expansion over older portions of the thallus. Protuberances can coalesce when they meet laterally. Cell fusions are scarce. Cells in the ventral plumose core are rectangular to trapezoidal in section (Pl. 1, fig. 1), 7–28 μm (mean 11.9 μm , s.d. 5.1) long and 4–14 μm (mean 8.9 μm , s.d. 2.5) in diameter (Table 1).

Cells of contiguous filaments in the peripheral region are laterally well aligned, giving to the thallus the aspect of a uniform grid (Pl. 1, figs 1–2). The cells are square to rectangular in section, 5–14 μm (mean 8.8 μm , s.d. 2) in diameter and 7–18 μm (mean 13.2 μm , s.d. 2.5) long (Table 1). Slight changes in the height of laterally aligned cells result in a weak zonation of the peripheral region (Pl. 1, fig. 2).

No epithallial cells have been recognized.

Reproductive structures. They consist of sporangial compartments (*sensu* Townsend *et al.* 1995) grouped in sori (Pl. 1, figs 2–3). Individual compartments are rectangular with rounded corners to elliptical or ovoid in longitudinal section and circular in transverse section (Pl. 1, fig. 3). They are 35–85 μm (mean 65.5 μm , s.d. 8.2) high and 21–46 μm (mean 36.6 μm , s.d. 4.8) in diameter (Table 1). Trapezoidal stalk cells occur at the base of some compartments (Pl. 1, fig. 3). Occasionally, a possible calcified septum separating the stalk cell from the sporangial compartment can be observed. Cells underlying the compartments are longer than other peripheral cells (18–35 μm ; mean 24.6 μm , s.d. 4). Calcified sporangial compartments are separated by up to eight (usually one to four) filaments of elongated cells. In longitudinal section compartments in sori are laterally aligned (Pl. 1, figs 2–3). Up to 51 compartments can be counted in a single sorus. No structures attributable to gametangial conceptacles have been observed.

Remarks. The features of the reproductive structures in the lectotype are characteristic of sporangial plants of *Sporolithon* Heydrich, 1897a (Woelkerling 1988; Townsend *et al.* 1994). According to Moussavian and Kuss (1990), *Sporolithon* is the correct generic name for corallines included by many authors in *Archaeolithothamnium* Rothpletz, 1891, since this latter name was not validly published. Verheij (1993) proposed a new family, Sporolithaceae, to separate *Sporolithon* from the rest of the Corallinales due to the simultaneous cruciate cleaving of its tetrasporangia. In addition, each tetrasporangium develops in a tetrasporangial chamber surrounded by calcified paraphysis (filaments) instead of developing in conceptacles. Townsend *et al.* (1995), in order to avoid confusing terms of reproductive structures, characterized the Sporolithaceae by 'tetrasporangia that produce cruciately arranged spores and develop within calcified sporangial compartments'. *Heydrichia* Townsend, Chamberlain and Keats, 1994, was established as a new genus belonging to this family. It was separated from *Sporolithon* by having more than one stalk cell in each sporangial compartment, among other features difficult to recognize in fossil material, such as the restriction of spermatangial systems to the male conceptacle floor.

Although the preservation potential of the several tetrasporangial stalk cells of *Heydrichia* in fossil plants is unknown at the moment, in the lectotype of '*Archaeolithothamnium brevium*' only one stalk cell can sometimes be observed at the bottom of the sporangial compartments, suggesting that this species should be assigned to *Sporolithon*. We therefore propose the new combination *Sporolithon brevium* (Lemoine) Aguirre and Braga for naming this species.

Since it was established, *A. brevium* has been referred to by Poignant *et al.* (1981) in Sardinia, in the only published illustration of the species other than the original by Lemoine (1939). This species was also included in Cretaceous floral inventories by Lemoine (1970) and Deloffre *et al.* (1977). Poignant (1985) analysed the supposed key features separating *brevium* from other *Sporolithon* species (as *Archaeolithothamnium*).

Sporolithon glangeaudii (Lemoine) Aguirre and Braga, comb. nov.

Plate 1, figures 4–6

Basionym. *Lithophyllum Glangeaudi* Lemoine (Matériaux pour la Carte Géologique de L'Algérie. 1^{re} Série Paléontologie (1939), p. 102, pl. 2, fig. 15; text-fig. 70).

Type material. This consists of a rock sample cut for thin sectioning, from the Miocene (Burdigalian) of Oued Nosara, 4 km south-east of Cherchel, Algeria (sample 10). Two thin sections from Glangeaud's Collection (Plaques 1 and 2, renumbered as 6437, probably by Emberger) and two from Emberger's Collection (no. 6437) are preserved.

Holotype. According to Article 9.1 in the ICBN, it is the sample figured and described by Lemoine (1939, p. 102, pl. 2, fig. 15; text-fig. 70). In the original description, Lemoine (1939) refers to other examples from Algeria and Andalusia (southern Spain) that could also belong to the same species. The holotype is a fruticose rhodolith embedded in a bioclastic micritic matrix. The algal nodule measured at least $90 \times 55 \times 40$ mm before being cut. The rhodolith is made up mainly of a single fruticose plant with branching and laterally coalescent protuberances, up to 28 mm long and 9 mm in diameter. The plant is heavily bored, probably by sponges. Some thin encrusting thalli of a *Mesophyllum* species are attached to the tips of the protuberances.

Vegetative anatomy. The thallus is monomerous. Plumose ventral cores develop in the sites of reinitiation of thallus growth (Pl. 1, fig. 4). Core thickness is $71\text{--}75$ μm , although locally it may be only 50 μm . Cell filaments run parallel to the substratum in the ventral part of the core, then curve upwards to give way to the peripheral region. The cells are rectangular, $14\text{--}28$ μm (mean 21.3 μm , s.d. 5.4) long and $4\text{--}11$ μm (mean 7.1 μm , s.d. 1.9) in diameter (Table 1). Cells of adjacent filaments are sometimes connected by cell fusions.

The peripheral region is well developed. Filaments in the protuberances are radially arranged and curve outwards to become perpendicular to the protuberance surface. Cells measure $7\text{--}21$ μm (mean 13.6 μm , s.d. 3.2) long and $4\text{--}11$ μm (mean 7.2 μm , s.d. 2.4) in diameter (Table 1). Cell fusions are scarce. The alignment of cells of adjacent filaments is poorly defined in some areas of the thallus (Pl. 1, figs 4–5).

Reproductive structures. The observable reproductive structures in the holotype consist of groups (sori) of calcified sporangial compartments (Pl. 1, figs 5–6). Individual compartments are rectangular with rounded corners to elliptical in longitudinal section, $57\text{--}71$ μm (mean 63.9 , s.d. 10) high and $28\text{--}32$ μm (mean 30.2 μm , s.d. 2.5) in diameter (Table 1). They developed on distinct stalk cells (Pl. 1, fig. 5) laterally aligned with elongated cells, $25\text{--}28$ μm (mean 26 μm , s.d. 1.8) long, forming a distinct layer. Some sporangial compartments are separated from the stalk cells by a calcified septum (Pl. 1, fig. 5). One compartment shows a Y-like internal structure (Pl. 1, fig. 6) that may represent the remains of a cruciately septate tetrasporangium, diagnostic of the Sporolithaceae (Keats and Chamberlain 1993; Verheij 1993; Townsend *et al.* 1995).

Some groups of laterally aligned elongated cells (up to 28 μm long) dispersed in the protuberances can be interpreted as sori primordia.

Remarks. Despite the original generic assignment of this species made by Lemoine (1939), the presence of sori of calcified sporangial compartments in the holotype places this species in the family Sporolithaceae. The occurrence of single stalk cells at the base of sporangial compartments suggests that the species should be included in *Sporolithon* and referred to as *Sporolithon glangeaudii* (Lemoine) Aguirre and Braga (the second 'i' at the end of the specific epithet is added following Recommendation 60C.1(b) of the ICBN).

Subsequent authors assumed the original generic assignment of this species and some plants with uniporate sporangial conceptacles have been illustrated as *Lithophyllum glangeaudi* by Johnson (1964b), and as *Lithophyllum* cf. *glangeaudi* by Johnson (1957, 1964c) and Buchbinder (1977), or included as *Lithophyllum* in Neogene floral accounts from the western Pacific and the Mediterranean (Elliott 1960; Vannucci *et al.* 1983). None of these reports can be considered as accurate records of *S. glangeaudii*.

Sporolithon liberum (Lemoine) Aguirre and Braga, comb. nov.

Plate 1, figures 7–8

Basionym. *Archaeolithothamnium liberum* Lemoine (Matériaux pour la Carte Géologique de L'Algérie. 1^{re} Série Paléontologie (1939), p. 61, pl. 1, fig. 14; text-fig. 26).

Type material. One fragment of a small algal nodule (sample 6) and one thin section from Ehrmann's Collection (Plaque 1, renumbered as 2347, probably by Emberger) is conserved in a box with a label in Lemoine's script on which the term 'type' appears under the name of the species. An additional thin section from the same example is found in the Emberger's Collection (sample no. 2347). The sample comes from Eocene sandstones and marls with nummulites from Bou Djebaa, Algeria.

Holotype. The only sample of the type material described and figured by Lemoine (1939, p. 61, pl. 1, fig. 14; text-fig. 26) is a small rhodolith with protuberances, cut for thin sectioning and now measuring $26 \times 23 \times 15$ mm.

The rhodolith is made up of many encrusting to warty coralline plants growing one upon another and on invertebrate skeletons. These algal plants belong to several genera according to the current generic taxonomy of corallines. However, in the thin section from Erhmann's Collection studied by Lemoine (1939), sections of protuberances of a coralline alga with sori of sporangial compartments are conspicuous and correspond to the original description of the species better than the other thalli present. It is impossible to ascertain whether the sections belong to a single thallus or several different thalli but this (these) specimen(s) should be considered the holotype of the species (Articles 8.1 and 9.1 in the ICBN).

Vegetative anatomy. The corallines in the holotype collection have dorsiventral monomerous thalli with a basal core of filaments that run parallel to the substrate for a short distance and then curve upwards to become perpendicular to the thallus surface in the peripheral region (Pl. 1, fig. 7). Cells from the ventral core measure 10–32 μm (mean 17.5 μm , s.d. 5.6) long \times 4–11 μm (mean 8.5 μm , s.d. 2.1) in diameter (Table 1). The thickness of the core changes from 57 μm to 213 μm , as a consequence of adaptation to substrate irregularities. Cell fusions are scarce.

In the peripheral region, cells of adjacent filaments are laterally well-aligned. This, together with the scarcity of cell fusions, confers to the longitudinal sections of this region the aspect of a regular grid (Pl. 1, fig. 8). In the protuberances cell filaments are radially arranged, curving outwards to become perpendicular to the external surface (Pl. 1, fig. 8). In the encrusting portions of the thallus, cells are rectangular in longitudinal section, measuring 14–25 μm (mean 19.9 μm , s.d. 3) long and 4–14 μm (mean 9 μm , s.d. 2.6) in diameter (Table 1).

Epithallial cells have not been recognized.

Reproductive structures. A single group of elliptical to ovoid calcified sporangial compartments can be clearly recognized in the section of a protuberance in Erhmann's thin section (Pl. 1, fig. 7). Poorly preserved or defined small groups of compartments occur in other protuberances. The compartments are irregularly distributed and laterally not well-aligned. They measure 57–71 μm (mean 61.5 μm , s.d. 8.2) high and 32–36 (mean 34.3 μm , s.d. 2.1) in diameter (Table 1). Single, poorly defined stalk cells occur at the base of some sporangial compartments.

Remarks. The vegetative and reproductive features of '*Archaeolithothamnium liberum*' are characteristic of *Sporolithon* (see remarks on *S. brevium*). Therefore, we propose the new combination *Sporolithon liberum* (Lemoine) Aguirre and Braga for naming this species.

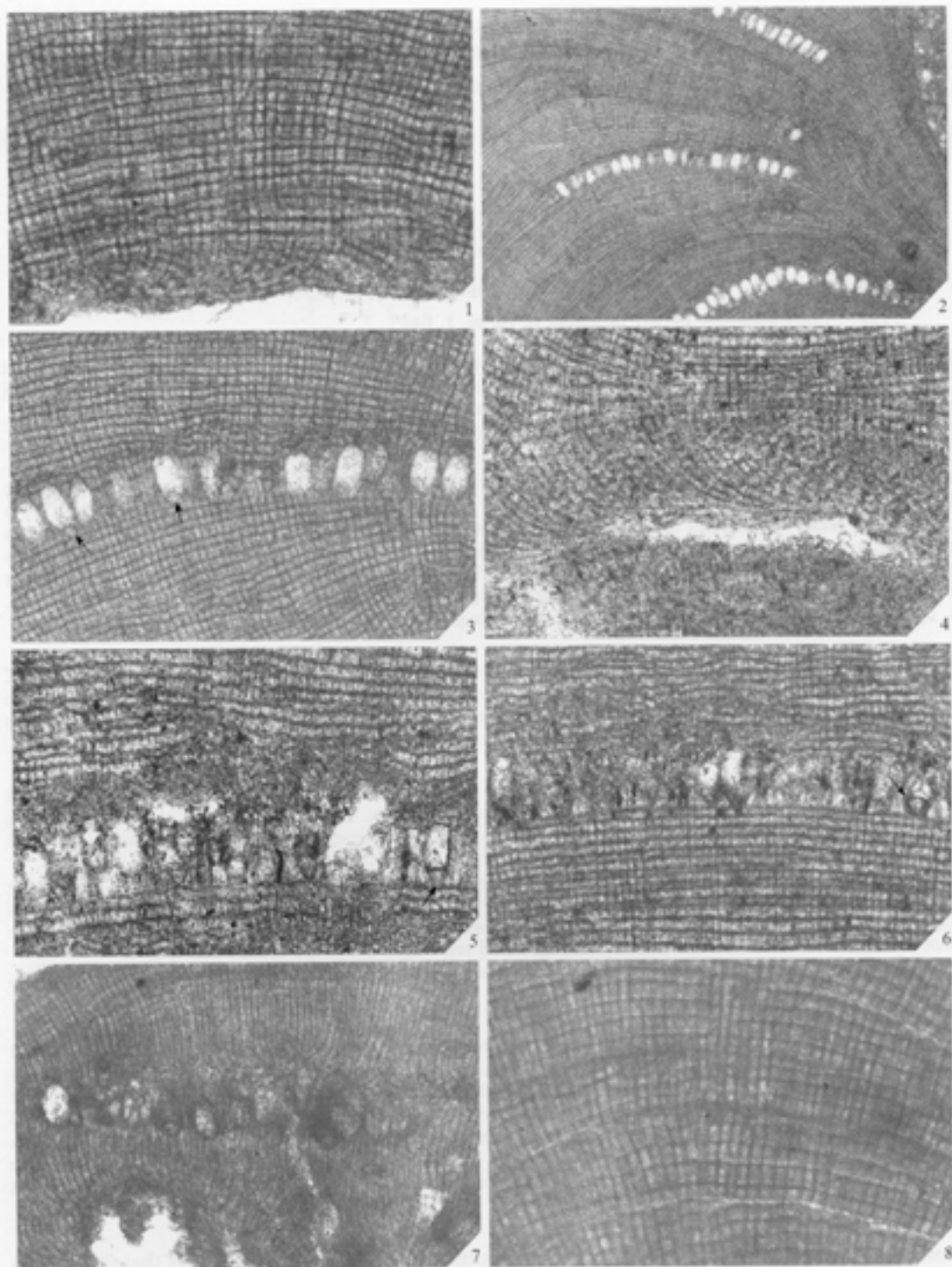
Johnson (1957) illustrated a coralline plant from the Eocene of Saipan as *A. cf. liberum*. Johnson (1964a, 1966) described the species without illustration from two other Paleogene localities in the western Pacific.

EXPLANATION OF PLATE I

Figs 1–3. *Sporolithon brevium* (Lemoine) comb. nov. (= *Archaeolithothamnium brevium* Lemoine); lectotype, Sample 11 (thin section no. 860), Emberger's Collection; Turonian of Mansourah, Monts des Aurès, Algeria. 1, plumose ventral core and peripheral filaments with laterally well-aligned cells; \times 140. 2, section of a thallus protuberance with filaments radially arranged and three sori of sporangial compartments; \times 40. 3, detail of the central sorus in figure 2; note trapezoidal stalk cells at the base of some compartments (arrows); \times 110.

Figs 4–6. *Sporolithon glangeaudii* (Lemoine) comb. nov. (= *Lithophyllum Glangeaudi* Lemoine); holotype, Sample 10, Emberger's Collection; Miocene (Burdigalian), Oued Nosara, 4 km south-east of Cherchel, Algeria. 4, thin section CE-10a; plumose core arising from peripheral filaments and expanding over older thallus portions; \times 130. 5, thin section CE-10a; sorus of sporangial compartments; note the trapezoidal stalk cell at the base of a compartment (arrow); \times 120. 6, thin section from Emberger's Collection no. 6437; sorus of sporangial compartments. Note the Y-like internal structure of a compartment (arrow) that may represent a cruciately septate tetrasporangium; \times 110.

Figs 7–8. *Sporolithon liberum* (Lemoine) comb. nov. (= *Archaeolithothamnium liberum* Lemoine); holotype, Sample 6, Emberger's Collection; thin section from Erhmann's Collection (*Plaque* 1, renumbered as 2347, probably by Emberger); Eocene, Bou Djebaa, Algeria. 7, thallus section with poorly preserved ventral plumose core (bottom centre) and peripheral filaments surrounding a sorus of sporangial compartments; \times 100. 8, detail of peripheral filaments in a thallus protuberance; note that cells of adjacent filaments are laterally well-aligned; \times 140.



AGUIRRE and BRAGA, *Sporolithon*

Family CORALLINACEAE Lamouroux, 1816
Subfamily MELOBESIOIDEAE Bizzozero, 1885
Genus LITHOTHAMNION Heydrich, 1897b

Lectotype species. *Lithothamnion muelleri* Lenormand ex. Rosanoff, 1866, p. 101, pl. 6, figs 8–11; designated by Woelkerling (1983, p. 193, figs 29–33).

Lithothamnion betieri Lemoine, 1939

Plate 2, figures 1–4

1939 *Lithothamnium Betieri* Lemoine, p. 70, pl. 1, figs 1, 7.

Type material. This consists of two algal nodules (samples 4 and 5), cut for thin sectioning, and some small fragments remaining from cutting, from the Miocene of Hammar Semounet and Chabet Akt el Mahdi (Algeria). One very poorly preserved thin section from Ehrmann's Collection (*Plaque* 12, renumbered 2358, probably by Emberger) is also part of the conserved type material.

Lectotype. The thin section from Lemoine's type material is badly damaged and it is not possible to determine from which of the three samples described by Lemoine (1939) it was taken. We have made a thin section from each of the preserved nodules (thin sections CE-4 and CE-5) and only in one (CE-4 from sample 4) can reproductive structures be observed. According to Articles 9.2 and 9.9 in the ICBN, we select as lectotype the biggest algal nodule (sample 4, figured by Lemoine (1939, pl. 1, fig. 1) in which the sporangial conceptacles occur. It is from the Upper Miocene of Hammar Semounet. The small nodule (sample 5, in Lemoine 1939, pl. 1, fig. 7) was considered by the author as a juvenile stage (Lemoine's manuscript on the sample label).

External appearance. The lectotype plants occur in a lumpy rhodolith with a nucleus made up of fragments of diverse coralline algae, bryozoans, foraminifers, serpulids and molluscs. According to Lemoine (1939), only the most external coralline plants belong to *L. betieri*. These are superimposed thalli of encrusting to lumpy plants with protuberances up to 5 mm high and 8 mm in diameter.

Vegetative anatomy. Monomerous plants with plumose ventral core 177.5 μm to 213 μm thick (Pl. 2, fig. 1). Cell fusions between cells of adjacent filaments are conspicuous (Pl. 2, fig. 1). Cells are rectangular, 7–21 μm (mean 12.8 μm , s.d. 3.3) long and 4–11 μm (mean 7.5 μm , s.d. 2.2) in diameter (Table 1). Cell filaments oriented parallel to the substrate at the bottom of the plumose core curve upwards into the peripheral region.

The peripheral region is well developed, formed by rectangular cells, 7–14 μm (mean 9.8 μm , s.d. 2.5) long and 4–11 μm (mean 6.3 μm , s.d. 2.1) in diameter (Table 1). Changes in cell length result in zonation, but lateral alignment of cells of adjacent filaments is poor and disturbed by many cell fusions (Pl. 2, fig. 2). In the protuberances, cell filaments are radially arranged and cell-length zones are arched and lensoid.

Epithallial cells, preserved at the lower surfaces of some protuberances, are flat and probably flared (Pl. 2, fig. 3).

Reproductive structures. Multiporate conceptacle chambers occur in a protuberance of a broken thallus covered by the outermost thalli of the lectotype rhodolith (thin section CE-4) (Pl. 2, fig. 4). The vegetative characters in this thallus leave no doubt about its conspecificity with the most external coralline plants. Conceptacles are rectangular, with rounded corners in longitudinal section. They measure 431–647 μm (mean 501 μm , s.d. 102) in diameter and 216–277 μm (mean 231 μm , s.d. 31) high (Table 1). Conceptacles protruded on the thallus surface at the time of their formation (Pl. 2, fig. 4) but some became buried by subsequent overgrowth of the thallus. Conceptacle roofs are flattened to mound-like and are made up of six or seven cell-long filaments perpendicular to the surface.

Remarks. The multiporate tetra/bisporangial conceptacles in the lectotype indicate that this species belongs to the subfamily Melobesioideae. Lemoine (1939) gave the measurements of some

conceptacles in one sample from the Pliocene of Djebel Zeboudj that she included in the original species material. Although she did not refer to the conceptacle morphology, they were probably multiporate as well, according to the generic concepts that she followed (Lemoine 1939, pp. 37, 39). Within the melobesioids, flat and probably flared epithallial cells, such as those observable in the lectotype of the species, are characteristic for *Lithothamnion* Heydrich, 1897*b* (nom. cons. in substitution of *Lithothamnium* Philippi, 1837, nom. rejic., Woelkerling 1983) and, therefore, this species should be named *Lithothamnion betieri* Lemoine.

Plants with affinities to this species were illustrated by Buchbinder (1977, pl. 2, fig. 1) from the Miocene of Israel. The species was also reported in a coralline algal inventory from the Neogene of southern Spain (Segonzac 1990).

Genus MESOPHYLLUM Lemoine, 1928

Lectotype species. *Mesophyllum lichenoides* (Ellis) Lemoine, 1928, p. 251; designated by Ishijima (1942, p. 174).
Basionym: *Corallium lichenoides* Ellis, 1768, p. 407, pl. 17, figs 9–11.

Mesophyllum curtum Lemoine, 1939

Plate 2, figures 5–7

1939 *Mesophyllum curtum* Lemoine, p. 92, pl. 2, fig. 13; text-fig. 61.

Type material. This consists of one fragment of a small algal nodule (sample 2) and some remains from cutting for thin sectioning, one thin section from Ehrmann's Collection (*Plaque* 8 ter, renumbered as 2352), and one from Emberger's Collection (no. 2352).

Lectotype. In the original description of the species, Lemoine (1939) referred to two Tortonian localities: Saint Denis du Sig and Kef bel Kobei, both in Algeria. However, she figured and described only the sample from Saint Denis du Sig (sample 2, pl. 2, fig. 13; text-fig. 61), which is the one preserved and is here selected as lectotype. This is a rhodolith made up of several thalli of encrusting to warty plants growing one upon another and on a bioclastic micritic matrix. The small protuberances are up to 8 mm long and 2 mm in diameter. All plants in the nodule seem to be conspecific.

Vegetative anatomy. Plants in the lectotype material have a dorsiventral monomerous thallus with a coaxial continuous ventral core (Pl. 2, fig. 5) and a well-developed peripheral region (Pl. 2, fig. 6). In longitudinal sections the core thickness is highly constant, varying from 92 μm to 213 μm (mean 178 μm). The cells in the core are rectangular to trapezoidal in longitudinal section, measuring 18–28 μm (mean 20.9 μm , s.d. 2.4) long and 4–11 μm (mean 8.1 μm , s.d. 2.3) in diameter (Table 1). They are arranged in concentric arcs with good alignment of cells of adjacent filaments. Cell filaments curve downwards to the substrate and upwards, giving way to the peripheral region (Pl. 2, fig. 5). Cell fusions are conspicuous.

In the encrusting peripheral portion cells measure 7–14 μm (mean 10.6 μm , s.d. 2.3) long and 4–11 μm (mean 6.3 μm , s.d. 2.1) in diameter, whilst in the centre of the protuberances, where filaments are radially arranged, they reach up to 18 μm long (Table 1). Changes in length of cells of contiguous filaments produce conspicuous zonation of the encrusting portions and protuberances (Pl. 2, fig. 6). However, the lateral extent of zones is short and their shape is very variable, giving the peripheral region an irregular aspect.

Reproductive structures. Numerous multiporate tetra/bisporangial conceptacles occur irregularly distributed in the thallus. They are very variable in longitudinal section, from trapezoidal with rounded corners to rectangular, elliptical and even round (Pl. 2, figs 6–7). They are also irregular in transverse section although tending to be round. They measure 187–427 μm (mean 279.7 μm , s.d. 48.8) in diameter and 133–253 μm (mean 204.4 μm , s.d. 24.4) high (Table 1). The conceptacles protruded above the thallus surface (Pl. 2, figs 6–7). The conceptacle roofs, seven or eight cells thick, have many long and narrow cylindrical pores, up to 12 in

transverse section (Pl. 2, fig. 7). They are 35–64 μm (mean 52.8 μm , s.d. 9.5) long and 7–21 μm (mean 16.8 μm , s.d. 4.5) in diameter. All conceptacle chambers remained empty after burial by subsequent plant growth.

No gametangial conceptacles have been observed.

Remarks. Woelkerling and Harvey (1992, 1993) have focused the generic delimitation of *Mesophyllum* inside the subfamily Melobesioideae on features of spermatangial ontogeny and morphology, avoiding the use of the presence of a coaxial core of filaments as characteristic for *Mesophyllum*. According to these authors, *Mesophyllum* includes melobesioids with monomerous construction, no haustoria, no flared epithallial cells and vegetative initials as long or longer than cells immediately underneath. These vegetative characters are shared by *Clathromorphum* Foslie, 1898 and *Synarthrophyton* Townsend, 1979 but, in addition, *Mesophyllum* is delimited by having 'spermatangial initials overlain by a layer of protective cells; spermatangial conceptacle roofs formed centripetally from groups of peripheral filaments and spermatangial branches simple' (Woelkerling and Harvey 1993, p. 575). The occurrence of a coaxial core, considered diagnostic for *Mesophyllum* since it was established by Lemoine (1928), would not be significant from a taxonomic point of view, since in some plants it is not a persistent character and changes from a coaxial to a non-coaxial core can be observed (Woelkerling and Harvey 1992). Nevertheless, *Mesophyllum* is the only genus of melobesioid in which a coaxial arrangement is always present even if only in part of the ventral core. The coaxial organization occurs consistently at least in some portions of the core filaments in the type species, *M. lichenoides* (Ellis) Lemoine, 1928, and other species included in the genus on the basis of the above-mentioned spermatangial characters (Woelkerling and Harvey 1993). Even if this vegetative feature is not considered a key character in delimiting the genus it can be accepted as an additional one (see, for example, Chamberlain and Keats 1994, table 2), as no other melobesioid is known to have this type of core organization except for very sporadic occurrences in *Synarthrophyton* plants (May and Woelkerling 1988).

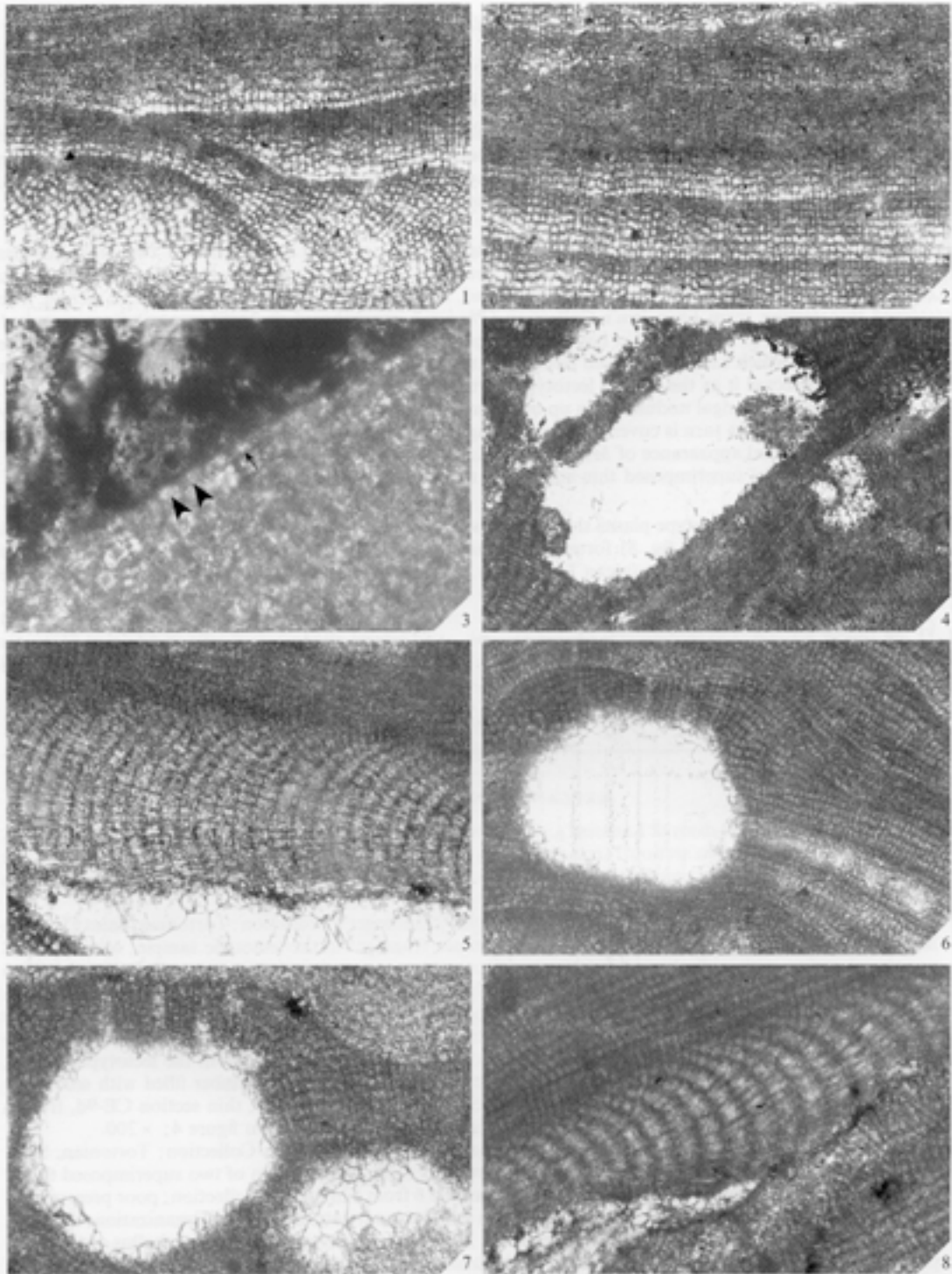
In fossil melobesioids the presence of coaxial arrangement in the core, such as that observable in *M. curtum*, is the only character readily preservable to separate *Mesophyllum* from other genera that share with it other vegetative features such as monomerous construction and long subepithallial initials (Braga *et al.* 1993). Therefore, we confirm the generic assignment made by Lemoine (1939) when establishing the species. *M. curtum* is easily identifiable by the irregular morphology of the conceptacle chambers. After its establishment, only Johnson (1966) has referred to this species in the Miocene of Borneo. However, the features of Johnson's figured specimen seem inappropriate to ascertain its relationships to *M. curtum*.

EXPLANATION OF PLATE 2

Figs 1–4. *Lithothamnion betieri* Lemoine (= *Lithothamnium Betieri* Lemoine); lectotype, Sample 4, Emberger's Collection; Upper Miocene of Hammar Semounet, Algeria; thin section CE-4. 1, plumose ventral core and strongly zoned peripheral region; note abundant and conspicuous cell fusions; $\times 120$. 2, zoned peripheral filaments; $\times 120$. 3, flat (arrow) and probably flared (arrowheads) epithallial cells; $\times 550$. 4, multiporate conceptacle slightly protruding on the thallus surface; $\times 100$.

Figs 5–7. *Mesophyllum curtum* Lemoine; lectotype, Sample 2, Emberger's Collection; thin section 2352, Emberger's Collection; Tortonian, Saint Denis du Sig, Algeria. 5, coaxial ventral core; $\times 140$. 6, section of zoned peripheral region and buried conceptacle that protruded on the thallus surface at time of development; $\times 120$. 7, buried conceptacle sections; note the marked difference in section shape with conceptacle in figure 6; also note flat roofs with narrow cylindrical pores; $\times 170$.

Fig. 8. *Mesophyllum sancti-dionysii* Lemoine (= *Mesophyllum Sancti Dionysii* Lemoine); lectotype, Sample 1, Emberger's Collection; thin section 7 (renumbered as 2360), Ehrmann's Collection; coaxial ventral core; $\times 120$.



AGUIRRE and BRAGA, *Lithothamnion*, *Mesophyllum*

Mesophyllum sancti-dionysii Lemoine, 1939

Plate 2, figure 8; Plate 3, figure 1

1939 *Mesophyllum Sancti Dionysii* Lemoine, p. 84, pl. 3, figs 2, 5–6.

Type material. This contains three algal nodules (samples 1, 7 and 8) and three additional rock fragments that may be the remains of cutting of two of the algal nodules for thin sectioning. One thin section from Ehrmann's Collection (*Plaque 7*, renumbered as 2360, probably by Emberger) and two from Emberger's Collection (no. 2360), all from the Upper Miocene (Tortonian) of Saint Denis du Sig, Algeria, have also been preserved.

Lectotype. From the original collection Lemoine illustrated the external appearance of two algal nodules (samples 1 and 7, pl. 3, figs 5 and 2 respectively in Lemoine 1939) and a microphotograph of a thin section (Lemoine 1939, fig. 6). Both algal nodules are preserved, but we have not found the figured thin section. The preserved thin section from Ehrmann's Collection (*Plaque 7*, renumbered as 2360) was cut from sample 1 according to the label of this sample in Lemoine's script. Therefore this is the only preserved sample from the type collection for which Lemoine studied both the external appearance and the microscopic features, which is why we have selected it as the species lectotype (Articles 9.2, 9.9 and Recommendation 9A in the ICBN). This is a fragment of an algal nodule made up of an unattached protuberant coralline growth surrounded by bioclastic micrite which in turn is covered by encrusting coralline plants. The thin section studied by Lemoine and the figured external appearance of *Mesophyllum Sancti Dionysii* correspond to the outermost algal cover. This consists of several superimposed thin encrusting thalli, some having encrusting laminar branches.

Vegetative anatomy. The lectotype plants show a dorsiventral monomerous thallus with a continuous, coaxial core in ventral position (Pl. 2, fig. 8) formed by rectangular to slightly trapezoidal cells, 14–39 μm (mean 25.9 μm , s.d. 4.8) long and 4–14 μm (mean 7.9 μm , s.d. 2.4) in diameter (Table 1). In longitudinal sections the core thickness is highly constant, varying from 107 to 250 μm (mean 178 μm). Cell fusions are conspicuous.

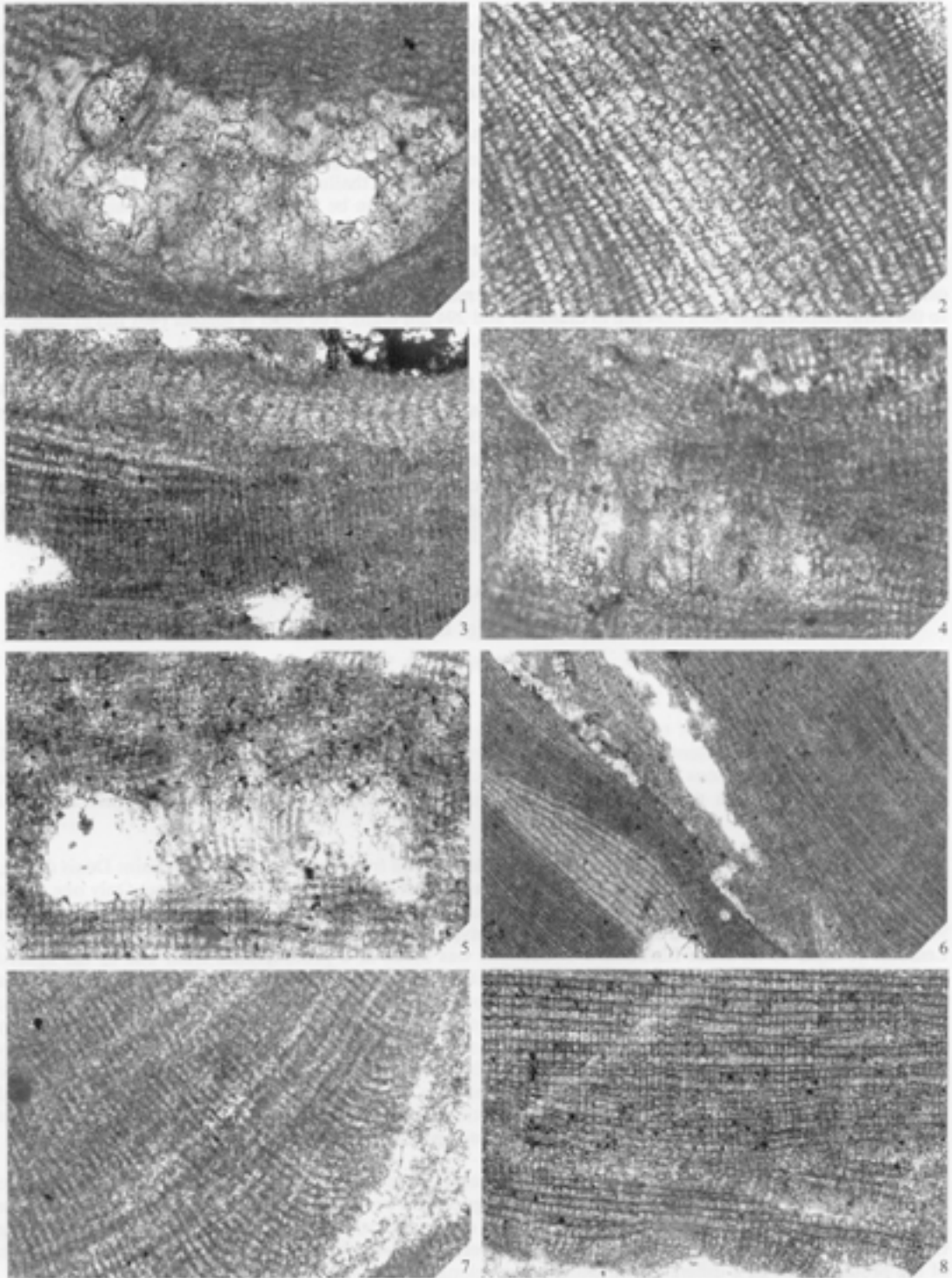
The peripheral region is well developed. It consists of square cells, 7–18 μm (mean 11.2 μm , s.d. 2.5) long and 4–11 μm (mean 8.1, s.d. 1.8) in diameter (Table 1), with good lateral alignment of cells of adjacent filaments and cell fusions (Pl. 2, fig. 8). Changes in length of laterally aligned cells cause a weak zonation of the peripheral region. These zones have a wavy appearance when they overlie conceptacles.

EXPLANATION OF PLATE 3

Fig. 1. *Mesophyllum sancti-dionysii* Lemoine (= *Mesophyllum Sancti Dionysii* Lemoine); lectotype, Sample 1, Emberger's Collection; thin section 7 (renumbered as 2360), Ehrmann's Collection; multiporate conceptacle with roof slightly concave upwards; the bulbous structure to the upper left (arrow) can be interpreted as the remains of a spore; $\times 120$.

Figs 2–5. '*Lithophyllum Sigi*' Lemoine; lectotype, Sample 9, Emberger's Collection; Tortonian, Saint Denis du Sig, Algeria. 2, thin section CE-9a, from a protuberance fragment in the lectotype sample; weakly zoned peripheral region with well-aligned cells from adjacent filaments; note conspicuous cell fusions (arrows) indicating that this species cannot be assigned to *Lithophyllum* in its modern circumscription; $\times 180$. 3, thin section CE-9c, from a protuberance fragment in the lectotype sample; coaxial core expanding over the surface of a protuberance; it is uncertain whether this core is an overgrowth from the same protuberance thallus or belongs to a different coralline species; $\times 140$. 4, thin section 2361, from the lectotype sample; structure that may represent an aborted conceptacle or an old conceptacle chamber filled with secondary tissue; it remains uncertain whether this conceptacle was uniporate; $\times 160$. 5, thin section CE-9d, from a protuberance fragment in the lectotype sample; structure similar to the one in figure 4; $\times 200$.

Figs 6–8. '*Mesophyllum Ehrmanni*' Lemoine; lectotype, Sample 3, Emberger's Collection; Tortonian, Saint Denis du Sig, Algeria. 6, thin section 6 bis from Ehrmann's Collection; section of two superimposed thalli; direction of growth towards top right; $\times 50$. 7, thin section 6 from Ehrmann's Collection; poor preservation prevents clear identification of primigenous filaments and the exact nature of thallus organization; direction of growth towards top left; $\times 150$. 8, thin section no. 2353 from Emberger's Collection; thallus section with probable dimerous organization; note the good alignment of cells of adjacent filaments; direction of growth towards top of figure; $\times 120$.



AGUIRRE and BRAGA, coralline algae

Reproductive structures. Numerous relatively well-aligned multiporate tetra/bisporangial conceptacles occur in the peripheral region of the lectotype. They measure 240–627 μm (mean 471.4 μm , s.d. 114.8) in diameter and 160–267 μm (mean 219.4 μm , s.d. 30.4) high (Table 1). Conceptacle chambers are bean-like or elliptical in outline. Conceptacles protruded from the thallus surface at the stage they were formed. Later growth of peripheral filaments adapted to these protrusions giving a wavy aspect to the peripheral region. Conceptacle roofs, comprising up to six layers of cells, are flat or slightly concave upwards (Pl. 3, fig. 1). Pore tubes are conical, measuring 63 μm long and 32–35 μm (mean 33.7 μm , s.d. 2.5) in basal diameter. Most conceptacles are filled with irregular large cells (21–71 μm , mean 49.3 μm , s.d. 12.6, long and 11–32 μm , mean 21.1 μm , s.d. 6.3, in diameter) that can be interpreted as secondary growths of the thallus after spore release (Lemoine 1939). However, in one conceptacle a bulbous structure (Pl. 3, fig. 1) can be interpreted as the remains of a spore (142 μm high and 71 μm in diameter).

In one thin section from Emberger's Collection two thalli with uniporate conceptacles but similar in vegetative anatomy to plants with tetra/bisporangial conceptacles can be interpreted as gametangial and/or carposporangial plants. One of these conceptacles protrudes slightly on the thallus surface and is similar in size to the tetra/bisporangial ones (534 μm in diameter and 294 μm high). The other is smaller (461 μm in diameter and 192 μm high) and protrudes strongly on the dorsal surface.

Remarks. As in the previously discussed case of *M. curtum*, the occurrence of a coaxial core in the lectotype plants of *M. sancti-dionysii* supports its inclusion in *Mesophyllum*. Therefore this species should be referred to as *M. sancti-dionysii* Lemoine.

Plants of this species have been illustrated from the Miocene of Lebanon (Edgell and Basson 1975) and northern Italy (Fravega and Vannucci 1987). In the latter region the species has been reported in some coralline algal accounts (Fravega and Vannucci 1982; Fravega *et al.* 1984, 1993). Plants with affinities to *M. sancti-dionysii* from Israel were figured by Buchbinder (1977).

SPECIES OF UNCERTAIN CIRCUMSCRIPTION

Lithophyllum Sigi Lemoine, 1939

Plate 3, figures 2–5

1939 *Lithophyllum Sigi* Lemoine, p. 103, pl. 2, fig. 9.

Type material. This consists of two rock fragments containing unattached fruticose and branching coralline plants and eight small fragments of fruticose protuberances (all this material was considered to be sample 9). In addition, two thin sections from Ehrmann's Collection (*Plaques* 15 and 15 ter, renumbered as 2361), one of them (*Plaque* 15) with no algal content, and one section from Emberger's Collection (no. 2361) are conserved.

Lectotype. From the many samples in the original collection, all from the Tortonian from Saint Denis du Sig, Algeria, Lemoine figured two examples (pl. 2, fig. 9) and made two thin sections from them. Only one of the figured examples (the one to the left in pl. 2, fig. 9) is preserved (included in sample 9). Following Articles 9.2 and 9.9 in the ICBN, this is here selected as lectotype. The preserved thin section from those studied by Lemoine (*Plaque* 15 ter from Ehrmann's Collection) was made in a protuberance from one of the figured plants. The sample preserved has several broken protuberances but it is uncertain whether the thin section was made in one of them. The plant cut in this thin section is conspecific with the one cut by Emberger (sample 2361), but two of those that we have cut from other protuberance fragments (thin sections CE-9a–CE-9g) may belong to other coralline species. However, the growth form of both examples figured by Lemoine is very similar and it is therefore reasonable to assume that the two plants belong to the same species. The lectotype is an unattached fruticose plant, 30 mm long. Protuberances, up to 6 mm in diameter, branch repeatedly and thin out at the tips. The plant is embedded in a bioclastic micritic matrix and it is difficult to ascertain, without breaking the sample, whether all the protuberances emerging from the matrix belong to the same plant.

Vegetative anatomy. Cell filaments in the protuberances are radially arranged. Cells of adjacent filaments are aligned laterally and slight changes in the length of aligned cells promote a weak zonation (Pl. 3, fig. 2). In one thin section from a protuberance of a plant probably conspecific with the lectotype there is a thin encrusting thallus with coaxial arrangement (Pl. 3, fig. 3). However, it is impossible to decide whether it is an overgrowth of the protuberance or a different encrusting plant belonging to another species.

Cells in the protuberances are 7–14 μm (mean 10.7 μm , s.d. 2.1) long and 4–7 μm (mean 5.5 μm , s.d. 1.8) in diameter (Table 1). Cell fusions are abundant and conspicuous (Pl. 3, fig. 2).

Reproductive structures. No reproductive structures occur in the sample studied by Lemoine (1939). In thin section 2361 from Emberger's Collection there are several poorly preserved structures representing aborted developmental stages of conceptacles or old conceptacle chambers filled with secondary tissue (Pl. 3, fig. 4). Similar structures occur in thin sections CE-9' and CE-9d (Pl. 3, fig. 5). Some of them seem to correspond to uniporate sporangial conceptacles, but their actual nature is highly uncertain (Pl. 3, figs 4–5). They measure 177–394 μm (mean 297.3 μm , s.d. 89.8) in diameter and 85–142 μm (mean 110.9 μm , s.d. 23.4) high (Table 1).

Remarks. The absence of well-preserved conceptacles precludes any certain generic assignment of this species. However, the presence of cell fusions in the peripheral region of the syntypes indicates that this species does not belong to the subfamily Lithophylloideae and cannot be attributed to *Lithophyllum*. If the poorly preserved structures observable in Emberger's thin section actually correspond to uniporate sporangial conceptacles this species should be considered as a member of the subfamily Mastophoroideae.

No reports of this taxon have been made since it was established.

Mesophyllum Ehrmanni Lemoine, 1939

Plate 3, figures 6–8

1939 *Mesophyllum Ehrmanni*, Lemoine, p. 85, pl. 1, figure 3, text-figs 52–54.

Type material. One algal nodule (sample 3) and three very small fragments remaining from cutting the sample for thin sectioning are preserved. It comes from the Tortonian of Saint Denis du Sig, Algeria. The original material also includes three thin sections from Ehrmann's Collection (*Plaques* 6, 6 bis and 6 ter, renumbered as 2353) and one thin section from Emberger's Collection (no. 2353).

Lectotype. When describing the species Lemoine refers to two samples. One of them (sample 3), figured by Lemoine (1939, pl. 1, fig 3; text-figs 52–53) is the one conserved at Nantes and labelled in Lemoine's script as type of the species. The three sections from Ehrmann's Collection and the one from Emberger's Collection were made from this sample. The other sample described by Lemoine (1939, text-fig. 54), which she assigned to the species with some doubt, was inside a nodule mainly composed of *Lithothamnium magnum* and does not seem to be preserved. The first sample is a rhodolith, measuring now 70 × 60 × 55 mm, that consists of a bioclastic micritic nucleus engulfing unattached fruticose thalli covered by thick encrusting algal plants. Lemoine (1939) refers to these latter in her description of the species and, therefore, they are here selected as the lectotype (Articles 8.1, 9.2 and 9.9 in the ICBN). The encrusting thalli curve around the fruticose thalli in the nucleus giving way to broad protuberances.

Vegetative anatomy. Plants have a dorsiventral monomerous and dimerous organization (Pl. 3, figs 6–8). Plumose ventral cores (Pl. 3, fig. 6) are poorly developed (35–71 μm thick). The filaments run parallel to the substrate for a very short distance and curve upwards to a very thick peripheral region. Core cells are 7–14 μm (mean 11.6 μm , s.d. 2.3) long and 4–11 μm (mean 7.9 μm , s.d. 1.8) in diameter (Table 1).

Cells of adjacent filaments in the peripheral region are usually well aligned (Pl. 3, figs 6, 8). Cell fusions are very scarce. Cells are rectangular, with uniform size, 7–14 μm (mean 10.7 μm , s.d. 2.5) long × 4–11 μm (mean 6 μm , s.d. 1.8) in diameter (Table 1). However, slight changes in cell length produce very weak zonation of the peripheral region.

Reproductive structures. Lemoine (1939) considered the lectotype plant to have been sterile. In fact, no reproductive structures can be observed in the thin sections from the original Ehrmann's Collection, in the one from Emberger's Collection or in the additional thin section that we prepared (sample CE-3). Close inspection of the algal nodule surface reveals no conceptacle structures. In the original description, Lemoine (1939) referred to multiporate conceptacles, drawn in her text-figure 54, only in the example covered by *Lithothamnium magnum*, which is not preserved. However, the attribution of this example to *Mesophyllum Ehrmanni* was

TABLE 2. Summary of the proposed taxonomic circumscription for the species studied.

| Lemoine's circumscriptions | Circumscription proposed in this paper | |
|-------------------------------------|--|--------------------------|
| Family Corallinaceae | | |
| <i>Archaeolithothamnium brevium</i> | <i>Sporolithon brevium</i> | Division RHODOPHYTA |
| <i>Archaeolithothamnium liberum</i> | <i>Sporolithon liberum</i> | Wettstein, 1901 |
| <i>Lithophyllum Glangeaudi</i> | <i>Sporolithon glangeaudii</i> | Class RHODOPHYCOPSIDA |
| | | Rabenhorst, 1863 |
| | | Order CORALLINALES |
| | | Silva and Johansen, 1986 |
| | | Family SPOROLITHACEAE |
| | | Verheij, 1993 |
| <i>Lithothamnium Betieri</i> | <i>Lithothamnium betieri</i> | Division RHODOPHYTA |
| <i>Mesophyllum Sancti Dyonisii</i> | <i>Mesophyllum sancti-dyonisii</i> | Wettstein, 1901 |
| <i>Mesophyllum curtum</i> | <i>Mesophyllum curtum</i> | Class RHODOPHYCOPSIDA |
| | | Rabenhorst, 1863 |
| | | Order CORALLINALES |
| | | Silva and Johansen, 1986 |
| | | Family CORALLINACEAE |
| | | Lamouroux, 1816 |
| | | Subfamily MELOBESIOIDEAE |
| | | Bizzozero, 1885 |
| <i>Lithophyllum Sigi</i> | Uncertain circumscription | |
| <i>Mesophyllum Ehrmanni</i> | | |

doubtful even for the author of the species (Lemoine 1939). Therefore, the nature of the reproductive structures in this species remains uncertain, as far as the type material is concerned.

Remarks. The absence of reproductive structures in the conserved type material prevents any definite generic assignment for this species. In addition, the lack of a ventral coaxial core suggests that this species does not belong to the genus *Mesophyllum*. Although Lemoine (1939) referred to a fertile plant when establishing the species and even drew some multiporate conceptacles, the conspicuity of the latter with the preserved type of *M. Ehrmanni* was doubtful even for Lemoine (1939). Therefore, it seems appropriate to consider the nature of the reproductive structures of the species and its circumscription as uncertain.

No subsequent reports of this species have been made.

CONCLUDING REMARKS

Emberger's Collection at the University of Nantes contains the type material of eight coralline algal species from the 27 new ones described by Lemoine (1939) from the Cretaceous and Cenozoic deposits of Algeria. This is one of the very few preserved collections of the original fossil material of Mme Lemoine, who established at least 108 fossil coralline algal species from the Lower Cretaceous to the Pleistocene.

We have typified six species according to the ICBN rules (Greuter 1994), selecting lectotypes from the original syntypes. The remaining two species were based upon a single specimen which has to be considered as the holotype. The types are redescribed and illustrated focusing on characters relevant in modern taxonomy of fossil corallines, completing Lemoine's original descriptions and illustrations. Revision of the types with present-day taxonomic criteria and nomenclature has resulted in changes of generic and family adscription of three species whilst three others remain

within the same taxa to which were assigned by Lemoine (1939) (Table 2). Finally, no diagnostic generic characters occur in two species types and therefore the nature of these taxa is uncertain (Table 2).

These results demonstrate the difficulties and, sometimes, the inadequacy of using taxa established a long time ago upon features which are not considered diagnostic in modern taxonomy. The results also confirm the necessity of reassessing the precise nature of many coralline algae taxa introduced in the palaeontological literature, by revising the preserved original collections and avoiding the use of taxa with no conserved type material.

Acknowledgements. We are very grateful to Patrick Génot who offered us the opportunity of studying Lemoine's types from the Emberger Collection at the University of Nantes. We are indebted to Dr W. J. Woelkerling for his helpful comments of the first version of the manuscript that have improved it. The manuscript has been enhanced by the corrections and changes suggested by the *Palaeontology* referees, whose efforts we sincerely appreciate. We also thank Christine Laurin for the revision of the English text.

REFERENCES

- AGUIRRE, J., BRAGA, J. C. and PILLER, W. 1996. Reassessment of *Palaeothamnium* Conti, 1946 (Corallinales, Rhodophyta). *Review of Palaeobotany and Palynology*, **94**, 1–9.
- BIZZOZERO, G. 1885. *Flora Veneta Crittogamica*. Part 2. Seminario, Padova, 255 pp.
- BOSENCE, D. W. J. 1983. Coralline algae from the Miocene of Malta. *Palaeontology*, **26**, 147–173.
- BRAGA, J. C. and AGUIRRE, J. 1995. Taxonomy of fossil coralline algal species: Neogene Lithophylloideae (Rhodophyta, Corallinales) from southern Spain. *Review of Palaeobotany and Palynology*, **86**, 265–285.
- BOSENCE, D. W. J. and STENECK, R. S. 1993. New anatomical characters in fossil coralline algae and their taxonomic implications. *Palaeontology*, **36**, 535–547.
- BUCHBINDER, B. 1977. Systematic and palaeoenvironments of the calcareous algae from the Miocene (Tortonian) Ziqlag Formation, Israel. *Micropaleontology*, **23**, 415–435.
- CHAMBERLAIN, Y. M., IRVINE, L. M. and WALKER, R. 1988. A redescription of *Lithophyllum crouanii* (Rhodophyta, Corallinales) in the British Isles with an assessment of its relationship to *L. orbiculatum*. *British Phycological Journal*, **23**, 177–192.
- and KEATS, D. W. 1994. Three melobesoid crustose coralline red algae from South Africa: *Leptophyllum acervatum* (Foslie) comb. nov., *L. foveatum* sp. nov. and *L. ferox* (Foslie) comb. nov. *Phycologia*, **33**, 111–133.
- DELOFFRE, R., POIGNANT, A. F. and TEHERANI, K. 1977. Algues calcaires de l'Albo-Aptien au Paléocène de l'Iran Central. *Bulletin des Centres de Recherches Exploration-Production Elf Aquitaine*, **1**, 29–57.
- EDGEELL, H. S. and BASSON, P. W. 1975. Calcareous algae from the Miocene of Lebanon. *Micropaleontology*, **21**, 165–184.
- ELLIOTT, G. F. 1960. Fossil calcareous algal floras of the Middle East with a note on a Cretaceous problematicum, *Hensonella cylindrica* gen. et sp. nov. *Quarterly Journal of the Geological Society, London*, **127**, 217–232.
- ELLIS, J. 1768. Extract of a letter from John Ellis Esquires, F.R.S. to Dr Linneaus of Upsal, F.R.S. on the animal nature of the genus of zoophytes, called *Corallina*. *Philosophical Transactions of the Royal Society of London*, **57**, 404–427, pls 17–18.
- FOSLIE, M. 1898. Systematical survey of the lithothamnia. *Kongelige Norske Videnskabers Selskab Skrifter*, **1898**, 1–7.
- FRAVEGA, P., GIAMMARINO, S. and VANNUCCI, G. 1984. Episodi ad « algal balls » e loro significato al passaggio arenare di Serravalle-Marne di S. Agata fossili a nord di Gavi (Bacino Terziario del Piemonte). *Atti della Società Toscana di Scienze Naturali, Serie A*, **91**, 1–20.
- PIAZZA, M. and VANNUCCI, G. 1993. Importance and significance of the rhodolith bodies in the miocenic sequences of Tertiary Piedmont Basin. 197–210. In BARATTOLO, F., DE CASTRO, P. and PARENTE, M. (eds). Studies on fossil benthic algae. *Bolletino della Società Paleontologica Italiana*, special vol. **1**, 197–210.
- and VANNUCCI, G. 1982. Significato e caratteristiche degli episodi a rhodoliti al « top » del Serravalliano tipo. *Geologica Romana*, **21**, 705–715.
- 1987. Significato delle facies algali delle sequenze tardo serravalliane-tortoniane ad Ovest di Gavi (Bacino Terziario del Piemonte). *Bolletino della Accademia Gioenia Scienze Naturali*, **20**, 317–334.

- GREUTER, W. 1994. *International Code of Botanical Nomenclature (Tokyo Code) adopted by the Fifteenth International Botanical Congress, Yokohama, 1993*. Koeltz Scientific Books, Königstein, Germany, xviii + 389 pp.
- HEYDRICH, F. 1897a. Corallinaceae, insbesondere Melobesieae. *Berichte Deutsche Botanische Gesellschaft*, **15**, 34–71, pl. 3.
- 1897b. Melobesieae. *Berichte Deutsche Botanische Gesellschaft*, **15**, 403–420, pl. 18.
- ISHIJIMA, W. 1942. The first find of *Mesophyllum* from the Tertiary of Japan. *Journal of the Geological Society of Japan*, **49**, 174–176.
- JOHNSON, J. H. 1957. Geology of Saipan, Mariana Islands. Calcareous algae. *Professional Paper of the United States Geological Survey*, **280-E**, 209–246.
- 1964a. Eocene algae from Ishigaki-shima Ryukyu-retto. *Professional Paper of the United States Geological Survey*, **399-C**, i–iii, 1–13, pls 1–7.
- 1964b. Miocene coralline algae from northern Iraq. *Micropaleontology*, **10**, 477–485.
- 1964c. Fossil and Recent calcareous algae from Guam. *Professional Paper of the United States Geological Survey*, **403-G**, i–iii, 1–40, pls 1–15.
- 1966. Tertiary red algae from Borneo. *Bulletin of the British Museum (Natural History), Geology Series*, **2**, 257–280, pls 1–6.
- KEATS, D. W. and CHAMBERLAIN, Y. M. 1993. *Sporolithon ptychoides* Heydrich and *S. episporum* (Howe) Dawson: two crustose coralline red algae (Corallinales, Sporolithaceae) in South Africa. *South African Journal of Botany*, **59**, 541–550.
- LAMOUREUX, J. V. F. 1816. *Histoire des polypiers coralligènes flexibles, vulgairement nommés zoophytes*. F. Poisson, Caen, lxxxiv + 559 pp., 19 pls.
- LEMOINE, M. P. 1928. Un nouveau genre de Mélobésiées: *Mesophyllum*. *Bulletin de Société Botanique de France*, **75**, 251–254.
- 1939. Algues calcaires fossiles de l'Algérie. *Matériaux pour la Carte Géologique de l'Algérie. 1^{re} Série Paléontologie*, **9**, 1–128, pls 1–3.
- 1970. Les algues floridées calcaires du Crétacé du sud de la France. *Archives del Museo Nationale Histoire Naturelle, Paris, Série 7*, **10**, 129–240, pls 1–15.
- MAY, D. I. and WOELKERLING, W. J. 1988. Studies on the genus *Synarthrophyton* (Corallinaceae, Rhodophyta) and its type species, *S. patena* (J. D. Hooker and W. H. Harvey) Townsend. *Phycologia*, **27**, 50–71.
- MOUSSAVIAN, E. and KUSS, J. 1990. Typification and status of *Lithothamnium aschersoni* Schwager, 1883 (Corallinaceae, Rhodophyta) from the Paleocene limestone of Egypt. A contribution to synonymy and priority of genera *Archaeolithothamnium* Rothpletz and *Sporolithon* Heydrich. *Berliner Geowissenschaftliches Abhandlungen*, **120**, 929–942.
- PHILIPPI, R. 1837. Beweis dass die Nulliporen Pflanzen sind. *Archiven Naturgeschichte*, **3**, 387–393, pls 1–9.
- POIGNANT, A. F. 1985. Key for specific determination of Cretaceous *Archaeolithothamnium*. 162–167. In TOOMEY, D. F. and NITCKI, M. H. (eds). *Paleoalgology. Contemporary research and applications*. Springer-Verlag, Berlin.
- CHERCHI, A. and SCHROEDER, R. 1981. Les corallinacées Crétacées du Nord-ouest de la Sardigne. *Revue de Micropaléontologie*, **24**, 244–252.
- RABENHORST, L. 1863. *Kryptogamen-Flora von Sachsen, der Ober-Lausitz, Thuringen und Nordbohlen*. Abteilung I. E. Krummer, Leipzig, xx + 653 pp.
- ROSANOFF, S. 1866. Recherches anatomiques sur les Mélobésiées. *Mémoires de la Société Impériale des Sciences Naturelles de Cherbourg*, **12**, 5–112, pls 1–7.
- ROTHPLETZ, A. 1891. Fossile Kalkagen aus den Familien der Codiaceen und der Corallineen. *Zeitschrift der Deutsche Geologische Gesellschaft*, **43**, 295–322, pls 15–17.
- 1893. Über eine neue Pflanze (*Lithothamnium erythraeum* n. sp.) des Rothen Meeres. *Botanisches Zentralblatt*, **54**, 5–6.
- SEGONZAC, G. 1990. Algues néogènes bétiques. *Documents et Travaux Institut Géologique Albert-de-Lapparent*, **12–13**, 35–41.
- SILVA, P. C. and JOHANSEN, H. W. 1986. A reappraisal of the order Corallinales (Rhodophyceae). *British Phycological Journal*, **21**, 245–254.
- TOWNSEND, R. A. 1979. *Synarthrophyton*, a new genus of Corallinaceae (Cryptonemiales, Rhodophyta) from the southern hemisphere. *Journal of Phycology*, **15**, 251–259.
- CHAMBERLAIN, Y. M. and KEATS, D. W. 1994. *Heydrichia woelkerlingii* gen. et sp. nov. a newly discovered nongeniculate red alga (Corallinales, Rhodophyta) from Cape Province, South Africa. *Phycologia*, **33**, 177–186.

- WOELKERLING, W. J., HARVEY, A. S. and BOROWITZKA, M. 1995. An account of the red algal genus *Sporolithon* (Sporolithaceae, Corallinales) in Southern Australia. *Australian Systematic Botany*, **8**, 85–121.
- VANNUCCI, G., STOCKAR, R., PIAZZA, M. and FRAVEGA, P. 1983. La trasgressione tardo-oligocenica nella zona di Millesimo (Savona): caratteristiche e significato delle associazioni faunistiche ed algali. *Bolletino del Museo regionale di Scienze naturali – Torino*, **11**, 239–266.
- 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*. Volume 1. Deuticke, Leipzig, v + 201 pp.
- WOELKERLING, W. J. 1983. A taxonomic reassessment of *Lithothamnion* Philippi (Corallinaceae, Rhodophyta) based on studies on Philippi's original collections. *British Phycological Journal*, **18**, 165–197.
- 1988. *The coralline red algae: an analysis of the genera and subfamilies of nongeniculate Corallinaceae*. Oxford University Press, London and Oxford, 268 pp.
- and HARVEY, A. 1992. *Mesophyllum incisum* (Corallinaceae, Rhodophyta) in Southern Australia: implications for generic and specific delimitation in the Melobesioideae. *British Phycological Journal*, **27**, 381–399.
- 1993. An account of southern Australian species of *Mesophyllum* (Corallinaceae, Rhodophyta). *Australian Systematic Botany*, **6**, 571–637.
- IRVINE, L. M. and HARVEY, A. 1993. Growth-forms in non-geniculate coralline red algae (Corallinales, Rhodophyta). *Australian Systematic Botany*, **6**, 277–293.

J. AGUIRRE

J. C. BRAGA

Departamento de Estratigrafía y Paleontología
Facultad de Ciencias
Universidad de Granada
Campus Fuentenueva s.n.
18071 Granada, Spain
e-mail: jbraga@goliat.ugr.es

Typescript received 29 April 1997

Revised typescript received 1 September 1997