

Application of neontological taxonomic concepts to Late Eocene coralline algae (Rhodophyta) of the Austrian Molasse Zone

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ABSTRACT – Traditionally, different diagnostic characters have been used in the identification of fossil and Recent coralline algal genera. The taxonomy of fossil coralline algae has focused on well calcified features such as basal filaments and conceptacle perforation. In contrast, the taxonomy of Recent material uses a combination of several features with a low fossilization potential, such as epithallial cells and structures of sexual reproductive organs. In the studied material of the Late Eocene Austrian Molasse Zone *Lithoporella*, *Neogoniolithon*, *Spongites*, *Phymatolithon* and *Sporolithon* are identified and described applying features of neontological taxonomic concepts. These features are: (1) the arrangement of basal filaments; (2) the occurrence of cell fusions; (3) the relative length of subepithallial initials; (4) the conceptacle perforation; (5) the orientation of filaments around the conceptacle pore; and (6) the type of conceptacle roof formation. Some of these features were thought to be un preservable in fossil material until recently. The fossilization potential of diagnostic features and the identification of the documented genera and species are discussed in detail. Moreover, a checklist for the description of fossil taxa is provided. *J. Micropalaeontol.* 18(1): 67–80, June 1999.

INTRODUCTION

Until recently, several diagnostic characters used in present day coralline red algal taxonomy were thought to be un preservable in fossil material. Wray (1977) and Pognant (1984) therefore concluded that fossil and Recent coralline algae have to be classified in different ways. The taxonomy of fossil coralline algae has usually focused on calcified characters with a high fossilization potential such as the arrangement of basal filaments, the perforation of asexual conceptacles, and the occurrence of trichocytes (Wray, 1977). The taxonomy of Recent coralline algae, however, uses additional characters including cell connections, the shape of epithallial cells, the length of subepithallial initials, and the formation of sexual reproductive organs (see Figure 2) (Woelkerling, 1988; Braga *et al.*, 1993). Consequently, some genera and most species described from fossil material cannot be compared to any Recent taxon and, conversely, some Recent genera are not recognized in the fossil record. The unification of taxonomy of Recent and fossil corallines is crucial to the understanding of their phylogeny, palaeoecology and palaeobiogeography.

Braga *et al.* (1993) demonstrated, using the genus *Spongites* Kützing (1841) as an example, that key features of the taxonomy of present day corallines such as cell connections, epithallial cells and subepithallial initials are indeed preservable and can occasionally be recognized in fossil coralline algae. Since then, several studies have dealt with the identification of fossil taxa using diagnostic characters used in present day taxonomy (Bassi, 1995a, 1995b; Braga & Aguirre, 1995; Aguirre *et al.*, 1996; Basso *et al.*, 1996, 1997). Moreover, Braga *et al.* (1993) presented an identification key for fossil coralline algae that utilizes both traditional and neontological features. This key demonstrated that traditional characters still have to be used in certain cases in the identification of several fossil genera. This is due to the fact that several key features used in Recent taxonomy, such as the formation of sexual reproductive organs, have not yet been observed in fossil material.

This study aims to evaluate the identification key of Braga *et al.* (1993) and the applicability of characters used in present day

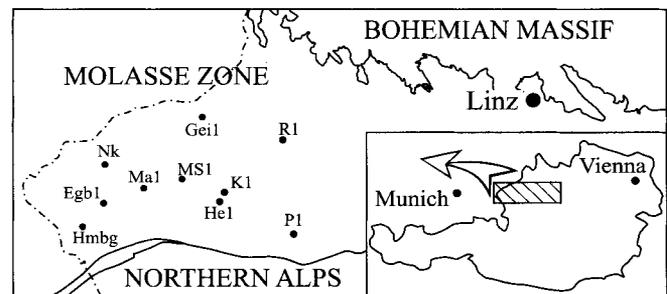


Fig. 1. Study area showing sampled deep wells and geological units. Inset shows the position of the study area in Austria.

taxonomy in the identification of fossil material. Using five genera it tries to bring us one step further in unifying fossil and present day coralline algal taxonomy. Moreover, it intends to provide a modern documentation of coralline algae of the study area to serve as a base for further actualistic approaches. We provide a checklist for the description of coralline algal species with all features known from fossil material (Table 2) and discuss the preservation potential of taxonomic features.

MATERIAL AND METHODS

The studied material comes from the Priabonian (Late Eocene) red algal limestones ('Lithothamnienkalk') of the Austrian Molasse Zone (Fig. 1) (Aberer, 1958; Malzer, 1981; Wagner *et al.*, 1986; Wagner, 1996). These red algal limestones are up to 80 m thick and were deposited on a mixed carbonate–siliciclastic ramp. They are known from deep wells of the Rohöl AG, Vienna (Austria) only (Wagner, 1980, 1996). A detailed study of the palaeoecology and facies of the red algal limestones is in preparation by the authors.

Two hundred palaeontological thin sections and several scanning electron microscope samples from 10 deep wells (Fig. 1) were studied. Cell and conceptacle dimensions were measured

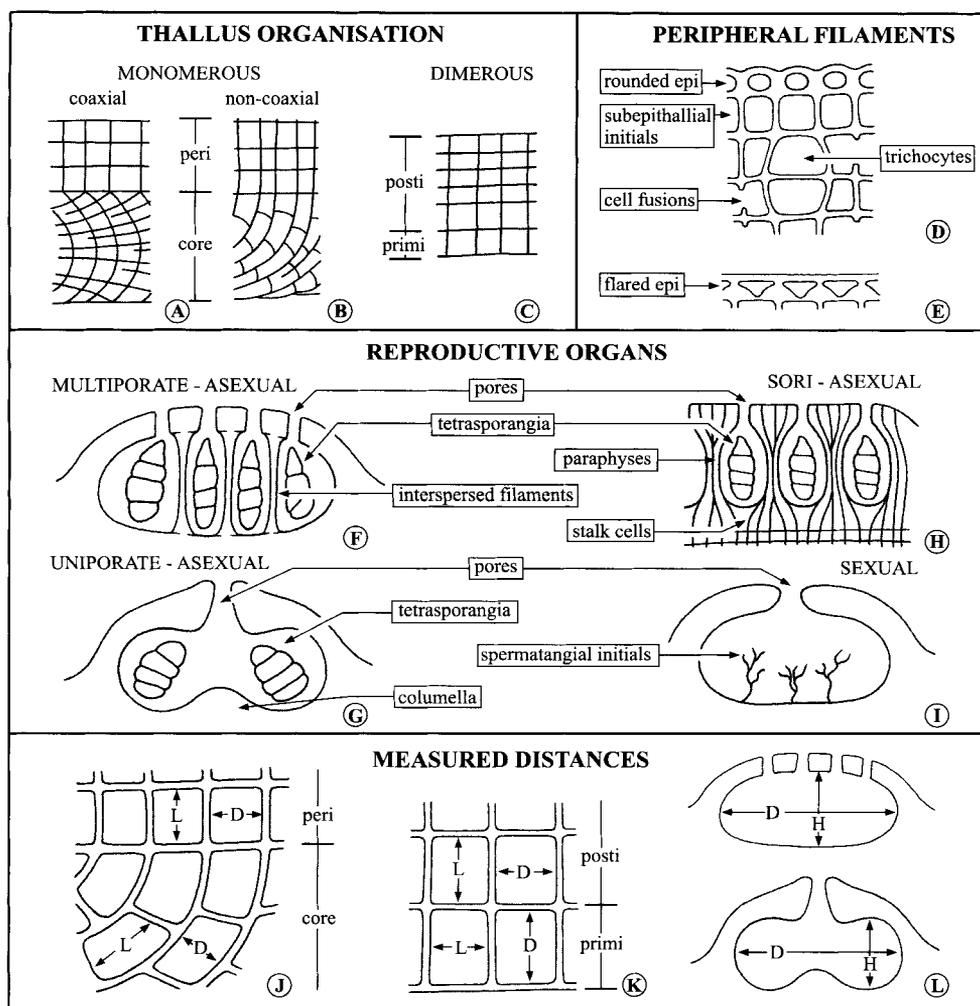


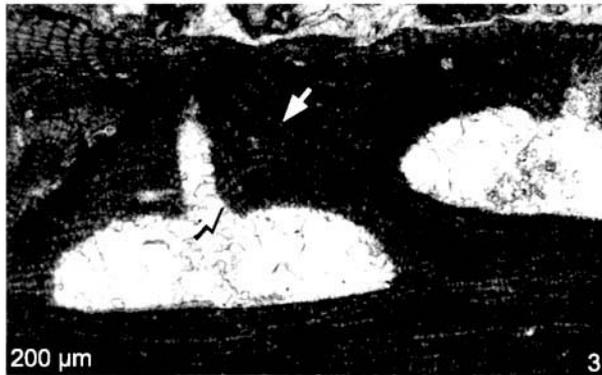
Fig. 2. Taxonomic features and measured distances of coralline algae. (A–C) Thallus organization. (A) Coaxial and (B) non-coaxial arrangement of monomerous thalli. (D, E) Shape and arrangement of epithallial cells and subepithallial initials. (F–H) Tetra/bisporangial reproductive organs are borne in (F) multiporate, (G) monoporate conceptacles or (H) are arranged in sori. (I) Sexual organs are borne in uniporate conceptacles. Gamete-producing cells (spermatangial initials) may be branched or simple. (J–L) Measurements. (J) Measurement distances in monomerous thalli, (K) dimerous thalli and (L) conceptacles (core = core filaments; peri = peripheral filaments; primi = primigenous filaments; posti = postigenous filaments; D = diameter; H = height; and L = length).

according to Fig. 2J–L. Measurements were made by a microscope at a magnification of $400\times$ to the nearest $1\mu\text{m}$. The maximum cell diameters of peripheral filaments were measured in sections perpendicular to the direction of filament growth, if possible. All other dimensions were measured in sections parallel to the growth direction. At least 20 cells of each cell type were measured, if possible. The mean (M) and standard deviation (SD) were calculated if a sufficient number of measurements could be made. The number of conceptacles was usually not sufficient to calculate M and SD. Cells of core filaments were measured only near the dorsal surface to avoid filament branching zones which may be difficult to recognize owing to the preservation. Cells of peripheral filaments were measured in the central parts of the thallus only, as the outer cell layers are usually micritized. Scanning electron microscope samples were prepared as described by Braga *et al.* (1993). Samples were polished and etched with 2% HCl for 10–30 seconds or with 7% EDTA for one minute. The optimal etching

time varied between the samples; the best results were obtained with HCl. Samples are stored at the Institute for Palaeontology, Vienna University.

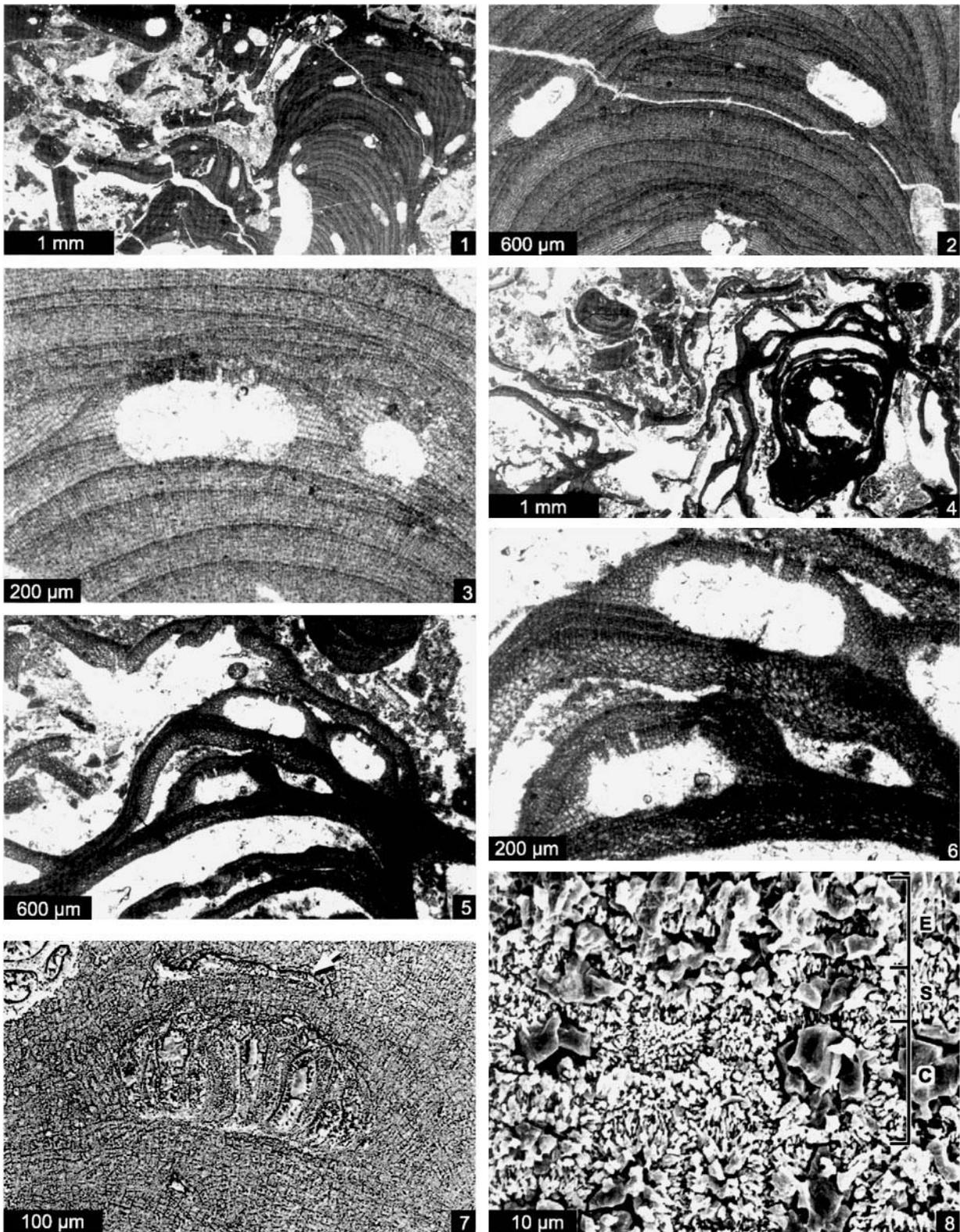
TERMINOLOGY OF TAXONOMIC FEATURES

The names of diagnostic anatomical features (Woelkerling, 1988; Braga & Aguirre, 1995) and growth forms (Woelkerling *et al.*, 1993) are summarized in the following, as they may be unfamiliar to most palaeontologists. Coralline algal thalli (i.e. plant bodies) are formed by adjacent filaments which are calcified and repeatedly branched. Consecutive cells within one filament are connected by primary pit connections; cells of adjacent filaments may be connected by secondary pit connections and/or cell fusions. Algal thalli can be dimerous or monomerous. Dimerous thalli (Fig. 2C) consist of unilayered basal primigenous filaments ('hypothallium' of older publications), from which the postigenous filaments ('perithallium' of older publications) arise dorsally at right angles. Primigenous



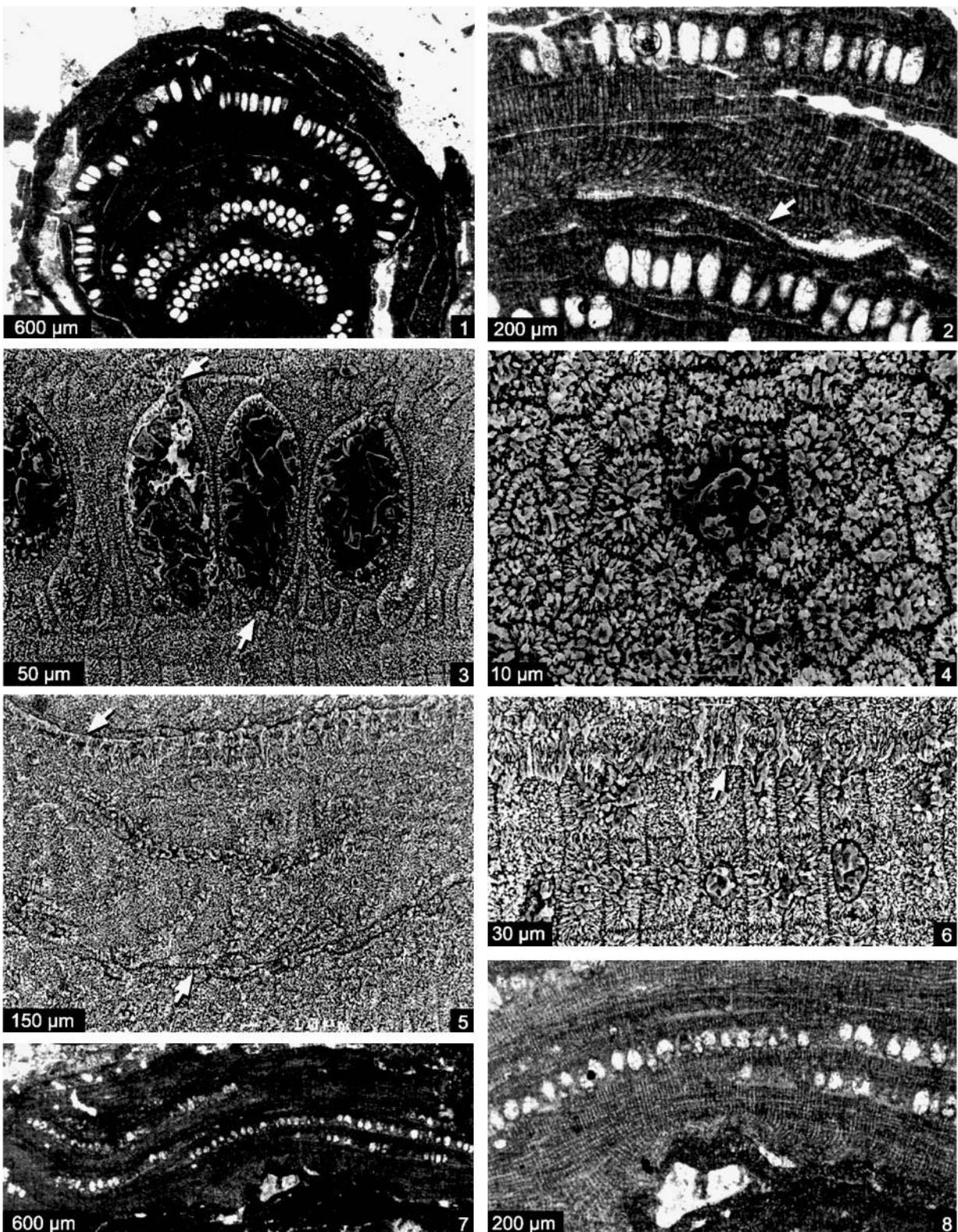
Explanation of Plate 1

Subfamily Mastophoroideae. fig. 1. *Lithoporella melobesioides*. Note large palisade cells (arrow) and postigenous filaments which occur around the conceptacles only. Arrow marks the filaments around the pore which are arranged subparallel to the outer roof surface. Sample MOL25. **figs 2–4.** *Neogonolithon* sp. **fig. 2.** Thallus with peripheral filaments occurring on both the dorsal and the ventral thallus portion and a tangentially cut conceptacle in the centre. Sample MOL292. **fig. 3.** Monoporate conceptacles. Note filaments around the pore (lower arrow) which are subparallel to the outer conceptacle roof (upper arrow). Sample MOL110. **fig. 4.** Scanning electron microscopy image of the coaxial core in longitudinal section showing a cell fusion (arrow). Sample MOL64ASEM. **figs 5, 6.** *Spongites* sp. 1. **fig. 5.** Thallus overgrowing *Lithoporella melobesioides*. Sample MOL380. **fig. 6.** Note the monoporate conceptacle completely raised above thallus surface. Sample MOL380. **figs 7, 8.** *Spongites* sp. 2. **fig. 7.** Protuberance with distinct growth rhythms in the upper part. Sample MOL209. **fig. 8.** Uniporate conceptacle with filaments around the conceptacle pore subparallel to the outer conceptacle roof. Note that the magnification is the same as in fig. 3. Sample MOL209.



Explanation of Plate 2

Subfamily Melobesioideae. **figs 1–3.** Melobesioideae gen. et spec. indet. **fig. 1.** Lumpy growth form. Sample MOL3A. **fig. 2.** Distinct growth rhythms in a protuberance. Sample MOL3A. **fig. 3.** Multiporate conceptacles are raised one-half above thallus surface. Sample MOL3A. **figs 4–8.** *Phymatolithon* sp. **fig. 4.** Characteristic layered to foliose growth form. Sample MOL291. **fig. 5.** Consecutive overgrowings of thalli. Sample MOL291. **fig. 6.** Multiporate conceptacles nearly completely raised above thallus surface. Sample MOL291. **fig. 7.** Scanning electron microscopy image showing preserved tetra/bisporangial conceptacles and interspersed filaments forming the conceptacle roof. Note the cement filled cavity above the roof (arrow). Sample MOL59SEM. **fig. 8.** Epithallial cells (E) and subepithallial initials (S) which are shorter than cells subtending them (C). Irregular shape of etched epithallial cells is caused by large crystals forming cell walls. This character allows a separation of epithallial cells from subepithallial initials. Compare Fig. 3. Sample MOL260. Sample MOL260SEM.



Explanation of Plate 3

Family Sporolithaceae. figs 1–6. *Sporolithon* sp. 1. **fig. 1.** Lumpy growth form. Sample MOL377. **fig. 2.** Non-coaxial core filaments in the centre and sori. Note row of epithallial cells (arrow) which are characterized by their transparency in thin section. Owing to their diffuse appearance, higher magnifications do not provide more details. Sample MOL377. **fig. 3.** Scanning electron microscopy (SEM) image of tetra/bisporangial conceptacles. Note basal stalk cell (arrow) and conceptacle pore (arrow). Sample MOL377SEM. **fig. 4.** SEM image showing a horizontal section of a conceptacle pore surrounded by rosette cells. Sample MOL377SEM. **fig. 5.** SEM image showing basal core filaments (arrow) and row of epithallial cells in the upper part (arrow). Sample MOL377SEM. **fig. 6.** SEM image showing regular cell rows of peripheral filaments and poorly preserved epithallium (arrow). Epithallial cells are recrystallized and replaced by large calcite crystals. Sample MOL377SEM. **figs 7, 8.** *Sporolithon* sp. 2. **fig. 7.** Encrusting growth form. Sample MOL220. **fig. 8.** Basal core filaments and sori. Note that the magnification is the same as in fig. 2. Sample MOL220.

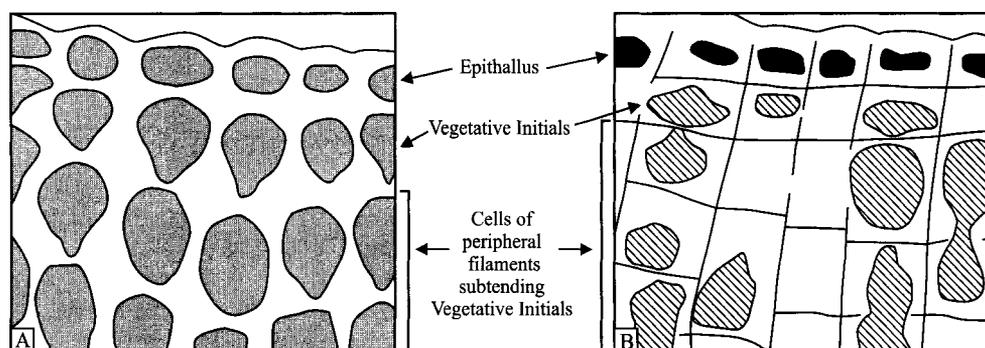


Fig. 3. Epithallial cells and vegetative initials. (A) Decalcified section of a Recent *Phymatolithon* showing the shape of epithallial cells and the length of vegetative initials compared to the length of cells subtending them. Cell luminae are marked by a greyish colour. Redrawn from Woelkerling (1988). (B) Epithallial cells and vegetative initials of a fossil specimen, redrawn from Plate 2, fig. 8. Primary cell luminae of epithallial cells are filled with micrite (black) and those of the vegetative initials and the cells of peripheral filaments are filled with sparry calcite (hatched). Note that the vegetative initials are as short as or shorter than the cells subtending them. See Plate 2, fig. 8 for scale.

filaments can be composed of palisade cells (i.e., cell diameter is higher than cell length; compare Fig. 2K; Plate 1, fig. 1). Monomerous thalli (Fig. 2A, 2B) consist of basal multilayered core filaments ('hypothallium' of older publications), which can be coaxial (i.e. they are arranged in tiers; Fig. 2A; Plate 1, figs 2, 4) or non-coaxial (Fig. 2B; Plate 2, fig. 6; Plate 3, fig. 5). Some derivatives of core filaments curve outward to form the peripheral filaments ('perithallium' of older publications). Meristematic cells (vegetative or subepithallial initials) terminate the filaments and increase filament length (Fig. 2D, 3; Plate 2, fig. 8). Epithallial cells are mostly uncalcified cells forming the thallus surface (epithallium) (Fig. 2D, 2E; Plate 2, fig. 8; Plate 3, figs 2, 5, 6). Trichocytes are potentially hair-producing enlarged cells (Fig. 2D, Fig. 3). Haustoria are cell extensions which absorb nutrients from a host plant.

In the reproductive cycle of corallines, both sexual gametes, asexual carposporangia and asexual sporangia occur (Woelkerling, 1988). Gametes (sexual) are produced by spermatangial initials (Fig. 2I) and are borne in uniporate conceptacles. Tetra/bisporangia (asexual) can be borne in either uniporate (Fig. 2G; Plate 1, figs 1, 3, 5–8) or multiporate (Fig. 2F; Plate 2, figs 1–7) conceptacles, or they are grouped in sori and formed by stalk cells (Fig. 2H; Plate 3, figs 1–3, 7, 8). Tetra/bisporangial conceptacles are formed by specialized groups of cells (initials); these initials are termed conceptacle primordia. Conceptacle roofs are formed by a columella (a group of decalcified filaments rising centrally from the conceptacle floor; Fig. 2G), by an elongation of decalcified filaments interspersed between the sporangia (Fig. 2F; Plate 2, fig. 7) or by filaments which surround and enclose the conceptacle chamber. Roofs of sori are formed by elongations of interspersed calcified filaments (paraphyses; Fig. 2H; Plate 3, fig. 3). Carposporangia are asexual reproductive organs which are formed by special filaments (gonimoblasts) and are borne in former sexual conceptacle chambers.

Growth form nomenclature follows Woelkerling *et al.* (1993). In the current study they are: encrusting (crustose without protuberances or branches; Plate 1, fig. 5; Plate 3, fig. 7), layered (several to many lamellate branches arranged in horizontally orientated layers; Plate 2, figs 4, 5), foliose (as layered, but lamellate branches are arranged at various angles to one

another; Plate 2, figs 4, 5), warty (warty protuberances that are <3 mm long and unbranched), lumpy (swollen protuberances that vary in length, rarely branched; Plate 3, fig. 1), fruticose (cylindrical protuberances > 3 mm long and branched), and arborescent (plants tree-like with a distinct hold-fast).

'Lamellate branches' are flattened branches with a dorsiventral organization in layered and foliose thalli (i.e. thalli without protuberances) (Plate 2, fig. 6). 'Branches' in fruticose plants are twig-shaped and affect protuberances only.

SYSTEMATIC PALAEOLOGY

Except for *Lithoporella melobesioides* (Foslie) Foslie (1909) and *Phymatolithon* sp., the described species could not be referred to any described Recent or fossil taxa. The designation of fossil species suffers from the problem that the vast majority of species are poorly described and type specimens are partially missing. Although there have been several recent efforts to revise and re-describe original material (e.g. Moussavian & Kuss, 1990; Piller, 1994; Rasser & Piller, 1994; Braga & Aguirre, 1995; Basso *et al.*, 1997), most fossil species cannot be identified with confidence.

Division **Rhodophyta** Wettstein, 1901
 Class **Rhodophyceae** Rabenhorst, 1863
 Order **Corallinales** Silva & Johansen, 1986
 Family **Corallinaceae** Lamouroux, 1812
 Subfamily **Mastophoroideae** Setchell, 1943

Diagnosis. Tetra/bisporangial conceptacles uniporate, cell fusions present (Woelkerling, 1988).

Genus *Lithoporella* (Foslie) Foslie, 1909

Diagnosis. Non-endophytic dimerous thallus which lacks haustoria; primigenous filaments composed of palisade cells; thallus 2–3(–5) cells thick; tetra/bisporangial conceptacles lack a columella; conceptacle roof formed by filaments interspersed between sporangia; postigenous filaments are restricted to branching zones and conceptacle walls (Woelkerling, 1988). Braga *et al.* (1993) characterize *Lithoporella* by a thin thallus and multiple overgrows of large primigenous cells.

Remarks. *Lithoporella* is well known in fossil material and can

be easily identified by its unistratose thallus with large cells.

Lithoporella melobesioides (Foslie) Foslie, 1909
(Plate 1, fig. 1)

1909 *Lithoporella melobesioides* (Foslie) Foslie: 59.

1957 *Lithoporella melobesioides* (Foslie) Foslie; Johnson: 234, pl. 37, fig. 5; pl. 43, figs 1–2; pl. 49, fig. 4.

1982 *Lithoporella melobesioides* (Foslie) Foslie; Turner & Woelkerling: 218 ff., figs 2, 4, 6, 7–11, 15–17, 20, 21, 25, 26.

1994 *Lithoporella melobesioides* (Foslie) Foslie; Rasser: 198, pl. 3, fig. 3.

Description. Growth form encrusting, either forming single thalli or multiple overgrowths.

Primigenous filaments show cell fusions. Cell length 11–20 μm ($M = 17$, $SD = 3$), cell height 27–54 μm ($M = 42$, $SD = 9$). Postigenous filaments occur around the tetra/bisporangial conceptacle chambers only (Plate 1, fig. 1), trichocytes absent. Epithallus not preserved. Tetra/bisporangial conceptacles completely raised above the thallus surface. Filaments around the conceptacle pores are subparallel to the outer roof surface. Length of cells in the conceptacle roof 14–36 μm , diameter 9–25 μm . Cells near the outer conceptacle roof surface usually longer than at the inner surface. Height of conceptacles, 130–180 μm , diameter, 410–420 μm ; pore length, 160 μm ; diameter, 110 μm . Type of conceptacle roof formation unclear. Sexual conceptacles and carposporangia unknown.

Remarks. *L. melobesioides* is one of the few species which is well known both in Recent and in fossil material. Nevertheless, it has to be treated carefully, as the status of most species in *Lithoporella* is uncertain (Woelkerling, 1988). This species is not abundant in the studied material. It overgrows corals and other coralline algae. Measured sample: MOL25.

Genus *Neogoniolithon* Setchell & Mason, 1943

Diagnosis. Thallus non-endophytic, lacking haustoria and palisade cells; core filaments coaxial (Woelkerling, 1988; Braga *et al.*, 1993). Penrose (1992) and Penrose & Chamberlain (1993) define *Neogoniolithon* mainly by simple (i.e. unbranched) spermatangial initials (compare Fig. 2I), which are borne on both the floor and roof of the conceptacles and gonimoblast filaments arising dorsally from fusion cells.

Remarks. The separation of *Spongites* from *Neogoniolithon* using the arrangement of core filaments (Braga *et al.*, 1993) is not accepted in present day taxonomy, which uses the structures of sexual reproductive organs instead (Penrose, 1992; Penrose & Chamberlain, 1993). Nevertheless, *Neogoniolithon* is the only genus of the Mastophoroideae with coaxial core filaments (Woelkerling, 1988).

Neogoniolithon sp.
Plate 1, figs 2–4

Description. Growth form encrusting to layered and foliose, tips of lamellate branches may fuse together. Thallus usually 700 μm thick, but in the conceptacle-bearing portions is up to 1.4 mm. Core portion 250–400 μm thick. Filaments curve towards both

the ventral and dorsal thallus surfaces (Plate 1, fig. 2). Cell fusions are abundant (Plate 1, fig. 4). Cell length 25–41 μm ($M = 31$, $SD = 5$), diameter 11–18 μm ($M = 13$, $SD = 2$).

Peripheral filaments are usually restricted to the dorsal surface, but may sometimes additionally occur on the ventral thallus portion (Plate 1, fig. 2). Peripheral portion 150–250 μm thick, no growth rhythms. Cell fusions occur, trichocytes absent. Cell length 9–16 μm ($M = 12$, $SD = 2$), diameter 7–11 μm ($M = 9$, $SD = 1$). Epithallial cells not preserved.

Tetra/bisporangial conceptacles: height 190–200 μm , diameter 600–620 μm . Pore length 144–190 μm , diameter 65–68 μm . Conceptacle floor 3–4 cell layers below thallus surface. Cell length of cells in the conceptacle roof 18–25 μm ($M = 21$, $SD = 3$), diameter 9–13 μm ($M = 11$, $SD = 1$). Filaments around the conceptacle pore subparallel to the conceptacle roof (Plate 1, fig. 3). No columella found. Type of conceptacle roof formation unclear, but appears not to be formed by filaments enclosing the conceptacle chamber (Plate 1, fig. 3). Sexual conceptacles and carposporangia were not seen.

Remarks. Traditionally (Wray, 1977), this genus would have been identified as *Lithophyllum* Philippi (1837) because cell fusions were not recognized in fossil material prior to the 1990s (Bosence, 1990; Braga *et al.*, 1993).

Only uniporate conceptacles without preserved reproductive organs were found in the studied material. It is not known if these are tetra/bisporangial (asexual) or gametangial (sexual) conceptacles. If they are gametangial conceptacles, which are always uniporate, the described genus may have multiporate tetra/bisporangial conceptacles which are not preserved in the studied material. Owing to the regular coaxial thallus, the described genus in this case would belong to *Mesophyllum* (although the coaxial core is no longer diagnostic for *Mesophyllum* Lemoine (1928), we apply the same arguments as for *Neogoniolithon*). If, however, the identified uniporate conceptacles are gametangial conceptacles of *Mesophyllum*, they would have to be formed from filaments which enclose the chamber (Woelkerling & Harvey, 1993). Owing to the filament structure in the walls of the identified conceptacles, this kind of formation can be excluded. We therefore refer this species to *Neogoniolithon*. Besides *Phymatolithon* sp., *Neogoniolithon* sp. is one of the most abundant species in the studied material. It forms coralline algal bindstones in association with the latter and occurs fragmented in most samples. Measured sample: MOL110.

Genus *Spongites* Kützing, 1841

Diagnosis. Non-endophytic thallus which lacks haustoria; thallus organization dimerous or monomerous; dimerous thallus portions lacking palisade cells; filaments around the conceptacle pore canals subparallel to the roof surface (Penrose & Woelkerling, 1992). Braga *et al.* (1993) additionally mentioned the presence of non-coaxial core filaments to separate *Spongites* from *Neogoniolithon*.

Remarks. *Hydrolithon* (Foslie) Foslie (1909) was considered to be congeneric with *Spongites* by Woelkerling (1988). Penrose & Woelkerling (1992), however, showed that both genera can be separated by the filament arrangement in the conceptacle roof. As it was shown by Braga *et al.* (1993) and by the current study,

this character can be applied to fossil material as well. The separation from *Neogoniolithon* is discussed above.

Spongites sp. 1
(Plate 1, figs 5, 6)

Description. Growth form encrusting, thallus organisation dimerous. Primigenous filaments unistratose, cell size variable. Cell length 18–40 μm ($M = 31$, $SD = 9$), diameter 9–22 μm ($M = 13$, $SD = 4$).

Postigenous filaments show cells with irregular cell walls, some, but not all cells of contiguous filaments joined by cell fusions, no growth rhythms and no trichocytes occur. Cell length 9–22 μm ($M = 14$, $SD = 4$), diameter 11–18 μm ($M = 13$, $SD = 2$). Subepithallial initials and epithallial cells not preserved. Tetra/bisporangial conceptacles uniporate with cylindrical pores. Filaments around the conceptacle pore are arranged subparallel to the conceptacle roof. Conceptacle floor 0–4 cell layers below thallus surface (Plate 1, fig. 6). Conceptacle height 150–160 μm , diameter 260–360 μm , no columella found. Cell length in conceptacle roof 9–18 μm ($M = 13$, $SD = 3$), diameter 7–13 μm ($M = 9$, $SD = 2$). Shape of pore channel unknown. Sexual conceptacles and carposporangia unknown.

Remarks. This species encrusts other coralline algae. It was found in three samples. Measured samples: MOL292, MOL380

Spongites sp. 2
(Plate 1, figs 7, 8)

Description. Growth form fruticose, diameter of protuberances 2–3 mm, length up to 10 mm; thallus monomerous. Core filaments non-coaxial, core portion usually 25–30 μm thick, sometimes up to 80 μm . Filaments only curve towards the dorsal thallus surface. Cell fusions present. Cell length 7–22 μm ($M = 13$, $SD = 6$), diameter 6–9 μm ($M = 7$, $SD = 1$).

Peripheral filaments: some parts of the thallus show growth rhythms with a thickness of 7–10 cell rows; cell length 6–11 μm ($M = 10$, $SD = 2$), diameter 7–9 μm ($M = 8$, $SD = 1$). Some cells of contiguous filaments are joined by cell fusions. Subepithallial initials and epithallial cells not preserved.

Tetra/bisporangial conceptacles uniporate, usually completely raised above thallus surface (i.e. conceptacle floor on the level of thallus surface; Plate 1, fig. 8). Conceptacle height 120–200 μm , diameter 500–550 μm . Pore length 150–180 μm , diameter 110 μm . Shape of pore channel most probably conical. Cell filaments around conceptacle pore are subparallel to the roof (Plate 1, fig. 8), measuring 11–18 μm ($M = 14$, $SD = 3$) in length and 4–5 μm ($M = 5$, $SD = 1$) in diameter. Filaments in distal portions of the roof are subperpendicular to the roof and show distinctively shorter cells: length 5–11 μm ($M = 9$, $SD = 2$), diameter 4–9 μm ($M = 5$, $SD = 2$). Sexual conceptacles and carposporangia unknown.

Remarks. *Spongites* sp. 2 was found in a single sample (MOL209).

Subfamily *Melobesioideae* Bizzozero, 1885

Diagnosis. Tetra/bisporangial conceptacles multiporate, cell fusions present (Woelkerling, 1988).

Melobesioideae gen. et spec. indet.
(Plate 2, figs 1–3)

Description. Growth form encrusting to warty and lumpy, thallus thickness in encrusting portions 0.3–0.4 mm. Protuberances are up to 3 mm in diameter and up to 5 mm long. Thallus organisation monomerous.

Core filaments non-coaxial, core portion usually 100–180 μm thick; filaments only curve towards the dorsal surface. Cell fusions occur. Cell length 11–18 μm ($M = 14$, $SD = 3$), diameter 11–13 μm ($M = 13$, $SD = 1$).

Peripheral region in encrusting portion 220–300 μm thick; growth rhythms occur, composed of up to 6 cells (Plate 2, fig. 3). Cell fusions abundant, trichocytes absent. Cell length 7–13 μm ($M = 10$, $SD = 2$), diameter: 7–13 μm ($M = 9$, $SD = 2$). Protuberances: growth rhythms from 4 to 12 rows occur. Cell fusions abundant. Cell length 13–18 μm ($M = 15$, $SD = 1$), diameter 7–11 μm ($M = 9$, $SD = 2$). Epithallium and vegetative initials not preserved.

Tetra/bisporangial conceptacles usually raised one half above the thallus surface (Plate 2, fig. 3). Conceptacle height 170–200 μm , diameter 350–600 μm ; roof thickness 55–90 μm . Pore diameter 11–13 μm . Length of cells in conceptacle roofs 7–9 μm ($M = 8$, $SD = 1$), diameter 5–10 μm ($M = 8$, $SD = 2$). Type of conceptacle roof formation unknown, sexual conceptacles and carposporangia unknown.

Remarks. In accordance with the traditional generic concepts of Wray (1977), this species would belong to *Lithothamnion*. However, this genus cannot be identified using present day concepts owing to the unpreserved epithallial cells and subepithallial initials. Owing to the non-coaxial core filaments, it can be referred to either *Lithothamnion* or *Phymatolithon* (see also remarks of *Phymatolithon*).

The described species is most abundant in 'Maerl'-type sediments (*sensu* Lemoine, 1910), forming isolated branches. Measured sample: MOL3a.

Genus *Phymatolithon* Foslie, 1898

Diagnosis. Plants lacking an arborescent growth form and haustoria. Thallus monomerous, core filaments non-coaxial, epithallial cells rounded or flattened, but not flared, subepithallial initials as short or shorter than underlying cells (Braga *et al.*, 1993; Wilks & Woelkerling, 1994). Irvine & Chamberlain (1994) additionally define *Phymatolithon* by the 'Phymatolithon-type' surface view of epithallial cells.

Remarks. Following Braga *et al.* (1993) this genus is indistinguishable from *Leptophytum* Adey (1966) in fossil material. This fact is reflected by the generic differentiation of Chamberlain & Keats (1994), who focus on growth form, surface view of epithallial cells, and whether the conceptacle initiation is 'shallow' or 'deep'. However, the cited authors also mention that the differentiation between *Leptophytum* and *Phymatolithon* is provisional. As Wilks & Woelkerling (1994) concluded that *Leptophytum* is not a distinct genus in the current state of research, it is not considered here. The occurrence of rounded epithallial cells and short subepithallial initials allows a distinct separation of *Phymatolithon* from other genera of this subfamily.

Phymatolithon sp.
(Plate 2, figs 4–8; Fig. 3)

1994 *Lithothamnion* sp.; Rasser: 198, pl. 3, figs 4, 5; pl. 2, fig. 6.
In press *Phymatolithon* sp.; Rasser & Piller

Description. Growth form encrusting to foliose (Plate 2, fig. 4) with a thallus thickness of usually 150 μm . Sometimes warty growth forms occur with 1.3–1.4 mm long and 1.5–0.8 mm thick protuberances. Thallus monomerous.

Core filaments predominantly curve towards the dorsal, sometimes towards the ventral thallus surface. Core portion 70–150 μm (mostly 100 μm) thick, in layered to foliose portions usually at least 50% of the thallus thickness (Plate 2, fig. 6). Cell fusions occur. Cell length 14–29 μm ($M = 19$, $SD = 4$), diameter 7–11 μm ($M = 9$, $SD = 1$). The peripheral region in encrusting portions is restricted to the dorsal part of the thallus; it is usually 50 μm thick, but also up to 150 μm . No growth rhythms occur. Cell length 7–16 μm ($M = 11$, $SD = 2$), diameter 5–13 μm ($M = 10$, $SD = 2$). Protuberances show 90–120 μm thick growth rhythms. Cell fusions abundant, trichocytes absent, cell rows not regular. Cell length 7–18 μm ($M = 11$, $SD = 3$), diameter 7–13 μm ($M = 9$, $SD = 2$). Vegetative initials as short or shorter than underlying cells (Plate 2, fig. 8). Cell length 7–9 μm , diameter 11–12 μm . The epithallium is one cell layer thick; the cells are rarely well preserved. The shape of epithallial cells is not clear, but they seem to be not flat (Plate 2, fig. 8). Cell length 8–9 μm , diameter 11–12 μm . Only a few measurable epithallial cells and vegetative initials were found in the studied material. Therefore, M and SD were not calculated.

Tetra/bisporangial conceptacles are multiporate, without a rim; old conceptacles may be buried within the thallus. Conceptacles distinctively raised above the thallus surface with a floor usually ten cell layers below the thallus surface (less frequently only five) (Plate 2, figs 5, 6). Height 100–160 μm , diameter 210–460 μm . Thickness of roof 45–70 μm , conceptacle pore diameter up to 27 μm . Length of cells in conceptacle roof 6–12 μm ($M = 9$, $SD = 3$), diameter 5–8 μm ($M = 7$, $SD = 1$). Conceptacle roof formed by filaments interspersed between sporangia (Plate 2, fig. 7). Sexual conceptacles and carposporangia unknown.

Remarks. As traditional concepts for fossil corallines do not take into account the occurrence of epithallial cells and subepithallial initials, this genus would, in the past, have been identified as *Lithothamnion*. This species is the same as described by Rasser (1994) as *Lithothamnion* sp. Growth form, anatomy, and conceptacle size are close to those of *Lithothamnion crispithallus* Johnson (1957), which, following this work, should now belong to *Phymatolithon*. A new combination would, however, require a study of the original material and this has not been included in the present study. *Phymatolithon* sp. is the most abundant species in the studied material, forming coralline algal bindstones together with *Neogonolithon* sp. Moreover, it is the dominant coral encruster. Measured samples: MOL12 and MOL291.

Family **Sporolithaceae** Verheij, 1993

Diagnosis. Non-geniculate, almost entirely calcified thalli; both

cell fusions and secondary pit connections occur; tetra/bisporangia formed between filaments, on one or more stalk cells, apical plug at tetra/bisporangial apex (Verheij, 1993).

Remarks. Verheij (1993) separated the family Sporolithaceae from the family Corallinaceae. Because of the preservation of calcified sori and paraphyses this family can easily be identified in fossil material.

Genus *Sporolithon* Heydrich, 1897

Diagnosis. Epithallial cells with flattened and flared cells and tetra/bisporangial conceptacles separated by interspersed calcified filaments (paraphyses) (Woelkerling, 1988); conceptacles arranged in sori (Verheij, 1993).

Sporolithon sp. 1
(Plate 3, figs 1–6)

Description. Growth form encrusting to lumpy (Plate 3, fig. 1). Diameter of protuberances: 0.7–2 mm at the base and 0.8–3.4 mm at the top. Thickness of encrusting thalli: up to 2 mm.

Core filaments strongly curve towards the dorsal, but never towards the ventral thallus surface (Plate 3, figs 2, 5). Thickness of core portion usually 30–50 μm , sometimes up to 100 μm . Irregular cell shapes, cell fusions occur. Cell length 20–36 μm ($M = 29$, $SD = 5$), diameter 11–13 μm ($M = 12$, $SD = 1$).

Peripheral portion 85–200 μm thick, mostly 100 μm . Cell shape rectangular; no growth rhythms and trichocytes occur; cell layers irregular; cell fusions occur. Cell length 25–30 μm ($M = 28$, $SD = 2$), diameter 10–16 μm ($M = 13$, $SD = 2$).

Some thalli show preserved epithallial cells which are characterized by brightish cell layers on the outermost thallus surfaces in thin section (Plate 3, fig. 2). Scanning electron microscope samples show that the epithallium is recrystallized and cells are replaced by large calcite crystals (Plate 3, figs 5, 6). Cell length approx. 7 μm , diameter approx. 13 μm . Owing to the poor state of preservation, the shape of epithallial cells cannot be identified.

Tetra/bisporangial conceptacles arranged in sori which rise approximately one-half above the thallus surface. Sori consist of 12–45 tetra/bisporangia (Plate 3, fig. 1). Old sori are not flaked off, but buried in the thallus. Sori usually arise from a layer of elongated cells (Plate 3, fig. 3). Conceptacle shape elongated ellipsoidal. Tetra/bisporangia height 110–130 μm , diameter 47–60 μm . Two pores with a diameter of 24 μm can be recognized in horizontal section, both of them surrounded by seven to eight rosette cells (Plate 3, fig. 4). One to six filaments (paraphyses) are interspersed between tetra/bisporangia (Plate 3, fig. 3). Number of cells in the paraphyses difficult to recognize. Most probably there are four cells with a length of 30–40 μm . Sexual conceptacles and carposporangia unknown.

Remarks. This species cannot be compared with any previous species of *Sporolithon*. It is not abundant in the studied material and usually encrusts bioclasts. Measured sample: MOL377.

Sporolithon sp. 2
(Plate 3, figs 7, 8)

Description. Growth form encrusting (Plate 3, fig. 7). Several

consecutive sori may occur within one thallus. Thallus thickness 0.8–1 mm. Core portion 50–70 μm thick. Cell dimensions not measurable owing to the poor preservation of core filaments.

Peripheral filaments are arranged in regular cell rows. Vertical filament walls are more distinct than the horizontal walls (Plate 3, fig. 8). Cell fusions abundant, trichocytes absent. Thickness of peripheral portion 350–500 μm . Cell length 10–16 μm ($M = 13$, $SD = 2$), diameter 7–9 μm ($M = 8$, $SD = 1$).

Epithallium not preserved.

Tetra/bisporangia arranged in sori with up to 35 tetra/bisporangia each. Sori completely raised above the thallus surface. Sori do not arise from a layer of elongated cells. Old sori are not flaked off, but buried in the thallus. Conceptacle height 63–70 μm , diameter 36–45 μm . One to nine filaments interspersed between the tetra/bisporangia. Number of cells in the paraphyses unclear; they seem to vary between three and five. Sexual conceptacles and carposporangia unknown.

Remarks. This species cannot be compared with any previous species of *Sporolithon*. Only a single thallus of *Sporolithon* sp. 2 was found in the studied material (MOL220).

IDENTIFICATION KEY

Tetra/bisporangial conceptacles arranged in sori: Family Sporolithaceae (1)

Tetra/bisporangial conceptacles not arranged in sori: Family Corallinaceae (2)

(1) Family Sporolithaceae

(1a) Tetra/bisporangial conceptacles 110–130 μm high and arise from a basal layer of elongated cells: *Sporolithon* sp. 1

(1b) Tetra/bisporangial conceptacles 60–70 μm high and do not arise from a basal layer of elongated cells: *Sporolithon* sp. 2

(2) Family Corallinaceae

(2a) Cells of contiguous filaments connected by cell fusions; tetra/bisporangial conceptacles uniporate: Subfamily Mastophoroideae (3)

(2b) Cells of contiguous filaments connected by cell fusions; tetra/bisporangial conceptacles multiporate: Subfamily Melobesioideae (4)

(3) Subfamily Mastophoroideae

(3a) Thallus dimerous with palisade cells, postigenous filaments only around conceptacles: *Lithoporella melobesioides*

(3b) Thallus dimerous, tetra/bisporangial conceptacle diameter 260–360 μm : *Spongites* sp. 1

(3c) Thallus monomerous and non-coaxial, tetra/bisporangial conceptacle diameter 500–550 μm : *Spongites* sp. 2

(3d) Thallus monomerous, core filaments coaxial: *Neogoniolithon* sp.

(4) Subfamily Melobesioideae

(4a) Vegetative initials as short or shorter than underlying cells, conceptacles nearly completely raised above thallus surface, conceptacle size 210–460 \times 100–160 μm : *Phymatolithon* sp.

(4b) Conceptacles usually raised one-half of their height above thallus surface, conceptacle size 350–600 \times 170–200 μm : *Melobesioideae* gen. et spec. indet.

DISCUSSION

Primigenous and core filaments

Except for the occurrence of palisade cells which helps to identify *Lithoporella* (Plate 1, fig. 1), the importance of the basal filament organization for the generic identification has decreased during the last decade. This is mainly true for the occurrence of coaxial and non-coaxial core filaments in monomerous thalli. The decreasing importance mainly affects the definitions of *Neogoniolithon* and *Mesophyllum*, which have traditionally been characterized by a coaxial core (e.g., Woelkerling, 1988). Some workers do not accept the validity of this feature for the identification of both *Neogoniolithon* (see Penrose, 1992) and *Mesophyllum* (see Woelkerling & Harvey, 1993), although the type species of both genera show distinct coaxial cores (Woelkerling, 1988). This character is therefore still used in Recent (e.g., Irvine & Chamberlain, 1993) and fossil (Braga *et al.*, 1993; Bassi, 1995a) taxonomy (Table 1).

Cell fusions

Interfilamental cell fusions (Fig. 2D; Plate 1, fig. 4) are diagnostic criteria for separating Recent subfamilies of Corallinaceae in combination with conceptacle perforation (Woelkerling, 1988). Since Bosence (1990) and Braga *et al.* (1993) showed that they are usually well preserved in fossil material, this character is now applied by palaeontologists (Bassi, 1995a, 1995b; Braga & Aguirre, 1995; Basso *et al.*, 1997). The recognition of this feature allowed Braga *et al.* (1993) to transfer *Lithophyllum albanense* Lemoine (1924) to *Spongites albanensis* and thus from the subfamily Lithophylloideae to the Mastophoroideae.

Trichocytes

Trichocyte (Fig. 2D) occurrence and arrangement have long been used to delimit genera within the Mastophoroideae, predominantly within the *Spongites* complex (Woelkerling, 1985). Chamberlain (1983) and Jones & Woelkerling (1984), however, showed that trichocyte occurrence varies within species and is influenced by environmental conditions. Trichocyte occurrences in the peripheral filaments are still used by Braga *et al.* (1993) to define *Neogoniolithon* and *Spongites*.

Subepithallial initials

The length of subepithallial initials with respect to the length of peripheral or postigenous cells subtending them is one of the most important characters used to separate genera within the Melobesioideae (Wilks & Woelkerling, 1994, 1995) (Table 1). As they are usually calcified, this feature can also be applied to fossil material (Braga *et al.*, 1993). The recognition of subepithallial initials, however, depends on the preservation of the overlying epithallial cells (Fig. 3).

Epithallial cells

The shape of the epithallial cells is an important feature used to identify *Lithothamnion* and *Sporolithon* (Woelkerling, 1988). Both of these taxa are characterized by flared, but not rounded, cell walls (Table 1). According to Braga *et al.* (1993) epithallial cells in *Sporolithon* are unknown in the fossil record. Several thalli of *Sporolithon* sp. 1 with preserved epithallia were found in the studied material (Plate 3, figs 2, 5, 6). The epithallial cells of

	<i>Lithop.</i>	<i>Spong.</i>	<i>Neogon.</i>		<i>Phym.</i>		<i>Sporol.</i>
	W	PW	P	W	WW	IC	W
GENERAL							
Nonendophytic, lacking haustoria	●	●	●	●	●		
Lacking arborescent growth form					●		
Thallus monomeric				●	●	●	
Thallus dimerous	●						
Thallus thickness	●						
BASAL FILAMENTS							
Composed of palisade cells	●						
Lacking palisade cells		●	●	●			
Coaxial core				●			
Non-coaxial core						●	
DORSAL FILAMENTS							
Subepithallial initials as short or shorter than underlying cells					●		
Epithallial cells flattened and flared							●
Epithallial cells rounded or flattened, not flared					●	●	
Epithallium " <i>Phymatolithon</i> -type" in surface view						○	
TETRA/BISPORANGIA							
Arranged in sori, persistent groups of calcified filaments are interspersed amongst sporangia							●
Lacking apical plugs		○					
Conceptacles develop from initials produced adventitiously within the thallus					○		
Conceptacle pore bordered by filaments arranged subparallel to conceptacle roof		●					
Conceptacle pore plugs not surrounded by differentiated cells						○	
Conceptacle lack a columella	●						
Conceptacle roof formed by elongation of filaments interspersed among sporangia	○						
SPERMATANGIA							
Simple and borne on both the floor and roof of male conceptacle chambers			○				
CARPOSPORANGIA							
Gonimoblast filaments arising dorsally from fusion cells			○				

Table 1. Characters used to identify the Recent genera *Lithoporella* (*Lithop.*), *Spongites* (*Spong.*), *Neogoniolithon* (*Neogon.*), *Phymatolithon* (*Phym.*) and *Sporolithon* (*Sporol.*). Circles indicate that the features are used to characterize the genus; closed circles indicate that the feature is known in fossil material; open circles indicate that it is known in Recent material only. References: W = Woelkerling (1988); PW = Penrose & Woelkerling (1992); P = Penrose (1992); WW = Wilks & Woelkerling (1994); and IC = Irvine & Chamberlain (1994). For details, see text.

this species are, however, recrystallized and replaced by large calcite crystals (Plate 3, figs 5, 6). Therefore, the shape of the cells cannot be recognized.

Epithallial cells in *Phymatolithon* sp. are slightly better preserved. In our material they can easily be identified and separated from subepithallial initials by large crystals forming the cell walls in the scanning electron micrograph (Plate 2, fig. 8; Plate 3, figs 5, 6; Fig. 3) and by their transparency in thin sections (Plate 3, fig. 2). Owing to the poor preservation, the shape of the cells cannot be recognized with confidence. However, unlike the epithallial cells described and figured by Braga *et al.* (1993) and Aguirre *et al.* (1996), they do not appear to be flat (Fig. 3). In the current study, epithallial cells helped to identify the underlying vegetative initials and thus indirectly allowed the designation of the genus *Phymatolithon*.

Conceptacles

Conceptacle perforation is a well known traditional feature used for the identification of both Recent and fossil genera (Wray, 1977) and subfamilies (Woelkerling, 1988; Bosence, 1990; Braga *et al.*, 1993). The orientation of conceptacle roof filaments around conceptacle pores is an important character in separating genera within the Mastophoroideae in present day taxonomy (Penrose & Woelkerling, 1992). Both *Neogoniolithon* and *Spongites* are characterized by filaments which are arranged subparallel to the roof surface (Braga *et al.*, 1993; Penrose & Woelkerling, 1992) (Table 1). This study proves that this feature can be well preserved in fossil material and enabled us to present the oldest record of *Neogoniolithon*.

Several fossil tetra/bisporangia have been described from multiporate conceptacles (e.g., Conti, 1947; Johnson, 1957;

	Thin section	SEM
GENERAL		
1. Growth form	●	
2. Thallus thickness	●	
3. Size of protuberances	●	
4. Thallus organisation monomerous or dimerous	●	
BASAL FILAMENTS		
5. Occurrence of palisade cells (dimerous thalli)	●	●
6. Filament arrangement coaxial or non-coaxial (monomerous thalli)	●	
7. Ventral or central position of core within the thallus (monomerous thalli)	●	
8. Thickness of core portion (monomerous thalli)	●	
9. Cell length and diameter	●	
10. Occurrence of cell fusions	●	●
DORSAL FILAMENTS		
11. Occurrence, arrangement, and size of trichocytes	●	
12. Occurrence and thickness of growth rhythms	●	
13. Thickness of dorsal region in thallus portions without protuberances	●	
14. Cell length and diameter both in encrusting and protuberant portions	●	
15. Occurrence of cell fusions	●	●
16. Length of subepithallial initials		●
17. Shape of epithallial cells		●
CONCEPTACLES		
18. Multiporate, uniporate, or grouped in sori	●	
19. Are old sori buried within the thallus or flaked off	●	
20. Occurrence of tetra/bisporangia or spermatangia	●	●
21. Occurrence of a rimmed conceptacle roof	●	
22. Height and diameter of conceptacles	●	
23. Amount to which conceptacles or sori are raised above thallus surface	●	
24. Thickness of conceptacle or sorus roof	●	
25. Length and diameter of pores	●	
26. Size of cells in conceptacle or sorus roof	●	
27. Formation of conceptacle roof (rarely observed)	●	●
28. Occurrence of a columella (uniporate conceptacles) (related to no. 27)	●	
29. Arrangement of filaments around conceptacle pore (uniporate conceptacles)	●	●
30. Pore shape cylindrical or conical (uniporate conceptacles)	●	
31. Number of paraphyses in sori	●	
32. Number of cells in paraphyses	●	●
33. Size of stalk cells in sori	●	●
34. Occurrence of an elongated cell layer from which stalk cells arise	●	

Table 2. Checklist for the description of fossil coralline algal taxa. Only those features are considered which are known from fossil material. Circles in the two right-hand columns indicate whether features can be observed in palaeontological thin sections or if scanning electron microscopy is necessary. For details, see text.

Mastrorilli, 1973; Lemoine, 1977; Bosence, 1983). Bosence (1983) presents both sexual and asexual conceptacles preserved in one thallus of *Lithophyllum*. Preserved gametangia and tetra/bisporangia borne in uniporate conceptacles are, however, unknown. This fact forced palaeontologists to interpret uniporate conceptacles as tetra/bisporangial only on the basis of the lack of multiporate conceptacles in the same thallus. In the current study we could indirectly exclude the gametangial nature of uniporate conceptacles in *Neogoniolithon* sp. Our designation of *Spongites* is, however, based on the lack of multiporate conceptacles. Consequently, we cannot exclude the possibility that both species we referred to *Spongites* have multiporate conceptacles which were not found owing to the low abundance of specimens in the studied material.

The kind of conceptacle roof formation is another important taxonomic feature. Roofs of multiporate conceptacles are formed by elongations of filaments interspersed between sporangia. After the release of sporangia these filaments in the conceptacle chambers are secondarily decalcified (Woelkerling, 1988) and thus usually not preserved in the fossil record. Interspersed filaments in conceptacles of *Phymatolithon* sp. are preserved in the studied material (Plate 2, fig. 7) as the tetra/bisporangia are not released and the conceptacle is buried within the thallus. The current study and the recognition of conceptacle primordia in fossil material (Aguirre *et al.*, 1996) suggest that even more reproductive characters are potentially preservable. Bosence (1983) described sexual conceptacles in *Lithophyllum* along with structures which appear to be carposporangia.

Further taxonomic studies of fossil coralline algae will have to focus on this topic.

Species identification

Owing to poor descriptions and different valuations of diagnostic criteria, the status of most fossil species is unclear and only a few Recent species have been traced back to the fossil (e.g. Braga & Aguirre, 1995; Basso *et al.*, 1996, 1997). The main problem is that traditional identifications of fossil species are usually restricted to characters such as cell and conceptacle dimensions (e.g. Lemoine, 1939; Conti, 1947; Mastrorilli, 1967; Bucur & Filipescu, 1994). However, these features alone are not used the identification of Recent species in fossil material. Table 2 summarizes all the diagnostic features which are known from fossil algae. The application of this checklist for the description of fossil taxa is a minor requirement in the recognition of Recent taxa in fossil material.

The identification of Recent species focuses on the combinations of several characters. Chamberlain (1994) separated species of *Spongites* by cell dimensions, occurrence of trichocytes, dimensions of filaments around conceptacle pores, growth form and colour. Species of *Phymatolithon* are separated by growth form, the amount to which tetra/bisporangial conceptacles are raised above the thallus surface, the occurrence of rimmed conceptacles (Chamberlain, 1994), whether old conceptacles are flaked off or buried in the thallus, colour (Irvine & Chamberlain, 1994), position of core filaments, shape of cells interspersed between tetra/bisporangial conceptacles, the occurrence of vegetative cells beneath the floor of tetra/bisporangial conceptacles and the thickness of conceptacle roofs (Wilks & Woelkerling, 1994). The identification of species in *Sporolithon* focuses on the number of cells that sori are raised above the thallus surface, the number of cells in paraphyses, the occurrence of a basal layer of elongated cells below tetra/bisporangia, the dimensions of tetra/bisporangia and whether old conceptacles are flaked off or not (Verheij, 1993; Townsend *et al.*, 1995).

We can show that all calcified features used to describe present day species are observable in well preserved fossil material. Growth forms can be recognized in two-dimensional sections (e.g., Plate 2, fig. 4) and the amount to which conceptacles are raised above the thallus surface can even be recognized if conceptacles are buried within the thallus (e.g. Plate 2, fig. 3). In some cases usually uncalcified features such as the filaments interspersed between sporangia are preserved (Plate 2, fig. 5). Reproductive features which are diagnostic for *Sporolithon* can easily be observed in scanning electron microscopy samples (Plate 3, fig. 3). Only the occurrence of vegetative cells beneath the floor of conceptacles has not yet been observed and the colour of thalli is obviously not applicable.

CONCLUSIONS

Combinations of six taxonomic features used in present day taxonomy are applied in the identification of five genera in fossil material: (1) the arrangement of basal filaments; (2) the occurrence of cell fusions; (3) the relative length of subepithallial initials; (4) conceptacle perforation; (5) the orientation of filaments around the conceptacle pore; and (6) the type of conceptacle roof formation.

The present study proves that most features used in the present day taxonomy of coralline algae can be applied to fossil taxa. The identification of certain fossil genera, however, still has to take into account traditional features which are no longer accepted in Recent taxonomy. This is because several phycologists tend to focus on taxonomic characters which are unknown in the fossil record. Our study also shows that the identification key of Braga *et al.* (1993) is a useful tool for the identification of fossil corallines which, however, has to be updated according to the latest published studies on present day taxonomy.

The most important features used to identify Recent species are easily observable in fossil coralline algae. Nevertheless, they are rarely applied to the identification of fossil taxa, even in modern studies. Therefore, we provide a checklist (Table 2) including all known features preserved in fossil material. Further documentations of fossil species will have to focus on these characters to trace back Recent species to the fossil record. This is crucial for the understanding of coralline algal phylogeny, palaeoecology and palaeobiogeography.

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