

# Designation of *Phymatolithon* (Corallinaceae, Rhodophyta) in fossil material and its paleoclimatological indications

Michael W. Rasser<sup>1</sup> and Werner E. Piller<sup>2</sup>

<sup>1</sup> Institute for Palaeontology, University of Vienna, Geozentrum, Althanstrasse 14, A-1090 Vienna, Austria

<sup>2</sup> Institute for Geology and Palaeontology, Karl-Franzens-University Graz, Heinrichstrasse 26, A-8010 Graz, Austria  
e-mail: werner.piller@kfunigraz.ac.at

**ABSTRACT:** The coralline genus *Phymatolithon* Foslíe 1898 (Corallinaceae, Rhodophyta) is a well-known present-day genus. Owing to the traditional taxonomic characters applied to fossil coralline algae it has, however, not been possible to identify this genus in fossil material until recently. This paper presents the first documentation of a fossil *Phymatolithon* by applying generic features used in present-day coralline algal taxonomy and discusses its separation from other genera in fossil material. These features are (1) arrangement of basal filaments, (2) occurrence of cell fusions, (3) relative length of subepithallial initials, (4) conceptacle perforation. The stratigraphic distribution of *Phymatolithon* could be extended from Lower Eocene to Recent. As it is a typical non-tropical genus in present-day environments, designation of *Phymatolithon* can give valuable indications for paleocological reconstructions. The studied material comes from Late Eocene red algal limestones of the Austrian Molasse Zone.

## INTRODUCTION

The genus *Phymatolithon* was established by Foslíe in 1898 and since then several Recent taxa have been referred to this genus (for review see Woelkerling (1988)). Adey (1970) revised the Foslíe herbarium and described the type species *P. polymorphum*. Woelkerling and Irvine (1986) defined the neotype of *Phymatolithon* and described *P. calcareum* as type species. Moreover, they conserved it against several superfluous substitute names such as *Apora*, *Nullipora*, and *Millepora*. The study of Wilks and Woelkerling (1994) summarised and defined the diagnostic features of *Phymatolithon* on the generic and species level.

Although *Phymatolithon* is well known in present-day environments (e. g., Adey 1966; 1970; Irvine and Chamberlain 1994; Wilks and Woelkerling 1994), the only indication of its fossil occurrence is the conclusion of Basso et al. (1997) and Vanucci et al. (1997) that the fossil *Lithothamnion operculatum* Conti 1950 is conspecific with the present-day *Phymatolithon calcareum*. Aguirre et al. (1993) additionally documented this species from the Pliocene of Spain. Nevertheless, a convincing documentation of the typical generic features in fossil material is still missing.

Diagnostic features used in present-day taxonomy were thought to be un preservable in the fossil record until recently (Braga et al. 1993, Braga and Aguirre 1995; Rasser and Piller, in press). Therefore, Wray (1977) and Poignant (1984) were of the opinion that the taxonomic characters to be considered in the identification of fossil coralline algae needed to be different from those used for modern corallines. Traditional concepts for fossil material (Wray, 1977), which focus on organisation of core filaments (former 'hypothallium') and conceptacle perforations, do not allow differentiation between *Phymatolithon*, *Lithothamnion* Heydrich 1897, *Clathromorphum* Foslíe 1898, *Leptophytum* Adey 1966, and *Synarthrophyton* Townsend 1979. Instead, they are all summarised as *Lithothamnion*. Braga

et al. (1993) proved that most of the diagnostic features used in present-day biological taxonomy, such as cell fusions and epithallial cells, can indeed be preserved and recognised in fossil material using scanning electron microscopy. The current paper supports this conclusion by presenting the first documentation of a fossil *Phymatolithon* using present-day generic concepts. Finally, the paleocological implications are discussed.

## MATERIAL AND METHODS

The studied material comes from the Late Eocene red algal limestones ('Lithothamnienkalk') of the western Austrian Molasse Zone (Aberer 1958; Malzer 1981; Wagner et al. 1986; Wagner 1996), which are only known from deep wells of the Rohöl AG Vienna, Austria. A detailed study on paleocology and facies of the red algal limestones is in preparation by the authors.

Two hundred thin sections and several SEM samples from 10 deep wells were studied. Cell and conceptacle dimensions were measured by a binocular microscope at a magnification of 400x. To avoid the effects of tangential sections the cell diameters of peripheral filaments were measured in sections perpendicular to the direction of filament growth. All other dimensions were measured in sections parallel to the growth direction. Forty cells of core filaments and peripheral filaments, respectively, were measured. Cells of peripheral filaments were only measured in the central parts of thalli, because the outer cell layers usually showed micritization. Only six conceptacles could be measured. Scanning electron microscope (SEM) samples were prepared as described by Braga et al. (1993). Samples were polished and etched with HCl 2% for 10 - 30 seconds or EDTA 7% for one minute, respectively. Optimal etching time varied between the samples. Samples are stored at the Institute for Palaeontology, University of Vienna, Austria.

## TERMINOLOGY OF ANATOMY AND GROWTH FORM

The terminology of vegetative and reproductive anatomy used in the current paper follows Woelkerling (1988). Monomerous thalli (i. e. plant bodies) consist of ventral core filaments (formerly 'hypothallium'), which run more or less parallel to the thallus surface with some derivatives curving outward to form the dorsal peripheral filaments (formerly 'perithallium'). Some parasitic genera may form haustoria (elongated cells) to absorb nutrients from a host plant. Cells of contiguous core filaments can be fused and are arranged in semicircular tiers (coaxial) or not (non-coaxial). Epithallial cells are mostly uncalcified cells forming the thallus surface (epithallium). Subepithallial initials (vegetative initials, meristematic cells) terminate the filaments and are situated directly below the epithallial cells. Tetra/bisporangia are asexual reproductive structures, which are borne in tetra/bisporangial conceptacles. The latter can be uni- or multiporate and may show a central columella.

The terminology of growth forms follows Woelkerling et al. (1993). Encrusting thalli lack protuberances or lamellate branches. Foliose thalli consist of lamellate branches (i. e. flattened branches with an internal dorsiventral organisation), which are arranged at various angles to one another. Warty plants are characterised by protuberances that are usually <3 mm long and unbranched. Arborescent thalli have a tree-like growth with a distinct holdfast.

## SYSTEMATIC PALEONTOLOGY

Division RHODOPHYTA Wettstein 1901  
Class RHODOPHYCEAE Rabenhorst 1863  
Order CORALLINALES Silva and Johansen 1986  
Family CORALLINACEAE Lamouroux 1812  
Subfamily MELOBESIOIDEAE Bizzozero 1885

**Diagnosis:** Tetra/bisporangial conceptacles multiporate; some but not all cells of contiguous filaments fused (Woelkerling 1988).

Genus *Phymatolithon* Fosløe 1898

Type species: *Phymatolithon calcareum* (Pallas 1766) Adey & McKibbin 1970

**Diagnosis:** Plants lacking an arborescent growth form and haustoria. Thallus monomerous, core filaments non-coaxial, epithallial cells not flared, subepithallial initials as short or shorter than underlying cells, tetra/bisporangial conceptacles develop from initials produced adventitiously within the thallus (Wilks and Woelkerling 1994).

**Occurrence of genus:** Lower Eocene of the Central Alpine Gosau Basin of Krappfeld (Carinthia, Austria; Rasser [1994], as *Lithothamnion* sp.); Late Eocene of the Alpine Foreland Basin in Upper Austria (current study). Basso et al. (1997) expected the fossil species *Lithothamnion operculatum* (Conti) Conti to be conspecific with the Recent *Phymatolithon calcareum* (Pallas) Adey and McKibbin. In that case the occurrence of *Phymatolithon* has to regard several Oligocene to Pleistocene occurrences, as listed by Basso et al. (1997).

Present-day species of *Phymatolithon* are recorded from the Northern Atlantic (e. g., Adey and Adey, 1973; Bosence, 1983b; Chamberlain, 1991; Irvine and Chamberlain, 1994), the Mediterranean (see Basso [1994] for review), and Southern Australia (e. g., Wilks and Woelkerling, 1994). In the tropics, it

occurs subordinately on the eastern Pacific shelf of North and South America (Adey, 1970).

**Stratigraphic range:** Lower Eocene to Recent.

*Phymatolithon* sp.

Plate 1, figures 1-7

*Lithothamnion* sp.- RASSER 1994, p. 198, pl. 3, figs 4, 5; pl. 2, fig. 6.

**Description:** Typical growth form is encrusting to foliose (pl. 1, fig. 1). Warty growth forms show protuberances, 1.3-1.4 mm long and 1.5-0.8 mm thick. Crusts are mostly unattached. Thalli show simple, reverse, or enforced crust division sensu Bosence (1983a), no crust fusion or bridging occurs. Thallus dorsiventral and monomerous, core filaments situated ventrally; peripheral filaments restricted to the dorsal thallus portions (pl. 1, fig. 2).

Core filaments predominantly curve towards the dorsal, sometimes towards the ventral thallus surface (pl. 1, fig. 2); core portion 70-150 µm (mostly 100 µm) thick and constitute at least 50 % of the thallus thickness in layered to foliose portions; cell length 14-29 µm (mean 19, standard deviation 4), cell diameter 7-11 µm (m. 9, sd. 1); cell fusions occur.

The peripheral region in encrusting portions is usually c. 50 µm thick but also up to 150 µm; no growth zones occur; cell length 7-16 µm (m. 11, sd. 2), cell diameter 5-13 µm (m. 10, sd. 2). Protuberances show 90-120 µm thick growth zones; cell fusions abundant (pl. 1, fig. 5), trichocytes absent, cell rows not regular; cell length 7-18 µm (m. 11, sd. 3), cell diameter 7-13 µm (m. 9, sd. 2). Subepithallial initials as short or shorter than underlying cells (pl. 1, figs 6, 7); cell length 7-9 µm, cell diameter 11-12 µm. The epithallium is one cell-layer thick (pl. 1, figs 4, 6 and 7), cells are rarely well preserved; cell shape diffuse, but not flat (pl. 1, figs 6, 7); cell length 8-9 µm, cell diameter 11-12 µm.

Tetrasporangial conceptacles are multiporate (pl. 1, fig. 2), without a rim, and may be buried within the thallus (pl. 1, fig. 3). Conceptacles are distinctively raised above the thallus surface with a floor usually ten cell layers below the thallus surface (less frequently only five). Internal diameter 210-460 µm (m. 344, sd. 68), height 100-160 µm (m. 127, sd. 24). 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). Some conceptacles show preserved tetrasporangia and filaments interspersed between them (pl. 1, fig. 3). Sexual conceptacles and carposporangia are unknown. Measured samples: MOL12 and MOL291.

**Remarks:** The occurrence of multiporate conceptacles, non-coaxial core filaments, relative length of subepithallial initials, and epithallial cells in a single layer allow the identification of the genus *Phymatolithon*. The species is the same as the one described by Rasser (1994) as *Lithothamnion* sp. from the Early Eocene of Carinthia (Austria). Growth form, anatomy, and conceptacle size are close to those of *Lithothamnion crispithallus* Johnson 1957.

**Occurrence of species:** Lower Eocene of the Central Alpine Gosau Basin of Krappfeld (Carinthia, Austria; Rasser [1994]) and Late Eocene of the Alpine Foreland Basin in Upper Austria (current study).

**Stratigraphic range:** Early to Late Eocene.

TABLE 1  
Characters of melobesioid genera with non-coaxial core filaments. For details see text.

	<i>Phymatolithon</i>	<i>Lithothamnion</i>	<i>Clathromorphum</i>	<i>Synarthrophyton</i>
Epithallium uni-layered	●	●		●
Epithallium multi-layered			●	
Epithallial cells not flared	●		●	●
Subepithallial initials as short or shorter than cells subtending them	●			
Subepithallial initials as long or longer than cells subtending them		●	●	●

## DISCUSSION

### Generic features of *Phymatolithon*

Braga et al. (1993) characterised *Phymatolithon* as having (1) multiporate tetrasporangial conceptacles, (2) a monomerous thallus with a non-coaxial arrangement of core filaments, (3) 'not flat' epithallial cells, and (4) a 'cell elongation down from the meristem'. All these features can be found in the described material.

Wilks and Woelkerling (1994) delimit *Phymatolithon* from other genera of Melobesioidae by a combination of six characters: (1) lack of an arborescent growth form, (2) haustoria absent, (3) thallus monomerous, (4) epithallial cells with rounded or flattened but not flared outer walls, (5) subepithallial initials are as short or shorter than their immediate inward derivatives, and (6) tetra/bisporangial conceptacles develop from cells produced adventitiously within the thallus. Only the latter feature could not be observed in the studied material; the shape of epithallial cells is diffuse but apparently not flared (pl. 1, figs 6, 7).

In addition to the features cited above, Irvine and Chamberlain (1994) define *Phymatolithon* by the 'Phymatolithon-type' surface view of epithallial cells and by the shape of cells surrounding the conceptacle pore plug. These characters are difficult to recognise in fossil material and have not yet been described.

### Separation from other genera

Traditional characters used to identify fossil coralline genera are the perforation of tetrasporangial conceptacles, the arrangement of basal filaments (formerly 'hypothallus'), the thickness of the peripheral region, and the occurrence of trichocytes (Wray 1977). On this basis, the species described here would have to be assigned to *Lithothamnion*, which is characterised by multiporate conceptacles and monomerous non-coaxial core filaments. Owing to this insufficiency of anatomical features, Johansen (1981) expected *Lithothamnion* to be a repository for a wide assortment of fossil crustose coralline algae. In fact, the restriction to the above mentioned characters does not allow separation of *Lithothamnion*, *Phymatolithon*, *Clathromorphum*, *Leptophyllum*, and *Synarthrophyton* which show non-coaxial core filaments.

The separation of *Phymatolithon* from other Melobesioidae is mainly based on the relative length of subepithallial initials (tab. 1). *Lithothamnion*, *Clathromorphum*, and *Synarthrophyton* are characterised by subepithallial initials, which are as long or longer than their immediate inward derivatives. Additionally, *Clathromorphum* has a multi-layered epithallium (Woelkerling, 1988; Braga et al. 1993). *Lithothamnion* shows flattened and flared epithallial cells (Wilks and Woelkerling 1995), and *Synarthrophyton* is characterised by tetrasporangia bearing apical plugs (Woelkerling and Foster 1989). These characters have a low fossilisation potential. The relative length of subepithallial initials is, however, a sufficient character to separate these genera from *Phymatolithon* (Basso, 1994). The separation from *Leptophyllum* is more problematical. According to Braga et al. (1993), *Phymatolithon* is indistinguishable from *Leptophyllum* in fossil material. This fact is reflected by the generic differentiation of Irvine and Chamberlain (1994), which focuses on the surface view of epithallial cells. However, Wilks and Woelkerling (1994) concluded that *Leptophyllum* is not a distinct genus, and Düwel and Wegeberg (1996) consider it as a younger synonym of *Phymatolithon*.

### Designation of species

Irvine and Chamberlain (1994) delimited species of *Phymatolithon* by external morphology, colour, and position and structure of tetrasporangial conceptacles. Wilks and Woelkerling (1994) also focus on external morphology and tetrasporangial conceptacles, but additionally made use of the vegetative anatomy. Both of these features can be recognised in fossil material.

The species described in the current study cannot be assigned to any known Recent species. The only present-day species of *Phymatolithon* with tetrasporangial conceptacles raised above the surface, that are not flaked off and that lack rimmed conceptacles, are *P. brunneum* Chamberlain and *P. masonianum* Wilks and Woelkerling. The conceptacles of *P. brunneum* are, however, smaller and the external morphology does not fit the studied species (Irvine and Chamberlain 1994). *P. masonianum* differs from the studied species by a centrally situated core portion (Wilks and Woelkerling, 1994).

The assignment to a fossil species suffers from the problem that the vast majority of species are poorly described and type specimens are often missing. Although there have been several ef-

forts to revise and re-describe original material (e. g., Moussavian and Kuss, 1990; Piller, 1994; Rasser and Piller, 1994; Braga and Aguirre, 1995; Basso et al., 1997), most fossil species cannot be identified with confidence. In terms of growth form, anatomy, and conceptacle size, the species that most closely corresponds to that described here is *Lithothamnion crispithallus* Johnson, which therefore would have to belong to the genus *Phymatolithon*.

#### Diagenetic overprint of diagnostic features

The preservation of epithallial cells in the studied material seems to result from the early micritization of the outer cell layers. A lack of micritization may result in submarine abrasion or a pressure solution of epithallial cells and subepithallial initials. This micritization causes, however, a diffuse appearance of cell walls in optical light microscope and irregular etching structures in scanning electron microscope (pl. 1, fig. 6).

#### Paleocological implications

Several attempts have been made to use the occurrence of coralline taxa for paleocological interpretations (e. g., Adey and Macintyre, 1973; Buchbinder, 1977; Taberner and Bosence, 1985; Manker and Carter, 1987; Rasser, 1994; Bassi, 1998). These interpretations have to be treated with caution, as until recently several fossil genera could not be identified with certainty (Braga et al., 1993; Rasser and Piller, in press). The possibility to designate *Phymatolithon* in fossil material suggests discussing the ecological requirements of this genus.

Several present-day species of *Phymatolithon* have distinct ecological requirements. For example, Adey and Adey (1973) differentiated between 'arctic-subarctic' and 'boreal' species of *Phymatolithon*. Other species show, however, a more widespread distribution. For example, *P. lenormandii* occurs from the 'arctic Norway' to the Mediterranean and the Canary Isles (Irvine and Chamberlain, 1994). The same problem occurs with other ecological parameters, like water depth (as a sum of different parameters) and salinity: *P. calcareum*, for example, occurs between 7 and 120 m water depth and may tolerate low salinity (Basso, 1994).

Consequently, paleocological interpretations on the generic level must be treated with caution. According to Adey (1970), Adey

and Macintyre (1973), Johansen (1981) and Adey (1986), *Phymatolithon* is typical for cold and warm temperate waters (for the definition of the temperate zone compare Betzler et al. [1997]). In the tropics, it subordinately occurs on the eastern Pacific shelf of North and South America (Adey, 1970). *Phymatolithon* has, however not been recorded from the Caribbean, the Indic Ocean, and the Western Pacific (e. g., Papenfuss, 1968; Littler, 1973; Gordon et al., 1976; Tsuda and Wray, 1977; Verheij, 1994).

#### CONCLUSION

This study provides the first documentation of *Phymatolithon* in fossil material by applying a sufficient combination of taxonomic features used in botany. It additionally supports the conclusion of Braga et al. (1993) that most of the characters used in botanical taxonomy can be recognised in fossil material. The designation of fossil *Phymatolithon* and its separation from other Melobesioideae depends on the preservation of epithallial cells and subepithallial initials which can be studied in SEM samples. The occurrence of rounded epithallial cells in a single layer and subepithallial initials which are as short or shorter than the underlying cells allows separation from *Lithothamnion*, *Clathromorphum*, and *Synarthrophyton*. Even if the shape of epithallial cells is not recognisable in fossil material, the relative length of subepithallial initials is a sufficient character to identify *Phymatolithon*.

*Phymatolithon* sp. cannot be referred to any present-day species, although characters used in present-day algae can be applied to fossil species. Possibly it could be referred to the fossil *Lithothamnion crispithallus* Johnson, in which case the latter would belong to *Phymatolithon*. A new combination, however, requires a revision of Johnson's original material, which would be an important approach for further studies.

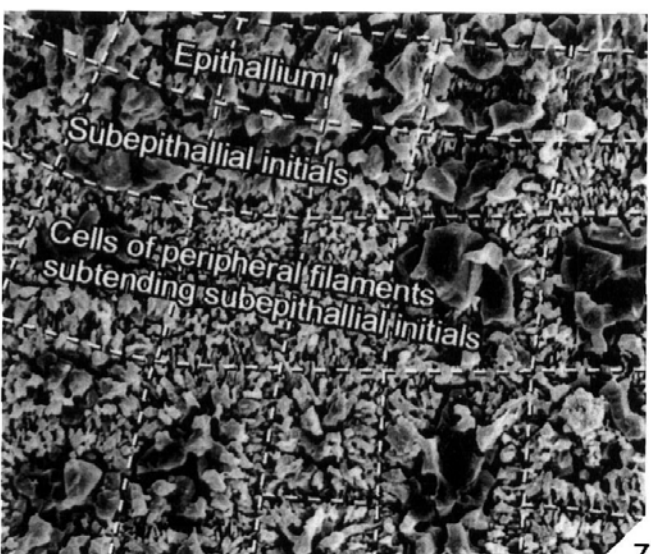
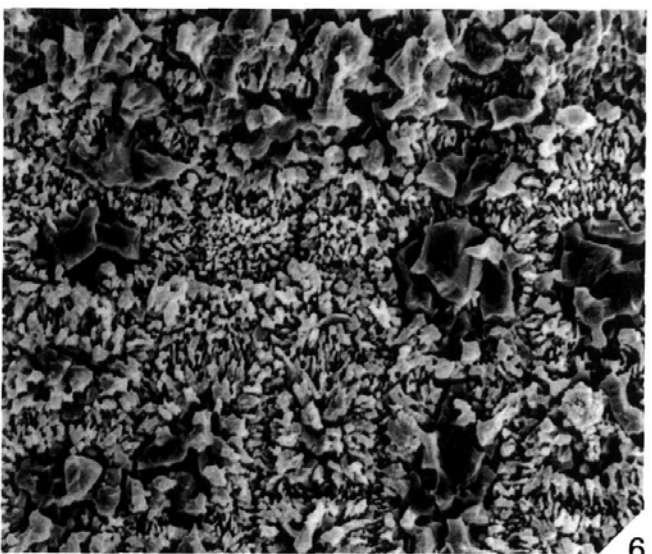
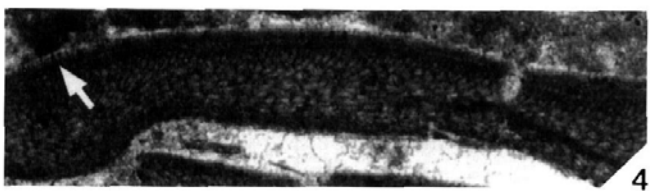
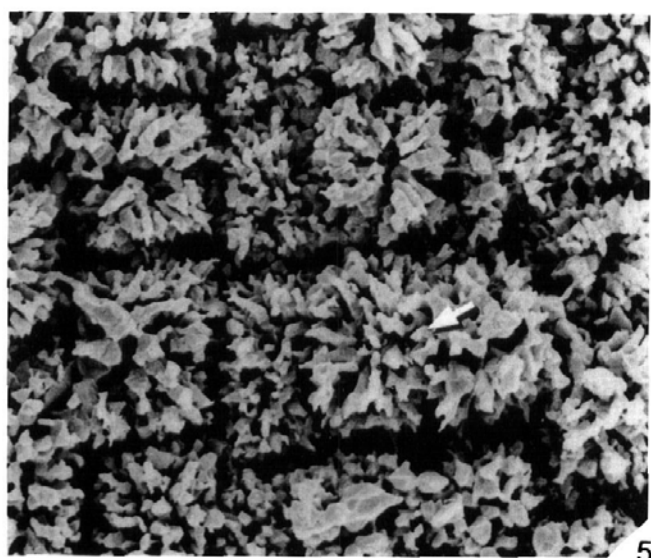
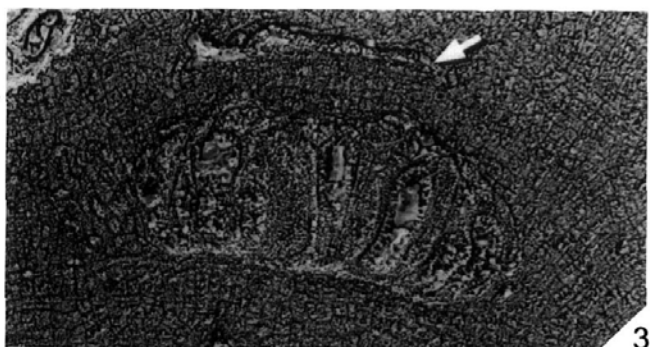
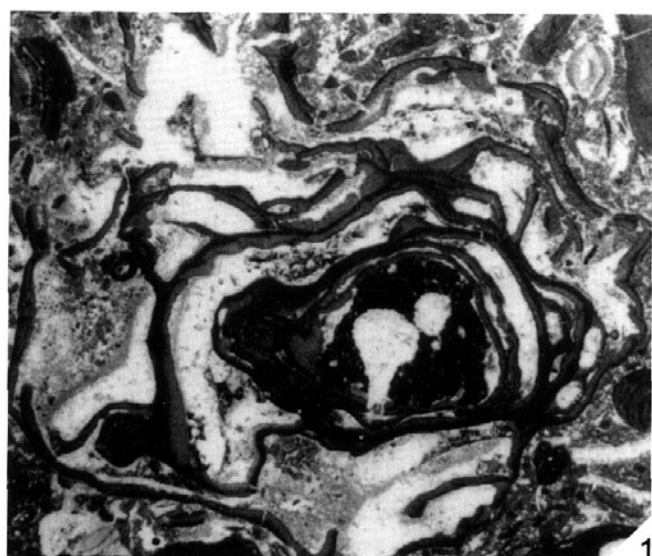
Paleocological interpretations are difficult even on the species level. A dominance of *Phymatolithon* in fossil material is, however, an indication for non-tropical rather than tropical environments.

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#### PLATE 1

- 1 Characteristic encrusting to foliose growth form of *Phymatolithon* sp.; sample MOL291;  $\times 15$ .
- 2 Detail of fig. 1, showing multiporate conceptacles and thallus organisation;  $\times 70$ .
- 3 Tetra/bisporangial conceptacle with preserved tetra/bisporangia and interspersed filaments; note the cement-filled cavity between conceptacle pores and overgrowing cell tissue (arrow); sample MOL59;  $\times 110$ .
- 4 Characteristic appearance of uni-layered epithallium in thin section (arrow); owing to the diffuse appearance, higher magnifications do not provide more details; sample MOL291;  $\times 70$ .
- 5 Cells of contiguous filaments are joined by cell fusion (arrow). Cell walls in SEM samples are usually etched by HCl, cell lumina filled by sparry calcite remain; sample MOL260;  $\times 1700$ .
- 6,7 SEM-image showing a uni-layered epithallium with 'not flared' epithallial cells and subepithallial initials which are as short or shorter than cells subtending them. Lines in fig. 7 mark the original cell walls which are etched by HCl (s. i. = subepithallial initials); sample MOL260;  $\times 1000$ .





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