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# STUDY OF LIVING CALCAREOUS ALGAE BY A PALEONTOLOGICAL APPROACH: THE NON-GENICULATE CORALLINACEAE (RHODOPHYTA) OF THE SOFT BOTTOMS OF THE TYRRHENIAN SEA (WESTERN MEDITERRANEAN).
## THE GENERA *PHYMATOLITHON* FOSLIE AND *MESOPHYLLUM* LEMOINE

DANIELA BASSO

*Key-words:* Taxonomy, Paleobotany, Corallinaceae, Recent, Tyrrhenian Sea.

*Riassunto.* Sono state studiate le Corallinaceae non articolate raccolte nel Tirreno settentrionale e centrale (Arcipelago Toscano e Isole Pontine) in 47 stazioni di profondità compresa tra 27 e 137 m. *Phymatolithon calcareum* (Pallas) Adey & McKibbin è stata rinvenuta vivente in 22 stazioni comprese tra 36 e 93 m di profondità, con massima abbondanza a -44 m, a nord di Palmarola. Sezioni longitudinali di rami hanno mostrato delle zonazioni regolari del tallo, attribuite ad alternanze stagionali dei ritmi di crescita e dell'entità della calcificazione delle pareti cellulari. Lo spessore di tali "bande" e la profondità di vita della specie appaiono correlati, ma tale correlazione non è costante. *Mesophyllum lichenoides* (Ellis) Lemoine è stata riconosciuta in due sole stazioni a circa 50 m di profondità, ma talli sterili attribuibili alla specie sono comuni nell'area investigata. Si descrive una nuova morfologia della specie come adattamento alla vita sui fondi mobili. Gli elementi diagnostici del tallo vegetativo e dei concettacoli delle due specie sono descritti attraverso l'analisi biometrica e illustrati con fotografie al Microscopio Elettronico a Scansione e al Microscopio Ottico.

*Abstract.* Living non-geniculate coralline algae were collected from 47 stations in the northern and central Tyrrhenian Sea (Tuscan Archipelago and Pontian Islands). Longitudinal sections of branches of *Phymatolithon calcareum* (Pallas) Adey & McKibbin show regular zonation, due to yearly cycles of growth. The alternating bands are generally thicker at shallower depth. A new morphology of *Mesophyllum lichenoides* (Ellis) Lemoine resulting from the adaptation to soft bottoms is described. The diagnostic elements of the vegetative thallus and the conceptacles of *P. calcareum* and *M. lichenoides* are described by biometry and Scanning Electron Microscope or Optical Microscope images. The geographic and bathymetric distribution of the two species is also given.

## Introduction.

Calcareous algae are common in the fossil record of ancient shelf environments, but corallinaceans have received little attention until recent times, when their importance as a paleoecological tool has been stressed (Adey & Macintyre, 1973). In addition

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- Dipartimento di Scienze della Terra, Università degli Studi, Via Mangiagalli, 34, 20133 Milano.

to traditional paleobotanical studies, it has been realized that crustose Corallinaceae are a widely distributed group with diversified environmental requirements, making them highly significant for paleoecological restorations.

In the last decade the growing interest in corallinaceans brought new attention to the old taxonomic problems that affect this algal group. Botanists undertook the revision of the most important genera of Corallinaceae, leading to major revisions of their taxonomy. In many cases these investigations, based on the original type collections, stressed the importance of some microscopic features for the identification of the higher taxa.

Systematic paleobotany could not overlook these results. Although botanists usually decalcify coralline thalli, in most cases comparison of details in the cellular organization of these algae with fossils is possible, since main features are conserved and still observable in the calcitic remain of corallinaceans, provided that suitable instruments are used for their investigation. For example, microscopic features such as cell fusions between contiguous filaments have been observed by Scanning Electron Microscope (SEM) in a common tertiary species (*Lithophyllum albanense* Lemoine 1923) allowing its correct identification as a mastophoroid and not, as previously thought, a lithophylloid genus (Braga et al., 1993).

Therefore, conceptual and methodological renewals call for new approaches, and fossil corallinacean taxa should be reassessed taking into account all diagnostic features of the biologic taxonomy that are recognizable in the calcitic remains.

The interest of the paleontologist on living corallinaceans is grounded on three considerations. First, diagenesis plays a major role in the quality of the preservation of the microscopic features in the fossil, but it is not clear even what is still recognizable soon after death and burial. That is to say that we have a very little knowledge of the effects of early taphonomic processes affecting corallinaceans. Any consideration on this subject must be grounded on a very good knowledge of morphology and structure of hard parts of living thalli.

Second, the study of the living corallinaceans of the Mediterranean was undertook since the early nineteenth century. Although some important contributions are available at present (Foslie, 1929; Hamel & Lemoine, 1952; Cabioch, 1972; Bressan, 1974) still the distribution of most taxa and sometimes even their anatomical features are poorly known. Moreover, since traditional methods of decalcification and sectioning of coralline algae often result in a distortion of shape and arrangement of the cells (Garbary & Veltkamp, 1980), the paleontological method on living species must be regarded as a complementary tool to the biological approach.

Third, paleoecological restorations rely on analogies with modern environments and biota. A better knowledge of the present-day organisms which are likely to undergo fossil preservation is the best tool for interpreting morphology, mode of life and ecological role of fossil organisms.

Observations of features of calcareous thalli in living mediterranean corallinaceans will allow the comparison between calcified and non decalcified thalli of the same living species, in order to assess the extent of the loss of diagnostic features and the biometric variability as function of the two different techniques (decalcified preparations vs. thin sections of non decalcified thalli).

Finally, it will be possible to give a key to define corallinacean species: the modern definition of the algal species should be grounded on the study of the natural population and its fluctuation around a mean, whilst too often corallinacean species (fossil and living) were erected on the basis of single specimens.

A special attention has been paid to circalittoral soft bottom species and to their distribution. The aim is to provide a tool for detailed near past evolution of many coastal environments, through the interpretation of ecological succession of assemblages, as partially recorded by the skeletal remains accumulated in the sediment.

Since the reliability of the reconstruction is maximum dealing with times when environmental setting and biota were close to the present ones, these data are expected to be very useful for paleoenvironmental restorations as far as Plio-Pleistocene times, at least.

## Material and methods.

Soft bottom samples were recovered by grab or dredge during the 1988-1990 cruises in the Tuscan Archipelago and the 1989 cruises in the Pontian Islands by the R/V Minerva. These cruises were runned in the framework of TSM project (Taphonomy and Sedimentology of the Mediterranean shelf; Basso et al., 1990). Sampling tools have been already described elsewhere (Basso et al., 1990; Basso, 1990).

The complete list of the 55 stations where living macroalgae were recovered can be found in Basso (1992). The distribution of the non-calcareous macroalgae collected at the same sites is discussed in Basso (1994).

Calcareous algae were found in 47 stations ranging from 27 to 137 m depth. The discussion of their distribution in the area is in progress (Basso, in prep.). Corallinaceans were picked up from the sample and dried in a ventilated site, far from direct light and heat.

For thin sections, calcareous thalli were imbedded in Epofix resin (Struers) before cutting, in order to preserve branching and avoid damage of vacuolar or delicate specimens. Then the thin section for observations under Optical Microscope (OM) was prepared following the standard procedures for stony material.

The correct orientation of the thallus is basic in order to obtain meaningful data; on this subject, references can be found, among others, in Afonso-Carrillo et al. (1984) and Chamberlain (1986).

For SEM observations, an oriented fragment of the thallus was obtained, and then mounted on the stubs by mean of graphite paste (Leit-C conductive carbon cement, Neubauer Chemicalen). Specimens were then gold coated. SEM Cambridge Stereoscan 250 was used.

Biometry is a major tool to separate corallinacean species of the same genus. When dealing with thick walled cells, the difference between dimensions of decalcified and non decalcified cells could be non negligible. Cells length (L) has been measured as the distance between the two primary pit connections; cells diameter (D) includes half of the calcified wall separating two adjacent cells. Since the growth of the hypothallial cells is parallel to the substrate, their length is oriented perpendicularly to the length of perithallial and epithallial cells. To avoid confusion, the diameter of hypothallial cells is called height (H) (Woelkerling, 1988). Abundance is given as total cover, i.e. $cm^2$ of bottom surface covered in projection by the living thalli of the given species.

## Systematic paleontology.

Evidence was given by Cabioch (1971, 1972, 1988) that the traditional division between geniculate and non geniculate forms of coralline (Lemoine, 1911, 1939; Conti, 1950; Hamel & Lemoine, 1952; Johnson, 1954 etc.) is not natural, since it has no morphogenetical ground. Cabioch observed that the crustose form is common to all corallines, geniculate or not, at least during early stages of ontogeny. That is to say that an anatomical feature appearing later (the presence of genicula) cannot be used as diagnostic feature at the highest taxonomic levels, following the Haeckel's law.

Many Authors criticized this purpose (Adey & Johansen, 1972; Johansen, 1981; Woelkerling, 1988), thus considering the presence of genicula as diagnostic at the subfamily level. The phylogenetic implications of the two opposed concepts are waiting for an answer and paleobotanists can obtain from the fossil record some decisive insights on the matter. In the absence of a definitive settlement of the question, one is faced with making a choice: "...the choice of which classification scheme to follow still must be based principally on arbitrary pragmatic considerations...choosing the most utilitarian construct from amongst those available" (Woelkerling, 1988, p.56). Since geniculate taxa commonly undergo a post-mortem disarticulation (i.e. allochthony can be frequent), and since they are by far less common as fossils, it seems reasonable and convenient to keep them separate from the crustose, non-geniculate taxa, even if this may not reflect the phylogenetical relationship among the genera.

Coralline taxonomy is undergoing major revisions, due to the application of new methods of investigation (SEM), to the recovery of type material that was believed lost, and to the application of a species concept grounded on populations rather than single specimens.

In this fluid situation, the citation of synonyms should only be made if the type specimen has been investigated. Thus synonymy will be limited here to publications where sufficient diagnostic data are given. In most papers of the last century and first decades of '900, Authors gave only a macroscopical description of coralline algae or, at best, an incomplete microscopical description that nowadays is not enough to define even the genus. Moreover, in some cases, the basionym corresponds to lost material, in other cases the original description was never followed by the revision of the type specimens. These basionyms were listed indicating in brackets the first paper with modern taxonomical basis where the original reference can be found.

### Order **Corallinales** Silva & Johansen 1986
### Family *Corallinaceae* Decaisne 1842
### Subfamily *Melobesioideae* sensu Woelkerling 1988

This subfamily encompasses non-geniculate species showing cell fusions between adjacent cells of parallel filaments. Secondary pit-connections are absent. Mature asexual conceptacles open at the roof by several pores, each pore corresponding to a sporangium. Before the release of the sporangia, the pores are occluded by pore-plugs. Sexual conceptacles with one pore.

### Genus *Phymatolithon* Foslie 1898 nom.cons.

Type species: *P. calcareum* (Pallas) Adey & McKibbin 1970

The neotype of *Millepora calcarea* Pallas 1776 was revised by Woelkerling & Irvine (1986a), who ascertained that it is conspecific with *Millepora polymorpha* Linnaeus 1767. The genera *Apora* Gunnerus 1768 and *Nullipora* Lamarck 1801 were based on *M. polymorpha*, thus on *M. calcarea*, and should have priority on *Phymatolithon* 1898. However, in order to stabilize nomenclature, the conservation of *Phymatolithon* against *Apora* and *Nullipora* was proposed (Woelkerling & Irvine, 1986a).

The genus encompasses all Melobesioideae possessing a non-coaxial hypothallus; perithallus with intercalary meristem formed by cells of the same length or shorter than the perithallial cells; epithallus terminating, when complete, with a large ovoid cell (Woelkerling, 1988). Asexual conceptacles developing from groups of adventitious initial cells, inside the perithallus (Adey, 1970; Cardinal et al., 1979).

### **Phymatolithon calcareum** (Pallas) Adey & McKibbin 1970

Pl. 1; Pl. 3, fig. 1-4

Basionym: *Millepora calcarea* Pallas 1766, p. 265 (Woelkerling & Irvine, 1986a).

1911 *Lithothamnium calcareum* - Lemoine, p.102 pro-parte (non *L. corallioides* Crouan 1867), pl. 1, fig. 3-5.
1915 *Lithothamnium calcareum* - Lemoine, p. 10.
1927 *Lithothamnion calcareum* f. *squarrulosa* - Funk, p. 430, pl. 11, fig. 4, 5.
1929 *Lithothamnion calcareum* - Foslie, p. 59, pl. 16, fig. 1-6, 9-28.
1952 *Lithothamnium calcareum* - Hamel & Lemoine, p. 85, fig. 47, pl. 15, fig. 1, 2.
1956 *Lithothamnium calcareum* - Huvé, p. 109.
1966 *Lithothamnium calcareum* - Cabioch, pl. 1, fig. A.
1970 *Phymatolithon calcareum* - Adey & McKibbin, fig. 1-3, 6.
1974 *Lithothamnium* (*Phymatolithon*) *calcareum* - Bressan, p.71, fig. 13 a-d.
1986a *Phymatolithon calcareum* - Woelkerling & Irvine, fig. 1-15.
1988 *Phymatolithon calcareum* - Woelkerling, p. 198, fig. 230.
1989 *Lithothamnium* (*Phymatolithon*) *calcareum* - Fravega & Vannucci, p. 717, fig. 3-5.

**External appearance**. The thallus is crustose to branched; it is commonly found as unattached branches or, sometimes, as nodules enveloping pebbles or biogenic remains. Branching density is extremely variable, as is the final shape of the rhodoid. The diameter of branches ranges from 1.5 to 3 mm.

**Microscopic anatomy**. The medial longitudinal section (L.S.) of a branch shows a medullary perithallus made of regular filaments of ovoid cells. The perithallus forming the periphery of the branch (cortex) has smaller cells that sometimes can undergo multiple fusions, resulting in large, irregularly "star-shaped" cells (Pl. 1, fig. 1).

A L.S. of a branch (Pl. 1, fig. 2) shows a clear zonation of convex, light and dark bands, that alternate following the growth of the thallus (Cabioch, 1966; Adey & McKibbin, 1970). This alternance of colour reflects a difference in cell size and thickness of cell walls (Tab. 1). Under SEM, light bands have smaller cells and a thicker calcification of the cell walls. Dark bands are thicker and are made of longer cells with thinner walls than those observed in light bands (Pl. 1, fig. 2). Under OM, at low magnification, long-celled zones may appear the lightest, because of larger voids (Pl. 3, fig. 1). The lower limit of each long-celled band is sharp, whilst the passage to the overlying thick-walled cells is very gradual. Freshly collected specimens show the cells inside the calcitic walls. They become soon dehydrated inside the vacuum chamber of S.E.M., thus crashing and producing several sphaeroidal remains (starch grains; Pl. 1, fig. 3).

The hypothallus is normally difficult to observe in branched specimens, but it can regenerate over damaged portion of the thallus, where it appears clearly multilayered (Pl. 1, fig. 4).

The shape of the epithallial cells is considered an important diagnostic character to separate the genus *Phymatolithon* from *Lithothamnion*. The epithallial cells should appear more or less convex or rounded in *Phymatolithon*, flattened and "eared" in *Lithothamnion* (Woelkerling & Irvine, 1986a). Epithallial cells are not calcified at their

DARK BAND PERITHALLUS (μm)

| L cell | L lumen | D cell | D lumen |
|---|---|---|---|
| 12 | 11.5 | 9 | 7 |
| 11 | 10 | 9 | 7 |
| 10 | 8.5 | 8.5 | 6.5 |
| 10 | 7.5 | 7.5 | 6 |
| 11.5 | 8 | 7 | 5.5 |
| 12.5 | 8 | 7 | 5.5 |

LIGHT BAND PERITHALLUS (μm)

| L cell | L lumen | D cell | D lumen |
|---|---|---|---|
| 10.5 | 7.5 | 11 | 5.5 |
| 8 | 6.5 | 7.5 | 5 |
| 8.5 | 6.5 | 10 | 6.5 |

Tab. 1 - A pair of bands in the perithallus of *Phymatolithon calcareum*, specimen DB 162, station min88edg024. Dimensions of the cells (μm) including the walls (L cell and D cell) compared with the dimensions of the lumen only (L lumen and D lumen).

upper surface, which is often sloughed off or collapsed, but conserve their lateral walls (Pl. 1, fig. 5). This means that, in absence of *post-mortem* transport and under condition of rapid burial, it should be possible that epithallus undergoes fossilization. Anyway, the difficulty to perform adequate observations of the epithallus, even in living specimens, makes this character poorly reliable in paleontology. However, the pattern of the subepithallial cell elongation is another diagnostic character that seems to be much easier to observe (Woelkerling & Irvine, 1986a), both in living and in fossil specimens. The subepithallial meristem is made of short cells and the inward derivatives continue to grow after the cutting off. Thus, they appear as one to three-four very short cells becoming longer inward, where they reach the normal perithallial size. This progressive elongation of the subepithallial cells is sufficiently apparent to allow generic assignment under both SEM and OM observations (Pl. 1, fig. 1; Pl. 3, fig. 2).

Asexual conceptacles are not rare, particularly in specimens found in deeper stations. Frequently these functional conceptacles are somewhat sunk in the surrounding perithallus, but sometimes they appear weakly raised. A characteristic feature under OM is a light line delimiting the upper side of the buried multiporic conceptacles (Pl. 3, fig. 3). It corresponds to the separation between the roof of the conceptacle and the overgrowing thallus (Pl. 1, fig. 6). This line is almost straight to concave-upward. Roofs are made of four-five cell layers, and shows several canals. Functional and buried (old) asexual conceptacles show convex lateral sides and flat bottom, as typical for the genus (Pl. 1, fig. 6; Pl. 3, fig. 4). The mean diameter of these conceptacles is approximately double than the height. This appears typical for the species (Woelkerling & Irvine, 1986a). After the releasing of spores, the empty chamber of conceptacles can undergo an early diagenetic deposition of boundles of $CaCO_3$ crystals.

Branched specimens of this species have been often confounded with the similar *Lithothamnion corallioides* Crouan & Crouan, but when observing under OM some mixed branches of the two species in the same thin section, the small dimension of the perithallial cells (Tab. 2), hardly distinguishable at low magnification, allows to quickly identify *P. calcareum*, even if not fertile.

| | | N | MEAN | (S.D.) | MODE | MIN. | MAX. |
|---|---|---|---|---|---|---|---|
| Ipothallial cells | L | 26 | 14 | (2.6) | 12.5 | 10 | 19 |
| | H | 26 | 6.73 | (1.29) | 6.25 | 4 | 9.3 |
| Perithallial cells | L | 58 | 9.66 | (2.6) | 12.5 | 6 | 19 |
| | D | 58 | 6.93 | (1.6) | 6.25 | 5 | 11 |
| Epithallial cells | L | 21 | 4.38 | (0.9) | 3.75 | 3 | 6.25 |
| | D | 21 | 8.25 | (2.39) | 7.5 | 5.75 | 16.25 |
| Asexual | D | 36 | 208 | (18.1) | 225 | 180 | 245 |
| conceptacles | H | 31 | 108 | (14) | 100 | 85 | 140 |
| Roof thickness | rt | 30 | 25 | (7.55) | 20 | 15 | 40 |

Tab. 2 - *Phymatolithon calcareum*. Dimensions of the diagnostic microscopic features of the species in the investigated area.

**Discussion**. Several forms of the species have been described on the basis of rhodolith shape, branching density and microscopic anatomy (Lemoine, 1911; Cabioch, 1966). Their significance was discussed by Bosence (1976, 1983) who suggested separating the taxonomy from macroscopic, environmentally-induced morphological variations. Woelkerling & Irvine (1986a) also suggested avoiding the use of infraspecific taxa and applicating Bosence's method for describing external morphology of branched corallinaceans. *P. calcareum*, although common, is not abundant in the studied area, so that no statistical evaluation of the occurrence of the different morphologies could be attempted.

Alternating bands in the thallus of corallinaceans are well known and attributed to seasonal differences in growth and wall thickness of cells (Giraud & Cabioch, 1979), during yearly cycles (Lemoine, 1911; Cabioch, 1966; Adey & McKibbin, 1970). Maximum growth rate occurs in early summer. Specimens of *P. calcareum* and *L. corallioides* living at 5-6 m depth along the Atlantic coast of Spain, proved to have a high rate of growth during summer whilst growth was very slow or absent during winter (Adey & McKibbin, 1970; Potin et al., 1990). Thus it is likely that thicker bands (the long-celled ones) form during spring/summer. The observed gradual transition from each long-celled band to the overlaying band with thick-walled cells suggests a gradual slackening of the growth rate during the fall and early winter, until the minimum is reached at the top of each short-celled band. The following spring, resumption of growth is marked by the sharp base of the developing long-celled (dark) band (Pl. 1, fig. 2). In branches showing a regular zonation one can assume that each pair of bands (one dark and one light) is formed in one year. Thus, it should be possible to calculate the approximate age of a branch, and the mean growth per year. The specimen taken as example in Tab. 1 shows 74 pairs of bands in a branch 8 mm long. It should be 74 years old, with a mean yearly growth of 108 $\mu$m per year. The comparison of band thickness (yearly growth) measured in specimens recovered at different depth from the investigated area and from Calvi (Corse) testifies to very slow growth, apparently related to the depth at which the algal branch was living (Text-fig. 1). However, some specimens collected at only 36 m depth and showing a very regular zonation had bands less thick than expected (Pl. 1, fig. 2). As well known, depth produces variation in several ecological factors, but it is not an ecological factor *per se*. The sample from which that specimen was collected was very rich in *Posidonia* debris. Thus, several elements other than depth (i.e. water turbidity and suspended matter, or presence of a phanerogame cover) could be responsible of the supposed slower growth of the corallinacean. Further investigations and controlled experiments will hopefully clarify the question.

**Geographical distribution and ecology**. The species is distributed along Atlantic and Mediterranean coasts, and it is found also in the north-eastern Pacific.

Millions of living and dead branched specimens growing *in situ* can form, with other branched corallinaceans, the algal bank called maërl, from a Breton word. In the Atlantic, the maërl developes at shallower depth (7-20 m; Cabioch, 1969, 1970, 1974)

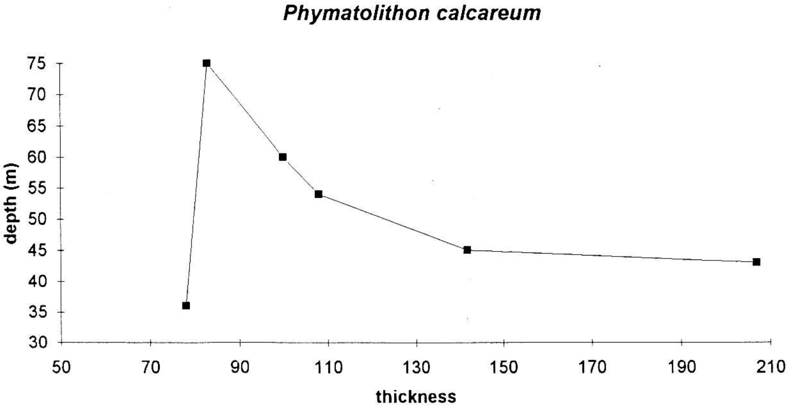

Fig. 1 - *Phymatolithon calcareum.* Mean thickness (μm) of each pair of bands (one dark plus one light) plotted versus the depth from which the specimen was collected.

than in the Mediterranean (about 40 m depth in the western basin, about 60 m in the eastern Mediterranean) (Jacquotte, 1962; Falconetti, 1970). In the Mediterranean, unattached corallines form the Association called *Phymatolitho-Lithothamnietum corallioidis* Giaccone 1965. This Association has been recorded from 30 to 90 m in the western Mediterranean, and down to over 120 m in the Eastern Mediterranean (Giaccone, 1968; Di Geronimo & Giaccone, 1994). The bathymetric distribution can be the result of differences in the penetration of light, since the species is found deeper in southern areas (Mediterranean versus Atlantic coasts of France) and in oligotrophic, transparent waters (eastern versus western Mediterranean). However, the most important condition for the development of maërl banks is the presence of currents (Jacquotte, 1962; Pérès & Picard, 1964; Falconetti, 1970; Pérès, 1982). These are mainly tidal currents along the Atlantic coasts of France (with several meters of tidal excursion twice a day), whilst, in the Mediterranean, where tides are not important, bottom currents enhanced by local morphology (in channels, around capes etc.) play the major role.

The species seems to tolerate small variations in salinity, since it can thrive in areas close to river mouths. During tank growth study the species ceased to grow at salinity of 24‰ (Adey & McKibbin, 1970).

The species was found living in 22 stations at depth ranging from 36 to 93 m (Tab. 3); thalli recovered at greatest depth were simple branches, living (pink colored) only on part of their surface. Asexual conceptacles were found more frequently on crustose thalli, growing on pebbles. The maximum abundance of living thalli was found at 44 m depth, north of Palmarola Island, in the Pontian Islands. More recent investigations lead to the discovery of a maërl bed living at 42 m depth, SW of the Isle of Elba.

**Stratigraphical distribution.** The species is recorded for marine sediments older than 14 ka (Late Pleistocene), recovered off the Pontian Islands (Corselli et al., 1994).

| STATION | DEPTH (M) | ABUND. (CM$^2$) |
|---|---|---|
| min89ebe197 | 36 | 6 |
| min89ebe127-128 | 43 | 6 |
| min89abe113 | 44 | 70 |
| min89abe104 | 51 | 4 |
| min89abe049b | 54 | 3 |
| min89abe105 | 60 | 8 |
| min90ebe044-45 | 60 | 1 |
| min89abe111 | 61 | 4 |
| min89ebe134-136 | 61 | 3 |
| min89ebe181 | 61 | 4 |
| min88edg024 | 45-63 | 30 |
| min89edg015 | 64-79 | 3 |
| min89ebe177 | 65 | 20 |
| min89ebe144-146 | 68 | 6 |
| min89abe103 | 69 | 2 |
| min89edg004 | 69 | 12 |
| min89edg002 | 73-78 | 9 |
| min89ebe019 | 75 | 14 |
| min90ebe038-039 | 76 | 4 |
| min88edg014 | 69-77 | 9 |
| min90ebe024 | 86 | 1 |
| min89abe109 | 93 | 6 |

Tab. 3 - *Phymatolithon calcareum.* Distribution and abundance in the investigated area. Abundance is given in cm$^2$ of bottom surface covered in projection by the living thalli of the species.

### Genus *Mesophyllum* Lemoine 1928

Type-species: *Mesophyllum lichenoides* (Ellis) Lemoine 1928

*Mesophyllum* is the only genus of Melobesioideae showing a coaxial organization of the hypothallus. This structure is due to the synchronous growth and division of the initial cells, in the marginal meristem (Cabioch, 1972; Woelkerling, 1988).

After the failure of all efforts to find the original Ellis collection, Woelkerling & Irvine (1986b) designated and described some neotype specimens of *M. lichenoides* collected in Cornwall (England).

### **Mesophyllum lichenoides** (Ellis) Lemoine 1928

Pl. 2; Pl. 3, fig. 5, 6

Basionym: *Corallium lichenoides* Ellis 1768, p. 407, pl. 17, fig. 9-11 (Woelkerling & Irvine, 1986b).

1837 *Lithophyllum expansum* Philippi, p. 388.
1866 *Lithophyllum lichenoides* - Rosanoff, p. 91, pl. 5, fig. 1-6; pl. 6, fig. 4, 5, 14.

1905 *Lithothamnion Philippii* - Foslie (pro-parte), p. 33, pl. 1, fig. 1.
1907 *Sphaeranthera lichenoides* Heydrich, p. 222, pl. 10, 11 (fide Lemoine, 1911).
1911 *Lithophyllum lichenoides* - Lemoine, p. 127, fig. 59-61.
1915 *Lithophyllum lichenoides* - Lemoine, p. 13, fig. 2, pl. 1, fig. 11.
1924 *Lithophyllum lichenoides* - Lemoine, p. 118, pl. 3, fig. 4; pl. 4, fig. 1, 2.
1928 *Mesophyllum lichenoides* - Lemoine, p. 252.
1929 *Lithothamnion philippii* - Foslie (pro-parte), p. 53, pl. 6, fig. 3.
1929 *Mesophyllum lichenoides* - Lemoine in Boergesen, p. 30.
1937 *Lithothamnion lichenoides* - Suneson, p. 62, fig. 37-41.
1952 *Mesophyllum lichenoides* - Hamel & Lemoine, p. 77, fig. 39, 40, pl. 13, fig. 5-7.
1970 *Mesophyllum philippii* - Adey, p. 25.
1973 *Mesophyllum lichenoides* - Adey & Adey, p. 363.
1974 *Mesophyllum lichenoides* - Bressan, p. 62, fig. 24.
1983 *Mesophyllum lichenoides* - Woelkerling, pp. 307-313, fig. 4-14.
1986b *Mesophyllum lichenoides* - Woelkerling & Irvine, pp. 382, fig. 1-27.
1989 *Mesophyllum lichenoides* - Fravega & Vannucci, p. 720, fig. 6.

**External appearance.** The species is most frequently found on hard substrates, where it commonly developes as thin, sometimes convoluted crusts (200-400 $\mu$m) loosely attached to other algae, plants or dead branched colonies of gorgonians; the formation of adventitious lamellae, funnel-shaped expansions and little flat lobes overgrowing the basal thallus is typical (Woelkerling, 1983; Woelkerling & Irvine, 1986b).

On soft bottoms the species shows different morphologies. Little unattached nodules, enveloping unrecognizable biogenic remains bear short, stout branches (Pl. 2, fig. 1, 2). The little overgrowing lobes occur sometimes also on unattached rhodoids, but adventitious lamellae and funnel-shaped expansions do not occur on these plants. This morphology can be compared with *M. canariense* (Foslie) Lemoine. The absence of adventitious lamellae is probably a consequence of the growth in contact with the sediment, since abrasion and occasional overturning prevent the formation of delicate thin expansions of the thallus.

At greater depth (80-100 m), in a quiet environment, the species forms some lamellate rhodoids due to the superposition of several thalli (Fravega & Vannucci, 1989).

**Microscopic anatomy.** A radial section of a lobe shows a coaxial hypothallus (Pl. 2, fig. 3) with a lower portion composed of rectangular cells arching toward the substrate, passing to oval cells in the core of the hypothallus and toward the perithallus. The height of hypothallial cells decreases toward the lower side of the hypothallus and toward the perithallus. The thickness of each hypothallus is about 100 $\mu$m.

The basal crust usually has smaller cells than the overgrowths (Woelkerling & Irvine, 1986b), and unattached rhodoids have smaller cells then those observed on the hard bottom specimens living at shallower depth (Tab. 4).

Cell fusions are large and evident, both in the hypothallus and in the perithallus.

The multilayered perithallus is thicker in free-living nodules than in the typical specimens from hard substrate, and it shows thick-walled cells (5-7 $\mu$m).

The asexual conceptacles develop in groups at the tip of the branch-like expansions. In surface view they appear more or less circular, depending on the degree of crowding. They are rised and have a flat roof (Pl. 2, fig. 4, 5). Sometimes the roof is sunken giving origin to a ring. Old conceptacles often show broken roofs. Little "plug

| | | N | Mean | (S.D.) | Mode | Min. | Max. |
|---|---|---|---|---|---|---|---|
| Ipothallial cells | L | 35 | 16.49 | (2.52) | 17.5 | 11.25 | 21.25 |
| | H | 35 | 6.66 | (2.39) | 8.75 | 3 | 11.25 |
| Perithallial cells | L | 50 | 10.35 | (2.07) | 12.5 | 6.25 | 13.75 |
| | D | 50 | 9.62 | (1.64) | 10 | 7.5 | 13.75 |
| Epithallial cells | L | 6 | 2.86 | (0.64) | 2.5 | 2.5 | 3.75 |
| | D | 6 | 10.8 | (1.02) | 10 | 10 | 12.5 |
| Asexual | D | 5 | 378.8 | (43.6) | 380 | 323 | 440 |
| conceptacles | H | 5 | 160 | (38.95) | 180 | 120 | 205 |
| Roof thickness | rt | 1 | 41 | | | | |
| (?) Cystocarpic | D | 1 | 430 | | | | |
| conceptacle | H | 1 | 240 | | | | |
| pore channel | l x d | 1 | 200 x 80 | | | | |

Tab. 4 - *Mesophyllum lichenoides.* Dimensions of the diagnostic microscopic features of the species in the investigated area.

cells", which are smaller than other roof cells have been remarked in the neotype plants (Woelkerling & Irvine, 1986b). These cells have been detected both in the soft-bottom specimens (Pl. 3, fig. 5) and in the more common, hard bottom plants (Pl. 3, fig. 6). The female conceptacles (cystocarpic) are rised, flask-shaped in L.S. (Pl. 2, fig. 6; Tab. 4). They were found empty, but the similarity with the shape and dimensions given by Woelkerling & Irvine (1986b) and the correspondence of all other characters of the thallus leave very little doubt on their identity.

**Discussion.** The species *Lithothamnion philippii* was erected by Foslie in 1897 without designating a type. It has been transferred to the genus *Mesophyllum* by Adey (1970). The selected holotype of *M. philippii* (Foslie) Adey is the same pictured in two Foslie's publications (1905, pl. 1, fig. 1; 1929, pl. 6, fig. 3) and, as stated in the caption, comes from the gulf of Naples. This picture showing the macroscopic feature of *Mesophyllum philippii* gives a good idea of one of the common aspects of the typical *M. lichenoides*, when growing on hard bottom. Moreover, no other species of *Mesophyllum* is recorded from the Mediterranean, thus, although no detailed studies of the type of *M. philippii* has been undertaken until now, little doubt exists that *M. lichenoides* and *M. philippii* (Foslie) Adey are conspecific. However, more than one form of *L. philippii* were described by Foslie. Adey revision (1970) apparently overlooked these forms. It is likely that one of them corresponds to the current concept of *L. philippii* (Hamel & Lemoine, 1952; Bressan, 1974). Moreover, Woelkerling (1993) has refused the validity of the typification of *L. philippii* proposed by Adey & Lebednik (1967) and by Adey (1970), because the selected types were collected three years after publication of the protologue, and at least 10 other collections predating the protologue are in Foslie's herbarium. Thus, even if *M. philippii* (Foslie) Adey is conspecific with *M. lichenoides*, the identity of *L. philippii* Foslie 1897 remains unchanged.

The species *Millepora agariciformis* Pallas was considered conspecific with *M. lichenoides* by a number of Authors, from the beginning of this century (Woelkerling

& Irvine, 1986b). Some unattached specimens of *M. lichenoides* from the British Isles have been reported under Pallas' specific epithet *agariciformis*. Pallas collected his material in the Mediterranean Sea (NE Algeria) and his original collection has disappeared, thus it is impossible to assess if *M. agariciformis* is conspecific with the specimens described here.

*Mesophyllum canariense* (Foslie) Lemoine 1928 shows several similarities with the specimens under this study. In particular, the presence of branches and the little size of the asexual conceptacles (D 200-400 x H 100 μm, Lemoine, 1929; D150-400 x H 75-130 μm, Masaki, 1968; Foslie's holotype: D up to 350 μm x H 90-110, Reyes & Afonso-Carrillo, 1993). However, perithallial and epithallial cell diameters are much smaller in *M. canariense*. Following Lemoine's description (1929) *M. canariense* lives firmly attached to rocks of the mesolittoral-upper infralittoral zone ("...les massifs de *M. canariense* sont fixés sur *Vermetus*....raboté par les vagues..."), in a completely different environment compared with Mediterranean relatively deep soft bottoms. Moreover, this species has never been found in the Mediterranean and comparison with other living species of *Mesophyllum*, to be undertaken by the biological method, is beyond the aim of this work. Thus it seems unlikely that the specimens under this study are related with *M. canariense*.

The material collected during this study shows some differences from the more common hard-bottom specimens of *M. lichenoides*: smaller size of hypothallial and perithallial cells, hypothallial cells passing from markedly rectangular to ovoid, more developed perithallus and smaller asexual conceptacles. Differences in size and shape of cells and conceptacles depending on the depth of life and/or on the life habit (attached versus unattached) are recorded in other species (Cabioch, 1966). Moreover, attached specimens of *M. lichenoides* also normally show a great degree of variability, even in the same plant.

Thus the specimens collected in the studied area are considered to result from the adaptations of the species *Mesophyllum lichenoides* to an unattached mode of life.

**Geographical distribution and ecology**. The species is not frequent in the studied area (Tab. 5). However, many thin sections showed well developed coaxial hypothalli with thin perithallus and no conceptacles that have been tentatively identified with *M. lichenoides* on the basis of cell shape and dimensions. Cell fusions and coaxial hypothallus may also be present in the mastophoroid *Neogoniolithon brassica-florida* (Harvey) Woelkerling, Penrose & Chamberlain, thus no sure identification can be made of non-fertile thalli, even if the vegetative anatomy is significantly different in the two species.

*M. lichenoides* is widely distributed along the Mediterranean and Atlantic coasts, from the lower mediolittoral zone down to 30-35 m, on hard bottom (Bressan, 1974). The species has been recorded on hard bottom at 65 m depth, and down to 80-100 m on soft bottoms in the Calvi Bay (Corse) (Fravega & Vannucci, 1989).

**Stratigraphical distribution**. *Lithothamnion lichenoides* (Ellis & Solander) Foslie is recorded in the Pleistocene of Saipan (Marianne Archipelago) (Johnson, 1957). However, since the species has never been recorded in the Pacific, it is possible that

| STATION | DEPTH (M) | ABUND. (CM$^2$) |
|---|---|---|
| min89abe092 | 48 | 2 |
| min88edg024 | 45-63 | 100 |

Tab. 5 - *Mesophyllum lichenoides.* Distribution and abundance in the investigated area. Abundance is given in cm$^2$ of the surface covered in projection by the thalli.

this identification is related to another species of *Mesophyllum. Mesophyllum lichenoides* has been found in Mediterranean marine sediments older than 14 ka (Late Pleistocene) (Corselli et al., 1994). Among Tertiary species, a comparison can be done with *M. commune* Lemoine 1939, described for the lower Miocene of Algeria. The presence of branches of 0.5-3 mm in diameter bearing little asexual conceptacles (D 325-500 x H 125-175 $\mu$m) and the comparable dimensions of perithallial and hypothallial cells would allow to consider the two taxa as conspecific. In this case, the stratigraphic distribution of *M. lichenoides* would show a considerable gap. Moreover, several dozen of fossil *Mesophyllum* have been described until now. Many of them were erected on the basis of differences that would be regarded now as the natural variation of one species. Thus the question requires further investigations.

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## PLATE 1

SEM photographs of *Phymatolithon calcareum* (Pallas) Adey & McKibbin.

Fig. 1 - Upper perithallus and epithallus in L.S. Multiple fusions (F) of perithallial cells are visible on the left. Specimen 2526892b15, station min89ebe134-136.

Fig. 2 - Zonation in the perithallus of a L.S. of a branch. Specimen DB 267, station min89ebe197.

Fig. 3 - Perithallial cell filaments uncompletely dried. Top left, the cell inside the calcitic wall is cracking but still entire; on right the cells are cracked and divided in several spheroidal remains. Primary pit connections (P) and fusions (F) are visible. Specimen DB 266 collected at 33 m water depth off Marettimo Island (Egads Archipelago).

Fig. 4 - Two ipothalli along a L.S. of a branch. Same specimen as in fig. 1.

Fig. 5 - Epithallial cells in surface view. The soft tissue has been sloughed off on the left, showing the calcitic walls filled with detritus. In the center of the picture the epithallial cells are not damaged, and the primary pit connection is visible. Same specimen as in fig. 1.

Fig. 6 - Apex of L.S. of a branch; two asexual conceptacles buried in the perithallus. The "line" overlying each conceptacle delimits the upper surface of the roof. The conceptacle on the right is filled with calcitic needles that have formed after the release of the spores, when the conceptacle cavity became permeable through the pore channels. Same specimen as in fig. 1.

## PLATE 2

*Mesophyllum lichenoides* (Ellis) Lemoine 1928.

Fig. 1 - Close-up photograph of the specimen 26892b19, station min88edg024. Some unrecognizable remains form the core of the rhodoid. The roundish excrescences at the top of the short branch-like expansions are the cystocarpic conceptacles (detail in fig. 6).

Fig. 2 - SEM photographs of the specimen 2526892b18, station min88edg024. An asexual thallus overgrown on a fragment of colony of the bryozoan *Sertella* sp. (note the flat shape of the thallus and the holes at the base of the branch-like expansions). The asexual conceptacles are crowded at the top of the branches. Bottom left, a conceptacle with broken roof.

Fig. 3 - Same as in fig. 2. Radial section of the basal crust. Bottom: detail of the coaxial hypothallus with the rectangular to ovoid cells. Middle: cell fusions in the perithallus. Top: two to three celled epithallus.

Fig. 4 - Same as in fig. 2. Detail of the surface view of a multiporate asexual conceptacle.

Fig. 5 - Same as in fig. 2. A section of an empty asexual conceptacle. Traces of the pore channels are visible in the roof.

Fig. 6 - SEM photograph of the same specimen as in fig. 1. A medial section of an empty cystocarpic (?) conceptacle.

## PLATE 3

Fig. 1 - *P. calcareum* (Pallas) Adey & McKibbin. L.S. of a branch. Zonation in the perithallus. Specimen DB181, ground section. OM photograph, scale bar = 200 µm.

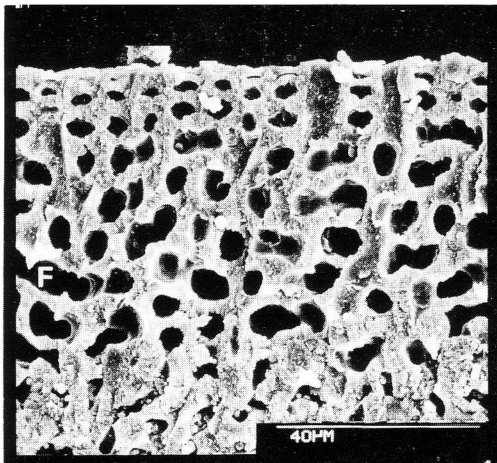
Fig. 2 - *P. calcareum* (Pallas) Adey & McKibbin. Progressive elongation of subepithallial cells. Specimen DB58, ground section. OM photograph, scale bar = 15 µm.

Fig. 3 - *P. calcareum* (Pallas) Adey & McKibbin. A fertile plant: several tetrasporangial (multiporic) empty conceptacles are buried in the thallus. Specimen DB51, ground section. OM photograph, scale bar = 100 µm.

Fig. 4 - *P. calcareum* (Pallas) Adey & McKibbin. Same as in fig. 3. Detail of a buried conceptacle. Scale bar = 15 µm.

Fig. 5 - *M. lichenoides* (Ellis) Lemoine. SEM detail of the roof of a tetrasporangial plant. Specimen 2526892b18.

Fig. 6 - *M. lichenoides* (Ellis) Lemoine. Same as in fig. 5. Specimen 4894b8, S. Fruttuoso (Ligurian Sea), on a vertical cliff at 15 m depth.



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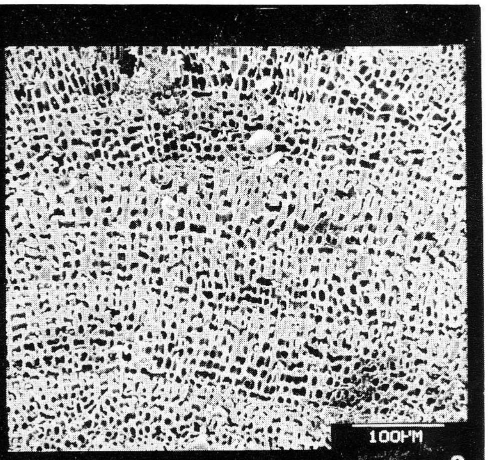

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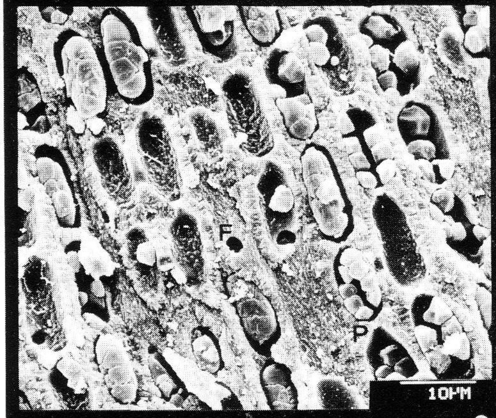

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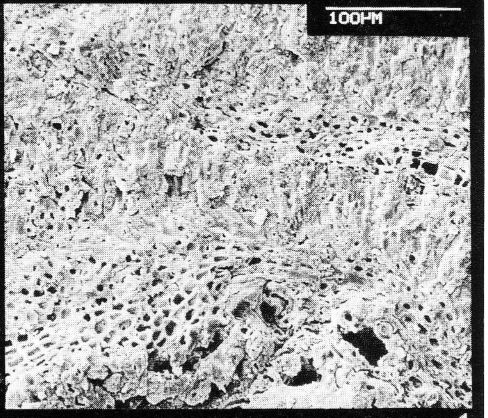

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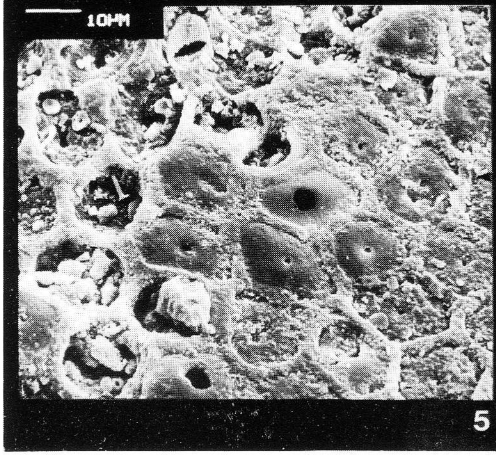

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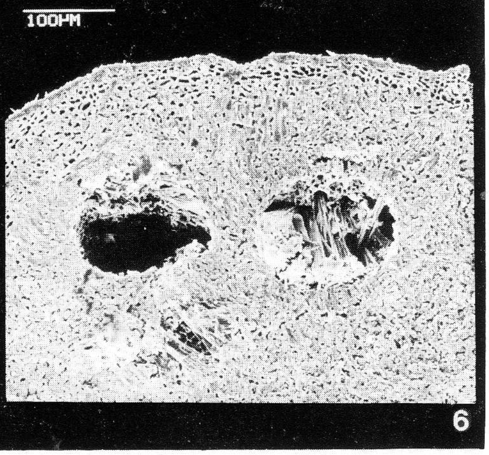

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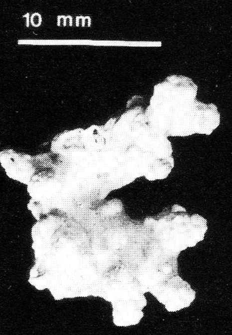

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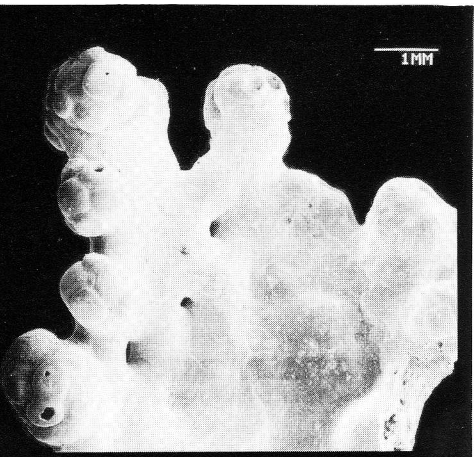

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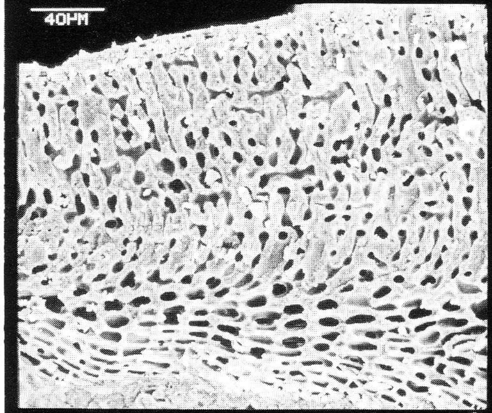

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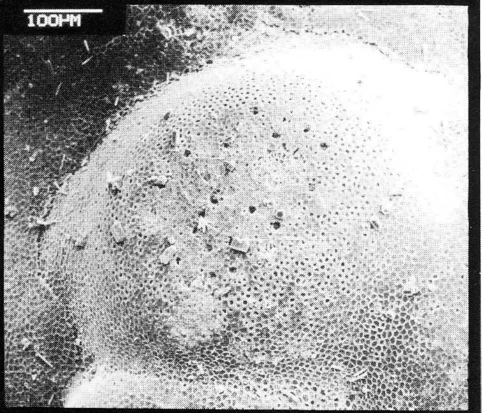

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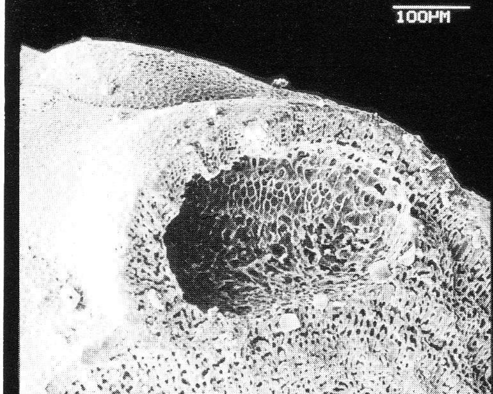

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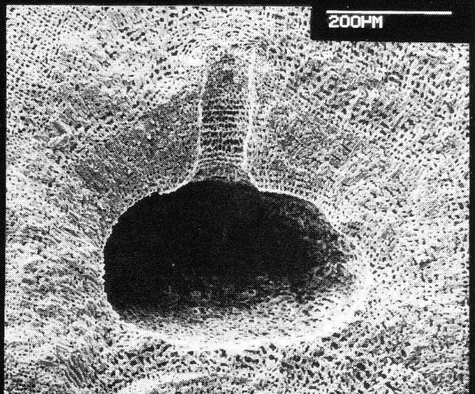

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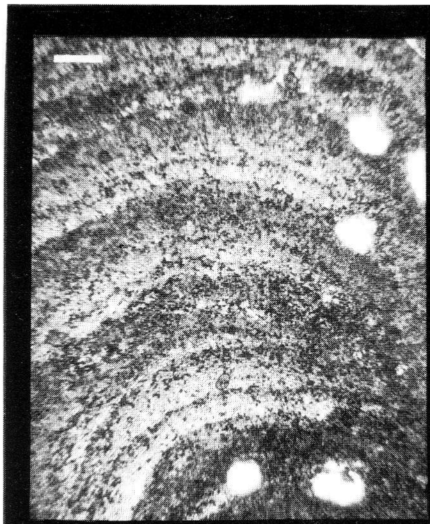
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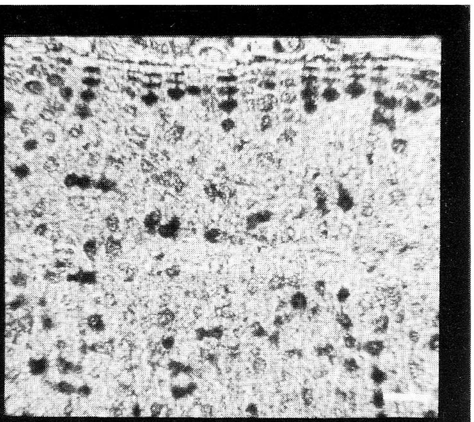
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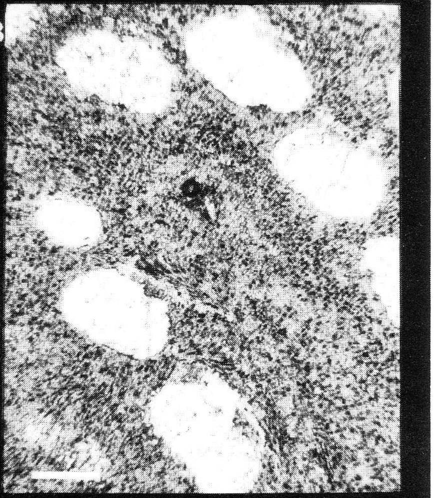
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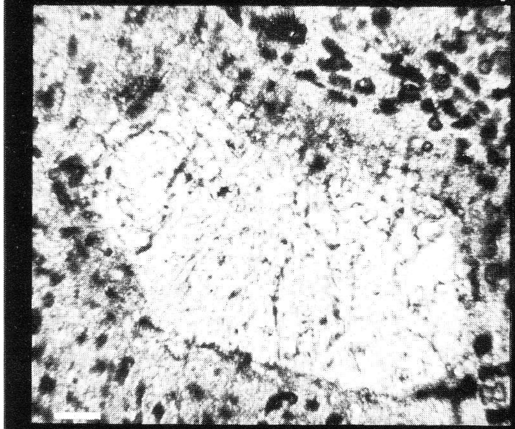
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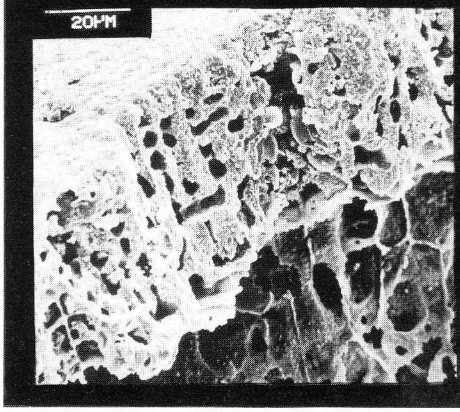

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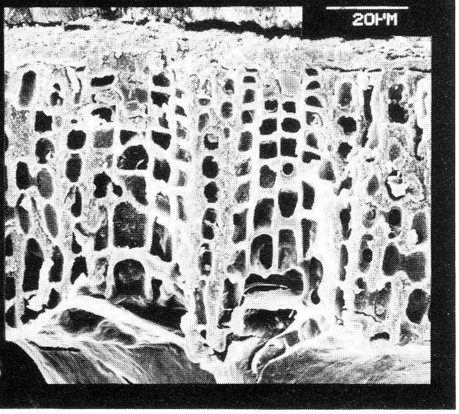

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