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LIVING CALCAREOUS ALGAE BY A PALEONTOLOGICAL APPROACH: THE GENUS *LITHOTHAMNION* HEYDRICH NOM. CONS. FROM THE SOFT BOTTOMS OF THE TYRRHENIAN SEA (MEDITERRANEAN)

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Key-words: Taxonomy, calcareous algae, Corallinaceae, Recent, Tyrrhenian Sea.

Riassunto. Sono state studiate le corallinacee non articolate raccolte nell'Arcipelago Toscano ed Isole Pontine in 53 stazioni di profondità compresa tra 27 e 137 m e tra 30 e 35 m di profondità nel maërl di Marettimo (Isole Egadi, Sicilia). *Lithothamnion corallioides* è stato rinvenuto vivente a Marettimo e in 10 stazioni comprese tra 44 e 93 m di profondità. *Lithothamnion fruticulosum* auctorum è stato ridescritto e identificato come *L. minervae* sp. nov., presente a Marettimo e in 23 stazioni tra i 27 e i 98 m di profondità. *L. philippii* Foslie è stato rinvenuto in 5 stazioni a profondità compresa tra 45 e 79 m. *Lithothamnion valens* Foslie è stato rinvenuto a Marettimo e in 9 stazioni localizzate tra 51 e 79 m di profondità, con massima abbondanza e con esemplari eccezionalmente sviluppati tra le isole di Ponza e Palmarola. Gli elementi diagnostici del tallo vegetativo e dei concettacoli delle quattro specie vengono per la prima volta descritti con un'analisi biometrica e illustrati con fotografie al Microscopio Elettronico a Scansione e al Microscopio Ottico. La zonazione del tallo, dovuta al regolare alternarsi di bande a cellule con pareti sottili e bande a cellule con pareti spesse, viene documentata in *L. corallioides*, *L. minervae* e *L. valens*.

Abstract. Living non-geniculate corallinacean algae recovered in the Tyrrhenian Sea (Tuscan Archipelago, Pontian Islands and Egads) have been collected at 53 stations ranging in depth from 27 down to 137 m and in the maërl of Marettimo (Egads), at 30-35 m depth. *L. corallioides* has been collected at Marettimo and in 10 stations ranging from 44 to 93 m depth. *L. fruticulosum* auctorum has been re-described and identified as *L. minervae* sp. nov., collected at Marettimo and in 23 stations ranging from 27 to 98 m depth. *L. philippii* Foslie has been identified in 5 stations ranging from 45 and 79 m depth. *L. valens* Foslie has been recognized at Marettimo and in 9 stations from 51 to 79 m depth, with maximum abundance and best developed specimens collected in the channel between the islands of Ponza and Palmarola. The diagnostic elements of the thallus of the four species are described by SEM and OM images and biometric data. The zonation of the thallus, due to alternating bands of thick-walled and thin-walled cells, is described in details for *L. corallioides*, *L. minervae* and *L. valens*.

Introduction.

In the last decade botanists revised the most important genera of Corallinaceae (among others: Woelkerling, 1988; Penrose & Woelkerling, 1992) leading to major upheavals on their taxonomy. The use of modern techniques (SEM) has supported some conceptual renewals that must be taken into account in the study of both fossil and living corallinacean taxa. All diagnostic features of the biologic taxonomy that are recognizable in the calcitic remains must be considered. The study of living corallinaceans by an actuopaleontological approach has a twofold result: to improve the knowledge of the morphology and distribution of the Mediterranean coralline algae and to give a sound actualistic basis for the more traditional research of paleobotanists and paleoecologists. Other comments on the conceptual framework of this study can be found in Basso (1995).

Material and methods.

Soft bottom samples were recovered by grab or dredge during 1988-1990 cruises in Tuscan Archipelago and 1989 cruises in the Pontian Islands by the R/V Minerva (CNR). These cruises were carried out in the framework of the TSM project (Taphonomy and Sedimentology of the Mediterranean shelf; Basso et al., 1990). Details concerning sampling tools, sampled sites, sample dimension, methods and SEM techniques are given in Basso (1995). In the Egads (western Sicily) samples have been collected by SCUBA along the western coast of the Island of Marettimo. Cell length (L) is the distance between the two primary pit connections; cell diameter (D) includes half of the calcified wall separating two adjacent cells. The dimension perpendicular to the length of the hypothallial cells is called heigth (H) (Basso, 1995). Abundance is given in square cm of surface covered in projection by the living thalli, given the difficulty to define the single plant (Boudouresque, 1970) (Tab. 1).

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Station	Depth (m)	*L.corallioides* (cm^2)	*L.minervae* (cm^2)	*L.philippii* (cm^2)	*L.valens* (cm^2)
min88abe012a	27		9		
min88abe017a	41		9		
min88edg04	36-49		8		
min88edg05	52-57		6	6	
min88edg014	69-77				3
min88edg024	45-63	30	200	200	
min88edg026	63-65	2			6
min90ebe024	86		16		
min90ebe041-043	63		12		
min90ebe044-45	60		2		
min90ebe046-047	56				12
min89abe060	68		17		
min89abe113	44	10			
min89abe104	51	4	37	2	4
min89abe049b	54	3	7		
min89abe092	48		9		
min89abe105	60		7		
min89abe109	93	2			
min89ebe042-043	68		3		
min89ebe044	63				1
min89ebe134-136	61	6	31		20
min89ebe144-146	68	4			
min89ebe158-159	46		18		
min89ebe127-128	43		8		
min89ebe174-176	74		7		
min89abe103	69		29		
min89edg002	73-78		46	14	243
min89edg004	69	2	12		9
min89edg012	90-98		4		
min89edg015	64-79	2	9	4	11

Tab. 1 - Stations and depth of recovery of the four species of *Lithothamnion*. Abundance is expressed in cm^2 of surface covered in projection by the coralline thallus (Boudouresque, 1970).

Systematic description

Synonymy is limited here to publications where sufficient diagnostic data are given to allow an unequivocal identification of species. Most papers of the last century and first decades of 1900 give a very poor description of coralline algae. These early contributions have been listed in synonymy only when the type material was revised and documented recently. When the basionym would correspond to lost material or when the first laconic protologue was never followed by the revision of the original specimens, these basionyms were listed indicating in brackets the first paper with modern taxonomical basis which includes the original reference.

Order Corallinales Silva & Johansen 1986
Family *Corallinaceae* Lamouroux 1812
Subfamily *Melobesioideae* Bizzozzero 1885

This subfamily encompasses non-articulated 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 uniporate.

Genus *Lithothamnion* Heydrich 1897 nom.cons.

Type species: *Lithothamnion muelleri* Lenormand ex Rosannoff 1866

For over one century Philippi's original collection was believed lost and therefore the genus *Lithothamnium* Philippi 1837 was not documented. Part of Philippi's types were recovered in Leida, together with Kützing's collection and subsequently revised (Woelkerling, 1983). The revision has shown that none of the specimens in Philippi's original collection corresponds to the modern circumscription of the genus *Lithothamnium*. The proposal to conserve *Lithothamnion* Heydrich against *Lithothamnium* Philippi in order to maintain the nomenclatural stability of a widely known genus (Woelkerling, 1985a) has been accepted by the XIV Intl. Botanical Congress in Berlin (Greuter et al., 1994).

The genus encompasses all Melobesioideae possessing a non-coaxial hypothallus; perithallus with intercalary meristem (easy to identify, since it is formed by cells longer than the underlying perithallial cells); epithallus with platy cells, with thick basal wall, frequently appearing flared (with more or less sharp corners) at the distal end. Multiporate asexual conceptacles developing from groups of intercalary initial cells (Cardinal et al., 1979). Sexual conceptacles uniporate.

Lithothamnion corallioides

Crouan P.L. & Crouan H.M. 1867

Pl. 1, 2; Tab. 2

1867 *Lithothamnium corallioides* Crouan & Crouan (*fide* Cabioch, 1966).
1915 *Lithophyllum solutum* - Lemoine, p. 13, fig. 3, pl. 1, fig. 9.
1919 *Lithophyllum solutum* - Lemoine, p. 108, pl. 3, fig. 1-3.
1952 *Lithophyllum solutum* - Hamel & Lemoine, p. 54, fig. 16, pl. 7, fig. 5.
1956 *Lithothamnium ? solutum* - Huvé, pl. 1, fig. a-b; pl. 2; pl. 3, fig. a-c; pl. 4, fig. a.
1960 *Lithothamnium australe* - Mastrorilli, p. 2, pl. 1, fig. 3; pl. 2, fig. 1-3; pl. 3, fig. 2; pl. 4, fig. 1.
1966 *Lithothamnium corallioides* - Cabioch, pl. 1, fig. B-C.
1970 *Lithothamnium coralloides* - Adey & McKibbin, fig. 4, 5, 7.
1974 *Lithothamnium corallioides* - Bressan, p. 74, fig. 12 a-d.
1989 *Lithothamnium corallioides* - Fravega & Vannucci, p. 719.

External appearance. The thallus is crustose to branched; it commonly occurs as unattached branches or, seldom, as nodules enveloping a pebble or a biogenic remain. The final shape of the rhodolith and the density of branching is extremely variable. In most cases the diameter of the rhodolith is 2 to 4 cm (Pl. 1, fig. 1). The diameter of branches is frequently around 1 mm and never exceeds 1.8 mm.

Microscopic anatomy. The hypothallus is thin (up to 60 µm), multilayered and non-coaxial. It can occur in the middle of a branch over some damaged portions of the perithallus. The perithallus is also multilayered. The medial longitudinal section (L.S.) of a branch shows a zoned medulla (Pl. 1, fig. 2, 6; Pl. 2, fig. 4). Long, thin-walled rectangular cells forming most of the medulla (Pl. 1, fig. 5) periodically alternate with thick-walled cells showing a reduction of the lumen size (Tab. 2). The transition from thin-walled to thick-walled cells is gradual, while the appearance of the following thin-walled cells is abrupt. Transverse section (T.S.) of branches frequently shows a central meniscus-like structure, originating by the convex layers of medullary cells (Pl. 1, fig. 3; Pl. 2, fig. 4). The large lumina of thin-walled medullary cells, frequently connected by multiple fusions, are easily detectable under low magnification (OM, x60) and very characteristic.

The perithallial cells which bend toward the surface of a branch become much smaller, forming the cortex (Pl. 1, fig. 3, 4, 6). Exceptionally long cells have been detected in the cortex of some specimens, in correspondence of irregularities of the thallus surface (Pl. 2, fig. 1). Cell fusions occur both in the hypothallus and in the perithallus (Pl. 1, fig. 4, 5; Pl. 2, fig. 3).

L. corallioides		n	mean	(s.d.)	mode		min	max
Hypothallial	L	25	20.5	(3.15)	22.5		14	25
cells	H	25	10.8	(0.85)	11.5		8	12
Perithallial	L	15	13	(4.29)	12		7	17
cells (cortex)	D	15	11.3	(1.15)	11.5		9	13
Perithallial	L	79	15.8	(5.01)	16.8	21.3	8	32
cells (medulla)	D	79	9.9	(2.55)	8.2	10.8	6.5	17.5
Epithallial cells	L	15	4.8	(1.39)	3		2.5	7
	D	15	6.9	(0.78)	7		5	8
Asexual	D	9	328.1	(59.78)	310		258	415
conceptacles	H	9	148.5	(16.15)	155		128	175
Roof thickness	rt	6	37.5	(2.08)	38		35	47
cell layers in roof		6	8	(0.82)	8		6	9

Tab. 2 - Sizes of the diagnostic microscopic features of *L. corallioides*. In the column mode, the small and large cells alternating in the perithallial cells of branches have been shown separately.

The epithallus is composed of a variable number of layers of flattened cells, the cells of the uppermost layer appearing "flared". Epithallial cells are not calcified at their surface, which is often sloughed off or collapsed, but their lateral walls are well calcified (Pl. 2, fig. 2, 3).

Asexual conceptacles are elliptical-rectangular in thin section. The roof of the conceptacle is convex and multiporate. It is made of 6 to 9 layers of cells becoming shorter (from 6 to 3 µm long) toward the external surface of the roof (Pl. 2, fig. 5, 6).

Discussion. Cabioch (1966, 1970) described two varieties (var. *corallioides* and var. *minima*) and several forms of the species. The var. *minima* should be characterized by branches with a homogeneous structure, not exceeding 1 mm in diameter. In the Baie de Morlaix *L. corallioides* var. *minima* thrives on fine sand and muddy bottoms (Cabioch, 1969, 1970). The var. *corallioides* cor-

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PLATE 1

Lithothamnion corallioides Crouan & Crouan.

Fig. 1 - Unattached branches and rhodoliths from Marettimo Is. (Egads, Sicily), 33 m depth. Scale bar = 1 cm.

Fig. 2 - Zonation of the perithallus of a L.S. of a branch. Marettimo Is. (Egads, Sicily), 33 m depth. SEM photograph, stub 121294b2.

Fig. 3 - Meniscus-like structure originated by the medullary, convex layers of cells. The meniscus is delimited by the smaller cortical cells. T.S. of a branch. Min89edg015, SEM stub 100691b8.

Fig. 4 - SEM detail of cortical cells of fig. 3. Note wall thickness.

Fig. 5 - SEM detail of long, thin-walled medullary cells of fig. 3. Note large cell fusions (f) and primary pit connections (p). Multiple cell fusions create a wide transversal connection among several cells (i.e. five cells within the white arrows).

Fig. 6 - Cortex cells in a L.S. of a branch. Top on the right. Marettimo Is. (Egads, Sicily). SEM photograph, stub 121294b2.

PLATE 2

Lithothamnion corallioides Crouan & Crouan.

Fig. 1 - Anomalous long cells (arrow) in the cortex of an unattached branch. Marettimo Is., 33 m depth. SEM photograph, stub 121294b2.

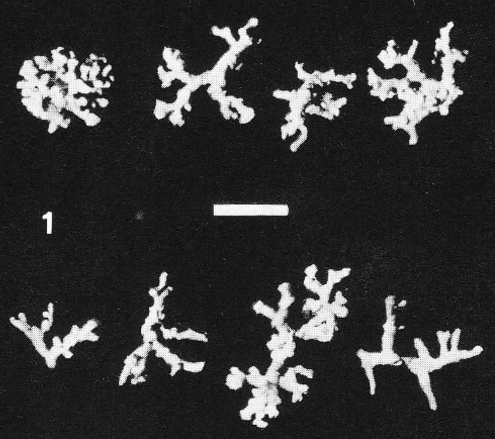
Fig. 2 - Surface view of epithallial cells. Same as fig. 1.

Fig. 3 - Epithallial and subepithallial cells in L.S. of a branch. Note the calcification of the lateral walls of epithallial cells. Same as fig. 1.

Fig. 4 - OM photograph of a L.S. (T.S. at the base) of a branch. Thin section DB93, Pontian Is., 78 m. Scale bar = 500 µm. Note the meniscus is detectable as a circular structure at the base of the branch. The cortex is also detectable as the compact margin which outlines the branch.

Fig. 5 - A multiporic conceptacle in surface view. The roof is partially crushed. Marettimo Is., SEM photograph, stub 121294b2.

Fig. 6 - SEM detail of fig. 5. Note the small cells of the conceptacle roof and the pores for the spore release.



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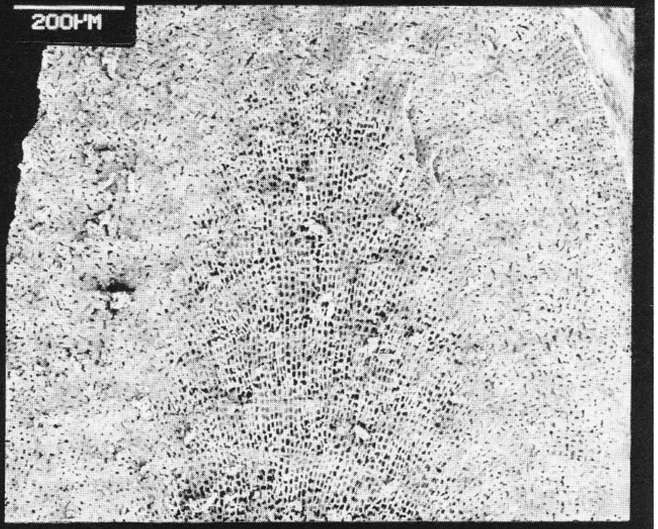

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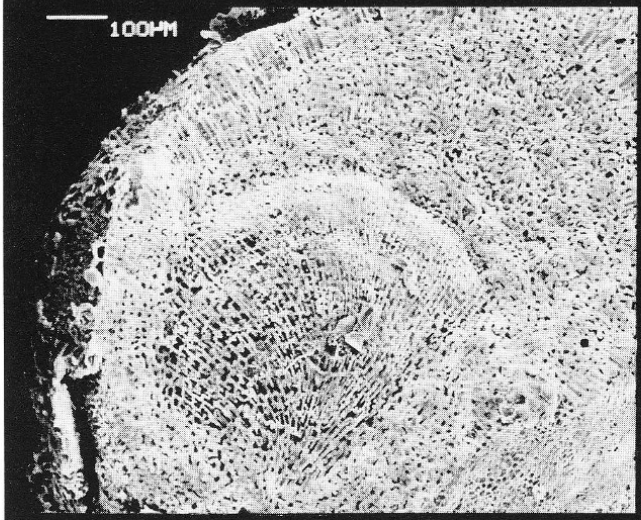

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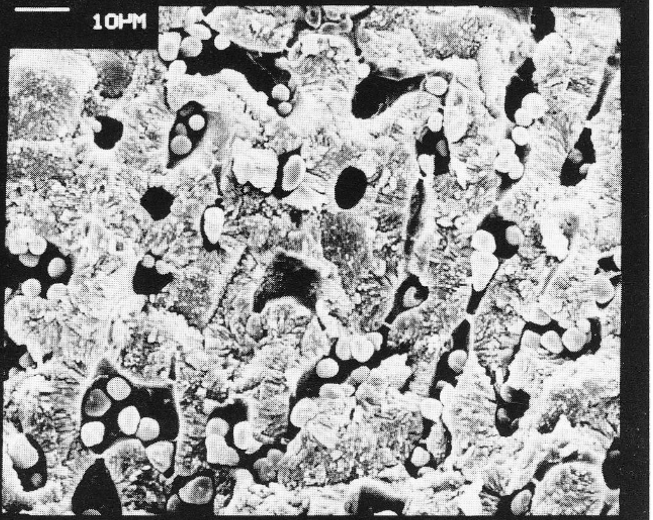

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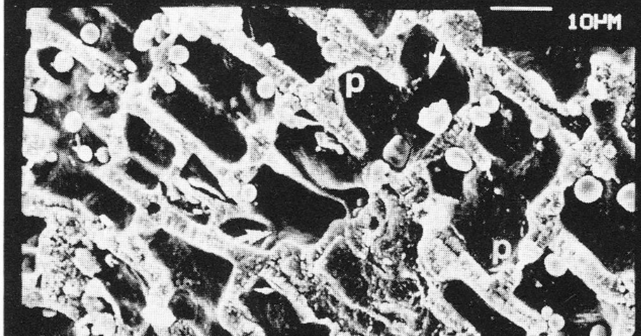

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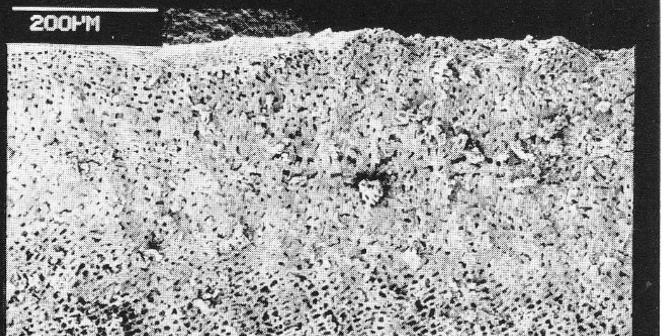

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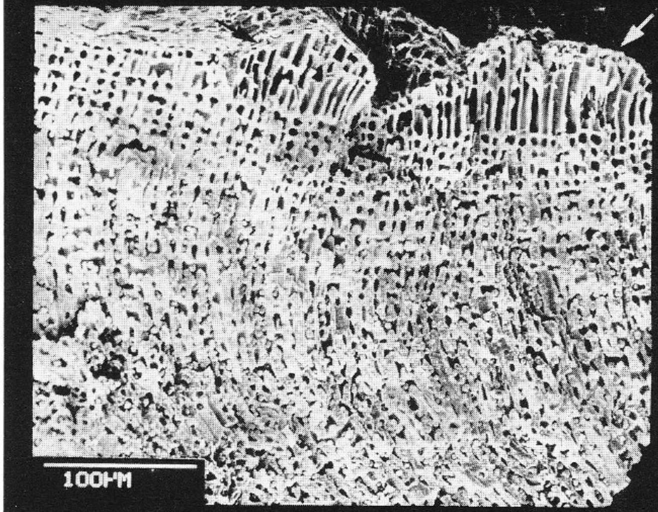

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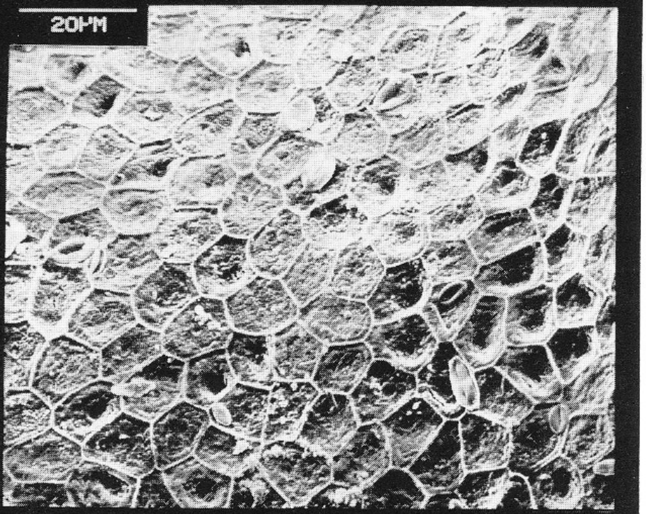

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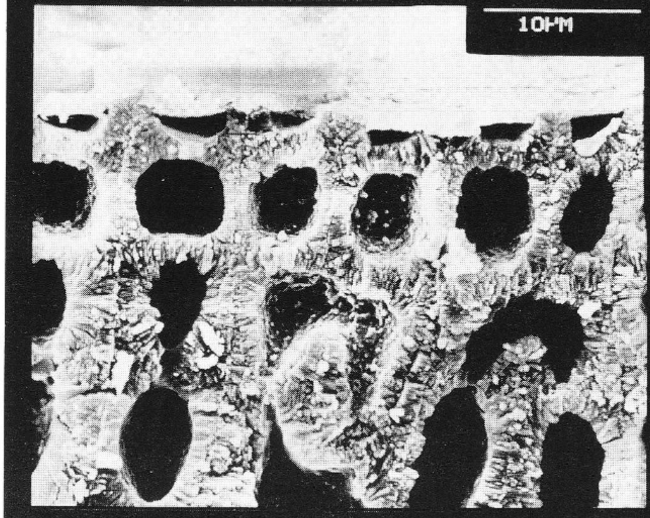

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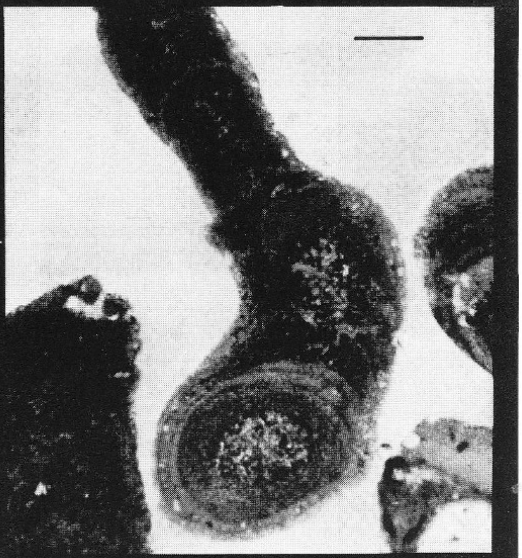

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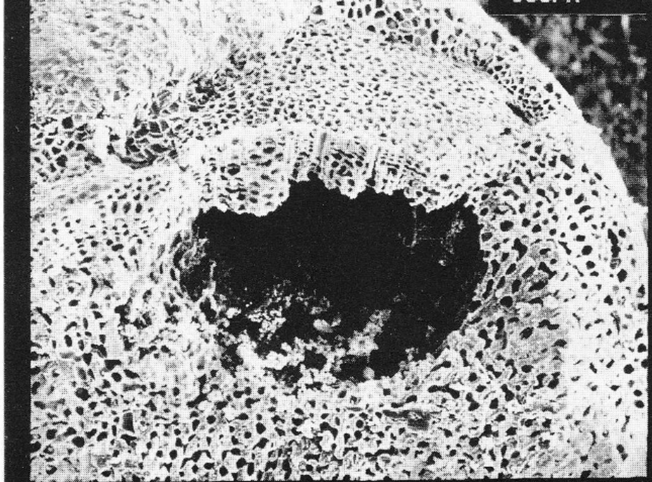

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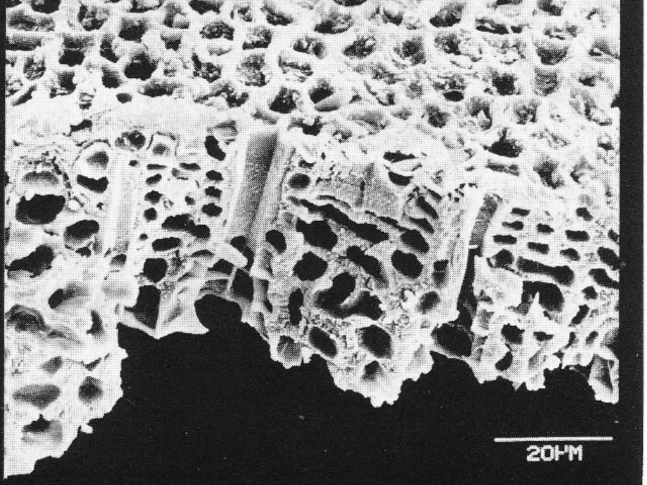

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responds to *Lithothamnium solutum* (=*Lithophyllum solutum*); this variety has thicker branches (up to 1.8 mm in diameter) with a clear zonation and thrives on coarse detritic bottoms (Cabioch, 1969, 1970).

Cabioch (1966) proposed to distinguish six forms of the var. *corallioides* (forma *subsimplex*, *subvalida*, *australis*, *corallioides*, *flabelligera*, *globosa*) on the basis of the shape of the rhodolith and its branching density, induced by the environmental conditions. The disadvantages deriving from this complicate nomenclatural framework discourage its use and suggest to adopt a morphological classification (Bosence, 1976, 1983; Woelkerling & Irvine, 1986).

Geographical distribution and ecology. The species is distributed along the Atlantic and Mediterranean coasts and northward to Norway. It is found also in the north-eastern Pacific (Bressan, 1974).

Living and dead branched specimens growing *in situ* can form the algal bank called maërl (Hamel & Lemoine, 1952; Cabioch, 1969). The growth rate of the species has been measured during an *in situ* experiment for one year, in the Bay of Brest (Atlantic coast of western Brittany, France): the calcium carbonate accretion rate has been estimated of 876 g m^{-2} $year^{-1}$, with the highest daily growth rate observed in July (Potin et al., 1990).

In the Tuscan Archipelago and Pontian Islands the species was found living in 10 stations at depth ranging from 44 to 93 m (Tab. 1); 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. *L. corallioides* is very abundant in the maërl of Marettimo (Egads, Sicily), at 33-35 m depth.

Stratigraphical distribution. The species is recorded for marine sediments older than 14 ka (Late Pleistocene), recovered off the Pontian Islands (Corselli et al., 1994). *Lithophyllum solutum* was recorded in the warm stages with *Strombus* (Tyrrhenian) of the Pleistocene of Taranto (Lemoine, 1919).

Lithothamnion minervae sp. nov.

Pl. 3, 4; Tab. 3

Lithothamnion fruticulosum auct. non *Spongites fruticulosa* Kützing 1841:

Lemoine, *Bull. Soc. Géol. France*, s. 4, v. 19, p. 104, fig. 3, 4; pl. 3, fig. 5, 8, 9. 1919.

Hamel & Lemoine, *Arch. Mus. Nat. Hist. Nat.*, s. 7, v. 1, p. 87, fig. 48. 1952.

Bressan, *Boll. Soc. Adriat. Sc. Nat.*, v. 59, n. 2, p. 68, fig. 16, 17. 1974.

Fravega & Vannucci, Atti 3 Symp. Ecol. Paleoecol. comunità bentoniche, p. 720. 1989.

External appearance. The thallus is crustose to branched, growing unattached or encrusting pebbles or biogenic remains. The species frequently forms rhodoliths 2-4 cm in diameter (Pl. 3, fig. 1), or occurs in multispecific larger rhodoliths. Branches are simple, more or less dense, with a diameter ranging from 1 to 3 mm and length up to 5 mm. Fertile (asexual) thalli are very frequent. Groups of asexual conceptacles are frequent, commonly occurring at the branch tips.

Microscopic anatomy. The hypothallus is formed of few (frequently three) layers of rectangular cells and is 40-50 µm thick. Its cells bend outward to form the multilayered perithallus of oval to rectangular cells (Pl. 3, fig. 2, 3). New hypothallus frequently occurs in the branches over some damaged surfaces.

The perithallus is zoned. Short, thick-walled cells pass abruptly to long, thin-walled cells. The transition to the next layer of short, thick-walled cells is gradual (Pl. 3, fig. 5). Large cell fusions (*sensu* Harvey et al., 1994) are numerous both in the hypothallus and in the perithallus (Pl. 3, fig. 2, 3).

The epithallus is made of two to three layers of ovoid to elliptical cells (L.S.) dividing outward from the intercalary meristeme. Cell fusions have not been observed in the surface layer of the epithallus (Pl. 3, fig. 6; Pl. 4, fig. 1, 2). In L.S. of branches several buried empty conceptacles can be observed. The perithallus overgrows the roof of empty conceptacles, leaving commonly some irregular cavities appearing approximately triangular in L.S. This feature is very characteristic and easy detectable under OM. The asexual conceptacles are prominent, with subcircular to elliptical outline in surface view, appearing rectangular to elliptical in L.S. of branches (Pl. 4, fig. 3-5). The formation of bundles of calcitic

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PLATE 3

Lithothamnion minervae sp. nov. MPUM no. 7513, holotype. Pontian Islands, dredge sample min89edg02, 73-78 m.

Fig. 1 - Dense branching of a spheric rhodolith. Scale bar = 1 cm.

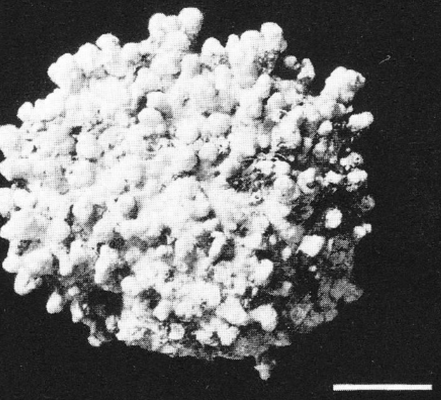
Fig. 2 - Rectangular cells of the hypothallus in surface view. SEM photograph, stub 121294b4.

Fig. 3 - SEM detail of fig. 2. Note cell fusions in the hypothallial cells.

Fig. 4 - SEM photograph of a L.S. of a branch. Note the irregular growth style and the zonation in the perithallus. Stub 121294b4.

Fig. 5 - SEM detail of the transition from the hypothallus to thick-walled perithallial cells and the abrupt transition from the latter to thin-walled perithallial cells with large lumina. Note the large cell fusions have almost the same size of the smallest cell lumina. Stub 121294b4.

Fig. 6 - SEM detail of the long-celled meristeme underlying two to three cell layers of the epithallus. Note the abrupt transition to the thick-walled cells of the inward band. Stub 121294b4.



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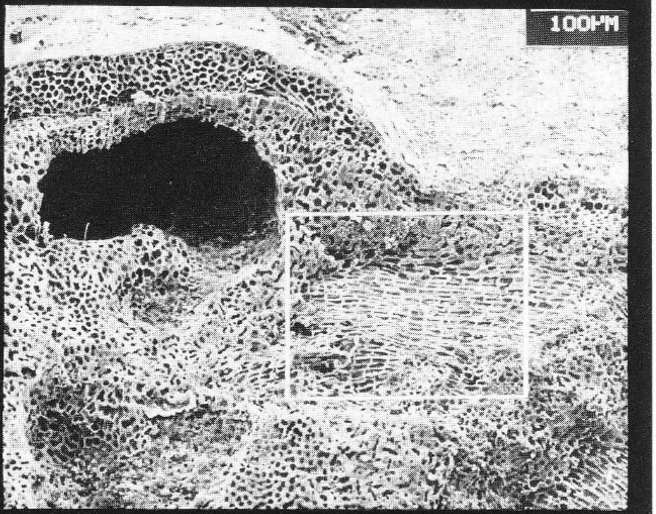

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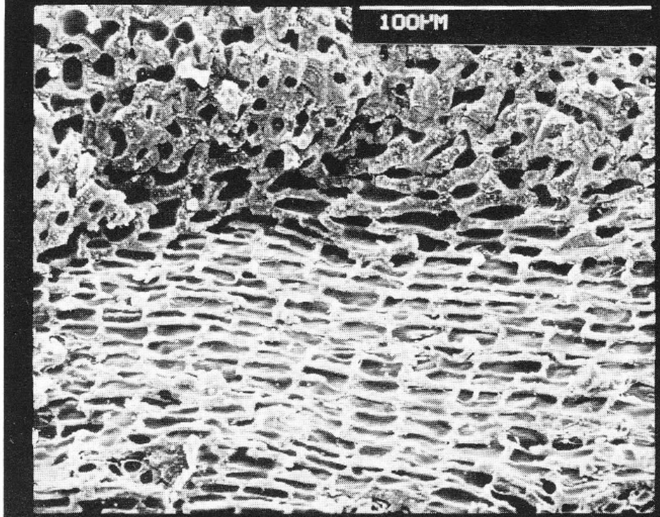

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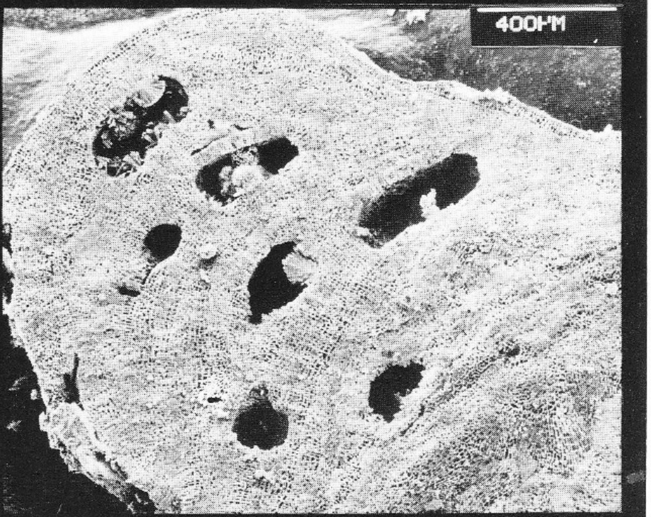

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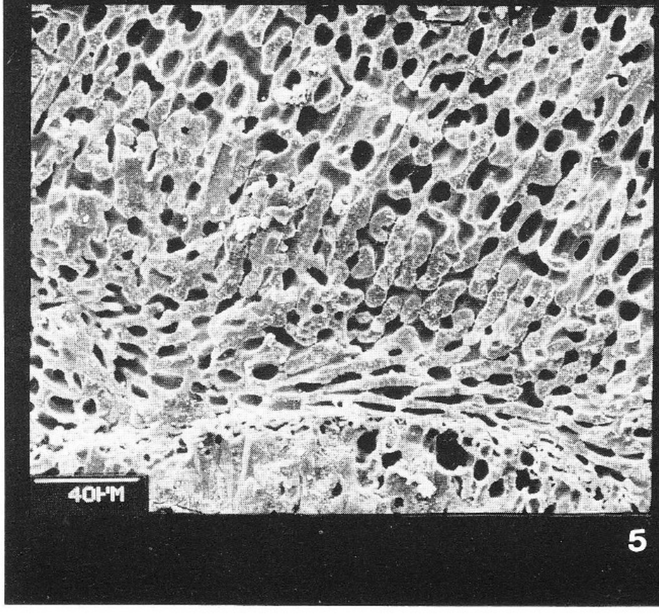

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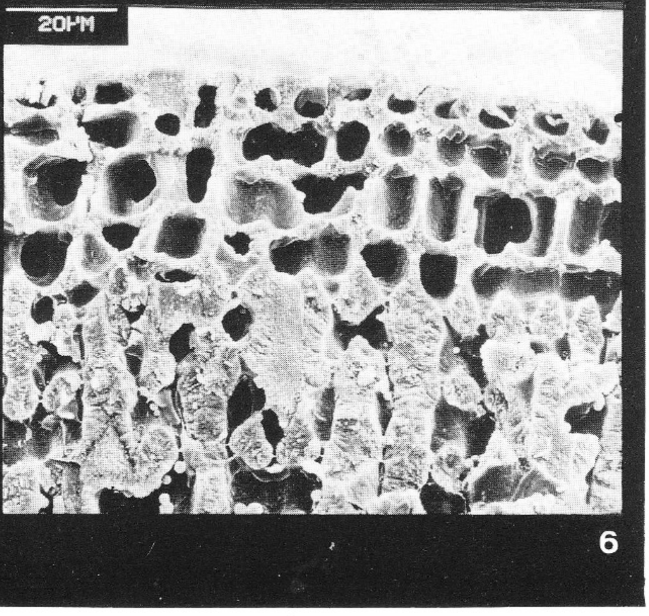

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crystals inside many empty conceptacles is allowed by the opening of the conceptacle to the external environment after the loss of the pore plugs and the release of the spores. The precipitation has been observed in both living and dead specimens, occurring more frequently inside buried conceptacles. The neo-formation of perithallus inside the old conceptacles is very rare (Pl. 4, fig. 4). The roof of the asexual conceptacles is made of 7-9 layers of elliptical to platy cells, becoming shorter (from 9 to 3.5 µm long) toward the external surface of the roof (Pl. 4, fig. 6).

Discussion. In analogy with the observations on *P. calcareum* (Basso, 1995), it would be possible to correlate the zonation of the perithallus, especially evident in branches, with periodic regular changes in the environmental conditions, probably related to the yearly cycle of seasons. One band of short cells and one band of long cells together might represent the yearly growth of the thallus, with the abrupt passage to thin-walled long cells representing the reappraisal of the growth after the winter quiescence (Pl. 3, fig. 4-6).

The holotype of *Spongites fruticulosa* Kützing (1841), on which *Lithothamnion fruticulosum* is based, has been revised by Woelkerling (1985b). On the basis of the occurrence of uniporate tetrasporangial conceptacles and cell fusions, *Spongites fruticulosa* (whose correct name is *Spongites fruticulosus*; ICBN 1994, art. 62.4; Penrose, 1991) became the type species of the reassessed genus *Spongites* (Woelkerling, 1985b, 1988). Therefore the name *Lithothamnion fruticulosum* (Kützing) Foslie was listed under synonymy of *Spongites fruticulosus* (Penrose, 1991), the type species of a different genus, and the correct name for the taxon to which Kützing's name has been misapplied had to be determined.

The occurrence of multiporate conceptacles in the Mediterranean specimens attributed to *Lithothamnion fruticulosum* by several Authors (Hamel & Lemoine, 1952; Bressan, 1974; Fravega & Vannucci, 1989) has been indirectly questioned by Penrose (1991). She noted that during the development of the uniporate tetrasporangial conceptacles of *S. fruticulosus* the pore is occluded by a "sieve-plug" of protecting material which, under low magnification and in surface view can be erroneously interpreted as multiporate. Moreover, it is known that old multiporate conceptacles can undergo the crashing of their roof, thus appearing uniporate. In consideration of these ambiguities, also due to the poor available illustrations of *L. fruticulosum* auctorum, it was possible to doubt the true identity of this species. Therefore a redefinition of the Mediterranean species commonly recognized as *L. fruticulosum* and of its relationship with the other Mediterranean species of *Lithothamnion* was needed.

The results of the biometric analyses (Tab. 3) and the OM and SEM observations reported above allow to place *L. fruticulosum* auctorum in the genus *Lithothamnion* and to conserve it as a separate species.

The research of a new specific epithet has been conducted at a first step by checking whether some of the synonyms of *L. fruticulosum* were suitable and available. The species *Melobesia fruticulosa* (Kützing) Decaisne 1842, *L. fasciculatum* β *fruticulosum* (Kützing) Hauck 1883, and *Paraspora fruticulosa* (Kützing) Heydrich 1900 are listed in the synonymy of *Spongites fruticulosus* Kützing 1841 by Penrose, 1991; therefore these names are not available.

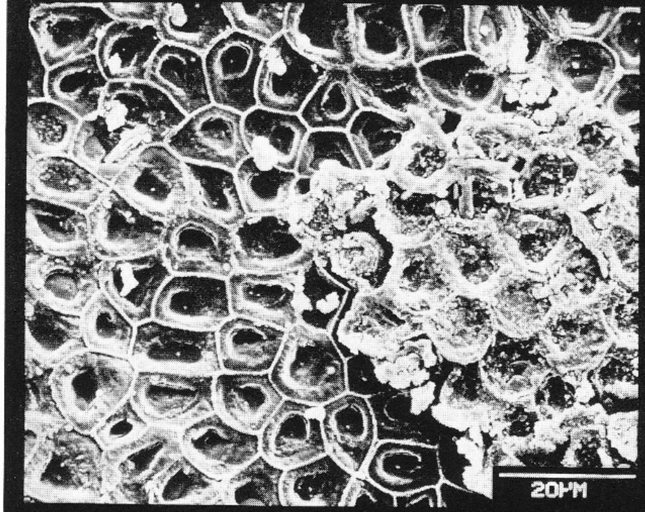
The species *Lithothamnion meneghinianum* Vinassa 1892 was considered conspecific with *L. fruticulosum* (Hamel & Lemoine, 1952; Bressan, 1974 under the name *L. meneghianum*, probably a mistake in transcription). Vinassa's original collection, once conserved at the Geological Institute of the Pisa University, has been lost (L. Ragaini, 1994, pers. commun.). The original description does not allow to identify even the genus and no illustration is given. Moreover, the species *L. fasciculatum* (Lamarck) Aresch var. *fruticulosum* is indicated in the protologue to be strictly related to *L. meneghinianum*. Therefore the use of this name would cause considerable taxonomical confusion. Since no available synonyms exist, *L. minervae* sp. nov. has been choosen to identify the Mediterranean species to which the name *L. fruticulosum* (Kützing) Foslie has been widely misapplied.

Diagnosis. *Lithothamnion incrustans arctissime adnatum, lapides cochleasque involvens, fronde ramosa, ra-*

PLATE 4

Lithothamnion minervae sp. nov.. MPUM no. 7513, holotype. Pontian Islands, dredge sample min89edg02.

Fig. 1 - Epithallus in surface view. SEM photograph, stub 121294b4.
Fig. 2 - Epithallus in L.S. Note the flared shape of the epithallial cell walls. SEM photograph, stub 121294b4.
Fig. 3 - Thallus structure and multiporic conceptacle shape. Note the triangular outline (L.S.) of the cavity left by the reappraisal of the vegetative growth over the conceptacle roof. Thin section DB 125, sample min88abe012a, Elba Is. (Tuscan Archipelago). OM photograph. Scale bar = 100 µm. MPUM no. 7514.
Fig. 4 - Thallus structure and multiporic buried conceptacles. Note zonation of the perithallus and the triangular cavity over one buried conceptacle. Bundles of calcitic crystals developed inside the empty conceptacles after the spore release. Note the uncommon neo-formation of perithallus inside a buried conceptacle (arrow). SEM photograph, stub 121294b4.
Fig. 5 - Detail of a buried conceptacle and its roof structure. SEM photograph, stub 121294b4.
Fig. 6 - Detail of fig. 5, the pores cross the roof. Note the short cells lining the pores.



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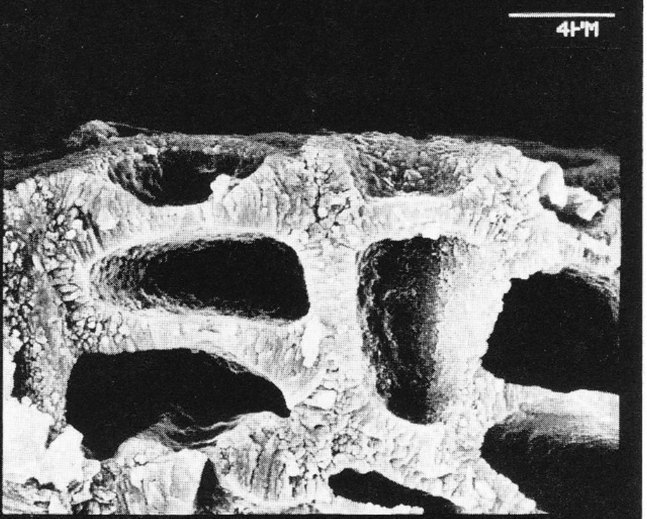

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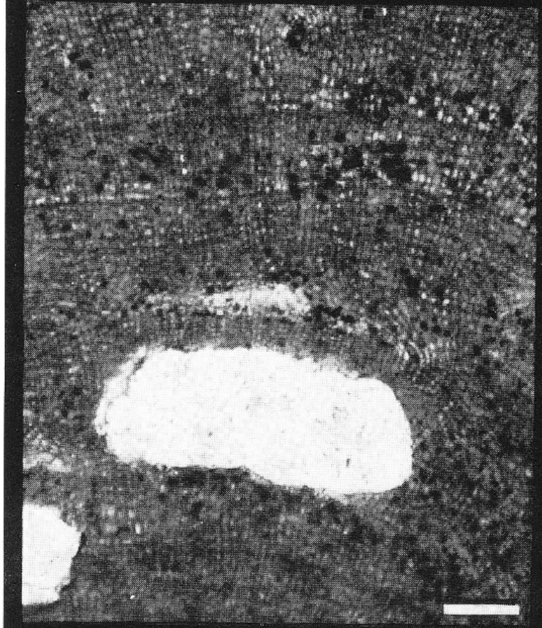

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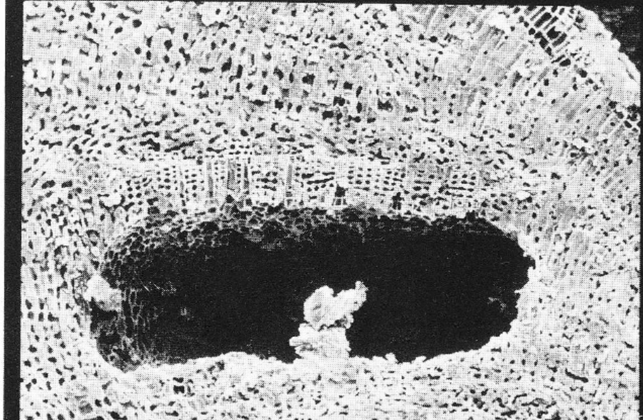

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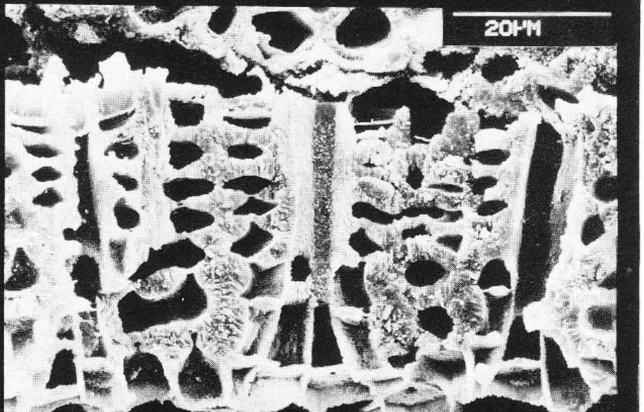

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L. minervae		n	mean	(s.d.)	mode		min	max
Hypothallial cells	L	433	19	(0.21)	18.75		13	25
	H	433	8	(0.07)	6.25		6	11
Perithallial cells	L	446	15	(0.17)	16.25		10	20
	D	446	8	(0.07)	8.75		5	11
Perithallial cells	L	470	16.5	(0.15)	15.5	18	13	24
(branches)	D	470	9	(0.04)	10	10	6	12
Epithallial cells	L	44	6	(0.46)	4.5		3.5	8
	D	44	10	(0.52)	8		7	13
Asexual	D	242	327	(8.32)	320		235	530
conceptacles	H	242	163	(4.22)	150		117	222
outside diameter	od	98	537	(20.5)	545		455	612
Roof thickness	rt	95	45	(2.27)	40		31	65
cell layers in roof		70	7	(0.19)	7		6	10

Tab. 3 - Sizes of the diagnostic microscopic features of *L. minervae*. In the column "mode", the small and large cells alternating in the perithallial cells of branches have been shown separately.

mis simplicibus, 1-3 mm latis, 1-5 mm elongatis. Conceptacula elevata, suae dimetientis (235-530 μm) circiter dimidiam partem alta, saepe praebentia aliquod triquetrum intervallum inter tectum atque thallum super eum inductum (ex caesura in longitudinem ramorum). Typus (MPUM 7513) ex Pontiis (Mare Mediterraneo) proveniens.

Thallus crustose to branched, tightly overgrowing on pebbles or biogenic remains. Branches simple, seldom dichotomous, 1-3 mm in diameter, up to 5 mm long. Anatomical characters as for genus. Differing from the other Mediterranean species of *Lithothamnion* in developing short, simple branches with abundant asexual conceptacles, inner diameter 235-530 μm, D/H≅2, elliptical in L.S. of branches, frequently with a triangular void left between their roof and the overgrowing thallus.

Derivatio nominis. The specific epithet honours the oceanographic activity of the R/V Minerva (CNR).

Holotype. The holotype (MPUM no. 7513; Pl. 3, fig. 1-6; Pl. 4, fig. 1, 2, 4-6) has been collected in the Pontian Islands (sample min89edg002, Tyrrhenian Sea, Western Mediterranean) and is conserved at the Paleontological Museum of the Dept. of Earth Sciences, University of Milan.

Geographical distribution and ecology. Following Bressan (1974), the species is distributed along the Atlantic and Mediterranean coasts of Europe. The species commonly occurs in the circalittoral coastal detritic bottoms (DC; Pérès & Picard, 1964), also together with the "maërl" species *Phymatolithon calcareum* and *L. corallioides*. A facies of the DC characterized by abundant rhodoliths of *L. fruticulosum* (= *L. minervae* sp. nov.), sometimes accompanied by the current-loving echinoid *Spatangus purpureus*, has been also described. Bottom currents seem to foster its presence (Pérès & Picard, 1964; Pérès, 1982). In the surveyed area the species is very common and has been recognized in 23 stations ranging in depth from 27 to 98 m (Tab. 1).

Stratigraphical distribution. The species has been recorded in the Pleistocene of Capo Milazzo and Ficarazzi (Sicily) (Lemoine, 1919) and has been found in the bottom sediments of the Mediterranean Sea older than 14 ka (Late Pleistocene) (Corselli et al., 1994).

Lithothamnion philippii Foslie 1898

Pl. 5; Tab. 4

1898 *Lithothamnion philippii* Foslie, p. 7 (*fide* Hamel & Lemoine, 1952).

1952 *Lithothamnium philippii* - Hamel & Lemoine, p. 83, fig. 44, pl. 14, fig. 7.

1974 *Lithothamnium philippii* - Bressan, p. 70, fig. 43.

External appearance. Crustose thalli, frequently thin (240 to 530 μm) and superposed, non branched. Short and irregular protuberances occasionally occur. The thallus frequently wraps up the substrate, which can be a soft bodied organism leaving an empty cavity after decay: a mass of sponge spicules has been observed inside some flat rhodoliths (Pl. 5, fig. 1). The large sized

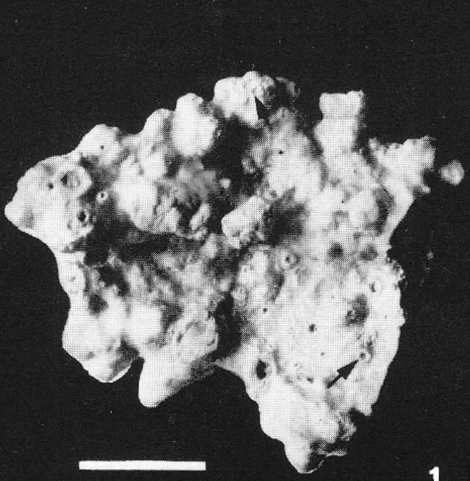
L. philippii		n	mean	(s.d.)	mode	min	max
Hypothallial cells	L	25	17.8	(5.36)	18	10	25
	H	25	11.3	(1.63)	12	6	15
Perithallial cells	L	25	11.6	(2.06)	12.5	5	18
	D	25	9.5	(1.55)	8	7.5	14
Epithallial cells	L	10	5.9	(0.44)	6.2	3.8	7
	D	10	9.69	(1.82)	10.7	6	13
Asexual	D	5	512	(186)	687	400	890
conceptacles	H	5	191	(19.23)	200	160	210
Roof thickness	rt	5	58.2	(1.5)	58.5	56	60

Tab. 4 - Sizes of the diagnostic microscopic features of *L. philippii*.

PLATE 5

Lithothamnion philippii Foslie 1898. Pontian Islands, dredge sample min89edg02.

Fig. 1	- A platy rhodolith. Note short protuberances and large conceptacles visible on the surface of the thallus (arrow). Scale bar = 1 cm.
Fig. 2	- A L.S. of a thin crust. SEM photograph, stub 020692b2.
Fig. 3	- A thallus overgrowing an old one. Note the cell fusions and the thickness of the cell walls. SEM, stub 020692b2.
Fig. 4	- Same as fig. 3. Detail of the perithallus, the thin-walled, large-celled meristem and the epithallus.
Fig. 5	- Asexual conceptacles in superficial view. SEM, stub 020692b4.
Fig. 6	- A senescent conceptacle is going to be buried by the new perithallus, with the formation of an annulate thickening. SEM, stub 020692b3.



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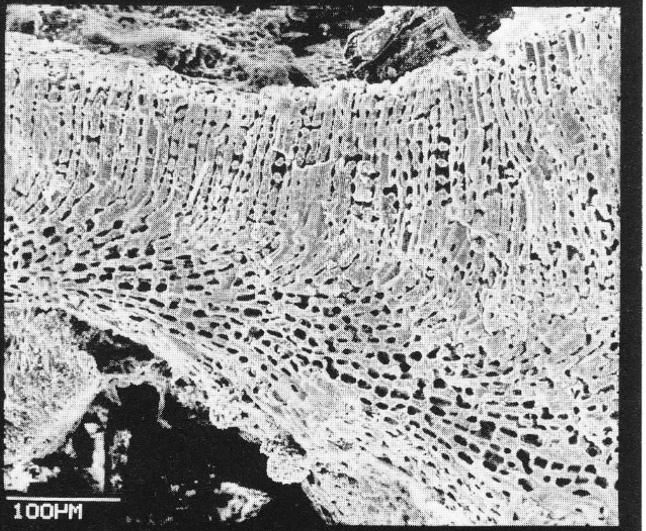

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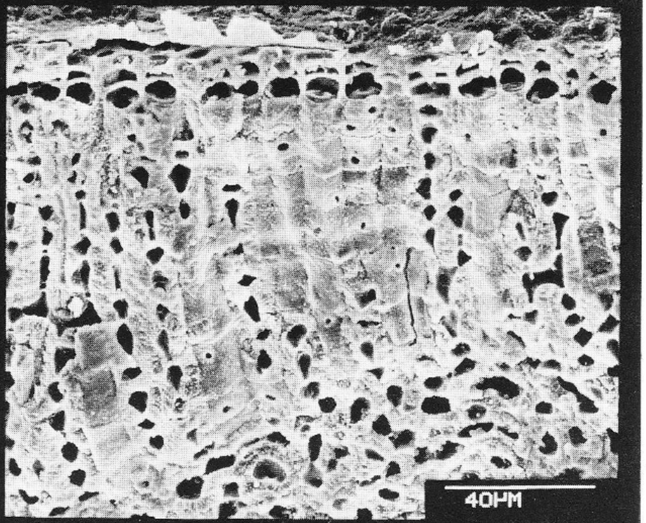

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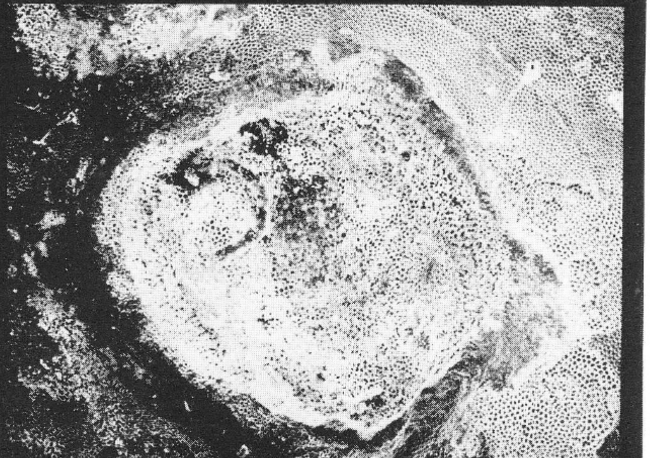

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asexual conceptacles are clearly visible as weakly risen, crater-like structures on the surface of fertile specimens.

Microscopic anatomy. The hypothallus is multilayered, well developed (thickness can exceed 100 μm), made of rectangular to ovoid cells (Pl. 5, fig. 2, 3). The multilayered perithallus is made of rectangular cells with thick walls. Cell fusions have been observed in both hypothallial and perithallial cells. The actively dividing, thin walled cells of the meristem produce shorter inward derivatives and squat, flared epithallial cells outward (Pl. 5, fig. 4).

Asexual conceptacles in superficial view (SEM) are circular to elliptical, weakly convex and pierced by about seventy pores (Pl. 5, fig. 5). An annulate thickening (ring) is more or less apparent at their periphery depending on the degree of development of the perithallus which is going to overgrow the conceptacle (Pl. 5, fig. 6). Observed external diameters range from 570 to 900 μm ("ring" included). The conceptacles appear irregularly rectangular in L.S.

Discussion. The recognition of this species has been based on Hamel & Lemoine (1952) and Bressan (1974) and therefore on the large size of the asexual conceptacles and the perithallial cells. Foslie's protologue is neither adequate nor sufficient for a modern definition of the species and does not contain the designation of the type. Foslie selected the type collection later (1900) from samples collected by A. Vickers in Naples (Woelkerling, 1993). Pictures of this collection appeared in two publications (Foslie, 1905; Printz, 1929). In the posthumous paper (Printz, 1929), four growth forms of *L. philippii* are illustrated: *typica*, *subdura*, *crispata* and *alternans*. *L. philippii* f. *alternans* has been considered conspecific with *Mesophyllum lichenoides* by Hamel & Lemoine (1952) on the basis of the coaxial hypothallus.

The only specimen of *L. philippii* f. *typica* appearing in both 1905 and 1929 Foslie's papers was studied by Adey (1970) during a revision of the Foslie's herbarium and selected as lectotype. Also this specimen showed a coaxial hypothallus, therefore inducing Adey to create the new combination *Mesophyllum philippii*. *M. philippii* Adey has been considered as a more recent synonym of *M. lichenoides* (Basso, 1995).

After a new revision of the Foslie's herbarium, Woelkerling (1993) rejected the validity of Adey's choice of the lectotype and selected some different specimens which became part of the Foslie's collection (coming from the Zoological Station at Naples) in 1895, therefore predating the Vickers collection. A detailed study of these newly selected types will hopefully clarify the definition of *L. philippii* Foslie.

Geographical distribution and ecology. Atlantic-Mediterranean (Bressan, 1974). In the Tuscan Archipelago and Pontian Islands the species has been collected from 45 down to 79 m depth.

Stratigraphical distribution. *L. philippii* has been recorded in the Pleistocene of Crotone (Lemoine, 1919).

Lithothamnion valens Foslie 1909

Pl. 6, 7; Tab. 5

1909 *Lithothamnion valens* Foslie, p. 3 (*fide* Lemoine, 1939).
1939 *Lithothamnion valens* - Lemoine, p. 341, fig. 2.
1952 *Lithothamnion valens* - Hamel & Lemoine, p. 97, fig. 62, pl. 20, fig. 5,6.
1974 *Lithothamnion valens* - Bressan, p. 76, fig. 15.

External appearance. Branched thalli growing unattached. The rhodoliths are frequently 1 to 3 cm in diameter but exceptionally large rhodoliths can reach more than 10 cm in diameter. Each rhodolith is made of stout branches more or less nodose, 4-10 mm in diameter, from few mm up to 6 cm long, coalescing at the base in groups of 4 to 5. Each group of branches is joint to the others at the core of the rhodolith (Pl. 6, fig. 1). The rhodolith of *L. valens* develops from a basal crust which frequently envelops some sediment. In one case a thallus was observed growing on a branching zoarium of a dead bryozoan colony (?*Myriapora truncata*).

Microscopic anatomy. The hypothallus is multilayered and non-coaxial, up to 100 μm thick. The perithallus can prostrate over some damaged portions of the thallus producing a new hypothallus inside the perithallus of a branch (Pl. 6, fig. 2, 3).

The perithallus is multilayered and zoned (Pl. 6, fig. 4). The medial L.S. of a branch shows a regular alternation of zones made of thin-walled rectangular cells (L 16-25 μm, wall thickness of 1-2 μm) separated by denser bands made of thick-walled cells (L 7-15, wall thickness of about 6 μm) with ovoid lumen (Pl. 6, fig. 5). Each band with thick-walled cells is repeated every 90-150 μm (rarely 30 μm), following the seasonal reduction of growth rate. The transition from thin-walled cells to thick-walled cells is gradual, whilst the transition to the following thin-walled cells is abrupt (Pl. 6, fig. 5, 6). Cell fusions are present both in the hypothallus and in the perithallus. Perithallial cell fusions are

L. valens		n	mean	(s.d.)	mode		min	max
Hypothallial cells	L	25	18	(4.19)	19		11	26
	H	25	8.2	(1.71)	7		5	11
Perithallial cells	L	70	15.6	(4.1)	13.5	16.6	7	25
	D	70	9.2	(1.77)	8.3	7.5	6	12
Epithallial cells	L	10	2.7	(0.16)	2.7		2.5	3
	D	10	8	(0.53)	8.7		7.5	9
Asexual	D	13	418	(186)	320		265	1000
conceptacles	H	13	169	(29.41)	130		100	210
Roof thickness	rt	4	52	(4.96)	54		45	56

Tab. 5 - Sizes of the diagnostic microscopic features of *L. valens*. In the column "mode", the small and large cells alternating in the perithallial cells of branches have been shown separately.

frequent and sometimes multiple (Pl. 7, fig. 1). Cell fusions are large (*sensu* Harvey et al., 1994) both in the thin walled and thick walled cells. The epithallus is made of 1-3 layers of flattened cells, the most superficial layer appearing "flared" (Pl. 7, fig. 2).

Most specimens are sterile, but the rare fertile thalli produce several asexual conceptacles, often grouped at the side of branches. Asexual conceptacles are multiporate, convex, subcircular to elliptical in surface view (Pl. 7, fig. 3-5). Their roof is opened by 20-30 pores. The empty conceptacle remains buried in the thallus and its cavity, elliptical to rectangular in L.S. of branches (Pl. 7, fig. 6), can be filled by calcitic crystals.

Discussion. As already suggested for *L. minervae* sp. nov., the yearly growth might correspond to a thin-walled band plus a thick-walled band. This assumption supports the hypothesis that thick-walled cells form during the winter and that the yearly growth stops before the spring resumption characterized by the thin-walled cells. Analogous observations have been reported for the calcitic thallus of *P. calcareum* (Basso, 1995).

The holotype of *L. valens* is made of three fragments and three slides, conserved at TRH. The type locality is not indicated and the container has the inscription "*Lithoth. crassum* Phil Adria" (Woelkerling, 1993). The slides, probably the same as mentioned by Lemoine (1939), do not show the diagnostic elements for a sure attribution to the genus (Adey, 1970). However, Lemoine had the opportunity to compare her material to a fertile type from Foslie's collection. This type was once conserved in the Museum of Trondheim and showed some convex, oval to subcircular sporangial conceptacles with diameter 300-600 µm in superficial view and many other details of the thallus, therefore allowing an unequivocal definition of the species (Lemoine, 1939). Therefore it is likely that Lemoine's description applies to a specimen that probably disappeared, and could not be revised later by Adey (1970) and Woelkerling (1993). Anyhow, Lemoine's concept of *L. valens* results to be based on the study of the relevant type material.

It is worth to mention that the revision of the type material of *L. crassum* Philippi, coming from the Mediterranean, allowed to place the species among the Lithophylloideae under the combination *Lithophyllum duckeri* Woelkerling. *L. duckeri* Woelkerling is conspecific with the Mediterranean endemic species *Pseudolithophyllum racemus* (Lamarck) Mendoza & Cabioch (Basso et al., in press). However, unattached sterile thalli of *P. racemus* and *L. valens* may have a very similar macroscopic appearance (Bressan, 1974) and it is possible that they have been confounded by early Authors. This could explain the script on the container of the holotype of *L. valens* Foslie.

Geographical distribution and ecology. The species is known only from the Mediterranean. In the study area it has been found in 9 stations ranging in depth from 51 to 79 m and in the maërl of Marettimo. The maximum abundance has been recovered in the channel between the Islands of Ponza and Palmarola, in the Pontian Archipelago. On the basis of the sedimentological characteristics of the stations where it was recovered, frequently together with a calcified peyssonneliacean (Basso, 1990), *L. valens* seems to prefer sandy and gravelly bottoms with little amount of mud in presence of bottom currents (SGCF and DC biocoenoses; Pérès & Picard, 1964).

PLATE 6

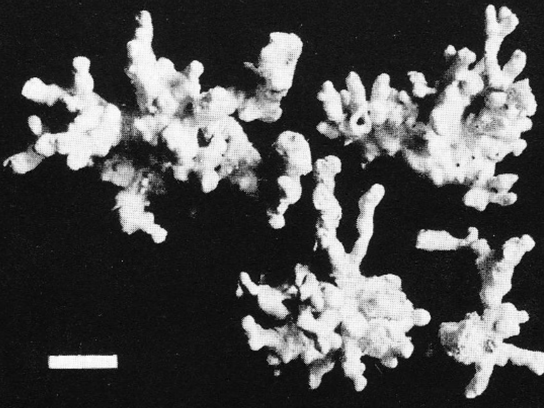
Lithothamnion valens Foslie 1909.

Fig. 1 - Exceptionally large, branched rhodoliths recovered at station min89edg02, Pontian Islands. Scale bar = 2 cm.
Fig. 2 - L.S. of a branch. A new hypothallus overgrows a damaged portion of the old thallus. Note the marked zonation of the perithallus. SEM photograph, stub 281191b1.
Fig. 3 - Detail of the hypothallus in fig. 2.
Fig. 4 - Zonation of the perithallus in a L.S. of a branch. Thin section DB180, OM photograph, scale bar = 200 µm. Station min89ebe044, Pontian Islands.
Fig. 5 - Detail of the abrupt transition from the thick-walled cells to the thin-walled cells in different bands of the zonate perithallus. SEM, stub 281191b1.
Fig. 6 - Detail of fig. 5. Note the different size of the cell fusions in the two types of perithallial cells. Large, thin-walled cells develop after the winter quiescence.

PLATE 7

Lithothamnion valens Foslie 1909.

Fig. 1 - Multiple cell fusions in the perithallus. SEM, stub 281191b1. Station min89edg02, Pontian Islands.
Fig. 2 - Flattened and eared epithallial cells. SEM, stub 281191b1.
Fig. 3 - Asexual multiporic conceptacles at the surface of a branch. SEM, stub 020692b11. Station min89edg02, Pontian Islands.
Fig. 4 - Detail of fig. 3.
Fig. 5 - Crater-like, senescent conceptacles. SEM, stub 020692. Station min89edg02, Pontian Islands.
Fig. 6 - An empty, buried conceptacle. Note its risen shape. Thin section DB180, OM photograph, scale bar = 100 µm. Station min89ebe044, Pontian Islands.



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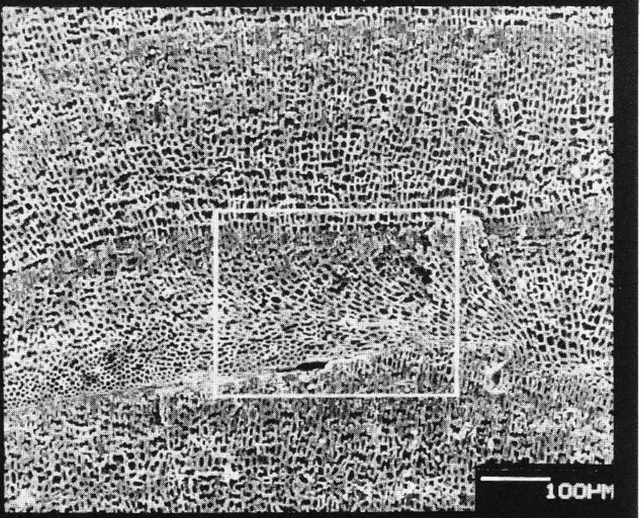

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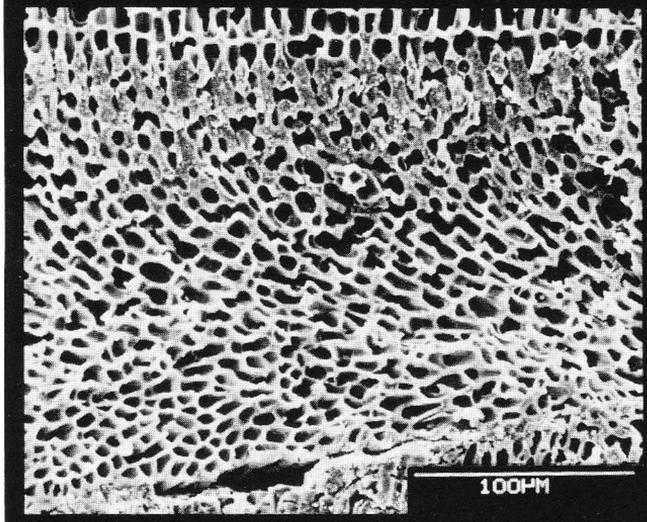

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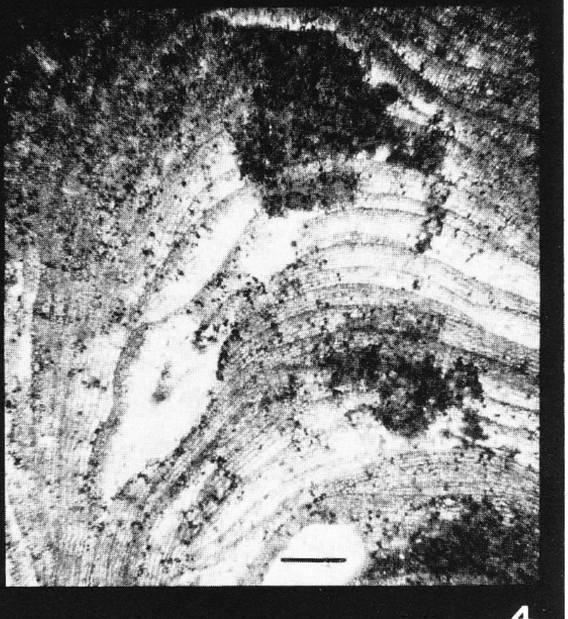

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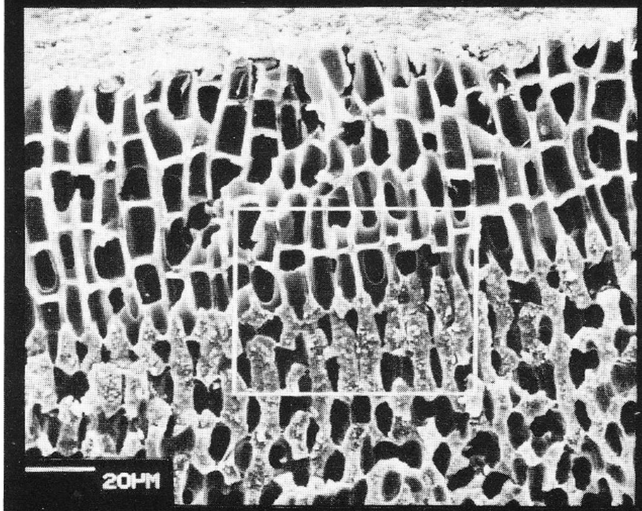

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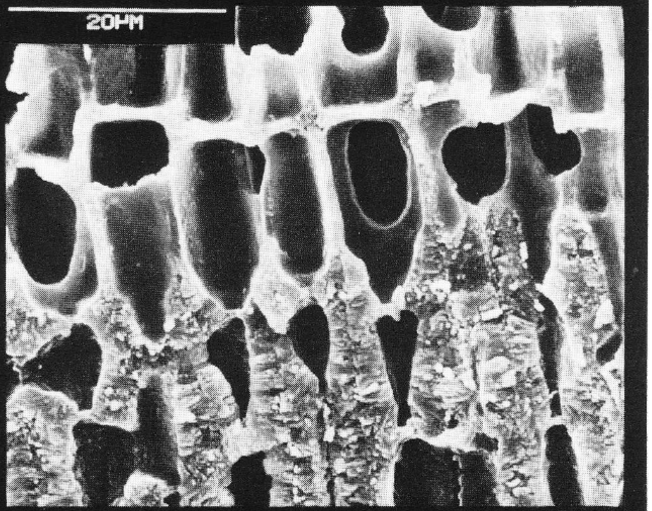

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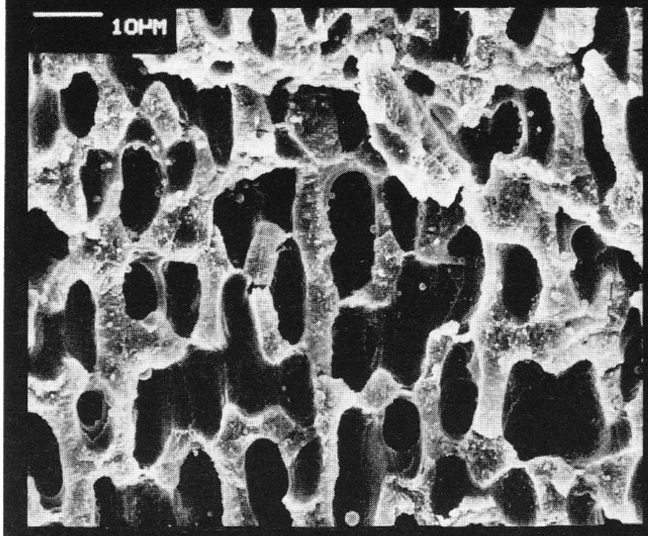

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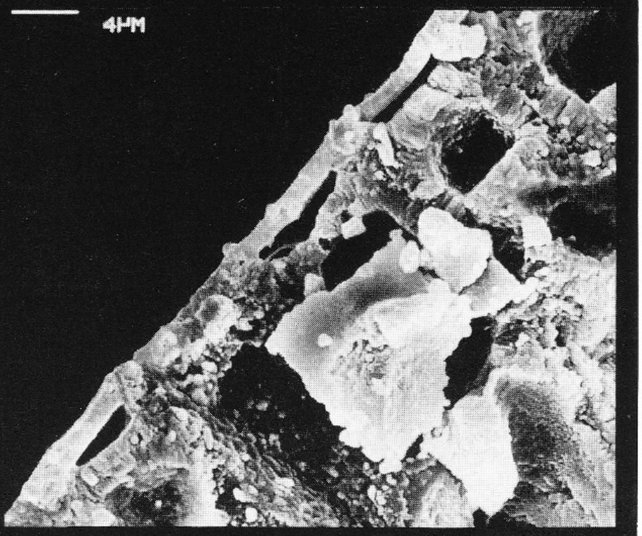

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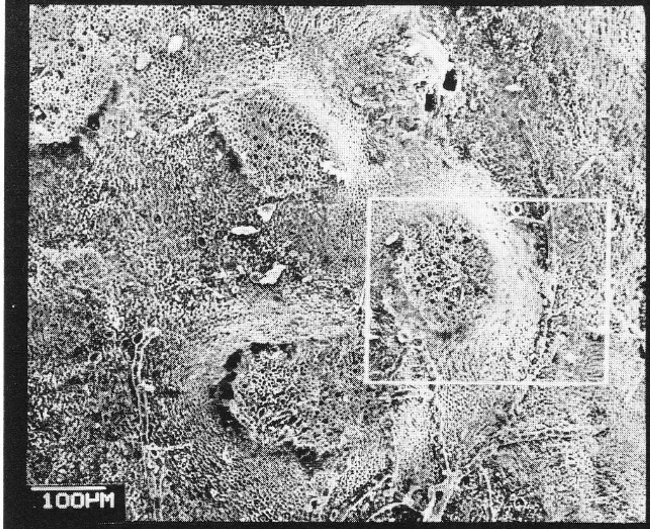

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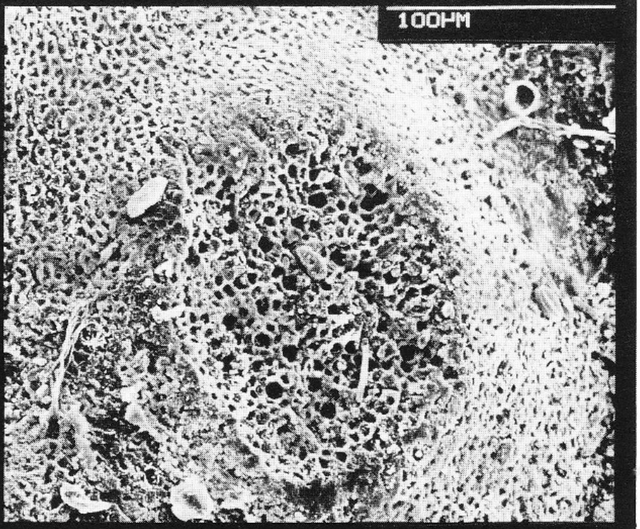

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Augier (1982) reports the occurrence of *L. valens* in association with the pelecypod *Chlamys commutata* in the Balearic Archipelago and along the coasts of Corse (France). This association has not been observed in the studied area. However, a new species of chiton (*Callochiton calcatus* Dell'Angelo & Palazzi, 1994) has been recovered together with the maximum abundance of *L. valens*. *C. calcatus* has been found also on the maërl bottoms of the Balearic Archipelago (Dell'Angelo & Palazzi, 1994), in Sicily and Elba Island. Since chitons are known to feed on calcareous algae, and since the most abundant calcareous alga in the sample was *L. valens*, this species might be preferably grazed by *C. calcatus*.

Stratigraphical distribution. The species is not known in the fossil record.

Conclusions.

On the basis of the information in this paper and in Basso (1995) a key is presented here for the identification of Mediterranean soft bottom Melobesioideae based on the characters observable on calcareous thalli, under OM (thin sections) and SEM. The genus *Melobesia*, encompassing very thin thalli with a unistratose hypothallus, is not considered.

L. minervae sp. nov. is described on the basis of newly collected material which corresponds to the species misidentified by some authors (among others: Lemoine, 1919; Hamel & Lemoine, 1952; Bressan, 1974) with the name *L. fruticulosum*, based on *Spongites fruticulosus* Kützing (the type species of *Spongites*).

A detailed description and illustration of the microscopical anatomy of *L. valens* and *L. philippii* is given for the first time.

Cell and conceptacle sizes are extensively used as diagnostic features, however, since evidence is given that the range of variability of each diagnostic feature is very wide (Tab. 2-5; Basso, 1995), they result to be not sufficient, though important, for species identification. Such numerical characters must be always based on many observations repeated on several specimens and should be accompanied by an accurate observation of the anatomical structure of the thallus. In particular, the shape and structure of the conceptacles are confirmed to be important diagnostic characters at species level.

The buried conceptacles of living thalli do not contain any trace of the original content. On the contrary, a very early diagenetic alteration, testified by the formation of bundles of crystals inside buried conceptacles, frequently occurs during the life of the thallus.

The zonation observed in the perithallus of most species of *Lithothamnion* results to be due to a variation of the thickness of the calcitic cell wall, associated to a change in shape and a reduction in size of the cell lumen. Under controlled experimental conditions, the growth zones (*anneaux de croissance*) observed in some species of *Fosliella* have been also explained with a variation in the thickness of the cell wall (Bressan & Tomini, 1981), probably depending on the rate of photosynthetic activity (Ikemori, 1970). However, the hypothesis concerning the correspondence of the observed growth zones to defined seasons needs further confirmation.

Identification key.

Asexual conceptacles multiporate, cell fusions present (secondary pit connections absent) (MELOBESIOIDEAE).

1. Hypothallus multistratose, predominantly coaxial.
Mesophyllum lichenoides

2. Hypothallus multistratose, non-coaxial.

α Terminal epithallial cells roundish or flat but not flared, progressive elongation of the subepithallial meristem inward derivatives. Conceptacles oval in outline (L.S.), with a very thin space (a white line in thin sections) marking the depression of the roof. Perithallial cells in branches hardly detectable under low magnification (thin sections, OM).
Phymatholithon calcareum

β Terminal epithallial cells flat and flared, with meristem cells longer than the cells below. Conceptacles oval to subrectangular in outline (L.S.), more or less prominent *(Lithothamnion)*.

a. Mainly branched (several orders of branching) thalli with rare, squarish conceptacles; perithallus zonate; medulla of branches mostly composed of long, thin-walled rectangular cells, easily detectable under low magnification (OM; D10 x L 21 μm) and a distinct cortex made of small cells.
Lithothamnion corallioides

b. Crustose thalli bearing thin and short (up to 3 mm wide and 5 mm long), simple branches with several buried conceptacles (D 320 x H 150 μm). Perithallus of branches irregularly zonate, not forming a distinct cortex. Thin (40-50 μm) hypothallus; intercalary hypothallus in branches overgrow old conceptacles, frequently leaving a triangular space (L.S.) over their roof.
Lithothamnion minervae sp. nov.

c. Crustose thalli (rare short protuberances) with large conceptacles (D 600 x H 190 μm). Zonation of the perithallus not evident, hypothallus well developed (100 μm).
Lithothamnion philippii

d. Thalli developing several nodose, diverging branches up to 1 cm in diameter and several cm long. Zonation of perithallus very marked, due to the alternation of large, rectangular, thin-walled cells (L 16-25 μm) and short, thick-walled cells (L 7-15 μm).
Lithothamnion valens

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