

REVISION AND RE-DOCUMENTATION OF M. AIROLDI'S SPECIES OF *LITHOPHYLLUM* FROM THE TERTIARY PIEDMONT BASIN

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Abstract. The species originally attributed by Airoldi (1932) to the genus *Lithophyllum* (*L. perrandoi*, *L. ligusticum*, *L. personatum* and *L. desitum*) are here re-examined on the basis of the original material, original descriptions and illustrations. *L. perrandoi* and *L. ligusticum* are considered to be conspecific and questionably retained in the genus *Lithophyllum*. We give priority to the name ?*L. perrandoi* Airoldi to honour the priest Don Perrando, who collected most of the fossils conserved in the Dip.Te.Ris of Genova. *L. personatum* and *L. desitum* do not belong to the genus *Lithophyllum* as presently circumscribed. *L. personatum* Airoldi is a female/carposporangial plant of a mastophoroid species resembling *Spongites fruticulosus* Kützing, and therefore we retain a dubitative identification with the new combination ?*Spongites personatus* (Airoldi). *L. desitum* is here placed in the genus *Mesophyllum* under the new combination *Mesophyllum desitum* (Airoldi). On the basis of its vegetative and reproductive features, *M. desitum* comb. nov. is here considered conspecific with *Mesophyllum obsitum* Airoldi.

Riassunto. La revisione dei tipi di *Lithophyllum perrandoi*, *Lithophyllum ligusticum*, *Lithophyllum personatum* e *Lithophyllum desitum* basata sul materiale, descrizioni e illustrazioni originali (Airoldi 1932) ha portato a considerare conspecifiche le specie *L. perrandoi* e *L. ligusticum*, che vengono mantenute nel genere *Lithophyllum* con formula dubitativa. Scegliamo di dare priorità al nome ?*L. perrandoi* Airoldi per onorare la memoria di Don Perrando, il parroco che collezionò la maggior parte del materiale attualmente conservato presso il Dip.Te.Ris di Genova. *L. personatum* e *L. desitum* non appartengono al genere *Lithophyllum*. *L. desitum* è posto in sinonimia con *Mesophyllum obsitum* Airoldi. *L. personatum* è una pianta femminile/carposporangiale della sottofamiglia Mastophoroideae, che presenta alcune somiglianze con la specie attuale *Spongites fruticulosus* Kützing. A causa della scarsità del materiale disponibile, attribuiamo la specie al genere *Spongites* con formula dubitativa, con la nuova combinazione ?*Spongites personatus* (Airoldi).

Introduction

The present paper is the third contribution to the revision of the material collected by Airoldi in the years 1930-32, and housed at the Department for the Study of the Territory and its Resources (Dip.Te.Ris.) of Genova University. Details on the history of the collection have been already given in Basso et al. (1998). The new species originally attributed by Airoldi to the genus *Lithophyllum* (*L. perrandoi*, *L. ligusticum*, *L. personatum* and *L. desitum*) are here revised on the basis of the original material, descriptions and illustrations.

Material and methods

The collection of fossil calcareous algae at the University of Genova was rearranged in 1967 and new numbering was added to most thin sections. The new number is written before the original given by Airoldi (e.g. the thin section originally numbered 162 by Airoldi, is now labelled 171/162). The rock fragments conserved together with the thin sections were not renumbered, although in some cases it was possible to find their exact correspondence. The original material considered for this study consists of six thin sections (4.7 x 2.7 cm) which include the type material of *L. perrandoi*, *L. ligusticum*, *L. personatum* and *L. desitum*, along with the macroscopic rock samples associated to the collection. SEM preparations (nine stubs) were obtained only from fragments corresponding to Airoldi's thin sections. SEM preparations followed the methods of Braga et al. (1993), which includes etching with HCL (2% vol.) on polished surface (Pl. 1, fig. 5). Some fragments have been observed on fresh fractures (Pl. 2, fig. 3).

The references in synonymy list includes only that literature providing species identification through adequate descriptions and illustrations or by direct control of relevant material in other collections conserved at the Dip.Te.Ris. Type localities are quoted from the original paper of Airoldi (1932). All published data for each species have

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been included in the section "Stratigraphic and geographic distribution". A new sampling has been performed at Squaneto (Mioglia, Savona) (Rovereto 1914), which is the *locus typicus* of *L. personatum*.

Within the paragraph "Stratigraphic distribution" we added separately those references which could not be checked because of the lack of descriptions and illustrations, and therefore excluded from further paleobiogeographic and stratigraphic considerations.

Tables of biometric data provide size range, mean (M) and standard deviation (SD) for cells in LRS (= Longitudinal Radial Section; Quaranta et al. 2007). The cell length (L) is measured as the distance between two primary pit-connections of the cell. The diameter (D) is the cell width measured perpendicularly to the length. Univariate statistics was not carried out for conceptacles size because of their rarity or inadequate orientation in the available material. Their size is reported in the tables together with the cell size; longitudinal sections that cut a conceptacle medially, along its pore canal, are defined as axial sections (= with visible pore canal; Afonso-Carillo et al. 1984).

Terminology of algal growth-forms follows Woelkerling et al. (1993), while taxonomy follows Woelkerling (1988), Woelkerling in Womersley (1996) and Irvine & Chamberlain (1994). Thallus nomenclature follows Basso et al. (2004).

Systematic palaeontology

Division **Rhodophyta** Wettstein, 1901

Class **Rhodophyceae** Rabenhorst, 1863

Order **Corallinales** Silva & Johansen, 1986

Family **Corallinaceae** Lamouroux, 1812 (emend. Harvey et al., 2003)

Subfamily **Lithophylloideae** Setchell, 1943

Genus *Lithophyllum* Philippi, 1837

Type species: *Lithophyllum incrustans* Philippi

?**Lithophyllum perrandoi** Airoldi, 1932

Pl. 1, 2; Tab. 1-3

Protologue. Airoldi 1932, p. 71, pl. 10, fig. 7a, b, pl. 11, fig. 1.

1932 *Lithophyllum ligusticum* Airoldi, p. 72, pl. 11, figs 2a-c, 3.

1968 *Lithophyllum ligusticum* - Mastroianni, p. 326, pl. 22, figs 1-4.

1968 *Lithophyllum perrandoi* - Mastroianni, p. 328, text fig. 31, pl. 23, figs 1-4.

1970 *Lithophyllum* cf. *perrandoi* - Francavilla, Frascari Riton-dale Spano & Zecchi, p. 675.

1970 *Lithophyllum ligusticum* - Vannucci, p. 456, pl. 5, fig. 4.

1983 *Lithophyllum ligusticum* - Bakalova, p. 62, pl. 6, fig. 2, not fig. 1.

1983 *Lithophyllum perrandoi* - Bakalova, p. 63, pl. 6, fig. 4, not fig. 3.

1987 *Lithophyllum ligusticum* - Fravega, Giammarino, Piazza, Russo & Vannucci, p. 56.

1987 *Lithophyllum perrandoi* - Fravega, Giammarino, Piazza, Russo & Vannucci, p. 56.

1987 *Lithophyllum* cf. *ligusticum* - Fravega, Giammarino, Piazza, Russo & Vannucci, p. 58.

1989 *Lithophyllum ligusticum* - Piazza, p. 166, pl. 7, fig. c.

1989 *Lithophyllum ligusticum* - Pisera & Studencki, p. 200, pl. 11, figs 2, 3.

1993 *Lithophyllum* cf. *ligusticum* - Vannucci, Stockar, Piazza & Fravega, tab. 1, p. 256.

1993 *Lithophyllum* cf. *perrandoi* - Vannucci, Stockar, Piazza & Fravega, tab. 1, p. 256.

1994 *Lithophyllum* cf. *ligusticum* - Fravega, Piazza, Stockar & Vannucci, tab. 2, p. 440.

1994 *Lithophyllum perrandoi* - Vannucci, Piazza, Fravega & Arnera, tab. 2, p. 102.

1997 *Lithophyllum ligusticum* - Stockar, p. 32, figs 14, 15.

1997 *Lithophyllum perrandoi* - Vannucci, Piazza, Pastorino & Fravega, tab. 1, p. 16.

1997 *Lithophyllum* cf. *perrandoi* - Vannucci, Piazza, Pastorino & Fravega, tab.1, p. 16, tab. 3, p. 24.

Holotype. Collection Airoldi (1930-32), thin section 162 re-labelled 171/162 (Pl. 1, fig. 1A).

Isotypes. Collection Airoldi (1930-32), thin section 168, re-labelled 174/168 and thin section 9 re-labelled 151/9 (Pl. 1, figs 1B-C).

Type locality. Rio Zunini, Sassello (Savona) (S Tertiary Piedmont Basin, Molare Formation).

Material. The original material consists of three thin sections (171/162, 151/9, 174/168). We obtained six SEM stubs (B10-31395, B1-8895, S1a-2004, S2a-2004, S1-2004, S2-2004) from the rock sample 162 in the original collection, corresponding to Airoldi's thin section 171/162.

In the protologue, Airoldi did not explicitly select a type, and since his illustrations show details of a fertile portion of thin section 171/162, this thin section is here recognized as the holotype (ICBN, McNeill et al. 2006, art. 9.1 and 9.13) (Pl. 1, fig. 2). The following description is based on the original material of *L. perrandoi* and its synonym, *L. ligusticum*.

Description. Thallus encrusting to warty (Pl. 1, fig. 2A) and locally lumpy, reaching several centimetres in diameter and thickness ranging from 120 to 1900 μm in the vegetative portions, 190 to 2000 μm in fertile portions. Most of the total thallus thickness corresponds to perithallial cells (= dorsal cell filaments perpendicular to the thallus surface).

Vegetative anatomy. Thallus apparently monomerous, with a dorsiventral organization. The hypothallium (= ventral core of filaments) is non coaxial, unidirectional and locally plumose (sensu Woelkerling 1988) (Pl. 1, figs 3, 4; Pl. 2, fig. 2). Hypothallium thickness ranging between 50-250 μm . The perithallium thickness is variable, with ranges between 50-1900 μm in sterile regions, and from 140 up to 1900 μm in fertile regions. Maximum thickness corresponds to protuberances.

Hypothallial cells sub-rectangular in LRS, with L 8-22 μm (M:14.7; SD:2.9) x D 3-10 μm (M:7.2; SD:1.5). Perithallial cells squarish, L 3-10 μm (M:5.0; SD:1.4) x D 3-9 μm (M:5.6; SD:1.5) (Tab. 1). The perithallium shows an inconspicuous zonation in the regions with laminar structure, where each band is composed of 5-6 cell layers. The zonation is more evident and irregular in protuberances, with bands of up to 15 cell layers (Pl. 1, fig. 3; Pl. 2, figs 1A, 4, 6).

SEM analysis of type specimens shows the occurrence of secondary pit-connections of about 1.8 μm in diameter, between cells of adjacent filaments (Pl. 1, fig. 5; Pl. 2, fig. 3). Trichocytes not observed. Epithallial

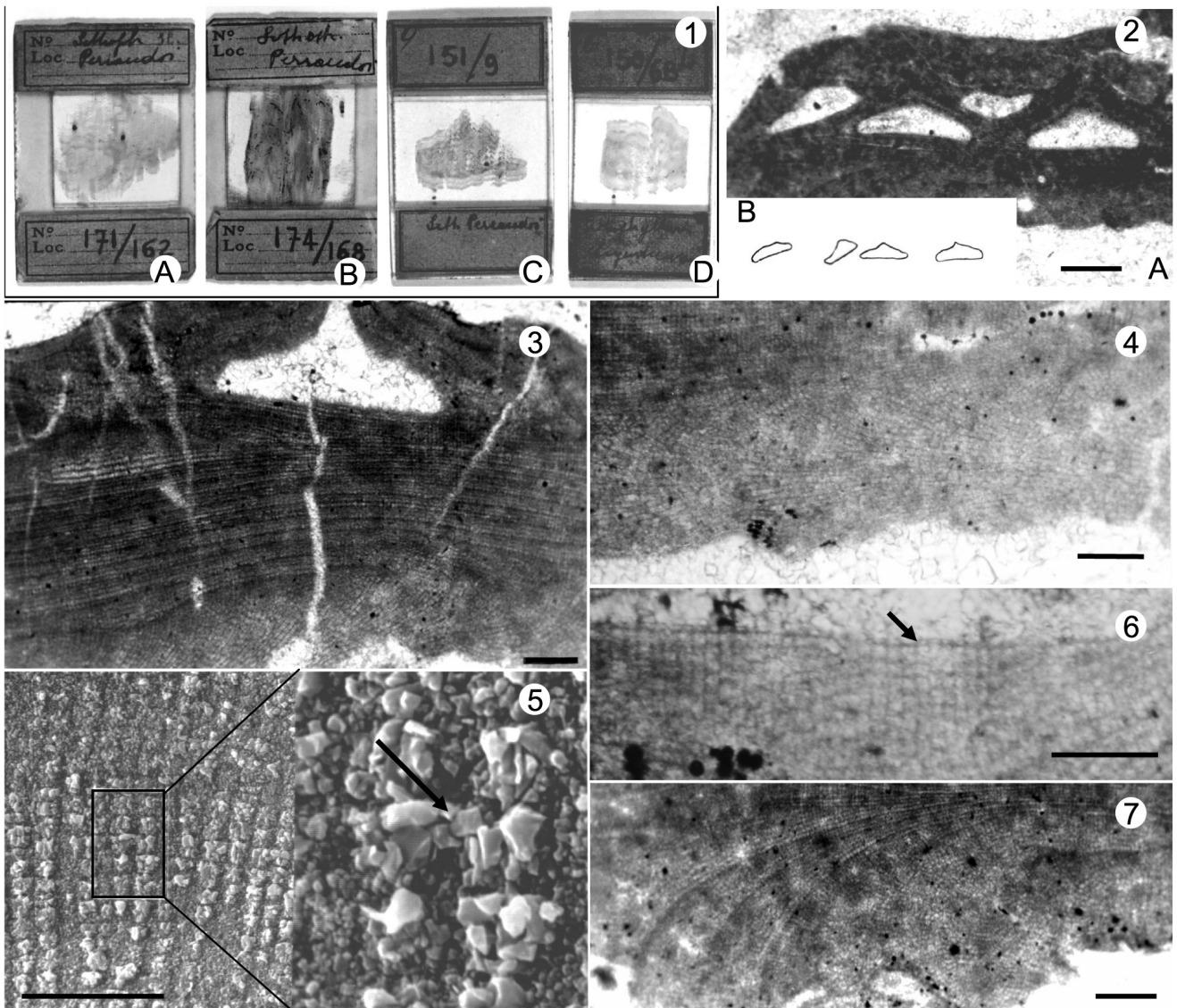


PLATE 1

?Lithophyllum perrandoi Airoidi

- Fig. 1 - Airoidi collection (1930-32). A) thin section 171/162 (holotype of *?L. perrandoi* Airoidi 1932). B) Thin section 174/168. C) Thin section 151/9 (isotypes of *?L. perrandoi*). D) Thin section 150/6A (holotype of *L. ligusticum* Airoidi 1932, subsumed in *?L. perrandoi* Airoidi). Thin sections are 4.1 x 2.7 cm.
- Fig. 2 - A) Holotype of *?L. perrandoi*. These conceptacles are the same as those illustrated by Airoidi in his protologue. Transmitted light optical microscope (OM) photograph, thin section 171/162. Scale bar = 250 μ m. B) Original drawing by Airoidi (1932, pl. 11, fig. 1).
- Fig. 3 - Note the plumose hypothallium organization and the zonation in the perithallium of *?L. perrandoi*. OM photograph, thin section from stub S1-2004. Scale bar = 100 μ m.
- Fig. 4 - *?L. perrandoi* Airoidi, holotype. The polystromatic, non-coaxial, apparently plumose hypothallium. OM photograph, thin section 171/162. Scale bar = 100 μ m.
- Fig. 5 - Mold of secondary pit-connections in a thallus of *?L. perrandoi* (arrow). SEM preparation as in Braga et al. (1993). SEM photograph, stub B1-8895. Scale bar = 50 μ m.
- Fig. 6 - *?L. perrandoi* Airoidi holotype. Preserved epithallial cells (arrow). OM photograph, thin section 171/162. Scale bar = 50 μ m.
- Fig. 7 - *?L. perrandoi* Airoidi holotype. The portion of thallus which was erroneously considered a coaxial hypothallium by Airoidi (1932). OM photograph, thin section 171/162. Scale bar = 100 μ m.

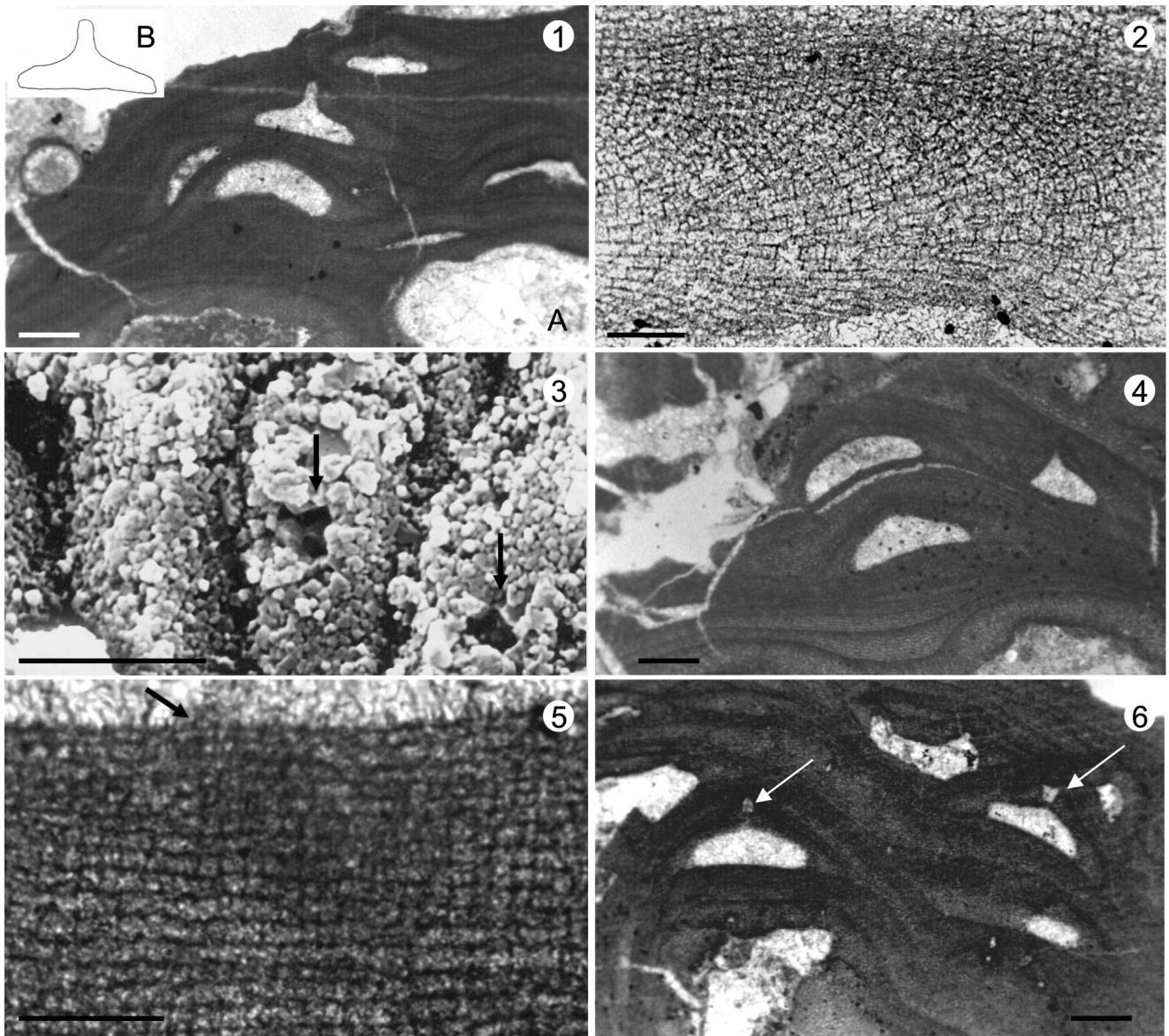


PLATE 2

Lithophyllum ligusticum Airoidi subsumed in ?*L. perrandoi* Airoidi

- Fig. 1A-B - *L. ligusticum* Airoidi, holotype. A) OM photograph, thin section 150/6A. Scale bar = 250 μ m. B) Original drawing by Airoidi (1932, pl. 11, fig. 2c).
- Fig. 2 - *L. ligusticum* Airoidi, holotype. Note the plumose organization of the hypothallium. OM photograph, thin section 150/6A. Scale bar = 50 μ m.
- Fig. 3 - *L. ligusticum* Airoidi. Note secondary pit-connections between cells of adjacent hypothallial filaments (arrows). Freshly fractured surface. SEM photograph, stub B5-31395. Scale bar = 10 μ m.
- Fig. 4 - *L. ligusticum* Airoidi, holotype. Sub-triangular conceptacle chambers with convex roof. OM photograph, thin section 150/6A. Scale bar = 250 μ m.
- Fig. 5 - *L. ligusticum* Airoidi, holotype. Preserved epithallial cells (arrow). OM photograph, thin section 150/6A. Scale bar = 50 μ m.
- Fig. 6 - *L. ligusticum* Airoidi, holotype. Conceptacles with visible pore canals with apical bulge (arrows). OM photograph, thin section 150/6A. Scale bar = 250 μ m.

Tab. 1 - Summary of biometric data obtained from merging the type material of *?Lithophyllum perrandoi* and its synonym, *L. ligusticum*. Size in micrometers (μm) from longitudinal radial sections. L = cell length; D = cell diameter (normal to the length) or conceptacle diameter; H = conceptacle height under the pore canal / or conceptacle central height when the pore canal is not visible; Hpc = height of the pore canal; n = number of observations; M = mean, SD = standard deviation.

		<i>?Lithophyllum perrandoi</i> Airoidi				
			Range	M	SD	n
Hypothallial cells	L		8-22	14.7	2.9	155
	D		3-10	7.2	1.5	
Perithallial cells	L		3-10	5.0	1.4	176
	D		3-9	5.6	1.5	
Sporangial conceptacles	axial at pore canal	D	320-520			12
		H	80-230			
	pore canal not visible	Hpc	20-150			29
		D	300-530			
	H	80-250				

cells apparently flat and non-flared (Pl. 1, fig. 6, Pl. 2, fig. 5).

Reproductive structures. Numerous uniporate conceptacles have been observed; they appear sub-triangular in axial section, with chamber floor usually flat or slightly convex. Conceptacle chambers with visible pore canal have a flat floor and diameter 320-520 μm x height 80-230 μm , plus the pore-canal length of 20-150 μm (Tab. 1). In the holotype the pore-canals are rare and difficult to identify (Pl. 1, fig. 2A). Conceptacle chambers without visible pore-canal are 300-530 μm in diameter and 80-250 μm in height. Pore canals can be constant in diameter or squat with an apical bulge. (Pl. 2, fig. 6). Columella not observed. The conceptacle chamber roof is raised about 150-250 μm from the thallus surface.

Remarks on type material of *L. perrandoi*. Some features of the original material are imprecisely described by Airoidi (1932). The author describes a hypothallium composed of cells organized in rather regular concentric series ("disposte in serie concentriche abbastanza regolari", Airoidi 1932, p. 71). However, we observed a clear vertical alignment of cells in most available specimens. In one case the thallus produces an apparently coaxial organization in correspondence with a change in growth direction (Pl. 1, fig. 7).

The cell and the conceptacle sizes reported by Airoidi can be confirmed, although we were not able to identify any hypothallial cell with a maximum length

of 27 μm . (Tab. 2)

Observations on Airoidi's original collection of *Lithophyllum ligusticum*, subsumed in *?Lithophyllum perrandoi*

Lithophyllum ligusticum Airoidi, 1932

Protologue. Airoidi 1932, p. 72, pl. 11, figs 2a-c, 3.

Holotype. Collection Airoidi (1930-32), thin section 6 re-labelled 150/6A (Pl. 1, fig. 1D).

Type locality. Rio Zunini (Sassello, S Tertiary Piedmont Basin, Molare Formation).

Material. The original material consists of one thin section (150/6A) (Pl. 1, fig. 1D) and a corresponding rock fragment (Airoidi collection fragment no. 6). Three SEM stubs (B5-31395, B6-8895, S3-2004) were obtained from rock fragments related to thin section 150/6A. In the protologue, Airoidi did not explicitly select a type, but as his illustrations show details of a fertile portion of the thin section 150/6A, this thin section is here recognized as the holotype (ICBN, McNeill et al. 2006, art. 9.1 and 9.13) (Pl. 2, fig. 1).

Description. Growth form warty or locally lumpy, thallus pseudoparenchymatous with a dorsiventral organization, monomerous.

Vegetative anatomy. Hypothallium non coaxial, pluristromatic (Pl. 2, fig. 2). Cells are rectangular in the hypothallium, passing to a sub-quadrate shape in the perithallial filaments, with L 10-20 μm (M:14.8; SD:2.8) x D 3-10 μm (M:6.5; SD:1.8) (Tab. 3). The peri-

Tab. 2 - *?Lithophyllum perrandoi* Airoidi, holotype thin section 171/162. Summary of biometric data. Size in micrometers (μm) from longitudinal radial sections. Abbreviations as in Tab. 1.

		<i>?Lithophyllum perrandoi</i> Airoidi (holotype)				
			Range	M	SD	n
Hypothallial cells	L		8-22	15.2	3.1	30
	D		6-9	7.2	1.0	
Perithallial cells	L		3-7	4.7	1.1	43
	D		3-7	4.8	1.1	
Sporangial conceptacles	axial at pore canal	D	430-520			2
		H	120-230			
	pore canal not visible	Hpc	70-130			9
		D	360-530			
	H	100-250				

		<i>Lithophyllum ligusticum</i> Airoidi (holotype)			
			Range	M	SD
Hypothallial cells	L	10-20	14.8	2.8	71
	D	3-10	6.5	1.8	
Perithallial cells	L	3-10	5.5	1.4	80
	D	4-9	6.5	1.3	
Sporangial conceptacles	axial at pore canal	D	430-500		8
		H	100-200		
		Hpc	20-150		
	pore canal not visible	D	300-520		18
	H	80-190			

Tab. 3 - *Lithophyllum ligusticum* Airoidi (subsumed in ?*L. perrandoi*), holotype thin section 150/6A. Summary of biometric data. Size in micrometers (μm) from longitudinal radial sections. Abbreviations as in Tab. 1.

thallium is zoned (Pl. 2, fig. 1A, 4, 6) with cells L 3-10 μm (M:5.5; SD:1.4) x D 4-9 μm (M:6.5; SD:1.3). Clear and numerous secondary pit-connections are common (Pl. 2, fig. 3). Trichocytes not observed. The epithallial cells are apparently flat and non-flared (Pl. 2, fig. 5).

Reproductive structures. The conceptacle chambers are uniporate and sub-triangular in section, with flat floor (rare, convex-upward, conceptacle chamber floors also occur) (Pl. 2, figs 1A, 4, 6). The long pore-canal (Tab. 3) has a constant diameter or appears squat with an apical bulge (Pl. 2, fig. 6). Columella not observed. The conceptacle chamber has D 430-500 μm x H 100-200 under axial sections (Tab. 3). The roof is raised 150-230 μm above the thallus surface.

Remarks on type material of *L. ligusticum*. The biometric data reported by Airoidi (1932) are confirmed (Tab. 3), with the exception of the maximum length of hypothallial and perithallial cells, which probably derive from the erroneous measuring of two consecutive cells of the same filament. Moreover, the growth form is warty to lumpy and the hypothallium is non-coaxial, contrarily to Airoidi's original description and drawing.

The taxonomic position of *L. perrandoi* and *L. ligusticum*. The growth-form, the vegetative and reproductive anatomy and the biometry of *L. perrandoi* and *L. ligusticum* are the same (compare Tab. 2 with Tab. 3 and Pl. 1, fig. 2A with Pl. 2, fig. 4). Airoidi (1932) already remarked the similarity, but kept the two species separated on the basis of the supposed fruticose growth-form of *L. ligusticum*. Therefore the two species must be considered conspecific (Tab. 6). Since no coded priority can be found between the two, we decide to retain *Lithophyllum perrandoi* Airoidi, 1932 and consider *L. ligusticum* as its synonym (McNeill et al. 2006, art. 11.5). This choice honours the memory of Don Perrando (the parish priest of S. Giustina-Savona) who collected most of Airoidi's material (1930-1932) and other important palaeontological and palaeoethnological collections presently conserved at the Dip.Te.Ris.

?*Lithophyllum perrandoi* Airoidi has secondary pit-connections, uniporate conceptacles and apparently

polystromatic, non-coaxial hypothallium. The present-day circumscription of the genus *Lithophyllum* is unclear, since the thallus is said to be monomerous with polystromatic hypothallium and/or dimerous with unistratose hypothallium (Woelkerling 1988 and Woelkerling in Womersley 1996) or primarily dimerous (Chamberline & Irvine in Irvine & Chamberline 1994). This ambiguity originates from the possible occurrence of a false hypothallium (Cabioch 1972; Athanasiadis 1999), which is formed of perithallial cell filaments arising a secondary monomerous dorsiventral growth (Chamberline & Irvine in Irvine & Chamberline 1994). It is often difficult to distinguish a false hypothallium of a dimerous plant from a polystromatic hypothallium of monomerous plant, even in living specimens of *Lithophyllum* (see Furnari et al. 1996, fig. 8; Woelkerling 1988, fig. 74; Athanasiadis 1999, fig. 6). Secondary pit-connections occur in Lithophylloideae and Sporolithaceae. Cell fusions have been not observed, and thus we could exclude that *L. perrandoi* belongs to the Sporolithaceae. The non-flared epithallial cells (Pl. 1, fig. 6, Pl. 2, fig. 5) would confirm this hypothesis, though with caution, since convincingly flared epithallial cells (e.g. Stockar 2000, pl. 1, fig. 4) are rarely observed in fossils. Finally, the vegetative anatomy of ?*L. perrandoi* differs from all the fossil *Sporolithon* species described so far from the same localities, and it is very unlikely that only the gametangial phase of another *Sporolithon* species entered the fossil record. However, given the uncertainty concerning the interpretation of an apparently polystromatic hypothallium of a monomerous thallus associated with secondary pit-connections, and the difficulties to ascertain the original shape of the epithallial cells in the fossil, we decide to retain a questionable attribution to the genus *Lithophyllum* with the name ?*L. perrandoi* as indication of taxonomic doubt (McNeill et al. 2006, art. 34.1).

Excluded references. Among the references mentioning ?*L. perrandoi*, we exclude the following records, because the material differs from the current circumscription of the species:

1) *L. cf. ligusticum* (Johnson 1961) from the Upper Eocene of Eniwetok (Marshall Islands);

2) *L. aff. ligusticum* (Beckmann & Beckmann 1966) from the Lower-Middle Eocene of Cuba;

3) Lemoine in Fallot et al. (1956, p. 1979) reports *Mesophyllum ligusticum* Air.? among the algal species of the Lower Eocene of Morocco, without any description and/or illustration. Later, Lemoine (1977, p. 19), records "*Mesophyllum ligusticum* (Airoldi) Lemoine 1956" in sediments of the Upper Eocene-Oligocene of the region of Radovis (Skopje, Macedonia), with reference to the paper of Fallot et al. (1956). Again, no illustration was provided. She described multiporate conceptacles in thalli which she considered to be conspecific with Airoldi's (1932) and Mastrorilli's (1968) material, specifying that their uniporate conceptacles could be gametangial. She never examined Airoldi's and Mastrorilli's original material. We exclude the attribution of *Lithophyllum ligusticum* Airoldi to the genus *Mesophyllum* because of the common secondary pit-connections observed in Airoldi's original material.

4) Records of *L. perrandoi* by Piazza (1989) from the Oligocene of Santa Giulia-Governo (Dego-Savona) and the Burdigalian of Bric Cardinelle (Ponzone-Alessandria), do not conform to the circumscription of the species as issued after the present revision.

5) The record of *L. cf. perrandoi* (Pisera & Studencki 1989) from the Middle Miocene (Badenian) of Korytnica and Chometow (Southern Poland) does not conform the circumscription of the species as issued after the present revision.

6) The comparison proposed by Bassi & Nebelsick (2000) with their *Spongites* sp. 2 is not tenable, since *L. ligusticum* Airoldi possesses secondary pit-connections and, moreover, much shorter perithallial cells.

Stratigraphic and geographic distribution. In this section we include only those references for which we could check the correct identification of the fossil alga (Fig. 1).

?*Lithophyllum perrandoi* occurs in the Paleogene. It is recovered in: ?Upper Eocene from Asenovgrad, S Bulgaria (Bakalova 1983) and Upper Eocene pebbles and boulders referred to the Ternate Fm. occurring in Quaternary sediment near Prella (Ticino, Southern Switzerland, Stockar 1997); Priabonian to ?Lower Oligocene from Barbarano (Colli Berici – NE Italy, Francavilla et al. 1970); an Oligocene pebble from the south-western moraine of Garda Lake deriving from the neighbouring "nullipore formations" (N Italy, Vannucci 1970). In the Tertiary Piedmont Basin (= TPB) ?*L. perrandoi* ranges from Oligocene Molare Fm. to the Lower Miocene Rocchetta Fm. and Visone Fm. In particular, in lower and middle Rupelian (SB21 according to the zonation of Cahuzac & Poignant 1997) and the upper Rupelian – Chattian and Chattian (biozone SB22A-SB23 and SB23) from different localities of the southern

	AGE	Bulgaria	Switzerland	NE Italy	Tertiary Piedmont Basin (TPB)		Poland
					Molare Fm.	Rocchetta Fm. and Visone Fm.	
MIOCENE	Serravallian						
	Langhian						
	Burdigalian						
	Aquitanian						
EOC OLIIGOCENE	Chattian						
	Rupelian						
	Priabonian						

Fig. 1 - Summary of stratigraphic and geographic distribution of ?*Lithophyllum perrandoi* Airoldi

margin of the TPB. In the SB21 of the Alessandria province (Prasco, Ovranò and Molare; Mastrorilli 1968; Vannucci et al. 1997). In the SB22A-23 of the Savona province (Dego, Sassello and Valzemola; Airoldi 1932; Fravega et al. 1987; Piazza 1989; Fravega et al. 1994). In the Chattian of Ponzone (Alessandria, Vannucci et al. 1997) and Millesimo (Savona, Vannucci et al. 1993). Within the Lower Miocene Rocchetta Fm., it is recorded from the Aquitanian near Millesimo (Savona, Vannucci et al. 1993) and in the Burdigalian near Spigno Monferrato (Alessandria, Vannucci et al. 1994) and from SB25 in the Visone Fm. of Bric Cardinelle (Ponzone-Alessandria, Piazza 1989). It is also recorded in the Middle Miocene (Badenian) of southern Poland near Korytnica and Chometow (Pisera & Studencki 1989). According to the above mentioned quotations, the paleobiogeography of ?*L. perrandoi* shows an Eocene distribution limited to the central and western sector of the Mediterranean Tethyan domain (S Bulgaria and Switzerland). The species seems confined in the western sector of the TPB during the Oligocene, and diffuses northernward into the central-western Paratethyan sector (S Poland) during the Badenian.

The following references could not be verified because of the lack of descriptions and illustrations, and therefore they have been excluded from further paleobiogeographic and stratigraphic considerations: Priabonian of Rohrdorf (Bavaria, near the German-Austrian boundary) (as *Lithophyllum cf. ligusticum*, Moussavian 1993); Upper Eocene – Lower Oligocene of Eastern Colli Berici ("Calcari e Calcareniti a Melobesie e Coralli") (as *Lithophyllum cf. perrandoi*, Ungaro 1978); Chattian of Millesimo (Savona) (as *Lithophyllum perrandoi* and *Lithophyllum ligusticum*, Lorenz 1964; 1968); Upper Burdigalian-Serravallian of St. Florent (N Corse) (*Lithophyllum ligusticum*, Mastrorilli in Bellini & Mastrorilli 1975) and of Bonifacio (Cala de Labra, S Corse) (*Lithophyllum perrandoi*, Mastrorilli in Bellini & Mastrorilli 1975). The Mastrorilli collection of mate-

rial from Corse (1975) is not present at the Dip.Te.Ris. and should be considered as lost.

Subfamily Mastophoroideae Setchell, 1943

Genus *Spongites* Kützing, 1841

Type species: *Spongites fruticosus* Kützing

?***Spongites personatus*** (Airoldi, 1932) comb. nov.

Pl. 3; Tab. 4

Basionym: *Lithophyllum personatum* Airoldi 1932, p. 73, pl. 11, fig. 4a, b, c.

1987 *Lithophyllum* cf. *personatum* - Fravega, Giammarino, Piazza, Russo & Vannucci, p. 59.

1996 *Lithophyllum* cf. *personatum* - Vannucci, Piazza, Fravega & Abate, tab. 1, p. 73.

Holotype. Collection Airoldi (1930-1932). Thin section 3 re-labelled 147/3 (Pl. 3, fig. 1).

Type locality. Squaneto (Mioglia, Savona, S Tertiary Piedmont Basin, Molare Formation).

Material. Airoldi's original collection (1930-1932) consists of a single thin section (147/3) (Pl. 3, fig. 1). Unluckily a new collection from Squaneto-Mioglia, which is the *locus typicus* of *L. personatum* contains only some poorly preserved fossil corallines which cannot help in clarifying the taxonomic position of *L. personatum*. However, the newly collected material appeared useful to indicate the Late Rupelian - Chattian age of the type locality.

In the protologue, Airoldi did not explicitly select a type, but as his illustrations show details of a fertile portion of the thin section 147/3, this thin section is here recognized as the holotype (ICBN, McNeill et al. 2006, art. 9.1 and 9.13) (Pl. 3, fig. 2).

Description. Plants encrusting, with vegetative thallus thickness ranging from 240 to 520 μm . The thickness varies from 650 to 950 μm in the fertile portions of the thallus (Pl. 3, fig. 2A).

Vegetative anatomy. Thallus monomerous, with a dorsiventral organization and non-coaxial, prevalently plumose hypothallium (sensu Woelkerling 1988) (Pl. 3, fig. 3). Hypothallium thickness ranging between 50 μm and 220 μm ; perithallium thickness ranging between 50-90 μm and 500-900 μm , with maxima in fertile portion of the thallus.

Hypothallial cells sub-rectangular, L 8-28 μm (M:14.3; SD:3.8) x D 4-10 μm (M:7.7; SD:1.3). Perithallium evidently zonate (Pl. 3, fig. 4), made of cells with L 5-18 μm (M:9.4; SD:2.1) x D 4-8 μm (M:7.1; SD:1.3) (Tab. 4).

Abundant cell fusions can be seen by OM, especially in the hypothallium (Pl. 3, fig. 5). Trichocytes not seen. Preserved epithallial cells appear prevalently rectangular, with meristematic cells of the same size of those subtending them (Pl. 3, figs 5, 6).

Reproductive structures. Conceptacles of very different shape and size occur in the holotype of *L. personatum* (Pl. 3, figs 4, 7), which we interpret as female/

carposporangial. Only one conceptacle chamber can be observed in axial section. It has a sub-triangular shape and thick chamber walls made of large cells. Its size is D 400 μm x H 220 μm with a pore canal 250 μm long (Pl. 3, figs 2A, 7; Tab. 4). It is raised 410 μm above the thallus surface. On the same thallus another similar conceptacle chamber, that we interpret as female, has D 220 μm x H 140 μm , and does not show the porecanal (Pl. 3, arrow in fig. 4). Other larger conceptacle chambers are diagonally cut and do not show their porecanal. They have flat to convex-upward floors, diameter ranging from 600-780 μm and height from 210 to 240 μm (Pl. 3, fig. 4; Tab. 4), and being much larger than the one in axial section are interpreted as mature carposporangial.

Remarks on type material of *L. personatum*.

Our observations partially disagree with Airoldi's protologue (1932). One discrepancy concerns the hypothallium organization, which is plumose and not coaxial. Despite the correspondence of the other anatomical details of the holotype with Airoldi's description (1932), and although the holotype hypothallium is cut at variable orientation (from transverse in Pl. 3, fig. 5 to LRS in Pl. 3, fig. 3) we could not observe any coaxial organization. It must be kept in mind that at that time (1932) the mastophoroids were not circumscribed yet and that a uniporate conceptacle, if not gametangial, had to belong to *Lithophyllum* (sensu Lemoine 1911: coaxial hypothallium and uniporate conceptacles). The size range of the vegetative cells does not correspond, since Airoldi reports hypothallial cells L 18-28 x D 8-14 and perithallial cells L 10-18 (23) x 8-14 (18) (compare with Tab. 4). Another difference is the size of conceptacle chambers, with sizes reported in the protologue (D 430-760 μm x H 200-220 μm) not completely corresponding to our observations (Tab. 4). Some rounded cells which were interpreted as possible spores by Airoldi, are actually cells of the conceptacle walls (Pl. 3, fig. 7), and this Airoldi's misinterpretation accounts for his overestimation of the minimum diameter of conceptacles.

The taxonomic disposition of ?*Spongites personatus*. The occurrence of cell fusions excludes *L. personatum* from the subfamily Lithophylloideae.

Conceptacles showing two contrasting shapes and size occur in the same thallus in the holotype of *L. personatum* (small and sub-triangular *vs.* large and ovoid; Pl. 3, figs 2A, 4, 7). This feature is commonly observed in the female/carposporangial plants of most corallines since cariogamy is followed by an increase in size and a change in shape of the female conceptacle becoming carposporangial.

A female/carposporangial thallus with adjacent vegetative cells filaments connected by cell fusions

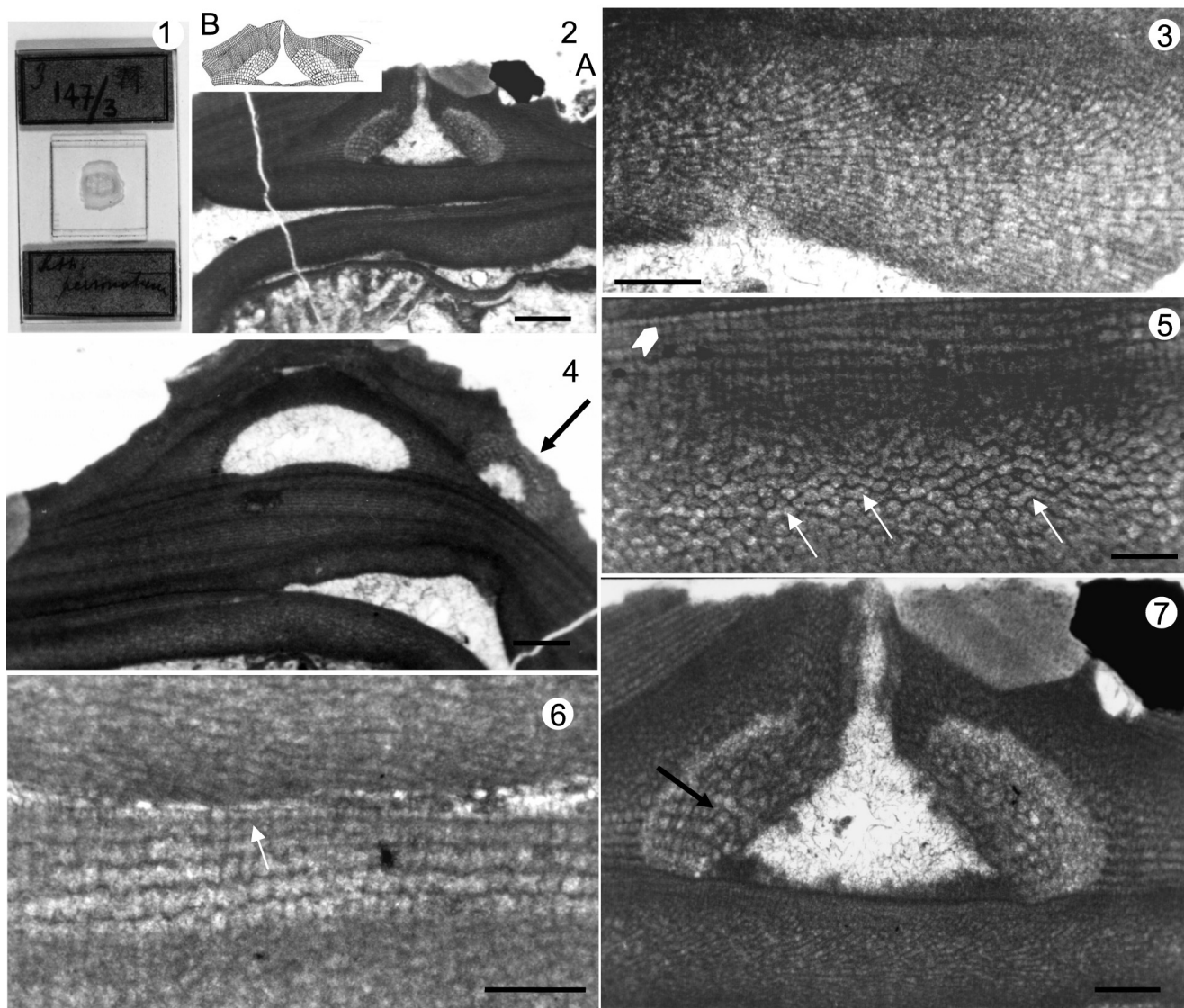


PLATE 3

?*Spongites personatus* (Airoldi) comb. nov. (= *Lithophyllum personatum* Airoldi), holotype

Fig. 1 - Holotype thin section 147/3. Actual size is 4.1 x 2.7 cm.

Fig. 2 - A) Fertile portion of ?*S. personatus*; the conceptacle is that illustrated by Airoldi (1932). OM photograph, thin section 147/3. Scale bar = 250 μ m. B) The original Airoldi drawing (1932 tav. 11, fig. 4c) of *L. personatum*.

Fig. 3 - Plumose hypothallium with large and numerous cell fusions. OM photograph, thin section 147/3. Scale bar = 100 μ m.

Fig. 4 - A large, presumed uniporate conceptacle chamber with convex-upward floor. Note the evident zonation of the perithallium and a smaller, incomplete conceptacle on top right (arrow), which has the same shape and structure of the conceptacle of fig. 2A. OM photograph, thin section 147/3. Scale bar = 250 μ m.

Fig. 5 - Note fusions in transversal section, connecting cells of adjacent filaments (arrows), and distally flat, non-flared epithallial cells (arrowhead). OM photograph, thin section 147/3. Scale bar = 50 μ m.

Fig. 6 - A thallus surface with preserved epithallial cells (arrow). OM photograph, thin section 147/3. Scale bar = 50 μ m.

Fig. 7 - Detail of the sub-triangular uniporate conceptacle chamber of fig. 2A. Note the large cells of the conceptacle walls (arrow). OM photograph, thin section 147/3. Scale bar = 100 μ m.

<i>?Spongites personatus</i> (Airoidi) (holotype)					
		Range	M	SD	n
Hypothallial cells	L	8-28	14.3	3.8	54
	D	4-10	7.7	1.3	
Perithallial cells	L	5-18	9.4	2.1	55
	D	4-8	7.1	1.3	
Conceptacles	Female axial at pore canal	D	400		1
		H	220		
	Carposporangial pore canal not visible	Hpc	250		
		D	600-780		4
	H	210-240			

Tab. 4 - *?Spongites personatus* (Airoidi), holotype thin section 147/3. Summary of biometric data. Size in micrometers (µm) from longitudinal radial sections. Abbreviations as in Tab. 1.

could belong alternatively to Sporolithaceae, Melobesioideae or Mastophoroideae. The preserved epithallial cells are distally flat and non-flared, thus pointing to the exclusion of the Sporolithaceae, though a particular note of caution must be used for the fossil plants (see comments under *L. perrandoi*).

Among the subfamily Melobesioideae, we should exclude *L. personatum* from the genus *Mesophyllum* for the non-coaxial hypothallium. Moreover, since the epithallial cells are flat and not flared and no pattern of progressive elongation is observed below the epithallial cell (Irvine & Chamberlain 1994) we can also exclude the genera *Lithothamnion* and *Phymatolithon*.

The currently accepted taxonomic biological characters separating *Spongites* from *Neogoniolithon* mostly rely on gametangial structures which are not preserved in the fossil. For this reason, it has been suggested to use a different circumscription for fossils belonging to these two genera, using the occurrence of a coaxial hypothallium as diagnostic for *Neogoniolithon* (Braga 2003). Within this taxonomic framework, *L. personatum* can be considered a species of *Spongites*.

In particular, we observed a strong resemblance of the small and triangular conceptacles of *L. personatum*, which have lateral walls made of large cells, with the characters of the female conceptacles of *Spongites fruticosus* Kützing (Basso & Rodondi 2006). Therefore we interpret *L. personatum* as a female/carposporangial mastophoroid. Given the scarcity of available material and the uncertainty of identification at the genus level, we use the formulation *?Spongites personatus* (Airoidi)

as indication of taxonomic doubt (McNeill et al. 2006, art. 34.1) (Tab. 6).

Stratigraphic and geographic distribution.

?Spongites personatus (Airoidi) appears to be restricted to the Oligocene Molare Fm. of the TPB (Fig. 2): it occurs in the Upper Rupelian – Chattian (biozones SB22A-SB23; Cahuzac & Poignant 1997) of Savona (Squaneto and Sassello; Airoidi 1932; Fravega et al. 1987), and in the Pietra da Cantoni Fm. of the Monferrato Complex: Aquitanian – Burdigalian of Terruggia and Rosignano (Alessandria, NW Italy) (Vannucci et al. 1996).

	AGE	Tertiary Piedmont Basin (TPB)	Monferrato complex
		Molare Fm.	Pietra da Cantoni Fm.
MIOCENE	Burdigalian		
	Aquitanian		
OLIGOCENE	Chattian		
	Rupelian		

Fig. 2 - Summary of stratigraphic and geographic distribution of *?Spongites personatus* (Airoidi)

<i>Mesophyllum desitum</i> (Airoidi) (holotype)					
		Range	M	SD	n
Hypothallial cells	L	15-20	17.3	1.3	20
	D	5-9	6.3	1.3	
Perithallial cells	L	7-9	7.6	1.0	20
	D	4-8	6.2	1.2	
Sporangial conceptacles	D	360-420			4
	H	130-160			

Tab. 5 - *Mesophyllum desitum* (Airoidi), subsumed in *Mesophyllum obsitum* Airoidi, holotype thin section 169/158. Summary of biometric data. Size in micrometers (µm). Abbreviations as in Tab. 1, but H = height of the multiporate conceptacle chamber.

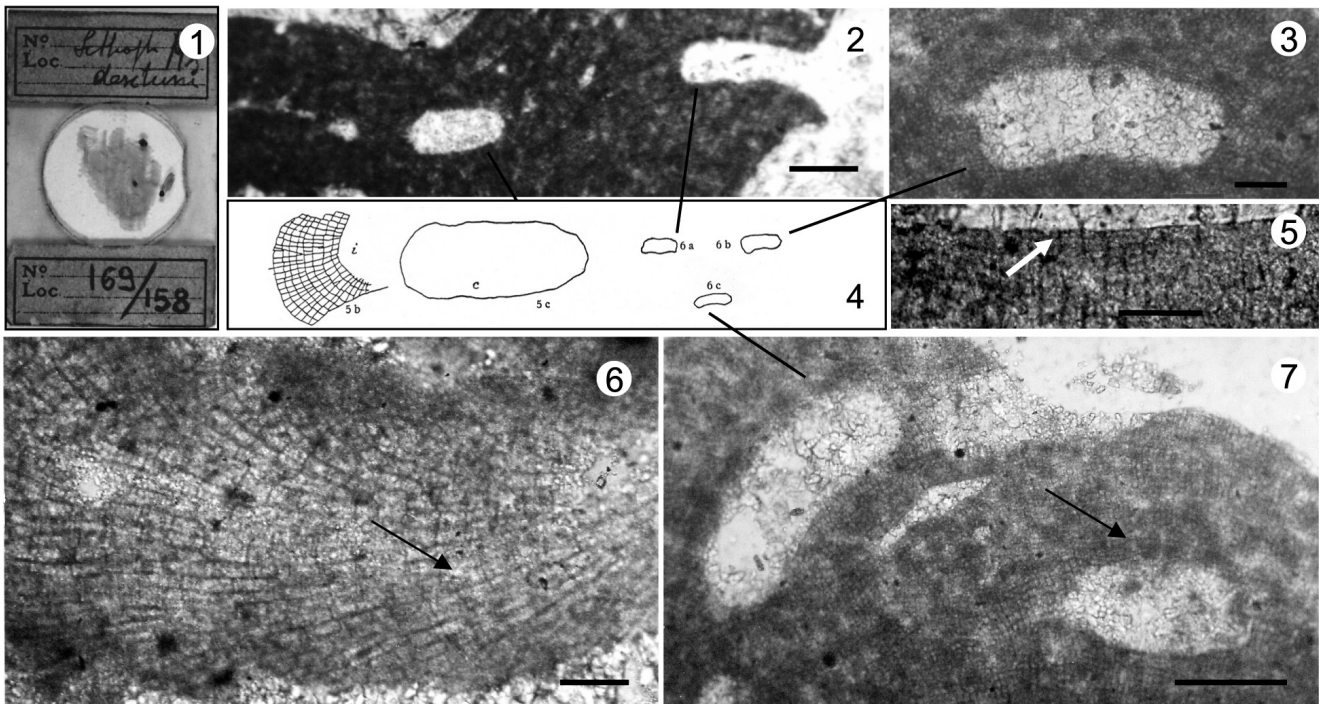


PLATE 4

Mesophyllum desitum (Airoldi) comb. nov. (= *Lithophyllum desitum* Airoldi) subsumed in *Mesophyllum obsitum* Airoldi, holotype

- Fig. 1 - The holotype thin section 169/158. Actual size is 4.1 x 2.7 cm. On top right note "Ms" in Mastrorilli's handwriting.
 Fig. 2 - Fertile portion of the holotype. The two conceptacles correspond to Airoldi (1932) drawings 5c and 6a (see Pl. 4, fig. 4). OM photograph, thin section 169/158. Scale bar = 250 μ m.
 Fig. 3 - Another conceptacle illustrated by Airoldi (see Pl. 4, fig. 4, 6b). OM photograph, thin section 169/158. Scale bar = 100 μ m.
 Fig. 4 - The original Airoldi's drawing (1932 tav. 11, figs 5-6) of *L. desitum*.
 Fig. 5 - Preserved epithallial cells (arrow). Note their flattened, non-flared, sub-rectangular shape. OM photograph, thin section 169/158. Scale bar = 50 μ m.
 Fig. 6 - The coaxial to plumose hypothallium with cell fusions (arrow). OM photograph, thin section 169/158. Scale bar = 50 μ m.
 Fig. 7 - Multiporate conceptacles. The one on left corresponds to Airoldi 1932 fig. 6c (see Pl. 4, fig. 4). The conceptacle on right shows numerous pore canals in the conceptacle roof (arrow). OM photograph, thin section 169/158. Scale bar = 100 μ m.

Family Hapalidiaceae Gray, 1864 (emend. Harvey et al., 2003)

Subfamily Melobesioideae Bizzozero, 1885

Genus *Mesophyllum* Lemoine, 1928

Type species: *Mesophyllum lichenooides* (Ellis) Lemoine

***Mesophyllum desitum* (Airoldi, 1932) comb. nov.**

Pl. 4; Tab. 5

Basionym: *Lithophyllum desitum* Airoldi 1932, p. 74, pl. 11, figs 5-6.

Holotype. Collection Airoldi (1930-1932). Thin section 158 re-labelled 169/158 (Pl. 4, fig. 1).

Type locality. Rio Zunini, Sassello (Savona) (S Tertiary Piedmont Basin, Molare Formation).

Material. The thin section 169/158 is the sole original material (Pl. 4, fig. 1). In the protologue, Airoldi did not explicitly select a type, and since his illustrations show details of conceptacles and hypothallial cells of the thin section 169/158, this thin section is here recognized as

the holotype (ICBN, McNeill et al. 2006, art. 9.1 and 9.13) (Pl. 4, figs 2-4, 7).

Description. Thallus encrusting to warty (Pl. 4, fig. 2), with variable thickness ranging from 340 μ m to 1500 μ m.

Vegetative anatomy. Thallus monomerous with dorsoventral organization. Several thalli are locally superposed. Cell fusions are evident in the hypothallium which is coaxial to locally plumose (sensu Woelkerling 1988) (Pl. 4, fig. 6); hypothallium thickness ranges between 50-240 μ m and hypothallial cells between 15-20 μ m in length (M:17.3; SD:1.3) and 5-9 μ m (M:6.3; SD:1.3) in diameter (Tab. 5). The perithallium thickness ranges between 60-300 μ m in sterile regions and up to 640 μ m in fertile regions. Perithallial cells measure L 7-9 μ m (M:7.6; SD:1.0) and D 4-8 μ m (M:6.2; SD:1.2). Zonation is not evident. The epithallial

Airoldi (1932)	Present name and disposition (this revision)
<i>Lithophyllum perrandoi</i>	? <i>Lithophyllum perrandoi</i> Airoldi
<i>Lithophyllum ligusticum</i>	? <i>Lithophyllum perrandoi</i> Airoldi
<i>Lithophyllum personatum</i>	? <i>Spongites personatum</i> (Airoldi) comb. nov.
<i>Lithophyllum desitum</i>	<i>Mesophyllum obsitum</i> Airoldi

Tab. 6 - Synopsis of the taxonomic dispositions and nomenclatural changes on Airoldi's species of *Lithophyllum*, issued from this revision.

cells are flat and not flared (Pl. 4, fig. 5). Trichocytes not observed.

Reproductive structures. Conceptacle chambers multiporate (Pl. 4, figs 2, 3, 7) ranging from 360-420 µm in diameter and 130-160 µm in height. The pore canals are up to 50 µm in length.

Remarks on type material of *L. desitum*. We were not able to locate the hypothallial cells with length of up to 29 µm reported in Airoldi's protologue. Airoldi did not describe the structure of the conceptacle roofs of *L. desitum* (uniporate *vs.* multiporate).

The taxonomic position of *Mesophyllum desitum*. The thin section 169/158 contains some poorly preserved thalli of crustose corallines. Airoldi (1932) published a sketch drawing of the species, where a coaxial hypothallium and some conceptacle chambers are shown. We recognized in the holotype section the coaxial hypothallium, with cell fusions and the conceptacle chambers, which are multiporate. Therefore we refer *Lithophyllum desitum* to the genus *Mesophyllum*. This taxonomic disposition was already suggested but not published by Mastrorilli, when she re-arranged the

Airoldi collection, as written in her hand-writing on the label of the thin section (Ms. = *Mesophyllum*) (Pl. 4, fig. 1).

In the same paper, Airoldi (1932) described *Mesophyllum obsitum*, which has been already revised in a previous paper (Basso et al. 1998). On the basis of the vegetative and reproductive features, we consider *Mesophyllum desitum* (Airoldi) nov. comb. conspecific with *Mesophyllum obsitum* Airoldi. The name *M. desitum* becomes a heterotypic synonym of *Mesophyllum obsitum* Airoldi.

Stratigraphic and geographic distribution. *Mesophyllum desitum* (synonym of *Mesophyllum obsitum* Airoldi) is known only from Airoldi's record (1932) in the Upper Rupelian - Chattian (SB22A-23) Molare Fm. of Sassello (Savona, NW Italy), in the TPB.

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