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REVISION AND RE-DOCUMENTATION OF M. AIROLDI'S SPECIES OF *MESOPHYLLUM* FROM THE TERTIARY PIEDMONT BASIN (NW ITALY)

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Riassunto. Airoldi (1930, 1932) descrisse ventitré specie di Corallinales fossili (Rhodophyta) provenienti dall'Oligocene del Bacino Terziario del Piemonte (Italia nord-occidentale); fra queste ben tredici erano nuovi taxa. Vengono qui ridescritti e ridocumentati *Mesophyllum fructiferum* Airoldi 1932 e *Mesophyllum obsitum* Airoldi 1932. La presenza di fusioni cellulari, concettacoli multipori e ipotallo (=ventral core of cell filaments) con organizzazione passante da coassiale a non coassiale consentono di confermare l'appartenenza di entrambe le specie al genere *Mesophyllum*.

Abstract. Airoldi (1930, 1932) described twenty-three fossil Corallinales (Rhodophyta) from the Oligocene of the Tertiary Piedmont Basin (NW Italy), including thirteen new species. In this paper *Mesophyllum fructiferum* Airoldi 1932 and *Mesophyllum obsitum* Airoldi 1932 are re-documented and re-described. The presence of cell fusions, multiporate conceptacles and a ventral core of cell filaments passing from coaxial to non-coaxial confirm that both species belong to the genus *Mesophyllum*.

Introduction.

This paper is the first of a series of contributions that re-examines the types of Corallinales described by the palaeontologists M. Airoldi, S. Conti and V. I. Mastrorilli from the University of Genova.

Between 1857 and 1910, Don Pietro Perrando (a priest who loved palaeontology) and Gaetano Rovereto (a geologist from the University of Genova) worked on Oligocene strata of the Tertiary Piedmont Basin and gathered a very valuable collection of Corallinales.

Marco Airoldi analysed this material and identified twenty-three taxa of Corallinales, thirteen of which were new species. In 1930 he published a short paper describing the new genus *Leptolithophyllum* and its type-species *Leptolithophyllum roveretoi*. Two years later Airoldi published the complete results of his studies in a large monograph (Airoldi, 1932), in which he described twelve new species of the genera *Archaeolithothamnium* (two species), *Lithothamnium* (three species), *Lithophyllum* (four species), *Mesophyllum* (two species) and *Leptolithophyllum* (one species).

As was typical for that time, the lengthy descriptions of the new species were accompanied by neither adequate illustrations (only drawings were provided) nor designations of the holotypes. This led to confusion in subsequent taxonomy and to considerable difficulties in species identification.

Fortunately, the largest portion of Airoldi's collection is well preserved and housed in the Department of Earth Sciences at the University of Genova, allowing revisions of the original material.

This paper focuses on the revision of original descriptions, iconographies, and taxonomic arrangement of the species originally attributed by M. Airoldi to the genus *Mesophyllum* (*M. fructiferum* and *M. obsitum*).

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. 154/14, with 14 being Airoldi's number and 154 the new number. No new labels were added to the original numbering on the corresponding rock fragments. In some cases, several rock fragments were preserved together under the same number, and it was very difficult to assess from which fragment the thin section was cut. Further observations by scanning electron microscope (SEM) and new thin sections were obtained only from fragments thought to be the originals used by Airoldi for his thin sections. SEM preparations followed the methods of Braga et al. (1993). Due to diagenetic alteration, SEM studies on the original material provided no information in addition to that already obtained using an optical microscope.

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Specimens questionably or incompletely identified by Airoldi were not considered in this work. The generic and suprageneric classification scheme, thallus nomenclature and growth form definitions follow Woelkerling (1988) and Woelkerling et al. (1993).

The list of synonyms and citations for each species includes only papers where descriptions and/or illustrations are provided. Type localities are quoted from the original works of Airoldi. All available published data for each species were included in the section "Stratigraphic and geographic distribution"; stratigraphic ranges were refined and revised, and formation names were included when known.

Systematic Palaeontology

Division **Rhodophyta** Wettstein 1901

Class Rhodophyceae Rabenhorst 1863

Order Corallinales Silva & Johansen 1986

Family *Corallinaceae* Lamouroux 1812

Subfamily *Melobesioideae* Bizzozero 1855

Genus *Mesophyllum* Lemoine 1928

Lectotype species - *Mesophyllum lichenoides* (Ellis) Lemoine 1928.

The genus *Mesophyllum* was delimited from other genera of Corallinaceae by Woelkerling (1988) on the basis of the following characters: genicula absent, haustoria absent, monomerous construction; plants with a predominantly coaxial core of filaments; outermost walls of epithallial cells rounded or flattened but not flared; cell fusions present between cells of adjacent filaments; secondary-pit connections absent; tetrasporangial/bisporangial conceptacles multiporate; tetrasporangia/bisporangia with mucilaginous plugs. Except for the occurrence of mucilaginous plugs, all these characters can be preserved and observed in fossil specimens. However, following Woelkerling & Harvey (1992; 1993) *Mesophyllum* is delimited from other genera of Melobesioideae by a combination of eight features, four of which concern the formation of the spermatangial conceptacle and other spermatangial characters, which cannot be observed in the fossils. Since the coaxial organisation of the ventral core of cell filaments has been shown to be rather variable, even within the same specimen (Woelkerling & Harvey, 1992), it has been considered of poor taxonomic value. However, the remaining four characters (haustoria absent; internal construction monomerous; outermost walls of epithallial cells rounded or flattened but not flared; vegetative initials usually as long or longer than cells immediately subtending them), though observable in the fossil, are not sufficient to delimit *Mesophyllum* from other genera of Melobesioideae. Therefore, it is necessary to use a combination of the above-mentioned characters, together with the predominantly coaxial morphology of the ventral core of cell filaments, to identify fossil specimens of *Mesophyllum*. In particular, it is possible to delimit *Mesophyllum* from: a) *Lithothamnion*, because *Lithothamnion* has a non coaxial organization of the ventral core and epithallial cells are flattened and flared; b) *Synarthrophyton* because *Synarthrophyton* has a predominantly non coaxial ventral core and small cell fusions visible only under particular orientation of the thallus; c) *Clathromorphum* because in *Clathromorphum* the ventral core is rarely coaxial and each cell filament terminates at the surface of the thallus with two or more epithallial cells.

Mesophyllum fructiferum Airoldi 1932

Pl. 1; Tab. 1

1932 *Mesophyllum fructiferum* Airoldi, p. 76; text fig. 2, pl. XII, fig. 1.
1932 *Mesophyllum suganum* (Rothpletz 1891) Airoldi, p. 75, pl. XI, text-fig. 1, fig. 7
1968 *Mesophyllum fructiferum* - Mastrorilli, p. 287, pl. XIII, fig. 1-2.
1980a *Mesophyllum fructiferum* - Fravega & Vannucci, p. 109, fig. 8.
1987 *Mesophyllum fructiferum* - Fravega et al., p. 51, fig. 14.
1989 *Mesophyllum fructiferum* - Piazza, p. 160, pl. 5, fig. a-b.
1989 *Mesophyllum fructiferum* - Pisera & Studencki, p. 198, pl. 8, fig. 3.

PLATE 1

Fig. 1 - *Mesophyllum fructiferum* Airoldi. Holotype, thin section 17. The thin section is broken. The script "17 *Mesoph. fructiferum*" is in Airoldi's handwriting. Magnification as in fig. 3.

Fig. 2 - *Mesophyllum fructiferum* Airoldi. Isotype, thin section 16. The script "16 *Mesoph. fructiferum*" is in Airoldi's handwriting. Magnification as in fig. 3.

Fig. 3 - Small rock sample n. 16, from which thin section 16 was obtained. Scale bar = 1 cm.

Fig. 4 - *Mesophyllum fructiferum* Airoldi. Overview of thin section 17, the holotype. Bottom right, Airoldi's original drawing (Airoldi, 1932, p. 77, fig. 2). Scale bar = 500 µm.

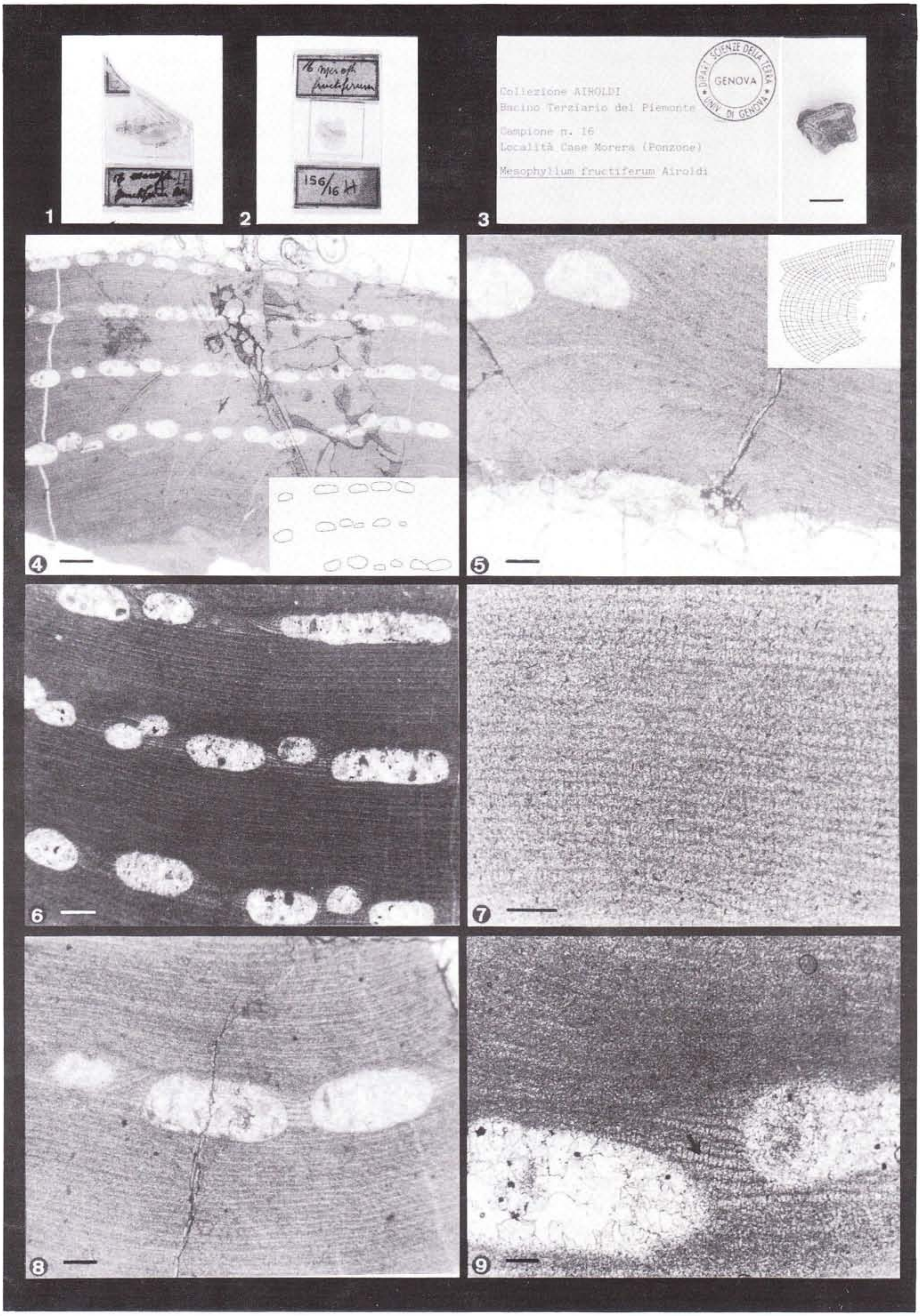
Fig. 5 - *Mesophyllum fructiferum* Airoldi. Detail of ventral core of thin section 17. Top right, Airoldi's original drawing (Airoldi, 1932, pl. XII, fig. 1a). Scale bar = 125 µm.

Fig. 6 - *Mesophyllum fructiferum* Airoldi. Overview of thin section 17N. Note sporangial conceptacles in regular rows and long cells between conceptacles. Scale bar = 200 µm.

Fig. 7 - *Mesophyllum fructiferum* Airoldi. Thin section 17N. Peripheral region. Note horizontal alignment of cells. Scale bar = 50 µm.

Fig. 8 - *Mesophyllum fructiferum* Airoldi. Detail of peripheral region and irregular zonation occurring around each conceptacle. Scale bar = 125 µm.

Fig. 9 - *Mesophyllum fructiferum* Airoldi. Detail of long cells with fusions (arrow) in a fertile portion of the peripheral region. Scale bar = 50 µm.


156/16 H
GENOVA
Collezione AIROLDI
Bacino Terziario del Piemonte
Campione n. 16
Località Case Morera (Ponzone)
Mesophyllum fructiferum Airoldi
1
2
3
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6
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9

Holotype - Coll. Airoldi, thin section 17, SEM stubs 31395b4 and 8895b7.

Isotype - Coll. Airoldi, one small fragment labelled 16 and related thin section 156/16.

Type locality - Late Rupelian-Chattian of Case Morera (SW Tertiary Piedmont Basin, Molare Formation).

Material.

The original material consists of two thin sections (17 and 156/16) and a small fragment of the rock sample related to section 156/16 (Pl. 1, fig. 1-3). Two more small rock fragments related to thin section 156/16 and 17 were used for the preparation of the SEM stub and one new thin section (17N). Airoldi did not explicitly select the holotype in the protologue, but the illustrations show details only of thin section 17 (Pl. 1, fig. 4, 5). Section 17 is therefore the holotype (ICBN, Greuter et al., 1994, art. 9.1).

Description.

Thin section 17 shows a thick, compact plant (possibly a single thallus) forming a small rhodolith. The rock in which the rhodolith was enclosed, a poorly sorted, coarse sandstone is observable at the margins of the section.

The plant is nongeniculate, encrusting, with a maximum thickness of 5 mm. The thallus is pseudoparenchymatous with dorsiventral internal organization; monomerous, with a coaxial to noncoaxial ventral core (sectioned transversely in most parts of the thin section), with a thickness ranging from 250 to 300 µm.

Cells of core filaments are 8-30 µm long and 5-15 µm in diameter (Table 1). The smallest cells are at the periphery and the longest cells in the central part of the core (Pl. 1, fig. 5).

The peripheral region has a variable thickness (max. 4250 µm). Cells are aligned horizontally, with horizontal cell walls more distinct than the vertical ones (Pl. 1, fig. 6, 8). Cell length ranges from 6 to 22 µm. The longest cells (20-22 µm) are present only in fertile portions of the thallus, between conceptacles (Pl. 1, fig. 6, 8, 9). In sterile portions of the thallus, where the horizontal arrangement is evident and no zonation occurs, layers of cells longer (11-15 µm) than the over- and underlying cells (6-10 µm) may be observed (Pl. 1, fig. 6-8). Cell diameter ranges from 5 to 9 µm. Epithallial cells are not preserved.

Cell fusions are visible locally in the ventral core. Cell fusions occur also in the peripheral region and are especially evident in very long cells close to conceptacles (Pl. 1, fig. 9), since in other zones the compact organization of cells and the effects of diagenesis make their observation difficult.

Sporangial conceptacles are multiporate (D 250-600 µm x H 140-270 µm) and occur in layers (Pl. 1, fig. 4, 6, Table 1). The D/H ratio ranges from 1.5 to 3.5. Cells between conceptacles are longer and cell filaments bend to follow the convexity of the conceptacles. This feature appears as an irregular zonation of the fertile portions of the thallus (Pl. 1, fig. 6, 8). In the genus *Mesophyllum*, larger cells close to the conceptacles are formed during early stages of conceptacle development (Woelkerling & Irvine, 1986, fig. 22; Woelkerling & Harvey, 1993, fig. 27B, C). The roof morphology appears to be mound-like or flattened. Rims are not apparent. Roof thickness is commonly 25-30 µm.

The isotype (thin section 156/16) shows the same general features as observed in the holotype. Differences are detected in the maximum total thickness of the thallus, which reaches only 1800 µm; in the maximum thickness of the ventral core (500 µm); and in the maximum thickness of the peripheral region not exceeding 1500 µm. Also, the long cells observed in single layers within the sterile thallus of the holotype are found only locally in the isotype and the organization of the thallus is less regular with an apparent, local zonation. In conceptacles, the D/H ratio ranges from 1.2 to 3.

Thin section 17N confirms the features observed in thin section 17.

Remarks.

Airoldi (1932, p. 77) described the species as "...crusts of little thickness, bearing slender branches as thin and long laminae..." (translated from Italian). There is no doubt that thin section 17 is the one illustrated in Airoldi's protologue (1932, fig. 2). However, no branching is evident in the holotype. This is probably due to a misinterpretation of the thallus structure.

Another discrepancy with Airoldi's protologue is in the range of core cell length: 15-33 µm. Our observations indicate 8-30 µm in the holotype and 8-25 µm in the isotype (Table 1).

Airoldi (1932, p. 75) described a specimen which he considered conspecific with *Lithothamnium suganum* Rothpletz (1891). Although he did not study Rothpletz's type material, he nevertheless assigned the species to the genus *Mesophyllum*. *Mesophyllum suganum* (Rothpletz) Airoldi is present in the collection as thin section 153, relabelled 164/153 in 1967. This thin section shows a thallus which corresponds in all details to *M. fructiferum* Airoldi. Airoldi separated the two species on the assumption that no hypothallus was observable in the specimen assigned to *M. suganum*. Actually, the hypothallus (i.e. the ventral core of filaments) is cut transversely, which may explain Airoldi's misinterpretation.

Stratigraphic and geographic distribution.

Paleocene - Morocco: Soko el Arba de Beni Hassan (Fallot et al., 1956). Late Rupelian and Chattian -

M. fructiferum		Holotype		Isotype	
		range	mean (s.d.)	range	mean (s.d)
Ventral core	L	8-30	16.5 (4.88) n=51	8-25	15.2 (5.49) n=25
	D	5-15	9.8 (2.11) n=54	8-11	09.8 (1) n=18
Periph. region	L	6-22	11.6 (4.78) n=19	6-25	13.2 (4.87) n=36
	D	5-9	7.3 (1.48) n=19	5-10	7.3 (1.73) n=19
Conceptacles	D	250-600	424.5 (105.2) n=20	230-640	447.3 (122.48) n=11
	H	140-270	212.5 (38.5) n=20	150-280	215.5 (44.57) n=11
	ratio D/H	1.5-3.5	2 (0.55) n=20	1.2-3	2.1 (0.51) n=11
Roof thickness		25-50		30	

Tab. 1 - *Mesophyllum fructiferum* Airoldi. Biometry of holotype and isotype specimens. Measures in µm. L=length, D=diameter, H=height, n=number of observations.

NW Italy: Tertiary Piedmont Basin, Molare Formation (Airoldi, 1932; Mastrorilli, 1968; Fravega & Vannucci, 1980a, 1980b; Fravega et al., 1987; Piazza, 1989; Vannucci, personal data on Molare, Spigno Monferrato and Mioglia areas). Early Miocene - NW Italy: Eastern Monferrato, Pietra da Cantoni Formation (Vannucci et al., 1997). Late Burdigalian-Langhian - Southern Poland: Korytnica Basin (Pisera & Studencki, 1989). Pliocene - NW Italy: "facies astiane" of central Piedmont (Vannucci et al., 1994).

Mesophyllum obsitum Airoldi 1932

Fig. 1; Pl. 2; Tab. 2

1932 *Mesophyllum obsitum* Airoldi, p. 78, pl. XII, fig. 2.
1958 *Mesophyllum obsitum* - Ogniben, p. 63, pl. XXVII, fig. 9a-b; pl. XXVIII, fig. 9c.
1968 *Mesophyllum obsitum* - Mastrorilli, p. 290, pl. XIII, fig. 3.
1970 *Mesophyllum obsitum* - Francavilla et al., p. 667.
1988 *Mesophyllum obsitum* - Studencki, p. 34, pl. 11, fig. 5.

Holotype - Coll. Airoldi, six fragments labelled 14 and one thin section 154/14; SEM stubs 31395b11, 31395b12, 8895b5.

Type locality - Late Rupelian-Chattian of Rio Zunini, Sassello (S Tertiary Piedmont Basin, Molare Formation).

Material.

The original material consists of six small fragments labelled 14, and one related thin section 154/14 (Pl. 2, fig. 1, 3); thin section 165/154 (Pl. 2, fig. 2) and three related small fragments (locality unknown). Airoldi (1932) illustrated only thin section 154/14, which is therefore the holotype (Fig. 1, Pl. 2, fig. 4, 8). The small rock fragments labelled 14, related to thin section 154/14, were used for the preparation of SEM stubs and two new thin sections (14N and 14AN).

Description.

The fragments labelled 14 were probably parts of a single rhodolith, about 5 cm in diameter, with a nucleus made of a coral fragment. A thin layered to foliose plant (total thickness about 1.5 mm) grows over this biogenic nucleus (fig. 1). Some benthic foraminifers and bryozoans occur in the spaces between the portions of the plant.

A single algal thallus (one of the layers composing the plant) is non geniculate, with a maximum thickness of 550 µm. Thallus pseudoparenchymatous with dorsi-

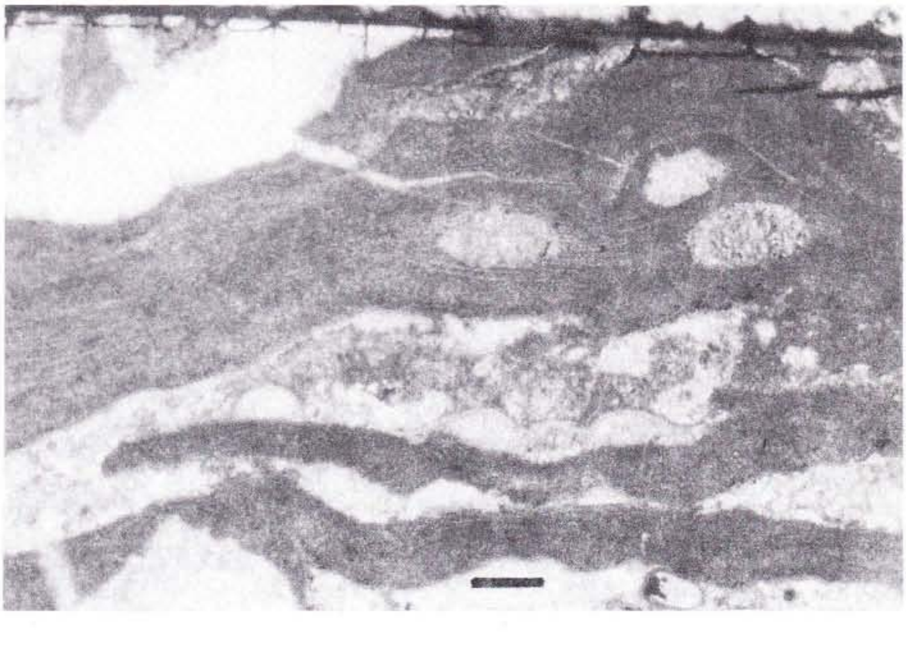


Fig. 1 - *Mesophyllum obsitum* Airoldi. Holotype, thin section 154/14. Scale bar = 200 µm.

M. obsitum		Holotype		Sections 14N - 14AN	
		range	mean (s.d.)	range	mean (s.d)
Ventral core	L	8-30	17.1 (5.91) n=75		
	D	7-12	8.3 (1.39) n=71		
Periph. region	L	5-20	8.9 (2.99) n=33		
	D	6-8	6.7 (0.8) n=25		
Conceptacles	D	240-360	283.3 (66.58) n=3	220-440	330 (57.07) n=15
	H	130-180	156.7 (25.16) n=3	120-250	166.6 (30.39) n=15
	ratio D/H	30-40	1.8 (0.43) n=20	1.76-2.66	1.99 (0.24) n=15
Roof thickness		25-50		20-40	

Tab. 2 - *Mesophyllum obsitum* Airoldi. Biometry of holotype and additional specimens in thin section 14N and 14AN. Measures in μm. L=length, D=diameter, H=height, n=number of observations.

ventral internal organization; monomerous, with a coaxial to noncoaxial ventral core, parallel to the surface of the plant, with a thickness ranging from 50 to 150 μm (Pl. 2, fig. 4, 5).

Cells of core filaments are 8-30 μm long and 7-12 μm in diameter. Smallest cells are at the periphery and longest cells (18-30 μm) in the central part of the core.

The peripheral region is 50-300 μm thick and reaches 420 μm in correspondence with conceptacles. Cell length is 5-20 μm. Cells 11-20 μm long are present only in fertile portions of the thallus, close to the conceptacles (Pl. 2, fig. 8). In the sterile, thickest portions of the thallus, layers of cells longer (10 μm) than the over- and underlying cells (6-7 μm) may be observed (Pl. 2, fig. 4); cell diameters range from 6 to 8 μm. Sterile portions of the thallus show a distinct horizontal cell alignment (Pl. 2, fig. 4, 6).

Cell fusions are evident in the ventral core and also occur in the peripheral region (Pl. 2, fig. 6). Epithallial cells are 6-8 μm in diameter and 3-5 μm long; they appear as a distinct layer of platy, rectangular cells (Pl. 2, fig. 7).

The few sporangial conceptacles occurring in the section are multiporate, elliptical with rounded lateral walls and flat floor (D 240-360 μm x H 130-180 μm) (Fig. 1; Pl. 2, fig. 8). The D/H ratio ranges from 1.38 to 2.25. Roof thickness is about 30 μm.

Thin section 165/154 and three related small fragments of unknown provenance are sterile and no diagnostic features were recognised.

Sections 14N and 14AN provide further information on the fertile portions of the thallus (Pl. 2, fig. 5, 9). Conceptacles range from 220 to 440 μm in diameter and from 120 to 250 μm in height. The D/H ratio ranges from 1.76 and 2.66. Roof thickness is 20-30 μm.

Section 14AN shows a maximum thickness of the peripheral region of 600 μm, with three layers of conceptacles.

Remarks.

As already noted for *M. fructiferum*, we found a discrepancy between our observations and the size of cells and conceptacles reported by Airoldi. This problem was already recognised by other authors (Ogniben, 1958). Later authors (Mastrorilli, 1968; Francavilla et al., 1970; Studencki, 1988) identified the species on the basis of Ogniben (1958), since they reported dimensional ranges fitting with Ogniben's description. Moreover, the conceptacle described and illustrated by Airoldi (1932, p. 78, pl. 12, fig. 2b) is simply a void between two interwoven portions of a thallus.

PLATE 2

Fig. 1 - *Mesophyllum obsitum* Airoldi. Holotype, thin section 154/14. The script "14" and "*Mes.*" at the top and "*Lithoph. obsitum*" at the bottom is in Airoldi's handwriting. Magnification as in fig. 3.

Fig. 2 - *Mesophyllum obsitum* Airoldi. Isotype, thin section 16. The script "*Lithoph. obsitum*" at the top and "*Mes.*" at the bottom is in Airoldi's handwriting. Magnification as in fig. 3.

Fig. 3 - Rock fragments labelled 14, from which thin section 154/14 was obtained. Scale bar = 1 cm.

Fig. 4 - *Mesophyllum obsitum* Airoldi. Thin section 154/14. Ventral core of cell filaments. Bottom right the original Airoldi's drawing (Airoldi, 1932, pl. XII, fig. 2a). Scale bar = 100 μm.

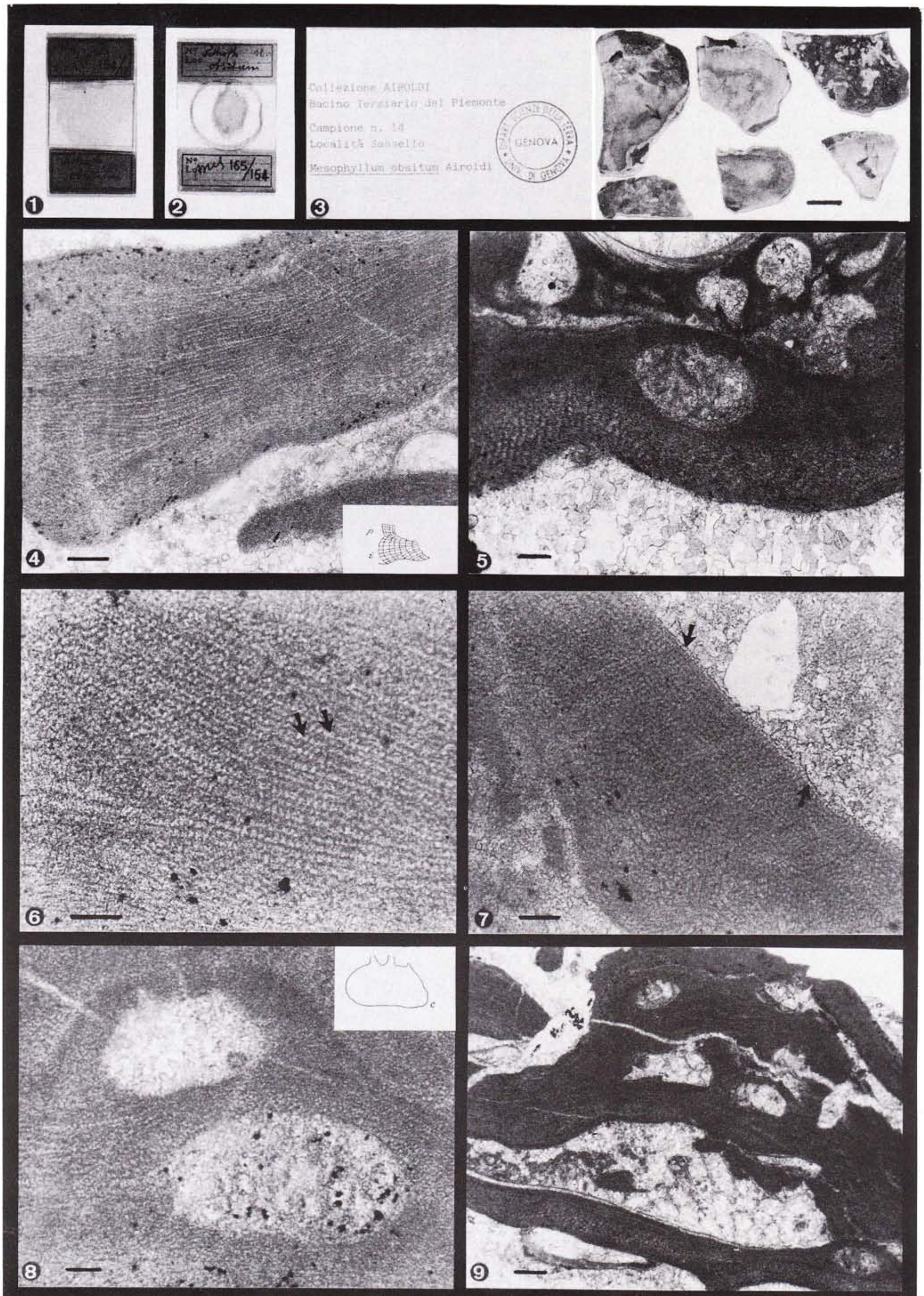
Fig. 5 - *Mesophyllum obsitum* Airoldi. Thin section 14AN. Ventral core and peripheral region with one multiporate conceptacle. Scale bar = 100 μm.

Fig. 6 - *Mesophyllum obsitum* Airoldi. Thin section 154/14. Cell fusions (arrow) in the peripheral region. Scale bar = 50 μm.

Fig. 7 - *Mesophyllum obsitum* Airoldi. Thin section 154/14. A single layer of epithallial cells is visible at the surface of the thallus (arrow). Scale bar = 50 μm.

Fig. 8 - *Mesophyllum obsitum* Airoldi. Thin section 154/14. Multiporate conceptacles. Top right the original Airoldi's drawing (Airoldi, 1932, pl. XII, fig. 2c). Scale bar = 50 μm.

Fig. 9 - *Mesophyllum obsitum* Airoldi. Thin section 14N. A thallus protuberance. Scale bar = 200 μm.


Collezione AIROLDI
Bacino Terziario del Piemonte
Campione n. 14
Località Sassello
Mesophyllum obsitum Airoldi
GENOVA
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Stratigraphic and geographic distribution.

Late Eocene - NE Italy: Colli Berici (Francavilla et al., 1970). Oligocene - NE Algeria: El Karn (Durand Delga, 1955). Late Rupelian and Chattian - NW Italy: Tertiary Piedmont Basin, Molare Formation (Airoldi, 1932; Mastrorilli, 1968; Lorenz, 1969; Fravega et al., 1994; Vannucci, personal data on Dego and Cairo Montenotte area). Lower Miocene - NW Italy: Tertiary Piedmont Basin, Rocchetta Formation (Vannucci et al., 1993). Middle Miocene - Central Poland: Pinczów Limestones (Studencki, 1988). Late Langhian-Serravallian - S Italy: Casertano, Mastroianni Formation (Ogniben, 1958).

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