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Morphology-anatomy of *Mesophyllum macroblastum* (Hapalidiaceae, Corallinales, Rhodophyta) in the Northern Adriatic Sea and a key to Mediterranean species of the genus

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Abstract – The coralline red alga *Mesophyllum* (Hapalidiaceae) is recorded for the first time from the Gulf of Trieste (Northern Adriatic Sea) and gametangial plants of *M. macroblastum* are recorded for the first time from the Mediterranean Sea. A morphological-anatomical account is provided, including comparisons with specimens from the western coast of Italy and with published data. Distribution and habitat information, comparison with Mediterranean species of *Mesophyllum*, and a dichotomous key to Mediterranean species are included along with brief comments on other species in the genus known to produce volcano-like tetrasporangial conceptacles.

Corallinales / Hapalidiaceae / Mediterranean Sea / *Mesophyllum macroblastum* / Northern Adriatic / taxonomy

Résumé – Le genre *Mesophyllum* (Hapalidiaceae), est signalé pour la première signalisation pour le Gulf de Trieste (Nord Adriatique) et un pied gamétangial de *Mesophyllum macroblastum* (Foslie) Adey est observé pour la première fois en Méditerranée. *M. macroblastum* est décrit et comparé avec des spécimens récoltés sur le littoral occidental de l'Italie. La distribution et des informations sur l'habitat, autant que la comparaison avec les espèces Méditerranéen de *Mesophyllum* sont reportées. Une clé dichotomique des espèces de *Mesophyllum* connues jusqu'au présent pour la Méditerranée est proposée avec des commentaires sur les autres espèces du genre qui produisent des conceptacles tétrasporangiaux en forme de volcan.

Corallinales / Hapalidiaceae / Mer Méditerranée / *Mesophyllum macroblastum* / Adriatique Nord / taxonomie

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INTRODUCTION

All five species of the coralline red algal genus *Mesophyllum* (Hapalidiaceae, Corallinales, Rhodophyta) reported from European waters by Cabioch & Mendoza (2003) are also reported to occur in the Mediterranean Sea. *Mesophyllum expansum* (Philippi) Cabioch & Mendoza is based on a type from an unknown locality in Sicily; *M. macroblastum* (Foslie) Adey was originally described from the Gulf of Naples (Tyrrhenian Sea); *M. alternans* (Foslie) Cabioch & Mendoza is typified by a specimen from Tangiers, Morocco, and *M. macedonis* Athanasiadis is based on a type from the Aegean Sea in Greece. The fifth species, *M. lichenoides* (J. Ellis) Marie Lemoine, is epitypified with a specimen from southern England (Woelkerling & Irvine 2007). Based on data in Cabioch & Mendoza (2003) and Bressan & Babbini (2003), *M. lichenoides* is distributed throughout the Mediterranean Sea, but Athanasiadis & Neto (2010: 337, 340) suggest that its occurrence in the Mediterranean requires confirmation. *M. expansum*, *M. macroblastum* and *M. alternans* are restricted to the western Mediterranean, and *M. macedonis* is reported only from its type locality (Pidgeon Cave, near Sarti, Greece). There is no published key to Mediterranean species of *Mesophyllum*.

Within the Adriatic Sea, there are unconfirmed records of *M. macroblastum* from an unspecified locality in the central Adriatic (Ercegovic, 1980; record repeated in Babbini & Bressan 1997 and in Furnari *et al.* 1999) and near Sušac Island in the southern Adriatic (Rac & Lovric, 2002). To date, however, no species of *Mesophyllum* has been reported from the Gulf of Trieste in the northern end of the Adriatic.

This paper presents an account on the first records of *Mesophyllum* from the Gulf of Trieste and the first record of gametangial plants of *M. macroblastum* from the Mediterranean Sea. Comparisons with recently collected specimens of *M. macroblastum* from the Tyrrhenian Sea (Pianosa Island) and with published data on the type (Gulf of Naples, Tyrrhenian Sea) and on specimens from Australia and New Zealand are included. Distribution and habitat data, along with comparisons with other Mediterranean species of *Mesophyllum*, a dichotomous key to Mediterranean species, and brief remarks on other species in the genus known to produce volcano-like conceptacles, are also provided.

MATERIALS AND METHODS

Gulf of Trieste samples were collected in August 2008 and April 2009 at the Trezza San Pietro (Fig. 1). For comparison, two additional tetrasporophytic specimens from Pianosa Island in the Tyrrhenian Sea (west coast of Italy) were also examined. All specimens were preserved in a 4% formaldehyde-seawater. Fragments of Gulf of Trieste material were analysed by scanning electron microscopy (SEM) after being prepared by air drying and then mounting them on aluminium stubs with acrylic adhesive. Stubs were sonicated with a Vitec sonicator to remove sediment and diatoms and then coated with gold/palladium (with S150 Sputter Coater, Edwards) prior to viewing in a LEICA Steroscan 430i at 20 kV. Tyrrhenian Sea specimens were prepared for SEM by air-drying fertile fragments of the thallus or small pieces of longitudinally fractured material and

Fig. 1. Sampling site: Trezza San Pietro - Gulf of Trieste (45º36, 2237N – 13º20, 3007E).

then mounting on aluminium stubs with « Fotobond » acrylic adhesive (Agfa-Gevaert). The stubs and materials were the coated with gold (Emitech K550) and observed with a Philips XL 20 SEM operating at 15 kV.

Anatomical terminology follows Woelkerling (1988) and growth-form terminology follows Woelkerling *et al.* (1993). Herbarium abbreviations are those used in Index Herbarium, formerly in print (Holmgren *et al.* 1990) and more recently online electronically (Holmgren & Holmgren 1998, continuously updated). Voucher specimens have been lodged at PC [Département Systématique et évolution (bâtiment de Cryptogamie), Muséum national d'histoire naturelle, Paris].

RESULTS AND DISCUSSION

Mesophyllum macroblastum (Foslie) Adey, 1970: 25.
Basionym: *Lithothamnion macroblastum* Foslie, 1897: 16.
Holotype: TRH (Department of Botany, Museum of Natural History and Archaeology, University of Trondheim, Trondheim, Norway), Foslie Herbarium, B16-2435.
Type locality: Gulf of Naples, Italy.

Specimens examined:
Gulf of Trieste (Northern Adriatic), Italy: Trezza San Pietro (45º36, 2237N – 13º20, 3007E), *leg. D. Poloniato*, April 2009, 15 m depth, PC 0116485. Trezza San Pietro (45º36, 2237N – 13º20, 3007E), *leg. D. Poloniato*, April 2009, 15 m depth, PC 0116486. Trezza San Pietro, (45º36, 2237N – 13º20, 3007E); *leg. D. Poloniato*, August 2008, 15 m depth, PC 0116487.

Tuscany (Tyrrhenian Sea), Italy: La Scarpa, Pianosa Island (Tuscan Archipelago) (42°34.861' N - 10°05.905' E), *leg D. Racano*, October 2006, 30 m depth, PC 0116488. La Scarpa, Pianosa Island (Tuscan Archipelago) (42°34.861' N - 10°05.905' E), *leg D. Racano*, October 2006, 30 m depth, PC 0116489.

Gulf of Trieste and Tyrrhenian Sea plants

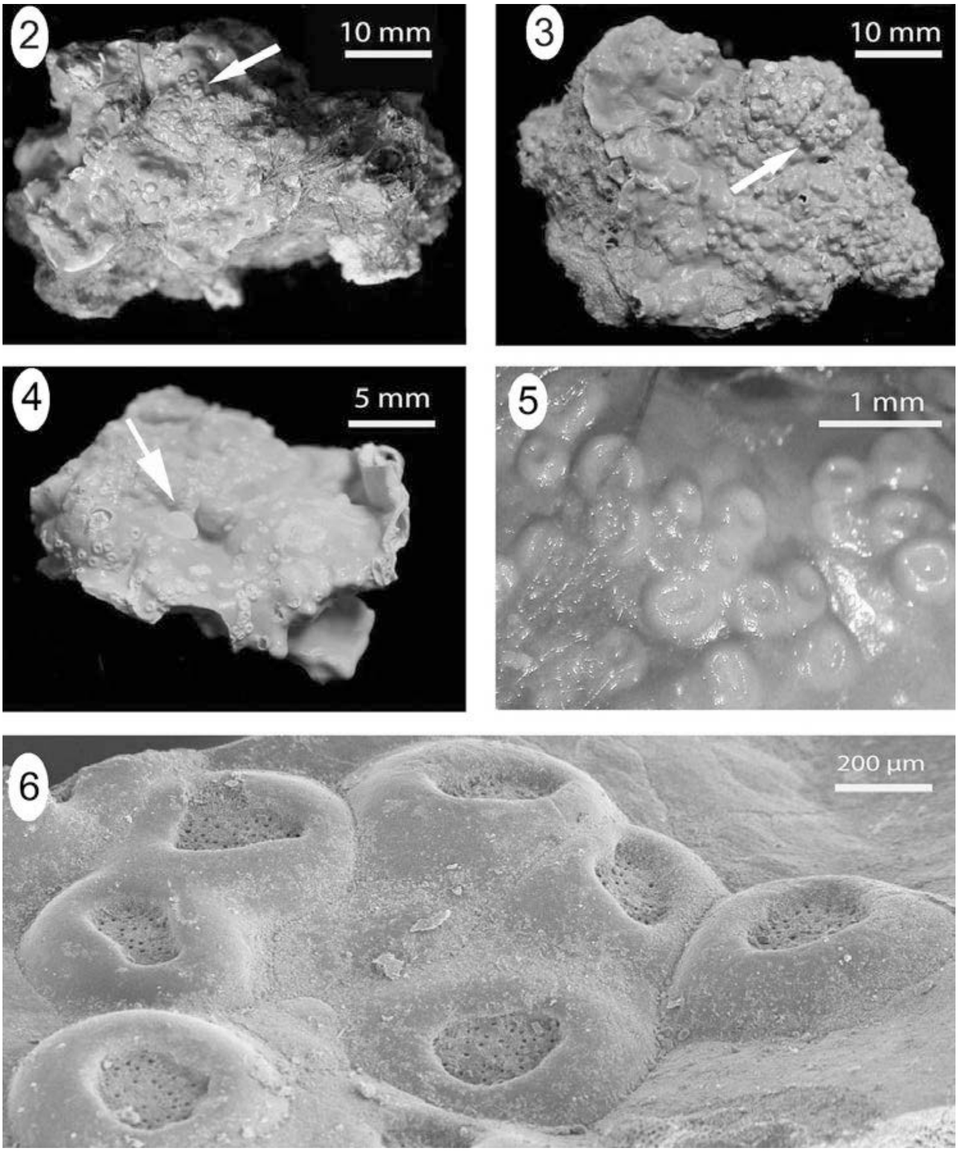
Vegetative features: Plants growing at Trezza San Pietro (Gulf of Trieste) are encrusting to warty or inconspicuously layered (applanate branching generally visible only in section) in growth form (Figs 2-3), grew attached to rock, and are up to 50 mm across and 0.2-0.8 mm thick. Pianosa Island (Tyrrhenian Sea) plants are similar, both epilithic and epizoic plants were collected, and several applanate branches are visible in surface view (Fig. 4).

Plants from both localities are pseudoparenchymatous and have a dorsiventral organization. They also have monomerous construction (Figs 9, 16, 17) with a single system of branched filaments forming a broad ventral or central core region and a perhiperal region in which core filaments or their derivatives curve outward towards the thallus surface. In the core region, filaments are coaxial, with cells of adjacent filaments aligned in arching tiers. Filaments terminate at the thallus surface in one or sometimes 2-3 epithallial cells with more or less flattened outer walls (Figs 11-12). When present, filaments with 2-3 epithallial cells occur in patches and are interspersed with patches of filaments with one epithallial cell. Epithallial cells are subtended by initials that are as long or longer than their immediate inward derivatives.

In surface view (Figs 10, 14, 15), cells (which may or may not be epithallial cells) are more or less polygonal. Like various other corallines (e.g. see Garbary & Veltkamp, 1980; Woelkerling & Irvine, 1986: 382; Wilks & Woelkerling, 1994: 200 & fig. 18; Wegeberg & Pueschel, 2002: 243, Table 1), distal walls of epithallial cells of *Mesophyllum* almost certainly are not calcified or are only lightly calcified. Consequently, in dried specimens and in specimens prepared for scanning electron microscopy, epithallial cells commonly collapse or are damaged or are lost. When this occurs, the underlying cell and the primary pit connection that originally linked that cell to the lost or damaged epithallial cell becomes visible (Figs 10, 14).

Within the thallus, cells of the same filament are always linked by primary pit-connections, while cells of adjacent thallus filaments (other than epithallial cells and subepithallial initials), are commonly but not always linked by cell fusions (Figs 9, 11).

Tentative evidence for the occurrence of a possible trichocyte (Fig. 14) was seen in a roof of a young multiporate conceptacle in a Tyrrhenian Sea plant. Trichocytes (see Woelkerling, 1988: 17) sometimes produce hair-like extensions that protrude above the thallus surface and eventually abscise or break off, leaving a pore-like hole that is visible in surface view. In the Tyrrhenian Sea plant, this pore like hole was about 3 μm in diameter and surrounded by 6 cells. By contrast, pores of tetrasporangial conceptacles are 10-12 μm in diameter and normally surrounded by 8-10 cells (compare Figs 14-15). We have not, however, seen trichocytes in sectional view, and no similar holes were seen in Gulf of Trieste plants. If confirmed by further study, this represents the first record of trichocytes in *Mesophyllum macroblastum*. Trichocytes have been recorded in several species of *Mesophyllum*, but their occurrence is not considered taxonomically significant (see Woelkerling & Harvey, 1993: 576-577).



Figs 2-6. *Mesophyllum macroblastum.* **2.** Encrusting tetrasporangial plants on rock. Note volkano-like conceptacles (arrow). **3.** Encrusting to warty plants on rock; note uniporate conceptacles (arrow). **4.** Tetrasporangial plant consisting of two main superimposed lamellae; note applanate branch (arrow). **5, 6.** Surface views of tetrasporangial conceptacles with sunken pore plates. (**2**, PC 0116486; **3**, PC 0116487; **4**, PC 0116488; **5-6**, PC 0116485).

A comparative summary of data on vegetative features and measured characters for Gulf of Trieste and Tyrrhenian Sea specimens examined during this study appears in Table 1.

Table 1. Comparative data for *M. macroblastum*: vegetative features. Sources: **(a)** Foslie, 1897; **(b)** Present study; **(c)** Woelkerling and Harvey, 1993; **(d)** Woelkerling, 1996; **(e)** Cabioch & Mendoza 2003; **(f)** Harvey *et al.*, 2003; **(g)** Harvey *et al.*, 2005; **(h)** Volpi & Benvenuti (2009); i) Farr *et al.* 2009. nd = no data

Feature / *Locality*	*Gulf of Trieste (Trezza S. Pietro) (b)*	*Tyrrhenian Sea (b) (h)*	*Gulf of Naples (Holotype TRH) (a) (c)*	*France (Port Cros and Corsica) (e)*	*Southern and south-eastern Australia (c) (d) (f)*	*New Zeland (g) (i)*
Habitat substratum	epilithic	epilithic or epizoic	epilithic	epilithic	epilithic or epizoic, epiphytic	epilithic or epizoic
depth range	to depths of 15-16 m	subtidal from depths of 5 m to at least 30 m	27-45 m	subtidal to 15, 30-40, 90 m	intertidal in pools and subtidal to 15 m (**c**), to depths of 27 m (**f**)	intertidal & subtidal to at least 18 m
Morphology thallus form	encrusting to warty	encrusting, layered to warty	earty	encrusting to warty, or lumpy	encrusting to layered, warty or lumpy (**c**)	encrusting to warty, layered or lumpy
thallus diameter	Up to 50 mm across	35-50 mm	40-50 mm	80 mm	Up to 83 mm (**c**), 90 mm (**f**)	Up to 105 mm across
thallus thickness	200-800 µm	200-1000 µm	100-450 µm (1000 µm)	nd	0.1-20 mm 9 (**c**), 1-4 mm (**f**)	nd
adhesion	mainly attached	mainly attached, or with free margins	mainly attached	mainly attached or with partly free margins	mainly attached (**c**)	mainly attached, or with free margins
Vegetative anatomy						
trichochytes	–	(+)	nd	–	–	–
cell fusions	+	+	+	+	+	+
core region						
type of growth	coaxial	coaxial	coaxial or non coaxial	coaxial or non coaxial	coaxial or non coaxial (**c**)	nd
thickness	190-220 µm	100-300 µm	200 µm	150 µm	nd	nd
cell- length	15-22	(13) 15-22 µm	nd	nd	8-42 µm (**c**)	nd
cell- breadth	5-9	6-8 µm	nd	nd	5-12 µm (**c**)	nd
peripheral region						
thickness	up to 220 µm	120-200 (630) µm	150 µm	500 µm	nd	nd
cell length	5-11 4-8 µm	(5) 10-18 (22) µm	nd	nd	5-12 µm (**c**)	nd
cell breadth	4-8 µm	4-8 µm	nd	nd	4-9 µm (**c**)	nd
Epithallial region						
cells in surface view	polygonal	polygonal	polygonal	polygonal	nd	nd

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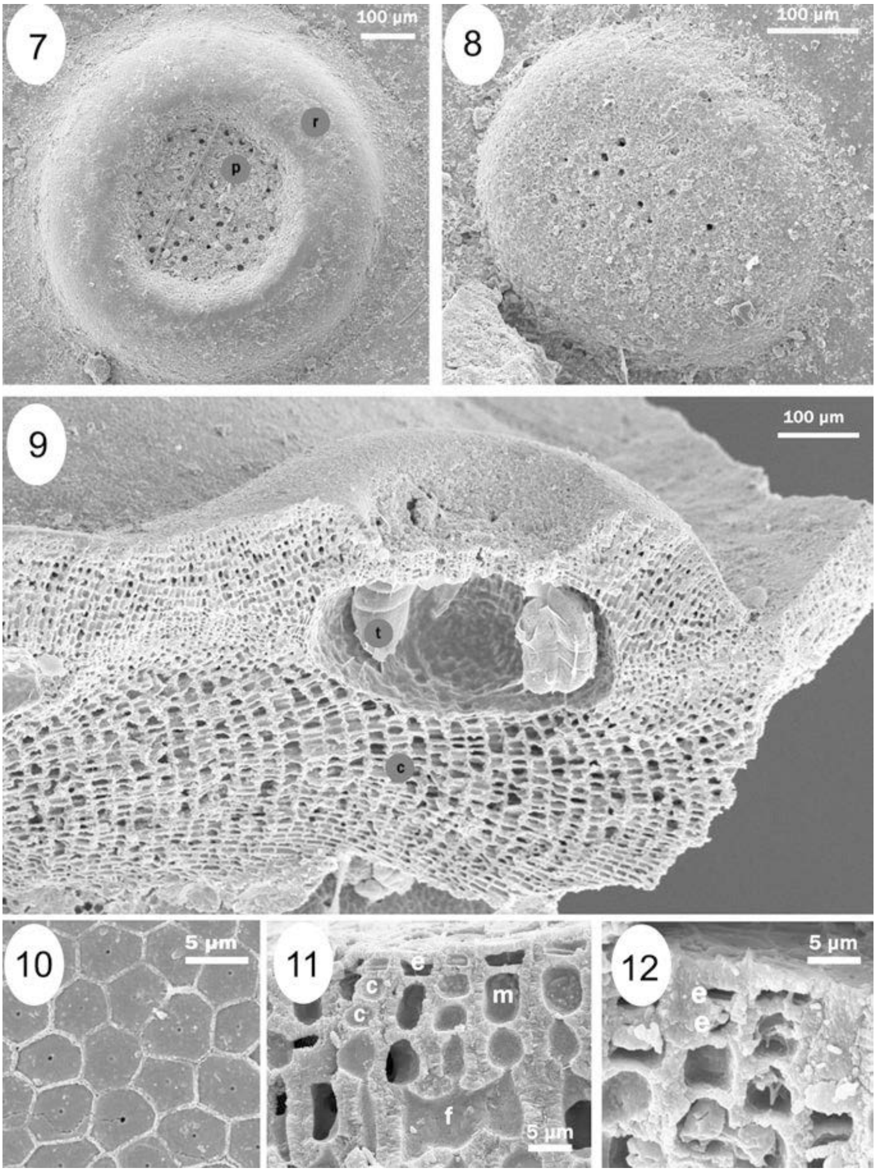
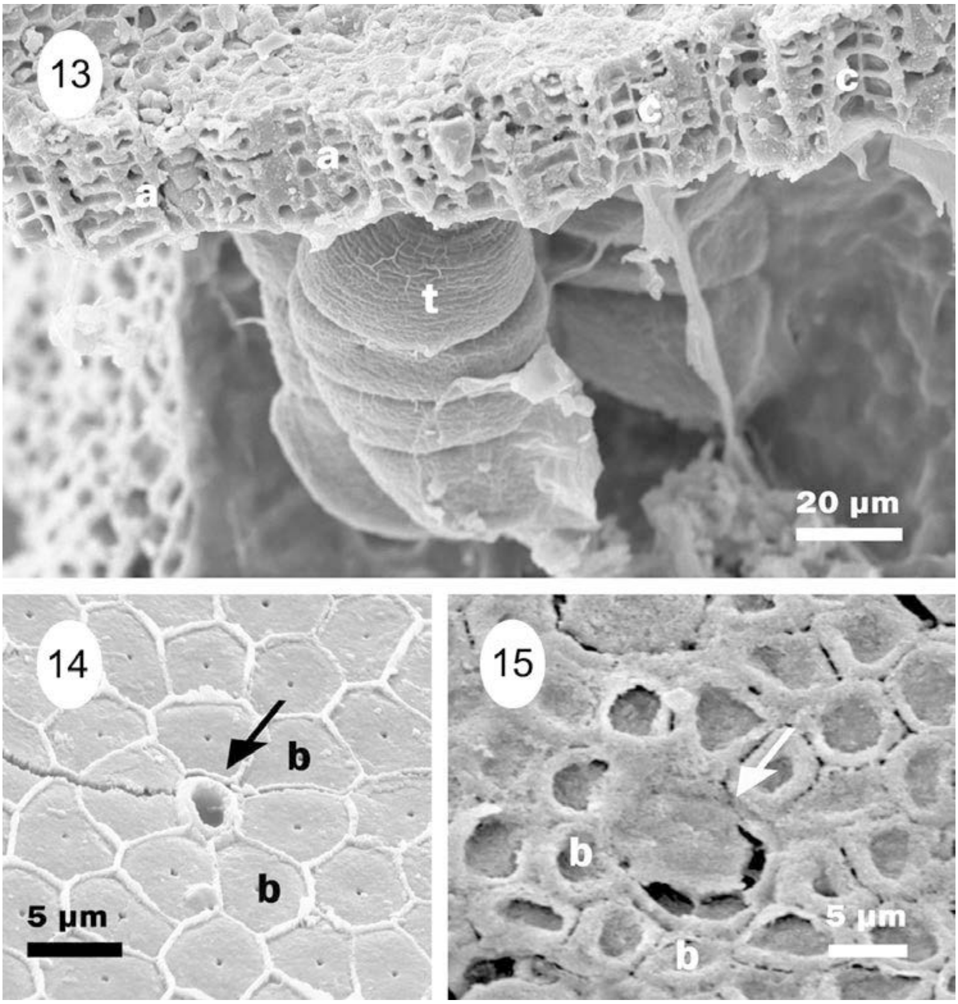
Feature / *Locality*	*Gulf of Trieste (Trezza S. Pietro) (b)*	*Tyrrhenian Sea (b) (h)*	*Gulf of Naples (Holotype TRH) (a) (c)*	*France (Port Cros and Corsica) (e)*	*Southern and south-eastern Australia (c) (d) (f)*	*New Zeland (g) (i)*
outer walls in section	flattened	flattened	nd	rounded to flattened	rounded to flattened (**d**)	rounded to flattened
number of cell layers	1-3	1	nd	nd	(1)	nd
cell diameter in surface view	6-9 µm	5-6 µm	nd	nd	5-7 µm (**f**)	nd
cell length	2-3 µm	2-3 µm	nd	nd	3-6 µm (**b**) 2-5 µm (**f**)	nd
cell breadth	5-8 µm	3-6 µm	nd	nd	nd	nd
Subepithallial initials: length compared to subtending cells	as long or longer	as long or longer	nd	nd	as long or longer (**c**)	as long or longer



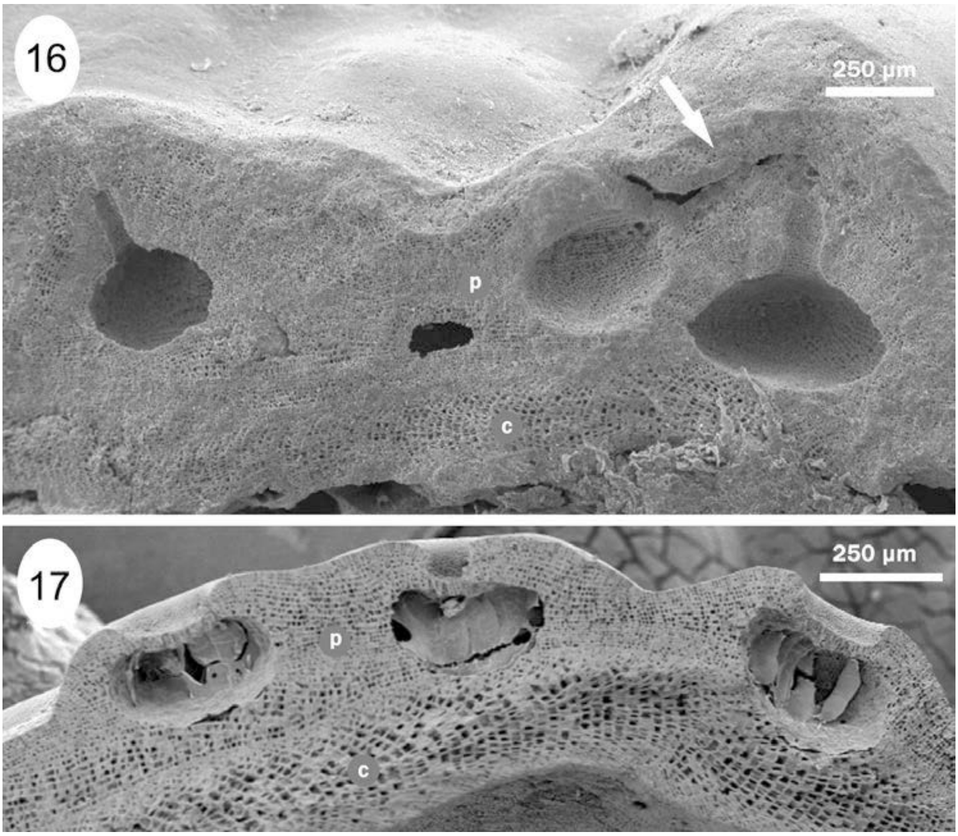
Figs 7-12. *Mesophyllum macroblastum*. **7.** Surface view of a tetrasporangial conceptacle with sunken pore plate (**p**) and peripheral rim (**r**). **8.** Surface view of a mound-like tetrasporangial conceptacle on same plant as conceptacle in Fig. 7. **9.** Longitudinal fracture through a plant showing a coaxial core region (**c**) with cells of adjacent filaments linked by cell fusions, and a mature conceptacle with tetraspores (**t**) and a sunken pore plate. **10.** Surface view of thallus showing polygonial cells. Note primary pit connections signifying where these cells were linked distally to epithallial cells (no longer present). **11.** Fracture showing flattened epithallial cells (**e**). Note subepithallial initials (**m**) slightly longer than their immediate inward derivatives, and cell-fusions (**f**) joining cells of adjacent filaments. Note also derivative cells (**c**) after division of initial cells. **12.** Fracture showing two layers of epithallial cells (**e**). (**7-9,** PC 0116485; **10, 11,** PC 0116486; **12,** PC 0116487).



Figs 13-15. *Mesophyllum macroblastum*. **13.** Tetrasporangia with zonately arranged spores (**t**). Note the pore plate showing rectangular cells lining pore canals **(c)**, with thinner cell walls if compared to other pore plate cells (**a**). **14.** Surface view showing cells with primary pit connections; epithallial cells no longer present (see text for details). Note a possible trichocyte pore (arrow) smaller than the bordering initials cells (**b**). **15.** Pore of a tetrasporangial conceptacle that is much larger than the bordering epithallial cells (**b**) and is still blocked by a tetrasporangial plug. Note collapsed or broken distal walls of epithallial cells. (**13,** PC 0116486; **14, 15,** PC 0116488).

Conceptacles: Plants with multiporate conceptacles (Figs 2, 5, 6, 7-9, 13, 17) were found both in the Gulf of Trieste and the Tyrrhenian Sea during the present study, and in addition, plants with uniporate conceptacles (Figs 3, 16) were collected in the Gulf of Trieste. The latter represent the first record of uniporate plants of this species in the Mediterranean Sea.

Tetrasporangial plants in the Gulf of Trieste and Tyrrhenian Sea had scattered to densely grouped multiporate conceptacles protruding above the



Figs 16-17. *Mesophyllum macroblastum*. **16.** Fracture showing gametangial conceptacles immersed only in peripheral region (**p**) or with chamber partly in contact with core (**c**). Note lamellate branch (arrow) overgrowing conceptacle roof. **17.** Longitudinal section through a plant showing tetrasporangial conceptacles that are either immersed in the peripheral region (**p**), or with the chamber base more or less in contact with the core region (**c**). (**16,** PC 0116487; **17,** PC 0116489).

surrounding thallus surface. Conceptacle chamber floors commonly are situated just above the coaxial core region of the thallus. Roofs of mature conceptacles are volcano-like with a perhiperal rim and a more or less sunken central pore-plate perforated by a number of pore canals (Figs 6, 13, 17). In surface view (Fig. 15), pore canals are bordered by 8-10 cells similar in shape and similar or slightly smaller in size than other epithallial cells in the pore plate. In sectional view (Fig. 13) pore canals in Gulf of Trieste plants were lined with cells that looked more or less square, appear very slightly larger than other conceptacle roof cells, and appear to have slightly thinner walls. In the Tyrrhenian Sea plants, cells lining pore canals were more or less square in sectional view, and appeared similar to or slightly larger in size to other conceptacle roof cells, which were more thick-walled. Mature conceptacles contain tetrasporangia with zonately arranged spores and apical plugs that block pore canals prior to spore release (Figs 9, 14, 17). Older conceptacles can become buried in the thallus.

Numerical and other data on Gulf of Trieste and Tyrrhenian Sea plants relating to mature tetrasporangial conceptacles is summarized in Table 2.

One Gulf of Trieste specimen (PC 0116485) with mature volcano-like multiporate conceptacles also had one multiporate conceptacle which in surface view was mound-like and did not have a sunken pore-plate (Fig. 8). This conceptacle was smaller in external diameter (360 × 420 µm) than nearby volcano-like conceptacles (540-790 µm in greatest external diameter), and it had only 10-12 evident pores in the roof rather than the 22-43 pores of nearby volcano-like conceptacles. We suspect that the mound-like conceptacle either was not fully mature or possibly was aberrant.

Another Gulf of Trieste specimen (PC 0116487) possessed uniporate rather than multiporate conceptacles. The uniporate conceptacles were more or less densely crowded and protruding above the surrounding thallus surface (Fig. 3). Unfortunately, these conceptacles appeared empty (Fig. 16), and thus we cannot be certain whether they are old male or old female/carposporangial conceptacles, although the conceptacle chamber diameter and height (Table 3) makes it more likely that they are female/carposporangial. In southern and south-eastern Australian plants (Woelkerling & Harvey, 1993; Harvey *et al.,* 2003), carposporangial conceptacles have similar dimensions while male conceptacles are smaller (see data in Table 3). Buried uniporate conceptacles also were observed (Fig. 16). This is the first Mediterranean Sea record of gametangial conceptacles in *Mesophyllum macroblastum*. In southern Australia, gametangial plants can be monoecious or dioecious (Woelkerling & Harvey, 1993; Woelkerling, 1996).

Comparisons with previous studies of *M. macroblastum*

Detailed studies of the type specimen, collected from the Gulf of Naples (Tyrrhenian Sea) have been published by Woelkerling & Harvey (1993), who also provided an account of the species in southern Australia, and by Cabioch & Mendoza (2003), who also provided an account of the species in the Mediterranean Sea. Gulf of Trieste and Tyrrhenian Sea specimens examined during the present study are largely concordant with the type material and other material studied by the above authors, leaving no doubt that these specimens belong to *Mesophyllum macroblastum*.

Woelkerling & Harvey (1993: 580, including table 5) concluded that the occurrence of volcano-like tetrasporangial conceptacles in which cells lining the pore canals were similar in size and shape to other cells in the conceptacle roof were diagnostic of *M. macroblastum*. Caboich & Mendoza (2003) reaffirmed that conclusion, and Gulf of Trieste and Tyrrhenian Sea specimens possess these characters.

Tables 1, 2 and 3 provide a summary comparison of data on *M. macroblastum* from the present study with available data on the type specimen and on the species from other recent studies. The extent of knowledge of the species varies from region to region. Thus, for example, gametangial plants are recorded only from the Gulf of Trieste, Australia and New Zealand, with most data coming from Australia. Not all studies include data for all characters listed in the Tables, and some variations are evident. In Table 1, for example, not all known growth-forms are reported for all regions, and non-coaxial as well as coaxial development is known in the holotype and plants from France and Australia, but non-coaxial growth was not evident in the Gulf of Trieste and Tyrrhenian Sea plants. Filaments terminating in more than 1 epithallial cell were observed in some Gulf of Trieste specimens but have not been explicitly reported from elsewhere. Filaments with more than one epithallial cell, however, are evident in scanning

Table 2. Comparative data for *M. macroblastum*: tetrasporangial features. Sources: **(a)** Foslie, 1897; **(b)** Present study; **(c)** Woelkerling and Harvey, 1993; **(d)** Woelkerling, 1996; **(e)** Cabioch & Mendoza 2003; **(f)** Harvey *et al.*, 2003; **(g)** Harvey *et al.*, 2005; **(h)** Farr *et al.* 2009. nd = no data

Locality / *Feature*	*Gulf of Trieste (Trezza S. Pietro) (b)*	*Tyrrhenian Sea (b) (h)*	*Gulf of Naples (Holotype TRH) (a) (c)*	*France (Port Cros and Corsica) (e)*	*Southern and south-eastern Australia (c) (d) (f)*	*New Zeland (g) (i)*
Tetrasporangial conceptacles						
shape	volcano-like[a]	volcano-like	volcano-like	volcano-like	volcano-like	volcano-like
external diameter	540-790 µm	560-760 µm	550-700 µm	550-570 µm	nd	nd
external height	80-110 µm	up to 200 µm	nd	nd	nd	nd
pore plate	170-330 µm	230-300 µm	nd	nd	nd	nd
peripheral rim thickness	(110) 130-170 µm	140-200 µm	nd	nd	nd	nd
peripheral rim height	40-80 µm	60-80 µm	nd	35 µm[b]	nd	nd
number of pores	22-43	39[b]	about 20 (a), nd (c)	nd	nd	nd
pore diameter	10-12 µm	11-13 µm	nd	nd	nd	nd
roof thickness	30 µm[b]	35-40 µm	30 µm[b]	nd	27-35 µm (**c**)	nd
number of cell layers in roof	6[b]	6-7	7-8	nd	4-5 (**c**), 6-7 (**f**)	nd
chamber diameter	310 µm[b]	300-400 µm	230 µm[b]	to 350 µm	145-270 µm (**c**)	(6)
chamber height	200 µm[b]	180-200 µm	164 µm[b]	nd	90-150 µm (**c**)	165-355 µm
disposition in thallus	in peripheral region or in contact with core region	in peripheral region or in contact with core region	in peripheral region	in peripheral region	in peripheral region (**c**) (**f**)	nd
old conceptacles buried	none observed	sometimes	nd	nd	commonly (**c**) (**f**)	nd

a. one mound-like conceptacle observed; b. based on one measurement.

Table 2. Comparative data for *M. macroblastum*: tetrasporangial features. Sources: **(a)** Foslie, 1897; **(b)** Present study; **(c)** Woelkerling and Harvey, 1993; **(d)** Woelkerling, 1996; **(e)** Cabioch & Mendoza 2003; **(f)** Harvey *et al.*, 2003; **(g)** Harvey *et al.*, 2005; **(h)** Farr *et al.* 2009. nd = no data *(continued)*

Locality / *Feature*	*Gulf of Trieste (Trezza S. Pietro) (b)*	*Tyrrhenian Sea (b) (h)*	*Gulf of Naples (Holotype TRH) (a) (c)*	*France (Port Cros and Corsica) (e)*	*Southern and south-eastern Australia (c) (d) (f)*	*New Zeland (g) (i)*
Bordering pore cells						
disposition	same level	same level	same level	same level	nd	nd
number of cells	8-10	9-10	nd	8-9		nd
appearance in surface view	like other epithallial cells or slightly smaller	like other epithallia cellsl	nd	nd	like other epithallial cells (**c**) (**d**) (**f**)	nd
appearance in section	squared, with thin walls	squared	squared	nd	squared (**c**) (**d**) (**f**)	rectangular
Other pore plate cells in section	rounded with thick walls	squared or rounded	squared	nd	squared (**c**) (**d**) squared to rounded (**f**)	rectangular
Tetrasporangia						
length	88-126 µm	130 µm[b]	nd	nd	81-135 µm	nd
breadth	49-64 µm	50 µm[b]	nd	nd	29-68 µm	nd

a. one mound-like conceptacle observed; b. based on one measurement.

Table 3. Comparative data for *M. macroblastum*: tetrasporangial features. Sources: **(a)** Foslie, 1897; **(b)** Present study; **(c)** Woelkerling and Harvey, 1993; **(d)** Woelkerling, 1996; **(e)** Cabioch & Mendoza 2003; **(f)** Harvey *et al.*, 2003; **(g)** Harvey *et al.*, 2005; **(h)** Farr *et al.* 2009. nd = no data

Locality / *Characters*	*Gulf of Trieste (Trezza S. Pietro) (b)*	*Tyrrhenian Sea (b)*	*Gulf of Naples (Holotype TRH) (a) (c)*	*France (Port Cros and Corsica) (e)*	*Southern and south-eastern Australia (c) (d)*	*New Zeland (g) (h)*
Female conceptacles						
chamber diameter	270-480 µm	nd	nd	nd	175-540 µm (**c**) (**d**)	nd
chamber height	190-280 µm	nd	nd	nd	54-270 µm (**c**) (**d**)	nd
roof thickness	120-250 µm	nd	nd	nd	80-205 µm (**c**) (**d**)	nd
number of cell layers in roof	14-34	nd	nd	nd	12-30 (**c**) (**d**)	nd
pore diameter	55-107 µm	nd	nd	nd	27-82 µm (**c**)	nd
carpogonial branches	nd	nd	nd	nd	2-3 celled (**c**) (**d**)	nd
Male conceptacles						
chamber diameter	nd	nd	nd	nd	243-310 µm (**c**) (**d**)	nd
chamber height	nd	nd	nd	nd	67-81 µm (**c**) 65-105 µm (**d**)	nd
roof thickness	nd	nd	nd	nd	62-108 µm (**c**) (**d**)	nd
number of cell layers in roof	nd	nd	nd	nd	11-16 (**c**) (**d**)	nd
pore diameter	nd	nd	nd	nd	27-46 µm (**c**)	nd
spermatangial filaments	nd	nd	nd	nd	unbranched (**c**)	unbranched

electron micrograph of the type (Woelkerling & Harvey, 1993: 623, fig. 17C) but were not recognized by those authors. These variations are not considered taxonomically significant.

Distribution and habitat

Published information on the distribution and habitat of *Mesophyllum macroblastum* in the Mediterranean Sea is limited. The species, first described as *Lithothamnion macroblastum* by Foslie (1897) from the Gulf of Naples (Italy), has been reported by Giaccone (1969, as *Lithothamnion*) in Sicily (Aci Trezza and Riserva dei Ciclopi), Ollivier (1929: 141 as *Lithothamnion*) from the Cote d'Azur (France) and Hamel & Lemoine (1953: 95, as *Lithothamnion*) from the Alpes-Maritimes (France). French specimens studied by Cabioch & Mendoza (2003, as *Mesophyllum*) were collected at Port Cros and Corsica and were growing on rocky and coralligenous bottoms at depths of 15-90 m.

Along the Tyrrhenian Sea and the French coasts of the Mediterranean, *M. macroblastum* may represent an important component of coralligenous assemblages (*sensu* Ballesteros, 2006; Volpi & Benvenuti, 2009), while in the eastern sector of the Mediterranean it appears to be a poorly documented species. The record (this study) of *M. macroblastum* on the Trezze at San Pietro in the northern Adriatic confirms the role of this species as a bio-constructor. According to Casellato and Stefanon (2008), the northern Adriatic biogenic outcrops, characterized by rich biocenoses, are comparable to the Mediterranean coralligenous assemblages but differ in having less conspicuous concretions of coralline algae. The Trezze of the Northern Adriatic Sea have been recently proposed as Sites of Community Interest (SCIs) in the context of the Habitats Directive of EU (Natura 2000, Interpretation Manual of European Union Habitats, Eur 25, October 2003, No 1180), and further studies are required for a better understanding of their evolution.

In Australia and New Zealand *M. macroblastum* has been collected in intertidal and subtidal habitats to 27 m deep on rocks, as epiphytes or on molluscs and sponges (Woelkerling & Harvey, 1993; Harvey *et al*., 2003; Harvey *et al*., 2005, Farr *et al.* 2009).

Additional substratum and habitat data are provided in Table 1.

Comparisons with other Mediterranean *Mesophyllum* species

Cabioch & Mendoza (1998, 2003) presented extensive information on the five species of *Mesophyllum* reported to occur in the Mediterranean, including data on the types of *M. alternans* (1998), *M. expansum* (1998, 2003), and *M. macroblastum* (2003). Additional data on the type of *M. macroblastum* was published by Woelkerling & Harvey (1993). The type of *M. lichenoides* has been studied by Woelkerling & Irvine (1986) (also see Woelkerling & Irvine, 2007), and the type of *M. macedonis* has been studied by Athanasiadis (1999). Cabioch & Mendoza (2003: 266, Table 1) also compared the principle characteristics of the five species, but they did not provide a species key.

Woelkerling & Harvey (1993: 577-580) concluded from an analysis of over 190 populations of species of *Mesophyllum* that characters associated with tetrasporangial conceptacle roof morphology and anatomy provided a reliable basis for delimiting southern Australian species of *Mesophyllum* from one another and from the type species of the genus (*M. lichenoides*). Subsequently, Chamberlain (2000: 377) confirmed the diagnostic value of these characters, also noting their adoption by subsequent authors, and Cabioch & Mendoza (1998: 219; 2003: 271) reaffirmed this conclusion in relation to Mediterranean species.

Within each species, Woelkerling & Harvey (1993) found that roof morphology and pore canal anatomy were constant in mature tetrasporangial conceptacles. Conceptacle roofs either were volcano-like with a peripheral rim and a sunken pore plate, or roofs were mound-like to flattened without a peripheral rim and sunken pore plate. In one species with volcano-like conceptacles (*M. printzianum*), Woelkerling & Harvey (1993: 595) also found, however, that peripheral rims may not be evident in very young conceptacles, and that in occasional conceptacles in some individuals, the rim was only marginally higher than the pore plate and thus hard to detect in surface view. In sections, by contrast, the rim and sunken pore plate always were evident.

Mature tetrasporangial conceptacles in *M. macroblastum* are volcano-like with rims that are conspicuous in surface view. With one exception (noted above), all Gulf of Trieste and Tyrrhenian Sea tetrasporangial conceptacles examined during the present study were volcano-like.

Woelkerling & Harvey (1993) also found three distinct patterns in relation to cells lining the pore canals:

1) cells lining pore canals are shorter and more squat than adjacent roof cells;
2) cells lining pore canals are narrower and more elongate than adjacent roof cells, especially near the base of the canal;
3) cells lining pore canals are similar in size and shape to other roof cells.

These patterns are illustrated diagrammatically in Fig. 18.

Pore canals in *M. macroblastum* fall into the third category, although some variation in this pattern was found during the present study. In the holotype (Woelkerling & Harvey, 1993: 624, fig. 18B) and southern Australian specimens

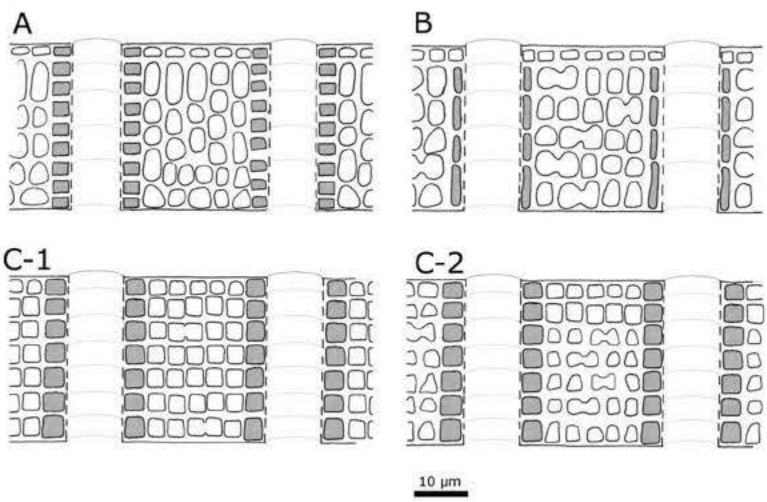


Fig. 18. Diagrams showing patters of pore canal structure: **A.** pore canals bordered by cells that are distinctly shorter and more squat than adjacent roof cells above the chamber; **B.** pore canals bordered by cells that are narrower and more elongate than adjacent roof cells above the chamber; **C1.** pore canals bordered by squared cells that are similar in size and shape to other roof cells of the pore plate; **C2.** pore canals bordered by squared cells as in C-1, but adjacent roof cells in pore plate with thicker cell walls and smaller lumens.

(e.g. Woelkerling & Harvey, 1993: 627, fig. 21 D) cells lining the pore canals as well as other roof cells all are comparatively thin walled and more or less square, as shown in Fig. 18C-1. In the Gulf of Trieste plants, roof cells not lining pore canals tend to be thicker walled and thus have smaller lumens and look slightly more irregular in shape, as shown in Fig. 18C-2. Roof cells away from pore canals in Tyrrhenian Sea specimens are intermediate in terms of wall thickness and lumen shape. Such variation has not been noted before, but appears presently to be of no taxonomic significance.

The five species of *Mesophyllum* known to occur in the Mediterranean can readily be delimited from one another (and specimens can readily be identified) using differences in tetrasporangial conceptacle roof morphology and tetrasporangial conceptacle pore canal anatomy. The dichotomous key below summarizes these differences.

Athanasiadis & Neto (2010: 340) recently reported that the number of cells surrounding pore canals is of diagnostic significance in separating *Mesophyllum expansum* from *M. lichenoides*. Athanasiadis & Neto (2010: 336, figs 12-14; 339, figs 26-29) also noted shape variation in cells lining the pore canals in both species and indicated (on p. 338) that cells lining the pore canals in *M. lichenoides* were generally smaller than neighbouring roof cells. Cells lining the pore canals of *M. expansum* were described (on p. 336) as 'differentiated or not', but no information relative to neighbouring roof cells was provided. In the dichotomous key below, we have incorporated their data on number of cells surrounding pore canals, but we have retained available published information for these two species on size of pore canal cells relative to cells of adjacent roof filaments. For completeness, we also have added data on the number of cells surrounding pore canals in *M. alternans* (sourced from Cabioch & Mendoza, 2003: 266, Table 1) and in *M. macedonis* (sourced from Athanasiadis, 1999: 241).

Key to species of *Mesophyllum* recorded from the Mediterranean Sea

1a. Tetrasporangial conceptacles volcano like, with a peripheral rim and a more or less sunken central pore plate 2

1b. Tetrasporangial conceptacles mound-like, with a flattened top that is not differentiated into a peripheral rim and a more or less sunken pore plate..... 3

  2a. Cells lining pore canals similar in size to or slightly larger than cells of adjacent conceptacle roof filaments; pore canals surrounded by 8-10 cells .... *M. macroblastum*

  2b. Cells lining pore canals much smaller than cells of adjacent conceptacle roof filaments; pore canals surrounded by 11-12 cells...... *M. alternans*

3a. Pore canals bordered by narrow elongate cells, especially near the base of the pore canal; pore canals surrounded by 4-6 cells............... *M. macedonis*

3b. Pore canals bordered by cells that are not elongate or narrow; pore canals usually surrounded by 7 or more cells.................................. 4

  4a. Cells lining pore canals generally similar in size to cells of adjacent conceptacle roof filaments; pore canals surrounded by (8) 9-11 (12) cells .... *M. expansum*

  4b. Cells lining pore canals generally much smaller than cells of adjacent conceptacle roof filaments; pore canals surrounded by (6) 7-8 (9-10) cells . ... *M. lichenoides*

CONCLUSIONS

M. macroblastum is one of five distinct species of *Mesophyllum* reported to occur in the Mediterranean Sea and the only species confirmed to occur in the northern Adriatic Sea. It also is one of two species in the Mediterranean known to produce volcano-like tetrasporangial conceptacles with peripheral rims and sunken pore-plates. The other species, *M. alternans*, which was studied in detail by Cabioch & Mendoza (1998), differs in that cells lining pore canals are much smaller in size than cells of adjacent roof filaments. In *M. macroblastum*, cells lining pore canals are similar in size or slightly larger than cells of adjacent filaments.

Four other species of *Mesophyllum* possess volcano-like tetrasporangial conceptacles with peripheral rims and sunken pore-plates: *M. printzianum* Woelkerling *et* Harvey (1993: 593) (also see Woelkerling, 1996: 204) from southern Australia, *M. capense* (Rosanoff) Chamberlain (2000) (also see Rosanoff, 1866:86, as *Lithophyllum*) from South Africa, *M. vancouveriense* (Foslie) Steneck & Paine (1986) (also see Athanasiadis *et al.,* 2004: 132), from the Pacific coasts of Canada and the USA, and *M. nitidum* (Foslie) Adey (1970: 25) (also see Foslie, 1901: 4, as *Lithothamnion*; Printz, 1929: pl. 6, fig. 10, as *Lithothamnion*; Yoshida & Baba, 1998: 599-600, Fig. 3-30, as *Mesophyllum*) from Japan. In *M. printzianum* and *M. capense*, cells lining pore canals in the type specimens are thinner (in sectional view), wider and more elongate than adjacent roof cells. Differences in those two species are summarized by Chamberlain (2000: 277). In *M. vancouvierense*, cells lining the pore canal in a Paine specimen (presumably #47A) from Tatoosh Island, Washington State, USA also were narrower and more elongate than other roof cells, but information on this feature in the lectotype apparently is lacking. Pore canal structure in the type of *M. nitidum* has not been examined in a modern context and thus the situation in this species requires clarification.

Over 140 species and infraspecific taxa have been ascribed to *Mesophyllum* according to Woelkerling (1996: 193), and Athanasiadis *et al.* (2004: 126) estimated that the genus accommodates more than 60 species worldwide. Most species, however, are poorly known. Consequently, broader comparisons of *M. macroblastum* with most other species ascribed to the genus are not possible at present.

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