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

GRAZIA VANNUCCI [1], FRANCESCA QUARANTA [1] & DANIELA BASSO [2]

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Abstract. The species originally attributed by Airoldi (1932) to the genus *Lithothamnion* (*L. roveretoi*, *L. obstrusum*, *L. stefaninii*) are here re-examined upon the original material, descriptions and illustrations. *L. roveretoi* and *L. obstrusum* are confirmed to belong to the genus *Lithothamnion*, on the basis of their epithallial and sub-epithallial morphology. *L. stefaninii* was moved by Fravega (1984) to the genus *Archaeolithothamnium*, under the nomen novum *A. airoldii.* In agreement with Fravega, we propose for *L. stefaninii* Airoldi the new combination *Sporolithon airoldii* (Fravega). According to ICBN, we select the epitype of *Sporolithon airoldii* (Fravega) comb. nov. containing both the gametangial and sporangial plants, since the holotype and isotype are ambiguous.

Riassunto. Le specie attribuite da Airoldi (1932) al genere *Lithothamnion* (*L. roveretoi*, *L. obstrusum*, *L. stefaninii*) sono revisionate sulla base del materiale, descrizione ed illustrazioni originali.

Per *L. roveretoi* e *L. obstrusum* si conferma l'appartenenza al genere *Lithothamnion* per la presenza di cellule epitalliche svasate e/o per le caratteristiche delle cellule sub-epitalliche.

L. stefaninii, già riferito da Fravega (1984) al genere *Archaeolithothamnium* con il nomen novum *A. airoldii*, viene qui denominato *Sporolithon airoldii* (Fravega) comb. nov. In base all'ICBN, per questa specie viene definito l'epitipo (contenente talli gametangiali e sporangiali) come tipo interpretativo, poiché olotipo e isotipo sono ambigui e non permettono una precisa definizione tassonomica.

Sulla base di tale revisione viene fornita la distribuzione stratigrafica e geografica delle specie.

Introduction

The present paper is the fourth contribution to the revision of 1930-32 Airoldi's original collection housed at the Department for the Study of the Territory and its Resources (Dip.Te.Ris.) of Genova University (Basso et al. 1998; Vannucci et al. 2000; Vannucci et al. 2008). Details on the history of the collection have been already given in Basso et al. (1998). The species originally attributed by M. Airoldi to the genus *Lithothamnion* (*L. roveretoi*, *L. obstrusum* and *L. stefaninii*) are here revised on the basis of the original type material, descriptions and illustrations. Specimens incompletely identified by Airoldi (1932: *Lithothamnion* sp.) have not been considered in this work.

Material and methods

The collection of fossil calcareous algae at the University of Genova was rearranged in 1967 and most thin sections were re-numbered. The new number is written before the original given by Airoldi (e.g. the thin section originally numbered 32 by Airoldi, is now labelled 160/32). The rock fragments conserved together with the corresponding thin sections were not renumbered.

The original material of *L. roveretoi* and *L. stefaninii* and *L. obstrusum* in Airoldi's collection consists of four thin sections (4.7 x 2.7 cm) and two rock samples. Three SEM stubs and thin section S4b-2004 were obtained from the rock fragment in the Airoldi's collection of *L. roveretoi*. Thin section S4b-2004 was also gold-coated and observed under SEM. The rock fragment in the Airoldi's collection of *L. stefaninii* was cut to obtain two thin sections (Fravega 1984) and four SEM stubs. SEM preparations follow the methods of Braga et al. (1993).

The synonymy list includes only those references that provide species identification through adequate description and illustrations or by direct control of relevant material.

Type localities are quoted from the original papers of Airoldi. All available published data for each species have been included in the section "Stratigraphic and geographic distribution". New samples have been collected at Mioglia and Varazze (Savona) (Rovereto 1914), the *locus typicus* respectively of *L. obstrusum* and *L. roveretoi*. Within the "Stratigraphic and geographic distribution" we added separately those references which could not be verified because of the lack of descrip-

1 Dip.Te.Ris. Univ. Genova, C.so Europa, 26, 16132 Genova, Italy. E-mail: vannucci@dipteris.unige.it
2 Dip.to di Sc. Geologiche, Univ. Milano-Bicocca, Piazza della Scienza, 4, 20126 Milano, Italy. E-mail: daniela.basso@unimib.it

tions and illustrations, and therefore excluded from further paleobiogeographic and stratigraphic considerations.

Cell measurements and abbreviations in biometric tables follow Vannucci et al. (2008). Univariate statistics was carried out for cells size in LRS (= Longitudinal Radial Section) and for the size of multiporate sporangial conceptacles, gametangial conceptacles and sporangia, and reported as size ranges, mean (M) and standard deviation (SD). The axial section of a uniporate conceptacle is the longitudinal section that cuts a conceptacle medially along the pore canal (= with visible pore canal; Afonso-Carillo et al. 1984).

Terminology of algal growth-morphology follows Woelkerling et al. (1993), while taxonomy follows Woelkerling (1988), Irvine & Chamberlain (1994), Womersley (1996) and Harvey et al. (2003). In particular, at the generic level we followed the key proposed by Braga et al. (1993) and Braga (2003). Thallus nomenclature follows Basso et al. (2004).

Systematic Palaeontology

Division **Rhodophyta** Wettstein, 1901
Class **Rhodophyceae** Rabenhorst, 1863
Order **Corallinales** Silva & Johansen, 1986
Family Hapalidiaceae Gray, 1864
(emend. Harvey et al., 2003)
Subfamily Melobesioideae Bizzozero, 1885
Genus *Lithothamnion* Heydrich, 1897 nom. cons.

Lithothamnion roveretoi Airoldi, 1932

Pl. 1, Tab. 1

Protologue. 1932 *Lithothamnium roveretoi* Airoldi, p. 66, pl. 10, figs 1a-c

1908 *Lithothamnium torulosum* Gümbel - Rovereto, p. 271

1914 *Lithothamnium torulosum* Gümbel - Rovereto, p. 98

1968 *Lithothamnium roveretoi* - Mastrorilli, p. 241, pl. 4, figs 3-4

? 1970 *Lithothamnium roveretoi* - Francavilla, Frascari Ritondale Spano & Zecchi, p. 664

1970 *Lithothamnium roveretoi* - Vannucci, p. 446, pl. 4, figs 3-4

? 1974 *Lithothamnium roveretoi* - Segonzac (in Segonzac & Charollais), pl. 20, figs 1-2

1980 *Lithothamnium roveretoi* - Fravega & Vannucci, p. 108, fig. 7

1983 *Lithothamnium roveretoi* - Bakalova, p. 56, pl. 3, fig. 4

? 1987 *Lithothamnium roveretoi* - Bucur, Mészáros & Costea, p. 33

1987 *Lithothamnium roveretoi* - Fravega, Giammarino, Piazza, Russo & Vannucci, p. 49

1987 *Lithothamnium* cf. *roveretoi* - Fravega, Giammarino, Piazza, Russo & Vannucci, p. 50

1988 *Lithothamnium roveretoi* - Fravega, Giammarino, Traverso & Vannucci, p. 210

1988 *Lithothamnium* cf. *roveretoi* - Fravega, Giammarino, Traverso & Vannucci, p. 211

1989 *Lithothamnium roveretoi* - Piazza, p. 155, pl. 4, fig. c

1989 *Lithothamnium* cf. *roveretoi* - Piazza, p. 158

? 1989 *Lithothamnion roveretoi* - Pisera & Studencki, p. 197, pl. 8, figs 1a-b

1993 "*Lithothamnium roveretoi*" - Vannucci, Stockar, Piazza & Fravega, tab. 1, p. 256, pl. 2, fig. a

1993 "*Lithothamnium* cf. *roveretoi*" - Vannucci, Stockar, Piazza & Fravega, tab. 1, p. 256

Lithothamnion roveretoi Airoldi (lectotype)		Range	M	SD	n
Hypothallial cells	L	13-20	16.9	2.1	45
	D	5-16	9.2	3.4	
Perithallial cells	L	4-15	7.8	2.7	56
	D	5-11	8.5	1.3	
Sporangial conceptacles	D	330-600	445.0	93.8	10
	H	100-130	123.0	10.6	

Tab. 1 - Biometric data of lectotype of *L. roveretoi*, thin section 145/A. The longest perithallial cells at the conceptacle sides (Pl. 1, fig. 6) are not considered here. Size in micrometers (µm) from longitudinal radial section, L=cell length; D=cell diameter (normal to length) or sporangial conceptacle diameter; H=sporangial conceptacle height; n=number of observations; M=mean; SD=standard deviation.

1994 *Lithothamnion roveretoi* - Vannucci, Piazza, Fravega & Arnera, tab. 2, p. 102

1996 *Lithothamnion roveretoi* - Vannucci, Piazza, Fravega & Abate, tab. 1, p. 73

1997 *Lithothamnion roveretoi* - Vannucci, Piazza, Pastorino & Fravega, tab. 4, p. 26, pl. 2, fig. b

? 1998 *Lithothamnion* sp.1 Bassi, p. 14, pl. 1, figs 1-6, pl. 2, fig. 1

? 2000 *Lithothamnion* sp.2 Bassi & Nebelsick, p. 112, pl. 4, figs 4-8

2000 *Lithothamnion* sp. Stockar, p. 414, pl. 1, figs 2-5

2003 *Lithothamnion roveretoi* - Vannucci, Quaranta, Piazza & Fravega, tab. 2, p. 38

Lectotype: Airoldi collection (1930-1932), thin section A, relabelled 145/A (Pl. 1, fig. 1).

Type locality: Varazze (Savona) (S Tertiary Piedmont Basin, Molare Formation).

Material: The original material consists of one thin section (145/A). Four SEM stubs of the original rock material of "*Lithothamnium torulosum*" from Varazze have been prepared, namely: B1-9697, S4c-2004, S4a-2004 and S4b-2004 (see also under "Material and methods"). Only a small fragment is left in its original condition. Unluckily new samples from Varazze, which is the *locus typicus* of *L. roveretoi,* resulted in a poor collection of fossil corallines and failed to recover new material of *L. roveretoi*. In the protologue Airoldi did not explicitly select a type. Although thin section 145/A does not contain the algal morphologies depicted by Airoldi (1932, pl. 10, fig. 1a-c) for *L. roveretoi* (Pl. 1, fig. 2), it represents the only element of the original Airoldi's collection, and therefore is here defined to be the lectotype (ICBN, Mc Neill et al. 2006, art. 9.2, 9.10).

Description. The fossil plant has an encrusting-warty growth form (Pl. 1, fig. 3), is 580-760 µm thick in the sterile portions of the thallus, reaching 480-1040 µm, where several layers of conceptacles occur. In some instances the thalli overgrow each other up to a thickness of 1.5 mm, creating more or less pronounced protuberances (Pl. 1, fig. 4).

Vegetative anatomy. Thallus monomerous**,** with dorsiventral organization. The hypothallium (ventral core of cell filaments) is non-coaxial, and ranges from 40 to 80 µm in thickness. The hypothallial cell filaments bend toward the thallus surface and are composed of rectangular to trapezoidal cells of 13-20 µm (M:16.9; SD:2.1) in length and 5-16 µm (M:9.2; SD:3.4) wide (Tab. 1) (Pl. 1, figs 4, 5). The peripheral region (dorsal

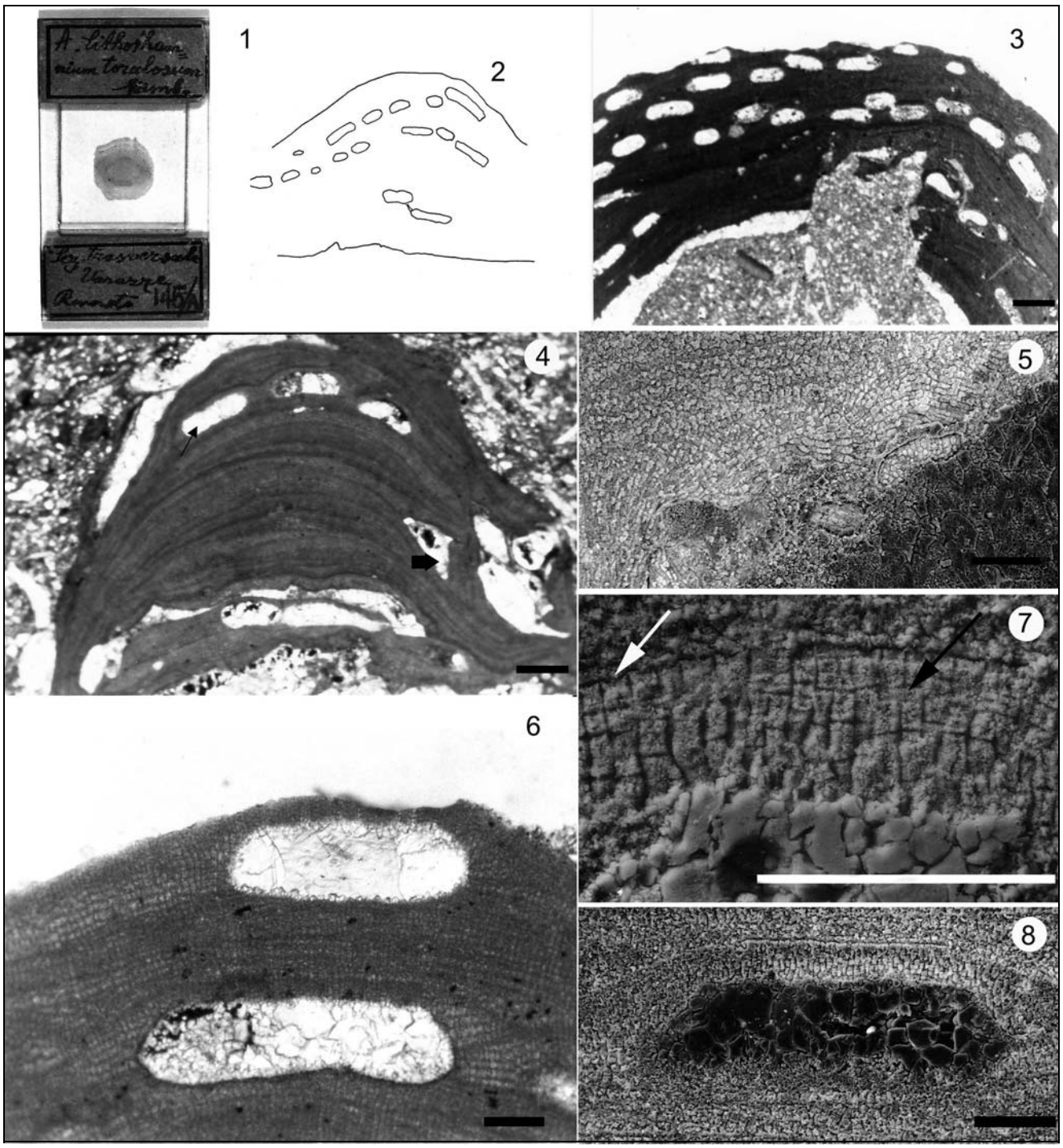

PLATE 1

Lithothamnion roveretoi Airoldi, 1932

Fig. 1 - Airoldi collection (1930-32). Thin section 145/A (lectotype of *L. roveretoi* Airoldi, 1932). The upper label reports the handwritten attribution to *L. torulosum* by Rovereto (1908-1914). Thin section is 4.1 x 2.7 cm.

Fig. 2 - Original drawing of *L. roveretoi* n. sp. (Airoldi, 1932, pl. 10, fig. 1C). This drawing could not be located in the only thin section presently conserved in the Airoldi collection (1930-32).

Fig. 3 - Lectotype. Transmitted light optical microscope (OM) photograph, thin section 145/A. Scale bar = 400 μm.

Fig. 4 - Portion of a protuberance. The hypothallium and the perithallial zonation are visible. Note the multiporate conceptacles (arrow) and the triangular cavity (arrowhead) produced by the perithallium overgrowing a foraminifer. OM photograph, thin section from stub S4b-2004. Scale bar = 250 μm.

Fig. 5 - Hypothallial cell filaments bending toward the peripheral region and toward the substrate. SEM photograph, stub B1-9697. Scale bar = 100 μm.

Fig. 6 - Multiporate conceptacle chambers in the lectotype. The "ladders" are visible at the conceptacle sides. OM photograph, thin section 145/A. Scale bar = 100 μm.

Fig. 7 - Flattened and flared epithallial cells (white arrow) and cell fusions (black arrow). SEM photograph, stub B1-9697. Scale bar = 100 μm.

Fig. 8 - Multiporate sporangial conceptacle. SEM photograph, stub B1-9697. Scale bar = 100 μm.

region=perithallium) is 500-700 µm thick in sterile portions of the thallus and 400-1000 µm in fertile portions; the perithallial cells are mainly sub-squared to locally rectangular. Their overall size is 4-15 µm (M:7.8; SD:2.7) in length and 5-11 µm (M:8.5; SD:1.3) in width (Tab. 1). At the lateral sides of the conceptacle chambers cells are longer, up to 11-18 µm (Pl. 1, fig. 6). This feature was defined *smagliature* (Italian word for ladders) by Conti (1950, pag. 56). The perithallium is weakly zoned, while in the protuberances the zonation becomes more marked (Pl. 1, fig. 4). Cell fusions are more frequently visible in the perithallium than in the hypothallium (Pl. 1, fig. 7). The epithallial cells are flat and locally flared (Pl. 1, fig. 7); the subepithallial initials are as long or longer than those subtending them. Trichocytes are not observed.

Reproductive structures. Several multiporate sporangial conceptacles have been observed. Their shape in LRS is elliptical, with flat roof and floor (Pl. 1, figs 3, 4, 6, 8, Tab. 1). Occasionally, more roundish sections of conceptacle chambers also occur. The conceptacles with preserved and visible pore canals have a diameter ranging between 330 and 600 µm (M:445; SD:93.8) and a height between 100 and 130 µm (M:123.0; SD:10.6). The pore canals are 40-60 µm long and about 10-20 µm wide. The conceptacle roof is formed by cells similar in size and shape to those of the surrounding perithallium, and has a thickness of 30-60 µm. The conceptacles are raised above the surrounding thallus surface of about 50-80 µm.

Remarks on Airoldi's original Collection of *Lithothamnium roveretoi*. The above described biometry of *L. roveretoi* confirms Airoldi's description (1932). The lectotype, however, shows a thinner hypothallium than that reported by Airoldi (1932), and it is more or less obliquely cut. Moreover, we could not locate any hypothallial cell 23 µm long, in contrast with Airoldi's report. As hypothesized by Airoldi, the conceptacles that he reports having 800 µm in diameter result from the fusion of two adjacent conceptacles. We could not observe any conceptacle filled by large-sized cells, as described by Airoldi (1932). Airoldi's unconfirmed observations could have been done on other thin sections, which are mentioned in the protologue but are presently lost.

Discussion. The vegetative and reproductive anatomy of the examined material belong to the genus *Lithothamnion.*

The species *Lithothamnium roveretoi* Airoldi is based on material originally collected and identified as *Lithothamnium torulosum* Gümbel 1871 by Rovereto (1908, p. 271; 1914, p. 98). Airoldi (1932, p. 67) observed that the structure of Rovereto's fossil coralline alga could not correspond to *L. torulosum* Gümbel, since that species would belong to the genus *Archaeolithothamnium* (=*Sporolithon*), as suggested by Rothpletz (1891) and subsequently accepted by Lemoine (1917).

We underline that:

1) Gümbel's description of *L. torulosum* (1871, p. 30, pl. 2, figs 6a, 6b) for a sample from the Oligocene of Thalberggraben includes and illustrates only the macroscopic features of the fossil plant and some possibly perithallial cells.

2) Rothpletz's description of *L. torulosum* (1891, p. 318, pl. 17, figs 2, 6) included several thalli from the Eocene of Bavaria (Kressenberg and Siegsdorf) and other localities. He compared this material with the holotype, which was deposited at the Munich Museum, and found a correspondence in characters and size of diagnostic features. In addition, Rothpletz describes and illustrates isolated sporangia in the material from Borgo Val Sugana (pl. 17, fig. 2) and describes some gametangial conceptacles in the Gümbel's material from Kressenberg and Thalberggraben (Rothpletz 1891, pl. 17, fig. 6). Rothpletz informally proposed the genus *Archaeolithothamnium* for plants possessing isolate sporangia as those occurring in the fossil coralline alga from Borgo Val Sugana.

3) Foslie (1900, pag. 8, note 2) states that "the section of the type specimen of *Lithothamnion torulosum* Gümb. pictured by Rothpletz, Foss. Kalkalg. t. 17, fig. 6 represents a true *Lithothamnion*..." with sporangial conceptacle chambers, not a gametangial *Archaeolithothamnion*, and consequently he lists the material (p. 12) as "L. torulosum Gümb. (Rothpl. ex parte)". In Foslie's opinion, the illustration on pl. 17, fig. 2 (Rothpletz, 1871) represents a different species: "A. Gumbeli Fosl. mscr. (L. torulosum Rothpl. ex parte)".

4) Lemoine (1917, p. 247) seems to ignore Foslie's comments (1900) listing "*Archaeolithothamnium torulosum* Gümb." among the Tertiary and Quaternary species.

5) Airoldi (1932) does not examine Gümbel's original material and follows Lemoine's conclusion (Lemoine 1917) that Gümbel's species belongs to the genus *Archaeolithothamnium.* However, though ignoring Foslie's conclusions (1900), he observes that the fossil coralline illustrated by Rothpletz (1891, pl. 17, fig.6) possesses multiporate conceptacles, and thus belongs to the genus *Lithothamnium*. He considers that the material collected by Rovereto (1908; 1914) is similar to that illustrated by Rothpletz (1891, pl. 17, fig. 6), nevertheless Airoldi describes Rovereto's material as the new species *L. roveretoi.*

Therefore it would be necessary to compare the type material of *L. roveretoi* with the type material of *L. torulosum* Gümbel, and with Rothpletz's material (1891) showing multiporate conceptacles. Unfortu-

nately, Gümbel's and Rothpletz's material related to *L. torulosum* is considered lost since 1912 (written personal communication to GV by Helmut Mayr, curator of the palaeontological collections of the Bayerische Staatssammlung für Paläontologie und Geologie (BSPM) of Munich, 2004).

Moussavian (1993, p. 3, pl. 1, figs 2a, 3b, 4) indicates and illustrates some specimens of "*Lithothamnion torulosum* (Gümbel) n. comb." from Bavaria, without providing any description.

Since *L. torulosum* Gümbel must be considered a *species inquirenda*, and since its circumscription is outside the aim of this paper, we re-describe here the species *L. roveretoi* Airoldi (1932) pending further investigation.

We also list in the references, though with caution, other described and/or figured specimens that are morphologically, structurally and dimensionally similar to *L. roveretoi*: 1) Francavilla et al. (1970) describe *Lithothamnium roveretoi* lacking a ventral "core"; however, the visible anatomy and its biometry are concordant with *L. roveretoi* as described here. 2) *L. roveretoi* as described and illustrated by Segonzac (in Segonzac & Charollais 1974) appears to be correctly identified; however this reference must be retained with caution, since the length range of the hypothallial cells (7-27 µm) is wider than that reported in the present revision and we could not locate any conceptacle as small as 112 µm in diameter. 3) The citation of *Lithothamnium roveretoi* by Bucur et al. (1987) should be retained with caution because of the thin hypothallium and unknown size of the hypothallial cells. 4) Pisera & Studencki (1989) do not provide any biometric data of their incompletely preserved *L. roveretoi* (no visible ventral core). The authors (Pisera & Studencki 1989) declared that their *L. roveretoi* corresponded to the biometry provided by Airoldi (1932), Mastrorilli (1968) and Bakalova (1983) but this identification should be treated with caution. 5) *Lithothamnion* sp. 1 in Bassi (1998) corresponds to *L. roveretoi* Airoldi, with hypothallial cells and conceptacles size at the upper limits of the herein reported range. Bassi (1998) considers *Lithothamnion* sp. 1 to be conspecific with *Lithothamnion* sp. 1 in Bassi (1995). The latter is excluded from synonymy with *L. roveretoi* Airoldi, since the hypothallial cells are completely outside the range observed in the lectotype of *L. roveretoi*. 6) *Lithothamnion* sp. 2 in Bassi & Nebelsick (2000) matches *L. roveretoi* Airoldi, although the mean length of the perithallial cells exceeds that of the type material. Bassi & Nebelsick (2000) consider their *Lithothamnion* sp. 2 to be similar to *Lithothamnion* sp. 2 (Bassi 1995) and *Lithothamnion* sp. 2 (Bassi 1998). We consider these two latter species not conspecific with *L. roveretoi*, because of the strongly discordant cell size.

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

Lithothamnion roveretoi mostly occurs in the Paleogene. It is reported from: Upper Paleocene from Montorfano (Como, Tabiago Fm., N Italy) (Stockar 2000); Upper Eocene from Massif des Bornes in Haute Savoie, SW France (Segonzac in Segonzac & Charollais 1974) and from Calcare di Nago Fm., NE Italy (Bassi 1998); Upper Eocene from Asenovgrad, S Bulgaria (Bakalova 1983); Priabonian from Cuciulat (NW Transilvania, W Romania) (Bucur et al. 1987); Priabonian to? Lower Oligocene from Barbarano, Colli Berici – NE Italy (Francavilla et al. 1970); Lower Oligocene from Gornji Grad (N Slovenia) (Bassi & Nebelsick 2000); in an Oligocene pebble from the south-western moraine of Garda Lake deriving from the neighbouring "nullipore formations" (NE Italy, Vannucci 1970).

In the Tertiary Piedmont Basin (= TPB) (NW Italy), *L. roveretoi* ranges from the Oligocene of Conglomerati di Savignone Fm. to the Lower Miocene of Visone Fm., and in particular within the Conglomerati di Savignone Fm. in lower and middle Rupelian (biozone SB21 of Cahuzac & Poignant 1997) of Costa Merlassino (Alessandria; Fravega & Vannucci 1980); within the Molare Fm. in lower and middle Rupelian (biozone SB21) and in upper Rupelian-Chattian and middle-upper Chattian (biozone SB22A-SB23 and SB23) of different localities of the southern margin of the TPB, namely, in the SB21 of Alessandria province (Ovrano,

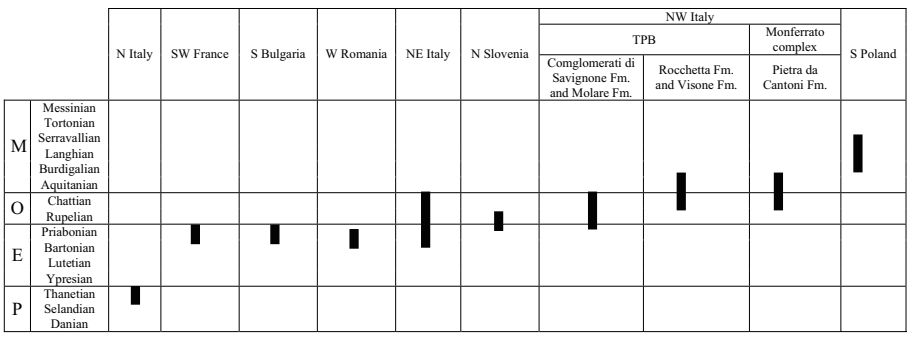

Fig. 1 - Summary of stratigraphic and geographic distribution of *Lithothamnion roveretoi* Airoldi.

Visone, Prasco, Carrosio; Mastrorilli 1968, Fravega et al. 1988), in the SB22A-23 and SB23 of Savona province (Varazze, Sassello, Dego, Millesimo; Airoldi 1932, Fravega et al. 1987, Piazza 1989, Vannucci et al. 1993, Vannucci et al. 2003) and in the Alessandria province (near Ponzone; Piazza 1989, Vannucci et al. 1997). Within the 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). Within the Visone Fm. in SB25 of Bric Cardinelle (Ponzone-Alessandria; Piazza 1989). It is recorded in the Pietra da Cantoni Fm. of the Monferrato complex (NW Italy): Aquitanian-Burdigalian of Terruggia and Rosignano (Alessandria; Vannucci et al. 1996). It is also recorded in the Middle Miocene (Badenian) of southern Poland near Korytnica (Pisera & Studencki 1989).

According to the above mentioned quotations, *L. roveretoi* occurs in the Upper Paleocene western sector of the western Mediterranean Tethyan domain; in the Upper Eocene and Oligocene is distributed in the western and northern sectors; during the Lower Miocene it appears confined to the western sector (TPB and Monferrato complex), and migrates northward into the Central Paratethys (S Poland) in the Middle Miocene.

The following references could not be checked because of the lack of descriptions and illustrations or inadequate illustrations, and therefore they have been excluded from further paleobiogeographic and stratigraphic considerations: Priabonian of Monte Baldo (Calcare di Nago Fm.) (*Lithothamnium roveretoi*, p. 124, Castellarin & Cita 1970); Upper Eocene – Lower Oligocene of eastern Berici Mounts (*Lithothamnium roveretoi,* p. 206; *Lithothamnium* cf. *roveretoi,* p. 205; Ungaro 1978); "middle" Oligocene of Hungary (*Lithothamnium roveretoi,* p. 435, pl. 53, fig. 1, Kriván-Hutter 1962).

Lithothamnion obstrusum Airoldi, 1932

Pl. 2, Tab. 2

Protologue. 1932 *Lithothamnium obstrusum* Airoldi, p. 68, pl. 10, figs 4a-e.

? 1968 *Lithothamnium obstrusum* - Mastrorilli, p. 243, pl. 5, figs 1-4

1997 *Lithothamnion* cf. *obstrusum* - Vannucci, Piazza, Pastorino & Fravega, tab. 1, p. 16.

2003 *Lithothamnion obstrusum* - Vannucci, Quaranta, Piazza & Fravega, tab. 2, p. 38.

Holotype: Airoldi collection (1930-1932), thin section 32, relabelled 160/32 (Pl. 2, fig. 1).

Type locality: Cemetery of Mioglia (Savona) (S Tertiary Piedmont Basin, Molare Formation).

Material: The original material consists of one thin section (160/32). New samples from the *locus typicus* of *L. obstrusum* failed to provide new material. In the protologue, Airoldi did not explicitly select a holotype, however, his illustrations show details of thin section 160/32 (Pl. 2, figs 2, 3, 4, 5), therefore this thin section is the holotype (ICBN, Mc Neill et al. 2006, art. 9.1, 9.13).

Description. Superposed thalli 100-250 µm thick (Pl. 2, fig. 6), with encrusting to warty growth-form (Pl. 2, fig. 2). The thickness increases to 1360-5430 µm in fertile portion of the thallus. The hypothallium is evident in the encrusting, superposed, sterile thalli (Pl. 2, fig. 6). In the superposed warty thalli it is rarely observed.

Vegetative anatomy. Thallus monomerous, with dorsiventral organization. Hypothallium (=ventral region) non-coaxial, unidirectional (*sensu* Woelkerling 1988), 30 to 200 µm in thickness (Pl. 2, fig. 7) composed of rectangular cells 8-20 µm (M:12.4; SD:2.4) long and 3-8 µm (M:5.3; SD:1.2) wide (Tab. 2). The peripheral region (=perithallium) is mostly not zoned; only in the protuberances faint zonations are observed (Pl. 2, fig. 2). The perithallium is 40-1250 µm thick when sterile, and up to 1250-5230 µm in fertile portions. The perithallial cells are sub-squared, 2-8 µm (M:4.5; SD:1.1) long and 3-9 µm (M:5.5; SD:1.4) wide (Tab. 2), and mostly not arranged in regular arrays (Pl. 2, fig. 8). Locally, some lenticular bands of longer cells (L 8-14 µm, D 4-10 µm) occur, mainly close to the hypothallium (Pl. 2, fig. 7). Cell fusions are more frequently seen in the perithallium (Pl. 2, fig. 9). Epithallial cells appear flat with subepithallial initials as long or longer than those subtending them (Pl. 2, fig. 9). Trichocytes are not observed.

Reproductive structures. Several multiporate, elliptical conceptacles occur, with flat floor and roof (Pl. 2, figs 2, 4; Tab. 2), although they can locally appear more roundish in LRS. Conceptacles with preserved pore canals are 380-640 µm (M:495.0; SD:89.6) in diameter and 90-220 µm (M:162.5; SD:41.6) in height. The pore canals are 20-60 µm long and 10-20 µm wide. The conceptacle roof is 30-60 µm thick and is formed by cells with the same size of those in the surrounding perithallium. The conceptacles are mostly raised above the surrounding thallus surface of about 50-180 µm.

Remarks on Airoldi's original collection of *Lithothamnium obstrusum.* The hypothallial cells in the type material are mostly shorter than those described by Airoldi (1932; 16-28 µm). The shape and size of conceptacles are in substantial agreement with Airoldi's protologue (1932). Airoldi's description of "sporangia in a conceptacle filled by cells" is actually referred to a foraminifer embedded in the thallus, in agreement with Mastrorilli (1968) (Pl. 2, figs 3, 5).

Discussion. On the basis of the present revision, *Lithothamnium obstrusum* Airoldi is confirmed to belong to the genus *Lithothamnion* as presently circum-

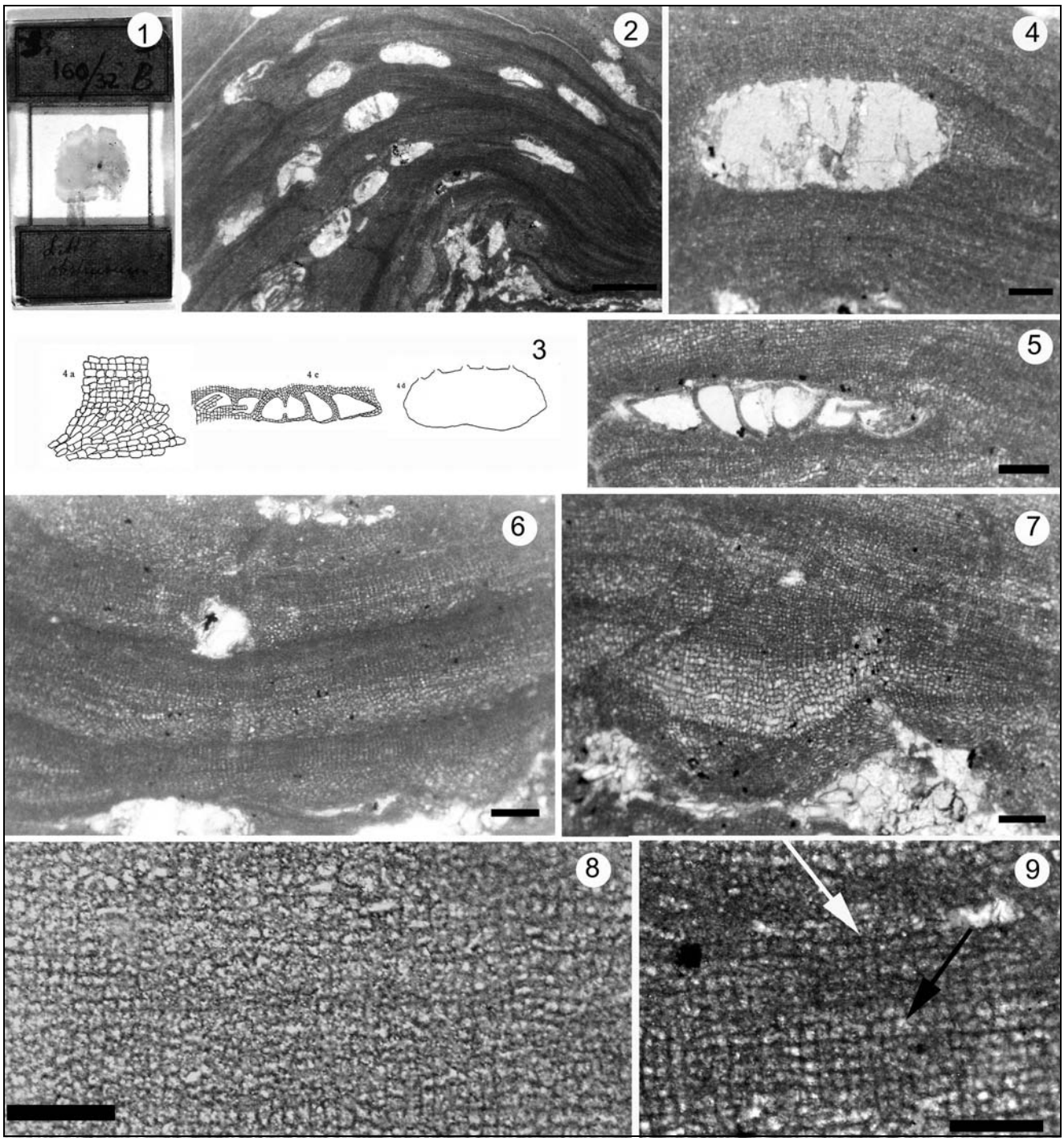

PLATE 2

Lithothamnion obstrusum Airoldi, 1932

Fig. 1 - Airoldi collection (1932-30). Thin section 160/32 (holotype of *L. obstrusum* Airoldi, 1932). Thin section is 4.1 x 2.7 cm.

Fig. 2 - Holotype. A protuberance with faint perithallial zonations. OM photograph, thin section 160/32. Scale bar = 600 μm.

Fig. 3 - *L. obstrusum* as depicted by Airoldi (1932, pl. 10, fig. 4a, 4c and 4d). The foraminifer in fig. 4c (compare Pl. 3, fig. 5) was interpreted by Airoldi to be sporangia in a conceptacle filled by large cells.

Fig. 4 - Detail of Pl. 2, fig. 2 showing a conceptacle illustrated by Airoldi, 1932, pl. 10, fig. 4d, (see also Pl. 2, fig. 3). OM photograph, thin section 160/32. Scale bar = 100 μm.

Fig. 5 - A foraminifer embedded in the perithallium. Compare Pl. 2, fig. 3. OM photograph, thin section 160/32. Scale bar = 100 μm.

Fig. 6 - Superposed portions of encrusting sterile thalli. OM photograph, thin section 160/32. Scale bar = 100 μm.

Fig. 7 - Non-coaxial hypothallium and lens-like bands of perithallial cells longer than the surrounding ones. OM photograph, thin section 160/32. Scale bar = 100 μm.

Fig. 8 - Perithallium showing the irregular arrangement of the cell filaments. The proximal and distal cell walls belonging to adjacent cell filaments appear locally aligned. OM photograph, thin section 160/32. Scale bar = 50 μm.

Fig. 9 - Flattened epithallial cells (white arrow) and subepithallial initials longer that the subtending cells. Note cell fusions (black arrow). OM photograph, thin section 160/32. Scale bar = 50 μm.

Lithothamnion obstrusum Airoldi (holotype)		Range	M	SD	n
Hypothallial cells	L	8-20	12.4	2.4	121
	D	3-8	5.3	1.2	
Perithallial cells	L	2-8	4.5	1.1	111
	D	3-9	5.5	1.4	
Sporangial conceptacles	D	380-640	495.0	89.6	16
	H	90-220	162.5	41.6	

Tab.2 - Biometric data of holotype of *L. obstrusum*, thin section 160/32. The longest perithallial cells in lenticular bands occurring near the hypothallium (Pl. 2, fig. 7) are not considered here. Size in micrometers (µm) from longitudinal radial section. Abbreviations as in Tab.1.

scribed. Reference to Mastrorilli (1968) is considered uncertain, since the 1967-1968 Mastrorilli's collection of *L. obstrusum* is badly preserved and improperly sectioned.

Stratigraphic and geographic distribution. In this section we include only those references for which we could check the correct identification of the fossil plant.

L. obstrusum is recorded exclusively in the Oligocene Molare Fm. at different localities of the southern margin of the Tertiary Piedmont Basin (NW Italy): in lower and middle Rupelian (SB21) of Bric La Valletta (SW Cassinelle, Alessandria) (Mastrorilli 1968) and Molare (Alessandria) (Vannucci et al. 1997); in upper Rupelian-Chattian (SB22A-SB23) of Mioglia (Savona) (Airoldi 1932), and in middle-upper Chattian (SB23) around Millesimo (Savona) (Vannucci et al. 2003).

The following references could not be verified because of the lack of descriptions and illustrations: Upper Eocene from Massif des Bornes (Haute Savoie, SW France) (Lemoine written communication, referenced in Segonzac & Charollais 1974, p. 118); Oligocene of Beni-Afeur (NE Algeria) (Durand Delga 1955, p. 346, as "*Lithothamnium obstrusum* Lem. du Lattorfien d'Italie").

Order **Sporolithales** LeGall & Saunders, 2009

Family Sporolithaceae Verheij, 1993

Genus *Sporolithon* Heydrich, 1897

Type species: *Sporolithon ptychoides* Heydrich

Sporolithon airoldii (Fravega) comb. nov.

Pl. 3, Tabs 3-5

Basionym: *Lithothamnium stefaninii* Airoldi, 1932, p. 62, pl. 10, figs 2, 3.

1968 *Lithothamnium stefaninii* - Mastrorilli, p.245, pl. 5, fig. 5.

1975 *Archaeolithothamnium stefaninii* (Airoldi) comb. nov. Mastrorilli in Bellini & Mastrorilli, p. 41, 43, fig. 4.3.

1984 *Archaeolithothamnium airoldii* nomen novum Fravega, p. 104, pl. 6, figs 1-5.

1987 *Archaeolithothamnium airoldii* - Fravega, Giammarino, Piazza, Russo & Vannucci, p. 46, fig. 12.

1988 *Archaeolithothamnium airoldii* - Fravega, Giammarino, Traverso & Vannucci, p. 207.

Holotype: Airoldi collection (1930-32), thin section 26, re-labelled 159/26 (Pl. 3, fig. 1A).

Isotype: Airoldi collection (1930-32), thin section 19, re-labelled 158/19 (Pl. 3, fig. 1B).

Epitype: Thin section 26/440 (Pl. 3, fig. 1C).

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

Material: The original material consists of two thin sections (159/26, 158/19). From the rock sample 26 of the original collection, corresponding to Airoldi's thin section 159/26, Fravega (1984) obtained two thin sections 26/440 (epitype) and 26/449. From the fragments of the same rock sample we obtained four SEM stubs B1-31395, B2-31395, B3-8895 and B8-8895. Only a small fragment of the original rock sample 26 is presently preserved.

In the protologue, Airoldi did not explicitly select the holotype, however, his illustrations match some details of a fertile portion of thin section 159/26, which is therefore designated as the holotype (ICBN, Mc Neill et al. 2006, art. 9.1, 9.13) (Pl. 3, figs 2A, B). The holotype thin section contains only gametangial thalli and the isotype is sterile, thus they are ambiguous and prevent a precise application of the name of the taxon. This situation requires the selection of an epitype according to ICBN article 9.7 (Mc Neill et al. 2006).

Section 26/440 contains both gametangial and sporangial thalli. This thin section was the original material used by Fravega (1984) to describe *Archaeolithothamnium airoldii* and is here selected as epitype of *Sporolithon airoldii* comb. nov. as interpretative type, under the ICBN article 9.7 (Mc Neill et al. 2006). The following description is based on the holotype, isotype and epitype.

Description. Thallus encrusting and locally warty (Pl. 3, fig. 3), up to 1340 µm thick and 3.5 cm as maximum length. Most of the total thallus thickness is composed of perithallium.

Vegetative anatomy. Thallus monomerous, with a dorsiventral organization. The hypothallium is non-coaxial, unidirectional (Pl. 3, fig. 2A) or locally plumose (*sensu* Woelkerling 1988). Hypothallium thickness ranges between 40-100 µm. The perithallium thickness ranges between 60-1240 µm. Hypothallial cells are rectangular, 6-18 µm long (M:11.0; SD:2.2) x 3-8 µm in diameter (M:5.3; SD:1.1) (Tab. 3). Perithallial cells are sub-squarish, 4-13 µm long (M:6.8; SD:1.8) x 3-9 µm in diameter (M:5.6; SD:1.4) (Tab.3). The perithallium often shows a regular array of horizontally and vertically aligned cells of adjacent cell filaments (Pl. 3, figs 4, 5). Perithallial zonation not observed. Cell fusions present (Pl. 3, figs 4, 6). Epithallial cells and trichocytes are not observed.

Reproductive structures. Elliptical sporangia (Pl. 3, fig. 7) formed within calcified compartments grouped in buried sori, each one 60-85 µm high (M:71.4; SD: 6.8) x 30-45 µm in diameter (M: 39.7; SD: 4.7) (Tab. 3). Only one complete sorus is conserved, with a maximum diameter of 560 µm. The surface of the sorus is raised 30 µm above the surrounding thallus surface. The sporan-

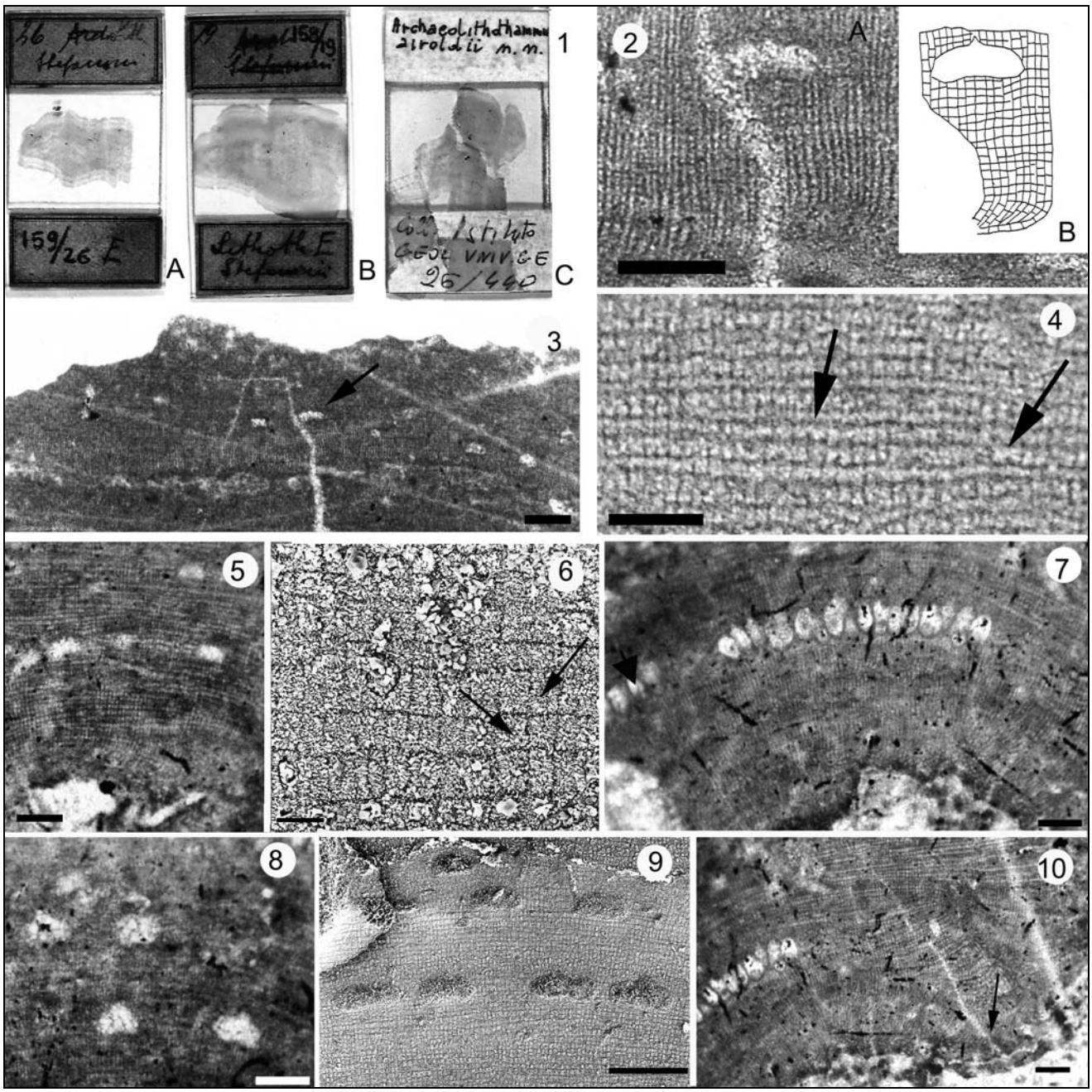

PLATE 3

Sporolithon airoldii (Fravega) comb. nov.

Fig. 1 - Airoldi collection (1930-32). A) Thin section 159/26 (holotype of *S. airoldii*). B) Thin section 158/19 (isotype of *S. airoldii*). C) Thin section 26/440 (epitype of *S. airoldii*). Actual size of thin sections is 4.1 x 2.7 cm.

Fig. 2 - A) Holotype. Gametangial thallus with non-coaxial hypothallium; the gametangial conceptacle is that in Airoldi's protologue. OM photograph, thin section 159/26. Scale bar = 100 μm. B) Original drawing by Airoldi (1932, pl. 10, fig. 3).

Fig. 3 - Holotype with superposed gametangial conceptacles. Arrow to indicate the conceptacle in fig. 2A. OM photograph, thin section 159/26. Scale bar = 200 μm.

Fig. 4 - Holotype. Perithallium with regular array of horizontally and vertically aligned cells of adjacent cell filaments. Note cell fusions connecting adjacent perithallial cells (arrows). OM photograph, thin section 159/26. Scale bar = 50 μm.

Fig. 5 - Epitype. Gametangial thallus showing organization of perithallial cells as in Pl. 3, fig. 4. OM photograph, thin section 26/440. Scale bar = 100 μm.

Fig. 6 - Cell fusions (arrows) in perithallial filaments. SEM photograph, stub B8-8895. Scale bar = 10 μm.

Fig. 7 - Epitype. Sporangial thallus with a buried sorus. Note the calcified septum separating the stalk cell (arrow). OM photograph, thin section 26/440. Scale bar = 100 μm.

Fig. 8 - Epitype. Gametangial thallus with uniporate conceptacle showing convex-upward floor. OM photograph, thin section 26/440. Scale bar = 100 μm.

Fig. 9 - Gametangial thallus. SEM photograph, stub B8-8895. Scale bar = 100 μm.

Fig. 10 - Epitype. Sporangial thallus showing non-coaxial hypothallium (arrow). OM photograph, thin section 26/440. Scale bar = 100 μm.

Sporolithon airoldii			Range	M	SD	n
Hypothallial cells		L	6-18	11.0	2.2	73
		D	3-8	5.3	1.1	
Perithallial cells		L	4-13	6.8	1.8	296
		D	3-9	5.6	1.4	
Sporangia		H	60-85	71.4	6.8	18
		D	30-45	39.7	4.7	
Gametangial conceptacles	pore canal visible	D	65-110	87.3	13.3	11
		H	25-50	37.3	8.2	
		Hpc	6-20	16.5	5.3	
	pore canal not visible	D	60-110	81.0	13.9	15
		H	20-55	38.3	9.0	

Tab. 3 - Summary of biometric data obtained from merging the type material of *S. airoldii* and its epitype. Size in micrometers (µm) from longitudinal radial section. L = cell length; D = cell diameter, (normal to the length) or sporangial diameter or gametangial conceptacle diameter; H = sporangial height or gametangial conceptacle height under the pore canal or gametangial conceptacle central height when the pore canal is not visible; Hpc = length of the pore canal; n = number of observations; M = mean, SD = standard deviation.

Sporolithon airoldii (holotype)			Range	M	SD	n
Hypothallial cells		L	8-18	11.8	2.1	33
		D	3-8	5.1	1.2	
Perithallial cells		L	5-13	7.7	2.0	80
		D	4-8	5.1	1.0	
Gametangial conceptacles	pore canal visible	D	80-110			5
		H	30-50			
		Hpc	6-20			
	pore canal not visible	D	70-90			7
		H	20-50			

Tab. 4 - Biometric data of holotype of *S. airoldii,* thin section 26/159. Size in micrometers (µm) from longitudinal radial section. Abbreviations as in Tab. 3.

gial pore is about 6.5 µm wide. A calcified septum separating the stalk cell from the sporangium is visible at the base of some sporangial compartments (Pl. 3, fig. 7). A basal layer of elongated cells does not occur at the base of sporangia. Sporangia appear rarely separated by sterile calcified filaments (paraphyses) composed of 1-2 cells, more often the sporangia are in contact (Pl. 3, fig. 7).

Uniporate gametangial conceptacles (Pl. 3, figs 2A, 8, 9), elliptical or sub-triangular in longitudinal section, with a short pore canal. The floor appears flat or sometimes convex upward (Pl. 3, fig. 8). Conceptacle chambers with visible pore canal are 65-110 µm in diameter (M:87.3; SD:13.3) and 25-50 µm in height (M:37.3; SD:8.2). The pore canal has a length up to 20 µm (M:16.5; SD:5.3). Conceptacle chambers without visible pore canal are 60-110 µm (M:81.0; SD:13.9) in diameter and 20-55 µm (M:38.3; SD:9.0) in height (Tab. 3).

Remarks on Airoldi's original collection of *Lithothamium stefaninii.* The holotype (thin section 159/26) shows several monomerous thalli with non-coaxial, unidirectional, locally plumose hypothallium (*sensu* Woelkerling 1988), 50-70 µm thick. Perithallium is 450 to 750 µm thick, where small uniporate conceptacles are buried. These conceptacle chambers appear with flat or slightly convex-upward floor. No zonation is observed. In agreement with Mastrorilli (1968, p. 247) the hypothallial cells never reach 28 µm in length as originally described by Airoldi (1932) (Tab. 4). The gametangial conceptacle that Airoldi described to have a diameter of 150 µm is actually formed by the fusion of two adjacent conceptacles. The isotype (thin section 158/19) is sterile and shows the same morphology and biometry as the holotype.

Remarks on the epitype of *Sporolithon airoldii.* In the epitype thin section the gametangial thalli (Pl. 3, figs 5, 8; Tab. 5) have non-coaxial and plumose hypothallium, 60 to 100 µm thick. The perithallium is not zoned and ranges from 100 to 1240 µm thick. Some uniporate gametangial conceptacles occur, with mostly flat floor, seldom convex upward (Pl. 3, fig. 8).

The rare sporangial thalli (Pl. 3, figs 7, 10; Tab. 5) have a non-coaxial, thin hypothallium (40-60 µm thick), rarely observed in LRS (Pl. 3, fig. 10). The perithallium is not zoned, ranging in thickness from 100 to 720 µm. Sporangia are grouped in sori, buried in the perithallium.

Selecting thin section 26/440 as epitype of *S. airoldii* is reasonable on the base of two observations: first, the vegetative anatomy and the biometry are consistent in the sporangial and gametangial thalli of the epitype (compare Pl. 3, figs 7, 10 with Pl. 3, figs 5, 8; Tab. 5); second, the gametangial thalli of the epitype are

Sporolithon airoldii (epitype)		Gametangial thallus				Sporangial thallus				
			Range	M	SD	n		Range	M	SD	n
Hypothallial cells		L	6-13	10.1	2.0	22	L	8-12			6
		D	4-7	5.4	1.0		D	4-6			
Perithallial cells		L	4-9	6.1	1.4	66	L	4-10	6.8	1.7	58
		D	3-8	5.2	1.0		D	3-7	5.0	1.0	
Sporangia							H	60-85	71.4	6.8	18
							D	30-45	39.7	4.7	
Gametangial conceptacles	pore canal visible	D	65-105			6					
		H	25-50								
		Hpc	10-20								
	pore canal not visible	D	60-110			8					
		H	30-55								

Tab. 5 - *S. airoldii,* epitype thin section 26/440. Summary of biometric data merged from gametangial and sporangial thalli. Size in micrometers (µm) from longitudinal radial section. Abbreviations as in Tab. 3.

consistent with those observed in the holotype (compare Pl. 3, figs 2A, 3 with Pl. 3, figs 5, 8 and Tab. 4 with Tab. 5).

Discussion. Airoldi (1932, p. 68) described the fertile parts of his new species *Lithothamnium stefaninii* as "piccoli concettacoli tondeggianti e reniformi, spesso muniti di un foro nel tetto" (= "small conceptacles, rounded and kidney-shaped, frequently bearing a hole on their roof") and he stated that the hypothallium and the perithallium are typical for the genus *Archaeolithothamnium*, but the fertile specimens show conceptacles and not isolated sporangia, thus pointing to the genus *Lithothamnium*.

Conti (1945, p. 63, note 3) was not sure about the placement of *L. stefaninii* in the genus *Lithothamnium* and he argued its possible inclusion in the genera *Lithophyllum* or *Archaeolithothamium*. Conti (1950, p. 114) lists *L. stefaninii* among the species of *Lithothamnium* with a dubitative formulation (*Lt.? stefaninii*).

Mastrorilli (1968, p. 247), in agreement with Conti (1950), also questioned the attribution of the species to the genus *Lithothamnium*. Later, Mastrorilli finds in the Miocene of Corsica some fertile sporangial thalli belonging to *L. stefaninii* and assign to Fravega the revision of the species. Mastrorilli anticipates Fravega's conclusions by publishing the new taxonomic disposition with the name *Archaeolithothamnium stefaninii* (Airoldi) comb. nov., specifying that Fravega was preparing a paper on the topic ("une note avec tous les reinsegnements va être publiée à ce sujet par M.lle Dr. P. Fravega"; Bellini & Mastrorilli 1975, p. 41, note 1).

Fravega (1984) concluded that *L. stefaninii* belongs to the genus *Archaeolithothamnium* by analyzing two thin sections prepared from Airoldi's original sample number 26, from which also the original thin section 159/26 was prepared. However, since the combination *Archaeolithothamnium stefaninii* was already established by Raineri (1929) for a species living in northern Somalia, and on the base of ICBN rules, Fravega (1984) establishes that the new name for *L. stefaninii* is *Archaeolithothamnium airoldii*. The current name for *Archaeolithothamnium stefaninii* Raineri 1929 is *Sporolithon stefaninii* (Raineri) Silva (Silva et al. 1996). In agreement with Fravega (1984) we propose for *Lithothamnium stefaninii* Airoldi 1932 the new combination *Sporolithon airoldii* (Fravega) comb. nov. (ICBN, Mc Neill et al. 2006, art. 53.1, 53.2).

Stratigraphic and geographic distribution. *Sporolithon airoldii* occurs in the Oligocene in the Molare Fm. of the Tertiary Piedmont Basin, NW Italy: it occurs in the lower and middle Rupelian (SB21) of Prasco and Ovrano (Alessandria) (Mastrorilli 1968) and of Val Lemme (Carrosio, Alessandria) (Fravega et al. 1988) and in the biozone SB22A-23 (upper Rupelian – Chattian) of Sassello (Savona) (Airoldi 1932; Fravega et al. 1987). It is also recorded in the upper Burdigalian-Serravallian of St. Florent (N Corsica) and of Bonifacio (Cala de Labra, S Corsica) (Mastrorilli in Bellini & Mastrorilli 1975).

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