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NEOGONIOLITHON CONTII COMB. NOV. BASED ON THE TAXONOMIC RE-ASSESSMENT OF MASTRORILLI'S ORIGINAL COLLECTIONS FROM THE OLIGOCENE OF NW ITALY (TERTIARY PIEDMONT BASIN)

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Key words: Corallinales, Mastophoroideae, Mastrorilli 1967-68 collections, taxonomy, stratigraphy.

Abstract. Recent anatomic observations of the types of *Lithophyllum contii* Mastrorilli, 1967, *Lithophyllum embergeri* Mastrorilli, 1968, *Mesophyllum flexile* Mastrorilli, 1968 and *Mesophyllum rigidum* Mastrorilli, 1968 urged their revision under modern taxonomic schemes. *Lithophyllum contii* Mastrorilli, 1967 is transferred to the subfamily Mastophoroideae and the new combination *Neogoniolithon contii* is proposed. *L. giammarinoi, L. embergeri, M. flexile* and *M. rigidum* are considered to be younger heterotypic synonyms of *L. contii*, originally established on the basis of anatomical details herein considered to be artefacts due to improper orientation of studied thalli.

Each species is critically analysed on the basis of original Mastrorilli's collections (Genoa University, Dip.Te.Ris.) and additional material collected at the type localities.

Riassunto. Recenti osservazioni di dettagli anatomici e morfologie incongruenti con l'inquadramento tassonomico originariamente attribuito a *Lithophyllum contii* Mastrorilli, 1967, *Lithophyllum embergeri* Mastrorilli, 1968, *Mesophyllum flexile* Mastrorilli, 1968 and *Mesophyllum rigidum* Mastrorilli, 1968 hanno reso necessaria la loro revisione basata su schemi sistematici moderni. Il risultato di questo lavoro consente di trasferire *Lithophyllum contii* Mastrorilli, 1967 nella sottofamiglia Mastophoroideae, sotto la nuova combinazione *Neogoniolithon contii.* Inoltre viene messo in luce che alcune differenze anatomiche, originariamente ritenute di valore diagnostico per l'istituzione delle altre specie esaminate, sono in realtà da attribuire all'imperfetta orientazione di talli osservati in sezione sottile. Pertanto è possibile considerare *L. giammarinoi, L. embergeri, M. flexile* e *M. rigidum* come sinonimi eterotipici più recenti di *L. contii.* Ciascuna specie qui trattata viene criticamente analizzata sulla base dell'anatomia microscopica e biometria rilevabili dal materiale conservato nella collezione originale Mastrorilli (Univ. Genova, Dip.Te.Ris.) e in materiale aggiuntivo proveniente dalle località tipo.

Introduction

The need to use the same diagnostic characters for the identification of living and fossil Corallinales urged paleoalgologists to undertake the revision and re-documentation of fossil type collections on modern basis and in light of current taxonomic criteria (e.g.: Piller 1994; Rasser & Piller 1994; Basso et al. 1997; Aguirre & Braga 1998; Basso et al. 1998; Vannucci et al. 2000; Bassi et al. 2005). Mastrorilli's original collections (1967 – 68) are located at the Department for the Study of the Territory and its Resources (Dip.Te.Ris.) of Genoa University. Recent observations of anatomical details and morphologies which were incongruous with the original taxonomic placement of *Lithophyllum contii* Mastrorilli, 1967, *Lithophyllum embergeri* Mastrorilli, 1968, *Mesophyllum flexile* Mastrorilli, 1968 and *Mesophyllum rigidum* Mastrorilli, 1968 urged their re-assessment under modern systematics. This paper is devoted to the description, re-documentation and critical revision of the above mentioned species of fossil Corallinales, based on Mastrorilli's original collections and additional material collected in the type localities.

Material and methods

The original material consists of 52 thin sections (4.7 cm x 2.7 cm) which include the type material of the studied species and macroscopic rock samples associated to the collection; from latter 53 dry-peels (25-45 cm^2 in average, following Brasier 1980) and 25 SEM stubs were obtained (following Braga et al. 1993). Further samples were collected at the type localities (24 thin sections of 4.6 cm x 2.7 cm

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and 6 cm x 4.5 cm; 131 dry-peels and 5 SEM specimens) with the primary aim to integrate the original collection with additional fertile thalli, since original conceptacle descriptions were inadequate.

Among the original material, each species is represented in several thin sections with different orientations. Since a correct orientation of the thallus is crucial in interpreting the organization of the ventral core (hypothallium), and in order to allow the comparison of biometric data, we distinguish longitudinal radial sections (LRS) and non-longitudinal radial sections (oblique sections). Different orientations of a coaxial hypothallium can be distinguished in oblique sections, that cause an apparent variability in size and arrangement of the hypothallial cells. For example, when the thallus is locally sectioned parallel or oblique to the basal plane (*sensu* Denizot 1968; Afonso-Carillo et al. 1984), the hypothallium shows horizontal cell walls aligned in rectilinear tiers (Pl. 1, Fig 5). When thallus is sectioned longitudinally but not radially, and/or it is observed in oblique section, the hypothallium shows horizontal cell walls arranged in sligthly arching to rectilinear tiers (Pl. 1, Fig. 6). In other cases, the hypothallium shows a transition from coaxial to plumose (*sensu* Woelkerling 1988) non-coaxial arrangement of the filaments (Pl. 1, Fig. 7).

Tables of biometric data provide dimensional ranges, mean (M) and standard deviation (SD) for cells size in LRS and in oblique sections. Although data on coralline anatomy must solely rely on properly oriented sections (LRS), we retain and present also data from non-longitudinal radial sections, since the recognition of artefacts due to improper orientation is crucial for the herein proposed synonymy of several Mastrorilli's species. The cell length (L) is measured as the distance between two primary pit-connections of the cell. The diameter (D) is the cell breath measured normal to the length. Univariate statistics was not carried out for conceptacles size because of their rarity or inadequate orientation in the available material. Their size is reported in the tables (Tabs 3-6) together with the cell size as observed with the same orientation in the same thallus where the conceptacles were found. Longitudinal sections that cut a conceptacle medially, along its pore canal, are defined as axial sections (= with visible pore canal; Afonso-Carillo et al. 1984). Kidney-shaped, sporangial conceptacle chambers typically show the maximum height (Hmax) in correspondence of the peripheral bulge, while a lesser height (H) is commonly measured at their centre, just below the pore-canal. In fossil material, we recognize trichocytes as cells that can occur solitary, in horizontal fields or in vertical row, possessing a much larger size in respect of the "normal" surrounding perithallial cells.

Terminology of algal growth-morphology follows Woelkerling et al. (1993), while taxonomy follows Woelkerling (1988), Irvine & Chamberlain (1994) and Womersley (1996). In particular, at the generic level we followed the key proposed by Braga et al. (1993), which however lacks several extant genera not recognized so far from the fossil record. Thallus nomenclature follows Basso et al. (2004).

Systematic Palaeontology

Division **Rhodophyta** Wettstein, 1901
Class **Rhodophyceae** Rabenhorst, 1863
Order **Corallinales** Silva & Johansen, 1986
Family Corallinaceae Lamouroux, 1812
Subfamily Mastophoroideae Setchell, 1943
Genus *Neogoniolithon* Setchell & Mason, 1943

Neogoniolithon contii (Mastrorilli) comb. nov.

Pls. 1, 2; Tabs. 1, 2

Basionym: *Lithophyllum contii* Mastrorilli 1967, p. 476, pls. 1, 2.

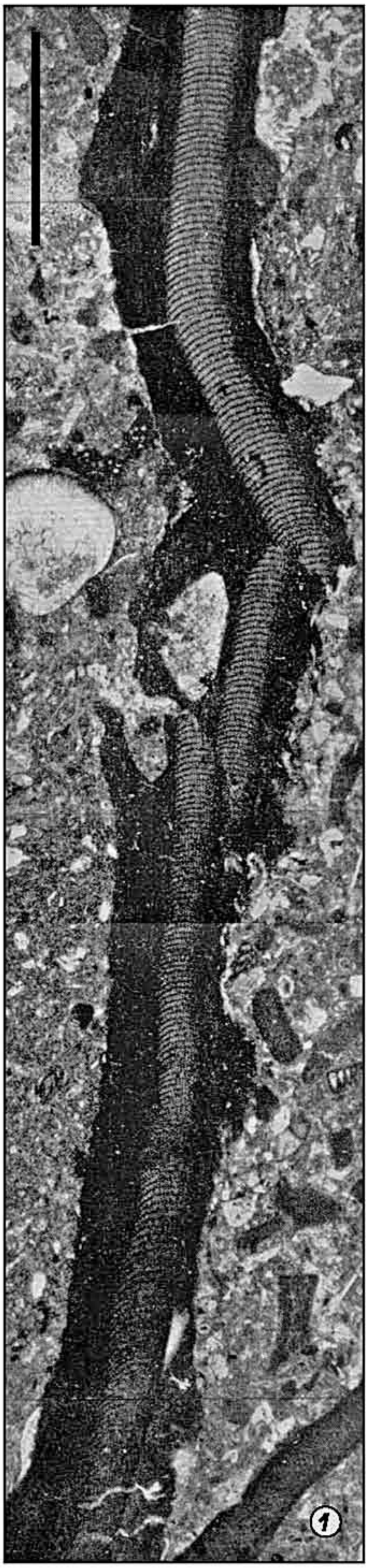
Synonyms and references:

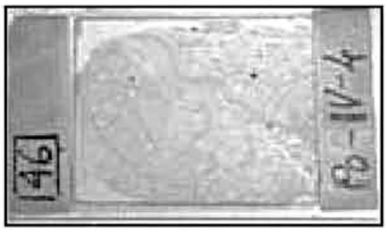
1968 *Lithophyllum contii* Mastrorilli, p. 338, pl. 25, fig. 4.
1968 *Lithophyllum embergeri* Mastrorilli, p. 349, text fig. 33, pl. 30.
1968 *Lithophyllum giammarini* Mastrorilli, p. 335, pls. 32-34.
1968 *Mesophyllum flexile* Mastrorilli, p. 307, pl. 18, fig. 1, non pl. 18, fig. 2.
1968 *Mesophyllum rigidum* Mastrorilli, p. 309, pl. 18, figs 3, 4.
1968 *Lithophyllum capederi* - Mastrorilli, p. 319, pl. 20, figs 1, 2, non *L. capederi* Lemoine, 1926.
1970 *Lithophyllum giammarini* - Vannucci, p. 464, pl. 7, figs 2, 3.
1970 *Lithophyllum giammarini* - Francavilla, Frascari Ritondale Spano & Zecchi, p. 672, pl. 86, figs 1, 2.
1970 *Mesophyllum* cf. *rigidum* - Francavilla, Frascari Ritondale Spano & Zecchi, p. 667, pl. 85, figs 2, 3.
?1972 *Lithophyllum johnsoni* - Orszag-Sperber & Poignant, p. 118 pl. 1, fig. 3.
1974 *Lithophyllum contii* - Segonzac (in Segonzac & Charollais), pl. 4.
1977 *Lithophyllum contii* - Lemoine, p. 16.
1977 *Lithophyllum giammarini* - Lemoine, p. 16.
1980 *Lithophyllum giammarini* - Fravega & Vannucci, p. 33.
1983 *Lithophyllum contii* - Bakalova, p. 59, pl. 5, fig. 6.
1983 *Lithophyllum embergeri* - Bakalova, p. 60, pl. 5, fig. 3.
1983 *Lithophyllum giammarini* - Bakalova, p. 61, pl. 5, fig. 4.
1983 *Mesophyllum rigidum* - Bakalova, p. 57, pl. 4, fig. 4.
1987a *Lithophyllum contii* - Fravega & Vannucci, p. 226, pls. 25-26.
1987b *Lithophyllum contii* - Fravega & Vannucci, p. 11.
1987 *Lithophyllum contii* - Fravega, Giammarino, Piazza, Russo & Vannucci, p. 54.

PLATE 1

Neogoniolithon contii:

Fig. 1 - Portion of the holotype thallus illustrated by Mastrorilli (1967). Thin section Po-IV-4/46. Scale bar = 950 µm.
Fig. 2 - Holotype. Thin section Po-IV-4/46. The section is mm 47 x 27.
Fig. 3 - S.E.M. photograph. Cell-fusions in the hypothallium (arrow). Stub 32 (sample Po-IV-5 associated to the collection). Scale bar = 50 µm.
Fig. 4 - Hypothallium in mostly LRS. Note regular coaxial arrangement. Cell-fusions (black arrow) and local intercalated small rectangular cells (white arrow). Thin section Po-IV-4/46. Scale bar = 100 µm.
Fig. 5 - Hypothallium in oblique sections. The horizontal cell walls are aligned in rectilinear tiers. Cell-fusions (black arrow) and local intercalated small cells (white arrow). Thin section Po-IV-4/46. Scale bar = 100 µm.
Fig. 6 - Hypothallium in oblique sections. The coaxial arrangement is still visible despite the imperfect orientation. Adjacent hypothallial cells appear arranged in slightly arching to rectilinear tiers. Cell-fusions (arrow). Thin section Po-VII-5/246. Scale bar = 170 µm.
Fig. 7 - Hypothallium in oblique sections. A transition appears from coaxial to non-coaxial, plumose arrangement of the hypothallium. Thin section Po-IV-8/122. Scale bar = 100 µm.





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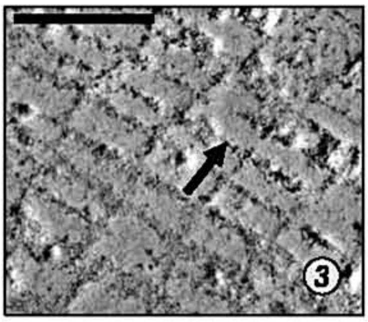

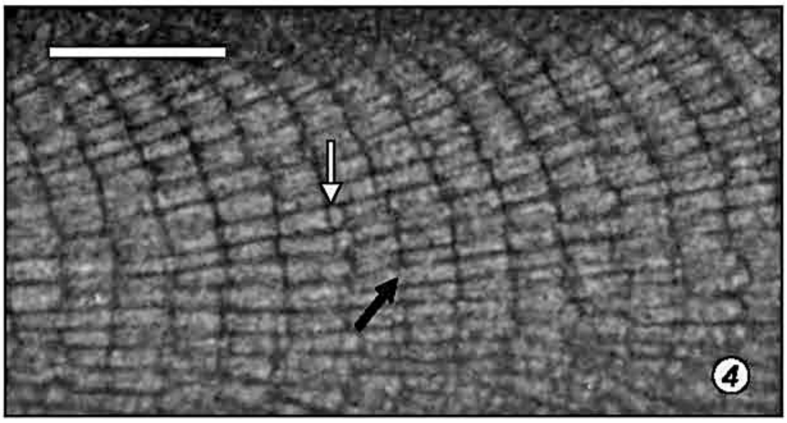

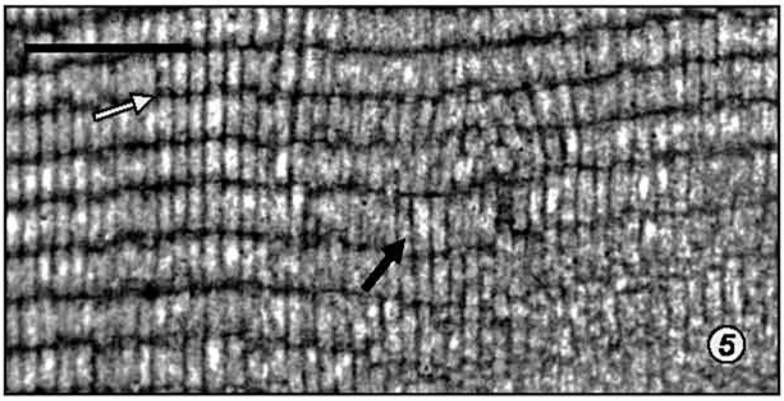

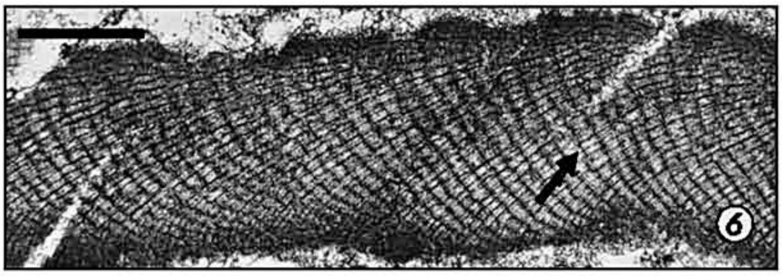

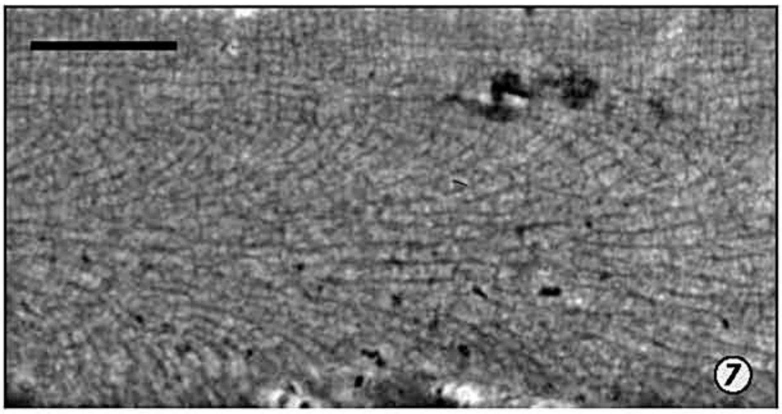

Neogoniolithon contii comb. nov.					
LRS		Range	M	SD	n
Hypothallial cells	L	12-38	26.8	3.6	404
	D	5-17	9.9	1.4	
Perithallial cells	L	4-12	7.1	1.7	394
	D	4-11	7.6	1.4	

Oblique sections		Range	M	SD	n
Hypothallial cells	L	18-40	27.8	4.2	241
	D	5-13	9.7	1.4	
Perithallial cells	L	4-18	7.0	1.9	198
	D	5-11	7.6	1.4	

Tab. 1 - Biometry of *N. contii*. Measures in µm. n = number of observations, M = mean, SD = standard deviation, L = cell length, D = cell diameter.

Neogoniolithon contii comb. nov.			
LRS		axial at p.c.	p.c. not visible
Sporangial conceptacles	D	600	340-720
	H	250	85-210
	Hmax	280	120-220
	Hpc	130	-
	n	1	6
Spermatangial conceptacles	D	100-380	200-400
	H	20-60	20-60
	Hmax	-	-
	Hpc	10-140	-
	n	12	8
Carpogonial conceptacles	D	480	450
	H	150	110
	Hmax	-	-
	Hpc	50	-
	n	1	1
Carposporangial conceptacles	D	800	820
	H	220	280?
	Hmax	-	-
	Hpc	260	-
	n	1	1

Tab. 2 - Biometry of reproductive structures of *N. contii*. Measures in µm. n = number of observations, D = conceptacle diameter, H = conceptacle height under the pore canal or conceptacle central height when pore canal is not visible, Hmax = maximum conceptacle height at the peripheral bulge, Hpc = pore canal height, p.c. = pore canal. The H of carposporangial conceptacle is reported with a question mark because of the oblique orientation.

1987 *Lithophyllum embergeri* - Fravega, Giammarino, Piazza, Russo & Vannucci, p. 55.

1988 *Mesophyllum* cf. *rigidum* Fravega, Giammarino, Traverso & Vannucci, p. 212.

1989 *Lithophyllum contii* - Piazza, p. 165, pl. 7a.

1997 *Lithophyllum contii* - Vannucci, Piazza, Pastorino & Fravega, tabs 1-2, p. 16, 21.

1997 *Mesophyllum* cf. *rigidum* - Vannucci, Piazza, Pastorino & Fravega, tab. 2, p. 21.

?1998 *Neogoniolithon* sp.2 - Bassi, p.18, pl. 6, figs 2-6.

Holotype. Ol. Ponzone '67 Collection, thin section Po-IV-4/46 (Pl. 1, fig. 2).

Isotypes. Ol. Ponzone '67 Collection, thin section Po-IV-4/47, 4/48.

Paratypes. Ol. Ponzone '67 Collection, thin section Po-IV-A/116; thin section Po-IV-1/2, 1/4, 1/5, 1/11; thin section Po-IV-2/12, 2/13; thin section Po-IV-3/6, 3/7, 3/8, 3/9; thin section Po-IV-5/133, 5/135, 5/136, 5/138; thin section Po-IV-7/128, thin section Po-IV-8/52, 8/123, 8/140; thin section Po-VI-B/312. Both the above mentioned thin sections and the SEM specimens obtained from the original and newly sampled material are preserved in Mastrorilli's Collection (1967-68) – Ol. Ponzone, at the Department for the Study of the Territory and its Resources (Dip.Te.Ris.), Genoa University.

Type locality. Oligocene of Bric Mazzapiede (Prasco-Alessandria), locality Case Tulle Maggi - Case Tulle Serra (station Po-IV-4) (Tertiary Piedmont Basin, Molare Formation).

Other examined material from the original Mastrorilli's collections, retained for the present description of *N. contii*, include the type material of *Lithophyllum giammarinoi* Mastrorilli (younger heterotypic synonym of *L. contii*, Fravega & Vannucci 1987a), *L. embergeri* Mastrorilli, *Mesophyllum flexile* Mastrorilli, *M. rigidum* Mastrorilli and specimens that Mastrorilli (1968) incorrectly identified as *Lithophyllum capederi* (see below).

Description. Growth-form foliose, thalli sometimes wrapped up, reaching several centimetres in length and 340-850 µm thick. The living plant was probably loosely attached or completely free from the substrate. In some specimens the derivatives of some core filaments curve towards the dorsal surface and others towards the ventral surface of the thallus, resulting in a bilateral growth of the peripheral region (= perithallium) and a more central position of the core (= hypothallium) within the thallus. In this instance the dorsal side of the perithallium is more developed then the ventral side. In some cases, small flattened lamellate

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PLATE 2

Neogoniolithon contii:

Fig. 1 - Uniporate sporangial conceptacle in LRS. The pore canal is axially cut. The filaments around the pore (arrow) are arranged sub-parallel to the conceptacle roof. Thin section Po-IV-4 / 46. Scale bar = 100 µm.

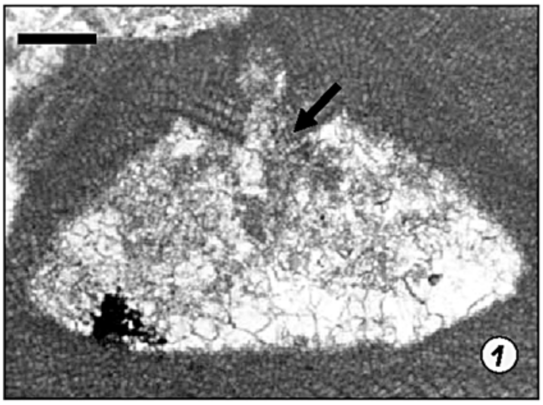
Fig. 2 - Sporangial conceptacle without visible pore canal, in oblique section. Note the "winged" appearance. Below the conceptacle, the hypothallial cells are cut perpendicularly to the direction of growth and elongation. Thin section Po-V-7/285. Scale bar = 100 µm.

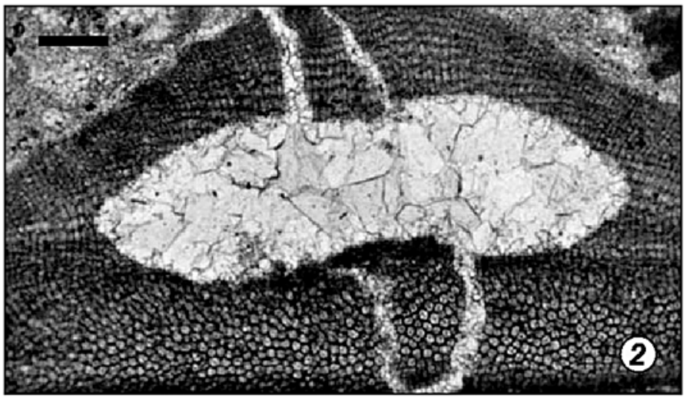
Fig. 3 - Sporangial conceptacle without visible pore canal. Thin section Po-IV-4/46. Scale bar = 100 µm.

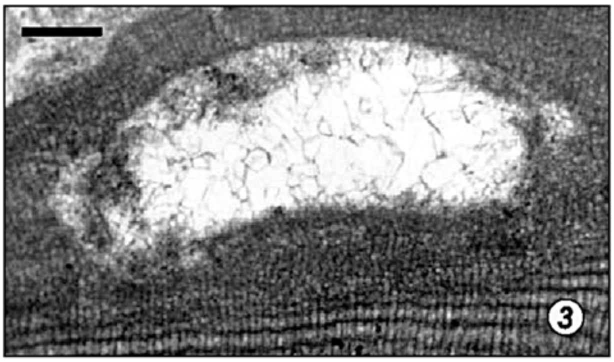
Fig. 4 - Sporangial conceptacle without visible pore canal. Note the sub-triangular outline. Thin section Po-IV-4/46. Scale bar = 100 µm.

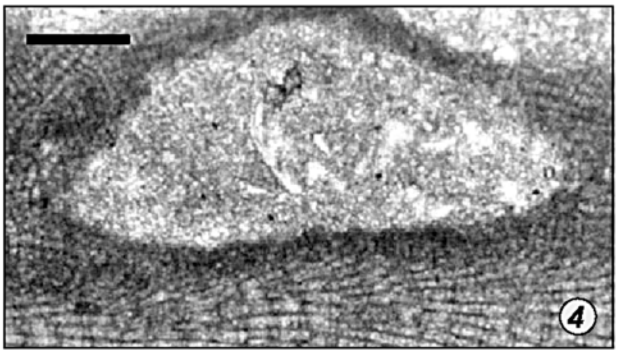
Fig. 5 - Presumed spermatangial conceptacle in LRS, axial section (pore canal visible). Thin section Po-V-7/282. Scale bar = 50 µm.

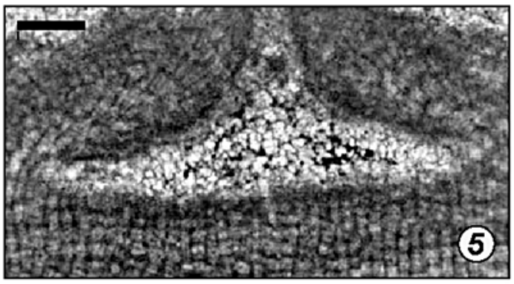
Fig. 6 - Presumed carpogonial (smaller) and carposporangial (larger) conceptacles. Thin section Po-IV-5/132. Scale bar = 400 µm.

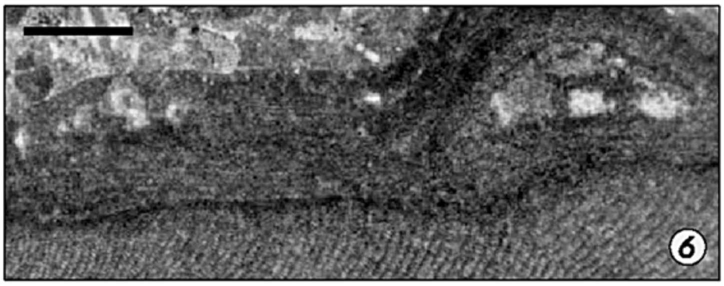












branches occur and develop more or less perpendicular to the basal lamella (Pl. 1, Fig. 1).

Vegetative anatomy. Pseudoparenchymatous thalli, with dorsiventral internal organisation, monomerous with a coaxial hypothallium. The thickness of the hypothallium varies from 120 µm to 620 µm and can locally reach 750-800 µm when the thallus is obliquely oriented.

The analysed thalli are sectioned both in LRS and oblique sections.

The hypothallial cells in LRS (Pl. 1, Fig. 4) are arranged in distinct arching tiers with L 12-38 µm and D 5-17 µm (Tab. 1). Under oblique orientations, cells are deformed appearing longer than in LRS (Tab. 1; Pl. 1, Figs 5-7).

Small rectangular cells of 2-5 µm in length locally occur in the hypothallium where they are occasionally interspaced among the longer hypothallial cells (Pl. 1, Figs 4, 5). They are interpreted as due to lateral division of cells, thus a feature with no diagnostic value. In most cases the bilateral or non-bilateral peripheral region (perithallium) is usually not zonated; a faint zonation is apparent in the thickest thalli. In particular, the sterile perithallial dorsal portions are 40-560 µm in thickness while the fertile ones are 110-700 µm. The ventrally developed perithallial portions are 20-240 µm in thickness. The perithallium consists of mainly horizontally arranged cells with horizontal partitions more distinct than the vertical ones, cell L 4-12 µm, D 4-11 µm (Tab. 1; Pl. 2, Figs 2, 3). There is no significant difference between cells of the perithallium developed towards the ventral surface and those developed in the dorsal surface.

Abundant cell-fusions occur, particularly visible in the hypothallium (Pl. 1, Figs 3-6).

Epithallial cells flattened but not flared locally occur, cell L 4 µm and D 6-7 µm; the subepithallial initials are as long as or locally longer than the underlying cells. Trichocytes were not observed.

All the additional studied material (new thin sections, SEM stubs and peels obtained from the samples of the original collection and further material sampled at the type locality) is consistent with the original Mastrorilli's thin sections and have the same structural, anatomical and dimensional description given above.

Reproductive structures. The reproductive structures in the original Mastrorilli's collection are interpreted, on the basis of their shape and size, as rare uniporate sporangial conceptacles, few male gametangial and very rare presumed carpogonial and carposporangial conceptacles. The only axial section of the sporangial conceptacle shows a pore canal partially inset in the chamber roof. This character is evident in the holotype and less clear in the additional material, probably because of the oblique orientation of the section. This conceptacle has sub-trapezoidal profile, D 600 μm, H 250 μm and Hmax 280 μm (Pl. 2, Fig. 1; Tab. 2). Pore canal is 130 μm high, it has a diameter at the base of 60 μm that becomes narrower (40 μm) and ends with a bulge of 60 μm of maximum diameter. The filaments around the pore are sub-parallel to the conceptacle roof (Pl. 2, Fig. 1).

The remaining sporangial conceptacles do not show the pore canal. However, their variable morphology is referable to uniporate chambers (Pl. 2, Fig. 2-4). Conceptacle D 340-720 μm, H 85-210 μm and Hmax 120-220 μm (Tab. 2). The conceptacle roof often protrudes more or less conspicuously above the surrounding thallus surface (about 220 μm) and no distinct columella occurs.

The presumed spermatangial conceptacles have a typical flattened sub-triangular morphology (Pl. 2, Fig. 5) with diameter of 100-380 μm, height of 20-60 μm and pore canal H 10-140 μm (Tab. 2).

The presumed carpogonial conceptacles are sub-triangular in section, with flattened floor. One of them shows an apparently complete pore canal H 50 μm, and a chamber D 480 μm x H 150 μm. In the other one the pore canal is not visible, D 450 μm x H 110 μm (Tab. 2). A conceptacle with flattened floor, convex-up roof and non visible pore canal occurs in the same thallus with the above described conceptacles, and is herein considered a possible carposporangial conceptacle (Pl. 2, Fig. 6) D 820 μm x about H 280 μm (Tab. 2). We also consider as carposporangial the conceptacle illustrated by Mastrorilli (1968, pl. 20, fig. 2) for a specimen that she erroneously identified as *Lithophyllum capederi,* and that we attribute to *N. contii* (see also remarks) (Tab. 2).

Conceptacles are rare in all the material investigated and in the additional material only 4 sporangial conceptacles out of 13 and 17 gametangial conceptacles out of 25 were properly oriented (axial section).

Tab. 3 - Biometry of types of *L. contii* in Mastrorilli's collection. Measures in μm. See Tabs 1-2 for abbreviations.

Lithophyllum contii Mastrorilli (type material)						
LRS			Range	M	SD	n
Hypothallial cells		L	12-38	25.5	4.0	332
		D	5-17	10.0	1.5	
Perithallial cells		L	4-12	7.4	1.6	334
		D	4-11	7.4	1.4	
Sporangial conceptacles	axial at pore canal	D	600			1
		H	250			
		Hmax	280			
		Hpc	130			
	pore canal not visible	D	340-720			4
		H	85-200			
		Hmax	120-220			
Spermatangial conceptacles	axial at pore canal	D	100-350			8
		H	20-60			
		Hpc	10-120			
	pore canal not visible	D	200-380			6
		H	20-40			

Oblique sections			Range	M	SD	n
Hypothallial cells		L	18-38	26.2	4.3	115
		D	5-12	9.6	1.3	
Perithallial cells		L	4-11	7.0	1.4	92
		D	5-10	7.3	1.5	
Sporangial conceptacles	pore canal not visible	D	550			1
		H	200			
Spermatangial conceptacles	axial at pore canal	D	220-320			2
		H	30-40			
		Hpc	20-140			
	pore canal not visible	D	350			1
		H	60			

Observations on Mastrorilli's original collections subsumed in *N. contii* comb. nov.

Lithophyllum contii Mastrorilli, 1967

Protologue. Mastrorilli 1967 p. 476, pls. 1-2

Holotype. Thin section Po-IV-4/46 figured in Mastrorilli 1967, pl. 2, fig.1

Isotypes, paratypes. See list of isotypes and paratypes as *Neogoniolithon contii.*

Heterotypic synonym. *Lithophyllum giammarinoi* Mastrorilli, 1968 (holotype thin section Po-V-7/282 figured in Mastrorilli 1968, pl. 33, figs 1-3, pl. 34, figs 1-2; isotypes Po-V-7/283, 7/285, 7/286 and paratypes Po-IV-A/120, Po-IV-2/12, Po-IV-8/122, 8/142, 8/144, 8/146), Fravega & Vannucci 1987a, p. 226, pls. 25, 26.

Growth form foliose, locally wrapped up (Mastrorilli 1967, pl. 1). Thallus pseudoparenchymatous with a dorsiventral organisation, monomerous. Cells connected by cell-fusions, easily observed in the hypothallium. The thin section of the holotype is oriented mostly in LRS. Cells of contiguous filaments of the hypothallium shows a coaxial arrangement in LRS, with hypothallial cells L 12-38 µm x D 5-17 µm (Pl. 1, Fig. 4). The observed appearance of the hypothallium in oblique sections derives from different orientations of the same cell organization and thus we refer them to the coaxial arrangement. As a consequence of the oblique orientation, size range of cells can vary significantly (Tab. 3). Small rectangular cells locally occur in the hypothallium.

Hypothallial filaments growing more or less parallel to the substrate and giving rise to peripheral cell filaments (perithallium) toward the dorsal surface or toward both the dorsal and the ventral surface of the thallus. In the latter situation the hypothallium is located more centrally along the thallus and the development of the perithallium is bilateral (Tab. 3; Mastrorilli 1967, pl. 1, fig. 2).

Perithallial cells L 4-12 µm x D 4-11 µm (LRS). Trichocytes were not observed.

Epithallial cells are rare, flattened but not flared (L 4 µm x D 6-7 µm). Subepithallial initials are usually as long as or rarely longer than their immediate inward derivatives.

Reproductive structures. Only one uniporate, supposed sporangial conceptacle has been identified. It has a sub-trapezoidal profile, D 600 µm, median H 250 µm, Hmax 280 µm. The pore canal is 130 µm in length with the proximal end inset in the sporangial chamber (Tab. 3; Mastrorilli, 1967, pl. 2, fig. 1). Rarely, sporangial conceptacles without visible pore canal show different morphologies due to the improper orientation (Tab. 3). Supposed spermatangial conceptacles are rare (D 100-350 µm x H 20-60 µm, pore canal 10-140 µm), with a general sub-triangular morphology and flattened floor (Tab. 3).

Remarks. Among the original Mastrorilli's material, thin section Po-IV-7/x is missing. Thin sections Po-IV-A/110, A/111, A/112, A/114, A/115, A/119, A/121, and Po-IV-1/1, 1/10, Po-IV-5/121, Po-V-2/290, Po-VI-B/308 are damaged or include poorly preserved algal fragments, sometimes impossible to identify. For this reason we exclude them from the list of the paratypes of *L. contii* and *L. giammarinoi* given by Mastrorilli (1968, pp. 340, 357).

Lithophyllum embergeri Mastrorilli, 1968

Protologue. Mastrorilli 1968 p. 349, text fig. 33, pl. 30, figs 1-4

Holotype. Thin section Po-VII-5/248 figured in Mastrorilli 1968, pl. 30, figs 2, 4 (non fig. 3).

Isotype. Thin section Po-VII-5/246 (figured in Mastrorilli 1968, pl. 30, fig. 1).

Paratypes. Po-IV-3/7 (figured in Mastrorilli 1968, pl. 30, fig. 3, non fig. 4), Po-IV-2/12; Po-IV-5/132; 5/133; Po-IV-8/142; 8/144.

Growth form foliose, thallus pseudoparenchymatous with a dorsiventral organisation, monomerous. Cells connected by cell-fusions, easily observed in the hypothallium. The holotype and paratypes designated by Mastrorilli (1968) do not show any LRS.

Hypothallium coaxial, rarely situated more centrally within the thallus. Mastrorilli (1968, pl. 30, figs. 1-4) provided illustrations of oblique sections of the species in the holotype thin section and in the paratypes (Tab. 4). Small rectangular cells locally occur in the hypothallium. As stated above, they are not a diagnostic character.

Lithophyllum embergeri Mastrorilli (type material)

Oblique sections			Range	M	SD	n
Hypothallial cells		L	22-40	30.2	3.8	66
		D	8-13	10.1	1.3	
Perithallial cells		L	4-10	6.3	1.6	70
		D	5-11	8	1.2	
Conceptacles	axial at pore canal	D	480			1
		H	150			
		Hpc	50			
	pore canal not visible	D	450-820			2
		H	110-280?			

Tab. 4 - Biometry of types of *L. embergeri* in Mastrorilli's collection. Measures in µm. See Tabs 1-2 for abbreviations.

The perithallium is developed dorsally or can be bilateral (Mastrorilli 1968, pl. 30). Epithallial cells not observed. Trichocytes not observed.

Reproductive structures. The only conceptacle described as sporangial and illustrated by Mastrorilli (1968, p. 351, fig. 33) has no visible pore canal and shows a chamber with flattened floor, D 820 µm x about 280 µm. However, one uniporate conceptacle has a subtriangular morphology, flattened floor, D 480 µm, H 150 µm and a pore canal H 50 µm. Another conceptacle without visible pore canal has similar shape and size (D 450 µm x H 110 µm) (Tab. 4).

Remarks. 1) The growth form and the vegetative anatomy and cell size observed in oblique sections are similar to those of *L. contii* with the same orientation (compare Tabs 3 and 4). 2) Uniporate conceptacles observed in the same thallus have very different size and shape and these two characters do neither match with the sporangial nor with the spermatangial conceptacles of *L. contii*. Since carpogonial conceptacles in Corallinales are known to change their shape and significantly increase their size after fertilization (becoming carposporangial), we interpret the two small conceptacles as carpogonial while the third and largest is supposed to be carposporangial.

Mesophyllum flexile Mastrorilli, 1968

Protologue. Mastrorilli 1968 p. 307, pl. 18, fig. 1, not fig. 2.

Lectotype. Thin section Po-IV-8/148 figured in Mastrorilli 1968, pl. 18, fig. 1, not fig. 2.

Paratypes. Thin sections Po-IV-5/135 and Po-IV-5/136.

The analysis of the holotype of *Mesophyllum flexile* revealed that the thalli do not correspond to the protologue, and that the type material is heterogeneous. Mastrorilli's protologue (1968, pl. 18) contains two photographs (figs 1, 2) representing different species. Mastrorilli's fig. 1 (1968) illustrates a foliose thallus with a distinct coaxial hypothallium. Mastrorilli's fig. 2 illustrates a portion of superposed algal crusts, with very thin non-coaxial hypothallium giving rise to a perithallium with distinct multiporate conceptacles. The two different coralline thalli were incorrectly interpreted by Mastrorilli (1968) as the same species because the thallus in fig. 2 shows a local and apparent continuity with another algal fragment which is similar to that in Mastrorilli's fig. 1.

The species illustrated in Mastrorilli (1968, pl. 18, fig. 2) shows a multistratose, non-coaxial hypothallium, cell fusions, multiporate conceptacles and subepithallial initials longer than the underlying cells, although the morphology of the epithallial cells is unclear. These characters collectively identify species belonging to the family Hapalidiaceae, subfamily Melobesioideae, possibly genus *Lithothamnion.* Cell size reported by Mastrorilli (1968) for the vegetative thallus are solely comparable to the thalli of fig. 2.

Lectotypification

Mastrorilli's photographs of the thalli included in the holotype that she designated (thin section Po-IV-8/148, figs 1 and 2) belong to different genera and families. Therefore we select the thallus illustrated in Mastrorilli's fig. 1 as lectotype of *Mesophyllum flexile* Mastrorilli, explicitly excluding the thallus illustrated in fig. 2, which we tentatively identify as *Lithothamnion* sp., pending further studies.

The lectotype of *Mesophyllum flexile* Mastrorilli

Growth form foliose, thallus pseudoparenchymatous with a dorsiventral organisation, monomerous. Cell connected by cell-fusions, easily observed in the hypothallium. Hypothallium coaxial observable in LRS lectotype section illustrated by Mastrorilli (1968, pl. 18, fig. 1) and in the paratypes not illustrated by her. Hypothallial cells L 20-32 µm and D 6-13 µm (Tab. 5). Among the normal hypothallial cells some small rectan-

Mesophyllum flexile Mastrorilli (type material)						
LRS			Range	M	SD	n
Hypothallial cells		L	20-32	26.1	3.8	48
		D	6-13	9.9	1.2	
Perithallial cells		L	5-10	6.9	1.5	36
		D	5-11	8.4	1.3	
Conceptacles	axial at pore canal	D	300-380			2
		H	30-60			
		Hpc	10-100			
	pore canal not visible	D	400			1
		H	50			

Oblique sections		Range	M	SD	n
Hypothallial cells	L	24-32	27.9	2.3	24
	D	5-12	8.9	1.5	

Tab. 5 - Biometry of types of *M. flexile* in Mastrorilli's collection. Measures in µm. See Tabs 1-2 for abbreviations.

Mesophyllum rigidum Mastrorilli (type material)					
LRS		Range	M	SD	n
Hypothallial cells	L	25-35	28.8	3.0	24
	D	8-12	9.6	1.5	
Perithallial cells	L	4-10	6.9	1.9	24
	D	4-8	6.9	1.4	
Conceptacle (pore canal not visible)	D	560			1
	H	210			

Oblique sections		Range	M	SD	n
Hypothallial cells	L	18-35	27.1	4.0	36
	D	7-12	10.1	1.3	
Perithallial cells	L	4-18	8.0	2.5	36
	D	5-9	7.6	1.2	

Tab. 6 - Biometry of types of *M. rigidum* in Mastrorilli's collection. Measures in µm. See Tabs 1-2 for abbreviations.

gular cells locally occur. Perithallium developed in mostly dorsal or locally dorsal and ventral surface of the thallus (bilateral organization). Perthallial cells are L 5-10 µm and D 5-11 µm (Tab. 5). Epithallial cells not observed. Trichocytes not observed.

Reproductive structures. Rare and poorly preserved uniporate conceptacles occur (undetected by Mastrorilli 1968), with a sub-triangular profile, flattened floor, D 300-380 µm, H 30-60 µm and pore canal H 10-100 µm (Tab. 5).

Remarks. 1) The growth morphology and cell biometry occurring in LRS and in oblique sections are comparable to those of *L. contii* (compare Tabs 3, 5). 2) The morphology and size of uniporate conceptacles are similar to the gametangial male conceptacles of *L. contii*.

Mesophyllum rigidum Mastrorilli, 1968

Protologue. Mastrorilli 1968 p. 309, pl. 18, figs 3, 4.

Holotype. Thin section Po-IV-8/52 figured in Mastrorilli 1968, pl. 18, figs 3, 4.

Isotypes. Po-IV-8/122, Po-IV-8/141.

Paratypes. Po-IV-5/131; Po-IV-5/138.

Growth form foliose, thallus pseudoparenchymatous with a dorsiventral organisation, monomerous. Cells connected by cell-fusions, easily observed in the hypothallium.

Hypothallium coaxial in LRS, with cell L 25-35 µm and D 8-12 µm (Tab. 6; Mastrorilli 1968, pl. 18, figs 3-4). Small rectangular cells occur among the normally-elongated hypothallial cells. Perithallium developed only dorsally. Perithallial cells in LRS L 4-10 µm and D 4-8 µm (Tab. 6). Epithallial cells and trichocytes not observed.

Reproductive structures. Out of the few fertile thalli of *M. rigidum* only one, included in the holotype, shows a well preserved, probably uniporate conceptacle (although without visible pore canal). The conceptacle chamber has flattened floor and slightly convex roof, D 560 µm and H 210 µm (Tab. 6). The "slim and short pore canals" observed by Mastrorilli (1968, p. 310) in the central portion of the roof are actually not visible (Mastrorilli 1968, pl. 18, fig. 3). On the basis of these "pore canals" Mastrorilli (1968) attributed the plant to the genus *Mesophyllum*. The remaining conceptacles included in the paratype underwent complete breakage of roofs and thus their nature (uniporate *vs.* multiporate) remains unknown.

Remarks. 1) The observed biometry of *M. rigidum* partially disagrees with the data given by Mastrorilli (1968), who reported a wider range for hypothallial cell size. The biometry of hypothallial cells measured in LRS and oblique sections is similar to that of *L. contii* in the same orientations (compare Tabs 3 and 6). 2) The only preserved conceptacle is morphologically and dimensionally comparable to the sporangial conceptacles of *L. contii*. 3) We exclude thin section Po-IV-8/145 from the list of paratypes indicated by Mastrorilli (1968) for *M. rigidum*, because of the poor preservation of the fossil.

Discussion

On the basis of habit, growth-form, thallus structure, vegetative and reproductive anatomy, we consider *Lithophyllum embergeri*, *Mesophyllum flexile* and *M. rigidum* as conspecific with *Lithophyllum contii. L. giammarinoi* is also conspecific with *L. contii*, in agreement with the conclusions of Fravega & Vannucci (1987a). The foliose growth-form and the large cells in coaxial hypothallium are prominent features that lead Mastrorilli to include her fossil material in the genera *Lithophyllum* and *Mesophyllum*. In a modern taxonomic framework, the occurrence of cell fusions excludes *L. contii* (and its above mentioned conspecific taxa) from the subfamily Lithophylloideae. Cell fusions, a coaxial hypothallium and a foliose growth-form are presently recognized in several taxa within the subfamily Melobesioideae and are common in the genus *Mesophyllum* Lemoine. However, Melobesioideae possess multiporate sporangial conceptacles and, despite our dedicated effort, no multiporate conceptacle was found in the studied material. It could be argued that the collections considered under this study are composed of gametangial plants only. Literature data on natural populations of extant corallines provide evidence that sporangial and gametangial plants are equally common or, in some cases, the sporangial plants prevail in number; therefore the hypothesis that only gametangial plants of a species enter the fossil record is unlikely. Moreover, the gametangial (carposporangial) conceptacles in *Mesophyllum* show a raised central part of the conceptacle floor (Woelkerling & Harvey 1993; "pedestal" in Athanasiadis & al. 2004) which was never observed in our material.

These considerations on the nature of the uniporate conceptacles, the occurrence of cell fusions, and the coaxial arrangement of the hypoythallium, collectively support a position of *L. contii* Mastrorilli within the subfamily Mastophoroideae. Among the genera listed in this subfamily, the genus *Neogoniolithon* is circumscribed by the following characters by Braga et al. (1993): "Tetra/bisporangial conceptacles uniporate, cell fusions, thallus composed of numerous layers of cells, pore canal of tetrasporangial conceptacles bordered by cell filaments subparallel to the roof surface and protruding into the canal, hypothallium coaxial...". The same diagnosis is given in Braga (2003), with the exception of the coaxial hypothallium that can be also non-coaxial (see Penrose 1992; Penrose & Woelkerling 1992). The occurrence of trichocytes is not considered diagnostic in the circumscription of coralline genera, though a general consensus on this matter is far to be reached (Basso & Rodondi 2006).

In plants showing a non-coaxial organization of the hypothallium, the distinction between *Neogoniolithon* and *Spongites* is possible only by the position of spermatangia or gonimoblast filaments inside the conceptacles. Unfortunately this character is not preserved in fossils. Also the occurrence of cells protruding into the canal is a diagnostic character (Womersley 1996), which is difficult to recognize in the fossil since these cells are usually not calcified. After these considerations, we conclude that, among the Mastophoroideae, the coaxial organization of the hypothallium should be retained as a major diagnostic character for the identification of the genus *Neogoniolithon.* As a consequence we transfer *Lithophyllum contii* Mastrorilli and its younger heterotypic synonyms *L. giammarinoi, L. embergeri, M. flexile* and *M. rigidum* under the new combination *Neogoniolithon contii* comb. nov.

The species that Mastrorilli (1968) incorrectly identified as *Lithophyllum capederi* Lemoine 1926 has also been included in the list of references because of its morphological and anatomical affinities with *N. contii* (foliose growth form, coaxial hypothallium, dorsal and dorsal – ventral peripheral region and cell-fusions). During the comparison, we were not able to observe hypothallial cells with mean length 35 µm, maximum 50 µm as indicated by Mastrorilli (1968; thin sections Po-IV-8/141, 8/146, 8/147, 8/150). The only conceptacle with visible pore canal (axial section, Mastrorilli 1968, pl. 20, fig. 2) with D 800 µm x H 220 µm and a pore canal of 260 µm in height, is similar to the herein supposed carposporangial conceptacle of *N. contii*, for the flattened floor and the large size (Fig. Pl. 2, Fig. 6). Moreover, *L. capederi* Lemoine (1926) has hypothallial cell lengths (15-22 µm) ranging below the mean lenght of hypothallial cells of Mastrorilli's *L. capederi* (M: 24.4; DS: 3.4 on 50 measures).

We also list in the references, though with caution, other figured specimens that are morphologically, structurally and dimensionally similar to *N. contii*:

1) Orszag-Sperber & Poignant (1972, tab. 1, fig. 3) point out and illustrate a specimen that they identify as *Lithophyllum johnsoni* Ishijima, 1954. They remark that it could be possible to misidentify this species with *L. contii* that, however, always shows bilateral peripheral region. However, we demonstrate here that bilateral peripheral region is not constant in *N. contii*. Moreover, since *L. johnsoni* in Orszag-Sperber & Poignant (1972) shows perithallial cell size falling within the range of *N. contii* and hypothallial cell size that fits better with the biometry of *N. contii* rather with that originally described for *L. johnsoni* (Ishijima, 1954) we are confident that the specimens figured by Orszag-Sperber & Poignant (1972) as *L. johnsoni* are correctly identified as *N. contii*.

2) The species *Neogoniolithon* sp. 2 considered to be similar to *L. contii* by Bassi (1998). Actually, the morphological and structural characters and the size of hypothallial cells and conceptacles of *Neogoniolithon* sp. 2 are comprised in those of *N. contii.* However, since the mean dimensions of the perithallial cells of *Neogoniolithon* sp. 2 are higher than those of *N. contii*, we consider with caution the possibility of their conspecificity. It is of note that (Bassi 1998) associated *Neogoniolithon* sp. 2 to other species that he described elsewhere, such as *Mesophyllum* sp. 2 (Bassi 1995) and *Neogoniolithon* sp. 1 (Bassi & Nebelsick 2000). In our opinion, however, further investigation is required, since these two species show perithallial cell size larger and not comparable to *N. contii.*

We exclude the following references from the synonymy with *N. contii*, because the material differs with the current circumscription of the species:

1) Segonzac in Segonzac & Charollais (1974, pl. 23) describes and illustrates *Mesophyllum rigidum.* Although the illustrations show great morphological similarities with *N.contii* the hypothallial cell size reported is much larger than that of *N. contii,* even considering the effect of oblique sections.

2) Lemoine (1977, p. 16) reports *Lithophyllum embergeri* with cell lengths of the perithallium much longer than those reported here for the type material of *L. embergeri*. Though it is possible that the reported cell size was taken at the core of lamellate branches (hypothallium), the lack of illustrations of Lemoine's specimens leaves the question unresolved.

3) Lemoine (1977, p. 20) describes specimens referred to *M. rigidum* for the morphology, structure and dimensional parameters. She points out a "très régulière" alternation of long and short cells in the hypothallium. In *N. contii* the shorter cells are locally and sporadically arranged and the reported dimensions of cells provided by Lemoine (1977) do not correspond, therefore this reference is excluded from the synonymy of *N. contii*.

4) Studencki (1988) describes a fertile specimen of *M. rigidum* (p. 34, pl. 11, figs 1, 3) with multiporate conceptacles with well visibile pore canals, and range of cell size much larger than that of *N. contii*. This material is obviously not conspecific with *N. contii*.

5) Studencki (1988) proposes to consider *Lithophyllum contii* figured by Mastrorilli (1967, only pl. 2, fig. 6) as synonym of *Lithophyllum lithothamnioides* Maslov (1962). We do not accept his proposal since *Lithophyllum lithothamnioides* Maslov is a poorly defined species, requiring further investigation.

Stratigraphic and geographic distribution

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

Neogoniolithon contii mostly occurs in the Paleogene. It is recovered in: ?Upper Eocene from Asenovgrad, S Bulgary (Bakalova 1983), Upper Eocene from Massif des Bornes in Haute Savoie, SW France (Segonzac & Charollais 1974) and from Calcare di Nago, N Italy (Bassi 1998); ?Upper Eocene – Oligocene from Radovis, Skopje – Macedony (Lemoine 1977); Priabonian to ?Lower Oligocene from Barbarano, Colli Berici – NE Italy (Francavilla et al. 1970); in an oligocene pebble from the south-western moraine of Garda Lake deriving from the neighbouring "nullipore formations", N Italy (Vannucci 1970); Oligocene from Tertiary Piedmont Basin of Molare Formation, N Italy, in particular according to the levels, in Lower and Middle Rupelian (SB21 according to the biozonation of Cahuzac & Poignant 1997) and the upper Rupelian – Chattian transition (biozone SB22A-SB23) from different localities of the southern margin of the Tertiary Piedmont Basin, nearby Ponzone – Prasco (Mastrorilli 1967, 1968; Piazza 1989; Vannucci et al. 1997), Sassello (Fravega et al. 1987; Fravega & Vannucci 1980; 1987a; 1987b), Val Lemme (Fravega et al. 1988) and Ovada (Fravega & Vannucci 1987a). The youngest occurrence is in the upper Burdigalian – Serravallian from eastern Corsica (Orszag-Sperber & Poignant 1972).

The following references could not be checked because of the lack of descriptions and illustrations, and therefore they have been cautiously excluded from further paleobiogeographic and stratigraphic considerations: Priabonian of Monte Baldo, Calcare di Nago (N Italy) (*Lithophyllum contii* p. 124; Castellarin & Cita 1970b); Priabonian of Rohrdorf, Germany – Austria frontier (*Lithophyllum contii* p. 3; *Lithophyllum embergeri* p. 3, Moussavian 1993); Upper Eocene – Lower Oligocene of eastern Colli Berici (*Lithophyllum giammarinoi* p. 205, 206; *Lithophyllum* cf *giammarinoi* p. 208; *Lithophyllum embergeri* p. 206, 208; *Mesophyllum rigidum* p. 206, 208; *Mesophyllum* cf. *rigidum* p. 208, Ungaro 1978); Lower Oligocene of Monte Baldo, Calcare di Monte delle Erbe (*Lithophyllum* cf. *giammarinoi* p. 107, Castellarin & Cita 1970a).

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