Cymopolia decastroi n. sp. and Cymopolia barattoloi n. sp. from the upper Maastrichtian of southeastern Salento (Apulia, southern Italy) with some remarks on the problem of species definition in fossil Dasycladales

Cymopolia decastroi n. sp. und Cymopolia barattoloi n. sp. aus dem oberen Maastricht des südöstlichen Salento (Apulien, S-Italien) mit Bemerkungen zum Problem der Artdefinition bei fossilen Dasycladales

by

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PARENTE, M., Cymopolia decastroi n. sp. and Cymopolia barattoloi n. sp. from the upper Maastrichtian of southeastern Salento (Apulia, southern Italy) with some remarks on the problem of species definition in fossil Dasycladales. — Beitr. Paläont., 19:161–179, 5 Figures, 1 Table, 3 Plates, Wien.

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Abstract

Two new species of *Cymopolia, Cymopolia decastroi* n.sp. and *Cymopolia barattoloi* n. sp., are described from upper Maastrichtian limestones outcropping in southeastern Salento (Apulia, southern Italy).

Cymopolia decastroi n. sp. is characterized by barrel-shaped segments, primary branches distinctly swollen for most of their length and large gametangia.

Cymopolia barattoloi n. sp. is mainly characterized by primary branches with a terminal widening.

Zusammenfassung

Zwei neue Arten der Gattung Cymopolia, Cymopolia decastroi n. sp. und Cymopolia barattoloi n. sp., werden von Kalken des Maastricht aus dem südöstlichen Salento (Apulien, S-Italien) beschrieben.

Cymopolia decastroi n. sp. ist durch faßförmige Segmente, primäre Äste, die den Großteil ihrer Länge deutlich verdickt sind, und große Gametangien charakterisiert.

Cymopolia barattoloi n. sp. ist hauptsächlich durch primäre Äste ausgezeichnet, die eine terminale Erweiterung zeigen.

1. Introduction

Two species of dasycladaleans, Cymopolia decastroi n.sp. and Cymopolia barattoloi n. sp., are described from upper Maastrichtian limestones outcropping in southeastern Salento (Apulia, southern Italy). Observations performed on well preserved and abundant material have allowed to give full account of their morphological variability in the studied samples. Comparisons between these two species, cooccurring in the studied samples, have been performed using both univariate and multivariate statistics. Comparisons with other species of the genus Cymopolia, showing similar primary branch morphology, are somewhat hindered by insufficient description and poor treatment of biometric data found in literature. This problem is particularly evident for Cymopolia barattoloi n. sp. owing to the poor knowledge of other fossil species of Cymopolia showing similar morphology of primary branches.

The case of *Cymopolia decastroi* n. sp. and *Cymopolia barattoloi* n. sp. is used to discuss some problems frequently arising in the definition and discrimination of fossil species of Dasycladales. Species described on poor material consisting of very few specimens are very difficult to handle and especially to compare with other species unless a purely typological approach is accepted. On the other side insufficient attention to statistical treatment of biometric data results in poor and inaccurate presentation of intraspecific morphological variability even when the material is abundant.

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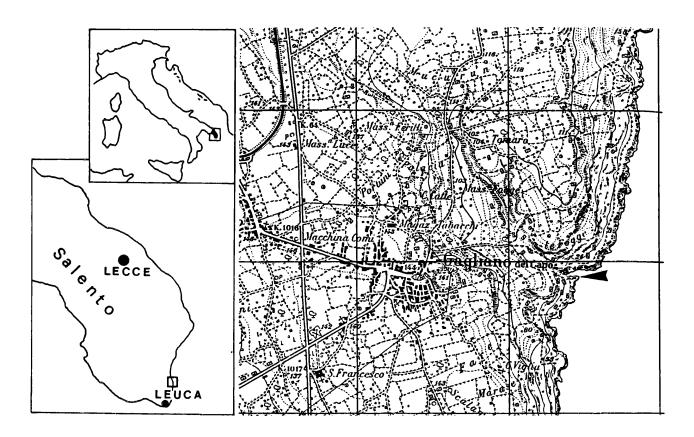


Figure1: Geographical setting of the type-locality of *Cymopolia decastroi* n.sp. and *Cymopolia barattoloi* n.sp. The ubication of sample A.8407 is indicated by the arrow in the topographical map (IGM map 1:25000, 223 I SE, "Alessano"; reproduced by permission of IGM, Istituto Geografico Militare: authorization n.3969, 8 march 1994).

2. Systematic description

Order Dasycladales PASCHER 1931 Family Dasycladaceae KÜTZING 1843 Genus *Cymopolia* LAMOUROUX 1816

Cymopolia decastroi n. sp. (Pl. 1, Figs. 1–7; Pl. 2, Figs. 1–10)

Origin of the name: The species is dedicated to Professor Piero De Castro (Dipartimento di Paleontologia, Università di Napoli Federico II) for his day by day inspiring teaching.

H o l o t y p e : Segment in oblique section figured in Pl. 1, Fig. 1 of this paper (thin section A.8407.34).

I s o t y p e s Segments from sample A.8407, thin sections A.8407.1- A.8407.59, partly figured in Pl. 1, Figs. 1–7 and Pl. 2, Figs. 1–10 of this paper.

Depository: The sample A.8407 and the thin sections prepared from it are deposited at the Dipartimento di Paleontologia, Università di Napoli Federico II, collection De Castro.

T y p e - l o c a l i t y: Southern flank of the Ciolo inlet, east of Gagliano del Capo, on the southeastern coast of Salento peninsula (Apulia, southern Italy); I.G.M. map 1:25000, 223 I SE "Alessano" (see Fig. 1 for geographical setting and ubication of the sample).

Type-material: The sample A.8407 has been

collected at the top of the Maastrichtian limestones outcropping in the Ciolo inlet, at about 20 m above sea level, just below the unconformity separating them from upper Oligocene limestones (PARENTE, 1993). It consists of a whitish limestone made by algal-foraminiferal packstone with coarse rudistid debris. Among the larger foraminifers the most significant species are Orbitoides apiculata, Omphalocyclus macroporus, Siderolites calcitrapoides and Lepidorbitoides socialis. This assemblage can be referred to the Orbitoides apiculata zone of VAN HINTE (1976) or to the Lepidorbitoides socialis zone of VAN GORSEL (1978) and is indicative of an upper Maastrichtian age. This age assignment is confirmed by the presence of rare specimens of Rosita contusa pointing to an age not older than the base of the Gansserina gansseri zone (CARON, 1985). Calcareous algae are represented by rare corallinaceans and abundant dasycladaleans (Cymopolia decastroi n. sp., Cymopolia barattoloi n. sp., Neomeris sp. and other not identified taxa).

D i a g n o s i s Thallus made by barrel-shaped to pear-shaped segments. Sterile segments on average smaller than fertile ones. Primary branches of central whorls composed by a short and thin peduncle followed by a swollen portion, akrophorous or slightly phloiophorous, constituting at least $^2/_3$ of the whole branch lenght. Primary branches of apical and basal whorls more slender and short. Inclination of primary branches changing from

about 90° in central whorls to 20–30° in apical whorls and 120–140° in basal whorls. Reproductive organs made by spheroidal to ovoid gametangia. Diameter of gametangia almost equal to that of terminal portion of primary branches: maximum in central whorls and decreasing toward both ends of the segment. Secondary branches shorter than primary ones; each tuft is composed by 5–7 branches.

Description

General characters of the calcareous skeleton: The calcified segments composing the thallus of *Cymopolia decastroi* n. sp. are generally barrel-shaped, very swollen in the middle and tapering at both extremities. In some sterile segments the calcareous skeleton is pear-shaped, i.e. they are more swollen in the lower part and show a neck in the upper part (Pl. 2, Figs. 4–5).

The central cavity of each segment is barrel-shaped too but less swollen. At the extremities of the segments it tapers in a constriction and then widens again. The terminal widening is more abrupt and pronounced at the basal end than at the upper end, especially in pear-shaped segments (Pl. 2, Figs. 4–5).

The calcareous skeleton envelops the primary branches, starting from their proximal ends, the reproductive organs, when present, and the secondary branches, except their distal ends. The calcification is rather thick in the proximal portion of primary branches but becomes very thin outwards especially in segments or portion of segments with swollen branches. It becomes a little stronger in the distal portion of secondary branches. The calcareous wall between adjacent pores of the same whorl is always thinner than the calcification between adjacent whorls. No difference has been observed as to these characters between fertile and sterile segments.

Sometimes the pores of the primary branches of the same whorl merge in an annular cavity with basal and upper wavy outlines subtilineating the position of the individual pores. This character is frequent in fertile segments (Pl. 1, Figs. 1–2, 4–5; Pl. 2, Figs. 1–3) but has been sporadically observed also in some sterile segments with swollen primary branches (Pl. 2, Figs. 7–8). This imperfect calcification is probably due to the lack of mucilage between branches very close or touching eachother.

The length of the segments varies from 1.530 mm to a maximum of about 2.80 mm. The number of whorls per segment varies from 11 to 16. All the other biometrical parameters are given in Tab. 1.

Inclination and distribution of primary branches in Cymopolia decastroi n. sp. varies both in the different portions of a segment and in different portions of the same branch. Generally a segment has two to four basal whorls with branches distinctly inclined downwards, three to six central whorls with branches almost perpendicular to the main axis, except for their peduncular portion, three to six

apical whorls with branches distinctly inclined upwards. The inclination of the branches is 80–90° in the central portion of the segments, decreases moving toward the upper end where it is 20–30° and increases toward the lower end where it is 120°–140°

In the central portion of some segments, especially in fertile ones with very swollen branches (Pl. 1, Figs. 1–4; Pl. 2, Fig. 2), but sometimes also in sterile segments (Pl. 2, Fig. 7), the primary branches have a distinctly curved course: the proximal portion has an inclination of 60°–70° then the branch becomes almost perpendicular to the main axis or even inclined downwards (Pl. 1, Figs. 1–2, lower portions). Moving towards the extremities of the segment the difference in inclination between the peduncle and the rest of the branch decreases and the branches show a more rectilinear course.

The primary branches are arranged in rather close simple whorls. The pores are alternating in subsequent whorls; this character is evident in oblique and tangential sections intersecting the proximal portion of the branches, close to their insertion on the central stem (Pl. 1, Fig. 1, 5). Moving outwards this arrangement is obscured by the close packing of the pores. The number of branches per whorl is 22–32 in fertile segments and 20-24 in sterile ones. The height between whorls is maximum in the central portion of the segments; moving towards the extremities of the segments the whorls are a little more closely spaced. This character can be observed in axial sections (Pl. 2, Figs. 4-5) or calculated from longitudinal-oblique ones after correction for the inclination of the cut as to the axis of the segment. Shape and size of primary branches: The shape of primary branches in Cymopolia decastroi n. sp. is highly variable. Different morphologies have been observed in different segments and in different portions of the same segment. In the central whorls of some fertile segments (Pl. 1, Figs. 1-2, 4; Pl. 2, Fig. 2), usually in the largest ones, and in some sterile segments (Pl. 2, Figs. 5, 7), the primary branch consists of a more or less short and thin cylindrical peduncle abruptly widening in a large akrophorous to slightly phloiophorous portion occupying at least $\frac{2}{3}$ of the branch length; the connection between the peduncle and the swollen portion of the branch is in lower position as to the vertical proximal section of the branch. In other segments the primary branches of central whorls have a longer cylindrical to slightly phloiophorous peduncle followed by a more or less developed and abrupt distal widening (Pl. 1, Fig. 3; Pl. 2, Fig. 4). Intermediate morphologies between these two extremes have been observed, including branches with a more regular phloiophorous morphology (Pl. 1, Fig. 7; Pl. 2, Fig. 6).

As a rule the branches of apical and basal whorls are thinner and shorter than the branches of central whorls in the same segment (Pl. 1, Figs. 1, 3, 7; Pl. 2, Figs. 2, 4–5).

	C. decastroi	C. decastroi	C. barattoloi	C. barattoloi
	n.sp.	n.sp.	n.sp.	n.sp.
	f	S	f	S
	1.428-2.756	0.841-1.606	0.918-1.938	0.612–1.222
D	1.951±0.379	1.208±0.233	1.216±0.268	0.811±0.139
	(13)	(15)	(12)	(11)
	0.523-0.994	0.280-0.625	0.331-0.790	0.242-0.433
d	0.712±0.143	0.456±0.100	0.460±0.130	0.337±0.069
	(12)	(15)	(12)	(11)
	0.302-0.438	0.263-0.485	0.324-0.421	0.316-0.485
d/D	0.378±0.045	0.380±0.062	0.376±0.032	0.416±0.052
	(12)	(15)	(12)	(11)
	0.408-0.746	0.236-0.535	0.268-0.574	0.166-0.344
e	0.586±0.103	0.376±0.089	0.378±0.073	0.237±0.046
	(12) 0.020-0.061	(15) 0.025–0.055	(12) 0.016–0.040	(11) 0.020–0.024
	0.020=0.061 0.044±0.013	0.025=0.035 0.035±0.010	0.010=0.040 0.031±0.009	0.020=0.024 0.021±0.002
pvm	(7)	(6)	(7)	(5)
	0.035-0.071	0.020-0.045	0.020-0.040	0.020-0.030
DWm.	0.053=0.071 0.052±0.011	0.020-0.043 0.032±0.010	0.028±0.007	0.026±0.005
pwm	(16)	(7)	(8)	(8)
-	0.081-0.151	0.061-0.101	0.030-0.131	0.020-0.040
$p^{1}/_{2}$	0.105±0.020	0.080±0.013	0.048±0.033	0.030±0.009
£ '2	(20)	(14)	(11)	(9)
	0.115-0.178	0.091-0.151	0.060-0.162	0.050-0.111
рум	0.149±0.024	0.121±0.016	0.095±0.038	0.072±0.022
	(7)	(9)	(8)	(6)
	0.101-0.212	0.081-0.162	0.071-0.111	0.0500.101
pwM	0.142±0.030	0.114±0.027	0.089±0.015	0.077±0.018
	(16)	(10)	(8)	(9)
	0.242-0.626	0.162–0.343	0.131-0.242	0.101-0.182
l	0.381±0.100	0.247±0.053	0.174±0.037	0.146±0.021
	(13)	(14)	(12)	(11)
	22–32	20–24	20–36	18-25
w	27.750±3.079	23±2	25±5.447	21.625±2.560
	(12) 0.110–0.208	(4) 0.091–0.162	(7) 0.079–0.141	(8) 0.081–0.151
h	0.110-0.208 0.145±0.027	0.091-0.162 0.129±0.020	0.079=0.141 0.111±0.025	0.081=0.131 0.105±0.018
11	(15)	(10)	(10)	(12)
	0.025-0.081	0.020-0.061	0.025-0.050	0.020-0.030
p'	0.045±0.014	0.030±0.012	0.036±0.007	0.024±0.005
Р	(15)	(16)	(14)	(9)
	0.172-0.404	0.061-0.232	0.081-0.303	0.071-0.151
1'	0.261±0.056	0.129±0.056	0.207±0.052	0.096±0.027
	(14)	(14)	(12)	(10)
	1.066-1.957	1.174-3.475	0.645-1.617	1.000-2.395
1/1'	1.477±0.303	2.156±0.712	0.893±0.305	1.668±0.443
	(13)	(14)	(12)	(10)
w'	6–7	5–6	4	4–5
w	(6)	(3)		(3)
	0.121-0.273	1	0.081-0.192	10/
ls	0.166±0.038		0.140±0.030	
	(13)		(14)	
	0.081-0.172		0.081-0.141	
dsv	0.136±0.030		0.103±0.020	
	(14)		(10)	
	0.111-0.162		0.081-0.101	
dsw	0.143±0.019		0.099±0.007	
	(14)		(8)	
	1.000-1.665		1.000-1.703	
ls / ds	1.210±0.208		1.361±0.194	
	(13)		(14)	
				

Table 1: Main biometrical parameters of Cymopolia decastroi n.sp. and Cymopolia barattoloi n.sp. given separately for fertile (f) and sterile (s) segments (sample A.8407). For each parameter the range is given in roman type, mean and standard deviation are given in bold type and the number of measurements in italics, between brackets. All size parameters are given in millimeters and have been taken in the most swollen portion of the segments. D: outer diameter of the segments; d: inner diameter of the segments; e: thickness of the calcareous wall; pv_m: vertical width of primary pores in the proximal portion; pwm: whorly width (="ampiezza verticillare" in BARATTOLO, 1981) of primary pores in the proximal portion; p¹/₂: width of primary branches at 1/2 of their lenght; pv_M: vertical width of primary pores in the distal portion; pw_M: whorly width of primary pores in the distal portion; l: lenght of primary branches; w: number of primary branches per whorl; h: distance between two subsequent whorls; p': width of secondary branches; l': lenght of secondary branches; w': number of secondary branches per tuft; ls: lenght of gametangia; dsv: vertical diameter of gametangia; dsw: whorly diameter of gametangia.

Moving towards the extremities of the segment the width of the median and distal portion of primary branches decreases while the width of the proximal portion is more or less the same as in the branches of central whorls. As a consequence the branches have a longer cylindrical to slightly phloiophorous peduncular portion and a more or less developed distal widening. In these branches the connection between the peduncle and the swollen portion of the branch is central in position as to the vertical section of the branch.

The transversal section of primary branches is circular to elliptical in the proximal portion and becomes distinctly subrectangular to trapezoidal in the swollen portion of the branches (Pl. 1, Figs. 1, 5; Pl. 2, Figs. 2-3).

Reproductive organs Cymopolia decastroi n. sp. is characterized by large subspherical to slightly ovoid gametangia. In fertile portion of segments each primary branch bears a gametangium in terminal position at the center of a tuft of secondary branches. The gametangium is directly attached to the apex of the primary branch without the interposition of a well defined peduncle. The size of the gametangia is maximum in central whorls and is positively correlated with the outer diameter of the calcareous skeleton and even more with the distal width of primary branches. The gametangia become smaller moving towards the extremities of the segments. Apical and basal whorls usually lack gametangia even in fertile segments (Pl. 1, Figs 3, 7; Pl. 2, Fig. 2).

Secondary branches Secondary branches are subcylindrical for most of their length then widen abruptly and probably form a cortex at their distal ends. They generally have the same inclination as the distal portion of primary branches that bear them: they are nearly perpendicular to the central stem in the central whorls, inclined upwards in upper whorls and downwards in lower whorls.

The length of secondary branches is maximum in central whorls; it decreases moving towards the extremities of the segments. Secondary branches are always shorter than primary ones.

Also the width of secondary branches, taken before their terminal widening, is maximum in central whorls; secondary branches of apical and basal whorls are a little thinner.

The number of secondary branches per primary branch can be observed with certainty only in tangential sections. In fertile segments each primary branch bears a tuft of 6–7 secondary branches (Pl. 1, Figs. 5–6). In sterile segments we have observed 5–6 secondary branches per tuft (Pl. 2, Figs. 9–10).

Reconstruction of the thallus: In the preceding paragraphs the main morphological characters of disarticulated segments of *Cymopolia decastroi* n. sp. have been described. Here some hypothesis are made on the morphology of the whole thallus on the basis of what is known about living species of *Cymopolia*.

In living species of the genus *Cymopolia* repetitive calcified segments are separated by periodic noncalcified constrictions providing the alga with flexibility (CRAMER, 1887; SOLMS-LAUBACH, 1893; BERGER & KAEVER,1992). It is therefore reasonable to assume that the segments of *Cymopolia decastroi* n. sp., preserved as isolated fossils, were originally linked by noncalcified articulations. Therefore the variability observed between segments (biometric and morphological) can be interpreted as variability between different segments of the same thallus and/or as variability between segments of different thalli.

Of the two known extant species, Cymopolia barbata has a branched thallus while Cymopolia vanbosseae is characterized by a simple thallus. Branching has never been reported in fossil Cymopolia species. Since it occurs in noncalcified articulations no trace is expected to be preserved in fossil material consisting only of disarticulated calcified segments. If we assume that Cymopolia decastroi n. sp. was characterized by a branched thallus it is reasonable that a difference between segments of the main axis and segments of the branches could account for at least part of the observed variability. In fact some of the published photos of Cymopolia barbata (LIDDLE, 1979; BERGER & KAEVER, 1992) show a quite remarkable difference in size of segments: the segments of the branches, especially those of higher order branches, are remarkably smaller than those of the main axis. Since most of the morphological parameters are positively correlated with the most important size-parameters (D and d) a difference in size of the segments could account for most of the morphological variability.

The hypothesis that in samples with Cymopolia elongata

from the Paleocene of eastern Majevica (NE Bosnia) the smaller segments could belong to lateral branches has recently put forward by RADOICIC (1991).

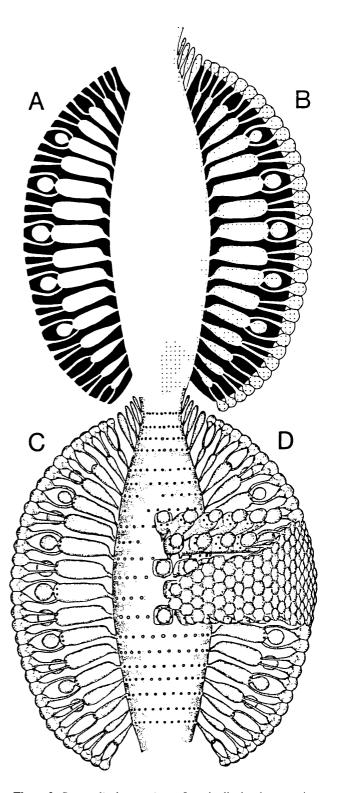


Figure 2: Cymopolia decastroi n.sp. Longitudinal and perspective reconstructions of two subsequent segments. A) calcareous skeleton in axial section. B) primary and secondary branches, gametangia and calcification (black) in axial section. C) longitudinal view of central stem, branches and gametangia without calcification. D) perspective view of branches, gametangia and cortex. (Approximately 30 x)

No information is available in literature as to the distribution of sterile and fertile segments in the plants of living *Cymopolia barbata* and *Cymopolia vanbosseae*. In *Cymopolia decastroi* n. sp. sterile segments are on average smaller than fertile ones, they might therefore be the younger segments of the axis or of the branches as contrasted with larger adult fertile segments.

In the Fig. 2 of this paper it has been attempted a reconstruction of two successive fertile segments of this species to represent in a synthetic and schematic way the tridimensional morphology deduced from the interpretation of the randomly oriented sections of segments. Of course this representation does not give account of the morphological variability between different segments discussed in the description and partly documented in the plates but allows, for example, to represent the morphological variation of some traits between different regions of the same segment (central whorls vs. apical and basal whorls). In Fig. 3 it is given a reconstruction of a transversal section.

C o m p a r i s o n s: The most remarkable character of *Cymopolia decastroi* n. sp. is the shape of primary branches. In the studied samples this character shows a fairly great variability (see shape and size of primary branches) but on the whole the species is characterized by primary branches swollen or widening outwards. The presence of a terminal widening in the primary branches is a character quite common in fossil *Cymopolia* species

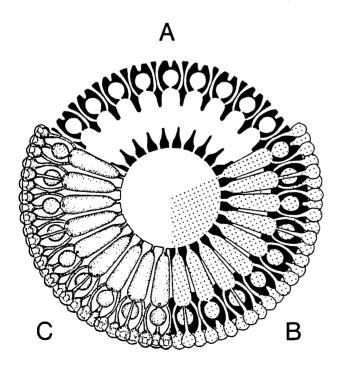


Figure 3: Cymopolia decastroi n. sp. Transversal and perspective reconstructions of the central whorl of a segment. A) sector of the whorl showing the calcareous skeleton in transversal section. B) central stem, primary and secondary branches, gametangia and calcification (black) in transverse perspective view. C) the same as B but without calcification. (Approx. 30 x)

but only few species show primary branches distinctly enlarged for most of their course: *Cymopolia eochoristosporica* ELLIOTT 1968 from the Maastrichtian of Arabian peninsula, *Cymopolia inflataramosa* SE-GONZAC 1968 from the Thanetian of French Pyrenees and *Cymopolia sirmiensis* RADOICIC 1987 from the Maastrichtian of the Dinarids.

For Cymopolia eochoristosporica only one specimen and a portion of another one were figured by ELLIOTT (1968). In order to make a more complete comparison I checked the type-material of this species, deposited at the British Museum (Natural History) of London. Unfortunately this material consists of only two thin sections in which C. eochoristosporica is represented by two longitudinal-oblique sections (corresponding to those figured by ELLIOTT, 1968) and a fragment of a tangential section. Nothing can be added to the original description on the basis of this material, however the measures of the biometric parameters have been repeated and completed. In particular the number of primary branches per whorl calculated from the two oblique sections is 21–22 whereas ELLIOTT (1968) indicated a range of 12–14.

Comparing Elliott's specimens with the largest fertile segments of *C. decastroi* n. sp., showing similar pore morphology and overall size, the most striking differences are the shape of the segments, the inclination of the primary branches, the number of primary branches per whorl and the size of gametangia:

- The segments of *C. eochoristosporica* are long and regularly cilindrical with up to 21 and more whorls per segment, while in *C. decastroi* n. sp. they are shorter, generally barrel-shaped and distinctly swollen in the middle, with no more than 16 whorls per segment.
- The primary branches are nearly perpendicular through the whole segment in *C. eochoristosporica* while in *C. decastroi* n. sp. only central whorls branches are perpendicular (see inclination of the branches).
- The number of primary branches per whorl and the size of gametangia are larger in *C. decastroi* n.sp. (see Figs. 4 b and f) while the height between whorls is smaller.
- C. inflataramosa differs from C. decastroi n.sp. in the shape of primary branches that lack a peduncle and are swollen from the very beginning, just after their insertion on the central stem. Moreover the average number of primary branches per whorl is lower and the gametangia are larger (see Figs. 4 b, d and f).

The published figures of *C. sirmiensis* resemble some of the segments of *C. decastroi* n. sp. but the 'funnel'-shaped primary branches of Radoicic's species represent only one of the pore morphologies observed in *C. decastroi* n. sp. and a rare one. Moreover in *C. sirmiensis* the width of secondary branches and the height between whorls are larger whereas the gametangia are smaller. On this basis it is preferred to consider the two species as distinct.

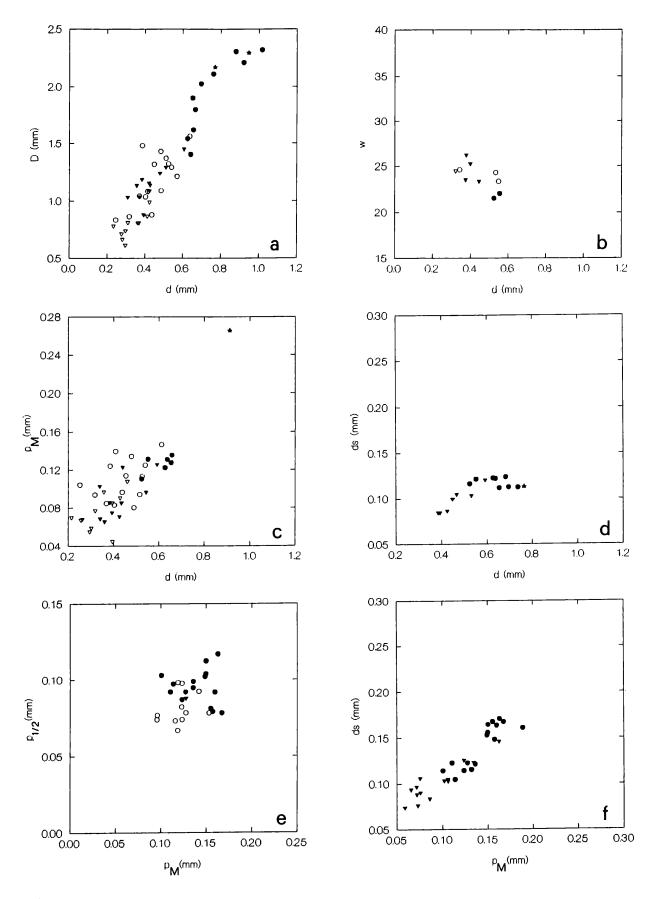


Figure 4: Bivariate scatterplots of the main biometric parameters. Legend – empty circles: sterile segments of C. $decastroi\ n$. sp.; black circles: fertile segments of C. $decastroi\ n$. sp.; empty triangles: sterile segments of C. $barattoloi\ n$. sp.; black triangles: fertile segments of C. $barattoloi\$

The differences between *Cymopolia decastroi* n. sp and *Cymopolia barattoloi* n. sp. are discussed in a following paragraph.

Cymopolia barattoloi n. sp. (Pl. 2, Figs. 11–15; Pl. 3, Figs. 1–15)

Origin of the name: The species is dedicated to Professor Filippo Barattolo, Dipartimento di Paleontologia, Università di Napoli "Federico II", for his precious contribution to the knowledges on fossil dasycladaleans. Holotype: Segment in axial section figured in Pl. 3, Fig. 3 of this paper (thin section A.8407.21).

Is o types: Segments from sample A.8407, thin sections A.8407.1–A.8407.59, partly figured in Pl. 2, Figs. 11–15 and Pl. 3, Figs. 1–12 of this paper.

Depository, type-locality and typem at erial: The same as for Cymopolia decastroi n. sp. Thallus made by moderately swollen Diagnosis barrel-shaped segments. Sterile segments on average smaller than fertile ones. Primary branches of central whorls composed by a thin cylindrical peduncle followed by a more or less well delimited distal swelling. Primary branches of apical and basal whorls always shorter and with a not very developed to absent distal swelling. Inclination of primary branches changing from about 90° in central whorls to 20-30° in apical whorls and 130-140° in basal whorls. Reproductive organs made by ovoid to ellipsoidal gametangia. Diameter of gametangia maximum in central whorls and decreasing toward both ends of the segment. Secondary branches may be shorter or longer than primary ones; each tuft is composed by 4–5 branches.

Description:

General characters of the calcareous skeleton: The thallus of Cymopolia barattoloi n. sp. is composed by barrel-shaped segments, moderately swollen in the middle and tapering at both extremities (Pl. 3, Figs. 1-3). Also the central cavity of these segments is moderately swollen in the middle; it tapers moving toward both the extremities and forms a constriction, then it widens again, with a more wide flaring at the lower end than at the upper end (Pl. 3, Fig. 3). In some sterile segments the most swollen part of the calcareous skeleton and of the central cavity is a little closer to the lower end (Pl. 2, Fig. 11).

The calcareous skeleton envelops the primary branches, starting from their insertion into the central stem, the reproductive organs, when present, and the secondary branches, except their distal end. The calcification is rather thick around the proximal and median portions of primary branches whereas it is very thin around their distal ends. In fact the distal ends of primary branches of the same whorl are often joined in a more or less continuous annular cavity; this character is very common in fertile segments (Pl. 3, Figs. 4–6, 8, 12) but it has been occasionally observed also in sterile ones (Pl. 2, Fig. 13).

The lenght of the segments in Cymopolia barattoloi n. sp.

varies from about 1.0 to 2.5 mm; the number of whorls per segment varies from 11 to 16. All the other biometrical parameters are given in Tab. 1.

In clination and distribution of primary branches in Cymopolia barattoloi n. sp. varies between different portions of the same segment. Primary branches of central whorls are almost perpendicular to the axial stem. The inclination increases moving toward the base of the segment; in the lowermost whorls the branches are distinctly inclined downwards with an angle of about 130–140°. Moving towards the upper end of the segment the inclination decreases: branches of the uppermost whorls have an inclination of about 20–30°.

Primary branches are distributed in simple whorls and alternate in subsequent whorls. The number of branches per whorl is 20–36 in fertile and 18–25 in sterile segments. The distance between whorls is maximum in central whorls; moving towards the extremities of the segments the whorls become a little more close each other (see for example Pl. 3, Figs. 1–3).

Shape and size of primary branches The shape of primary branches in Cymopolia barattoloi n. sp. shows a certain amount of variability, both between different segments and between different portions within the same segment. The most common morphology, observed in most of the fertile segments, except for their apical and basal whorls, is characterized by a long and thin cylindrical portion, occupying more than ¹/₂ of the total lenght of the branch, followed by a distinct terminal widening (Pl. 3, Figs. 1, 3–10, 12). In some fertile segments (see for example Pl. 3, Fig. 2) the terminal widening is not so well delimited and the swollen portion of primary branches in central whorls takes almost ¹/₂ of the total lenght of the branches. In sterile segments the terminal widening is usually present but never so well developed and delimited as in fertile ones (Pl. 2, Figs. 11-15). Moreover some sterile segments shows primary branches lacking a distinct widening also in central whorls (Pl. 3, Figs. 13, 15).

The morphology of primary branches in basal and apical whorls is more regular: moving away from central whorls the branches become thinner and shorter, the width of their terminal portion decreases and the branches become almost cylindrical (Pl. 2, Figs. 11–12; Pl. 3, Figs. 1–2). The lenght of primary branches is maximum in central whorls and decreases moving towards both ends of the segment.

Reproductive organs: Cymopolia barattoloi n. sp. is characterized by slightly ovoid to ellipsoidal gametangia. The size of reproductive organs is maximum in central whorls and decreases moving towards both the ends of the segments; apical and basal whorls usually lack gametangia even in fertile segments (Pl. 3, Figs. 1–2). Secondary branches are thin and subcylindrical for most of their length but their distal portion shows a progressive widening,

especially evident in their whorly section (= "sezione verticillare" in BARATTOLO, 1981) (see for example Pl. 3, Figs. 6, 8). They generally keep the same inclination as the primary branches bearing them: they are almost perpendicular in central whorls, inclined upwards in upper whorls and downwards in lower whorls (Pl. 3, Figs. 1–3). Secondary branches of apical and basal whorls are always a little thinner and remarkably shorter than branches of central whorls of the same segment.

The ratio I/I' is highly variable: secondary branches may be longer or shorter than primary branches in fertile segments (I/I' = 0.645-1.617) whereas they are almost always shorter in sterile segments (I/I' = 1.0-2.395).

The number of secondary branches per primary branch has been observed with certainty only on a few tangential sections: each tuft seems to be composed of 4–5 secondary branches, both in fertile and in sterile segments.

C o m p a r i s o n s: The segments of Cymopolia present in the studied samples have been attributed to two distinct species: Cymopolia decastroi n. sp. and Cymopolia barattoloi n. sp. The discrimination between these two taxa is mainly based on the shape of primary branches. Although this character shows a certain amount of variability in both the species Cymopolia decastroi n. sp. has been described as having primary branches distinctly swollen for most of their lenght whereas in Cymopolia barattoloi n. sp. the swollen portion of primary branches is restricted to a more or less well developed and delimited terminal widening.

The shape of primary branches can be represented through different sets of biometrical parameters. For example we could describe each branch through a set of four biometrical values that are the lenght of the branch and its widths at the proximal portion, at $\frac{1}{2}$ of the total branch length and at the terminal portion. Since the aim is to discriminate between segments bearing branches that are swollen only in the terminal portion and segments bearing branches that are swollen along most of their lenght we could also use as a single parameter the ratio $p_M/p_{1/2}$ This ratio will give values higher than 1 in the first case and close to 1 in the second case. As a consequence in a bivariate scatter plot of p_M/p¹/₂we will have a good separation between the segments attributed to Cymopolia decastroi n. sp. and those attributed to Cymopolia barattoloi n. sp. (see Fig. 4 e). As a matter of fact the only segments that this plot fails to discriminate are those figured in Pl. 3, Figs. 1–2: these segments are attributed to Cymopolia barattoloi n. sp. even if the shape of their primary branches is not so distinctive and most of their biometrical parameters plot in the field of C. decastroi n.sp. The reason for this decision is that both the shape of the segment and the shape of primary branches are remarkably different from those observed in segments of C. decastroi n. sp. having approximately the same inner diameter (compare for example Pl. 1, Fig. 1 with Pl. 3, Fig. 1).

After having tentatively assigned each of the segments of *Cymopolia* present in the studied sample to either of the

two taxa on the basis of the morphology of primary branches we see that almost all the biometric parameters allow to discriminate the two species, i.e. the statistical tests of comparison between the univariate distributions of these parameters allow to refuse the null hypothesis under a strict 0.01 level of confidence.

If we take a look at the bivariate distributions (Fig. 4) we see that most of them, and particularly $p_M/p_{1/2}$ and w/d, allow a good discrimination both considering separately and jointly fertile and sterile segments.

A principal component analysis taking into account the most relevant biometrical parameters allows to synthesize the data supplied by univariate and bivariate distributions and to strenghten the conclusion that the *Cymopolia* segments present in the studied sample represent two distinct species (see Fig. 5).

Summing up, and substituting words for numbers and graphs, the most important differences between *Cymopolia barattoloi* n. sp. and *Cymopolia decastroi* n. sp. are:

- -shape of primary branches in central whorls: only distally enlarged in *C. barattoloi* n. sp., swollen along most of their lenght in *C. decastroi* n. sp.
- ratio between the lenght of primary and secondary branches in central whorls: in *C. barattoloi* n. sp. primary branches may be shorter or longer than secondary in fertile segments but are always shorter in sterile segments; in *C. decastroi* n. sp. primary branches are always longer than secondary ones.
- number of primary branches per whorl: if we compare segments having more or less the same inner diameter the number of primary branches per whorl is remarkably higher in C. barattoloi n. sp. than in C. decastroi n. sp. If we take into consideration previously described species of the genus Cymopolia, C. barattoloi n. sp. may be compared with the species showing primary branches characterized by a terminal widening: C. miocenica (KARRER, 1868) MORELLET & MORELLET, 1926 from the Miocene of Romania; C. zitteli MORELLET & MORELLET, 1913, from the Lutetian and Auversian of Paris Basin; C. tibetica MORELLET, 1916, from the Maastrichtian of Tibet; C. edwardsi MORELLET & MORELLET, 1939, from the Eocene of the Cotentin (NW France); C. frugifera SEGONZAC, 1976, from the Thanetian of the French Pyrenees.

In this group *C. frugifera* sets apart for being characterized by the common occurrence of two gametangia per primary branch. The differences between the other species are more subtle and with some of them once more the comparisons are somewhat hampered by original descriptions and figures based on very few specimens and by poor presentation of biometric data.

From the description and figures of *C. miocenica* given by MORELLET & MORELLET (1926) nothing can be said on the morphology of primary branches, on their inclination and on the number of branches per whorl: as to biometrical parameters the only data given by the authors are the ranges of article length, outer and inner diameter.

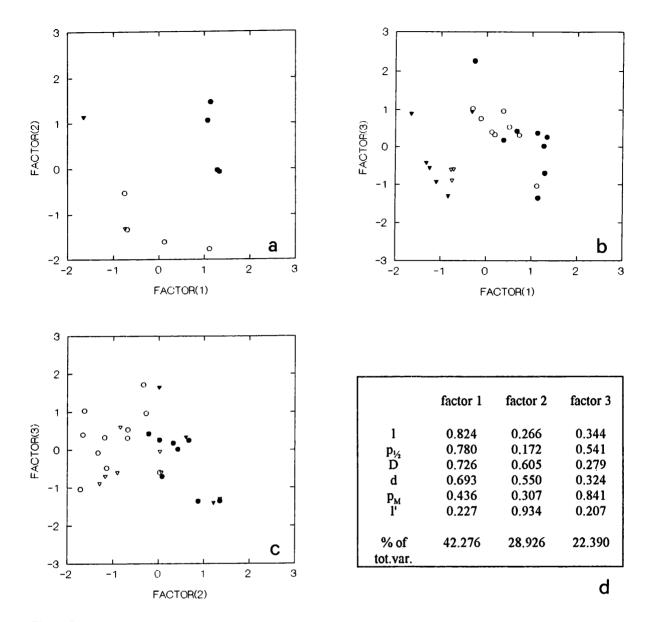


Figure 5: Principal component analysis. a-c: varimax rotated factor plots of the main biometric parameters of the *Cymopolia* segments of sample A.8407. d: rotated factor loadings and % of variance explained by each component. See caption to Fig. 2 for legend of symbols. Only some parameters have been used to avoid excessive reduction of number of cases owing to missing values. For the same reason for the width of primary branches at their distal portion it has been used p_M that is the greater value between pw_M and pv_M when both values were available, either of the two when only one was available.

Even if with some reserves deriving from the poor knowledge of this species it seems that the main differences with *C. barattoloi* n. sp. can be found in the lenght of primary branches (very short in *C. miocenica*) and in the size of the gametangia that are said to occupy almost the whole calcareous wall in *C. miocenica* whereas in *C. barattoloi* n. sp. the thickness of the calcareous wall is on average almost three times the lenght of gametangia (see Tab. 1).

C. zitteli is certainly the best known species in the group cited above: it has been recently redescribed and well figured by GÉNOT in several papers (1978, 1980, 1987). The most important differences between C. barattoloi n. sp. and C. zitteli may be found in the shape of gametangia, that are distinctly ovoid in C. zitteli (ls/ds generally approaches or exceeds the value of 2) and in the shape of the segments (barrel-shaped vs. cylindrical with a neck at

the base). Moreover in *C. zitteli* primary branches are inclined upwards through the whole segment whereas in *C. barattoloi* n. sp. only upper whorls have primary branches inclined upwards (compare Pl. 3, Fig. 2 in GÉNOT, 1980 with Pl. 3, Fig. 3 of this paper).

In the original description of Cymopolia tibetica (MO-RELLET, 1916) the internal morphology is illustrated by 5 drawings, 1 referring to a longitudinal section and 4 to transversal sections. The most important characters defining this species are shape and inclination of the primary branches, perpendicular to the central axis and showing a distinctly enlarged terminal portion, the rather low number of branches per whorl (9–12) and the very remarkable length attained by segments (up to 2.5 cm). On this basis C. barattoloi n. sp. differs from C. tibetica in the shape of the calcareous segments, short and barrel-shaped vs. long and regularly cylindrical, in the number of

primary branches per whorl, that is remarkably greater in the Apulian species, and in the inclination of primary branches that are always perpendicular in *C. tibetica* whereas they are perpendicular only in central whorls in *C. barattoloi* n. sp.

The original description of *C. edwardsi* is accompanied by a single figure showing a longitudinal section through a cylindrical segment. Plotting this only specimen in the bivariate scatter plots of *C. barattoloi* n. sp., it would set apart in having a much higher ratio d/D (see Fig. 4a), and a lower number of branches per whorl (see Fig. 4b). Moreover in *C. edwardsi* the branches are almost perpendicular whereas in *C. barattoloi* n. sp. branches of upper whorls are distinctly inclined upwards and those of basal whorls are inclined downwards. On this basis the two species are taken as distinct even if with some reserves deriving from the insufficient knowledge of *C. edwardsi*.

3. Discussion and conclusions

In the descriptions of *Cymopolia decastroi* n. sp. and *Cymopolia barattoloi* n. sp. we have stressed that these species are characterized by a fairly large morphological variability. This variability is chiefly expressed by shape and size of primary branches and by shape and size of the segments.

The intraspecific morphological variability observed in *C. decastroi* n. sp. and *C. barattoloi* n. sp. is a character common to other species of the genus (both living and fossil ones) as for example *C. zitteli*, *C. elongata* and *C. barbata*.

The great variability in shape and size of segments of *C. elongata* and *C. zitteli* in the Lutetian and Auversian of Paris Basin has been subtilineated by GÉNOT (1978, 1987). This same variability has been observed by RADOICIC (1991) in *C. elongata* samples from the Paleocene of NE Bosnia.

Variability in shape and size of segments in the living species *C. barbata* has been remarked by several authors. LIDDLE (1979) has reported statistically significant differences in shape and size of segments between intertidal and subtidal populations. Variability in shape of primary branches, and notably in the presence/absence and degree of terminal widening has been observed by SEGONZAC (1968) and GÉNOT (1978).

The intraspecific morphological variability shown by some characters in the above mentioned species of the genus *Cymopolia* raises some problems as to the definition and discrimination of fossil species in this genus. It is worth remembering that in the past some of these characters have been used to propose different genera or subgenera within the tribe *Cymopolieae* (MORELLET & MORELLET, 1913; PIA, 1927; KAEVER 1969). These problems have been already discussed by GÉNOT (1978) who refused the possibility to use at genus level characters that are seen to fall in the variability range of one species. In listing the main characters to be used in the definition

of the species within the genus Cymopolia, GÉNOT (1978) stressed the importance to use a set of characters, and not a single one, to avoid oversplitting. All the characters listed by GÉNOT (1978) may be defined as "shape & size" characters; all of them are expected and most of them have been positively demonstrated to show a certain amount of intraspecific variability in some known species, both fossil and extant (see above). This fact can not lead to their abandonment as not suited to define and discriminate species: in fossil dasycladaleans presence/ absence or category characters (like f.e. position of reproductive structures, type of branches distribution etc.) are always used at supraspecific level whereas discrimination of species within a genus is very often, if not always, based on "shape & size" characters. The recommendation to use set of characters instead of a single character is certainly valid but not sufficient. The intraspecific variability shown by "shape & size" characters calls for a more accurate description of fossil species of Cymopolia: their morphological variability must be described from samples consisting of numerous segments and the data must be correctly expressed in order to allow accurate comparisons between different species.

Regrettably, a correct statistical approach to biometric data is almost always lacking in paleontological descriptions of fossil dasycladaleans. The problems arising from this pitfall have been already subtilineated by ZORN (1977). In the paleontological literature on fossil dasycladaleans biometrical data are often expressed only by ranges of values: mean, standard deviation and number of measurements are often neglected thus hindering the use also of simple parametric tests of comparison by following researchers.

In the present paper two species of *Cymopolia*, cooccurring in the same sample, have been compared taking in consideration univariate, bivariate and multivariate distributions of biometrical parameters. Of course bivariate and multivariate distributions have shown to be much more useful than univariate ones (let alone simple ranges of value).

Moreover it has been shown how both for *Cymopolia decastroi* n. sp. and especially for *Cymopolia barattoloi* n. sp. comparisons with other species of the genus *Cymopolia*, showing similar primary branch morphology, are somewhat hindered by insufficient descriptions and poor treatment of biometric data found in literature.

In conclusion this case-study allows to draw some remarks that are thought to be more generally valid for species definition and discrimination in fossil dasycladaleans:

- Species descriptions based on very few specimens contain no information on intraspecific morphological variability thus preventing accurate definition and discrimination of species unless we accept a purely typological approach.
- Incorrect gathering and presentation of biometric data prevents accurate comparison by statistical tests even in the case of samples consisting of numerous specimens.

Since in fossil dasycladaleans presence/absence characters are usually given supraspecific value often the only way to differentiate species within a genus is to use "shape & size" characters. These characters can be appropriately described by biometric parameters and their variability is correctly expressed by the statistical distribution of these parameters.

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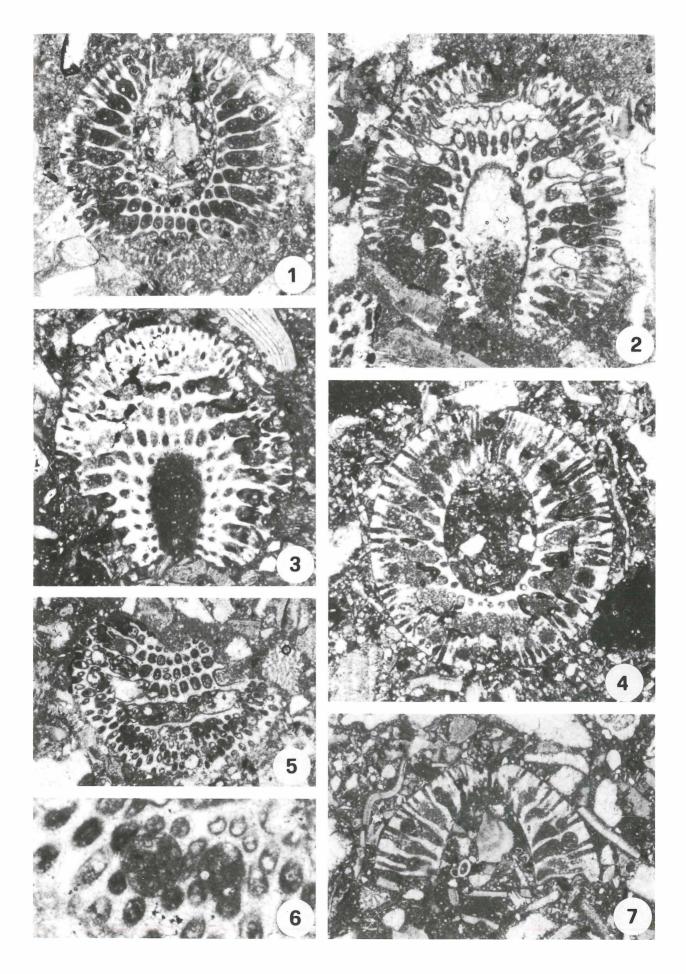
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PLATES 1-3

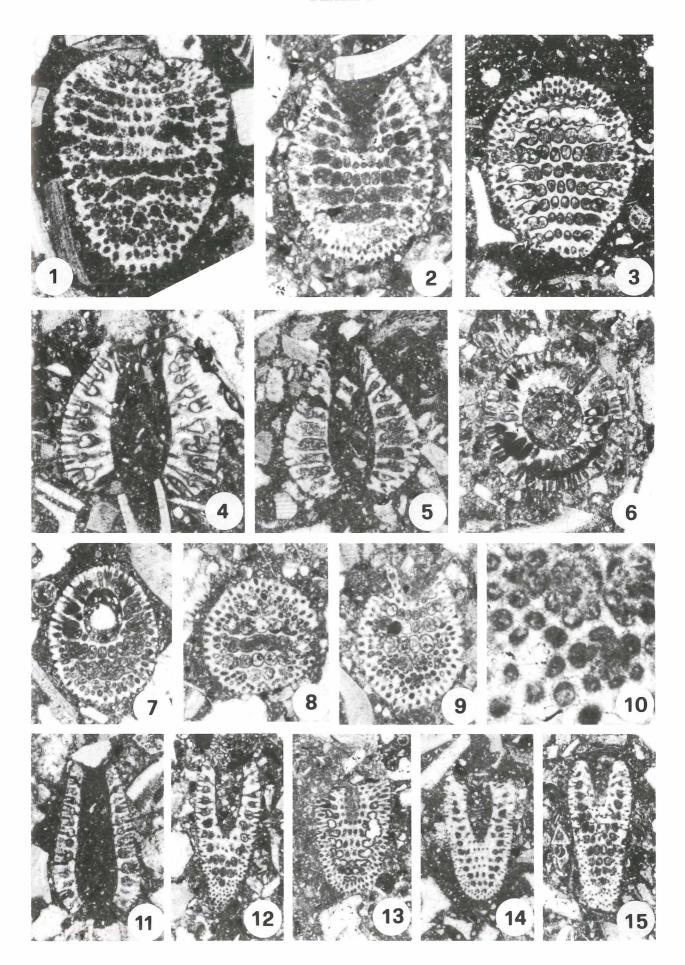
Cymopolia decastroi n. sp., upper Maastrichtian of southeastern Salento (Apulia, southern Italy).

- Fig. 1. Holotype; oblique-longitudinal section through a large-size fertile segment. Primary branches of central whorls have a curved course: their proximal portion is inclined upwards but the swollen portion bends downwards and becomes almost perpendicular to the axial stem or even inclined downwards. Moving toward the apex of the segment the difference in inclination between the proximal portion and the swollen part of the branch decreases. In the uppermost whorls primary branches have a rectilinear course and their inclination drops to 20–40° Thin section A.8407.33, magnification 25 x.
- Fig. 2. Isotype; slightly oblique tangential section through a large-size fertile segment. Notice the difference in inclination between the proximal, peduncular portion and the swollen part of primary branches. In the upper part of this section the pores corresponding to the swollen portion of primary branches of the same whorl merge in a cavity with wavy outline (the same feature can be seen in the lowermost part of the segment in Fig. 1). Thin section A.8407.34, magnification 25 x.
- Fig. 3. Slightly oblique tangential section through a large-size fertile segment. See what said above as to the inclination of primary branches. Thin section A.8696.8, magnification 25 x.
- Fig. 4. Oblique section through a large-size fertile segment. Notice how shape of primary pores, inclination of primary branches and size of gametangia change moving from central whorls towards apical whorls. Thin section A.8697.32, magnification 25 x.
- Fig. 5. Isotype; tangential section through central and upper whorls of a large-size fertile segment. Notice, in the middle of the section, the cavity formed by the pores corresponding to the swollen portion of primary branches of the same whorl. Thin section A.8407.18, magnification 25 x.
- Fig. 6. Detail of Fig. 5 showing large circular pores, corresponding to transversal sections of two adjacent gametangia, encircled by small pores corresponding to transversal sections of tufts of secondary branches. Each tuft is composed by seven secondary branches. Thin section A.8407.18, magnification 25 x.
- Fig. 7. Isotype; fragment of a slightly oblique longitudinal section through the uppermost part of a large-size fertile segment. Notice how apical whorls are made by thin primary branches distinctly inclined upwards and lacking gametangia. Thin section A.8407.10, magnification 25 x.



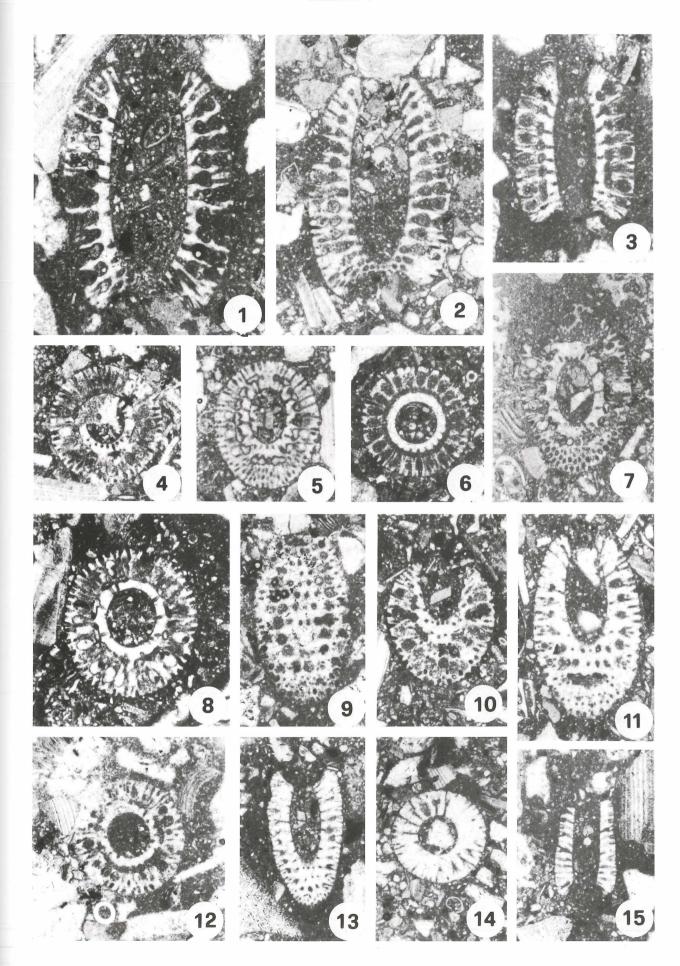
Figs. 1-10. Cymopolia decastroi n. sp., upper Maastrichtian of southeastern Salento (Apulia, southern Italy).

- Fig. 1. Isotype; tangential section through a fertile segment. Notice the cavity formed by the swollen portion of primary branches and the crowding of large size gametangia encircled by secondary branches in the lower portion of the figure. Thin section A.8407.26, magnification 25 x.
- Fig. 2. Isotype; tangential oblique section through a fertile segment. The uppermost three whorls in the figure, corresponding to the apical whorls of the segment, are seemingly devoid of gametangia. Thin section A.8407.58, magnification 25 x.
- Fig. 3. Tangential section through a fertile segment. Notice the cavity, formed by the swollen portion of primary branches, and the absence of gametangia in the upper whorls of the segment. Thin section A.8696.2, magnification 25x.
- Fig. 4. Isotype; longitudinal section through a sterile segment. The calcareous skeleton is pear-shaped. The central cavity is less swollen and more symmetrical; at the apex it makes a kind of neck while at the base it widens rather abruptly. Thin section A.8407.48, magnification 25 x.
- Fig. 5. Isotype; longitudinal section through a sterile segment. The calcareous skeleton is pear-shaped and the sections of the branches show remarkable differences in size, shape and inclination moving from central whorls towards both apical and basal whorls. Thin section A.8407.6, magnification 25 x.
- Fig. 6. Transversal section through a sterile segment or a sterile portion of segment. Notice how primary branches are distinctly longer than secondary ones. Thin section A.8697.30, magnification 25 x.
- Fig. 7. Isotype; oblique section through a small size sterile segment showing swollen primary branches and short secondary branches. Thin section A.8407.59, magnification 25 x.
- Figs. 8, 9. Isotypes; tangential sections through sterile segments showing swollen primary branches and tufts of secondary branches. Thin sections A.8407.35 and A.8407.39, magnification 25 x.
- Fig. 10. Detail of Fig. 9 showing tufts composed each by six secondary branches per primary branch. Thin section A.8407.39, magnification 100 x.
 - Figs. 11–15. Cymopolia barattoloi n. sp., upper Maastrichtian of southeastern Salento (Apulia, southern Italy).
- Fig. 11. Isotype, longitudinal section through a sterile segment. The calcareous skeleton is pear-shaped but less swollen than in *Cymopolia decastroi* n. sp. and remarkably thinner (compare with Figs. 4–5 of this plate). Primary branches are made by a thin peduncular portion followed by a distal widening. Thin section A.8407.49, magnification 25 x.
- Figs. 12–14. Isotypes; oblique sections through small size sterile segments. Primary branches are characterized by a well delimited distal widening. Thin sections A.8407.33, A.8407.16; magnification 25 x.
- Fig. 15. Oblique section through a sterile segment. Thin section A.8696a.3, magnification 25 x.



Cymopolia barattoloi n. sp., upper Maastrichtian of southeastern Salento (Apulia, southern Italy)

- Fig. 1. Isotype; longitudinal section through a large size fertile segment. The calcareous skeleton and the central cavity are barrel-shaped but less swollen than in *Cymopolia decastroi* n. sp. Primary branches show a rather well delimited distal widening. Shape, size and inclination of primary branches change moving from central whorls toward both apical and basal whorls. Thin section A.8407.32, magnification 25 x.
- Fig. 2. Isotype; longitudinal section through a fertile segment. In this specimen the distal widening of primary branches is not as well delimited as in the others segments attributed to this species. Thin section A.8407.10, magnification 25 x.
- Fig. 3. Holotype; longitudinal section through a medium size fertile segment. Primary branches are characterized by a well delimited distal widening. Notice how secondary branches are longer than primary ones. Thin section A.8407.21, magnification 25 x.
- Figs. 4, 8, 12. Subtransversal sections through fertile segments. The distal, widened portions of the primary branches of the same whorl merge in a more or less continuous annular cavity. Thin sections A.8697.9, A.8697.22 and A.8407.13, magnification 25 x.
- Figs. 5, 7. Isotypes; oblique sections through fertile segments. Notice the well delimited distal widening of primary branches. Thin sections A.8407.6, A.8407.38; magnification 25 x.
- Fig. 6. Isotype; transversal section through a fertile segment. The distal, widened portions of primary branches merge in a well delimited annular cavity; the whorly section of the gametangia is distinctly elliptical; secondary branches are longer than primary ones. Thin section A.8407.20, magnification 25 x.
- Fig. 9. Isotype; tangential section through a fertile segment. Thin section A.8407.18, magnification 25x.
- Fig. 10. Oblique section through the central and upper whorls of a fertile segment. Notice how apical whorls are devoid of gametangia. Thin section A.8697.1, magnification 25 x.
- Fig. 11. Isotype; oblique section. Thin section A.8407.8, magnification 25 x.
- Fig. 13. Isotype; oblique section through a sterile segment. In this specimen the distal widening of primary branches is very faint to nearly absent. Thin section A.8407.24, magnification 25 x.
- Fig. 14. Isotype; transversal section through a sterile segment. Thin section A.8407.8, magnification 25 x.
- Fig. 15. Isotype; longitudinal section through a small size sterile segment. Thin section A.8407.1, magnification 25 x.



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