

A NEW CALCITIC SPHINCTOZOAN SPONGE BELONGING TO THE
DEMOSPONGIAE FROM THE CASSIAN FORMATION (LOWER CARNIAN ;
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ABSTRACT

A new species of a coralline sponge, *Cassianothalamia zardini* n. gen. n.sp., from the Lower Carnian Cassian Beds (northern Italy) is described. The new species possesses a secondary thalamid basal skeleton with a spongocoel and the internal structure is constructed of horizontal elements (trabecula) and vesiculae. The microstructure of the basal skeleton is composed of an irregular high Mg-calcite. From the spicular skeleton aster-microscleres can be preserved. In rare cases, monaxonid megascleres can also be found. Therefore the new sponge is probably a representative of the demospongid order Hadromerida.

RÉSUMÉ

Une nouvelle espèce d'éponge coralline, *Cassianothalamia zardini* n.gen. n.sp., a été trouvée dans les couches du Carnien inférieur de Saint-Cassian. La nouvelle espèce possède un squelette basal thalamide secondaire muni d'une cavité pseudogastrique et sa structure interne est constituée d'éléments horizontaux (trabécules) et de vésicules. La microstructure de la partie basale du squelette est composée d'une calcite irrégulière à forte teneur en Mg. Les microsclères astéroïdes du squelette spiculaire peuvent avoir été conservés. On peut aussi trouver très rarement des mégasclères monaxonides. Par conséquent, cette nouvelle éponge est probablement un représentant de l'ordre Hadromerida des Démosponges.

KEY-WORDS : PORIFERA, CALCIFIED DEMOSPONGES, SYSTEMATICS, PHYLOGENY, CARNIAN, CASSIAN FORMATION, NORTHERN ITALY.

MOTS-CLÉS : PORIFERA, DÉMOSPONGES CALCIFIÉES, SYSTÉMATIQUE, PHYLOGÉNIE, CARNIEN, FORMATION DU SAINT-CASSIAN, ITALIE DU NORD.

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INTRODUCTION

The Cassian Beds are a famous locality in northern Italy for well-preserved macroinvertebrates. Since the last century many collectors (e.g. Wissmann & Münster 1841, Klipstein 1843-45, Leonardi 1943, Dieci *et alii* 1970, Cuif 1973, 1974, Fürsich & Wendt 1977, Zardini 1973) have discovered numerous fossils and more than 1000 invertebrate taxa have been identified. Besides the rich gastropod fauna, sponges are diverse and common. The coralline sponges are an important faunal element in certain outcrops, e.g. Seeland-Alpe near Schluderbach, Passo Giau and the Valle de Rimbianco near Misurina (for more data see Fürsich & Wendt 1977).

Most of the coralline sponges build patch reefs with an average size of 10 m and a thickness of some meters. Generally the preservation of organisms is moderate in these buildups. But in some places (Seelandalpe, Misurina, Passo Giau) erratic blocks of these patch reefs (« Cipit »-boulders) occur within the marls of the Cassian Formation (Fürsich & Wendt

1977). The preservation of the organisms within these blocks is often excellent ; most of the coralline sponges retained their original skeletal mineralogy (Scherer 1977, Cuif 1973, 1974, Wendt 1979).

The majority of coralline sponges have an aragonitic mineralogy with different types of microstructures (Wendt 1979). Calcitic coralline sponges are rare except for some « sphinctozoans ». Besides the coralline Calcarea, there are only two modern calcified demosponges, *Acanthochaetetes* and *Merlia* which have high Mg-calcite basal skeletons. The calcified demosponges are a highly polyphyletic group (Vacelet 1985, Reitner & Engeser 1985, Reitner 1987, Wood 1987) and it is important to establish the different phylogenetic lineages within these sponge morphotypes. One of the best studied examples is the *Verticillites* - *Vaceletia* - *Murguiathalamia* lineage which demonstrates the convergence of calcareous secondary basal skeletons (Reitner & Engeser 1985, Reitner 1987). The new form shows a further convergent calcareous skeleton within this lineage.

MATERIAL AND METHODS

The specimens were collected from the famous outcrops of the Seeland-Alpe near Schluderbach (Northern Italy). The specimens were found as either individuals in the marls or within the « Cipit »-boulders in their original life position. Nearly 50 specimens were collected and studied.

Half of the specimens were studied by petrographic microscope and three by scanning electron microscope (SEM). The polished surfaces of the specimens were etched with a weak acid (Titriplex-III-solution) and studied by SEM in order to recognize the

entrapped microscleres (method described in Reitner & Engeser 1987). The microstructure was studied in unetched fresh fractured surfaces. The geochemistry was determined by an Energy Dispersive X-Ray Analyzer (EDAX). The samples were coated with carbon and the specimens were analysed at 10 KV. Each analysis had an average of ca. 3000 counts/sec. The analyse time was 100 sec. The quantitative amount of Ca and Mg was determined with the method described by Neugebauer (1979).

SYSTEMATICS

Demospongiae SOLLAS

Subclass **Tetractinomorpha** LEVI

Order **HADROMERIDA** TOPSENT

Family **Cassianothalamiidae** nov. fam.

TYPE GENUS :

Cassianothalamia n. gen.

DIAGNOSIS :

Sponges with a secondary basal skeleton composed of an irregular high Mg-calcite. Aster-microscleres form the spicular skeleton. They can possess a spongoeol.

DIFFERENTIAL DIAGNOSIS :

See species description.

GENERA WITHIN FAMILY :

Only the type genus.

Genus *Cassianothalamia* n.gen.

TYPE SPECIES :

Cassianothalamia zardini n.gen., n.sp.

DERIVATIO NOMINIS :

After the type locality of the Cassian Formation and the Greek word « thalamos » = chamber.

DIAGNOSIS :

The more or less spherical hadromerid sponges possess a chambered calcitic basal skeleton with a central cavity (spongocoel). The spongocoel is only developed in the ontogenetic younger parts. The skeleton is constructed of vertical pillars which are connected on the bottom and the top to horizontal elements (chamber walls). In most specimens irregular vesiculae occur. From the spicular skeleton aster-microscleres (spheraster, sterraster ?) are present; megascleres, when present, are probably monactinal.

DIFFERENTIAL DIAGNOSIS :

See species description.

SPECIES WITHIN GENUS :

Cassianothalamia zardini n.gen., n.sp. only.

Cassianothalamia zardini n.gen., n.sp.

pl. 1, fig. 1 a-c

1985 — ?*Stylothalamia* n.sp. - Reitner & Engeser, p. 170; pl. 4, fig. 8-12.

DERIVATIO NOMINIS :

After Rinaldo Zardini (Cortina d'Ampezzo), the famous private collector of Cassian fossils.

HOLOTYPE :

Deposited in the Museo Comunale in Cortina d'Ampezzo, Coll. R. Zardini.

PARATYPES :

Two specimens are deposited in the Institute of Palaeontology of the « Freie Universität » in Berlin, no. IPFUB 87/1,2 (pl. 1, fig. 2,3).

LOCUS TYPICUS :

Seelandalpe near Schluderbach.

STRATUM TYPICUM :

Cassian Formation, Early Carnian.

DIAGNOSIS :

See genus diagnosis.

DESCRIPTION OF THE HOLOTYPE :

The specimen is uncut and exhibits a more or less spherical shape (pl. 1, fig. 1 a-c). The surface of the hadromerid thalamid sponge is perforated by numerous prosopores. On the apertural side of the sponge, the excurrent opening of the spongocoel is located. The apical side of the sponge has an irregular shape without any spongocoel opening. The calcitic basal skeleton of the sponge is conveniently fractured so that the pillars and chambers are visible.

The 3 mm diameter of the spongocoel is characteristic of this species; only a small variability in this dimension occurs.

Measurements (in mm)	holotype	other specimens N=50	
		min.-	mean- max.
Diameter (I) (perpendicular to the spongocoel)	14	(12.5-	16.6- 23)
Diameter (II) (parallel to the spongocoel)	10	(9 -	14.6- 18)
Diameter of the spongocoel	3	(3 -	3.25- 4.5)

DESCRIPTION OF PARATYPE I :

The specimen was cut horizontally through the spongocoel (pl. 1, fig. 3). The spongocoel is recognizable as a sediment-filled tube. The margin of the spongocoel is perforated by apopores. The apopores (exhalant) are bigger than the prosopores (inhalant). The horizontal cut through the sponge demonstrates the mode of growth through the orientation of the internal structures. Near to the spongocoel the inner chamber contains prosopores with a circular outline (pl. 2, fig. 4); this shows that this chamber is cut horizontally. The medial chambers appear to be cut obliquely while the outer chambers exhibit pillar structures (pl. 2, fig. 3) without circular outlines which indicates a vertical cut. Sponge growth therefore was probably as successive concentric chamber layers around the initial core of the calcareous skeleton.

The microstructure of the skeleton is totally irregular (pl. 3, fig. 1,7). The length of the high Mg-calcite

crystals is more or less 1 μm . In some cases the growth structure is lamellar (pl. 3, fig. 1). The space between the lamellae often exhibit thin sparitic layers which can be misidentified as simple monaxonic megascleres. Common borings within the calcitic skeleton can be confused with spicules also. But, there are rare monaxonic spicules entrapped within the outer portions of the calcitic chamber wall. The spicules are distinguishable from the borings and diagenetic features through their position in relation to the chamber wall. The body of the spicule extends from the inner portion of the wall into the pore space or it is contained in a protuberance on the pillar structure of the skeleton (pl. 3, fig. 8-10).

Within the outer parts of the calcitic skeleton very small (10-15 μm) crystal balls are present. In a few cases, with the SEM, these balls were determined to be aster-microscleres (for measurements, see below.).

DESCRIPTION OF PARATYPE II :

The specimen was cut vertically and shows the central cavity (spongocoel) (pl. 1, fig. 2). The ontogenetic oldest part of the sponge does not possess any spongocoel. The vesicular skeleton is linked to the ontogenetic oldest parts only (pl. 2, fig. 5). The sponge has asexual buds. The sponge grew on a bioclast in its original life position.

SPICULE PRESERVATION :

The spicules of *Cassianothalamia* are preserved as Fe- rich Low-Mg calcite pseudomorphs. The original siliceous spicules were dissolved within the ontogenetic older parts of the coralline sponges during very early diagenesis (Land 1976, Hartman 1979, Reitner 1987a). In most cases, the spicule molds are cemented by the epitactical growth of aragonite or Mg- calcite crystals of the basal skeletons (Reitner 1987a). In this case no spicule remains are preserved. In rare cases, some spicule molds, mostly within the ontogenetic younger parts of the basal skeleton, are cemented during late diagenetic processes. As a rule these cements are large -sized meteoric blocky Fe-calcite crystals. This case is documented in *Cassianothalamia*. With the Titriplex-etching method it is possible to separate the spicules because the small-sized crystals of the basal skeleton dissolve much faster than the large sized late diagenetic calcite crystals of the molds.

MEASUREMENTS (in mm) :

	paratype I min, mean, max.	paratype II min, mean, max.
Prosopores :	0.1- 0.15- 0.2	0.1- 0.17- 0.3
Apopores :	0.1- 0.19- 0.3	0.13- 0.2- 0.35
Length of the pillars :	0.5- 0.53- 0.56	0.5- 0.54- 0.57
Diameter of the pillars :	0.06- 0.1- 0.18	0.06- 0.11- 0.17
Inner diameter of the spongocoel :	3.5	4.0
Thickness of the chamber wall :	0.1- 0.13- 0.16	0.11- 0.14- 0.16
Diameter I :	36	25
Diameter II :	30	25
Size of the asiphonat early ontogenetic stage (n = 5) :		2.5- 3.4- 4.5
Scleres (in μm)		
Microscleres, diameter in all studied specimens (n = 43) :		8- 13- 25 μm
Megascleres, length (n = 4) :		180- 206- 245 μm

DIFFERENTIAL DIAGNOSIS :

This new species of a hadromerid calcitic coralline sponge differs in many ways from other closely related coralline sponges. The genus *Acanthochaetetes*, also a hadromerid coralline sponge, possesses, in contrast to the new species, an astrorhizal exhalant system, a chaetetid cross morphology of the basal skeleton, and tylostyle megascleres (Reitner 1984, Reitner & Engeser 1983, 1987).

There are certain similarities to coralline sponges with affinities to the genera *Verticillites*, *Stylothalamia*, *Vaceletia* (pl. 4, fig. 2, 3), and *Murguiathalamia*. All of these forms are coralline sponges with a sphinctozoid basal skeleton and a spongocoel analogous to the new species. The differences are the aragonitic mineralogy of the basal skeletons, different internal structures, e.g. a complicated exhalant channel system, and different spicular skeletons which are linked to the Ceractinomorpha and choristid Tetractinomorpha (Reitner & Engeser 1985, Reitner 1987). There are no affinities to the sphinctozoid Calcarea. Within the Calcarea no microscleres are observed.

POSSIBLE CASSIANOTHALAMIID SPHINCTOZOA

The review of the literature concerning « Sphinctozoa » with a high-Mg calcite skeleton is difficult because there is little or no data on calcite mineralogy, diagenesis, or the spicular skeleton. In most cases the plate figures are too small to allow a critical examination of the specimens described.

A cassianothalamiid « sphinctozoan » was reported by Radoicic (1966 : pl. 151) from the Early Jurassic of the Lovcen mountains (Yugoslavia). The specimen is named in the figure caption « *Pelleria bonomi* (VIALLI) Grubic » with *Pelleria* a nomen nudum (according Flügel 1971, Engeser & Neumann 1987). It is questionable whether it really can be attributed to « *Ellipsactinia* » *bonomi* VIALLI, 1938, whose systematic position is uncertain as well (Reitner & Engeser 1985).

Flügel (1969) described the « hydrozoan » *Actinostromarianina* ? *beauvaisi* from the « Senonian » (? Santonian) of the Gosau Basin (Austria) as showing a « circumlamellar » microstructure. The given photographs and the description indicate a sponge with a high Mg-calcite skeleton and stromatoporoid habitus. This specimen certainly cannot be referred to the genus *Actinostromarianina* LECOMPTE, 1952 (WOOD in press) but to a new genus.

Turnsek (1970) figured two specimens (*Actinostromaria turonica* TURNSEK, 1970, pl. 5, fig. 1-5, pl. 6, fig. 1-3) *Burgundostromaria zlatiborensis* TURNSEK, 1970, pl. 7, fig. 1-5, pl. 8, fig. 1-3, pl. 9, fig. 1-2, pl. 11, fig. 1-3) which possess a trabecular internal structure of the basal skeleton. The figures exhibit a micritic microstructure in the basal skeleton which indicates an original high Mg-calcite mineralogy. These forms are probably related to the new family Cassianothalamiidae.

From the Late Santonian of Romania Baltres (1973) reported an « *Actinostromarianina* ? cf. *beauvaisi* FLÜGEL. The specimen is certainly different from Flügel's described species and it might be better attributed to a new genus.

Steiger & Wurm (1980 : pl. 25, fig. 4, right specimen) figured an *Actinostromaria* sp. from the Late Jurassic Plassen limestones (Styria, Austria) which is micritized. It could have been composed of high Mg-calcite and therefore belong to a new genus, just as the questioned specimens of Flügel (1969) and Baltres (1973).

A specimen from the « Upper Carixian/Lower Domerian » form the Central Apennines that may belong to the new described family was figured by Pallini & Schianinotto (1981) ; however, no description and no determination was given.

Yabe & Sugiyama (1935 : pl. 17), Flügel (1964, pl. 11, fig. 3), and Turnsek & Barbulescu (1969 : fig. 1-5) figure specimens of *Actinostromaria tokadiensis* (YABE & SUGIYAMA) which are very similar to the new described species. All figured specimens exhibit a spongocoel, the characteristic pillar structure of trabecular « sphinctozoans » and a micritic microstructure of the basal skeleton which indicates a calcitic original mineralogy.

Specimens similar to those figured by Radoicic (1966) were described by Beccarelli Bauck (1986 ; pl. 3, fig. 1, specimen right above, pl. 3, fig. 4) from the Early Jurassic of the Southern Alps (named as *Stylothalamia* cf. *columnaris* and by Senowbari-Daryan & Schäfer (1986) from the Norian of the Isle of Sicily (« *Cryptocoelia* » ? sp. 1). All three forms might be referred to a new genus in the new described family Cassianothalamiidae.

Dictyocoelia manon (MÜNSTER, 1841) (Senowbari-Daryan & Schäfer 1983 : pl. 5, fig. 1) from the (?) Carnian of the « Pantokrator limestone » of Hydra (Greece) shows a strong micritization that is typical for high Mg-calcite. Other « sphinctozoans » and dasycladaceans of the « Pantokrator limestone » display either a neomorphic calcitic or original aragonitic structures. The systematic position is uncertain since no material was available for analysis. *Dictyocoelia* OTT, 1967 is a younger, objective synonym of *Solenolmia* POMEL, 1872 (Engeser 1986). Preliminary results from the Cassian Beds suggest an aragonitic skeleton for *Solenolmia manon* (MÜNSTER, 1841), the type species of the genus *Solenolmia* POMEL, 1872.

Two comparably well-known genera of Triassic sphinctozoans, *Uvanella* OTT, 1967 and *Zardinia* also exhibit high Mg-calcite skeletons. They probably can be grouped with the cassianothalamiid sphinctozoans.

The content of the family Cassianothalamiidae may be summarized as follows :

- new genus (Radoicic 1966 : pl. 151, Beccarelli Bauck 1986 : pl. 3, fig. 1, right above, fig. 4, Senowbari-Daryan & Schäfer 1986 : pl. 51, fig. 5) ;

- new genus (Flügel 1969, Baltres 1973, Steiger & Wurm 1980) ;
- *Cassianothalamia* n. gen.
- Genus *Uvanella* OTT, 1967
- Genus *Zardinia* DIECI, ANTONACCI & ZARDINI, 1968 ;

- Species *Actinostromaria tokadiensis* (YABE & SUGIYAMA, 1935).

The *Stylothalamia* specimen with a micritic basal skeleton described by Gautret (1985) is undoubtedly aragonitic and therefore not linked to the new family Cassianothalamiidae.

PALEOBIOLOGY

The living sponge tissue of *Cassianothalamia* resides within the calcareous skeleton comparable with sponges possessing a stromatoporoid basal skeleton. This is in contrast to sponges with a chaetetid basal skeleton which possess only a thin tissue veneer on the surface of the basal skeleton.

The ontogenetic oldest parts of the basal skeleton in *Cassianothalamia* is not occupied by living tissue. The boundary between the dead skeleton and the living parts is marked by the presence of vesicular structures (pl. 2, fig. 5). In some cases the whole basal skeleton is filled by these vesicular structures. This indicates that the thickness of the living sponge tissue was not constant but fluctuated. These changes in the amount of living tissue may have been due to ecological crises during the life time of the sponge. In most cases this vesicular feature is restricted to the ontogenetic oldest parts.

Some stromatoporoid basal skeletons, as well as many « sphinctozoans » from the Paleozoic and Triassic (Ott 1967, Seilacher 1962, Rigby & Potter 1986, Senowbari-Daryan & Schäfer 1983, 1986) contain these vesicular structures. In the modern « stromatoporoid » haplosclerid sponge *Calcifibrospongia*, the boundary between the dead skeleton and the living tissue is marked by a special aragonitic layer (Reitner 1987a).

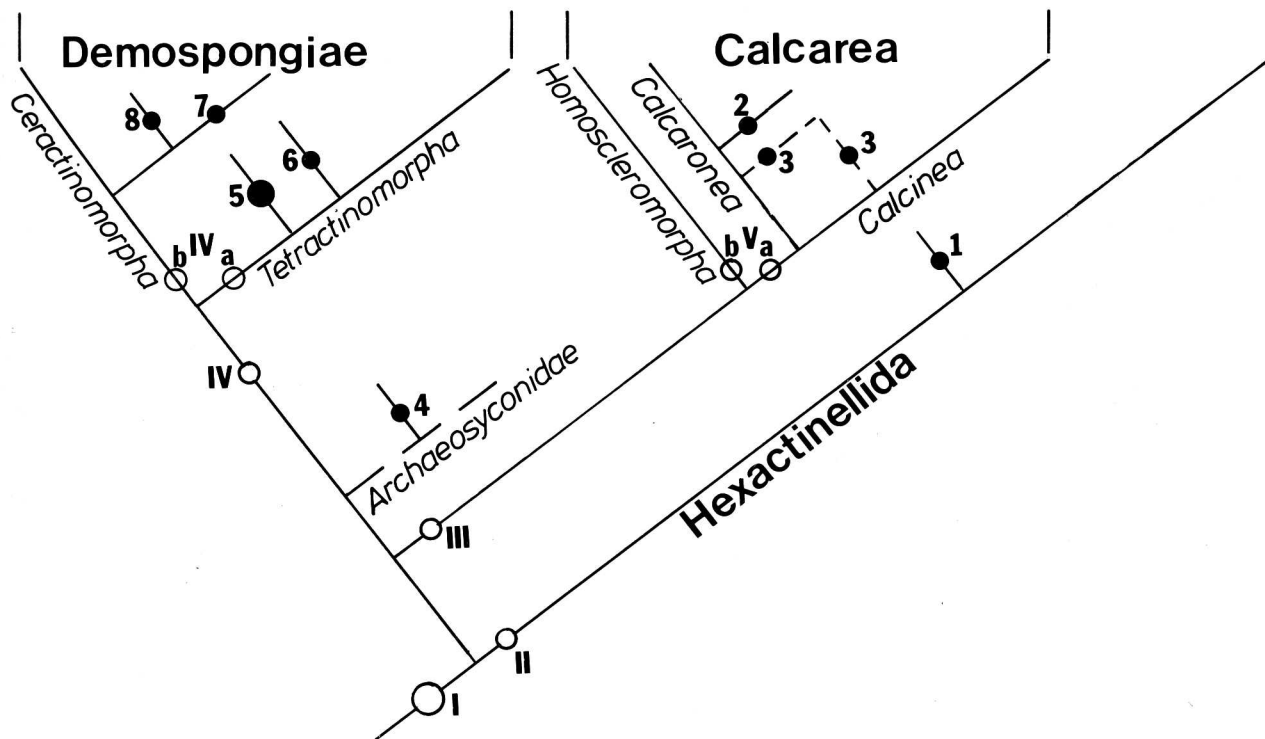
Within the modern sphinctozoid sponge *Vaceletia*, the living tissue is observed in the ontogenetic youngest parts of skeleton (Vacelet 1979) and the vesicular structures have never been observed. The parts without living tissue are cemented in vivo by irregular aragonite crystals (pl. 4, fig. 2).

The exhalant system of *Cassianothalamia* and *Vaceletia* is nearly similar. Both species possess larger apopores open to the central cavity, the spongocoel (pl. 2, fig. 6, 7). In *Verticillites* a special canal system is developed within the spongocoel wall (Reitner & Engeser 1985) and the astrorhizal pattern usually found in

Chaetetids and Stromatoporoids is not present. The formation of the basal skeleton of *Cassianothalamia* is probably comparable with the modern *Vaceletia* (pl. 4, fig. 3). In *Vaceletia* the ontogenetic youngest part of the aspicular organic-skeleton will be mineralized by aragonite. The biomineralization is not controlled by special cells and is probable analog to the mineralization observed in some calcareous algae (Flais 1977, Reitner 1987a, b) but without any control by photosynthesis. The presence of circular nuclei within the calcareous skeleton of *Cassianothalamia* may mark the position of the organic pillars of the probably collagenous skeleton. These pillars were sparsely mineralized between the organic fibers within and more heavily calcified around the outer ring of the pillars (compare *Vaceletia* in pl. 4, fig. 3). The center of these pillars rarely contain megascleres (pl. 3, fig. 10). The absence of megascleres within the organic skeleton indicates a solid primary collagenous tissue.

Only some microscleres are entrapped within the outer portion of the calcareous skeleton of *Cassianothalamia* (pl. 3, fig. 2-6). The same feature of selective entrapping of microscleres is observed in the Late Albian *Acanthochaetetes*. The microscleres are enriched selectively within the tabulae. The microstructure of the tabulae is totally disorganized in contrast to the microstructure of the vertical wall elements. The microstructure of the tabulae is very similar to the microstructure of the outer portions of the calcareous skeleton and the microstructure of the vesicular skeleton of *Cassianothalamia*. The skeleton formation is probably controlled by the pinacoderm layer.

Asexual budding in *Cassianothalamia* is common (pl. 1, fig. 4). This feature is common in all sphinctozoid sponges independent of their systematic position. In most cases the buds are nearly the same size. In some cases small buds are observed upon adult specimens (pl. 2, fig. 1). Besides normal asexual budding, there is a further possibility of bud formation which is



Text-fig. 1 —Phylogenetic cladogram representing the evolutionary developments of the major sponge groups (modified from Soest 1984 and Reitner 1987).

The open circles represent plesiomorphic features.

I : First occurrence of scleres ;

II : Parenchymella larvae of the Hexactinellida, hexactine scleres ;

III : Blastula/Amphiblastula larvae of the Calcarea and Homoscleromorpha ;

IV : Parenchymella larvae of the Demospongiae. The circles with a bar represent synapomorphic features - IVa : Oviparous parenchymella - IVb : Viviparous parenchymella - Va : Caltrops scleres (CaCO₃) in calcareous sponges - Vb : Caltrops scleres (SiO₂) in siliceous Homoscleromorpha. Black circles represent the convergent feature of a thalamid skeleton.

1 : *Casearia* without any calcareous basal skeleton ; 2 : e.g. *Barroisia* ; 3 : Paleozoic and Mesozoic « sphinctozoans » with uncertain affinities, e.g. *Amblysiphonella* ; 4 : Archaeocyathids, e.g. *Tabulacyathus taylori* ; 5 : *Cassianothalamia zardinii* ; 6 : *Murguiathalamia* ; 7 : *Vaceletia crypta* ; 8 : *Vascothalamia*.

Cladogramme phylogénétique représentant les développements de la majorité des groupes d'éponges (modifié d'après Soest 1984 et Reitner 1987). Les cercles vides désignent des caractères plésiomorphes.

I : première apparition de sclères ;

II : larve parenchymella d'Hexactinellida, sclères hexactines ;

III : larve blastula/amphiblastula des Calcarea et des Homoscleromorpha ;

IV : larve parenchymella des Demospongiae. Le cercle barré désigne des caractères synapomorphes. IVa : parenchymella ovipare. IVb : parenchymella vivipare. Va : sclères caltropes (CaCO₃) dans les éponges calcaires - Vb : sclères caltropes (SiO₂) dans une Homoscleromorpha. Les cercles noirs désignent un caractère convergent avec un squelette thalamide.

1 : *Casearia* sans aucun squelette basal calcaire ; 2 : par ex. *Barroisia* ; 3 : Sphinctozoaires paléozoïques et mésozoïques ; 4 : Archæocyathides, par ex. *Tabulacyathus taylori* ; 5 : *Cassianothalamia zardinii* ; 6 : *Murguiathalamia* ; 7 : *Vaceletia crypta* ; 8 : *Vascothalamia*.

restricted to the smaller type of buds. Within the basal skeletons of *Acanthochaetetes* there are internal gemmulae (« storage cells » Vacelet 1987). With these undifferentiated cells the sponge can survive during a food crisis. From these cells new sponges can develop as small buds upon the surface of the dead basal skeleton. The same type of survival strategy is developed within *Merlia normani* and *Petrobiona massiliana* (Vacelet 1987).

Cassianothalamia is an important part of the coral-line sponge community of the Seeland-Alpe patch reefs and related Ciptit-Boulders. Up to 15 % of the observed sponge fauna are specimens of *Cassianothalamia* which growth on firmgrounds like other coral-line sponges, bioclasts or lithoclasts (pl. 2, fig. 2, pl. 4, fig. 1). In other localities of occurrences of Cassian-patch reefs or Cipit Boulders this species is rare or not observed.

PHYLOGENY

(Text-fig. 1)

The « Sphinctozoa » are sponges with a thalamid skeleton. The development of this skeletal type occurs at least six times in the Porifera (Reitner 1987b). There are representatives in the Class Calcarea (e.g. *Barroisia*), in the different subclasses of the Class Demospongiae (ceractinomorph « sphinctozoans » : *Vaceletia crypta*, *Stylothalamia*, *Verticillites* ; tetractinomorph « sphinctozoans » : *Murguiathalamia*, *Boikothalamia*), in the archaeocyathids (e.g. *Dictyosycon*, *Tabulacyathus*), and in one species of the Hexactinellida that does not have a calcareous skeleton (*Casearia*).

To demonstrate the convergent development of the calcareous basal skeletons, phylogenetic systematics is used. The cladogram presented here is based on the theory of Soest (1984) and Reitner (1987b). The monophyletic origin of the calcareous basal skeletons suggested by Soest (1984) is not probable (discussion in Reitner 1987b). Within the coralline sponges (calcified demosponges and calcified Calcarea), the calcareous skeletons occur in different taxa independently and always exhibit fundamental differences in the microstructure and the mineralogy (Hartman & Goreau 1970, 1975, Vacelet 1985, Reitner & Engeser 1983, 1985, Reitner 1987a,b, Wood 1987). However the process of biomineralization is mostly simple and probably indirectly influenced by the soft tissue only.

An intracellular control of the construction of the basal skeleton is observed in *Astrosclera* only (Lister 1900, Jones 1979, Reitner 1987a).

The calcareous skeletal formation within the modern sclereless ceractinomorph « Sphinctozoan » *Vaceletia crypta* is simple (Vacelet 1979, Gautret 1985, Reitner & Engeser 1985). *Vaceletia* possesses a well-developed primary organic skeleton. This organic skeleton will be passively calcified by irregular aragonite. This type of skeletal formation is probably similar in *Cassianothalamia*. The only difference is the skeletal mineralogy. But this feature is phylogenetically unimportant, because aragonite and high Mg-calcite skeletons occur in different lineages of the coralline sponges. Both features occur convergently within the coralline sponges. Only the scleres and the scleres arrangement can be used for phylogenetic reconstruction. The observed microscleres are characteristic for the order Hadromerida (Tetractinomorpha). Within the Tetractinomorpha further fossil genera have developed a thalamid trabecular basal skeleton but with an aragonite mineralogy and megascleres forming the pillar structure (*Murguiathalamia*) (Reitner & Engeser 1985, Reitner 1987b). The new genus *Cassianothalamia* demonstrates a further convergence of a thalamid calcareous basal skeleton which can be classified within the modern sponge classification.

CONCLUSIONS

1. *Cassianothalamia zardini* n. gen. n. sp. is a new sphinctozoid coralline sponge from the Lower Carnian Cassian Formation in Northern Italy. The basal

skeleton is composed of irregular arranged high Mg-calcite crystals.

2. The spicular skeleton is composed of monaxonic megascleres and aster microscleres (sphaeraster, steraster ?). This spicular skeleton is characteristic for the order Hadromerida (Tetractinomorpha, Demospongiae).

3. Sponges grow on frimgrounds like corals or other coralline sponges. They are very common in the Cipit-Boulders of the Seeland-Alpe near Schluderbach (Northern Italy). In some of these boulders *Cassianothalamia* takes up fifteen percent of the rock by volume.

4. Small buds on the surface of large specimens are common and are significantly smaller in size than buds growing on older adult specimens. These same

type of buds are observed within the genus *Acanthochaetetes* and are linked to a special survival strategy using internal « gemmulae ».

5. The soft tissue resided within the upper part of the calcareous skeleton. The « stromatoporoid » vesicular skeleton marks the boundary between the dead and the living part of the basal skeleton.

6. The sphinctozoid basal skeletons are developed within the Calcarea and all subclasses of the Demospongiae. This type of basal skeleton has no phylogenetic significance. The term « Sphinctozoa » describes a special type of basal skeleton only. Therefore this term should not be used to describe a taxon.

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REFERENCES

- BALTRES A. (1973) - Inventarul hydrozoarelor si chaetidelor din România. Dari seama sedint., 3. *Paleont.*, Bucarest, **59** : 5-33.
- BECCARELLI BAUCK L. (1986) - Stylothalamien aus dem unterjurassischen Misone-Kalk der Südalpen, Italien. *Palaeontographica*, A, Stuttgart, **192** : 1-13.
- CUIF J.P. (1973) - Histologie de quelques sphinctozoaires (Porifères) triassiques. *Geobios*, Lyon, **6** : 115-125.
- CUIF J.P. (1974) - Rôle des sclérosponges dans la faune récifale du Trias des Dolomites (Italie du Nord). *Geobios*, Lyon, **7** : 139-153.
- DIECI G., ANTONACCI A. & ZARDINI R. (1970) - Le spugne cassiane (Trias medio-superiore) della regione dolomitica attorno a Cortina d'Ampezzo. *Boll. Soc. Paleont. Ital.*, Modena, **7** : 94-155.
- ENGESER T. (1986) - Nomenklatorische Notiz zur Gattung *Dictyocoelia* OTT 1967 (« Sphinctozoa », Porifera). *N. Jb. Geol. Paläont. Mh.*, Stuttgart, **1986** : 587-590.
- ENGESER T. & NEUMANN H.-H. (1987) - Ein neuer verticillitider « Sphinctozoe » (Demospongiae, Porifera) aus dem Campan der Krappfeldgosau (Kärnten, Österreich). *Mitt. Geol. Paläont. Inst. Univ. Hamburg*, **61** : 149-159.
- FLAJS G. (1977) - Die Ultrastrukturen des Kalkalgen-skeletts. *Palaeontographica*, A, Stuttgart, **160** : 69-128.
- FLÜGEL E. (1964) - Ein neues Vorkommen von Plassenkalk (Ober-Jura) im Steirischen Salzkammergut, Österreich. *N. Jb. Geol. Paläont. Abh.*, Stuttgart, **120** : 213-232.
- FLÜGEL E. (1969) - Hydrozen mit circumlamellarer Mikrostruktur aus den Gosau-Schichten (Senon) des Gosau-Beckens (Oberösterreich/Salzburg). *Verh. geol. B.-A.*, Vienna, **1969** : 126-131.
- FLÜGEL E. (1971) - Review of « Radoicic, Rajka : Microfaciès du Jurassique des Dinarides externes de la Yougoslavie ». *Zentralbl. Geol. Paläont.*, part III Paläont., Stuttgart, **1968** : 98.

- FÜRSICH F.T. & WENDT J. (1977) - Biostratiny and Palaeoecology of the Cassian Formation (Triassic) of the Southern Alps. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, Amsterdam, **22** : 257-323.
- GAUTRET P. (1985) - Organisation de la phase minérale chez *Vaceletia crypta* (VACELET) démosponge, sphinctozoaire actuelle. Comparaison avec des formes aragonitiques du Trias de Turquie. *Geobios*, Lyon, **18** : 553-562.
- HARTMAN W.D. (1979) - A new sclerosponge from the Bahamas and its relationship to Mesozoic stromatoporoïds. *Coll. inter. CNRS*, Paris, **291** : 467-474.
- HARTMAN W.D. & GOREAU T.F. (1970) - Jamaican coralline sponges : their morphology, ecology and fossil relatives. *Symp. zool. Soc. London*, **25** : 205-243.
- HARTMAN W.D. & GOREAU T.F. (1975) - A Pacific tabulate sponge, living representative of a new order of sclerosponges. *Postilla*, New Haven, **167** : 1-21.
- JONES C. (1979) - The Microstructure and Genesis of Sponge Biominerals. *Coll. internat. CNRS*, Paris, **291** : 425-447.
- KIRPATRIK R. (1911) - On *Merlia normani*, a sponge with a siliceous and calcareous skeleton. *Quart. Journ. microscop. Sci.*, London, **56** : 657-702.
- KLIPSTEIN A.V. (1843-45) - Beiträge zur geologischen Kenntnis der östlichen Alpen. *Giesen*, 311 p.
- LAND L.S. (1976) - Early dissolution of sponge spicules from reef sediments, North Jamaica. *J. sed. Petrol.*, **48** : 337-344.
- LEONARDI P. (1943) - La fauna Cassiana di Cortina d'Ampezzo. Parte I. Introduzione geologica e lamelli-branchi. *Mem. Inst. Geol. Univ. Padova*, **15** : 1-78.
- LECOMPTE M. (1952) - Révision des Stromatoporoides Mésozoïque des Collections Dehorne & Steiner. *Inst. roy. nat. Belgique*, Brussels, **28** : 1-39.
- LISTER J.J. (1900) - *Astrosclera willeyana*, the type of a new family of sponges. In : WILLEY A. (ed.), *Zoological Results*, Cambridge. **4** : 461-482.
- OTT E. (1967) - Segmentierte Kalkschwämme (Sphinctozoa) aus der alpinen Mitteltrias und ihre Bedeutung als Riffbildner im Wettersteinkalk. *Bayer. Akad. Wiss., math.-naturwiss. Kl.*, N.S., Munich, **131** : 1-96.
- NEUGRBAUER J. (1979) - Drei Probleme der Echinodermigenese : Innere Zementation, Mikroporenbildung und Übergang von Magnesiumcalcit zu Calcit. *Geol. Rundschau*, **68** : 856-875.
- PALLINI G. & SCHIAVINOTTO F. (1981) - Upper Carixian-Lower Domerian Sphinctozoa and Ammonites from some Sequences in Central Apennines. In : FARINACCI A. & ELMI S. (eds), *Rosso Ammonitico symp. Proc.*, Rome : 521-539.
- RADOICIC C. (1966) - Microfaciès du Jurassique des Dinarides Externes de la Yougoslavie. *Geologija*, Zagreb, **9** : 5-349.
- REITNER J. (1984) - Mikrofazielle, palökologische und paläogeographische Analyse ausgewählter Vorkommen flachmariner Karbonate im Basko-Kantabrischen Strike Slip Fault-Becken-System (Nordspanien) an der Wende von der Unterkreide zur Oberkreide. *PhD Diss. Geowiss. Fak. Univ.*, Tübingen, 211 p.
- REITNER J. (1987a) - *Euzkadiella erenoensis* n.gen. n.sp. ein « Stromatopore » mit spikulärem Skelett aus dem Oberapt von Ereño (Prov. Guipuzcoa, Nordspanien). *Paläont. Z.*, Stuttgart, (in press).
- REITNER J. (1987b) - The polyphyletic origin of the « Sphinctozoans ». - In : Proc. 3rd internat. Conf. Sponge Biol., *Smithsonian Inst. Press*, Washington, (in press).
- REITNER J. & ENGESER T. (1983) - Contributions to the systematics and the paleoecology of the family Acanthochaetidae Fischer, 1970 (order Tabulospongida, class Sclerospongiae). *Geobios*, Lyon, **16** : 773-779.
- REITNER J. & ENGESER T. (1985) - Revision der Demopongier mit einem thalamiden, aragonitischen Basalskelett und trabekulärer Internstruktur (« Sphinctozoa » pars). *Berliner geowiss. Abh.*, A, Berlin, **60** : 151-193.
- REITNER J. & ENGESER T. (1987) - Skeletal structures and habitats of Recent and fossil *Acanthochaetetes* (« sclerosponges », subclass Tetractinomorpha). *Coral Reefs*, **6**, New York : 13-18.
- RIGBY K.J. & POTTER A.W. (1986) - Ordovician Sphinctozoan sponges from the Eastern Klamath Mountains, Northern California. *Jour. Paleont.*, Tulsa, **47** p.
- SCHERER M. (1977) - Preservation, alteration and multiple cementation of Triassic aragonite skeletons from the Cassian Beds (Southern Alps) : petrographic and geochemical evidence. *N. Jb. Geol. Paläont. Abh.*, Stuttgart, **154** : 213-262.
- SEILACHER A. (1962) - Die Sphinctozoa, eine Gruppe fossiler Kalkschwämme. *Akad. Wiss. Lit. Mainz, Abh. math.-naturw. Kl.*, Mainz, **1961** : 721-790.
- SENOWBARI-DARYAN B. & SCHÄFER P. (1983) - Zur Sphinctozoen-Fauna der obertriadischen Riffkalke

- (« Pantokratorkalke ») von Hydra, Griechenland. *Geologica et Palaeontologica*, Marburg, **17** : 179-205.
- SENOWBARI-DARYAN B. & SCHÄFER P. (1986) - Sphinctozoen (Kalkschwämme) aus den norischen Riffen von Sizilien. *Facies*, Erlangen, **14** : 235-284.
- SOEST R.W.M. VAN (1984) - Deficient *Merlia normani* KIRPATRIK, 1908, from the Curaçao Reefs, with a discussion on the phylogenetic interpretation of sclerosponges. *Bijdragen tot de Dierk.*, Amsterdam, **54** : 211-219.
- STEIGER T. & WURM D. (1980) - Faziesmuster oberjurassischer Plattform-Karbonate (Plassenkalke, Nördliche Kalkalpen, Steirisches Salzkammergut, Österreich). *Facies*, Erlangen, **2** : 241-282.
- TURNSEK D. (1970) - Cretaceous Hydrozoa from the Zlatibor Mountain in West Serbia. *Raz. Diss.*, Ljubljana, **8** : 194-208.
- TURNSEK D. & BARBULESCU A. (1969) - Upper Jurassic Hydrozoa in Central Dobrogea (Romania). *Geologija-Raz. Porocila*, Ljubljana, **12** : 73-84.
- VACELET J. (1979) - Description et affinités d'une éponge sphinctozoaire actuelle. *Coll. inter. CNRS*, Paris, **291** : 483-493.
- VACELET J. (1985) - Coralline sponges and the evolution of Porifera - *In* : CONWAY MORRIS S., GEORGE J.D., GIBSON R. & PLATT H.M. (eds.), The origins and relationships of lower invertebrates. *Syst. Assoc. Sec. Vol.*, Oxford, **28** : 1-13.
- VACELET J. (1987) - The storage cells of calcified relict sponges - *In* : Proc. 3rd internat. Conf. Sponge Biol., *Smithsonian Inst. Press*, Washington, (in press).
- WENDT J. (1979) - Development of skeletal formation, microstructure, and mineralogy of rigid calcareous sponges from the Late Palaeozoic to Recent. *Coll. inter. CNRS*, Paris, **291** : 449-475.
- WISSMANN H.J. & MÜNSTER G. (1841) - Beiträge zur Geognosie und Petrefacten-Kunde des südöstlichen Tirol's vorzüglich der Schichten von St. Cassian. *Beitr. Petrefacten-Kde*, Bayreuth, **4** : 1-152.
- WOOD R.A. (1987) - The position of Mesozoic Stromatopoids in the Porifera. *In* : Proc. 3rd internat. Conf. Sponge Biol., *Smithsonian Inst. Press*, Washington, (in press).
- YABE H. & SUGIYAMA T. (1935) - Jurassic stromatopoids from Japan. *Sci. Rep. Tohoku Imp. Univ. Japan*, Tokyo, **2**, ser. (Geol.), **14** : 135-192.
- ZARDINI R. (1973) - Fossili di Cortina, Atlante degli Echinodermi Cassiani (Trias medio-superiore) della regione dolomitica attorno a Cortina d'Ampezzo, Cortina d'Ampezzo, 29 p.

PLATE 1

Cassianothalamia zardinii n.gen. n.sp.

Fig. 1 a-c — **Holotype** ; Lower Carnian, Cassian Formation ; Seeland-Alpe near Schluderbach (Dolomites).

a : apertural view ; b : side view ; c : apical view.

Holotype ; Carnien inférieur, formation de Saint-Cassian ; Seeland-Alpe près de Schluderbach (Dolomites).

a : vue de l'ouverture ; b : vue latérale ; c : vue apicale.

Scale = 4 mm.

Fig. 2 — **Paratype II** ; Seeland-Alpe near Schluderbach. Vertical section showing the spongocoel cavity.

Paratype II ; Seeland-Alpe près de Schluderbach. Section verticale montrant la cavité pseudogastrique.

Scale = 3,5 mm.

Fig. 3 — **Paratype I** ; Seeland-Alpe near Schluderbach. Horizontal cut.

Paratype I ; Seeland-Alpe près de Schluderbach. Coupe horizontale.

Scale = 4 mm.

Fig. 4 — **Oblique cut through two sponge buds showing the spongocoel cavities.**

Coupe oblique à travers deux bourgeons d'éponge montrant les cavités pseudogastriques.

Scale = 2 mm.

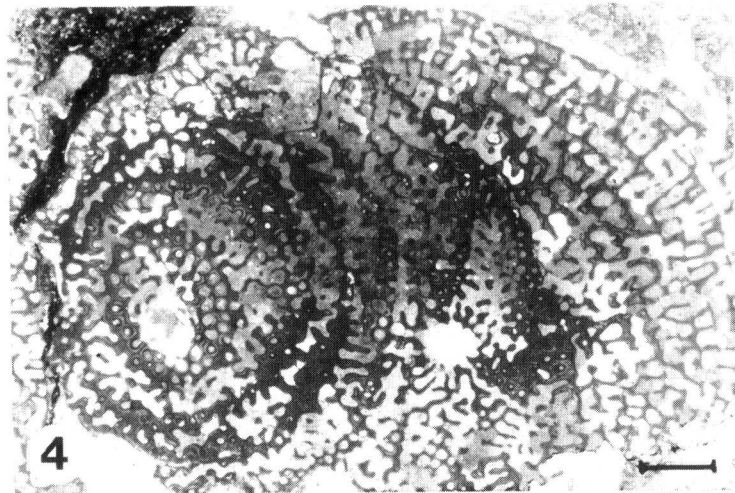
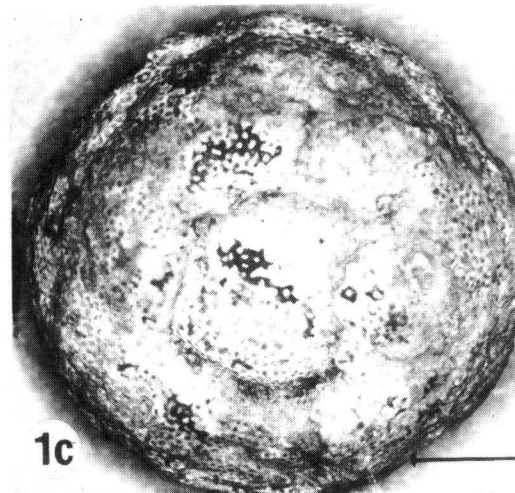
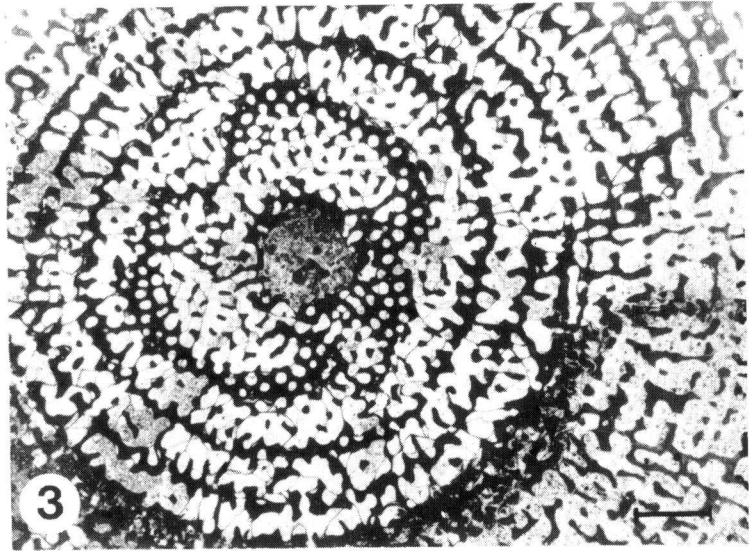
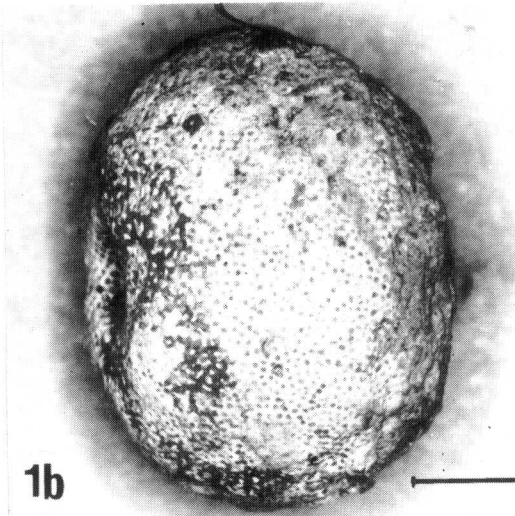
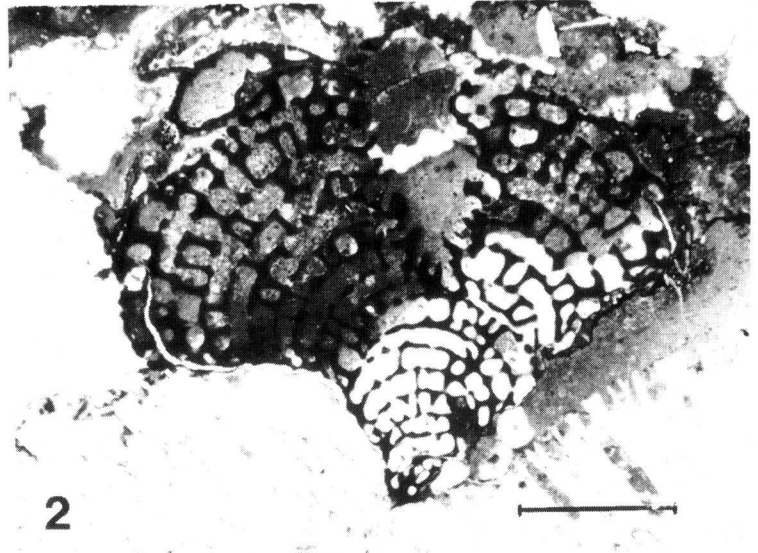
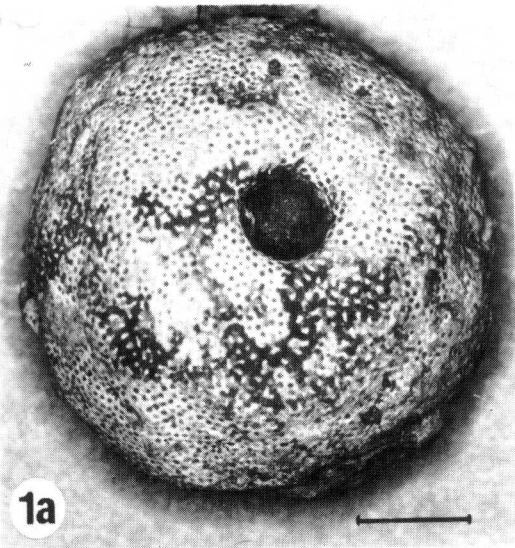


PLATE 2

Fig. 1 — **Adult specimen of *Cassianothalamia* with two asexual buds.** Seeland-Alpe near Schluderbach.

Spécimen adulte de *Cassianothalamia* avec deux bourgeons asexués. Seeland-Alpe près de Schluderbach.

Scale = 2 mm.

Fig. 2 — **Juvenile specimens of *Cassianothalamia* attached to a clast.**

Spécimens juvéniles de *Cassianothalamia* fixés à une roche clastique.

Scale = 2 mm.

Fig. 3 — **Vertical section showing the pillar structures in *Cassianothalamia*.**

Section verticale montrant les structures de *Cassianothalamia*.

Scale = 200 μ m.

Fig. 4 — **Horizontal cut through a chamber wall of *Cassianothalamia* exhibiting the prosopores.**

Coupe horizontale à travers la paroi d'un alvéole d'une *Cassianothalamia* montrant les prosopores.

Scale = 100 μ m.

Fig. 5 — **Horizontal cut through the ontogenetic early stage of the basal skeleton of *Cassianothalamia* demonstrating the vesicular skeleton.**

Coupe horizontale à travers le stage ontogénique jeune du squelette basal d'une *Cassianothalamia* montrant le squelette vésiculaire.

Scale = 200 μ m.

Fig. 6 — **Vertical cut of the spongocoel cavity of *Cassianothalamia*.**

Coupe verticale de la cavité pseudogastrique d'une *Cassianothalamia*.

Scale = 1 mm.

Fig. 7 — **Horizontal cut of the spongocoel cavity of *Cassianothalamia*.**

Coupe horizontale de la cavité pseudogastrique d'une *Cassianothalamia*.

Scale : 1 mm.

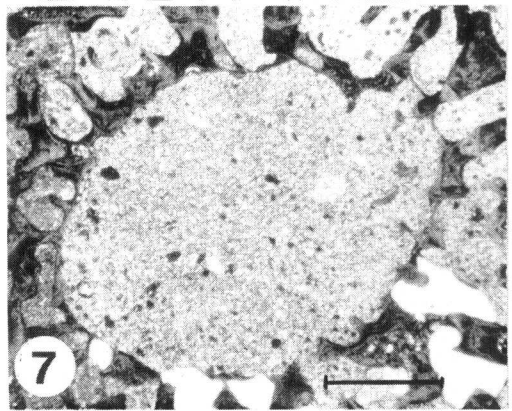
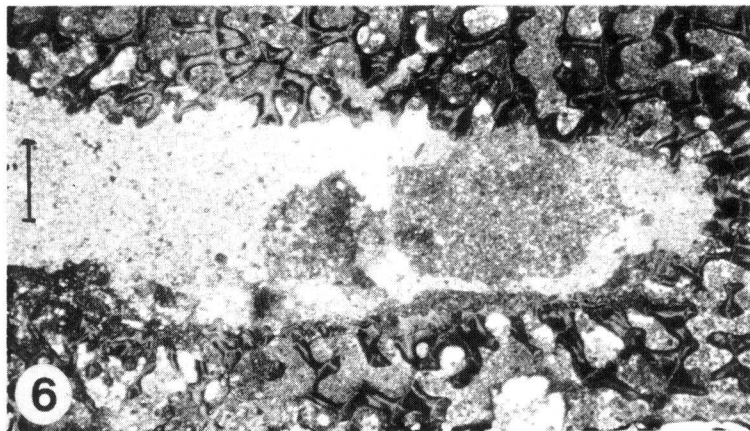
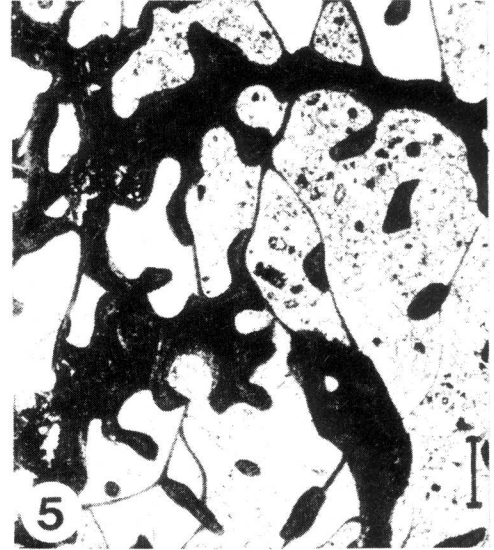
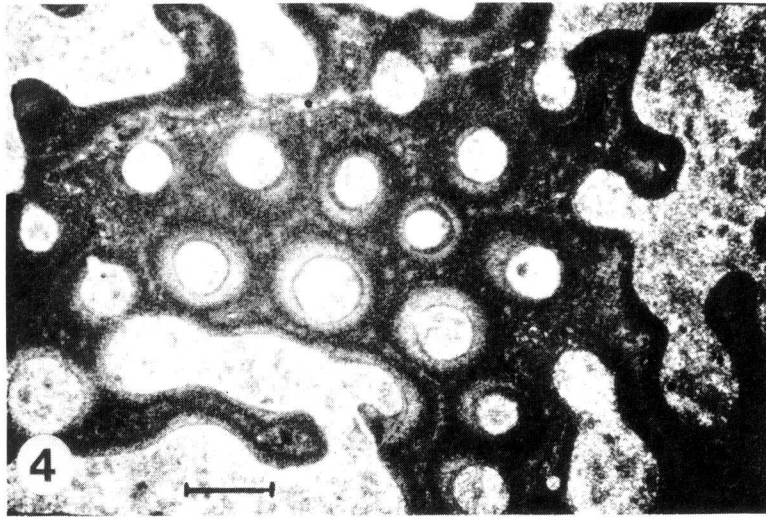
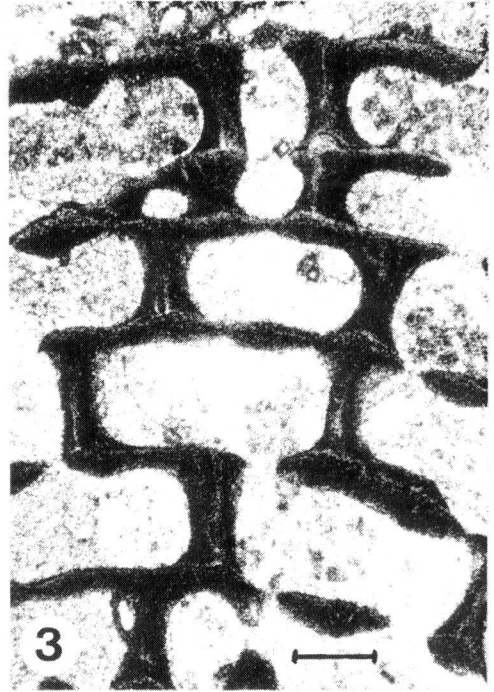


PLATE 3

Fig. 1 — **Horizontal section through a vertical pillar of *Cassianothalamia* demonstrating the central core surrounded by the dense mineralized outer portions.**

Section horizontale à travers un pilier vertical de *Cassianothalamia* montrant le noyau central entouré de parties externes fortement minéralisées.

Scale = 50 μ m.

Fig. 2 — **Aster microsclere of *Cassianothalamia* embedded within the outer wall of the mineralized portion of the pillar.**
Microsclère astéroïde d'une *Cassianothalamia* encastrée dans la paroi externe de la partie minéralisée du pilier.

Scale = 10 μ m.

Fig. 3-5 — **Sterraster microscleres of *Cassianothalamia*.**

Sterraster-microsclères de *Cassianothalamia*.

Scale : fig. 3 = 10 μ m ; figs. 4, 5 = 30 μ m.

Fig. 6 — **Spiraster microsclere of *Cassianothalamia* etched with Titriplex-Solution III.**

Spiraster-microsclère d'une *Cassianothalamia* attaquée par une solution de Titriplex III.

Fig. 7 — **Aster microscleres of *Cassianothalamia* within the outer wall of the mineralized portion of a pillar.**

Microsclères astéroïdes d'une *Cassianothalamia* dans la paroi externe de la partie minéralisée du pilier.

Fig. 8 — **Intramural monaxonic megasclere of *Cassianothalamia*. Arrows delineate the length of the sclere.**

Mégasclère monaxone intramurale de *Cassianothalamia*. Les flèches indiquent la longueur du spicule.

Scale = 50 μ m.

Fig. 9 — **An incompletely entrapped megasclere from the basal skeleton of *Cassianothalamia* (arrows indicate the non entrapped part of the sclere).**

Une mégasclère prise en partie dans le squelette basal d'un *Cassianothalamia* (les flèches indiquent la partie non-inclus du spicule).

Scale = 50 μ m.

Fig. 10 — **Intramural monaxonic megasclere of *Cassianothalamia*.**

Mégasclère monaxone intramurale de *Cassianothalamia*.

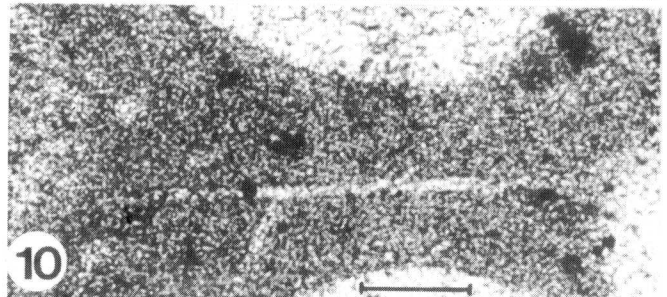
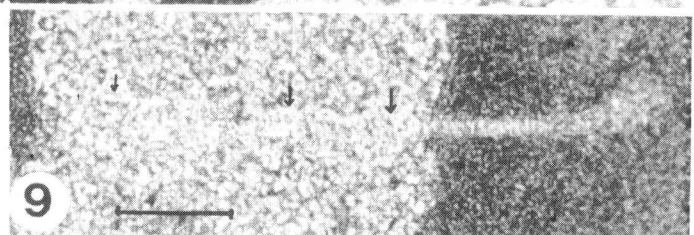
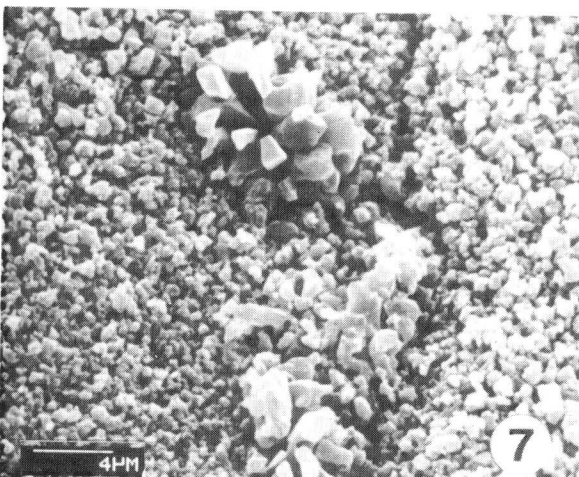
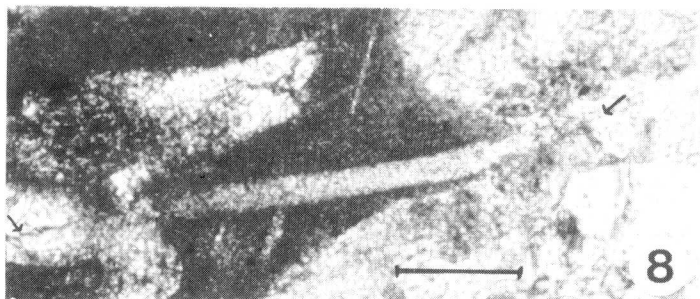
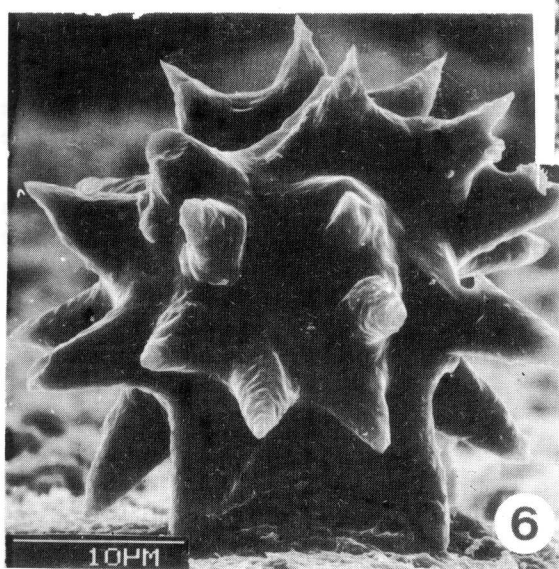
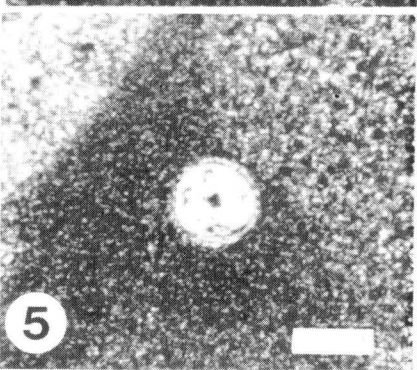
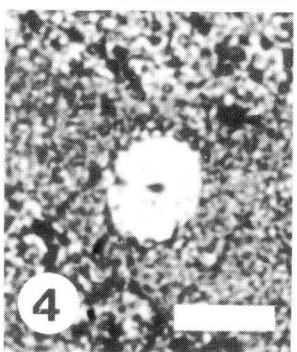
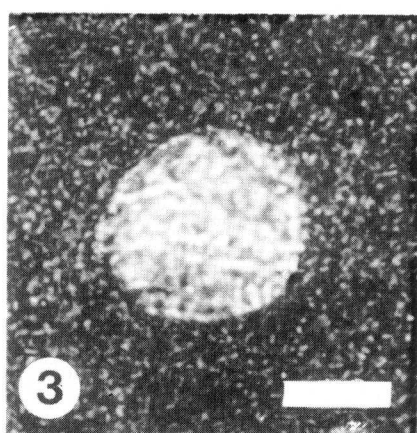
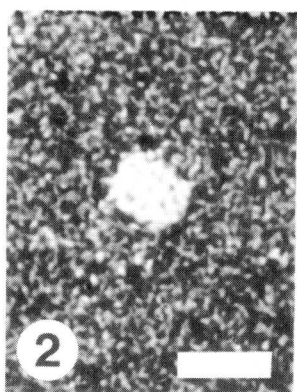
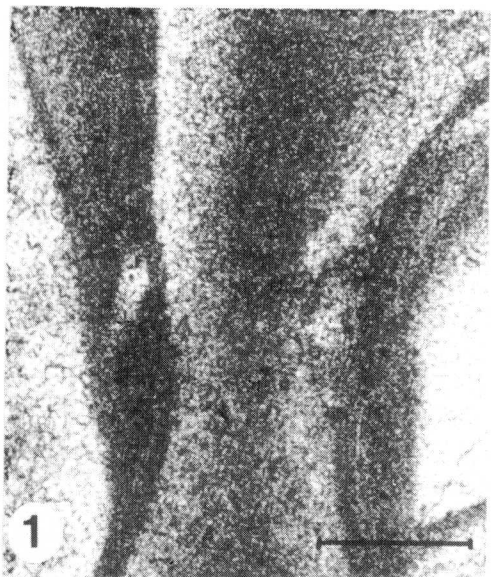


PLATE 4

Fig. 1 — Specimens of *Cassianothalamia* (C) in life position.

A : *Precorynella* sp.

B : encrusting foraminifera.

D : crusts of blue-green algae.

E : original cavities filled with micritic mudstone.

Spécimens de *Cassianothalamia* (C) trouvés dans leur milieu de vie.

A : *Precorynella* sp.

B : foraminifère fixé.

D : croûtes d'algues bleues et vertes.

E : cavités d'origine remplies de micrites.

Scale = 1 cm.

Fig. 2 — Vertical view of *Vaceletia crypta* (VACELET) (Lizard Island, Australia) demonstrating the lower dead portion and the upper living portion of the skeleton (arrow points toward the boundary).

Vue verticale de *Vaceletia crypta* (VACELET) (île Lizard, Australie) montrant la partie inférieure morte et la partie supérieure vivante du squelette (la flèche indique la limite entre les deux parties).

Fig. 3 — Pillar of *Vaceletia crypta* (Lizard Island) with core (C) and the enveloping soft tissue (A). Note the small holes on the upper surface of the broken pillar. These holes are evidence of a primary organic skeleton. The folding (B) along the outer wall of the pillar denotes the former elasticity of the organic tissue.

Pilier de *Vaceletia crypta* (île Lizard) avec le noyau (C) et le tissu mou le recouvrant (A). Notez les petits orifices sur la surface supérieure du pilier rompu. Ces cavités mettent en évidence un squelette organique primaire. Les plis (B) le long de la paroi externe du pilier montrent l'élasticité primaire du corps organique.

