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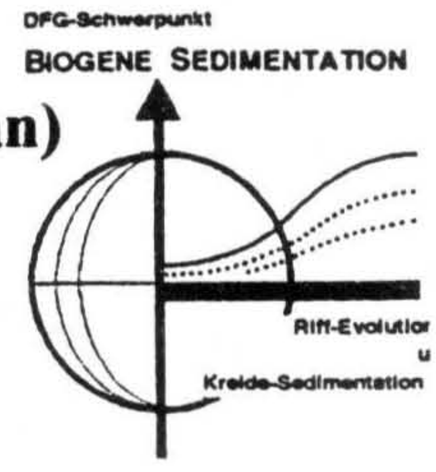
Palaeobiological Reconstructions of selected Sphinctozoan Sponges from the Cassian Beds (Lower Carnian) of the Dolomites (Northern Italy)



S. MÜLLER-WILLE & J. REITNER

Palaeobiological reconstruction of selected Sphinctozoan Sponges from the Cassian Beds (Lower Carnian) of the Dolomites (Northern Italy).- Staffan MÜLLER-WILLE & Joachim REITNER, Berliner geowiss. Abh. (E) 9: 253-281; Berlin.

Abstract: Palaeobiological models of four selected species of sphinctozoan coralline sponges from the Cassian Beds (Lower Carnian, Dolomites) have been established using, among others, luminescence techniques. The latter has been succesfully used to estimate the organic content and diagenetic history of the skeletons. Recent investigations yield the differentiation of three steps in the secretion of the skeleton in coralline sponges, according to which skeletal elements can be classified. The identification of these elements renders information on the way of secretion of the basal skeleton, the relative position of the soft tissue, and the function of the skeleton. Two basic types of sphinctozoan organisation can be distinguished: a matrix type, where a rigid framework, secreted in an organo-spicular matrix penetrates the soft tissue (as in stromatoporoid coralline sponges) and a cortex type, where the skeleton is secreted by a spezialized subdermal layer (cortex) surrounding the sponge body. These organizational types bear no phylogenetic implication.

Zusammenfassung: Es wurden paläobiologische Modelle von vier ausgewählten Arten sphinctozoider Schwämme aus den Cassianer Schichten (Unteres Karn, Dolomiten) unter Zuhilfenahme von Lumineszenzmethoden erstellt. Diese konnten mit Erfolg zur Abschätzung des Gehalts an organischen Stoffen und der diagenetischen Geschichte der Basalskelette eingesetzt werden. Neuere Untersuchungen erlauben die Unterscheidung von drei Schritten in der Genese des Basalskeletts der corallinen Schwämme, die zu einer Klassifikation der Skelettelemente herangezogen werden können. Eine Identifikation der jeweiligen Elemente entsprechend dieser Klassifikation liefert Informationen über die Art der Sekretion des Basalskeletts, die relative Position des Lebendgewebes und die Funktion des Skeletts. Zwei grundlegende Organisationstypen können innerhalb der Sphinctozoen unterschieden werden: ein Matrix-Typ, bei dem das Basalskelett in einer organo-spikulären Matrix sekretiert wird, die den Weichkörper durchzieht (ähnlich den stromatoporoiden "Coralline Spongien") und ein Cortex-Typ, bei dem die Sekretion des Basalskeletts in einer spezialisierten, subdermalen Schicht (Cortex), die den Weichkörper umgibt, stattfindet. Diese Organisationstypen haben keine phylogenetischen Implikationen.

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1 Introduction

The Sphinctozoa erected by STEINMANN 1882 are a mainly fossil group of sponges with an aragonitic or Mg calcitic basal skeleton, which is built up by chambers. Though the sponge affinities of this taxon have been known since long time, due to occasional findings of scleres in some representatives, it remained an enigmatic group up to the discovery of the recent species *Vaceletia crypta*. This can be explained by the fact that the sphinctozoans represent a highly polyphyletic taxon. As most workers had assumed monophyly for this sponge group on the ground of the similarities in skeletal organization, they encountered conflicting characters, leading to great difficulties in solving questions concerning the biology and phylogeny of these animals. Examples are the controversial discussions about sclere mineralogy (STEINMANN 1882, RAUFF 1914) or soft tissue organization (RAUFF 1914, SEILACHER 1962).

Because the sphinctozoan coralline sponges play an important role as reefbuilders in Permian and Triassic times (0TT 1967a, SENOWBARI-DARYAN & RIGBY 1988), an understanding of their biology is crucial for facial analysis of bioherms of this time. Since the (re)-discovery of coralline sponges in the beginning of the sixties an actualistic approach to the palaeobiological reconstruction of coralline sponges has been possible. The new information was readily taken up by palaeontologists working on fossil representatives (like ZIEGLER (1964b) for pharetronids or OTT (1967) for sphinctozoans), but not until the discovery of the recent demosponge *Vaceletia crypta* (VACELET 1977) and thorough investigations of scleres in fossil species (e.g. REITNER 1987b,1990) it became clear that the sphinctozoans are highly polyphyletic. This fact makes it necessary, to expect different life strategies in different sponge taxa with sphinctozoid basal skeletons. To avoid the pitfalls of deductions from phylogenetic assumptions four species have been selected from the rich and well preserved fauna of the Cassian Beds, representing at first glance different "end members" of sphinctozoan organization. Assuming that all stem from

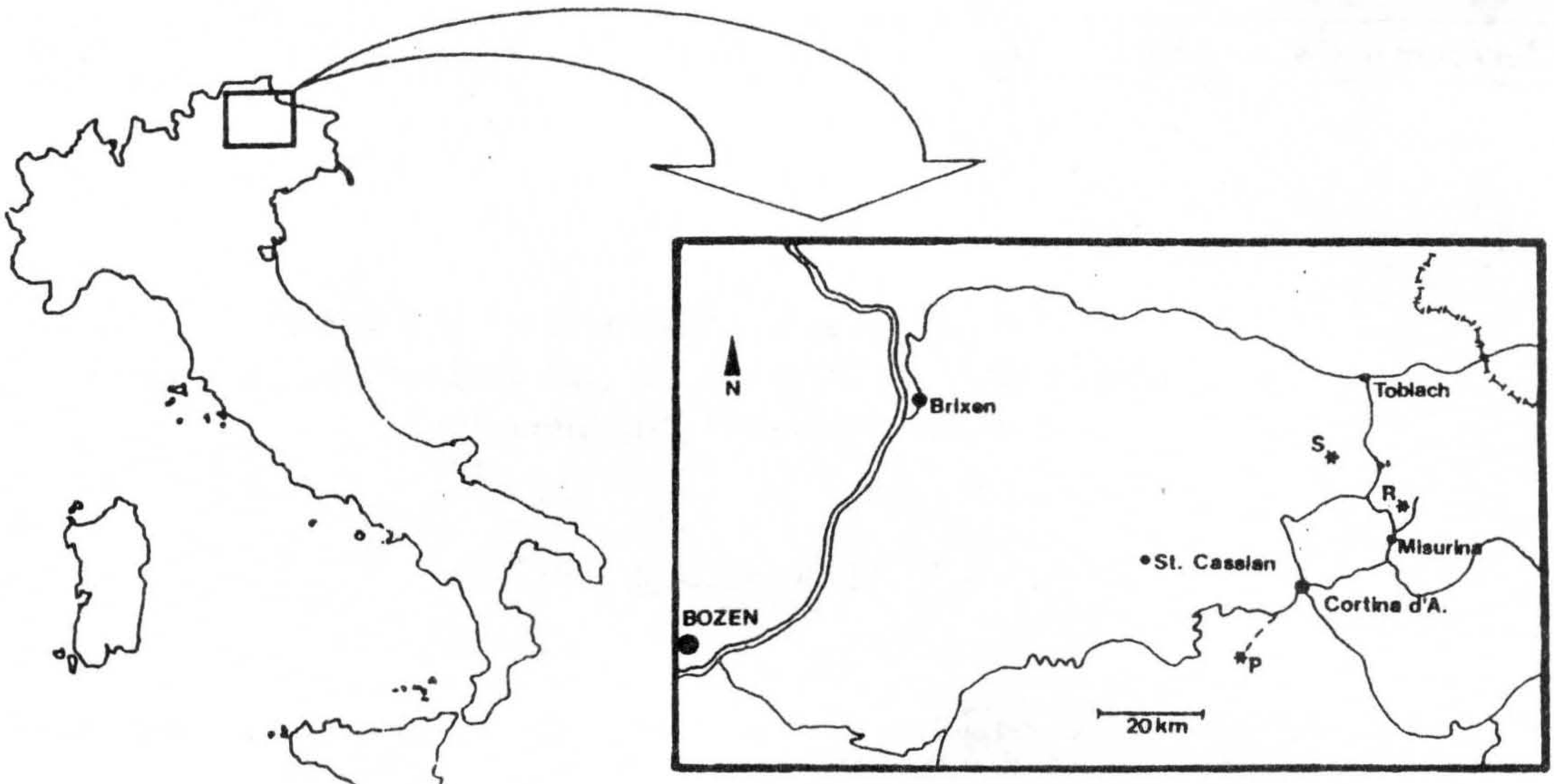

Fig. 1: The material used in this study is originated from three locations with "erratic boulders" with Cassian fauna (Carnian, Triassic). **S** = Seelandalpe (Alpe di Specie) **R** = Vale di Rimbianco **P** = Passo Giao

different lineages, a palaeobiological model has been established for each of them, in the end leading to the differentiation of organizational grades (sensu SIMPSON 1961).

Therefore the species were, as far as possible, only assigned to higher taxa in the system of the Porifera by characters of spiculation.

2. Material

The material was collected by J. Reitner from three locations in the Dolomites near Cortina d'Ampezzo (see fig.1). They have long been famous for a very rich and excellently preserved invertebrate fauna, the Cassian fauna, in the Cassian Beds of lower Carnian age. Unfortunately this fauna appears only in so called "erratic boulders", i.e. they are exposed in blocks of up to several cubic meters volume embedded in an argillaceous matrix, which makes facial and stratigraphic correlation difficult. To date it seems the most probable, that they stem from small biostromes or bioherms which arose in shallow water at the transition between the Upper Cassian Dolomite, where existing basins had been filled with platform debris and the base of Dürrenstein Dolomite, with its onset of a new transgression phase, thus being of Julian age (*austriacum*-zone). Others interpreted them as small patch reefs in the back reef area or as Cipit boulders transported into the basins of the Upper Cassian dolomite (see fig.2; for further information see FÜRSICH & WENDT 1977, BOSSELINI 1989, RUSSO et al. 1991). An overview over the sponge fauna of the Cassian Beds is given by DIECI et al. (1968).

The investigated thin sections are deposited at the Institut für Paläontologie at the Freie Universität Berlin.

3. Methods

The observations for this study were taken only from thin sections, using normal as well as polarized light. Additionally, luminescence techniques were applied. These techniques have been in use in carbonate sedimentology only since a short time, so that some technicual and explanatory annotations are necessary.

Luminescence is the capability of certain minerals, to emit light when excited by an energy source due to certain impurities of the crystal lattice. Techniques can be distinguished according to the excitation source. For this study ultraviolet and further short wave length light and an electron beam were used as energy sources. Good general informations about luminescence techniques are contained in MARSHALL (1988) and MACHEL et al. (1991).

The luminescence caused mainly by ultraviolet light from a Hg-high pressure lamp (epifluorescence) is generally believed to be caused by the excitation of organics inclosed in carbonates (van GIJZEL 1979). We got best results using two different non-UV filter sets to determine the auto-

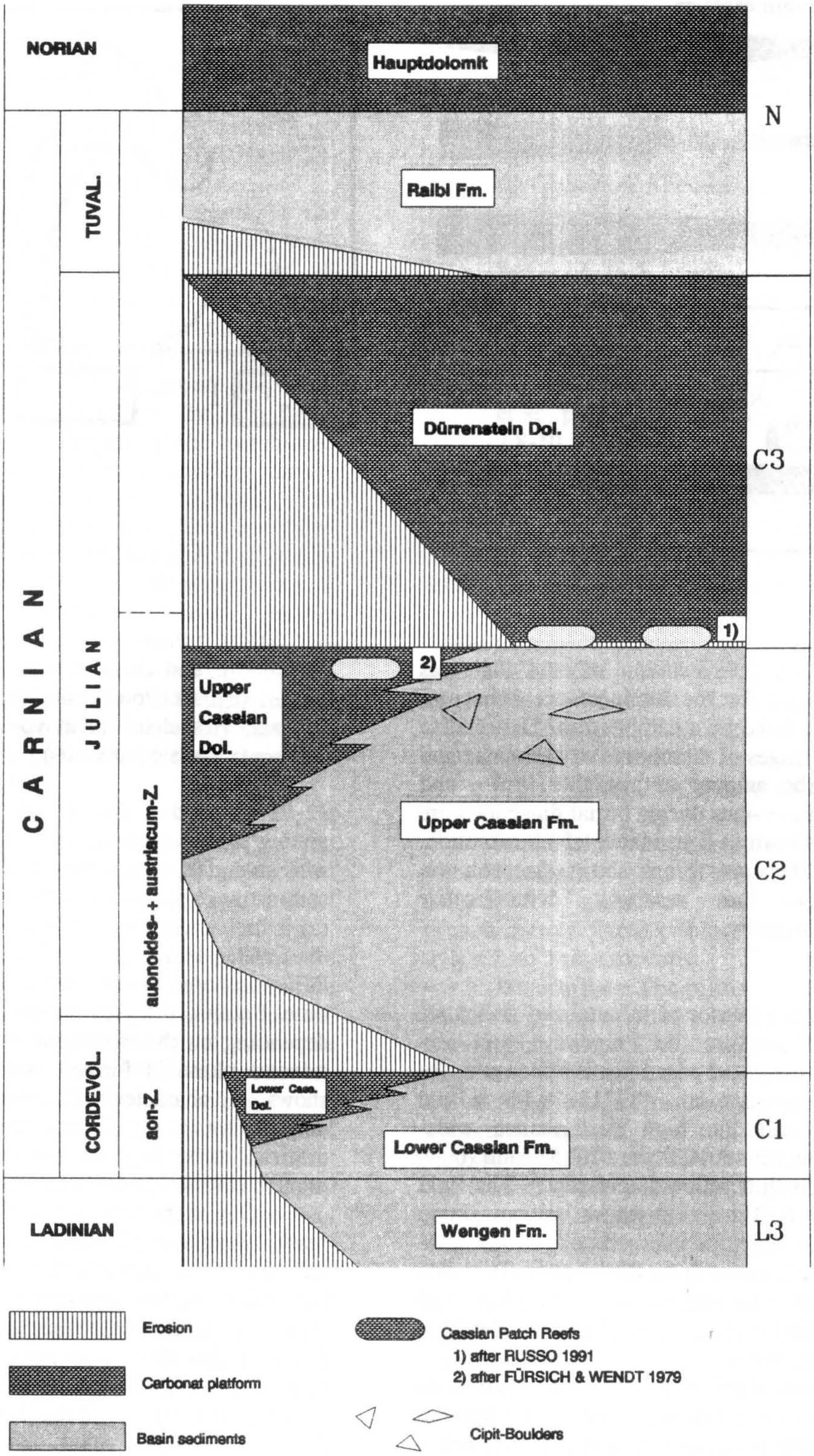

Fig. 2: Stratigraphic scheme of the Carnian of the Southern Alps with the proposed source for the "erratic boulders" with Cassian fauna. (combined from FÜRSICH & WENDT 1977 and RUSSO et al. 1991)

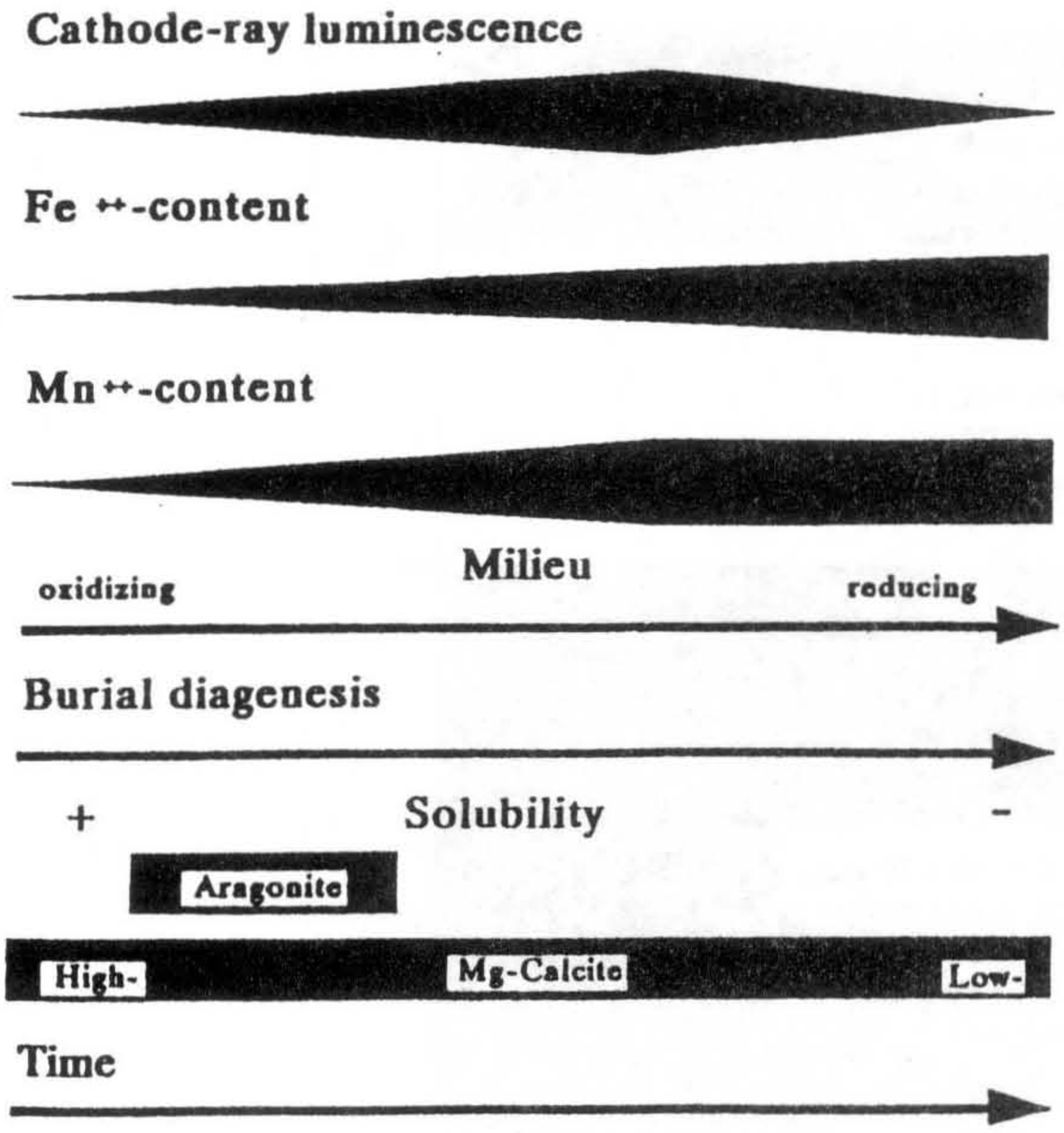

Fig. 3: The interpretation scheme that was used for the luminescence behaviour created by a cathode ray. The relative ranges of dissolution of cabonates and the amount of available Mn++ and Fe++-ions during burial diagenesis are shown in dependance of Eh-evolution. The upper graph shows the evolution of the resulting luminescence intensity.

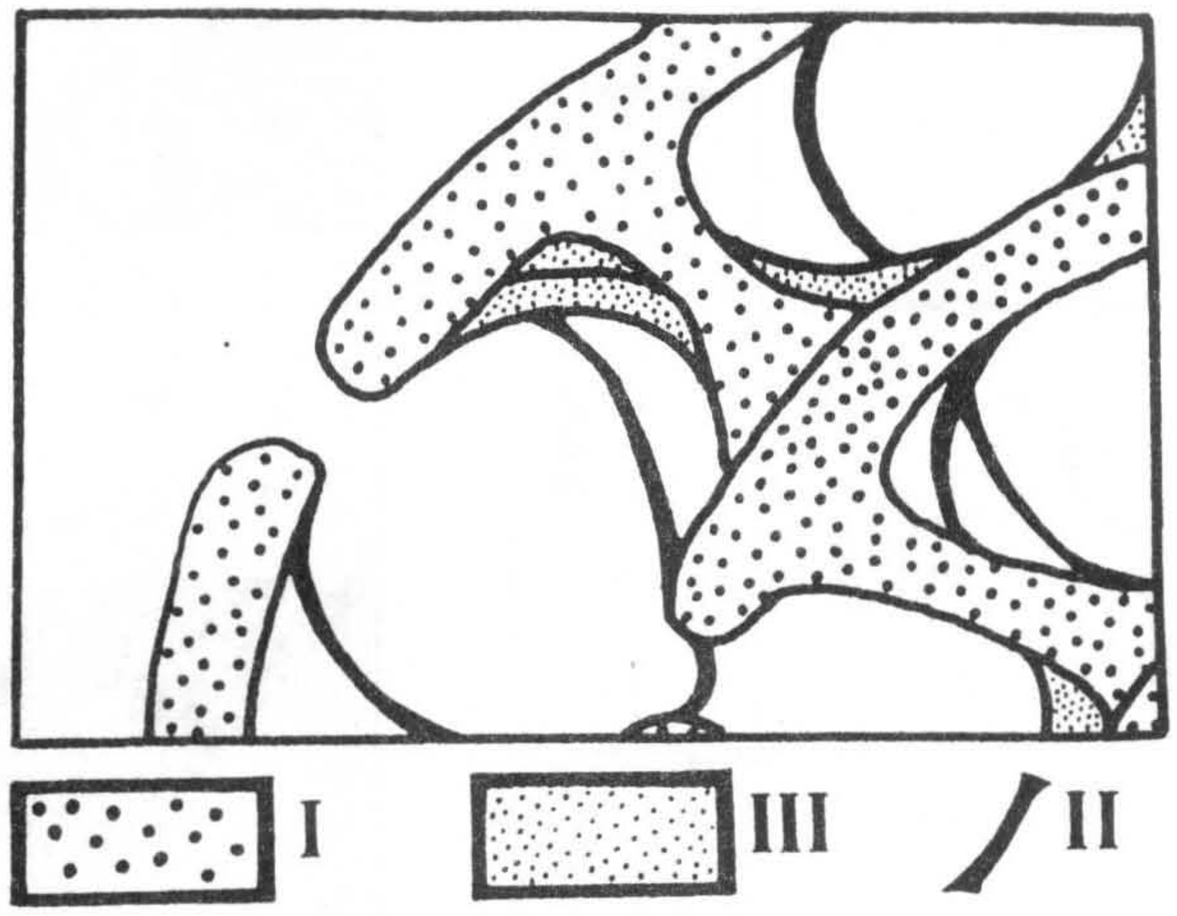

Fig. 4: Genetic classification of basal skeleton in the "Coralline Sponges" as shown in a trabecular sphinctozoan. **I**: primary basal skeleton with trabecules and chamber-roof II: secondary basal skeleton (vesicules) **III**: tertiary basal skeleton (synvivo-diagenetically filled vesicular voids)

epifluorescence behavior of mineralized skeletons. These two filters are the longewave high-performance narrow-band pass filter BP 546nm / 12 / LP 590nm (green, no. 487715) with a red fluorescence and the high performance wide-bandpass filter BP 450-490 nm / LP 520 nm (blue, no. 487709) with a yellow fluorescence. The light source was a Hg-high-pressure vapour lamp attached to an Axiophot microscope (ZEISS). Photographs were taken with an Ektachrome Tungsten film 160 ASA. The intensity of emitted light can be used to estimate the content of organic matter in the skeletal carbonate.

The second energy source used is that of an electron beam produced in a cathode, the luminescence resulting being called cathodoluminescence (CL). The investigations were made at the Institut für Interdisziplinäre Paläontologie at Erlangen, kindly supported by Dr. J. MEHL, using a Technosyn 8200 Mk II apparatus, equiped with a cold cathode. The polished and not covered thin sections were bombed with electrons in an He-atmosphere at O.17-0.20 torr pressure at a voltage of 12-15 kV and a current of 420-450 µA, thus getting stable conditions. Photographs were taken with an Agfachrome 1000 RS film (1000 ASA). In contrast to Hg-lamp light the energy of a cathode-ray is high enough to excite Mn^{++}-ions enclosed in the $CaCO_3$-lattice. This effect may be subdued, if Fe^{++}-ions are present in the lattice at the same time. Because the presence of Mn^{++} and Fe^{++} is depending on the diagenetic milieu, in which the mineral phase is formed, the CL of carbonates shows a characteristic evolution with burial diagenesis (see fig. 3), making interpretations on original mineralogy of carbonate phases and a relative chronology of diagenetic events possible.

One of the results from this study is, that the main advantage gained by the use of the two techniques for palaeobiological investigations is the much higher resolution of certain microstructural details in the skeleton. Additionally UV-L and further short wave ligth can successfully be used to estimate the content of organic material in skeletal carbonates, giving some hints on their genesis. CL yields good results concerning the degree and relative chronology of diagenetic alterations of the skeleton, also leading to informations on the original mineralogy.

4. Terminology

For microstructural types the terminology according to JONES (1979) was used, while for skeletal elements of sphinctozoans the terminology worked out by FINKS (1983) and SENOWBARI-DARYAN (1990) was taken over.

Nevertheless, recent developments in the research of coralline sponges afford some modifications. It seems to hold valid for all coralline sponges, that skeletogenesis is ocurring in three steps: a first one, in which a rigid, coherent framework is built, in which the sponge houses (primary basal skeleton). In a second step basal parts of the skeleton are left by the soft tissue leaving behind thin, unpermeable membranes inserted into the primary basal skeleton, mostly called vesicula (secondary basal skeleton). The resulting voids in the primary skeleton are filled with e.g. mucopolysaccharids and other acidic macromolucules, which induce the third step of skeletogenesis. This step comprises passive calcification events, so that the voids can completely be filled up with calcium carbonate in the end (tertiary basal skeletons). By their relative position skeletal elements can be readily classified according to during which of the three steps they were built (see fig. 4).

The described genetic classification is important in two respects: Firstly it allows interpretations on skeletogenesis, the position of the living sponge relative to the skeleton, and on the function of the skeleton in palaeobiological investigations. Secondly it forces to discriminate structures that seem similar, but are different in origin and function. An example for this are the numerous types of filling tissue found inside the chambers of sphinctozoans. While the reticular, trabecular and septal filling tissue belong to the primary basal skeleton, vesicular, "spore like" and "pisolithic" belong to the secondary. Tubular filling tissues can be formed by the secondary or primary basal skeleton. An identification of these two may lead to severe misinterpretations, because tubular structures in the primary skeleton may serve as an aquiferous system, while tubes originating from the secretion of the secondary basal skeleton can never have this function, due to the unpermeability of these skeletal structures.

5. Systematic descriptions

Phylum Porifera GRANT 1872
Classis Demospongiae SOLLAS 1875
Subclassis Tetractinomorpha LEVI 1973
Ordo Astrophorida SOLLAS 1887
Familia Geoiidae GRAY 1867
Genus *Cassianothalamia* REITNER 1987a
Cassianothalamia zardinii REITNER 1987a
(Text-fig. 5, pl. I, pl. IV/fig. 1-3)

1985 *?Stylothalamia* n. sp.: REITNER & ENGESER, p.170, pl.4, fig.8-12
1987a *Cassianothalamia zardinii* n.g. n.sp.: REITNER, p.571 ff., pls 1-3
1988 *Cassianothalamia zardinii* REITNER: ENGESER & APPOLD, p.73 ff., pls 1-2
1989 *Cassianothalamia zardinii* REITNER: GAUTRET & CUIF, p.4 ff., pl.1, fig.1, pl.2, figs 1-2,6, pl.3, figs 2-3
1989 *Cassianothalamia zardinii* REITNER: SENOWBARI-DARYAN, p.481, text-fig.3, pl.2, figs 9-10, pl.7, figs 1-6, pl.8, figs 9-10
1990 *Cassianothalamia zardinii* REITNER: CUIF et al., p.24 ff., text-figs 2E, 3E, 4, pl.1, figs 2,8-10, pl.2, fig.5
1990 *Cassianothalamia zardinii* REITNER: SENOWBARI-DARYAN, p. 136, text-fig.8, pl.5, figs 1-6, pl.6, figs 9-10, pl.24, fig.8, pl.51, fig.9-10, pl.52, fig.1-5
1990 *Cassianothalamia zardinii* REITNER: REITNER, p.34, text-fig.1
1991a *Cassianothalamia zardinii* REITNER: REITNER, p.202
1991 *Cassianothalamia zardinii* REITNER: RUSSO et al., pl.52, figs 4-5, pl.53, figs 1-6
1992 *Cassianothalamia zardinii* REITNER: REITNER, p. 140, text-fig.28, pl.15

Material: 44 specimens in 14 thin sections were investigated, whereof 4 were stained with a solution of alizarine-s and potassium-hexa-cyanoferrate-III. Autoepifluorescence was observed in 8, CL in 3 thin sections.

Description: The primary basal skeleton of *C. zardinii* is constructed of 0.4 mm flat chambers, whose roofs, pierced by exopores of 0.1-0.2 mm diameter, are sustained by 0.1-0.3 mm wide trabecules (for exact dimensions see table 1). The trabecules rest on the roof of the preceding chamber, sharply separated from the latter. While the chambers are widely overlapping, they form half-spherical aggregates up to 3 cm in diameter. This ideal form can be modified by the form of small crypts, in which this sponge houses (see pl. I), by differential growth, occuring, when the basal skeleton is overgrown by encrusters, and by budding. If *C. zardinii* reaches a certain size, a central spongocoel is formed, which contains endopores of slightly larger diameter than that of the exopores. The material of the primary basal skeleton is a dense, irregular micrite (REITNER 1987a observed crystal sizes of 1 µm). Epi-fluorescence is very bright which shows that organics, responsible for the secretion of the skeleton, are still contained. CL shows only low luminescence, hinting at a little diagenetic alteration. Both observations point at an original mineralogy of high-Mg calcite, which already was

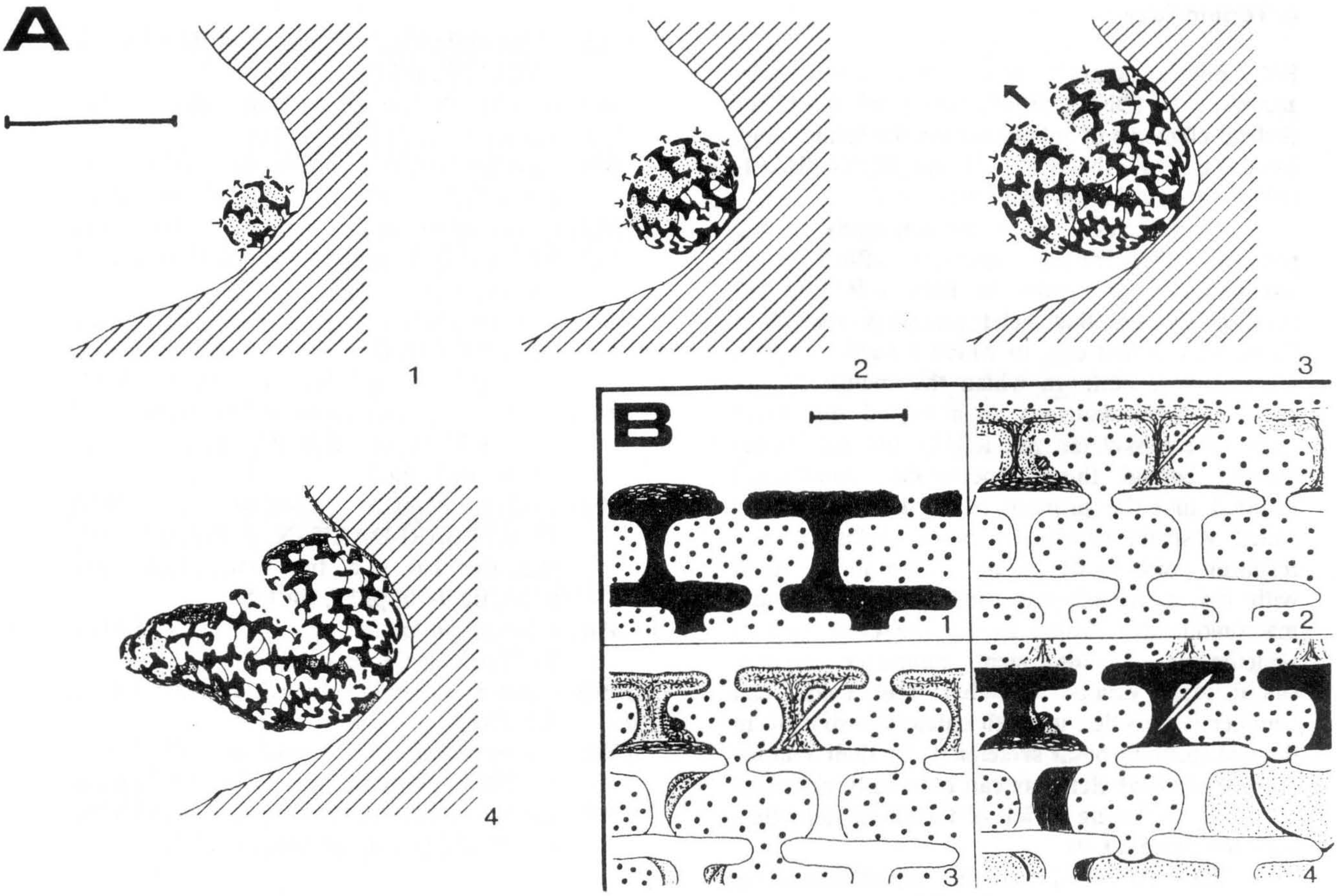

Fig. 5: **A:** Growth strategy of the basal skeleton of *Cassianothalamia zardinii* **B:** Biomineralization process of *Cassianothalamia zardinii* (For explanation see text)

postulated by REITNER (1987a) and ENGESER & APPOLD (1988), who speak of 15-25 Mol-% $MgCO_3$. In some cases the trabecules show areas of recrystallisation at their flanks and in the top, where they broaden to form the segment roof. In these areas there is no epifluorescence and CL, probably due to late diagenetic Fe^{++}-uptake (earlier cements show brightly luminescing rims).The trabecules always show a thin, denser envelope. In very thin thin sections one can observe, that thread-like structures of reddish-brown colour run through the central part of the trabecules and spread into the segment roofs, surrounding the exopores.

The secondary and tertiary basal skeleton is secreted to a very variable extent. While almost completely missing in some specimens, it fills up nearly all of the skeleton's inner voids in others. The secondary skeleton comprises vesicula, that are inserted into the primary skeleton, clearly attached to the primary elements and arranged in "fronts". The latter show no clear orientation, but may run obliquely through the skeleton. Voids, isolated from the environment by primary and secondary skeletal elements, are usually sediment-free or may be filled with skeletal carbonate of the tertiary basal skeleton. If they remain hollow, they often show a different succession of early diagenetic cements, than voids in contact with the surrounding medium.

Both secondary and tertiary basal skeleton show the same mineralogy, luminescence characteristics and microstructure as the primary, except for the tertiary basal skeleton being distinctly laminated under normal and epifluorescence light.

The primary as well as the secondary and tertiary skeleton are able to entrap encrusters (mostly *Girvanella*-like, thin micritic crusts), sediment particles and in rare cases scleres. The latter always are slightly sigmoid monaxones and totally replaced by late diagenetic, non-luminescent Fe-calcite, pointing at an original siliceous mineralogy. Secretion of secondary and tertiary basal skeleton, disturbance of the architecture of the primary basal skeleton and encrustation are clearly correlated.

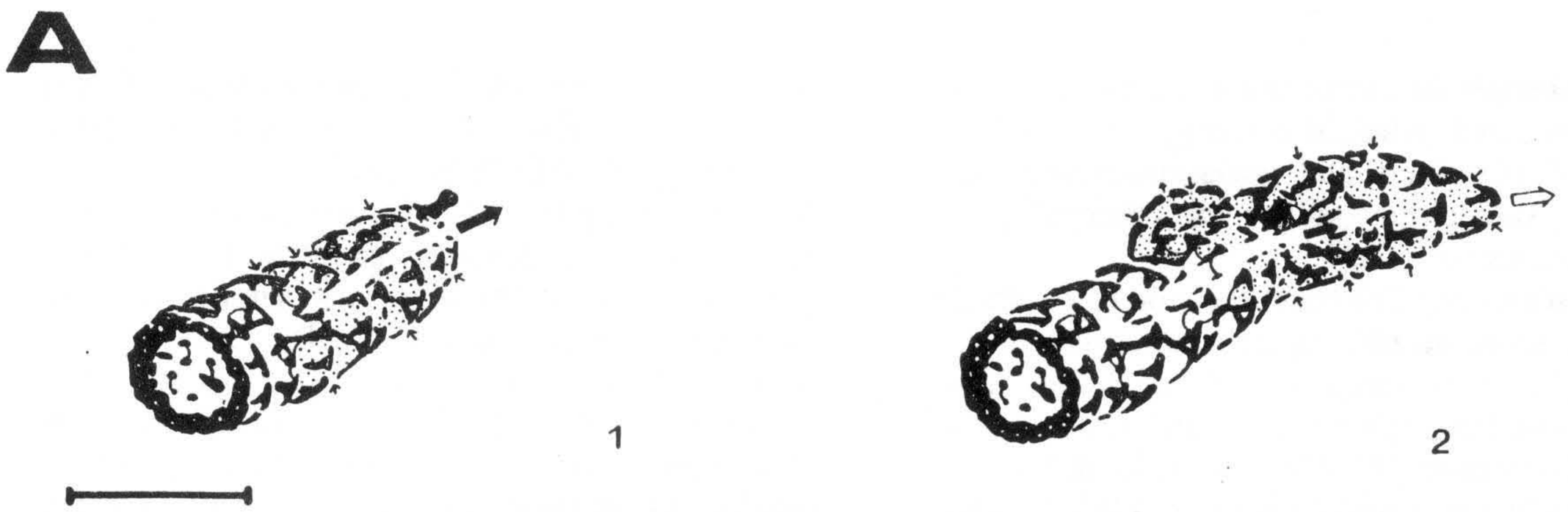

Fig. 6: **A**: Growth strategy of the basal skeleton of *Cryptocoelia zitteli* **B:** Biomineralization process of *Cryptocoelia zitteli* (for explanation see text)

Remarks: REITNER (1992) assigned *C. zardinii* to the Geoiidae, due to the finding of sterraster microscleres in some specimens. The species has until now been found in the lower Carnian Cassian beds, the Upper Carnian Lechkogel beds (ENGESER & APPOLD 1988) and in Norian Cipit boulders in Turkey (SENOWBARI-DARYAN 1990).

Demospongiae inc. sed.

Genus *Cryptocoelia* STEINMANN 1882
Cryptocoelia zitteli STEINMANN 1882
(Text fig. 6, plate II/fig. 1 & 2, pl. IV/fig. 4 & 5)

1882 *Cryptocoelia zitteli* n. gen n. sp.: STEINMANN, p.176, pl.7, fig.5, pl.5, fig.4
1967a *Cryptocoelia zitteli* STEINMANN: OTT, p.42, pl.9, fig.5-7
1968 *Cryptocoelia zitteli* STEINMANN: DIECI et al., p.149, pl.33, fig.2
1971 *Cryptocoelia zitteli* STEINMANN: JABLONSKY, p.342, text-figs 8-9
1973 *Cryptocoelia zitteli* STEINMANN: JABLONSKY, p.185, pl.1, figs 1-2, pl.2, figs 1-2
1973 *Cryptocoelia zitteli* STEINMANN:WOLFF, text-fig.4/3
1974 *Cryptocoelia zitteli* STEINMANN: ASSERETO & MONOD, text-fig.14/A
non 1978 *Cryptocoelia zitteli* STEINMANN: SENOWBARI-DARYAN (in: FLÜGEL et al.), p.171, pl.24, fig. 4, pl.26, fig.1, pl.28, fig.3-4
non 1980 *Cryptocoelia zitteli* STEINMANN: SENOWBARI-DARYAN, pl.3, fig.3
1980 *Cryptocoelia zitteli* STEINMANN: DULLO (in: DULLO & LEIN), pl.1, fig.8, pl.3, fig.3
1981 *Cryptocoelia zitteli* STEINMANN: SENOWBARI-DARYAN, pl.1, fig.1-2
non 1981 *Cryptocoelia zitteli* STEINMANN: SENOWBARI-DARYAN, pl.2, fig.2
1981 *Cryptocoelia zitteli* STEINMANN: TURNSEK et al., pl.10, fig.2,4
1983 *Cryptocoelia zitteli* STEINMANN: SENOWBARI-DARYAN & SCHÄFER, p.183, pl.6, fig.3
1983 *Cryptocoelia zitteli* STEINMANN: HENRICH, pl.5, fig.1
1987 *Cryptocoelia zitteli* STEINMANN: DULLO et al., pl.3, fig.9/A
1990 *Cryptocoelia zitteli* STEINMANN: SENOWBARI-DARYAN, pl.29, figs 3-4, pl.34, fig.1
non 1990 *Cryptocoelia zitteli* STEINMANN: SENOWBARI-DARYAN, pl.29, fig.1A
1991 *Cryptocoelia zitteli* STEINMANN: BOIKO et al., p. 140, pl.41, pl. 42, fig 1

Material: 10 specimens in 12 thin sections were investigated, whereof 6 were stained with a solution of alizarine-s and potassium-hexacyano-ferrate-III. Autoepifluorescence was observed in 6, CL in 3 thin sections.

Description: The basal skeleton of *C. zitteli* shows the same overall appearance as that of *C. zardinii*, i.e. it is composed of ca. 1 mm flat chambers overlapping each other and sustained by somewhat irregular 0.1-0.2 mm wide trabecules and pierced by small round exopores of 0.1-0.2 mm diameter. Through the skeleton runs a retro-siphonate, narrow (0.8 mm in diameter) spongocoel with endopores. In contrast to *C. zardinii* these chambers form up to 1 cm wide cylinders wich may be branched. The bases of the trabecules are sharply separated from the roof of the preceding chamber by thin micritic lines (probably of microbial origin, because they sometimes contain filamentous structures), while their tops broaden to form the segment roof.

The secondary and tertiary basal skeleton contains the same elements like *C. zardinii*, i.e. vesicula and laminated deposits of skeletal carbonate inside the voids of the primary and secondary basal skeleton. Vesicula are often seen to close off ontogentic older parts of the skeleton. Here too, there is a correlation between disturbance of skeletal architecture, encrustation (*C. zitteli* is very often incrusted by small *Tubiphytes*-skeletons) and secretion of secondary and tertiary skeletal elements. In one specimen it was possible to observe a monaxone sclere, built into a trabecule of the basal skeleton. It is assumed to belong to *C. zitteli*, because other foreign particles were never seen being incorporated into the skeleton. It shows the same diagentic alteration as those in *C. zardinii*, thus probably being of originally silicious composition.

Despite the great similarities in general appearance, *C. zitteli* can clearly be distinguished from *C. zardinii*, due to its peculiar microstructure. The primary skeletal elements are quite distinctly laminated, i.e. they are composed of discrete elements, having a dark envelope and containing coarser crystalline, thus lighter, material. In specimens of good preservation, Autofluorescence is very bright in the coarser crystalline inner part of these elements. In specimens with stronger diagenetic alteration, CL shows bright colours in these areas, of the same colour and intensity as early diagenetic cements, pointing at relatively early solution events.

Some specimens are totally recrystallized by late diagenetic non-luminescent Fe-calcite. In these cases skeletal elements are only distinguishable by pyrite secreted in small crystals around them, in some instances even tracing the lamination. The strong recrystallization of some specimens and early diagenetic recrystallization events point, when contrasted with the preservation of Mg calcitic *C. zardinii*, at an originally aragontic mineralogy of the basal skeleton.

Remarks: With the discovery of a siliceous spicule in *C. zitteli*, a demosponge affinity is highly probable (hexactinellids are not known to form calcareous basal skeletons). By its peculiar microstructure it is clearly set off from other sphinctozoan groups. To avoid confusion with other species (e.g. *Solenolmia manon*, which is similar in general appearance), only species described in literature, which show this lamination, were taken up into the synonmy list. Wether all species contained in the family Cryptocoelidae erected by SENOWBARI-DARYAN (1990) possess this distinctive feature, which might be an acceptable argument for monophyletic origin, seems doubtful.

C. zitteli is a frequent part of biohermal limestones from the Ladinian-Carnian western Tethys (DULLO et al. 1987, TURNSEK 1984) and the upper Triassic of the southwestern Pamir (BOIKO et al. 1991). Other species of this genus are known from the Norian and Rhaetian of Sicily (SENOWBARI-DARYAN 1980, 1990).

Genus *Jablonskya* SENOWBARI-DARYAN 1990

Jablonskya andrusovi (JABLONSKY) 1975

(Text-fig. 7, pl. II/fig. 3-5, pl. III/fig. 2)

1975 *Colospongia andrusovi* n. sp.: JABLONSKY, p.267 ff., pls 1-3
1978 *Follicatena cautica* OTT: SENOWBARI-DARYAN (in: FLÜGEL ET AL.), p.167, pl.28, fig.2
1981 *Colospongia andrusovi* JABLONSKY: SENOWBARI-DARYAN, pl.5, fig.2
1983 *Colospongia andrusovi* JABLONSKY: SENOWBARI-DARYAN & SCHÄFER, p.181, pl.2, figs 2,7
1987 *Colospongia andrusovi* JABLONSKY: DULLO et al., p.532, pl.4, fig.2
1989 *"Colospongia" andrusovi* JABLONSKY: SENOWBARI-DARYAN, p.475, pl.2, fig.8, pl.11, figs 7-9
1990 *Jablonskya andrusovi* (JABLONSKY): SENOWBARI-DARYAN, p.140, text-fig. 15, pl.9, figs 7-9, pl.49, figs 1,3-4, pl.51, fig.8
1991 *Colospongia andrusovi*: RUSSO et al., pl.50, fig.2, pl.51, fig.4
partim 1992 *Celyphia submarginata* (MÜNSTER): REITNER, p. 131 ff., text-fig. 24/e-f, text-fig. 25/a, pl. 10, fig.1; non: text-fig. 24/a-d, text-fig. b, pl.10, figs 2-5, pls 11-12

Material: 11 specimens (partly fragmented) in 5 thin sections were investigated, whereof 4 were stained with a solution of alizarine-s and

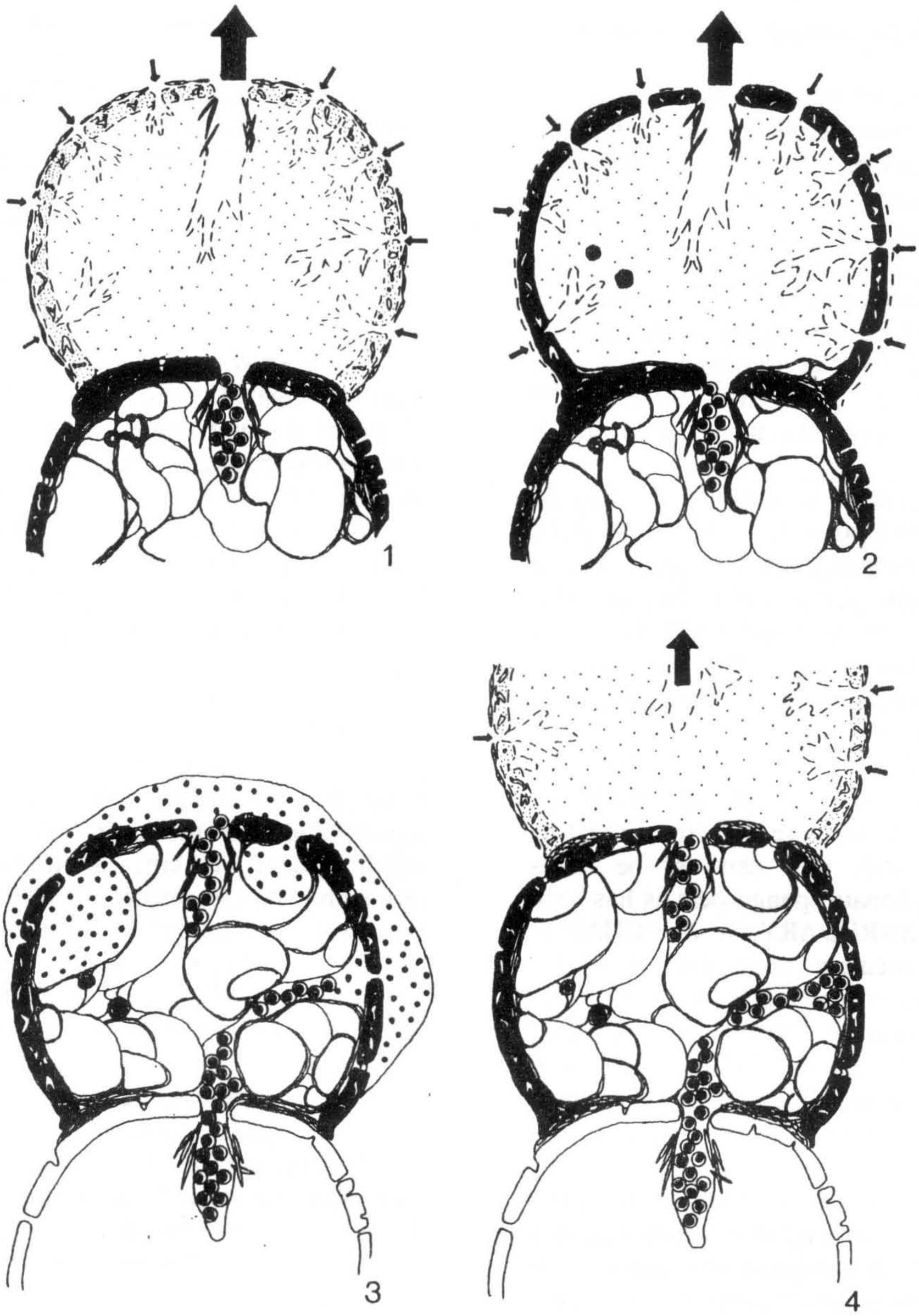

Fig. 7: Growth strategy of the basal skeleton of *Jablonskya andrusovi* (For explanation see text)

potassium-hexacyanoferrate-III. Intensive autoepifluorescence was observed in 4, CL in 2 thin sections.

Description: *J. andrusovi* possesses a primary basal skeleton, that is composed of several spherical or barrel-formed segments of up to 1 cm diameter, arranged in a catenulate manner. The walls have a thickness of ca. 0.4 mm and are pierced by a lot of regularily arranged exopores of 0.1 mm diameter. In the top of the segment or losely spaced on the outer walls appear larger, up to 1 mm wide openings (oscula), surrounded by a collar-like extension of the wall. The walls contain irregularily branching 0.05 wide "channels", which never lead outside the wall. It was shown by SENOWBARI-DARYAN (1989), that these are not spicules, due to their ultrastructure, so that he consequently termed them as "pseudospicules". The microstructure of the primary basal skeleton is irregular micritic, being of an original high-Mg calcite composition (11 Mol% $MgCO_3$ after RUSSO et al 1991), like in *C. zardinii*. Autoepifluorescence shows high intensity, especially in the described "channel-like" structures, pointing at contained organics, while CL is only weak, a hint at little diagenetic alteration. This primary basal skeleton is not secreted, where it rests on a substrate, be it a preceding segment or an alien substrate. Succeeding chambers are often separated

by thin layers of grumeleuse micrit containing sediment particles.

The segments of the primary skeleton are mostly filled with dense vesicular filling tissue - only one small specimen lacking these structures - comprising the secondary basal skeleton. These vesicula are ca 0.2 mm, at the maximum 0.4 mm thick, adding an inner layer of up to 0.7 mm thickness to the segmental walls of the primary basal skeleton and thus closing the exopores. It is also formed at the base of segments, such that intersegmental walls gain the three-layered appearance. Vesicules can also be contained inside the exopores.

The vesicules show an arrangement with the concave sides pointing out of the segment. In some cases one or two exopores are left open, with a succession of vesicules pointing towards them with their concave side. The last voids, being in contact with the environment by these open exopores are often filled with sediment. They sometimes have a tubular form, leading to the osculum at the top of the preceding osculum. Similar tubular structures may run through the center of segments, interconnecting them. Because they are formed by impermeable vesicules, they can not be interpretated as retrosiphonate spongocoels as has been done by SENOWBARI-DARYAN & SCHÄFER (1983). At the osculum they are frequently sustained by bundles of monaxone scleres, pointing back into the chamber.They were probably primarily siliceous, as shown by their replacement by highly luminescent (CL) early diagenetic cements and non-luminescent late diagenetic Fe-calcite.

Another frequent and peculiar structure are small, roundish objects of up to 0.4 mm diameter and with a laminated appearance. They are in close contact to the vesicular filling tissue, actually being formed by it and may contain small sedimentary particles as cores. They thus resemble the elements of the pisolithic filling tissue of *Pisothalamia* described by SENOWBARI-DARYAN & RIGBY (1988).

Remarks: The Mg calcitic mineralogy distinguishes *J.andrusovi* clearly from the Genus *Colospongia,* with which it shares a lot of other characteristics. The closure of the exopores by the secondary basal skeleton and their rarer appearances in vertical sections often provoked confusions with other aporate sphinctozoans such as *Follicatena* (SENOWBARI-DARYAN 1978) and *Celyphia submarginata* (REITNER 1992).

Up til now *J. andrusovi* has only been found in Carnian reef limestones of the Western Tethys (Dolomites, Northern Calcareous Alps, Carpathians, former Yugoslavia and Turkey).

Porifera inc. sed.

Genus *Amblysiphonella* STEINMANN
Amblysiphonella strobiliformis DIECI et al. 1968
(text-fig. 8, pl. III/fig. 1, 3 & 4, pl. IV/fig. 6)

1968 *Amblysiphonella strobiliformis* n. sp.: DIECI et al., p.142, text-fig.9, pl.29, figs 1-3, pl.33, fig.3

Material: 5 specimens in 3 thin sections were investigated, all being stained with a solution of alizarine-s and potassium-hexacyonoferrate-III. Auto-epifluorescence was observed in 2 thin sections, CL in 1.

Description: *A. strobiliformis* has a catenulate primary basal skeleton, whose flat chambers are of trapezoidal form and of up to 2.8 cm width and up to 4 mm height. The segments get broader with ontogeny while staying constant in height. Each segment, sometimes separated by a layer of micritic crusts, rests on the preceding one with the narrower end, such that the whole skeleton gets funnelshaped with a clear outer segmentation. If the chambers reach a certain width (about 1 cm) a narrow secondarily retrosiphonate spongocoel is installed, which later (at a segment width of ca 2 cm) widens to form a funnel in the segment roof (primarily retrosiphonate). The segment walls are about 0.6 mm thick, getting much thicker at the upper edges of the segments. In their outer portion they contain irregular branching pores of 0.05 mm diameter, while the segment roof is pierced by openings of up to 0.23 mm diameter. The spongocoel wall is quite thin and penetrated by irregular pores. The skeleton is rooted by skeletal material intruding into pores of the substrate.

The microstructure of the primary basal skeleton is spherulitic with spherulits of 0.1 mm diameter. Due to intensive diagenetic alteration by replacement in form of Fe-calcite, auto-epifluorescence as well as CL show weak luminescence colours, a hint to originally aragonitic composition. In some instances, spherulits contain small cores of intense epifluorescence, caused by remaining organics.

The secondary and tertiary basal skeleton are weakly developed in *A. strobiliformis*. Only some of the chambers contain thick vesicula, which close off large, basal parts in the respective chamber. Inside these spaces, the inner side of the segmental wall may be covered with another layer of skeletal carbonate with an orthogonal microstructure. It is interpreted as the tertiary basal skeleton, being produced by epitactic growth of the spherulits in voids left by the living tissue of the sponge. The same process is responsible for the fact, that a lot of pores of the outer walls are closed secondarily.

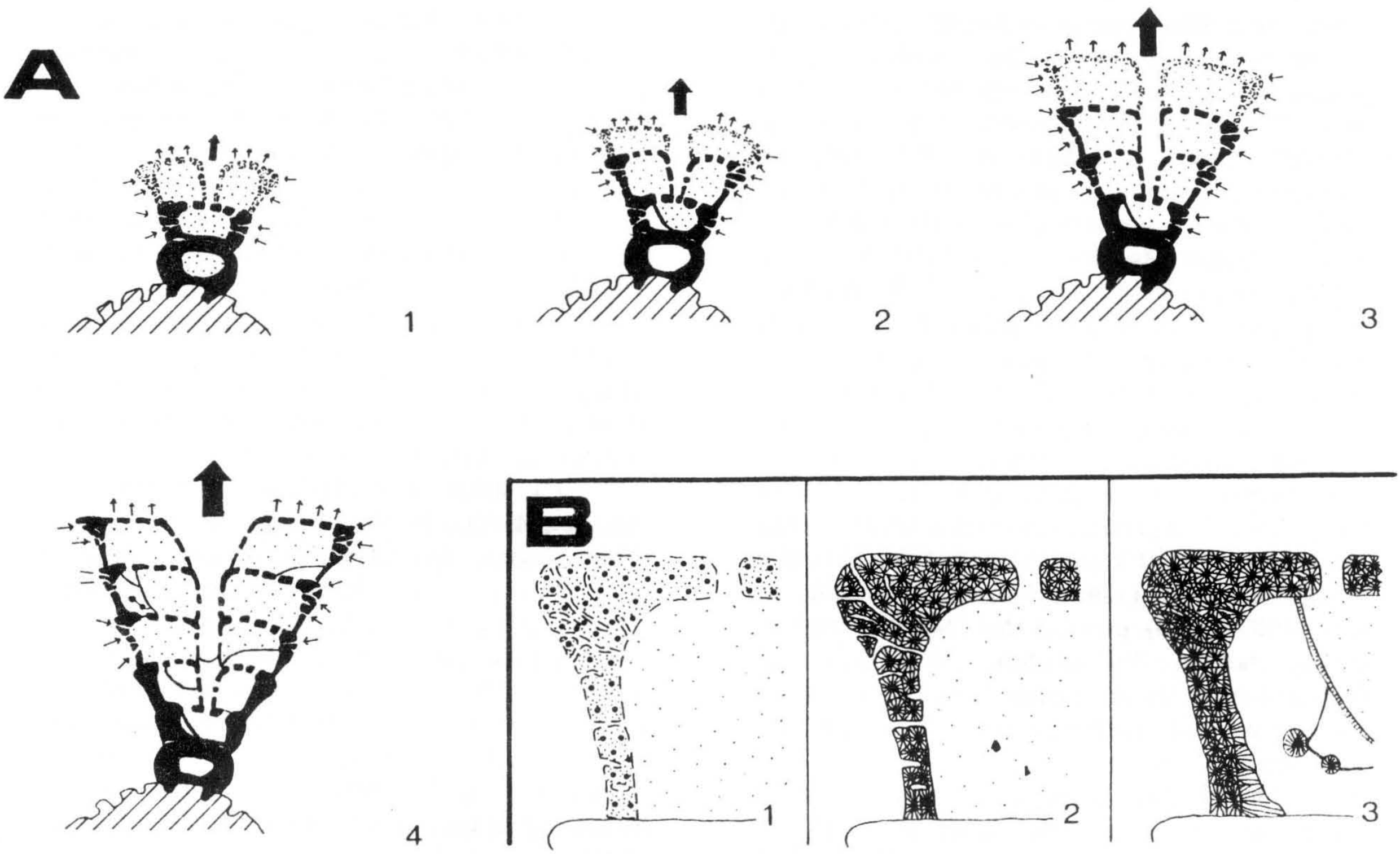

Fig. 8: **A:** Growth strategies of the basal skeleton of *Amblysiphonella strobiliformis* **B:** Biomineralization process of *Amblysiphonella strobiliformis* (for explanation see text)

6. Palaeobiological reconstructions

6.1. Palaeobiological interpretation of general features of sphinctozoan coralline sponges

Sphinctozoans, with their chambered basal skeleton, have long been interpreted as sponges, though their closer affinities remained doubtful. In some cases there were proposals to ascribe them to hydrozoans (*C. zitteli*; STEINMANN 1882) or even to algae (*Celyphia submarginata*; RAUFF 1914). Arguments for their poriferan origin where spicules (*Barroisia*; RAUFF 1914) or tubular systems inside the chambered skeleton combined with a system of exo- and endopores (SEILACHER 1962, OTT 1967a). The latter can be used as an argument, because it implies a filtering life habit (compare experimental results of BALSAM & VOGEL, 1973, referring to archaeocyathids). Further evidence for the above assumption came from the (re-)discovery and close examination of recent poriferans with calcareous basal skeletons and especially of the sphinctozoan *Vaceletia crypta*. All species described in this study show either of these features and microstructural similarities to recent coralline sponges, so that their poriferan nature is confirmed.

As has been noted earlier, this study tries to outline palaeobiological models for different sphinctozoan species separately, so that details will follow in the succeding sections. But two general features are common to all sphinctozoans, such that their interpretation is best dicussed in this section. These are the possession of a chambered basal skeleton and the formation of vesicula.

The formation of massive, calcareous, basal skeletons is known from a variety of sponges today. Basically the secretion of such a skeleton should

follow the general pattern, proposedly valid for all metazoans and given by the following model (following WHEELER & SIKES 1989): Ca^{++}-ions attach to free carboxyl-groups of the so-called soluble matrix (i.e. soluble in EDTA-solution) formed by polypeptids in an ordered manner. The structure and composition of these polypeptids (ß-sheets) determines the nucleation rate and mineralogy (aragonite or calcite) of the resulting precipitate. To develop the ability of the soluble matrix to capture Ca^{++}-ions, a second set of organic macromolecules, the insoluble matrix, is needed, on which the soluble matrix can be attached. Details for this process are still unknown for sponges, but it seems probable that exo-pinacoderm cells produce the soluble matrix, while specialized cells of lophocyte or collencyte origin ("large cells with granules" in *Acanthochaetetes*, REITNER 1991b) provide the insoluble matrix. During the described process, the participating organic substances are enriched in the precipitate, and can be made visible by using epifluorescence microscopy.

As this luminescence can be observed in all species under examination here, it is highly probable, that a similar process is responsible for their skeletogenesis. It was especially RAUFF who argued in a very polemic manner for a diagenetic origin of calcareous basal skeletons, especially in his very detailed work on *Barroisia* (RAUFF 1914). That the basal skeletons of sphinctozoans were produced by the organisms themselves can be derived from two other facts too. These are the frequent overgrowth by epizoans (SEILACHER 1962, ZIEGLER 1964a) and by borings (STEINMANN 1882, OTT 1967a). In this study a boring occured only once in *C. zardinii*, but epizoans are very frequent (mainly micritic crusts of microbial origin, *Tubiphytes* and coralline sponges in some cases). As a matter of fact, these two arguments do not show, that the skeleton was produced during lifetime, but that calcification had to occur shortly after or during death at the latest. Another important interpretation, that can be derived from encrustations and borings of each individual chamber is, that each chamber of a sphinctozoan is the result of a discrete calcification step. This lead HERAK (1944) to regard the single chamber as representing the individual, while the whole skeleton represented a colony of first order (called "Person"), which in turn can form branching colonies of second order.

The basal skeleton in coralline sponges serves three main functions:

1. It enhances the resistability against mechanical stress. SCHUHMACHER & PLEWKA (1981) computed a far higher resistability against mechanical stress of the basal skeleton in *Ceratoporella nicholsoni*, a chaetetid coralline sponge, than in scleractinians.

2. It provides the sponge with a permanent substrate, which can be resettled after ecological crisis or scavenging. Some coralline sponges are known to store special cells for reproduction and nutrition ("thesocytes", known from *Acantho-chaetetes wellsi, Merlia normani* and *Petrobiona massiliana*, VACELET 1991, REITNER 1992). Experimental results on this topic where gained by JACKSON & PALUMBI (1979).

3. The basal skeleton can be seen as a container for Ca^{++}-waste deposits, which occur during metabolic Ca^{++}-detoxification by the sponge. This is especially true for the tertiary basal skeleton (for discussion see REITNER 1992).

The mechanical strength of the skeleton is considerably diminuished by the segmentation in sphinctozoans. The advantage of this strategy of skeletogenesis is, that the organisms gain a much higher speed in vertical growth. This is the reason why sphinctozoans are generally more readily found in bafflestones than in true framestones. At least this is true for the material underlying this study, with the exception of *C. zardinii*, which houses in small crypts in coralline sponge-hydrozoan framestones (compare FAGERSTRØM 1984).

Except for possessing a basal skeleton, there is hardly any other feature common to all coralline sponges. The only exception is the possession of vesicula, which is also known from skeletons of archaeocyaths, scleractinans, brachiopods, bryozoans and rudists (ZIEGLER & RIETSCHEL 1970). Their distinct nature, which lead us to designate them as secondary basal skeleton, has been recognized early. SEILACHER (1962) and OTT (1967a) interpreted them as residues of an retreating epithelium, in analogy to the scleracti-nians. In *Vaceletia crypta* they are known to be formed by thin organic lamella, which are produced by the basal endopinacoderm, and separate the upper part of the skeleton inhabitated by the sponge tissue from the basal part, which has been left by the sponge during upward retreat and is filled with an organic mucus (VACELET 1979, REITNER 1992; compare also SENOWBARI-DARYAN 1990). They are impermeable, which also can be seen in fossil species, as voids delimited by vesicula are nearly always sediment-free in contrast to other voids. Due to their formation at the base of the living tissue, they are of great value in palaeobiological reconstruction, because they enable to detect strategies of retreat in the basal skeletons.

The function of such lamellas is primarily to separate parts of the basal skeleton, which can not be supplied with food, from the remaining living tissue. This is shown by specimens in our material, where vesicula are formed in the vicinity of encrustations covering the pores, and of contact zones with other skeletalized organisms. Food

crises may also force the organism to retreat from the basal parts of skeletons, and last but not least the sponge may reach its maximum size of the soft body, which leads to the same result. The remaining voids below the vesicula are filled with an organic mucus, which may calcify in a later stage (tertiary basal skeleton). Because the secretion of the tertiary basal skeleton may be interpreted as a Ca^{++}-detoxification (see above), the vesicula may also have an osmoregulatory function.

The interpretation of vesicula is complicated by the fact, that there are similar structures called tabulae in chaetetid *Acanthochaetetes wellsi*, which are formed by the basal exopinacoderm, and enclose thesocytes (see above). The importance of this strategy will be discussed in the section on *J. andrusovi*.

6.2. Palaeobiology of *Cassianothalamia zardinii* (text-fig. 5)

The basal skeleton of *C. zardinii* shows very close similarities to the recent sphinctozoan species *Vaceletia crypta* in all respects, except for its mineralogy being Mg calcitic. This already lead REITNER (1987) and ENGESER & APPOLD (1988) to compare these two forms. Nevertheless the basal skeleton has to be seen as a convergence, due to their known systematic positions, which shows the high systematic value of skeleton mineralogy.

Like *Vaceletia crypta*, *C. zardinii* erects its flat chambers successively, as is shown by the clear separation line between the base of trabecules and the roof of the preceding chamber as well as by enclosed encrusters. The creation of a new chamber may have occured according to the following scheme, in analogy to *Vaceletia crypta* and as shown by fine structures: Part of the soft tissue emigrates from the already existing chamber and erects an organic matrix, preforming the later skeleton. This organic matrix is composed of an organic envelope (sometimes seen as a thin redbrown line bordering the primary basal skeleton) containing a central thread forming a network of organic fibres extending into the roof and the flanks of the trabecule (in some cases seen in fossil material). The whole envelope is filled with organic mucus, which induces the calcification progressing from the center outwards. Remaining organics can be seen by auto-epifluorescence in the resulting precipitate. The recrystallization areas in the trabecules may be due to an incomplete calcification. The internal structure of theresulting skeleton is very regular, but gets irregular, if the calcification process is disturbed (encrustation, rapid vertical growth).

The overall form of the skeleton is half-spherical, but may be changed by the form of the crypt inhabitated or by encrustations. *C. zardini* shows a high potential of regeneration by asexual budding. That this is provided by reproductives enclosed by the vesicules is not plausible, because the latter are not permeable and fragmented specimens are very rare. The resettlement was rather due to remaining soft tissue in the surficial regions of the skeleton. The spongocoel, formed in late ontogenetic stages, served the reduction of the way the water current had to pass through the living tissue. In analogy to *Vaceletia crypta* the exopores can be interpreted as prosopores and the endopores as apopores. In earlier ontogenetic stages the function of apopores may have been taken over by apical pores. The diameter of these pores (140µm) does surely not represent that of the ostia, because the latter have diameters of only 50 µm (HARTMANN 1982). It is much more plausible that the skeleton was enclosed by a thin exopinacodermal layer, narrowing the pores.

The vesicula were most probably produced as described for *Vaceletia crypta* above. Their position shows, that the living tissue of *C. zardinii* could inhabit several chambers. Position and extent of the living portion of the skeleton fluctuated highly, showing distinct phases of retreat, probably due to food crises or similar factors. The correlation of encrustation or other factors of growth disturbance and the secretion of a secondary and tertiary basal skeleton proves, that the latter play a role in the physiological reaction potential of the organism, when exposed to ecologic stress. In some cases it was observed, that the secondary and tertiary basal skeleton enclose alien particles and scleres, functionally reminding of pearls. The encapture of spicules shows no systematic orientation, so they play no integral part in skeleton formation.

6.3. Palaeobiology of *Cryptocoelia zitteli* (text-fig. 6)

In spite of the overall similarity in skeletal architecture with *C. zardinii*, *C. zitteli* shows a very different strategy of skeletogenesis. While the skeleton is also formed by flat, clearly distinguished chambers, supported by trabecules, the elements of the primary skeleton are laminated. These structures point to the fact, that the skeleton of each segment was raised successively by joining discrete elements, and not in a rash, progressing manner as in *C. zardinii*. In specimens of good preservation, these elements are shown by auto-epifluorescence to resemble small cushions, provided with an envelope and filled with carbonate material rich in organics. The assertion of OTT (1967a), that the trabecules grow downwards is not plausible, and surely due to section effects. Rather the segment was built upwards by piling up the elements.

A recent pendant is not known to the authors. Only the secretion of calciumcarbonate in an extrapinacodermal layer of mucus, as observed in *Acanthochaetetes*, may serve as an interpretation. This would mean, that the elements, constituting the trabecules, where formed in a small void between the basal pinacoderm and the already finished part of the basal skeleton. An alternative could be, that small containers with an envelope of organic material were produced by the organism, and then stacked to form the skeletal elements. The organic mucus inside these containers then induced calcification. Here, as in *C. zardinii*, the calcification of the secondary and tertiary skeleton followed the same basic process as that of the primary basal skeleton, as is shown by the occurrence of the same microstructural and luminescence features.

The appearance of vesicules, a tertiary basal skeleton, and scleres have to be interpreted as in *C. zardinii*. That vesicula close off greater parts of the skeleton from the surrounding is rare. This may be due to the cylindrical, branchy habit, which reduces the distance between exo- and endopores. Additionally to this the narrow, retrosiphonate spongocoel served the same function. This growth form is also responsible for the fact, that *C. zitteli* is able to inhabit a milieu of higher sedimentary input. A rapid vertical growth is also seen in the much greater segment height, which frequently has the consequence, that the trabecules get highly irregular. *Tubiphytes*, which is very often seen enclosed in the skeleton, was most certainly a commensal, and points to quite long growth interruptions between the erection of segments.

6.4. Palaeobiology of *Jablonskya andrusovi* (text-fig.7)

After the two sphinctozoan species described in the previous sections, which have a skeleton composed of flat segments sustained by trabecules, we now turn to a "typical" sphinctozoan with a primary basal skeleton built up by spherical, hollow chambers. *J. andrusovi* is very similar to *C. zardinii* in skeletal mineralogy (Mg calcite), microstructure (irregular micritic with some laminations), diagenesis, and organic content (both skeletons with intense auto-fluorescence and remains of organic matrix in form of red-brown fibres). The only difference in these respects seems to be the occurence of "pseudospiculae" in the walls of *J. andrusovi*, which are interpreted as an additional element of the organic matrix responsible for calcification. Although these facts suggest, that skeletogenesis occured in the same way in both mentioned species, it is unplausible, that *J. andrusovi* should construct its segmental walls by an organic matrix, raised by a not yet differentiated cell assemblage emigrated from the preceding chamber, because such a structure would be extremly instable. It is more plausible, that the calcification occured in the cortex of an individual already established with an active choanosome on the preceding chamber. This special way of basal skeleton formation will be discussed in more detail in the next section.

The exopores, piercing the walls of *J. andrusovi*, do not show the dimensions of ostia (max. 50 µm). Thus it is problematic to decide, wether they were inhalant or exhalant openings. In the text fig.7 illustrating the palaeobiology of *J. andrusovi*, the first alternative was favoured, although it is as likely, that the real inhalant ostia lay in the cortex around the exopores, having been closed during calcification. That they are represented by the channel-like struktures in the chamber wall is unprobable, because these never lead outside the wall. The larger openings in the apex of the chambers and on their side were surely exhalant openings or oscula.

The most striking feature of *J. andrusovi* is its secondary basal skeleton, developed as a dense vesicular filling tissue. The following observations, partly already made by SENOWBARI-DARYAN (1990) and FINKS (1990) are important for the interpretation:

1. If one assumes, that vesicula represent remains of a retreating soft tissue with the concave side showing into the direction of retreat, the soft tissue was withdrawn from the chamber in phases, beginning at the base of the chamber and progressing upwards and outwards.

2. By this process the exopores are closed by a vesicular layer covering the inside of the chamber walls. Three cases can be distinguished: The pore is closed inwards from the outside, the pore is closed outwards from the inside and the pore remains open.

3. The vesicular filling tisue forms tubular sytems, which interconnect segments or lead outside and are attached to oscula.

From these observations the following picture about the skeletogenesis of *J. andrusovi* arises: In the beginning stands a fully differentiated individual, provided with a subdermal cortex and resting on the preceeding chamber. At a certain point, not exactly fixable, the cortex calcifies with the exception of the contact area to the substrate (where probably no cortex was formed). Later, the soft tissue withdraws from the newly built chamber, leaving behind vesicula. Partly soft tissue, resting on the chamber walls (probably the exopinacoderm) is drawn into the chamber by this process. The soft tissue leaves the chamber through some exopores and the oscula. At the oscula, the exhalant channels leading towards them are pictured by vesicula, including scleres stabilizing them. In the end, a new individual is established on the newly left chamber.

This behaviour can be interpreted as a special case of a well known phenomenon in sponges, the tissue regression. During this process the soft tissue is reduced, thereby losing its choanosomal organization and changing a lot of cell types into archaeocytes. Such tissue reductions are called forth by (seasonal) ecological crises and/or reproductive phases (for more detailed information see SIMPSON 1984). A special case of tissue reduction is the production of reductiae in *Ephydatia fluviatilis*, where large voids appear in the sponge tissue during the metamorphosis, lined by endopinacoderm (as seen from illustrations in WEISSENFELS 1989). This endopinacoderm may well have been responsible in *J. andrusovi* for secretion of vesicula. The seasonal occurence of such processes explains segmentation in this case in an elegant way.

The tubular systems enclosed in the vesicular filling tissue show that the basal skeleton probably still had some storage function, either for nutritive and/or reproductive cells. Such storage function of the basal skeleton are known from a number of recent coralline sponges (*Acantho-chaetetes, Merlia,* and *Petrobiona*, see VACELET 1990, REITNER 1989, 1991a) and gemmulae, special reproductive cells also known from marine species in the recent, were found in the fossil sphinctozoan *Celyphia submarginata* by REITNER (1992). If this were the case in *J. andrusovi,* it is possible, that the vesicula were secreted by the exopinacoderm, in analogy to the tabulae of *Acanthochaetetes*, which seclude the stored theso-cytes from the rest of the soft tissue. The frequent occurrence of fragmented specimens may have been a way of propagation for the reproductives (propagation by fragmentation is also known in recent sponges, see BATTERSHILL & BERG-QUIST 1990).

Another function of the dense vesicular filling tissue was of course to stabilize the hollow chambers. It can additionally be observed, that ve-sicula are secreted around intruded foreign particles to form pisoid-like structures. They would thus have a function as pearls.

6.5. Palaeobiology of *Amblysiphonella strobili-formis* (text-fig. 8)

Like *J. andrusovi*, *A. strobiliformis* has a primary basal skeleton composed of large, hollow chambers arranged in a catenulate manner. Nevertheless it is different in not possessing such a dense vesicular filling tissue. If we assume, that the secondary skeleton is always secreted, when the soft tissue retreats, several chambers of *A. strobiliformis* must have been inhabited at the same time. This is additionally suggested by the spongocoel penetrating most of the segments. The exopores point at the following course of the water current: the narrow channels on the side of the chamber were inhalant pores, while the wider exopores in the segment roof and the endopores in the spongocoel functioned as exhalant pores. This interpretation is possible, because in contrast to *J. andrusovi*, the exopores show a clear differentiation in size.

The difficulty in explaining the secretion of large, hollow chambers was already hinted at in the preceding section. To solve this question, we first turn to the spherulitic microstructure of *A. strobiliformis*. Such a microstructure is known from the recent coralline sponge *Astrosclera willeyana*, where the spherulits, composing the basal skeleton, are secreted around seed nuclei containing high amounts of organics (GAUTRET 1986). Their existence in *A. strobiliformis* is proved by the appearance of centers with intense auto-fluorescence inside the spherulits. These seed nuclei are produced intracellularily (according to REITNER (1991b) in vacuols of special cells derived from the pinacoderm, according to WOOD (1991) in surficial archaeocytes) and then transported to their destination, where they grow on epitactically until they merge. This would mean, that *A. strobiliformis* possessed a specialized subdermal zone as the zone of destination for the seed nuclei. Such subpinacodermal zones are well known from a number of sponge taxa and called cortex (for details see SIMPSON 1984). According to VACELET (1971) a cortex has the function to protect and stabilize the sponge.

Thus the growth of *A. strobiliformis* can be described in the following way: In a fully differentiated sponge provided with a cortex, calcification starts with the intracellular production of seed nuclei by specialized cells. The seed nuclei are transported into the cortex and start to grow epitactically. Because it is known, that the possession of a cortex may inhibit growth, it is probable, that calcification marks a point where the maximum of growth is reached. This is also suggested by the very constant height of the segments. After calcification the soft tissue extends out of the newly formed chamber.

Except for chamber height, *A. strobiliformis* shows a clear ontogeny in the succeeding chambers: the breadth of each segment is continually increased. If a certain breadth is reached, a secondary retrosiphonate spongocoel is installed, which later widens to form a primary retrosiphonate spongocoel. This clearly shows, that the installation of a spongocoel is a function of chamber volume, in the way, that it reduces transport ways of the filtered water in the chamber. The occasional appearance of vesicules, shutting off basal parts of large chambers, may have served the same function.

The capability to grow epitactically is retained by the spherulits. This is shown by the

fact, that the narrow inhalant channels are closed by epitactic growth, and by the formation of an additional inner layer of the walls of an orthogonal microstructure (as part of the tertiary basal skeleton). In both processes remains of organic substances in dead portions of the basal skeleton may have been of great importance. The pisoidal structures, fixed to the vesicular filling tissue, have to be interpreted as pearls, like in *J. andrusovi*.

6.6. Comparison with other coralline sponges

Because comparisons always are in need of a thorough classification the following one of architectural types in fossil and recent coralline sponges is proposed, mainly resting on the works of REITNER & KEUPP (1989), REITNER (1992) and WOOD (1991)

1. the crustal type: The basal skeleton is produced by biomineralization occuring at the base of the soft tissue. Two subtypes can be distinguished:

a) simple crustal type: simple, solid crusts are secreted (known from *Hispidopetra*); *Ceratoporella* mediates to the chaetetid crustal type by inserting tubes into its basal crust.

b) chaetetid crustal type: The basal crust contains tubes subdivided by horizontal tabulae; surficial astrorhizae may be developed (known from *Acanthochaetetes, Merlia* and fossil chaetetids).

2. the matrix type: biomineralization occurs in an organo-spicular matrix, penetrating the sponge tissue. The following subtypes exist:

a) stromatoporoid matrix type: the encrusting basal skeleton is composed of vertical and horizontal elements forming a more or less regular network. Threedimensional astrorhizae systems or mamelones may occur (known from Minchinellidae, *Astrosclera, Calcifibrospongia* and fossil stromatoporoids).

b) inozoid matrix type: branching basal skeletons with an internal structure like that of stromatoporoids. Prominent channel systems may penetrate the whole skeleton (early ontogenetic *Astrosclera*, fossil inozoans and some fossil stromatoporoids).

c) sphinctozoid matrix type: Horizontal and vertical elements of the basal skeleton are arranged to form a chambered skeleton, sometimes penetrated by spongocoels (known from recent *Vaceletia crypta* and some fossil sphinctozoans).

The archaeocyaths (if sponges at all), established as a separate type by WOOD (1991), can be identified as representatives of the matrix type.

The first two studied species, *C.zardinii* and *C. zitteli*, with their trabecular skeletons, are easily fitted into this scheme as representatives of the sphinctozoid matrix type. This is also true for the fossil taxa Verticillitidae and Vaceletiidae, established by REITNER & ENGESER (1985), as is shown by comparisons with *Vaceletia crypta*. From these two taxa *C. zardinii* is only different in spiculation and mineralogy of the basal skeleton. Other fossil taxa of the same architectural type are *Solenolmia ("Dictyocoelia") manon* and the genus *Zardinia*, which even shares the same mineralogy of the basal skeleton with *C. zardinii*. Interesting comparisons can also be made with archaeocyaths (see DEBRENNE & VACELET 1984, ZHURAVLEV 1989).

C. zitteli with its very special mode of biomineralization can only be compared with a few fossil representatives in this respect. There are only some members of the family Cryptocoeliidae and some Palaeozoic stromatoporoids with a similar laminated microstructure.

In contrast the two other studied species, *J. andrusovi* and *A. strobiliformis*, represent a third basic architectural type within the coralline sponges, which we call the cortex type. It is characterized by the fact, that biomineralization of a basal skeleton occurs in a specialized, subdermal zone of the more or less spherical sponge individual. Thus the classical sphinctozoans are distributed in this classification among two groups, notwithstanding possible transitional forms. The cortex type is not known from the recent.

The growth strategy of *J. andrusovi* with its retreat from the chambers, is well known from other fossil taxa. As examples may serve: the genus *Colospongia* (see OTT 1967b) from the Triassic and the genus *Salzburgia* (see SENOWBARI-DARYAN & DI STEFANO 1988). There are also great similarities with the glomerate sphinctozoan *Alpinothalamia* (see SENOWBARI-DARYAN 1990).

A. strobiliformis, last but not least, represents the most widespread type of sphinctozoan, being composed of more or less hollow chambers, pierced by numerous pores. With its aragonitic basal skeleton of a spherulitic microstructure it is part of the family Sebargasiidae, responsible for the sphinctozoan radiation in the Upper Carboniferous and the Permian (FINKS 1990). If they compose a monophylum is doubtable though, after all we know about the strong tendency of sponges, to develop secondary basal skeletons in independent evolutionary lineages. Of interest is the interpretation of pisoid-like structures inside the skeleton of *A. strobiliformis* as pearls, which liken structures in *Amblysiphonella? bullifera* (SENOWBARI-DARYAN & RIGBY 1988) and the "spore-like" filling tissue of *Intrasporeocoelia* described by RIGBY et al. (1988). If the interpretation is true, these structures should not have a high systematic value. The same is true for the pisoid-like structures in *J. andrusovi*, which are

also known from the Permian *Pisothalamia* (SENOWBARI-DARYAN & RIGBY 1988).

The model given for *J. andrusovi* may also serve to get a better understanding of the sphinctozoans, which possess an aporate skeleton. A lot of them have a prominent vesicular filling tissue, so that it is very plausible, that a calcification of the cortex without keeping pores open forced the soft tissue to retreat from the skeleton through the larger openings (probably oscula) always present in these taxa (compare *Follicatena cautica* in OTT 1967a, *Gyrtiocoelia beedi* in SENOWBARI-DARYAN & DI STEFANO 1988, and *Gyrtiocoelia typica* in FINKS 1990). In some aporate taxa with a spherulitic microstructure (Thaumastocoelidae, OTT 1967a) the loss of pores may be due to the epitactic growth of the spherulits.

The possession of pores may serve as a feature to subdivide the sphinctozoans of cortex type into further groupings:

3) the cortex type: biomineralization of the basal skeleton occurs in the cortex of more or less spherical individuals. The following subtypes can be distinguished:

a) primarily aporate cortex type: The calcified cortex contains no pores, but only occasional openings (probably oscula).

b) secondarily aporate cortex type: pores in the calcified cortex are closed during retreat of the soft tissue from the chamber by vesicula.

c) porate cortex type: pores are left open during the calcification of the cortex and the vesicula.

7. Conclusions

1. The erratic boulders with Cassian fauna from the lower Carnian of the Dolomites contain a diverse fauna of sphinctozoans, which are suitable for palaeobiological reconstructions due to their excellent preservation.
2. Luminescence techniques are successfully be used for investigations in biomineralization, because of their capability to resolve certain structures better than by normal light. Additionally they render the possibility to estimate the role of organics in biomineralization and the course of diagenesis.
3. The comparison of sphinctozoans with recent "Coralline Sponges" is very valuable for the reconstruction of their palaeobiology. The insight in genetic relationships forces to modify the traditional classification of basal skeletons. One of the consequences is the introduction of a new terminology for the elements of basal skeletons. Three different components can be distinguished: the primary basal skeleton (forming a rigid network), the secondary basal skeleton (vesicules, spread up in the former) and the tertiary basal skeleton (passively secreted carbonates in parts of the basal skeleton, which have been left by the living tissue).
4. *Cassianothalamia zardinii* REITNER is a sphinctozoan with a trabecular architecture. Its basal skeleton is analogous to that of recent *Vaceletia crypta* (VACELET). The Mg calcitic, irregular-micritic basal skeleton is built by the calcification of an organic matrix, which penetrates the living tissue.
5. *Cryptocoelia zitteli* STEINMANN erects its aragonitic, trabecular basal skeleton by a successive stacking of discrete elements, which results in a lamellar microstructure.
6. *Jablonskya andrusovi* (JABLONSKY) erects its Mg calcitic, irregular-micritic chambers by the calcification of a cortex. Later the tissue emigrates from the chamber, in connection with a tissue regression (triggered by ecologic or reproduktive cycles). During this the hollow chamber is filled up with vesicules, which close of the exopores. The basal skeleton possibly posessed a container function.
7. *Amblysiphonella strobiliformis* DIECI et al. constructs its chambers by the transport of intracellularily secreted, aragonitic seed nuclei into a cortex. Inside the cortex the seed nuclei grow epitactially to form spherolites. A greater part of the basal skeleton is constantly inhabitated.
8. The analysed taxa can be seen as models for the greater part of sphinctozoans. As a consequence the morphological subdivision of the "Coralline Sponges" into organizational types has to be modified: while the sphinctozoans with a trabecular architecture alongside the stromatoporans represent those coralline sponges, which secrete their skeleton in an organic matrix, penetrating the living tissue (matrix type), others consist of large hollow chambers, thus representing another type. Here the calcification happens in a subdermal cortex (cortex type). Inside this group of coralline sponges three subtypes can be distinguished: the porate, the primary aporate and the secondary aporate. Taxa with a prominant internal, primary skeleton as well as uviform and glomerate forms mediate to the matrix type. In the third type of coralline sponges, the crustal type, taxa of sphinctozoid architecture are not known.

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Plate I

Fig. 1: *Cassianothalamia zardini* REITNER 1987
Two specimens growing together and being separated from each other by vesicula. They show several growth phases due to resettlement of the basal skeleton. The specimen to the left is restricted in growth by encrustations, such that only a small rest is allowed to grow on in a columnar manner (arrow). The volume of this part of the basal skeleton is reduced by vesiculae. Scale bar is 3 mm.

Fig. 2: *Cassianothalamia zardini* REITNER 1987
Specimen with a regular primary basal skeleton structure. The secondary and tertiary skeleton fill up nearly all of the skeleton's voids. The whole specimen is surrounded by micritic crusts. Scale bar is 2 mm.

Fig. 3: *Cassianothalamia zardini* REITNER 1987
Part of a *Girvanella*-like crust growing on a segment roof. It is enclosed by the base of a trabecule of the following segment. Scale bar is 250 µm.

Fig. 4: *Cassianothalamia zardini* REITNER 1987
A monaxone sclere [1], a sedimentary particle [2], and *Girvanella*-like crusts [3] are enclosed by elements of the secondary and tertiary basal skeleton. The skeletal architecture is disturbed. Scale bar is 250 µm.

Fig. 5: *Cassianothalamia zardini* REITNER 1987
Two specimens, one dwelling in a small gap between a stromatoporoid and a chaetetid coralline sponge. The overall form of the basal skeleton matches the form of the gap. Only the ontogenetically youngest chambers were inhabitated as shown by vesicula closing off the older chambers from intruding sediment (arrow). Scale bar is 2 mm.

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Plate II

Fig 1: *Cryptocoelia zitteli* STEINMANN 1882
Oblique section through a specimen. The lamellar microstructure of the basal skeleton is clearly recognizable [1], as well as the narrow, retrosiphonate spongocoel [arrow]. The ontogenetic older parts of the skeleton on the rightside are cut horizontally and show the irregular, somewhat septal arrangement of the trabecules [2] and a dense secondary basal skeleton (vesicula). The segment roofs are covered by thin, micritic crusts. Scale bar is 2 mm.

Fig 2: *Cryptocoelia zitteli* STEINMANN 1882
A sclere integrated into the primary basal skeleton [arrows]. It protrudes from the sediment and is covered by the micritic crust also covering the segment roof. The originally siliciouis spicule is replaced by Fe-calcite. The basal skeleton contains vesicula [1] and deposits of the tertiary basal skeleton [2]. Scale bar is 1 mm.

Fig. 3: *Jablonskya andrusovi* (JABLONSKY) 1973)
Specimen with four chambers. The chamber walls [1] consist of micritic, irregular Mg calcite and contain a dense vesicular filling tissue constituting the secondary basal skeleton [2]. This forms a second inner layer of the chambers, such that intersegmental walls gain a three-layered appearance. The chamber walls are pierced by numerous pores (see tangential sectrion of a wall above specimen) which are closed by the secondary basal skeleton. The vesicular filling tissue contains pseudopisoids [3] and tubular systems [arrows]. Scale bar is 5 mm.

Fig. 4: *Jablonskya andrusovi* (JABLONSKY) 1973)
Dense vesicular filling tissue; the thicker vesicula show lamination [arrow]. The pores below on the right side are closed by the vesicular inner layer of the chamber wall [2]. The vesicula point out of the segment with their concave sides. The vesicular void at the far right communicates with the surrounding environment by a pore left open [1]. Scale bar is 1 mm.

Fig. 5: *Jablonskya andrusovi* (JABLONSKY) 1973)
Pseudopisoid and vesicula inside a chamber. The pseudo-pisod shows a circumlamellar structure and is in direct contact with the vesicula. It contains a sedimentary particle as a core [1]. Scale bar is 250 µm.

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2

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1

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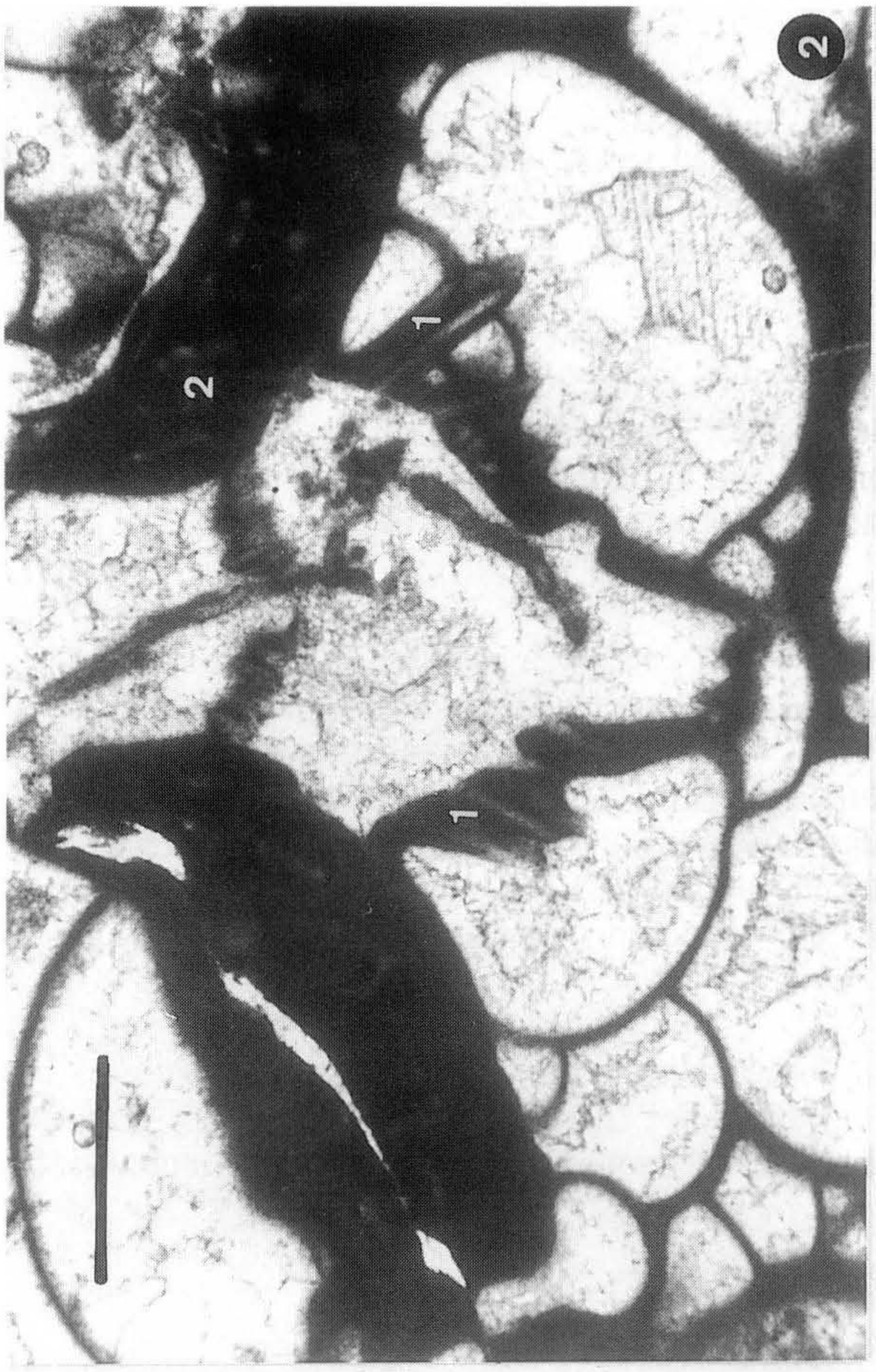
Plate III

Fig. 1: *Amblysiphonella strobiliformis* DIECI et al. 1968
Whole specimen with a spongocoel [1], which develops from a primary retrosiphonate to an secondarily retrosiphonate. The chambers are trapezoidal, broadening upwards while keeping a constant height. The upper edges of the chambers are thickened. The outer walls contain labyrinthous pores, while the segment roofs contain wider, straight pores. Inside the chambers are some vesicules and pseudo-pisoids [arrow]. The first segment roots in a bryozoan [2]. Growth is renewed on the spongocoel of the youngest chamber. Scale bar is 5 mm.

Fig. 2: *Jablonskya andrusovi* (JABLONSKY) 1973)
Part of a vesicular tube directly beneath an osculum. The tube is formed by vesicula and sustained by collar-like arranged scleres [1]. The osculum possesses an elevated rim. The chamber walls contain irregular, channel-like voids [2]. Scale bar is 500 µm.

Fig 3: *Amblysiphonella strobiliformis* DIECI et al. 1968
Outer part of a chamber, which has been secluded by a vesiculum [1]. The vesiclular void contains pseudo-pisoids of spherulitic microstructure [2] and and an inner wall layer of orthogonal to clinogonal microstructure [4] added to the spherulitic segment wall. Scale bar is 500 µm.

Fig. 4: The outer edge of a chamber. The wall contains labyrinthous, sometimes branching pores. The spherulitic microstructure of the aragonitic basal skeleton is discernable. Scale bar is 500 µm.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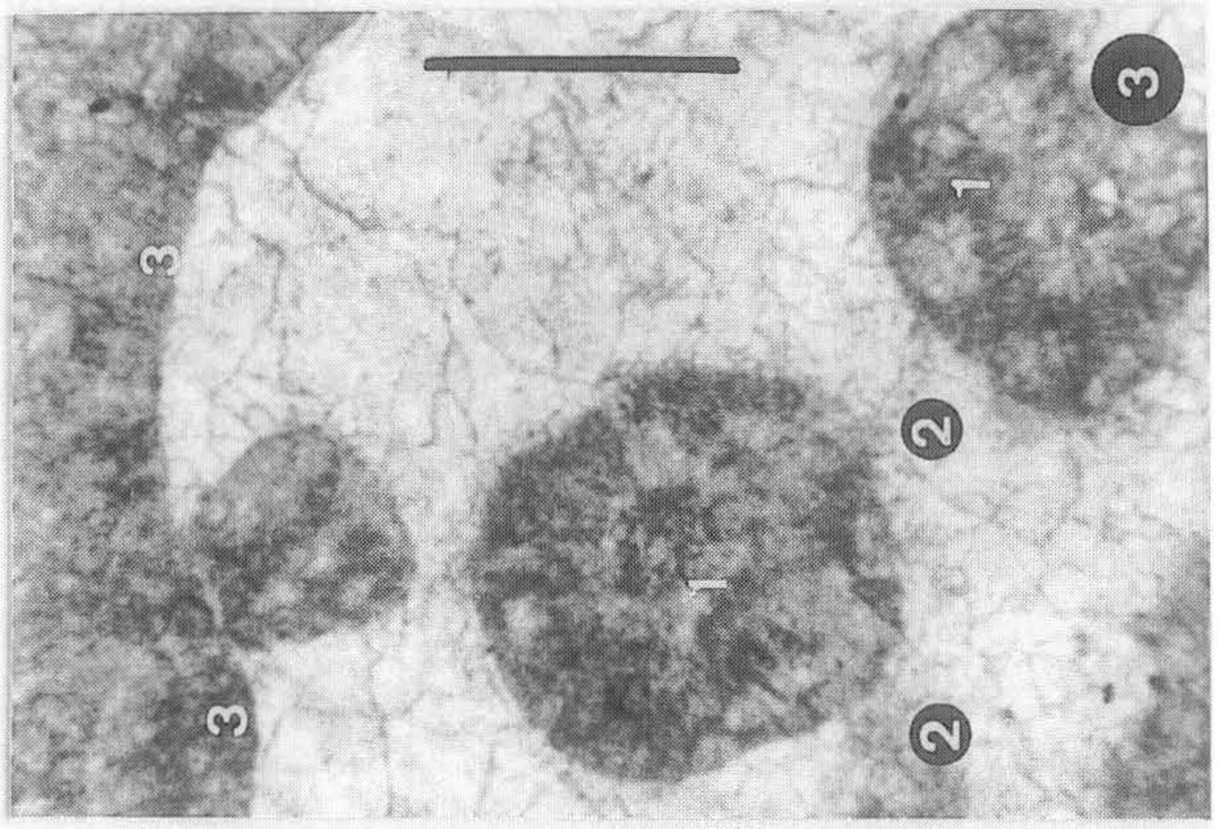
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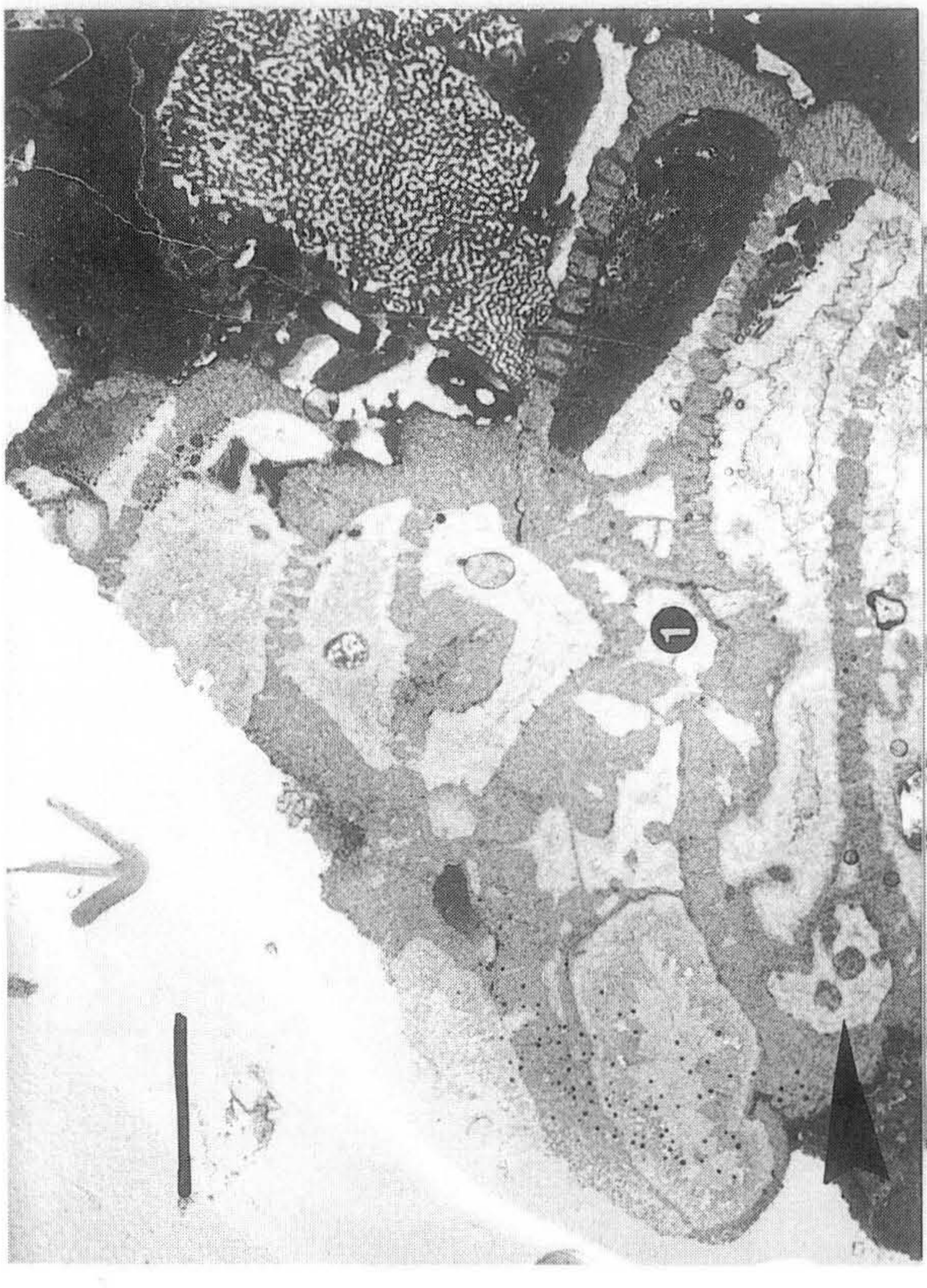
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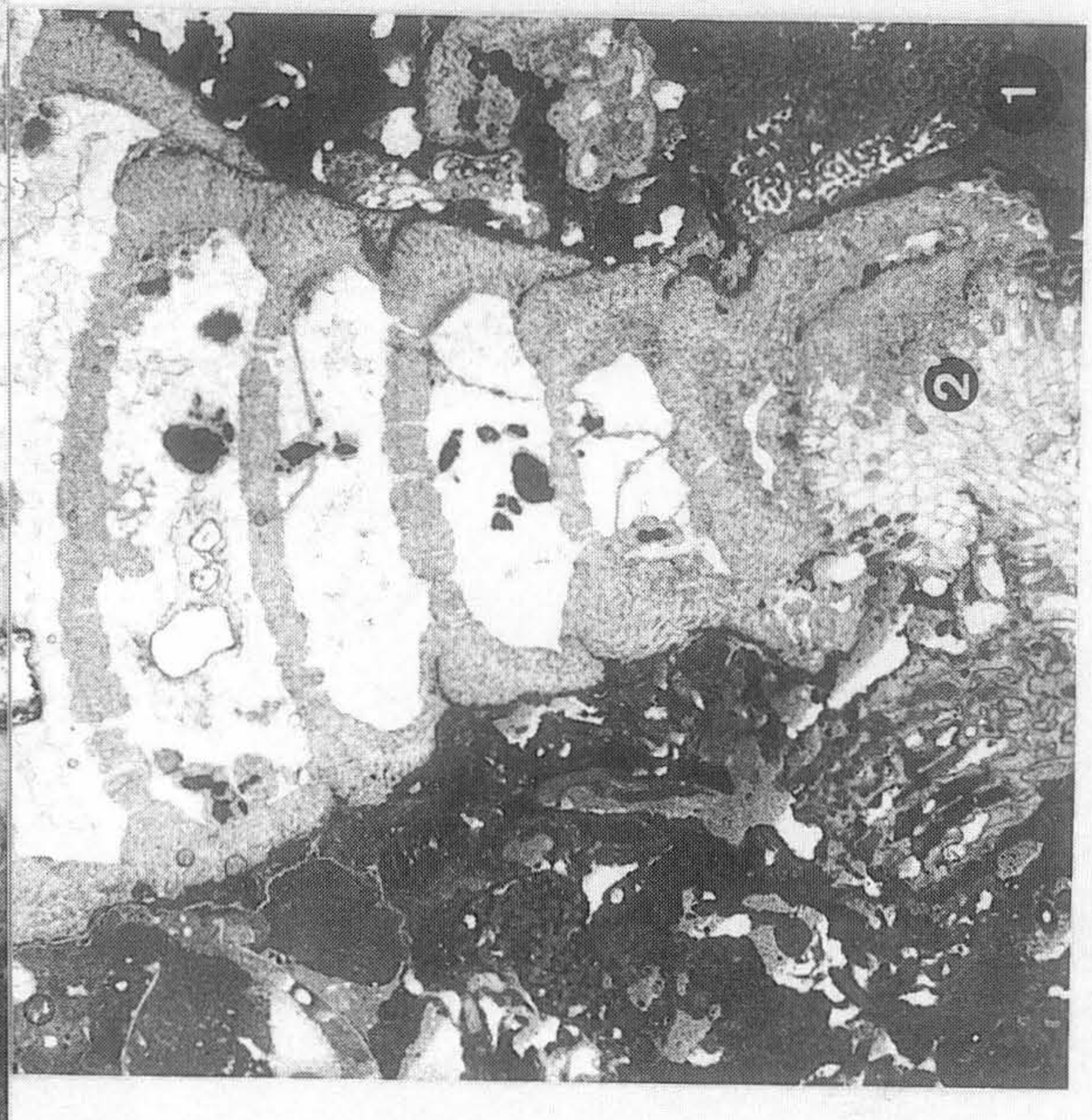
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Plate IV

Fig. 1: *Cassianothalamia zardini* REITNER 1987
A monaxone sclere entrapped in the primary basal skeleton. The sclere is passing through a void between two trabecula. The originally silicious sclere appears non-luminescent under epifluorescence (yellow fluorescence, high performance wide-band pass filter BP 450-490 nm, LP 520 nm) due to replacement by Fe-calcite. Scale bar is 125 µm (auto-epifluorescence photograph).

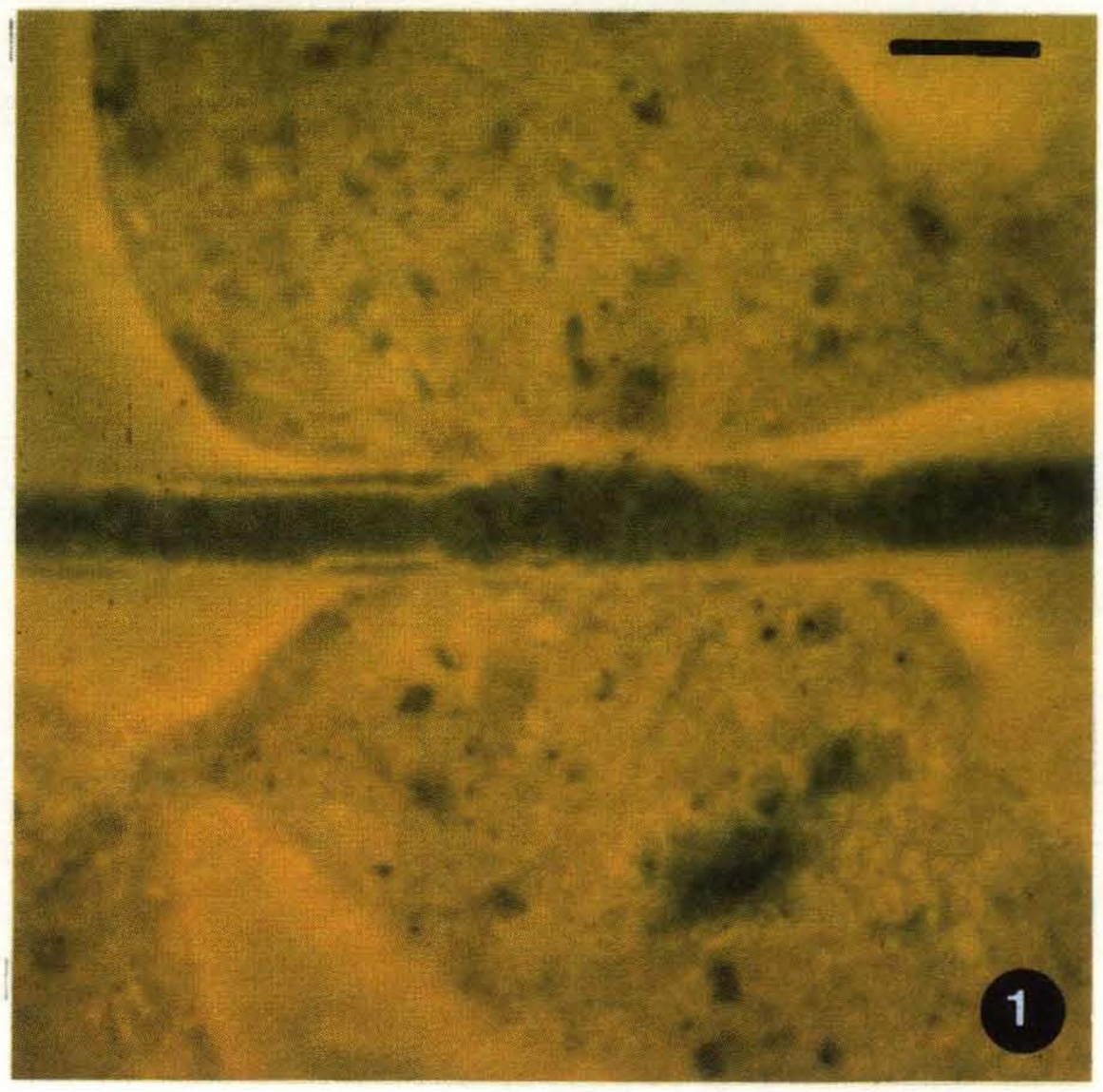
Fig. 2: *Cassianothalamia zardini* REITNER 1987
Part of the periphery of the specimen in pl. I, fig. 2 under epifluorescence.Voids in the primary basal skeleton are filled with highly luminescent material from the secondary and tertiary basal skeleton. The tertiary skeleton shows a stepwise decrease in luminescence intensity towards the center of voids. Voids filled with diagenetic cements show no luminescence. Scale bar is 125 µm.

Fig 3: *Cassianothalamia zardini* REITNER 1987
Part of the primary basal skeleton with vesicula (secondary basal skeleton). The elements of the primary basal skeleton show a somewhat stronger luminescent rim. Voids of the skeleton are filled with early diagenetic cements in two phases: 1. a palisade cement with low luminescence [1], 2. a non luminescent bladed calcite with a brightly orange luminescing rim [2]. This sequence is developed with much higher thicknesses inside the voids closed off by skeletal elements. In the last cementation phase a non-luminescent Fe-calcite is deposited [4]. Scale bar is 250 µm (combined normal light and cathode-ray luminescence photograph).

Fig. 4: *Cryptocoelia zitteli* STEINMANN 1882
The lamella of the primary basal skeleton show a bright luminescence under the cathode-ray [2], enveloping weakly luminescent zones. Colour and intensity of the luminescence corresponds to that of early diagenetic cements [arrow]. The envelopes of the trabecules and the vesicula themselves show hardly no luminescence. Scale bar is 500 µm (cathode-ray luminescence).

Fig 5: *Cryptocoelia zitteli* STEINMANN 1882
Two trabecules with distinct lamination. Auto-epifluorescence light one recognizes, that the trabecules are constructed by distinct "cushions", which possess a weak luminescent outer envelope [2] and a brightly yellow luminescing interior [1]. Between the trabecules vesicula [4] and deposits of the tertiary basal skeleton [3] have been deposited. Scale bar is 125 µm.

Fig. 6: *Amblysiphonella strobiliformis* DIECI et al. 1968
Outer wall under epifluorescence (BP 450-490; LP 520).showing labyrinthous pores filled with brightly luminescent grumeleuse micrite [1]. The primary basal skeleton is strongly recrystallized and thus of low luminescence, except for some brightly luminescent centers of spherulits [arrow]. Scale bar is 125 µm.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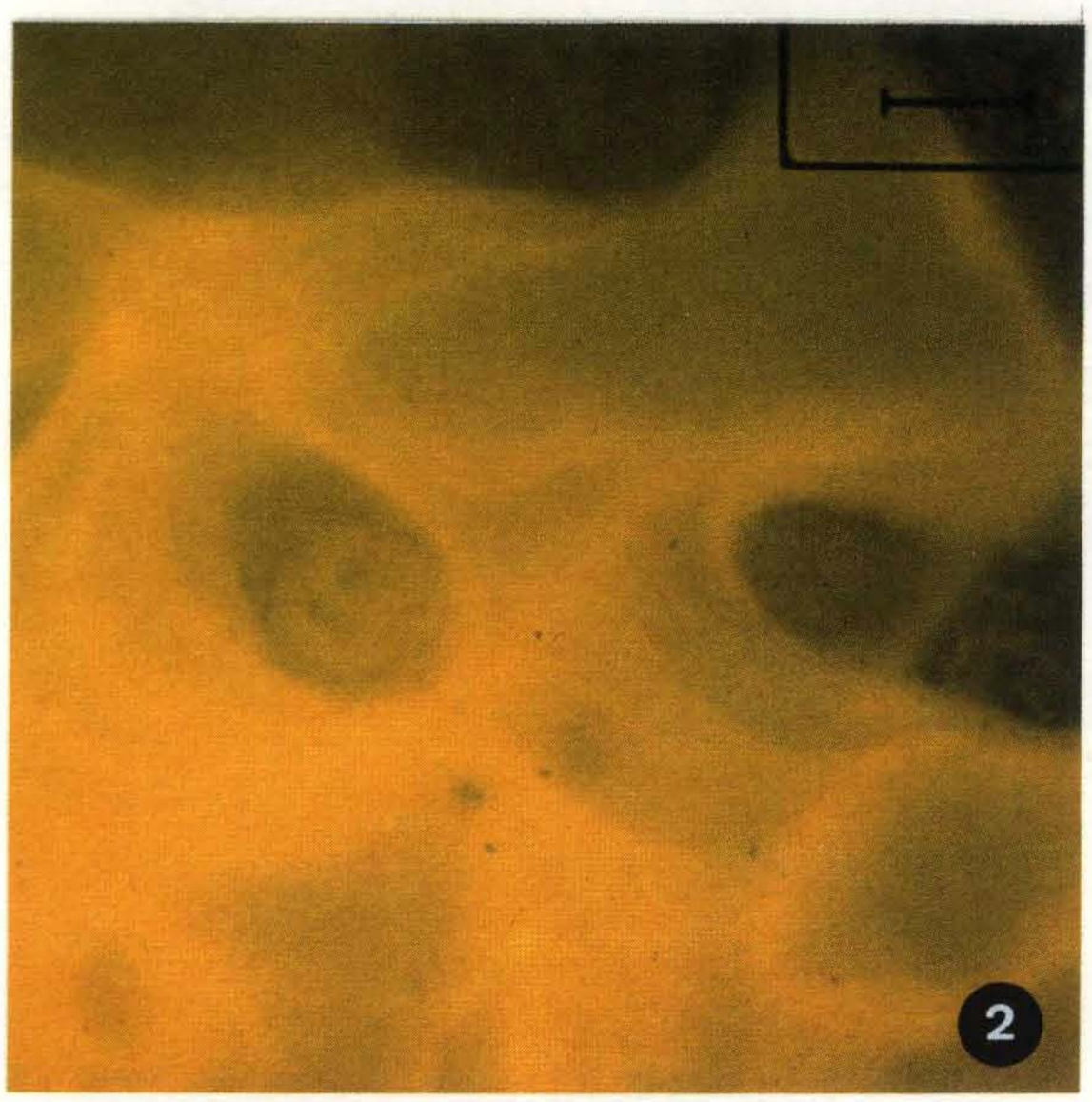
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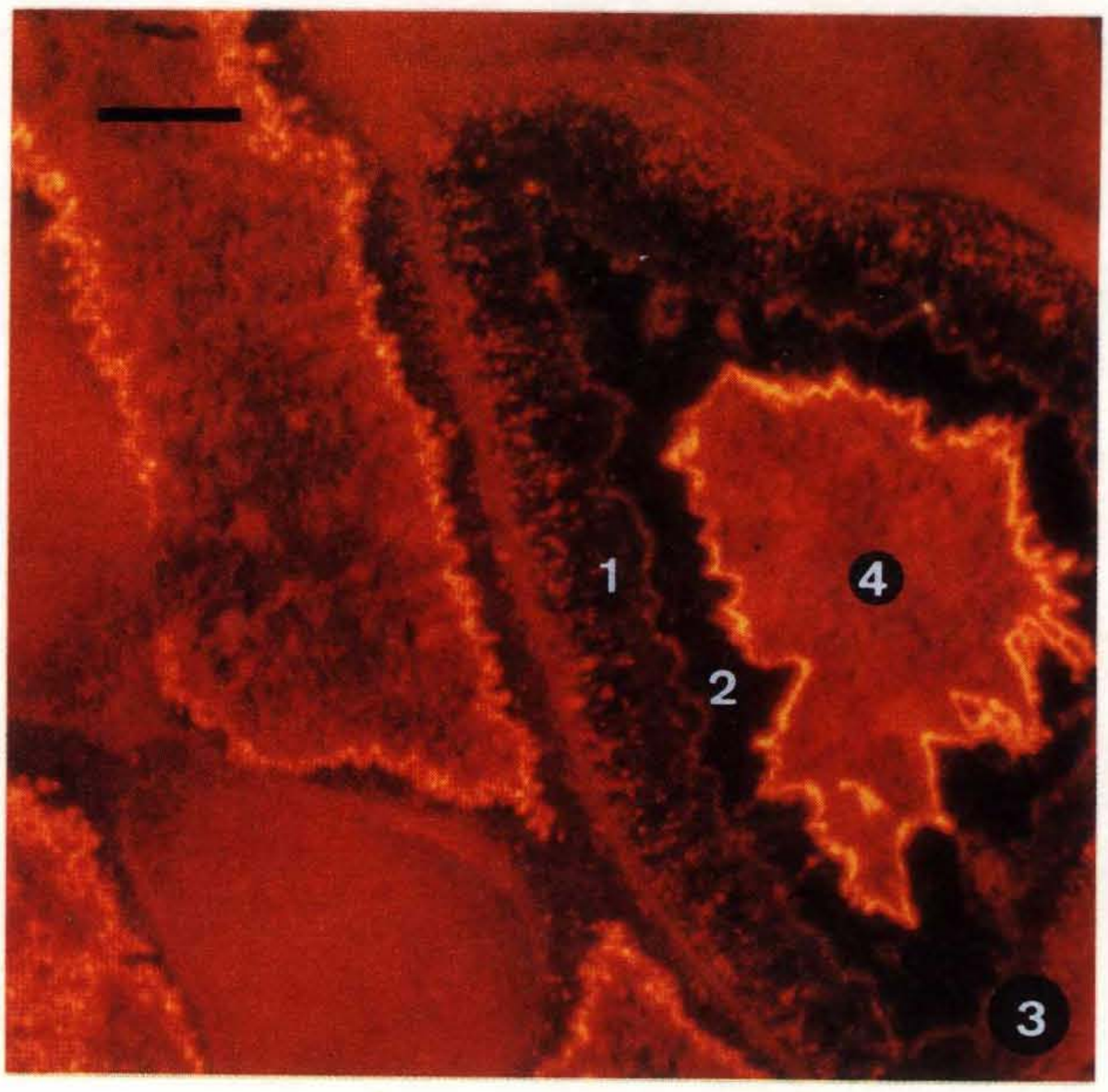
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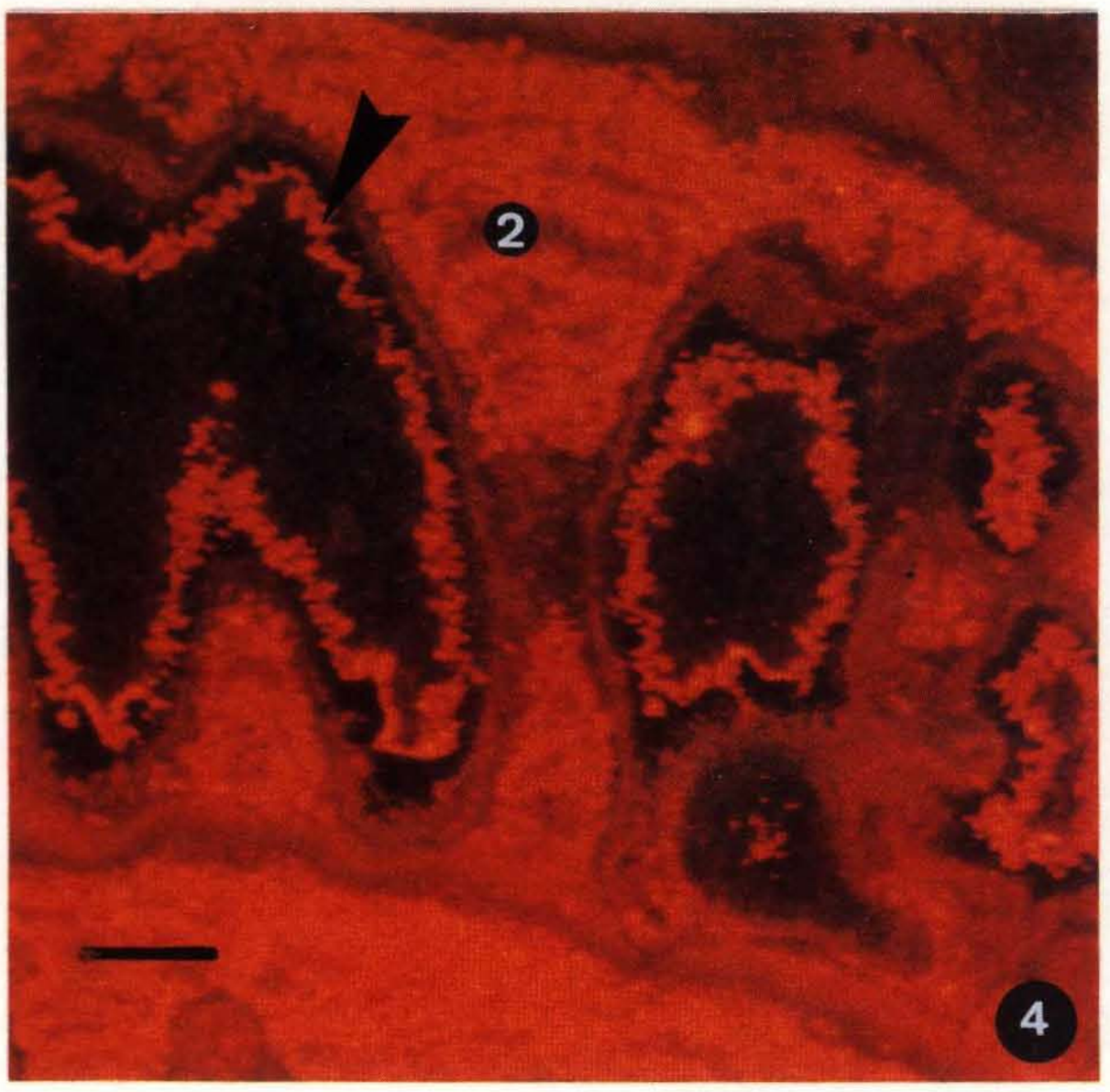
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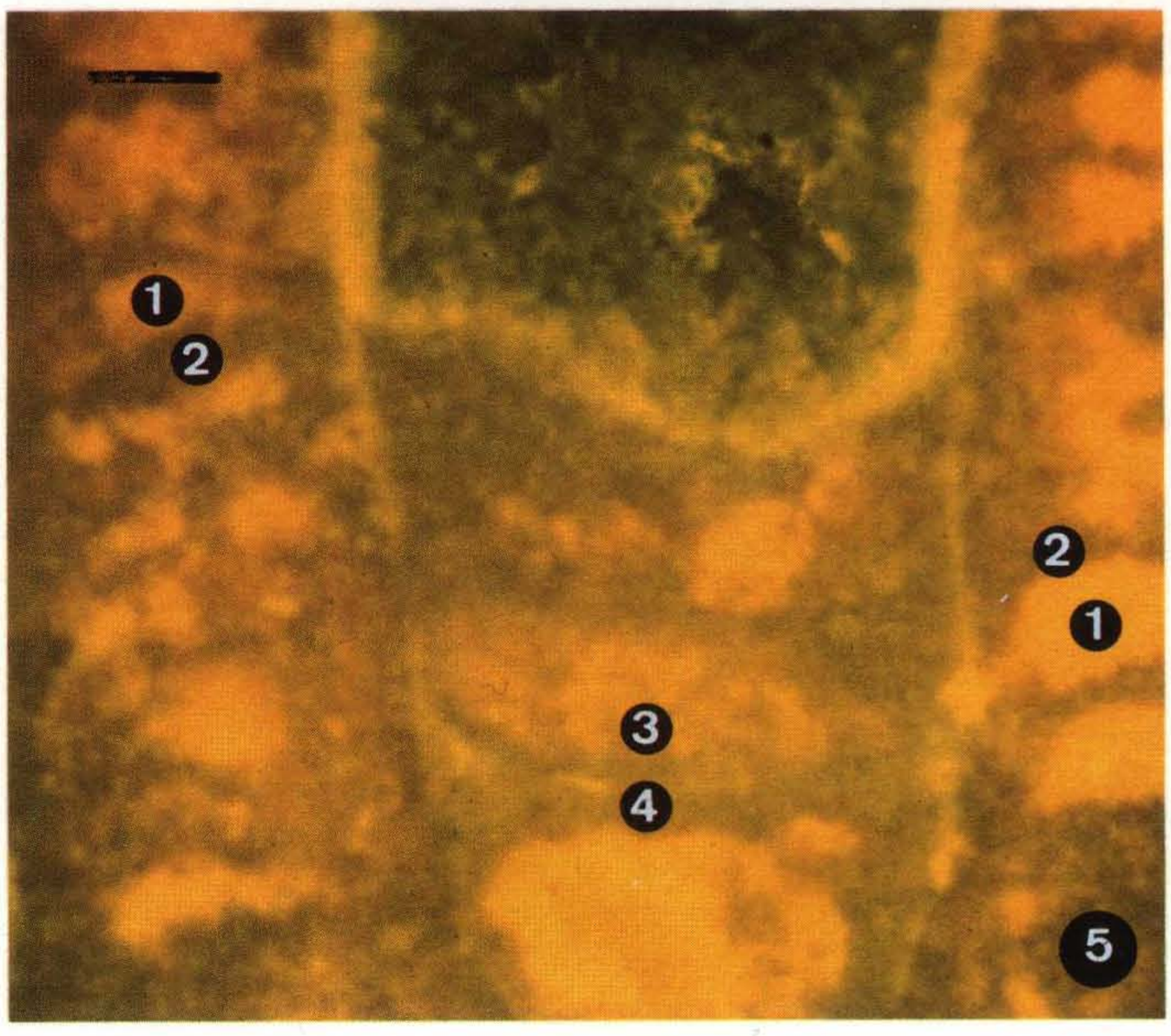
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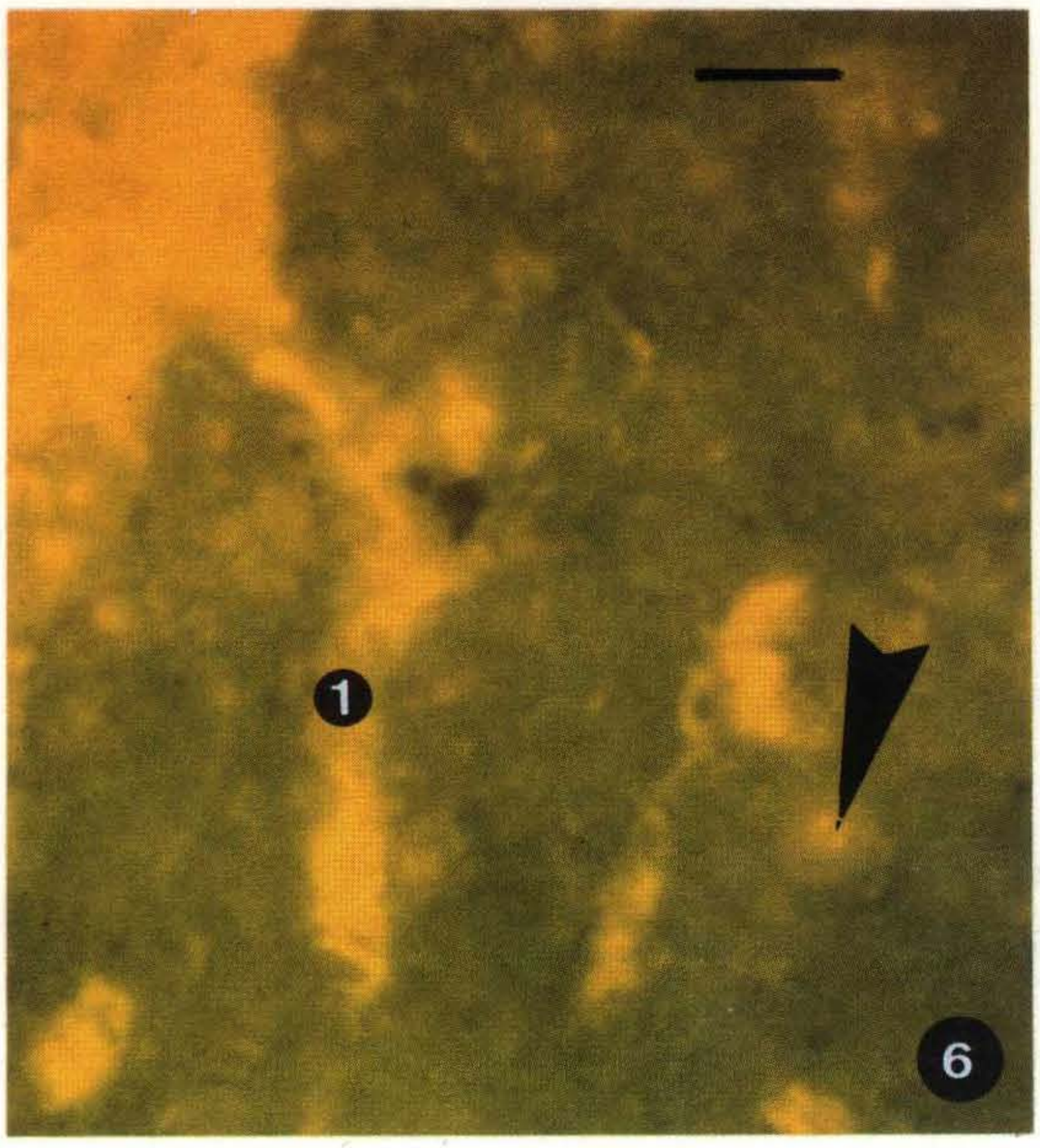
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