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Bimineralic (calcareous and phosphatic) skeleton in Late Ordovician Bryozoa from Sardinia: Geological implications

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KEY WORDS — Bryozoa, Late Ordovician, Sardinia, Phosphatic skeleton, Cryptocyst, Geological implications.

ABSTRACT — The study of Palaeozoic Bryozoa from the Upper Ordovician of Sardinia was carried out by integrating the traditional thin section description with the SEM observation of single zooecia or zoarial remnants, isolated by acid acetic technique. This technique was made possible by the presence of a bimineralic (calcareous and phosphatic) skeleton, which is interpreted as the result of the primary mineralization of the membranous part of the cryptocyst originally very rich in phosphorus. The frequent records of phosphatic bodies in Bryozoa lead us to hypothesize the possibility that some Bryozoa secreted, at least in the Palaeozoic, a phosphatic skeleton in response to particular environmental conditions. The deposition of calcium phosphate occurred in the zooecial cavity owing to the change in chemical conditions between the regeneration and degeneration phases.

RIASSUNTO — [Scheletro a duplice composizione mineralogica (calcarea e fosfatica) in briozoi dell'Ordoviciano superiore della Sardegna: implicazioni geologiche] — *Lo studio di briozoi paleozoici dell'Ordoviciano superiore della Sardegna viene condotto integrando la tradizionale descrizione in sezione sottile con l'osservazione al SEM di singoli zoeci e frammenti zoariali isolati con la tecnica dell'acido acetico diluito. Tale tecnica è stata resa possibile dalla presenza negli esemplari sardi di pareti e strutture di fosfato di calcio (oltre a quelle calcitiche) interpretate come dovute alla mineralizzazione primaria di una struttura originariamente organica (parte membranosa della criptocisti) e ricca in fosforo. Le frequenti citazioni in letteratura della presenza di corpi fosfatici nei briozoi ci portano ad ipotizzare la possibilità che alcuni briozoi secernessero, almeno nel Paleozoico, uno scheletro a duplice composizione mineralogica (calcarea e fosfatica) in risposta a particolari condizioni geologico-ambientali (ambienti ad alta percentuale di fosforo). La precipitazione di fosfato di calcio avverrebbe nelle cavità zoeciali a seguito del mutare delle condizioni chimico-fisiche fra la fase di degenerazione e quella successiva di rigenerazione.*

INTRODUCTION

In the 'seventies, and 'eighties, we collected several types of apparently problematic fossils from various outcrops in the Upper Ordovician sequence of Sardinia text-fig. 1). They were extracted from the rock using the technique for the recovery of conodonts. After dissolving the rock in acetic acid and the separation of the residues with bromoform and other heavy liquids, these fossils (submicroscopic tubes of varying morphology and size) were collected in the heavy fration and, on chemical and mineralogical analyses, they turned out to be phosphatic. In a previous paper (Conti & Serpagli, 1984), these phosphatic tubes were interpreted as *zooecial linings* belonging to different bryozoan colonies. Following new data and interpretations (Conti & Serpagli, 1987), it seems, however, more correct to use the term *phosphatic skeleton* because not involving connections with the calcareous wall.

The shape of these phosphatic zooecial tubes varies considerably and it is possible to recognize 10 informal morphological types (text-fig. 5) in longitudinal view:

1) irregularly prismatic;
2) irregularly cylindrical;
3) conical;
4) pyramidal;
5) cylindrical with the cap-like apparatus at the top (Conti & Serpagli, 1987);
6) contorted to irregularly flexuous;
7) cup-like;
8) flask-like;
9) roughly cylindrical or funnel-shaped;
10) curved conical, expanding from a flattened side.

The small phosphatic zooecia were either full of matrix and dark brown in colour or empty and transparent, isolated or grouped in small colonies.

The purpose of this paper is both to demonstrate that most of the phosphatic problematica reported in literature are remains of bryozoan colonies and to stress an uncommon technique (acid etching of the rock and SEM observation) in the study of this group of colonial fossils. An hypothesis is proposed in order to explain the formation of the phosphatic skeleton (considered of primary origin) and the relationship between phosphatic deposition and environmental conditions.

PHOSPHATIC BODIES AND ZOOECIAL LININGS IN BRYOZOA: A REVIEW

Sollas (1879) gave a full description of «oolitic granules» present in some zooecia of Ceramoporidae (Cystoporata) from Silurian of Rymney (Great Britain), regarding them as calcitic.

Etheridge & Foord (1884) published a detailed description of *Favositella interpuncta* (Quenstedt) (Cystoporata) from the Wenlock Limestone of Dudley (Great Britain) pointing out that the frequent communication pores were filled with spherules in concentric layers of material, which they supposed to be chalcedony (beeckite). Bassler (1911), reporting the presence of such spherules in Silurian ceramoporids, stated that they had nothing to do with the bryozoan itself and that they were of siliceous composition.

The mineralogical composition of these concentric spherules was only supposed and it was necessary to wait the revision work of Oakley (1934), where a mineralogical analysis of such spherules («pearl-like bodies») was carried out. They turned out to be phosphatic and, more precisely, with a composition varying from dahllite to collophanite. The phosphatic spherules reported by Oakley (1934) were recorded in several species of Cystoporata, Cryptostomata and Trepostomata from different Silurian outcrops from Great Britain and Gotland (Sweden). According to this author, phosphatic spherules were more abundant in autozooecia than in mesozooecia and they were generally located at the bottom of the zooecial chamber, either resting on a diaphragm or below it and sometimes related to brown bodies. Oakley regarded these phosphatic spherules as zooecial calculi, comparable to such pathological structures as human gall-stones, which were formed in the coelomic fluid when this lost its buffering properties owing to polypide degeneration.

Spjeldnaes (1950) considered the phosphatic spherules present in cryptostomes and trepostomes from the Silurian strata of Gotland as corroded fish scales and not as zooecial calcular precipitates.

Lewis (1926) described a ceramoporid (*Bolopora undosa*) with a phosphatized skeleton from basal Arenig rocks of Upper Ordovician from Wales, later interpreted by Hofmann (1975) as an oncolitic accretion.

Phosphatic bodies, quite similar to zooecial spherules, were also found associated with conodonts (Glenister *et al.*, 1976), suggesting that their origin was probably unrelated to the systematic group but linked with the chemical composition.

Besides phosphatic spherules, called «Oakleyit» by Eisenack (1965), (a complete description is given by Oakley, 1966 and Spjeldnaes, 1984), phosphatic zooecial linings are also present in Bryozoa.

Eisenack (1964) found in the Silurian of Gotland conical (*Phosphaconus*), cylindrical (*Phosphatuba*) and slightly contorted (*Phosphasipho*) phosphatic tube-like fossils, which have been interpreted as zooecial phosphatic linings belonging to different genera of Bryozoa (Martinsson, 1965; Conti & Serpagli, 1984). Their appearance, in longitudinal view, is laminated, sometimes with the laminae confluent with phosphatic spherules, when they occurred. Not all zooecial linings, however, are of phosphatic nature and Cumings & Galloway (1915) used the term «cingulum» to indicate calcareous secondary thickening continuous with the diaphragms and cystifragms lining the zooecial walls of the Trepostomata. These authors believed the «cingulum» as a senile feature having the purpose of reducing the zooecial lumen.

In a short review of the occurrence of phosphatic substances in Lower Palaeozoic metazoans, Müller (1964) reported apatitic bodies in *Favositella* (Cystoporata, previously attributed to Cyclostomata).

Martinsson (1965) recognized phosphatic zooecial linings in the genus *Ptilodictya* from Wenlockian and Ludlovian strata of Gotland. According to the swedish author, zooecial linings and «pearl-like globules» had similar features and were formed at the surface of the inner epithelium during lifetime of the polypides. He hypothesized, moreover, that apatitic linings and similar structures were very common in the phylum Bryozoa and their rare indications were to be placed in relationship to their fragility and to the fact that the acid-digest technique was rarely used in the study of Bryozoa. Martinsson (1965) also stated that phosphatic linings were laminated, with the laminae parallel to the zooecial axis and variable in thickness along the zooecium.

Gorka (1969), using the acetic acid technique, recovered phosphatic tube-like problematica from Ordovician erratic boulders from Poland and she established three new genera (*Labyrinthotuba, Phosphotesta* and *Oxytuba*) without realizing that these were zooecial linings (Dzik, 1981; Conti & Serpagli, 1984). She noted, however, a similarity between the Polish specimens and those described by Eisenack (1964). According to Gorka (1969), the phosphatic laminae are normal to the growth direction of the zooecial walls and they have a chemical composition that varies from dehrnite to francolite.

Mc-Kinney (1969) reported a dark-coloured membranous lining observed in the transverse section of a mesozooecial cavity belonging to a trepostome (*Tabulipora*) from the Upper Mississippian of the Alabama (U.S.A.), and considered it different from cuticular structures and brown bodies.

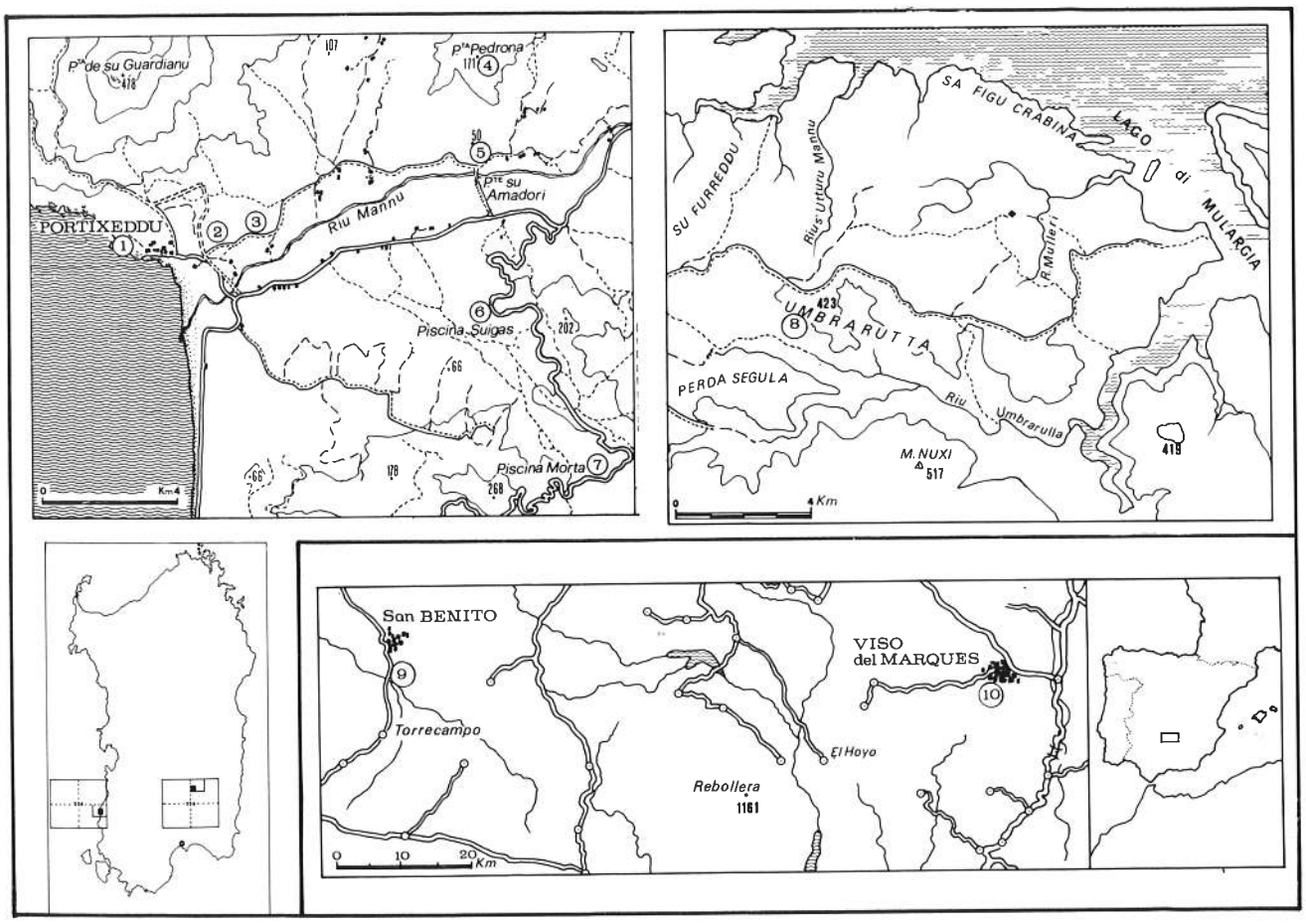
Rhodes & Bloxam (1971) regarded the calcium

phosphate present in zooecial linings from the Lower Silurian of Cincinnati (U.S.A.) as secondary.

The calcareous wall of tubular Bryozoa (Stenolaemata) was divided by Boardman (1971) into two distinct parts: 1) the cortex, occurring in virtually all Palaeozoic Bryozoa and defined as the outermost unit of the zooecial wall, consisting of concentrically curved laminae that range from inclined to transverse in orientation to the zooecial axis; 2) the lining (Boardman, 1960b), which is not always present and defined as the calcareous wall-unit between cortex and zooecial cavity and consisting of laminae that are generally parallel to the zooecial axis. The contact between the laminae of the lining and those of the cortex can either be continuous or discontinuous and, in the latter case, the laminae in a parallel direction gradually pinch out on the inner surface of the cortex (Boardman, 1971, fig. 1). The laminae of diaphragms and cystifragms may continue without break either into the laminae of the cortex or of the lining when the latter is present. In this case, the term lining includes terms such as: wall-diaphragm unit, cingulum, etc. and it is only an empirical term that does not imply primary-secondary relationship with the cortex.

Boardman (1971, p. 11) reported apatitic linings from Devonian trepostomes from the Antarctic and suggested that these structures were originally membranous and mineralized during the organism's lifetime. In support of this hypothesis, Boardman (1971, 1973) recorded several examples among fossil Bryozoa, where the mineralization of part of the outer or of the inner body-wall, such as cystifragms, funnel-shaped structures, diaphragms and zooecial linings occurred. The thickness of these apatitic linings was, sometimes, much greater than analogous membranous structure (cryptocyst) observed in Recent cyclostomes, and Boardman suggested that diagenetic changes could have altered the original thickness of the inner membrane in fossil Bryozoa. Boardman (1971, pl. 1, fig. 5c) reported also the presence of a stained membrane lining the zooecial wall of a degenerated autozooid belonging to a Recent disporellid cyclostome from the Pacific.

According to Lowenstam (1972), some problematic organisms such as *Stenothecopsis*, generally attributed



Text-fig. 1 - Map showing location of fossiliferous outcrops in Sardinia (1-8) and Spain (9,10): 1) Caletta di Portixeddu; 2) Bunker; 3) Vasca Anguille; 4) Punta Pedrona; 5) Ponte su Amadori; 6) Piscina Suigas; 7) Piscina Morta; 8) Lago di Mulargia; 9) San Benito; 10) Viso del Marques.

to Hyolithelminths (Bengtson, 1979 considered them able to secrete phosphatic tubes) could, in fact, be Lophophorates (phoronids or zooecial linings of early Bryozoa). Lowenstam (1972, 1981), probably following Oakley's data (1934), discovered an amorphous dahllite precursor in Palaeozoic Bryozoa.

Utgaard (1973) described «membranous linings» in abandoned autozooecial chambers of Cystoporata from Upper Devonian of France and Permian of Australia. The «membranous linings» were both complete (the whole zooecial cavity was lined) and incomplete (the zooecial cavity was only partly lined). In the first case the membranous lining covered the basal diaphragms and the autozooecial walls and sometimes also the aboral side, surrounding completely the abandoned chambers. There were therefore diaphragms enclosed between oral and aboral linings. According to Utgaard (1973) the complete linings, often rich in pyrites and with membranous subspherical swellings, were primary and secreted by the zooidal epithelium, while the incomplete ones would more likely have been secondary.

Hynda (1973) reported phosphatic problematica (= phosphatic zooecial linings, Conti & Serpagli, 1984) from Ordovician of Volynia (U.S.S.R.), which were very similar to the ones previously recognized by Gorka (1969).

Müller (1974), too, while reviewing phosphatic organisms present in the Palaeozoic, took into account Gorka's (1969) phosphatic problematica.

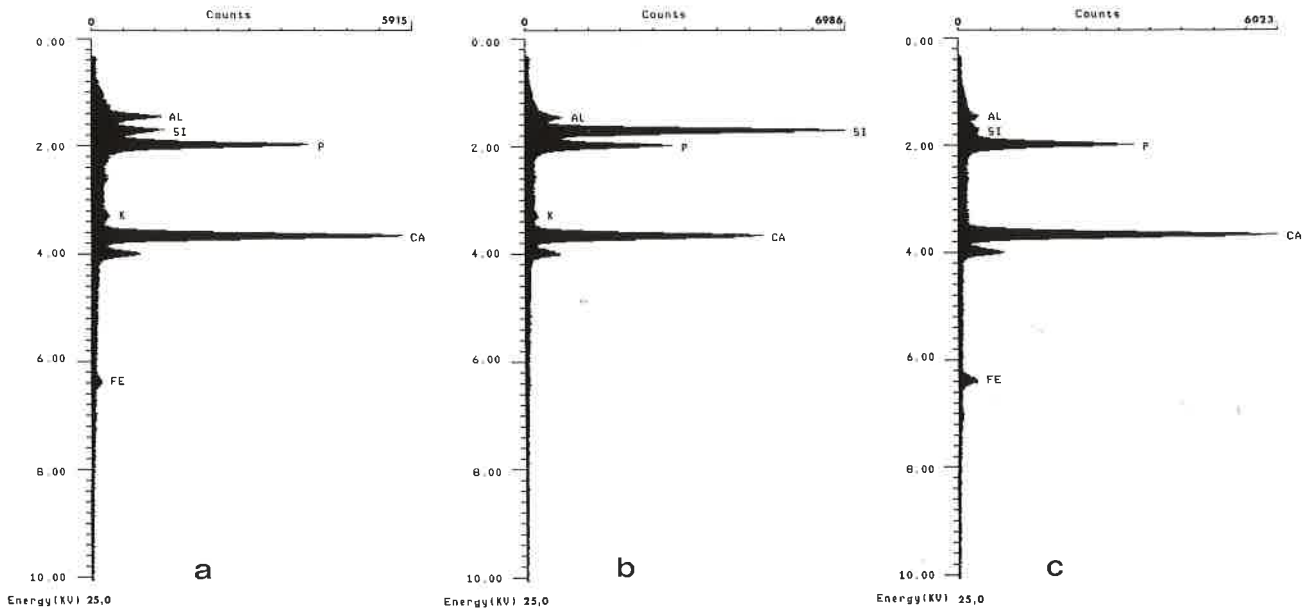
Wass (1975) described concentric spherules («cyst-like bodies») and phosphatic linings in Permian trepostomes from Tasmania and he noted that the lining appeared to be tuberculose on the side of the zooecial cavity but smooth on the side of the cortex. This author interpreted both structures as secondary and probably remnants of a foreign organism (*Tasmanites*).

While looking for conodonts, Bischoff (1978) found from the Ordovician of Öland (Sweden) and from Silurian and Lower Devonian of Australia phosphatic tubes, interpreted as phosphatized remains of a new species (*Septodaeum siluricum*) belonging to a new subclass (Septodaearia) of Anthozoa. Such small fossils were demonstrated to be zooecial tubes of *Hallopora elegantula* by Conti & Serpagli (1984, 1987).

Dzik (1981) ascribed the phosphatic problematica, described by Gorka (1969), to different genera of trepostome Bryozoa. The same interpretation was followed by Conti & Serpagli (1984), who recognized other phosphatic problematica as zooecial linings.

Spjeldnaes (1984) reported phosphatic zooecial linings of cryptostomes from Ordovician erratic boulders of Gotland, some of which were grouped into small colonies. He believed that the phosphatic bodies were formed while the bryozoans were still alive, probably by deposition of apatite on a protein (collagen) matrix.

Finally, Conti & Serpagli (1987) regarded the cap-like apparatus of *Hallopora elegantula* due to the phosphatization of the peritoneum of the cryptocyst.



Text-fig. 2 - X-ray analyses (EDAX) of some zooecial tubes: a) zooecial walls of (*Anaphragma meneghinii*) from Punta Pedrona, IPUM 21408; b) Zooecial infillings of the specimen of a; c) Zooecial infillings of the specimen of text-fig. 3a.

TECHNIQUES AND MINERALOGICAL DATA

Most of the studied material comes from different outcrops (text-fig. 1) of the Iglesiente-Sulcis regions (SW Sardinia) and from one new outcrop close to Mulargia lake (more or less at the Trexenta-Sarcidano-Quirra junction) in south-central Sardinia. In this last outcrop, recently discovered by Prof. S. Barca (Cagliari University), thin calcareous episodes inside the terrigenous sequence of Sardinian Ordovician are developed. Few specimens were also collected from the Upper Ordovician of Spain (San Benito and Viso del Marques) where one of us has under study a large conodont collection (text-fig. 1). For more details on sampling localities and geological setting, the reader is referred to the papers of Conti & Serpagli (1984) and Havliceck *et al.*, (1987).

Phosphatized zooecial tubes were either dissolved out of sediment with dilute acetic or formic acid or extracted mechanically using thin steel needles, cleaned ultrasonically in a weak detergent, dried in acetone and coated with gold for examination under the scanning electron microscope. Specimens prepared for the EDAX microanalysis were embedded in an epoxy resin and then lapped to get polished sections.

In order to state the chemical composition of the fossils under study two investigation methods were used:

1) direct mineralogical analysis of the zooecial walls and infillings (brown bodies, spherules and cuticular structures).

2) chemical microanalysis (EDAX linked to SEM) of the zooecial walls and infillings.

Mineralogical analyses using an optical microscope showed that the zooecial walls were always made of a microcrystalline aggregate of a perfectly cristallized mineral that had all the features of one member of the apatite family (collophanite?). At X-rays, on the other hand, the zooecial walls seemed to correspond to idroxyapatite and carbonate-apatite.

Inside of the zooecia, the infilling-matrix consisted of quartz and apatite, plus a mineral of 7 Å which could be kaolinite or chlorite. On the outer side of the apatitic walls, pyrite in perfect cubic crystals plus a clay mineral of 7 Å (kaolinite or chlorite) and a very small amount of a 10 Å mineral (illite) have been noted. The analysis also showed a content of apatite higher in the zooecial walls than in the matrix. (Such data have been provided by Proff. P. Gallitelli and N. Morandi, University of Bologna, on the basis of specimens supplied by one of us, many years ago - 1967).

Chemical analyses (qualitative and semiquantitative at X-rays) were carried out at the Instrument Centre of Modena University where several specimens were examined (X-ray maps of Ca and P elements were limited to some of these). The zooecial wall was almost completely composed of phosphorus and calcium in amount varying from 18% to 32% (P) and from 34% to 64% (Ca), besides small content of Fe and K (text-fig. 2a). The values of Al and Si were not very significant since these two elements were used to lap the material under study. The infillings had more or less the same phosphatic composition of the wall, except for occasional increasing of Si and Fe which reach 45% and 4% respectively (text-fig. 2b, c).

X-ray maps of some autozooecia showed that P and Ca have the same distribution in the walls as well as in the infillings (text-fig. 3).

SYSTEMATIC DESCRIPTION

The bryozoans described in the following pages are part of the palaeontological collection of Modena University. Figured specimens are stored in the Museum of the Institute of Palaentology under the catalog numbers IPUM 19882-21604.

The different types of phosphatic zooecia till now recovered were recognized to belong to five species of Trepostomata and to one species of Cryptostomata:

Anaphragma meneghinii (Vinassa de Regny)
Hemiphragma irrasum (Ulrich)
Hallopora elegantula (Hall)
Bithopora sardoa (Vinassa de Regny)
Genus et species indet.
Graptodictya sp.

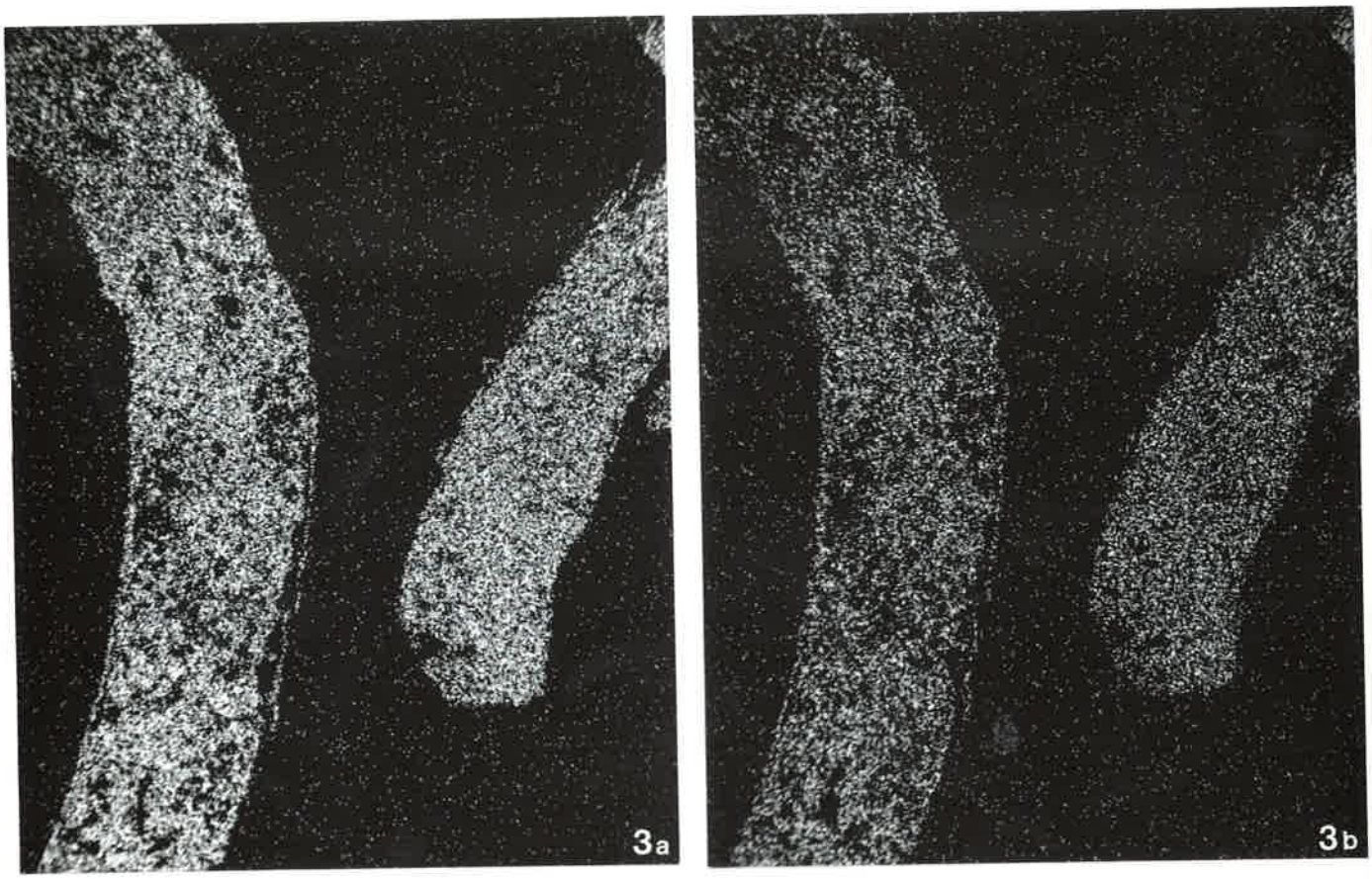
A description of the species based on SEM and thin section observations, when available, is given in the following pages. The Bryozoa (types included) of the Vinassa de Regny's collection (1942), normally stored in the Palaeontological Museum of Pavia University, have been temporarely borrowed from us in order to carry out a complete revision of the whole assemblage. The synonym-lists of the following pages have been therefore compiled studying the types of the Vinassa's collection.

Class STENOLAEMATA Borg, 1926
Order TREPOSTOMATA Ulrich, 1882
Family TREMATOPORIDAE Miller, 1889
Genus ANAPHRAGMA Ulrich & Bassler, 1904

Type-species *Anaphragma mirabile* Ulrich & Bassler, 1904

ANAPHRAGMA MENEGHINII (Vinassa de Regny)
Pls. 1-3; Pl. 11, figs. 1-2; Pl. 12, fig. 5; Text-fig. 5A.

1942 *Acantotrypa (Acantotrypina) Meneghini* - VINASSA DE REGNY, pp. 1038, figs. 6-8; text-fig. F.
1964 *Phosphaconus dentiformis* - EISENACK, p. 172, pl. 16, figs. 4-7.



Text-fig. 3 - X-ray maps of two zooecial tubes (*Hallopora elegantula*) from Caletta di Portixeddu, IPUM 21390, 21391, x 65: a) Showing distribution of Ca in zooecial walls and infillings; b) Showing distribution of P in zooecial walls and infillings.

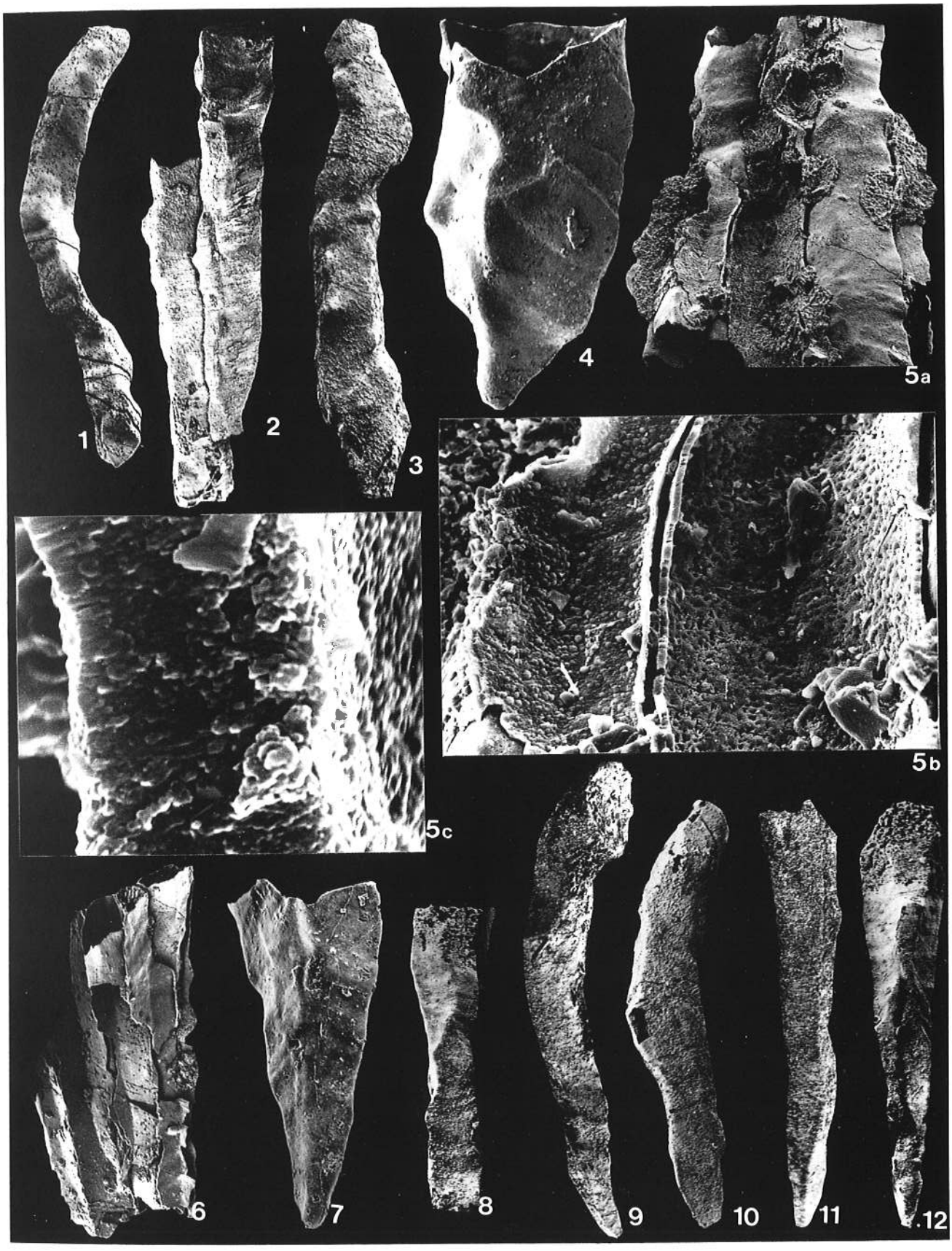
1964 *Phosphaconus lamellosus* - EISENACK, p. 173, pl. 17, fig. 2.
1969 *Oxytuba varians* - GORKA, p. 91, pl. 24, figs. 1-5, 7; text-fig. 44a, d-f.
1973 *Oxytuba varians* - HYNDA, p. 253, fig. 1 o-s.

SEM description — The type 1 (see introduction) consists of autozooecia isolated or grouped into small zoarial fragments, subpolygonal to polygonal in cross section, with wavy walls and polygonal to subcircular apertures (Pl. 1, figs. 1-3). Sometimes crenulations are well developed (Pl. 1, fig. 4). Specimens showing zooecial cavities emphasize the absence of diaphragms (Pl. 1, figs. 5a-6), as is also shown by the lack of their insertion on the outer surfaces of the phosphatic walls (Pl. 2, fig. 2). The phosphatic walls are smooth on the outside (Pl. 2, fig. 6a, 6b, 7), while the inside is rough and tuberculose (Pl. 2, fig. 8) and sometimes characterized by thin perforations (Pl. 1, fig. 5b).

Zoarial fragments consist of autozoecia containing pyrite crystals, phosphatic spherules and cuticular structures in their body cavities (Pl. 2, fig. 3; Pl. 11, fig. 2).

EXPLANATION OF PLATE 1

Figs. 1-12 - *Anaphragma meneghinii* (Vinassa de Regny). 1) Autozooecial tube with wavy walls and a slight reduction in zooecial diameter, IPUM 21530, Lago di Mulargia, x 30; 2) Autozooecial tubes showing a prismatic shape, endozone, IPUM 21604, Bunker, x 30; 3) Autozooecial tube with wavy walls showing the beginning of the exozonal curvature, IPUM 21595, Caletta di Portixeddu, x 30; 4) Detail of an autozooecial apex showing wall crenulations: compare with zooecial apex of pl. 3, fig. 2, IPUM 21470, Caletta di Portixeddu, x 100; 5a) Zoarial fragment showing the morphology of the phosphatic skeleton, IPUM 21467, Caletta di Portixeddu, x 80; 5b) Detail of two zooecial cavities of the same zoarial fragment showing small perforations and infillings of communication pores (in the middle): the latter are located inside the empty space between phosphatic walls, occupied, before etching by the calcareous wall, x 300; 5c) Detail of the phosphatic wall of the right zooecium, x 10000; 6) Zoarial fragment, IPUM 21511, Caletta di Portixeddu, x 60; 7) Detail of an autozooecial apex, IPUM 21552, San Benito, x 100; 8-12) Autozooecial tubes, one of which is completely preserved, IPUM 21503, 21442, Bunker, 21540 Lago di Mulargia, 21443, 21504, Bunker, x 30.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The Type 4 consists of pyramidal autozoecia isolated or grouped into small zoarial fragments (Pl. 2, fig. 4a), with the oral part rapidly reaching the maximum zoecial diameter (0.3-0.4) (Pl. 1, figs. 4, 7, 8, 10-12), which is very similar to this of the autozooecia of the Type 1. The phosphatic walls show the same features noted on the Type 1 (Pl. 2, figs. 4a-4b).

The presence of more complete zoarial fragments shows that pyramidal autozooecia (Type 4) continue in their adult part in irregularly prismatic autozooecia (Type 1) at various levels of the colony emphasizing the A1 budding pattern (apparently disordered interzooecial budding) of Mc-Kinney (1977) (Pl. 1, fig. 9; Pl. 2, figs. 7-9; text-fig. 5A).

The «complete» autozooecia (apical part = Type 4 + mature part = Type 1) have an average length of 2-3 mm.

Mesopores are difficult to distinguish from autozooecia because of the absence of calcareous diaphragms (Pl. 2, fig. 5), while rare phosphatic diaphragms (Pl. 2, fig. 8) are sometimes present. In all available zoarial fragments the acanthopores are never visible, because connected to the calcareous wall, dissolved out during the preparation technique.

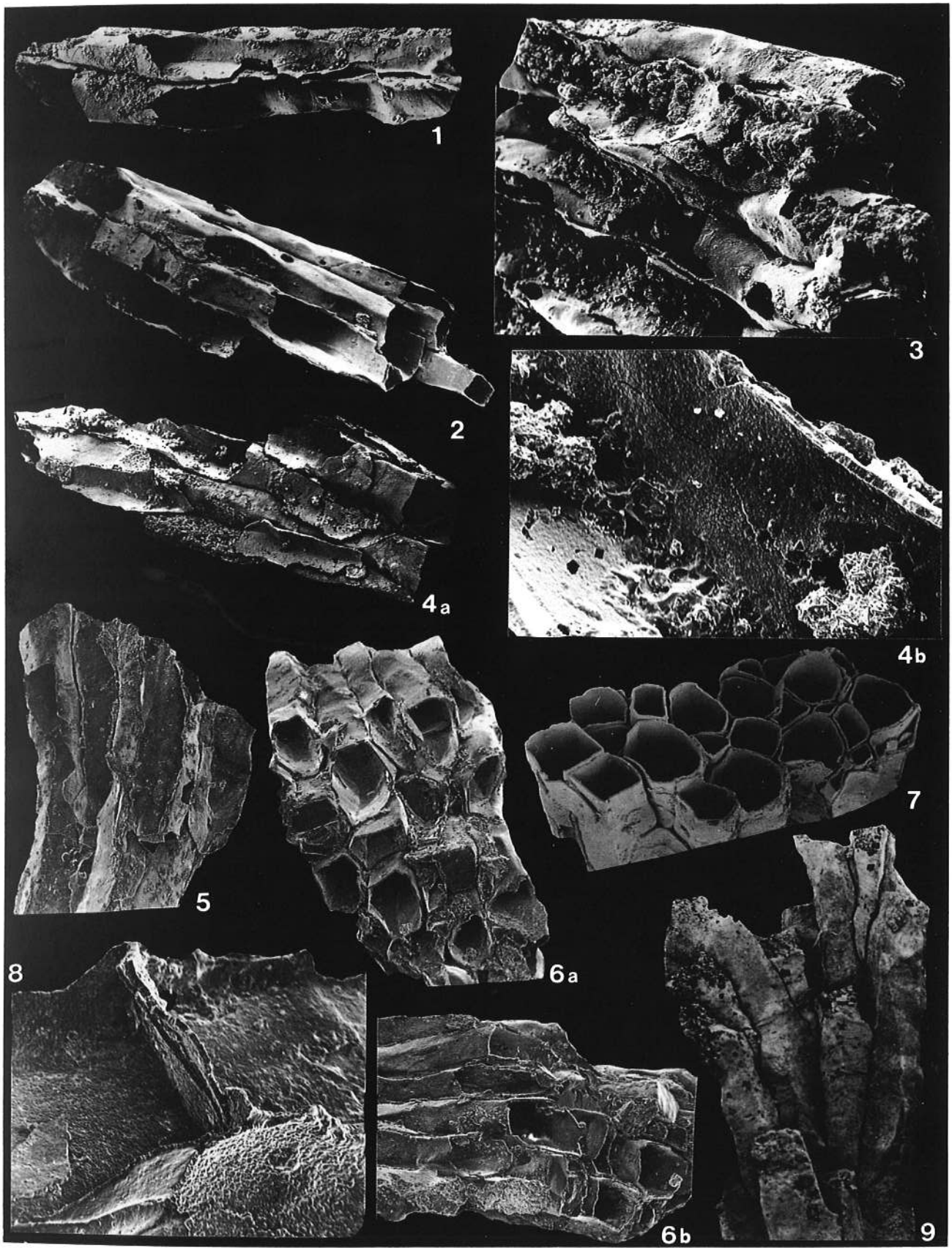
Thin section description — Zoaria ramose with strong subcylindrical branches (average diameter 30-40 mm) dividing rather frequently. Maculae not a conspicuous feature, distinguished only by the size of their zooecia and by their depressed area. Zooecial apertures angular to subangular, with rather thick walls, 8-10 zooecia in 3 mm. In longitudinal section the striking feature is the almost complete absence of diaphragms in both autozooecia and mesopores (Pl. 3, fig. 1a). Mesopores (0.15 mm diameter) with planar diaphragms (3 to 4), located at the exozone (Pl. 3, fig. 1a) are rare. Autozooecial apical parts show a rapid expansion to normal size (0.3 mm diameter) (Pl. 3, fig. 1b). Acanthopores small and only occasionally well shown at the surface; in transverse section acanthopores are 2-3 per autozooecium and usually situated at the junction angles (Pl. 3, fig. 2a-3a). Dark phosphatic walls of autozooecia and mesopores are very common both in axial and in peripheral regions, but have not been observed in acanthopores (filled with laminar calcite) (Pl. 3, figs. 1c, 2b, 3b; Pl. 12, fig. 5). Brown bodies and cuticular structures are often located in autozooecia (Pl. 3, fig. 1b). Laminae of zooecial walls form generally a U-shaped pattern in longitudinal section, but sometimes a V-shaped is also recognizable. For this reason the genus *Anaphragma* has, time to time, been considered as belonging to the suborder Amalgamata or to the suborder Integrata. Boardman (1960a) and Owen (1962) showed the uselessness of such a systematic subdivision.

In the axial region the walls are thin (0.04 mm) and wavy; crenulations are less frequent in the exozone, where the walls become greatly thickened (0.12 mm) and considerable laminated tissue is developed upon the inner sides; dark zooecial boundaries are also visible (Pl. 3, fig. 1a). Longitudinal sections show an astogenetic pattern (apparently disordered interzooecial budding) as described by Mc-Kinney (1977) (Pl. 3, figs. 1a-1b). In transverse section autozooecia have a polygonal to subpolygonal outline (Pl. 3, figs. 2a-3a).

Discussion — The Sardinian species is distinguished from the type-species *A. mirabile* essentially by the very small number of mesopores, by their dimensions (the Sardinian ones are larger), by the occasional presence of diaphragms and, rarely, by the presence of phosphatic (originally membranous) diaphragms in the autozooecia. Interesting to note that under normal conditions of preservation (Bryozoa without phosphatic skeleton) the species *Anaphragma meneghinii* would appear without any indications of diaphragms and would be considered to lack these structures for taxonomic purposes. *Anaphragma shucknellensis* Owen (1962) is distinguished form *A. meneghinii* by the presence of calcareous diaphragms in the autozooecia and by the absence of acanthopores. *A. portranense* Ross (1966) differs because

EXPLANATION OF PLATE 2

Figs. 1-9 - *Anaphragma meneghinii* (Vinassa de Regny). 1) Autozooecial tubes showing phosphatic bodies in their walls, IPUM 21469, Caletta di Portixeddu, × 60; 2) Zoarial fragment, IPUM 21575, Caletta di Portixeddu, × 60; 3) Detail of zooecial infillings displaying brown phosphatic bodies, IPUM 21579, Caletta di Portixeddu, × 90; 4a) Zoarial fragment, IPUM 21509, Piscina Morta, × 60; 4b) Detail of the same specimen showing phosphatic walls and bodies inside one autozooecial tube, × 400; 5) Zoarial fragment displaying the absence of diaphragms in autozooecial tubes, IPUM 20174, Caletta di Portixeddu, × 60; 6a) Zoarial fragment showing the typical astogenetic pattern of the genus *Anaphragma* and a terminal phosphatic diaphragm, IPUM 20172, Lago di Mulargia, × 60; 6b) Another view of the same specimen, × 60; 7) Zoarial fragment displaying the A1 (Mc Kinney, 1977) interzooecial budding: note the space among phospatic walls previously occupied by the calcareous wall; tubes are joined by the phosphatic linings of the communication pores, IPUM 21478, Caletta di Portixeddu, × 60; 8) Detail of a compound phosphatic diaphgragm: note no calcareous wall is present in between; on the right a double phosphatic wall is present, probably corresponding to the position of the peritoneum and inner epidermis, IPUM 20166, Caletta di Portixeddu, × 325; 9) Zoarial fragment displaying the configuration of zooecial tubes, IPUM 21474, Bunker, × 20.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of its considerable abundance of mesopores and by bearing acanthopores equally scattered all over the colony. The specimens with a straight wall described by Eisenack (1964) under *Phosphaconus dentiformis* e *P. lamellosus* and those illustrated by Gorka (1969) and Hynda (1973) under *Oxytuba varians* represent the apical parts of autozooecia that can be attributed both to *Anaphragma meneghinii* and to *Hemiphragma irrasum*. No valid elements for distinction have been till now recognized. The specimens with wavy walls have been considered to belong to *A. meneghinii* (being apical parts of autozooecia of the axial region).

Genus HEMIPHRAGMA Ulrich, 1893

Type-species *Hemiphragma irrasum* Ulrich, 1893

HEMIPHRAGMA IRRASUM (Ulrich, 1893)
Pl. 4; Text-fig. 5B

1886 *Batostoma irrasa* - ULRICH, pp. 94-95.
1893 *Hemiphragma irrasum* - ULRICH, pp. 299-300, pl. 24, figs. 5-19.
1897 *Hemiphragma irrasum* - SIMPSON, p. 592, figs. 190-193.
1911 *Hemiphragma irrasum* - BASSLER, pp. 284-286, figs. 172-173.
1913 *Hemiphragma irrasum* - ZITTEL & EASTMAN, p. 443.
1942 *Hemiphragma irrasum* - LOEBLICH, p. 443, pl. 63, fig. 19.
1953 *Hemiphragma irrasum* - BASSLER, p. G114, fig. 77, 4a-d.
1964 *Phosphaconus dentiformis* - EISENACK, p. 172, pl. 16, figs. 4-7.
1964 *Phosphaconus lamellosus* - EISENACK, p. 173, pl. 17, fig. 2.
1968 *Hemiphragma irrasum* - BORK & PERRY, pp. 342-343, pl. 4, figs. 1-3, 5.
1969 *Labyrinthotuba kozlowskii* - GORKA, pp. 82-86, pl. 21, figs. 1-8; pl. 22, figs. 1-4, 6-9; pl. 29, figs. 1-5; text-figs. 34-37.
1969 *Oxytuba varians* - GORKA, p. 91, pl. 24, fig. 1; text-fig. 44D-E.
1971 *Hemiphragma irrasum* - MC-KINNEY, pp. 276-279, pl. 61, figs. 7-8; pl. 62, figs. 1-6.
1973 *Labyrinthotuba kozlowskii* - HYNDA, pp. 252-253, fig. 1i-n.

SEM description — The Type 1 consists of prismatic autozoecia with straight walls (Pl. 4, fig. 3), whereas Type 4 of pyramidal autozoecia having the same features as described for *Anaphragma meneghinii* except for the absence of crenulations (Pl. 4, fig. 1).

The Type 6 is generally formed by isolated subcylindrical to cylindrical autozooecia with flexuous to irregularly contorted walls and closely spaced hemiphragms (about 4 in 0,5 mm) (Pl. 4, figs. 8-10, 11-13, 15-16). Hemiphragms are shelf-like transverse extensions of the phosphatic walls that arise alternately from proximal and distal sides of the autozooecium and extend part of the way across the zooecial chamber (Pl. 4, figs. 8-10, 15-16). The free edge of the hemiphragms located in the basal part of an autozooecium is generally straight or only slightly curved and greatly expanded (they occlude the zooecial cavity almost completely) (Pl. 4, figs. 12-13), while, the free edge of the hemiphragms located in the oral part of an autozooecium is irregularly sinuous and curving both in oral and aboral direction in order to occupy about half of the zooecial cavity (Pl. 4, figs. 8-10). Cuticular phosphatic structures and brown bodies are often observed between two or more successive hemiphragms (Pl. 4, fig. 7a).

The phosphatic walls are generally smooth on the outside and tuberculose on the inside (Pl. 4, fig. 7b).

The presence of more complete zoarial fragments shows that pyramidal autozooecia (Type 4), after continuing in their adult part as Type 1, end in the oral portion, first in autozooecia with straight hemiphragms and then with sinuous hemiphragms (Type 6), usually located in the exozone of the colony (Pl. 4, figs. 2, 4-7, 11). Autozooecial length is about 1.3 mm and diameter about 0.35 mm in the endozone. The study of a complete colony (Pl. 4, fig. 14) showing the A1 budding pattern described by Mc-Kinney (1977) and the exozonal position of the hemiphragms has led us to the designation of the above-mentioned fragments to *Hemiphragma irrasum*.

The problematica described by Eisenack (1964), Gorka (1969) and Hynda (1973) belong to different zoarial portions of *H. irrasum*.

Family HALLOPORIDAE Bassler, 1911
Genus HALLOPORA Bassler, 1911

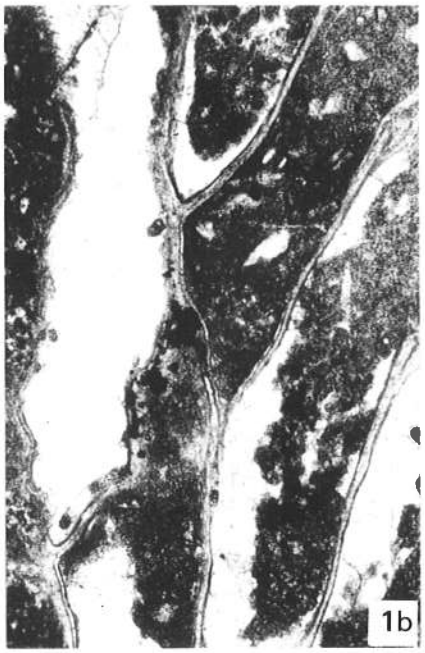
Type-species *Callopora elegantula* Hall, 1852

HALLOPORA ELEGANTULA (Hall, 1852)
Pls. 5-8; Pl. 11, figs. 3-7; Pl. 12, figs. 7-8; Text-figs. 4-5C.

EXPLANATION OF PLATE 3

Figs. 1-3 - *Anaphragma meneghinii* (Vinassa de Regny). 1a) Zoarial view showing the endozone and exozone, IPUM 19994, Caletta di Portixeddu, × 15; 1b) Detail of the same specimen showing phosphatic and calcareous walls as well as the crenulations of the walls, × 65; 1c) Detail of the same specimen displaying large acanthopores, × 65; 2a) Transverse section showing polygonal zooecial tubes, IPUM 20041, Bunker, × 65; 2b) Detail of the same specimen showing the phosphatic skeleton inside zooecial tubes but not inside acanthopores, × 160; 3a) Transverse section: note the abundance of phosphatic bodies inside autozooecial tubes, IPUM 20009, Caletta di Portixeddu, × 75; 3b) Detail of the same specimen showing phosphatic walls and acanthopores, × 160.

1a



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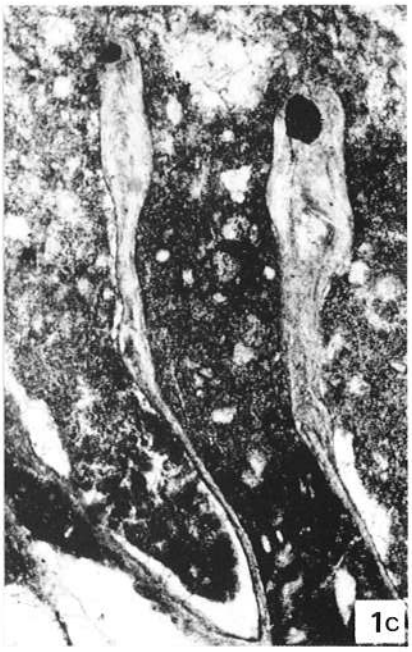

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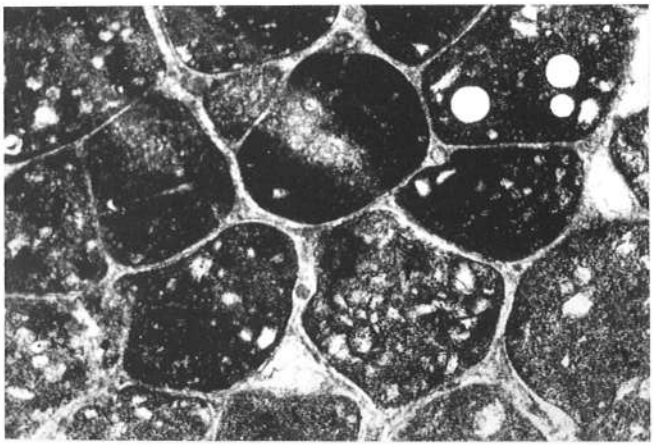

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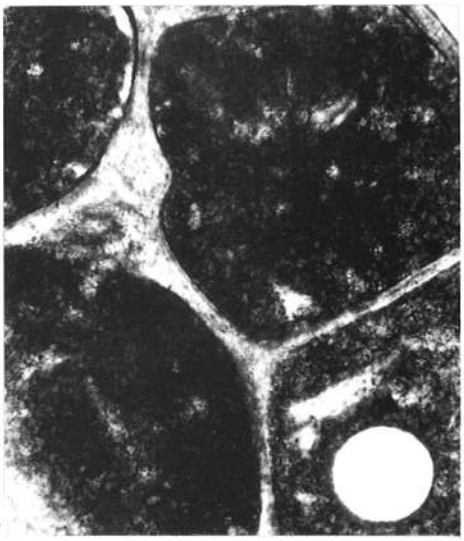

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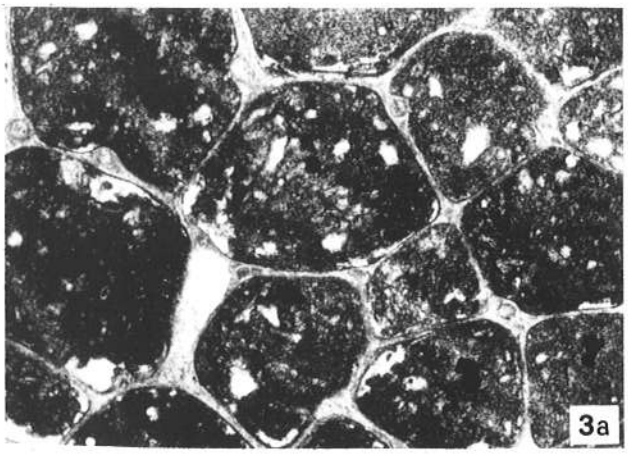

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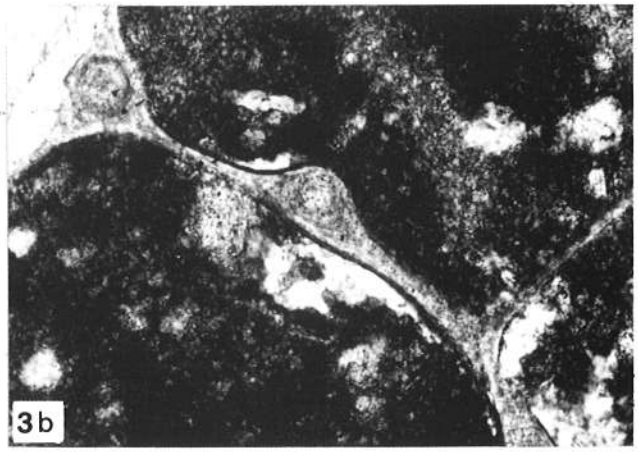


3b

1851 *Calopora elegantula* - SILLIMAN *et al.*, p. 400.
1851 *Chaetetes fletcheri* - EDWARDS & HAIME, p. 271.
1852 *Callopora elegantula* - HALL, pp. 144-145, pl. 40, fig. 1a-m.
1910 *Monticulipora (Callopora) Taramellii* - VINASSA DE REGNY, pp. 11-12, pl. 2, figs. 1-7.
1914 *Hallopora Taramellii* - VINASSA DE REGNY, p. 206, pl. 1, fig. 4.
1942 *Hallopora Taramellii* - VINASSA DE REGNY, p. 1038.
1973 *Hallopora elegantula* - CORNELIUSSEN & PERRY, pp. 191-203, pl. 5, figs. 1-16; pl. 6, figs. 1-15; pl. 7, figs. 1-15; text-figs. 17-25; cum syn.
1978 *Hallopora elegantula* - ASTROVA, p. 69, pl. 9, fig. 1a-c.
1978 *Septodaeaum siluricum* - BISCHOFF, pp. 229-257, pl. 4, figs. 50a-51; pl. 5, figs. 52-54; pl. 6, figs. 55a-56d; pl. 7, figs. 57a-58b; pl. 8, fig. 60a-d.
1984 *Hallopora elegantula* - CONTI & SERPAGLI, pp. 8-16, pls. 1-6; text-figs. 2-7.
1987 *Hallopora elegantula* - CONTI & SERPAGLI, pp. 1-20, figs. 1-9.

SEM description — The Type 2 consists of cylindrical autozooecia isolated or grouped into small zoarial fragments with generally straight walls (Pl. 5, figs. 1, 6, 8, 9).

Specimens showing zooecial cavities emphasize the presence of diaphragms (Pl. 5, fig. 12). The phosphatic walls are smooth on the outside, while the inside is rough and tuberculose (Pl. 11, figs. 7a-7b), sometimes with extremely small pores (Pl. 5, fig. 9b).

Zoarial fragments show the presence of numerous polygonal mesopores with closely spaced diaphragms; mesopore shape is adapted to the spaces left free by the autozooecia (Pl. 5, fig. 9a; Pl. 6, fig. 4a).

The Type 3 consists of conical autozooecia isolated (Pl. 5, figs. 2, 4, 7) or grouped into small zoarial fragments, usually associated to the Type 5 (Conti & Serpagli, 1984, Pl. 2, fig. 3). Autozooecial walls may be straight or slightly curved with the features seen for Type 2. Oral portions of the autozooecia are slightly expanded. Closely spaced diaphragms (mesozooecial pattern) occur in the elongate initial part of an autozooecium and become progressively more widely spaced when the zooecium reaches an intermediate or nearly maximum diameter (autozooecial pattern).

Zoarial fragments show the presence of mesopores completely identical to those described for Type 2 (Pl. 5, fig. 5).

The Type 5 consists of cylindrical autozooecia isolated or grouped into small zoarial fragments having the oral end terminating with the cap-like apparatus, described by Conti & Serpagli (1987) (Pl. 5, fig. 10a). The phosphatic walls are the same as Type 2 and 3 except that, on the outside, near the cap-like apparatus, they show small conical cavities interpreted as casts of autozooecial spines (Conti & Serpagli, 1984; 1987) (Pl. 5, fig. 10b). The autozooecia are generally curved and are extremely expanded in the oral portion (Pl. 5, fig. 3).

Zoarial fragments show the presence of both diaphragms and mesopores (Pl. 5, fig. 11).

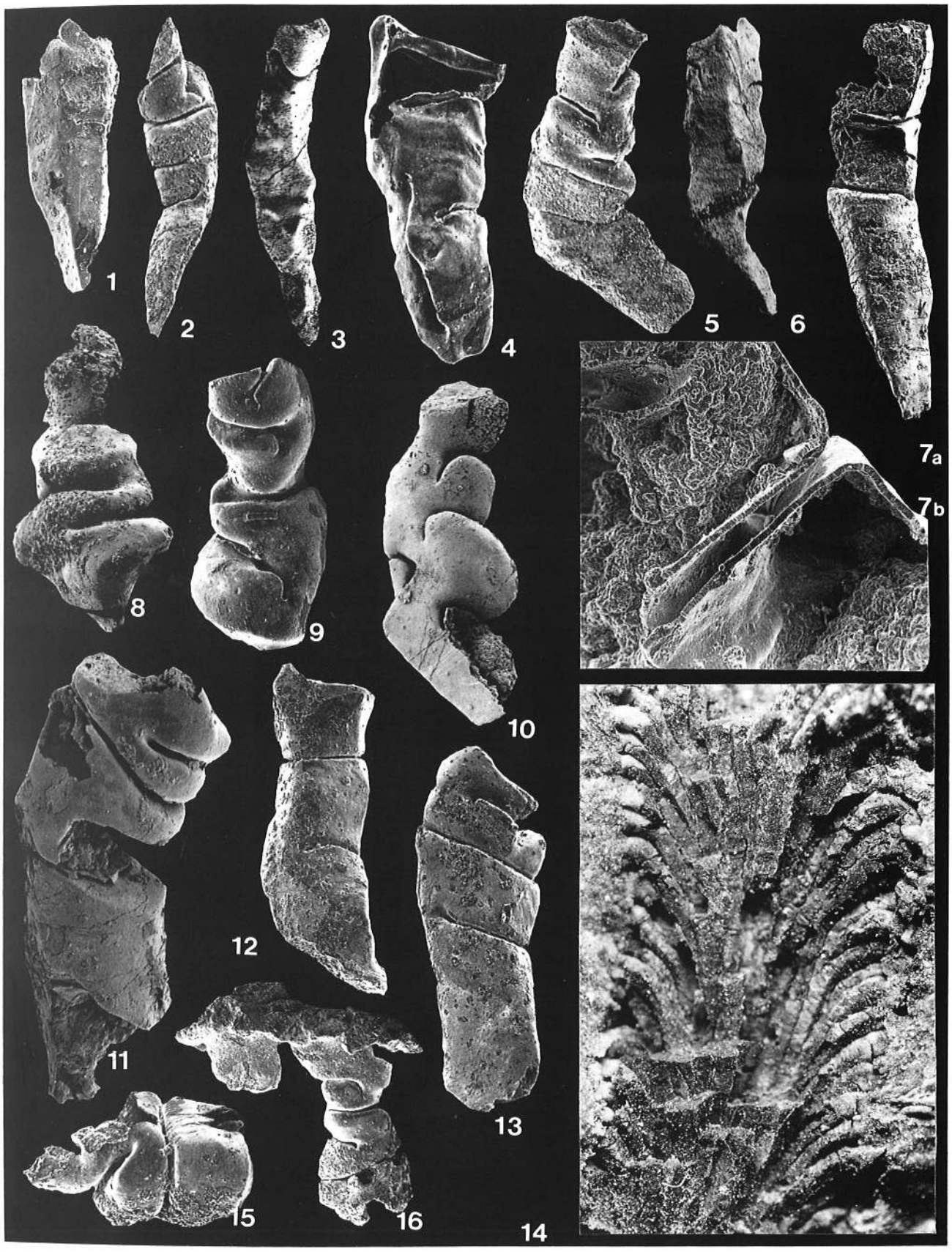
The Type 7 consists of cup-like zooecia with straight walls and circular section, having the oral end open or closed by a concave diaphragm; (see Conti & Serpagli, 1987, fig. 2 for a diagrammatic reconstruction).

The presence of more complete zoarial fragments shows that conical autozooecia (Type 3 = apical part) continue in their adult section either in irregularly cylindrical autozooecia (Type 2) and/or in cylindrical autozooecia closed by a terminal diaphragm (cap-like apparatus) (Type 5) bearing buds on the top (Type 7) (Conti & Serpagli, 1987, fig. 5e-f) (text-fig. 5C).

Zoaria erect, solid and ramose, dichotomous branching, with oval, elliptical or circular branches – maximum diameter ranging from 10 to 23 mm. Branches per specimen ranging from 2 to 16. Zoarial surface smooth, absence of monticules and maculae. Zooecial openings mostly circular ending with an ornamented cap-like apparatus consisting of two concentric rings linked by radial ridges (Pl. 5, fig. 10a). Above the apparatus, new zooecia (mesopores and autozooecia) can develop

EXPLANATION OF PLATE 4

Figs. 1-16 - *Hemiphragma irrasum* (Ulrich). 1) Autozooecial tube showing the apical end and one hemiphragm, IPUM 20167, Caletta di Portixeddu, × 75; 2) Complete autozooecial tube (apical end + planar hemiphragms), IPUM 20132, Caletta di Portixeddu, × 50; 3) Apical portion of one autozooecial tube with one hemiphragm, IPUM 21538, Lago di Mulargia, × 30; 4) Autozooecial tube displaying the curvature of the phosphatic walls in one hemiphragm, IPUM 20126, Caletta di Portixeddu, × 100; 5) Autozooecial tube with sinuous hemiphragms, IPUM 20136, Caletta di Portixeddu, × 45; 6) Complete autozooecial tube with the apical end, IPUM 21546, Lago di Mulargia, × 30; 7a) Autozooecial tube showing phosphatic infillings, IPUM 20135, Caletta di Portixeddu, × 65; 7b) Detail of the same specimen showing the phosphatic walls and cuticular structures; the empty space located inside the phosphatic compound hemiphragms was formerly occupied by calcareous matter, × 335; 8-10) Autozooecial tubes displaying hemiphragms, some of which occupying the whole zooecial lumen, IPUM 21458, 20128, 21453, Piscina Suigas, × 75; 11) Detail of one autozooecial tube, IPUM 21452, Caletta di Portixeddu × 100; 12, 13) Autozooecial tubes with planar hemiphragms, IPUM 20131, 20130, Piscina Morta, × 75; 14) Colony showing the astogenetic pattern: note the hemiphragms located in the exozone and the absence of mesopores, IPUM 19910, Caletta di Portixeddu, × 15; 15) Portion of one autozooecial tube showing sinuous hemiphragms, IPUM 20125, Caletta di Portixeddu, × 75; 16) Autozooecial tubes showing sinuous hemiphragms located at their terminal end (exozone), IPUM 20134, Caletta di Portixeddu, × 30.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Text-fig. 4 -Hypothetical and diagrammatic reconstruction of different phosphatization modes from two generalized zooecia of *Hallopora elegantula*.

by budding and are always located in the most peripheral part of the colony (Conti & Serpagli, 1984, Pl. 2, figs. 3, 7-9). Medium length of zooecial tubes from 2 to 5 mm; occasionally a length of about 10-15 mm can be reached in the axial part of the colony; average diameter of 0.35 mm, terminal expanded end 0.45 mm. Astogenetic pattern A2 of Mc-Kinney (1977) (apparently disordered budding of intrazooecial mesozooecia) (Pl. 6, figs. 1-3). Mesopores polygonal, elliptical, round and generally isolating adjacent zooecia. Mesopore maximum width, approximately, less than 0.2 mm (average from 0.05 to 0.1 mm). Mesopore openings commonly restricted or covered on zoarial surface by concave diaphragms. Acanthopores absent.

The thin sections figured on Pls. 7, 8, 12 (figs. 7, 8), will be mostly used for the description of the phosphatic skeleton and, therefore, you can refer to Conti & Serpagli (1984) for the complete thin section description of this species.

Family BATOSTOMELLIDAE Miller, 1889
Genus BYTHOPORA Miller & Dyer, 1878

Type-species *Bythopora dendrina* James, 1878

BYTHOPORA SARDOA (Vinassa de Regny)
Pl. 9; Pl. 12, figs. 4, 6; Text-fig. 5D

1942 *Monotrypa sardoa* - VINASSA de REGNY, pp. 1035-1036, pl. 2, fig. 10; text-fig. d.

SEM description — The Type 6 consists of subcylindrical autozooecia usually grouped into small zoarial fragments (Pl. 9, figs. 1-6, 10), characterized by variable cross sectional diameter (0.1-0.2 mm) and wavy walls. The crenulations can be so marked that autozooecia can show a flask-like appearance (Pl. 9, figs. 5, 8a, 11a).

Zoarial fragments show a B1 budding pattern as described by Mc-Kinney (1977) (large axial zooecia progressively partitioned distally with autozooecia at more restricted cross sectional diameter in endozonal periphery). Consequently, the straighter and longer autozooecia occur in the axial region while those with a more wavy walls and a more strongly restricted cross section belong to the peripheral region (Pl. 9, figs. 2, 7a, 8a).

Mesopores and acanthopores completely absent.

Phosphatic walls are generally smooth on the outside (Pl. 9, figs. 9, 11a), but rough on the inside (Pl. 9, figs. 7b-11b) and sometimes they are perforated (communication pores) in the apical part of the autozooecia (Pl. 9, fig. 8b). Phosphatic linings of communication pores are seldom visible (Pl. 9, fig. 7b).

Thin section description — Very slender cylindrical branches bearing zooecial openings in a very thin peripheral region located at 45°-60° to the axial region. The width of a branch varies from 1 to 2 mm. Autozooecia usually without diaphragms, sometimes rare diaphragms are present in the axial region. Slightly

wavy zooecial walls can occur; sometimes the crenulations can be so marked that the autozooecial longitudinal section can show a flask-like appearance (Pl. 12, figs. 4, 6). The considerable constriction in size, noted along the longitudinal axis of some autozooecia, could be functionally analogous to the diaphragms: this would explain the absence of diaphragms in specimens with strongly wavy walls. Very shallow mesozooecia may occur in the outermost peripheral part of the colony (pl. 12, figs. 4, 6). Astogenetic pattern B1 as described by Mc-Kinney (1977) is recognizable in most of the specimens. Acanthopores-like structure are not clearly visible.

Discussion — *B. sardoa* is quite similar to the type-species in shape and zoarial size but it differs from *B. dendrina* and other species of the genus mainly in the crenulations of the walls, which originate a variable cross section of the autozooecia, and by the presence of mesopores, usually located into the channeled interspaces.

Family MONTICULIPORIDAE Nicholson, 1881
Genus et Species indet.
Pl. 10; Text-fig. 5E

Zooecial phosphatic linings of autozooecial chambers of monticuliporids.

SEM description — The Type 9 consists of roughly cylindrical or funnel-shaped autozooecia (0.1-0.2 mm diameter), usually empty and transparent, with flexuous walls (Pl. 10, figs. 4, 5, 7, 9-12) and probably represent phosphatic linings of flask-shaped chambers closed by terminal, basal, cystoidal and funnel-shaped phosphatic diaphragms (Pl. 10, figs. 1, 3, 8, 10). The phosphatic autozooecia occasionally have a flattened side (Pl. 10, fig. 9) and their walls are usually smooth both on the outside and on the inside, where a dark-coloured infilling (cuticular phosphatic structures) can occurs; in some cases the phosphatic walls are rough and tuberculose (Pl. 10, figs. 11b-11c).

Some autozooecia have a funnel-shaped oral end (Pl. 10, figs. 2, 3, 4) and other ones can end with spinelike appendages (Pl. 10, figs. 13a,-13b). Phosphatic terminal vestibular membranes and the final portion of the membranous sac can be present inside the autozooecial cavity and confluent with the phosphatic skeleton (Pl. 10, fig. 6).

Some autozooecia are joined by a spongy structure (Pl. 10, figs. 1b, 5).

Order CRYPTOSTOMATA Vine, 1884
Family ESCHAROPORIDAE Karklins, 1983
Genus GRAPTODICTYA Ulrich, 1882
Type-species *Ptilodictya perelegans* Ulrich, 1878

GRAPTODICTYA sp.
Pl. 11, figs. 4-6; Pl. 12, figs. 1-3

SEM description — The Type 10 consists of curved, conical autozooecia expanding from a flattened side (mesotheca) along a linear stem of the colony. The circular zooecial openings are closed by an hemiseptum; the budding pattern is typical of bifoliate cryptostomes. The phosphatic walls are usually straight and smooth (Pl. 11, figs. 4-6).

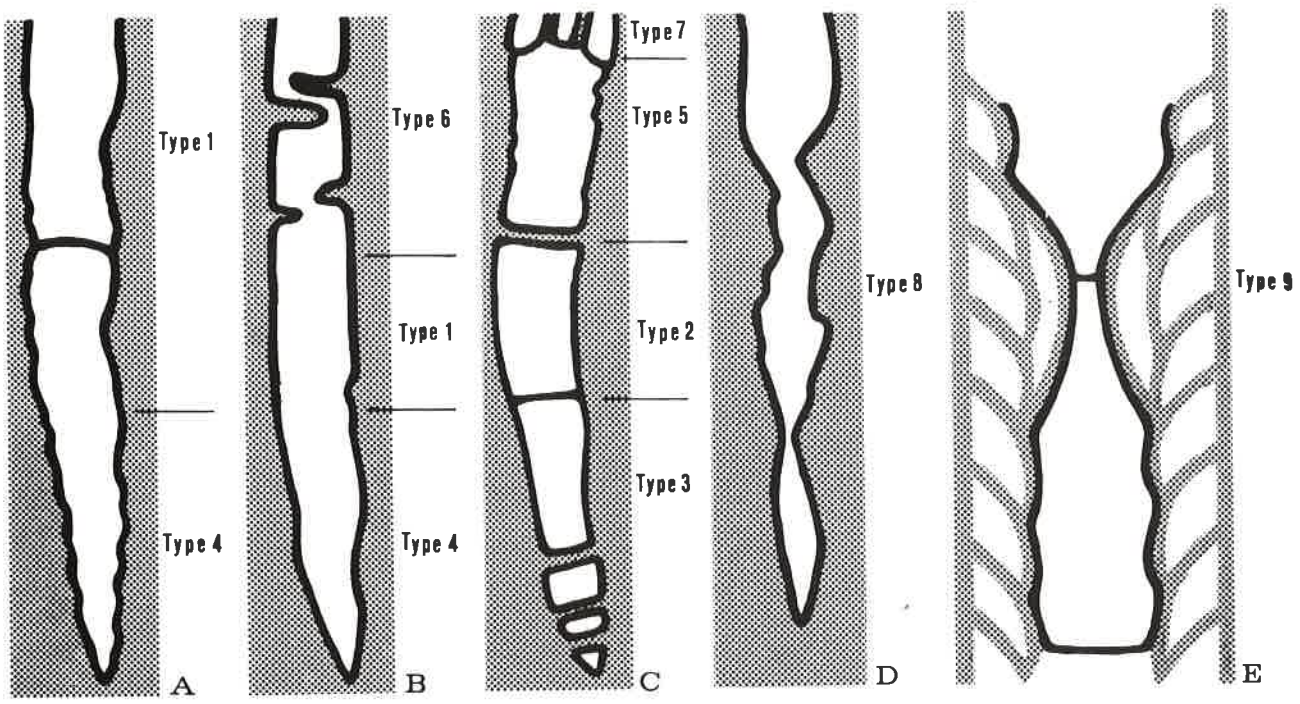
Thin section description — Zoaria branched, anastomosing irregularly; mesotheca with a sinuous longitudinal pattern, commonly zigzag in transverse section in some specimens. In endozones, autozooecia range from straight to sinuous, generally alternated with mesotheca and having a subelliptical to subcircular cross section (Pl. 12, figs. 1-3). In exozones, autozooecia occur at angles between 80° and 90° to zoarial surface. Superior hemisepta usually common, variable in shape and thickness; basal diaphragms generally absent. Extrazooecial skeleton deposits very common usually located on zoarial margins (Pl. 12, fig. 1).

DESCRIPTION OF THE PHOSPHATIC SKELETON

SEM DESCRIPTION

The phosphatic skeleton is generally smooth on the outside (Pl. 1, fig. 5a; Pl. 6, fig. 4a; Pl. 9, fig. 9; Pl. 10, fig. 1b; Pl. 11, fig. 5), while is often rough and tuberculose on the inside (Pl. 2, fig. 4b; Pl. 9, fig. 7b; Pl. 10, fig. 11b; Pl. 11, fig. 7b). It may be perforated by minute vertical or lateral communication pores that connect two adjacent zooecial cavities indicating a high degree of colonial dominance achieved by Palaeozoic trepostomes (Pl. 1, fig. 5b; Pl. 6, fig. 4b). The pore structure is characterized by a star-shaped plug and communications exist at the side of this plug (Pl. 5, fig. 9b). There seems to be no order in the distribution of the communication pores which must not be confused with the intrazooecial spines of *H. elegantula* (Pl. 5, fig. 10b). The phosphatic linings of lateral communication pores look like to irregularly shaped *appendages* crossing the calcareous wall, which appears as an empty space since it was dissolved by acid etching (Pl. 2, figs. 6a, 7; Pl. 6, figs. 1a, 1b, 1c). These phosphatic *appendages* explain the preservation of phosphatic zooecial tubes not only as isolated individuals but also grouped together in zoarial fragments after acid etching.

A careful examination of the inside of the phosphatic walls shows phosphatic spherules similar to those



Text-fig. 5 - Diagrammatic reconstruction of various autozooecia showing informal morphological types: A) *Anaphragma meneghinii*; B) *Hemiphragma irrasum*; C) *Hallopora elegantula*; D) *Bithopora sardoa*; E) Monticuliporid (probably *Peronopora* or *Prasopora*) (from Boardman, 1971, fig. 5, modified). Figure not to scale.

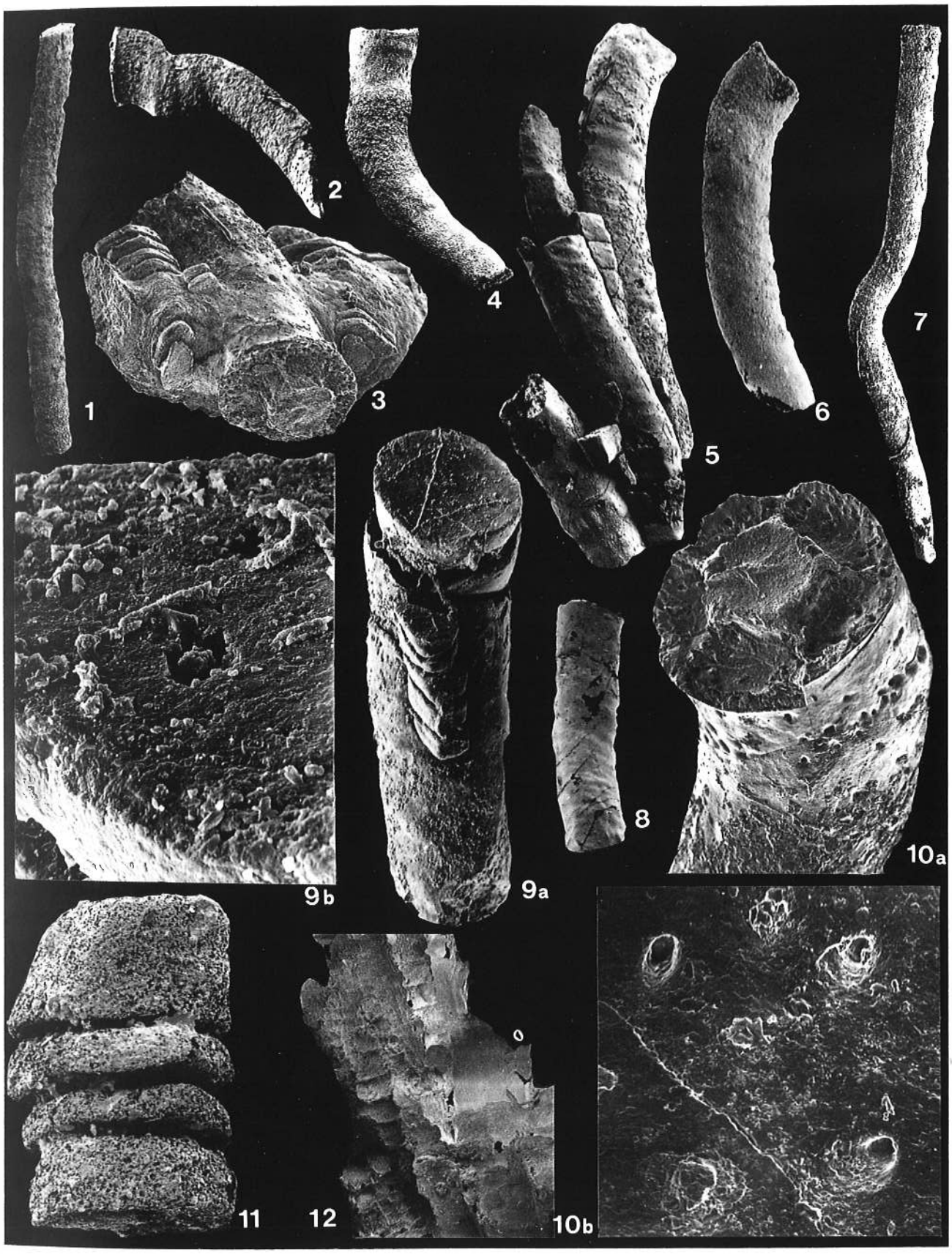
(pearls-like bodies) reviewed by us in the previous pages (Pl. 2, fig. 4b; Pl. 9, fig. 11b).

Autozooecial cavities display a lumpy infilling having the same mineralogical composition of the walls, as proved by chemical analyses (Pl. 2, fig. 3; Pl. 4, fig. 7b; Pl. 6, fig. 4b). This infilling, very rich in pyritic crystals, corresponds to the cuticular structures and other degenerated remains of the polypide, usually showed in thin section. The phosphatic skeleton is unlaminated, consisting of prismatic crystals parallel to each other and normal to the attitude of the laminae of the calcareous cortex (Pl. 1, figs. 5b, 5c; Pl. 6, fig. 4c); the thickness of the walls varies from 0.002 to 0.006 mm. The arrangement of the crystals indicates that the phosphatic skeleton has been deposited after the laminar calcareous wall.

In most cases, the phosphatic skeleton perfectly line the adjacent calcareous structures: A)-walls (Pl. 8, fig. 1a), B)-intrazooecial spines (Pl. 5, figs. 10a-10b), C)-cystifragms and funnel-shaped diaphragms (Pl. 10), D)-cystoidal diaphragms, E)-basal and terminal diaphragms (Pl. 5, figs, 11-12; Pl. 10, figs. 1a, 3, 5, 7, 9), F)-

EXPLANATION OF PLATE 5

Figs. 1-12 - *Hallopora elegantula* (Hall). 1) Autozooecial tube probably located in the endozone, IPUM 21584, Vasca Anguille, × 15; 2, 6, 8) Autozooecial tubes closed by terminal diaphragms: apical part not preserved, IPUM 21594, 21522, 21527, Lago di Mulargia, × 30; 3) Zoarial fragment displaying one circular autozooecium with the cap-like apparatus and polygonal mesopores, IPUM 20194, Caletta di Portixeddu, × 100; 4) Autozooecial tube lacking the cap-like apparatus, IPUM 21587, Piscina Morta × 30; 5) Zoarial fragment showing autozooecial and mesozooecial tubes, IPUM 21498, Caletta di Portixeddu, × 40; 7) Autozooecial tube belonging to the endozone, IPUM 21589, Caletta di Portixeddu, × 15; 9a) Detail of a zoarial fragment showing one large autozooecium and one polygonal (cross section) mesopore: note the empty space (before etching occupied by calcareous wall) between two successive phosphatic diaphragms, IPUM 21592, Ponte su Amadori, × 100; 9b) Detail of the mesozooecial tube showing two vertical communication pores, × 1100; 10a) Autozooecial tube with the cap-like apparatus: note the casts of the autozooecial spines, IPUM 20191, Caletta di Portixeddu, × 160; 10b) Detail of the casts of the autozooecial spines, × 770; 11) Detail of a mesopore, IPUM 21454, Punta Pedrona, × 140; 12) Zoarial fragment displaying the typical astogenetic pattern of the Halloporidae, IPUM 20178, Lago di Mulargia, × 25.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hemiphragms (Pl. 4). In other cases, the phosphatic skeleton is present without any adjacent calcareous skeleton and therefore there are structures consisting only of calcium phosphate: A)-cap-like apparati (Conti & Serpagli, 1984; 1987) (Pl. 5, figs. 8, 10a), B)-terminal vestibular membranes (Pl. 10, fig. 6), C)-cystoidal diaphragms (Pl. 6, figs. 5a-5b), D)-basal and terminal diaphragms (Pl. 2, figs. 6a, 8). In these cases, it would be better to use the general term *phosphatic skeleton* or *originally membranous structures* (Boardman, 1971, 1973; Utgaard, 1973) rather than the term *lining*, as used by the most of the authors. The phosphatic deposition is usually compound (located on oral and aboral side of different types of diaphragms).

The study of compound phosphatic diaphragms consisting of two adjacent layers confluent with the phosphatic walls (Pl. 2, figs. 6a, 6b, 8; Pl. 6, figs. 5a, 5b; Pl. 10, fig. 11c), without calcareous diaphragms in between, lead to the conclusion that the phosphatic skeleton is analogous to the membranous part of the inner body-wall (cryptocyst).

It is also important to note that a bimineralic skeleton, consisting both calcareous and phosphatic walls, etched according to the conodontological routine and observed by SEM, is very useful in the study of originally soft parts like tentacles (Conti, 1983), membranous diaphragms, remains of polypide-like structures, perimetrical attachment organs (Conti & Serpagli, 1987), membranous part of the inner body-wall (cryptocyst). All these new informations certainly aid in understanding the biology of Palaeozoic Bryozoa and can partly modify their systematic subdivisions.

THIN SECTION DESCRIPTION (Text-fig. 4)

Longitudinal section — Light-brown phosphatic walls distinctly darker than the adjacent calcareous walls, with a thickness from 0.002 to 0.006 mm, are distributed both in the axial and in the peripheral region of the colony; their thickness is generally greater in autozooecia than in mesozooecia (Pl. 7, figs. 1a-1b; Pl. 8, fig. 3; Pl. 12, fig. 8).

In some cases (walls, spines, diaphragms and cystifragms), the phosphatic skeleton perfectly line the adjacent zooecial calcareous structures becoming a real phosphatic zooecial lining (Pl. 3, figs. 1a, 1b, 2a, 2b; Pl. 12, fig. 7).No calcareous zooecial lining are seen. In other cases, there are terminal and basal diaphragms (Pl. 7, fig. 2; Pl. 8, fig. 6), terminal vestibular membranes (Pl. 8, fig. 2), cap-like apparati (Conti & Serpagli, 1987), cuticular structures and other polypide remains (Pl. 7, figs. 3a-4) consisting only of calcium phosphate confluent with the phosphatic walls without any adjacent corresponding calcareous structures. For example, in phosphatic compound diaphragms there is a direct contact of two originally membranous layers, without a calcareous diaphragm in between (Pl. 7, figs. 2, 5; Pl. 8, figs. 2, 6).

The phosphatic skeleton is tuberculose and often characterized by the presence of roughly circular spherules; it may be in direct contact with the calcareous walls or wholly or partially separated by a white layer which estinguishes at crossed Nicols at different times from it (Pl. 8, fig. 3).

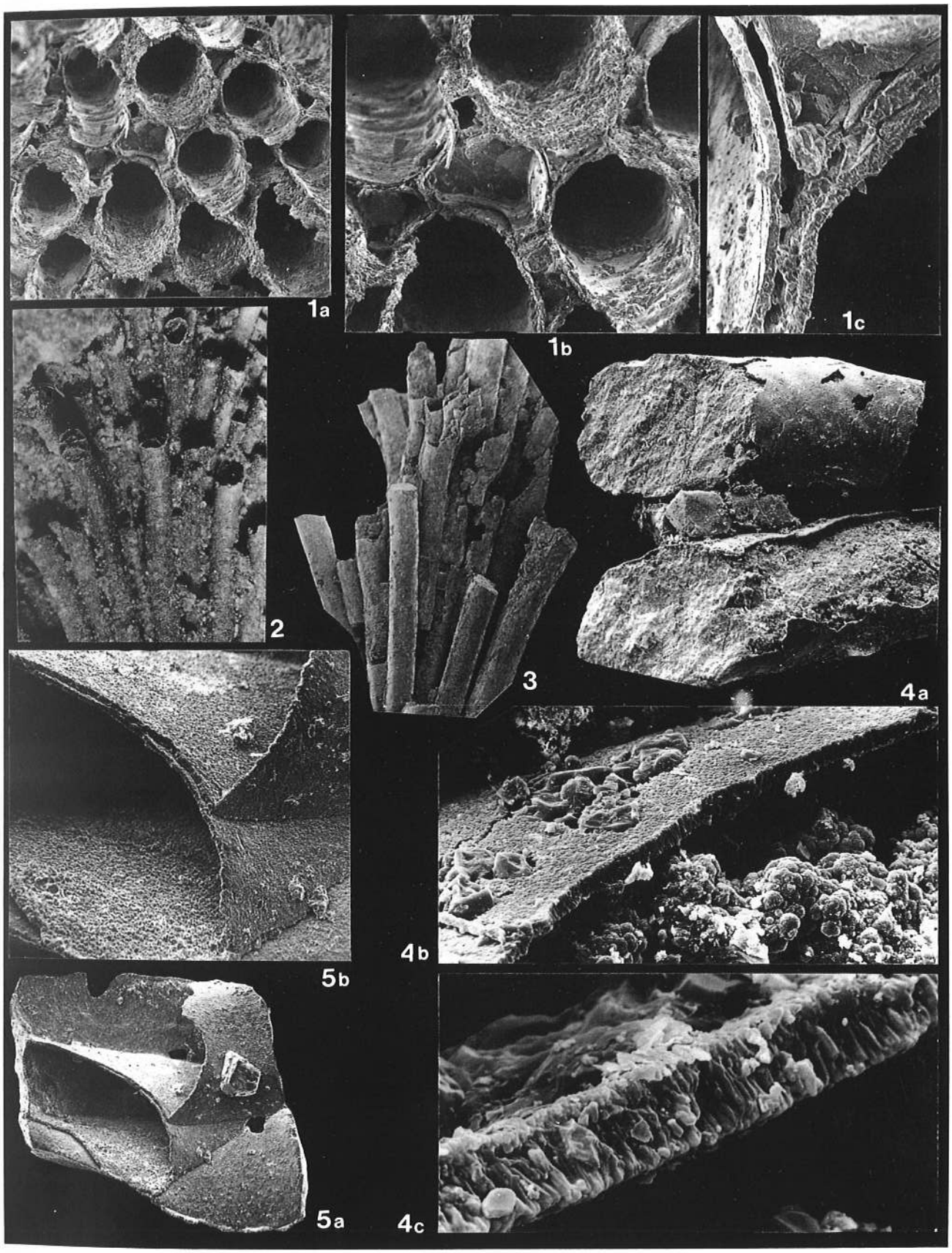
The phosphatic skeleton is usually complete and compound (Pl. 7, fig. 1a) in this way, the zooecial cavities are closed into isolated compartments (Pl. 8, fig. 3). Phosphatic deposition is never confluent with the calcareous laminae of the cortex and estinguishes at cross Nicols always at different times from them.

Transverse section — The phosphatic walls appear in two different positions: 1)-adjacent to the calcareous walls (Pl. 8, figs. 1a, 4), 2)-separated by a white layer along the whole or part of their length (Pl. 8, figs. 1b, 5). They present the same optical and morphological features seen in the longitudinal section. The inside is rough, characterized by spherules and brown bodies that often abut on remains of the membranous sac and other cuticular structures (Pl. 7, fig. 4). Sometimes phosphatic walls appear to be doubled (Pl. 8, fig. 1b) and they occur both in autozooecia (generally with a greater thickness) and in mesopores (Pl. 12, figs. 7-8).

EXPLANATION OF PLATE 6

Figs. 1-4 - *Hallopora elegantula* (Hall). 1a) Zoarial fragment showing the configuration of zooecial tubes, IPUM 20123, Caletta di Portixeddu, × 35; 1b) Detail of the same specimen showing phosphatic diaphragms in two mesopores, × 70; 1c) Detail of the same specimen showing the phosphatic walls, × 360; 2) Zoarial fragment displaying two circular autozooecia with cap-like apparati, IPUM 19882, Caletta di Portixeddu, × 15; 3) Zoarial fragment displaying the astogenetic pattern of the genus *Hallopora*, IPUM 20124, Punta Pedrona, × 15; 4a) Zoarial fragment displaying two autozooecial tubes and one mesopore in between, IPUM 21596, Caletta di Portixeddu, × 75; 4b) Detail of the same specimen showing the phosphatic cuticular structures and communication pores, × 1100; 4c) Detail of the same specimen showing the phosphatic wall, × 4000.

Fig. 5 - *Hallopora* sp.; 5a) Autozooecial fragment showing one phosphatic cystoidal diaphragm, originally membranous, without calcareous wall in between, IPUM 20133, Punta Pedrona, × 135; 5b) Detail of the same specimen showing two phosphatic layers closely connected, × 325.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The phosphatic walls are equally distributed throughout the colony while they are always absent in acanthopores, and never laminated (Pl. 12, fig. 5).

PRIMARY DEPOSITION OF THE PHOSPHATIC SKELETON

Interpretation

On the basis of the following considerations, it becomes clear that the phosphatic skeleton is primary, that is, secreted during the lifetime of the colony.

1) The phosphatic skeleton does not, as it happens in most cases, only line the oral and aboral side of calcareous diaphragms as well as zooecial walls becoming a real lining, but it also occurs without the interposition of the calcareous deposition. There are, therefore, basal (Pl. 2, fig. 8), cystoidal (Pl. 6, fig. 5b; Pl. 10, fig. 11c), terminal (Pl. 7, fig. 5), convex (Pl. 8, fig. 6), perforated diaphragms, cap-like apparati (Pl. 5, figs. 8, 10a), terminal vestibular membranes (Pl. 8, fig. 2; Pl. 10, fig. 6) located at different ontogenetic stages, made up only of calcium phosphate and never confluent with the laminae of the calcareous skeleton (Pl. 3, fig. 1c).

The only possible explanation of the deposition of such a phosphatic skeleton is that it was an originally membranous structure, probably analogous to the peritoneum of the cryptocyst, mineralized at different times from the secretion of calcareous walls during polypide degeneration phases.

2) Some of the membranous structures previously recorded could have functioned only by preserving their organic nature. In fact:

2A) Terminal vestibular membranes (Pl. 10, figs. 3, 6) as well as perimetrical attachment organs (cap-like apparati) would certainly not have allowed tentacle eversion if they had originally been mineralized. The functional morphology of the cap-like apparatus during zoarial life and its successive mineralization during a particular stage of polypide degeneration has already been discussed (Conti & Serpagli, 1987). It is interesting to note that the phosphatic cap-like apparatus derived from the mineralization of the peritoneum of the cryptocyst, which is the only membranous structure involved in the formation of a perimetrical attachment organ (Boardman, 1973).

2B) Cystifragms and funnel-shaped diaphragms are considered originally membranous, that is remnants of orificial terminal walls or membranous sacs (Boardman, 1971, 1973), and related to tentacle eversion. In agreement with Boardman (1973), their mineralization occurred during the phase of polypide degeneration. In Sardinian specimens the mineralization (phosphatization) involves the membranous part of the cryptocyst which can or not line the calcareous skeleton.

The hemiphragms of *H. irrasum* can also be placed in connection with tentacle eversion (Boardman, 1971). The alternate curvature of the autozooecial walls would create more restricted zooecial cross sections, favouring the increasing of the coelomic pressure and consequently tentacle eversion (Pl. 4, fig. 5). Moreover, the occurrence of cuticular structures between two successive hemiphragms (Pl. 4, fig. 7b) proves the existence of soft parts located in this restricted coelomic cavity. On the other hand, in other cases, (hemiphragms extending to two thirds of the zooecial cavity) (Pl. 4, fig. 8), the coelomic space available is too restricted in order to containing feeding polypides and probably they represent pouches containing excreting products of metabolism (brown bodies) which were lost during growth of the zooecium related to degeneration-regeneration cycles (Dzik, 1981).

3) The position of the phosphatic skeleton in relation to the calcareous one and the zooecial cavity shows that the mineralization of the originally, membranous structures, previously examined, started from both oral and aboral side. The only membranous structure closely connected to the calcareous skeleton, and forming membranous diaphragms or other organic structures trasverse in orientation to the zooecial cavity is the membranous part of the cryptocyst consisting of inner epidermis and peritoneum. For instance, the cap-like apparatus of *Hallopora elegantula* is the result of

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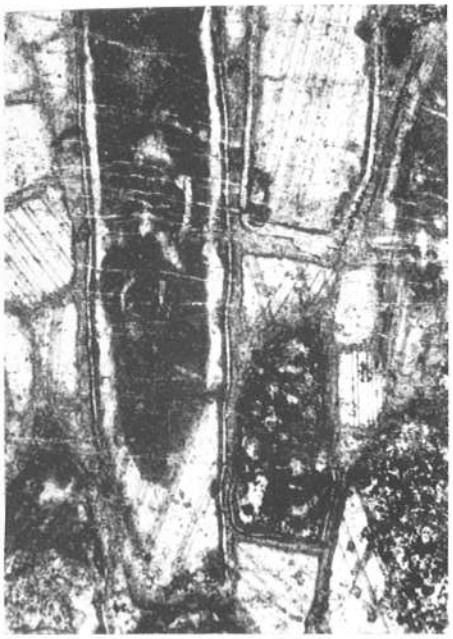
EXPLANATION OF PLATE 7

Figs. 1-5 - *Hallopora elegantula* (Hall). 1a) Longitudinal section displaying phosphatic cuticular structures and phosphatic bodies, IPUM 19966, Caletta di Portixeddu, × 75; 1b) Detail of the same specimen showing zooecial phosphatic walls, × 185; 2) Longitudinal section displaying phosphatic walls and one phosphatic diaphragm, IPUM 20004, Piscina Morta, × 75; 3a) Longitudinal section showing phosphatic cuticular structures and the astogenetic pattern of the genus *Hallopora*, IPUM 20115, Caletta di Portixeddu, × 25; 3b) Detail of the same specimen showing the relationship between phosphatic and calcareous walls: note the presence of a phosphatic terminal diaphragm, × 75; 4) Tangential section displaying phosphatic cuticular structures: note several membranous sacs transversely cutted, IPUM 20105, Caletta di Portixeddu, × 25; 5) Longitudinal section showing a large development of phosphatic granular bodies and one phosphatic hemiphragm abutting into the phosphatic walls, IPUM 19971; Caletta di Portixeddu, × 75.



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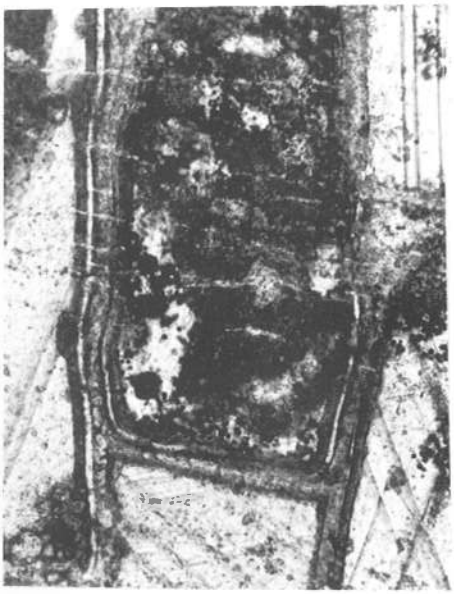

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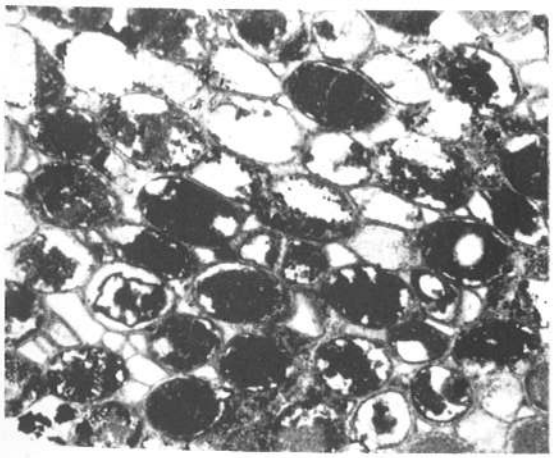

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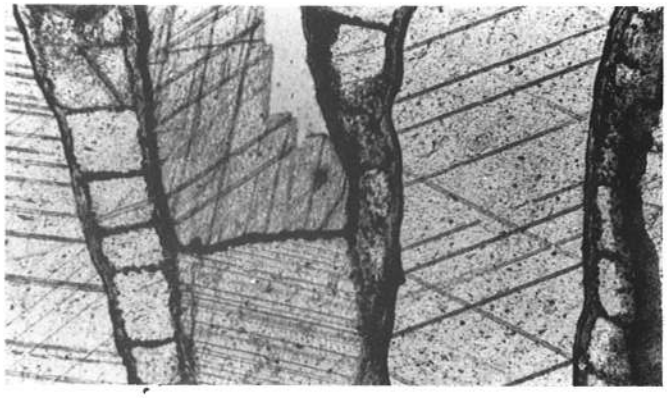

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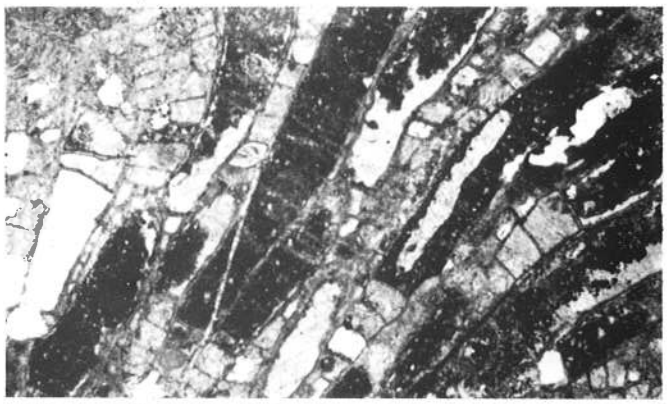

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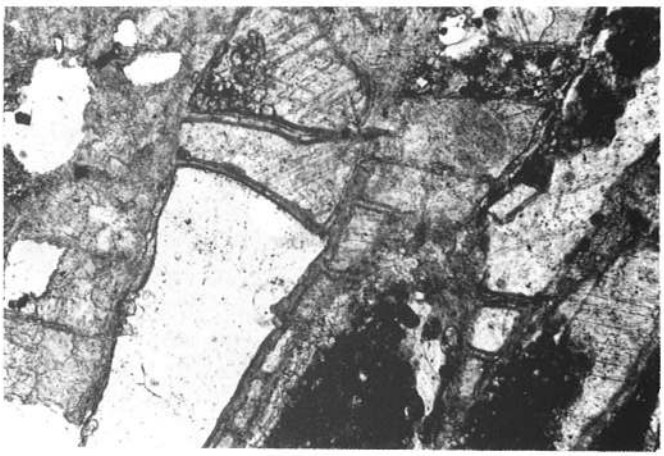

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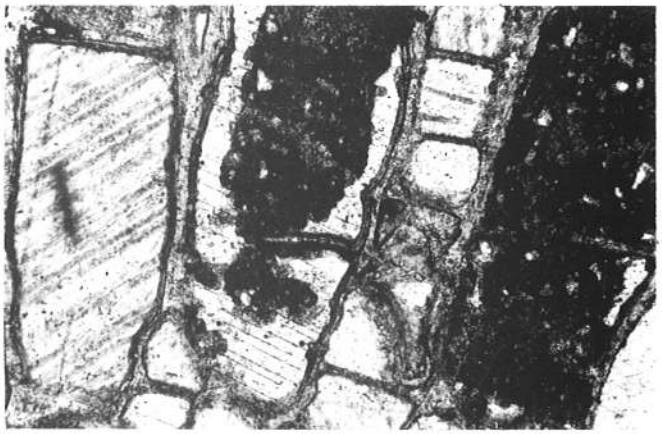

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the mineralization of the peritoneum (Conti & Serpagli, 1984, 1987). The explanation of the frequent detachment of the phosphatic skeleton from the calcareous one (Pl. 7, fig. 1b; Pl. 8, fig. 1b) could be due to the interposition of the protein sheet (Taverner-Smith & Williams, 1972) or of the inner epidermis, or, more probably, to a progressive mineralization and hardening of the peritoneum (= phosphatic skeleton).

4) The analyses carried out (text-fig. 2) and the careful examination of the Sardinian specimens show also that the structures occurring inside the zooecial cavity (spherules, brown bodies, remains of cystides and tentacles) have the same chemical composition as the phosphatic walls and that their arrangement is not related to any preferential positions (Pl. 2, fig. 3). These structures can be found both at the bottom of the zooecial cavity (Pl. 7, fig. 3a) and attached to the walls (Pl. 2, fig. 4b) indicating that the degeneration of soft parts occurred in a liquid environment and their deposition was not only influenced by the gravity force. On the other hand, if we hypothesize a secondary phosphatization, it should have occurred in an environment where organic structures should have been previously destroyed. Nevertheless, in several papers (Mc-Kinney, 1969; Boardman *et al.*, 1983) the preservation of membranous structures is often reported. This preservation, favoured by the protection of the diaphragms and by anoxic conditions, is very common in Sardinian specimens. Under particular conditions, it is possible to note the preservation of phosphatic tentacles (Conti, 1983, figs. 1-2) and cystides (Pl. 7, fig. 4).

5) The discovery of communication pores, lined by phosphatic membranes confluent with the phosphatic skeleton (Pl. 1, fig. 5b; Pl. 5, fig. 9b; Pl. 6, fig. 4b; Pl. 9, fig. 8b; Pl. 12, fig. 8), connecting two adjacent zooecial cavities, can be only explained if this skeleton is analogous to the membranous part of the cryptocyst.

6) A further support of the primary origin of the phosphatic skeleton in Bryozoa is related to the abundance of phosphatic bodies in the fossil record. They are in fact reported from Middle and Upper Ordovician, Lower and Upper Silurian, Lower and Upper Devonian, Lower Carboniferous and Permian from several geographical areas: France, Norway, Sweden, Great Britain, Poland, Russia, Spain, Sardinia, U.S.A., Australia, Tasmania, Antarctica and also from Recent samples of Pacific Ocean.

7) Phosphatic structures occur in all Palaeozoic orders of Bryozoa (Trepostomata, Cryptostomata, Cystoporata and Cyclostomata) indicating their general spreading inside the whole phylum.

In order to have a further support, we examined two samples bearing Bryozoa from the Upper Silurian of Skane (Sweden) and from the Upper Ordovician of Kentucky (U.S.A.). After etching them with the technique used in order to yield conodonts, we noted that the first sample showed only the presence of some scolecodonts, while the second one displayed a lot of phosphatic zooecia belonging to different genera and species of Bryozoa. As Martinsson (1965) pointed out, it may be possible that most of the phosphatic zooecia were destroyed by gas bubbles during the conodontological routine, and therefore, they would probably be much more abundant than what till now reported by the authors.

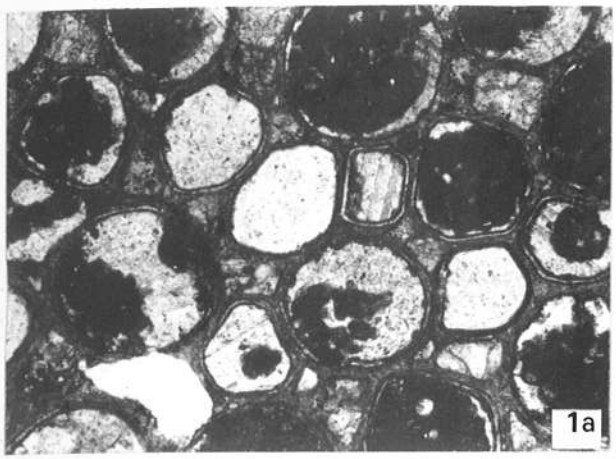
8) Phosphatic walls are never found inside acanthopores: this is full agreement with their connection to the calcareous laminae and with the absence of membranous part (peritoneum) of the inner body-wall (cryptocyst) inside them (Pl. 3, figs. 2b-3b).

9) The thickness of the phosphatic skeleton and the occurrence of phosphatic cuticular structures is greater in autozooecia than in mesopores (Pl. 7, figs. 3a, 4), in agreement with the greater thickness of the peritoneum in the former (related to tentacle eversion) than in the latter.

10) The phosphatization of originally membranous structures does not always occur during the zoarial ontogeny. For example, not all the autozooecia of *Hallopora elegantula* display a phosphatized perimetrical attachment organ (terminal diaphragm) with the function of a supporting base for new buds (Conti & Serpagli, 1987, fig. 5a) and, on the other hand, some zooecia have higher phosphatic contents than other ones. It is probable, therefore, that there is a particular colony dominance on the phosphatization mechanism

EXPLANATION OF PLATE 8

Figs. 1-6 - *Hallopora elegantula* (Hall). 1a) Transverse section displaying the phosphatic walls and cuticular structures, interpreted as probable remains of the polypide, IPUM 19976, Caletta di Portixeddu, × 75; 1b) Detail of the same specimen showing the phosphatic walls, × 160; 2) Longitudinal section of the same colony of fig. 1, displaying a phosphatic vestibular membrane with partial remain of the membranous sac, × 75; 3) Detail of fig. 3 of pl. 7 showing phosphatic walls and cuticular structures, × 65; 4) Transverse section displaying phosphatic walls and more or less wide cystide remains, IPUM 19993, Bunker, × 75; 5) Transverse section showing detail of the phosphatic walls and cystide remains, IPUM 20001, Caletta di Portixeddu, × 160; 6) Longitudinal section showing one convex phosphatic diaphragm, IPUM 20103, Piscina Suigas, × 100.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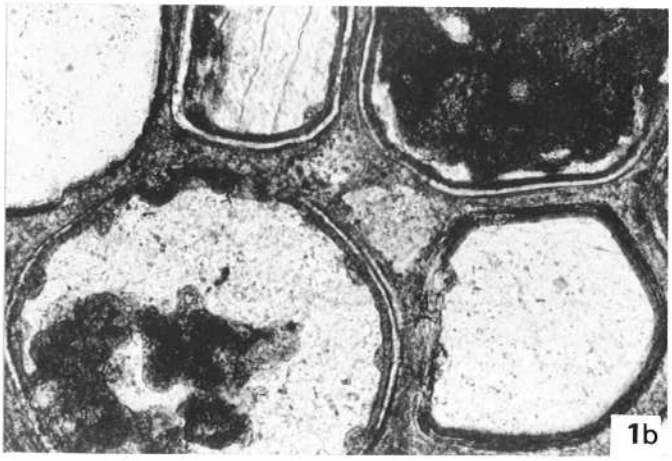
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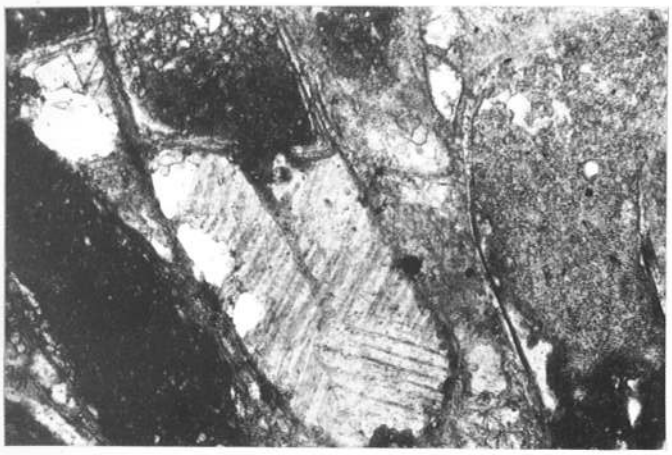
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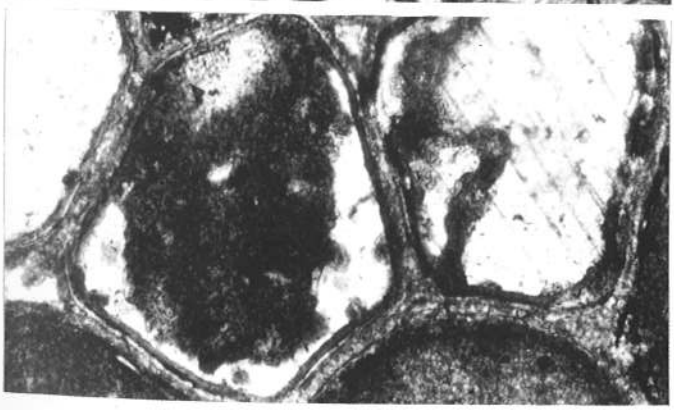
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as hypothesized by some authors (Oakley, 1934; Martinsson, 1965; Spjeldnaes, 1984).

It seems to be demonstrated that the phosphatic skeleton is the result of the phosphatization of the peritoneum of the cryptocyst during the degeneration phase of the polypide. It is probable that the phosphatization was complete involving also the inner epidermis. There are, in fact, specimens with a very thick or doubled phosphatic wall (Pl. 8, fig. 1b), that could represent more important phosphatic episodes, related to particular environmental conditions.

Discussion

In order to explain which kind of complex mechanism give rise to the phosphatization of the membranous part of the cryptocyst, it is necessary to suppose that the cells constituting bryozoan soft parts were originally rich in phosphorus. Some authors reported in fact the occurrence of phosphorus and/or phosphates in bryozoan soft parts.

Clarke & Wheeler (1922) found small amount of phosphorus in Recent cheilostomes from the North Atlantic.

Silèn (1947) described some Recent Bryozoa displaying high amount of phosphoric acid used to perforate calcareous shells.

Vinogradov (1953) reported the presence of phosphates in Palaeozoic Bryozoa but, according to him, they had a secondary origin.

Saudray & Buffandeau (1958) published the results of interesting analyses carried out on Recent ectocysts of cheilostomes and ctenostomes, which revealed different stages of mineralization and sometimes, they were very rich in phosphates (10% on average); among ctenostomes (group beginning in the Palaeozoic), the phosphate content was higher than carbonate one.

The first sufficiently exhaustive review of the chemical composition of Bryozoa (skeleton and soft parts) was carried out by Schopf & Manheim (1967). The authors indicated a phosphorus content of the soft parts, generally around 1%, increasing to 3% in particular brackish environments usually located near estuaries. Such amount of phosphorus could be related to the large digestion of diatoms or other photosynthetic microorganisms usually rich in phosphorus.

Schopf & Allan (1970) noted that high phosphorus contents could be concentrated in limited portions of the zooecial walls in Recent cheilostomes. The high phosphorus values seemed to occur only in the early-formed part of the lateral wall. Therefore, the phosphorus could be systematically enhanced or decreased in different growth stages of the same individual.

Rhodes & Bloxam (1971) stated that the phosphorus values in Recent Bryozoa varied from traces to 2.78%, whereas noted a significant increase in fossil zooecial tubes (7-20%).

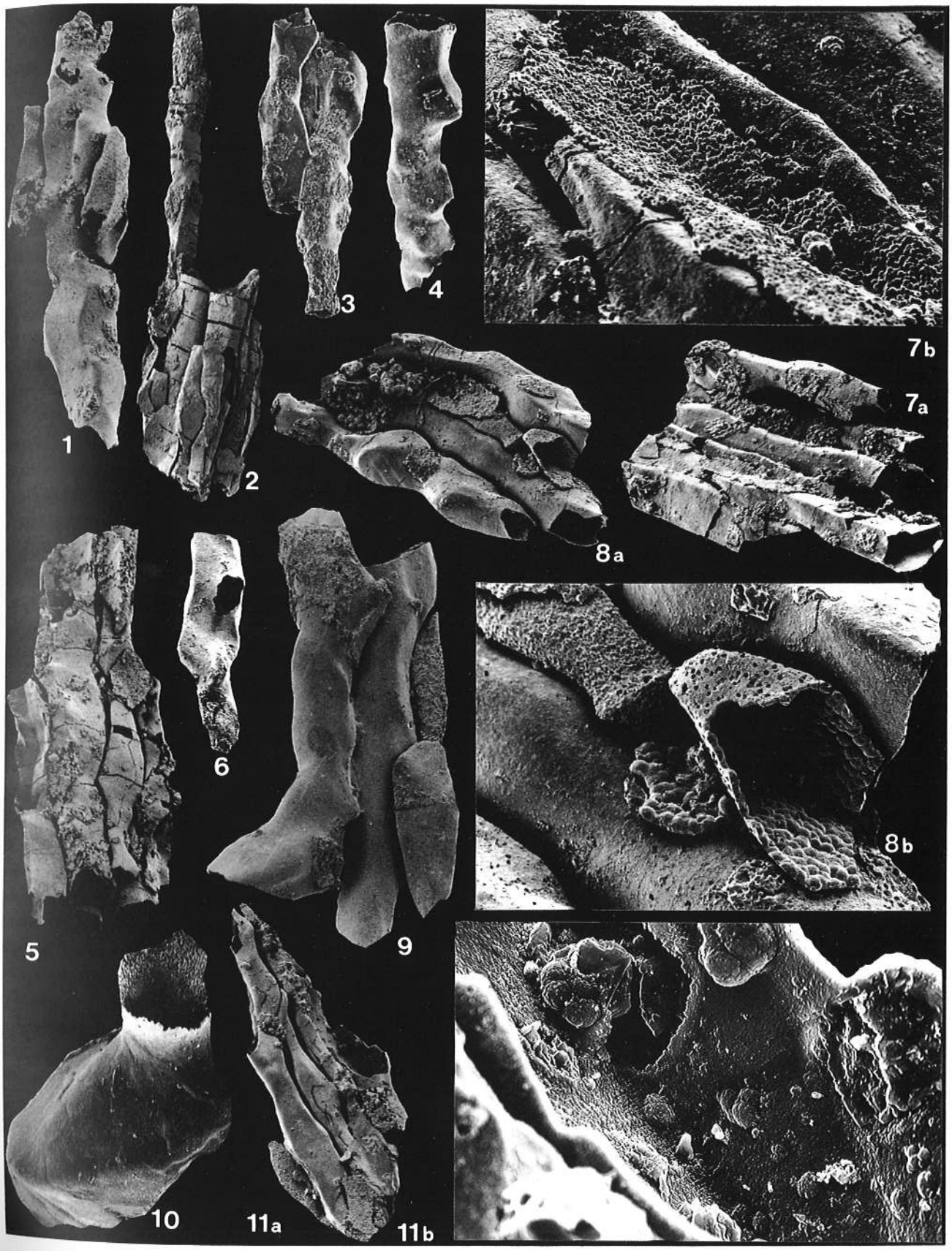
From the above review, it seems to emerge that phosphorus values are higher in Palaeozoic Bryozoa than in Recent ones.

Throughout the animal and plant kingdoms, phosphorus plays a major and essential role in the life processes. It is necessary to the principal metabolic functions of living organisms (production of cell energy and change from ADP to ATP) and it is an essential component of the nucleic acids (Simkiss, 1964; Rhodes & Bloxam, 1971). Pyrophosphates, glycerophosphates and polyphosphates have been observed in cell membranes and are involved in fundamental cell activities (Cavero & Spedding, 1983). Some of these phosphatic substances are used to pump excess calcium out of cells as it is a strong inhibitor of cell reproduction (Nyers, 1987).

As a matter of fact, the first and simplest mechanism used by cells to get rid of excess calcium (abundant since the Precambrian, as testified by calcareous stromatolites) is to deposit it in the body-walls as calcium phosphate or calcium carbonate (Nyers, 1987). One of the many hypotheses of the appearance of skeleton-bearing animals at the beginning of the Cambrian (Bengtson, 1977; Glaessner, 1984) is based on the need of cells to get rid of elements that were

EXPLANATION OF PLATE 9

Figs. 1-11 - *Bithopora sardoa* (Vinassa de Regny). 1) Zoarial fragment showing frequent variations of zooecial diameter, IPUM 21425, Piscina Morta, × 75; 2) Zoarial fragment showing several autozooecial tubes and their flask-like shape, IPUM 21475, Caletta di Portixeddu, × 60; 3, 4) Fragments of autozooecial tubes, IPUM 20168, 20169, Caletta di Portixeddu, × 85; 5) Zoarial fragment displaying the astogenetic pattern B1 of the genus *Bithopora*, IPUM 21473, Lago di Mulargia, × 75; 6) Autozooecial tube showing the apical part, IPUM 21562, Lago di Mulargia, × 50; 7a) Zoarial fragment, IPUM 21581, Caletta di Portixeddu, × 60; 7b) Detail of the same specimen showing the phosphatic walls, × 325; 8a) Zoarial fragment showing several autozooecial tubes and their flask-like shape, IPUM 21557, Caletta di Portixeddu, × 60; 8b) Detail of the same specimen showing the phosphatic walls, × 200; 9) Zoarial fragment, IPUM 21422, Lago di Mulargia, × 110; 10) Detail of one autozooecial tube, IPUM 21556, Lago di Mulargia, × 110; 11a) Zoarial fragment, IPUM 21446, Caletta di Portixeddu, × 60; 11b) Detail of the same specimen displaying the phosphatic walls and the bodies located inside an autozooecial cavity, × 530.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noxious to their vital functions. Even today, for instance, some organisms are able to deposite harmful substances in their skeleton in extremely polluted environment (Simkiss & Taylor, 1981).

GEOLOGICAL IMPLICATIONS

Many authors emphasize that calcium phosphate is one of the first chemical substances used by organisms in building hard parts (Lowenstam, 1981). According to Cook & Shergold (1984) and Kazmierczak *et al.*, (1985), there was, on the Precambrian-Cambrian boundary, a close relationship between deposits of phosphorites (Sheldon, 1981) and skeletal evolution. Following this point of view, many data of the composition of the original environment that led to the appearance of phosphatic shells could be derived from the factors affecting the phosphorite deposition.

The main hypotheses on the origin of phosphorites are essentially four (Sheldon, 1980; Kennett, 1982): 1) special events, such as catastrophic destruction of life or volcanic addition of fluorine to the sea; 2) supply of phosphate to the sea from rivers; 3) diagenetic processes (Bushinskiy, 1935; Kennedy & Garrison, 1975; Baird, 1978; Swirydczuk *et al.*, 1981): like the replacement of carbonate by phosphate in anoxic biogenic sediments; 4) formation of phosphorites directly from high phosphorus deep waters, upwelled to the shelf edge (about 150 m) by dynamic oceanic circulation (Bentor, 1980). Such phosphate rich waters also caused abnormous explosions of phytoplankton organisms.

The study of the depositional conditions of phosphorites integrated with laboratory experiments aid in understanding the mechanisms that regulate the calcium phosphate deposition (Simkiss, 1964; Gulbrandsen, 1969; Rhodes & Bloxam, 1971; Sheldon, 1980; Nancollas *et al.*, 1983). The solubility of phosphates is markedly increased by increasing acidity (apatite normally precipitates at pH of 7.8), and carbon dioxide pressure an by decreasing temperature, and water hardness (magnesium is a strongly limiting factor in the phosphatic deposition).

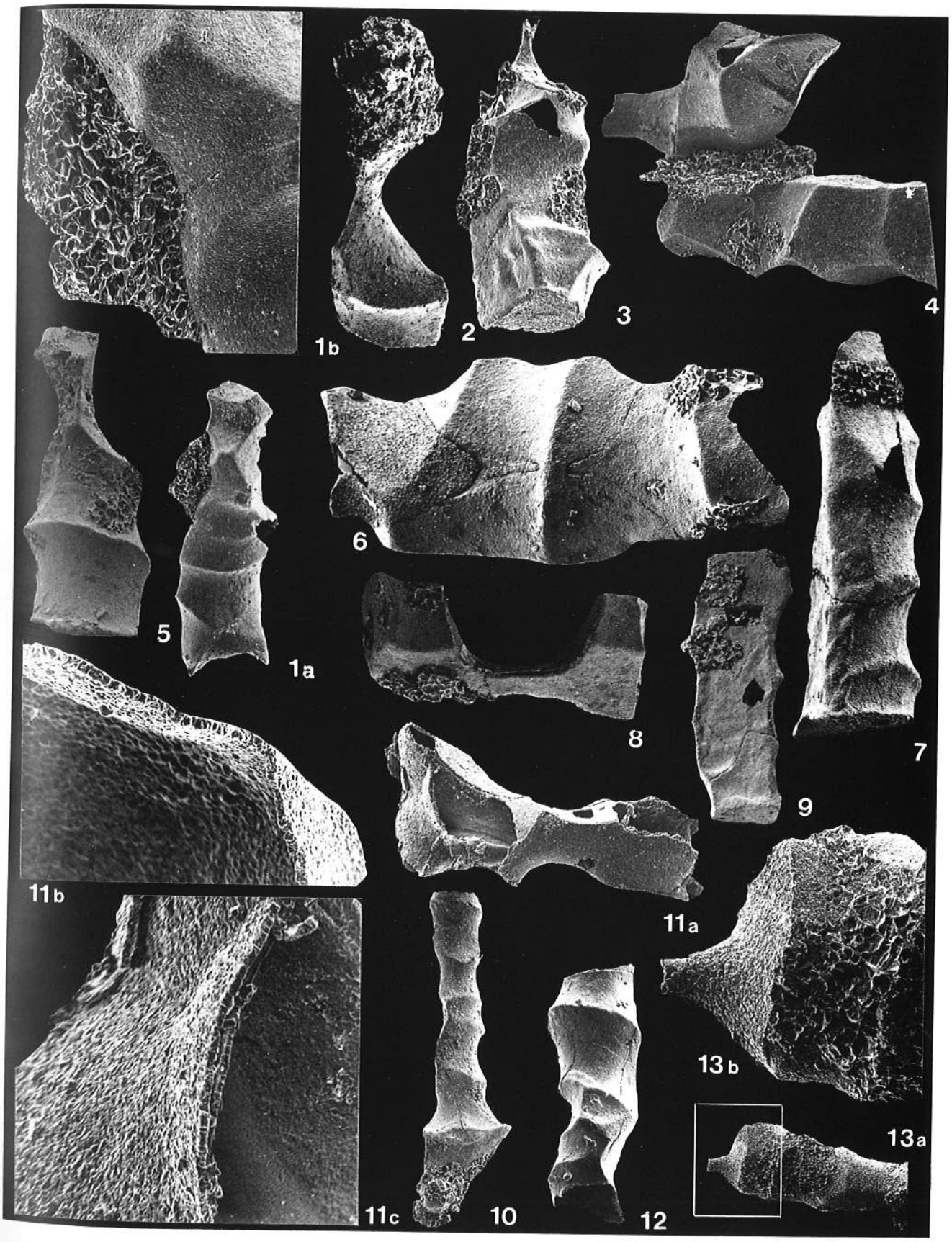
It is well known that at the beginning of the Cambrian, two thirds of the metazoans secreted a calcium phosphate skeleton and this was possibly related to different reasons, such as the atmospheric pressure of carbon dioxide much higher than today (Müller, 1964; Sheldon, 1980) and a lower concentration of magnesium. This is confirmed by the fact that the first successive calcareous skeletons were secreted in calcite (magnesium acts as crystal poison for calcite) (Dodd & Schopf, 1972) and today the high concentration of magnesium inhibits phosphate deposition (Bentor, 1980), in favour of aragonite. Calcium carbonate occurring in early Bryozoa was calcitic with a low magnesium content (Sandberg, 1977).

A further possibility is related to high phosphorus waters formed in the deep ocean following a prolonged period of anoxia (Sheldon, 1980; Nyers, 1987), probably due to the existence of a super-continent that limited oceanic circulation and vertical mixing of the water. The phosphorus was transferred to shallow waters primarely by mechanisms like upwelling related to a period of enhanced oceanic overturn (Cook & Shergold, 1984).

The high phosphate values in the photic zone could consequently inhibit carbonate calcification (Simkiss, 1964; Glaessner, 1984) and forcing the organisms to deposit calcium phosphate in their skeleton (Lowenstam & Weiner, 1983). In this connection, Bachra *et al.*, (1963) explained the mutual exclusion of crystallized calcium phosphates and carbonates in the same tissues by the inhibiting action of orthophosphates on carbonate crystallization. They also showed experimentally that aragonite and calcite were produced only under conditions of low phosphate concentration and that high phosphate contents inhibited calcite deposition, even at high calcium concentrations.

EXPLANATION OF PLATE 10

Figs. 1-13 - Genus et species indet. of Monticuliporids; phosphatic linings of flask-shape chambers. 1a) Autozooecial chamber capped by one terminal phosphatic diaphragm, IPUM 20147, Caletta di Portixeddu, × 65; 1b) Detail of the same specimen showing the spongy structure attached to the autozooecial wall, × 325; 2, 5, 8) Details of flask-shape chambers, IPUM 21428, 21479, 21483, Punta Pedrona, × 110.; 3) Autozooecial phosphatic chamber showing funnel-shape and basal diaphragms, IPUM 20137, Caletta di Portixeddu, × 130; 4) Two autozooecial chambers joined by the spongy structure, IPUM 20156, Caletta di Portixeddu, × 75; 6) Detail of an autozooecial chamber displaying the prints of the terminal vestibular membrane (right) and of the membranous sac (left) filled by phosphatic cuticular structures, IPUM 21486, Punta Pedrona, × 180; 7) Lateral view of one flask-shape chamber, IPUM 21438, Punta Pedrona, × 120.; 9) Dorsal view of one flask-shape chamber, IPUM 21482, Caletta di Portixeddu, × 85; 10) Autozooecial chamber, IPUM 20139, Caletta di Portixeddu, × 65; 11a) Autozooecial chamber displaying cystoidal diaphragms, IPUM 20155, Caletta di Portixeddu, × 65; 11b) Detail of the phosphatic wall of the same specimen, × 650; 11c) Detail of the cystoidal phosphatic diaphragm, × 650; 12) Autozooecial chamber terminating with a small appendage (something like the funicular system?), IPUM 21485, Bunker, × 50; 13b) Detail of the same specimen displaying the spongy structure, × 150.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The successive decrease in phoshporus content, occurring in Middle Cambrian seas, favoured the mineralization of the calcite (Stehli, 1956; Lowenstam, 1981; Cook & Shergold, 1984) and the increasing of calcitic skeletons.

While the reasons for the beginning of such a period of oceanic overturn are unclear, two hypotheses are possible (Cook & Shergold, 1984): 1) a phase of continental drift which provided an ocean-continent configuration, possibly with a narrow latitudinal near-equatorial ocean (Prototethys); 2) the final glaciation of the late Proterozoic. Probably the formation of a supercontinent, located near the South Pole in the late Proterozoic, could have been a possible trigger mechanism. During the successive postglacial period the rising of the sea-level and the formation of extensive shallow epicontinental seas in providing areas for colonization as well as traps for the phosphatic deposition (Cook & Shergold, 1984) could have played an important role.

It is reasonable that micro- and macro-environments, similar to those of the Precambrian-Cambrian boundary, could have occurred in several times during Earth history (Sheldon, 1980). In such environmentals conditions, organisms able to deposit calcium phosphate and therefore decreasing the toxicity of waters were undoubtedly favoured.

Following such geological considerations three hypotheses may be suggested for Bryozoa during the Palaeozoic:

A) The life environment of Bryozoa was very rich in phosphorus;

B) Bryozoa had high amounts of phosphorus available in their soft parts;

C) Bryozoa, as a recessive and not a dominant genetic character, could secrete a phosphatic skeleton in particular environmental conditions, stressing their systematic relationships not only to inarticulate brachiopods, but also to deuterostomes.

Interesting to point out that the bivalve (*Pinctada martensii*) was able to mineralize the first larval shell (prodisoconch 1st) by phosphate (dahllite), the second larval shell (prodisoconch 2nd) by calcite and the adult shell by calcite and aragonite (Lowenstam, 1972).

It is logical that the three hypotheses should be connected: nutrients rich in prosphorus → bryozoan membranes rich in phosphorus → phylogenetic possibility of phosphatic secretion. The fact that Bryozoa with bimineralic skeleton were sometimes the dominant organisms of palaeocommunities (Spjeldnaes, 1984), leads us to conclude that Bryozoa were able to colonize, more efficiently than other organisms, high phosphorus environments (upwelling zones, estuaries, brackish waters, etc.). In this view Bryozoa may have acted as «phosphatic sinks» and scavanged a considerable part of the phosphorus in circulation in the environment where they lived (Spjeldnaes, 1984).

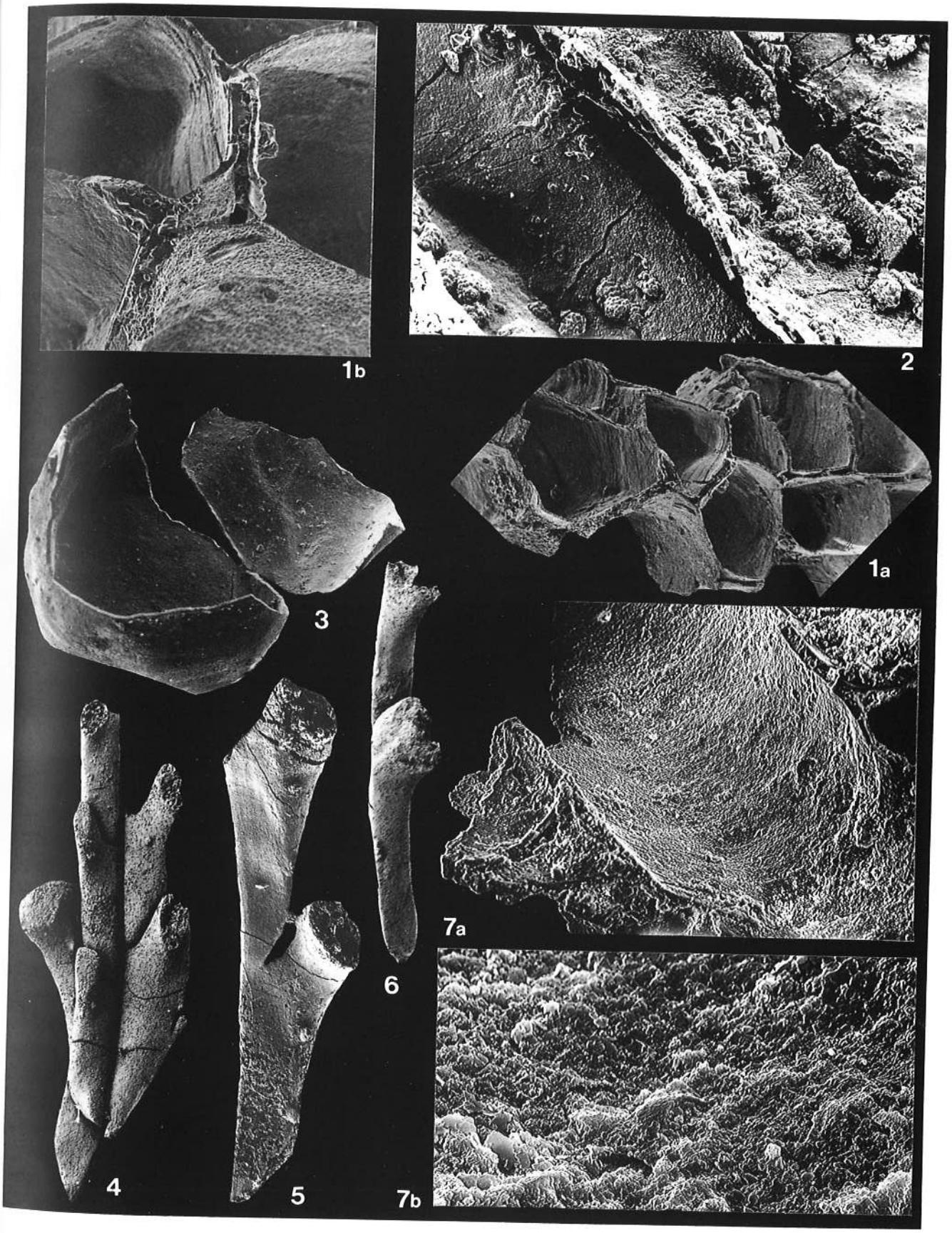
An hypothetical reconstruction of the chemical-physical conditions that led to the phosphatic deposition in Sardinian Bryozoa could be as follows. During the polypide life, there was a growth of zooecial calcareous walls in high phosphorus conditions. On reaching particularly high concentrations, some phosphatic compounds acted as crystal poison for carbonate calcification (Simkiss, 1964) and prevented the crystalline growth of calcareous walls. For instance, in the coccolithes, some phosphatic compounds prevent the mineralization of the soft parts (Black, 1968). Living organisms adopt two mechanisms in order to stop such a prevention (Simkiss, 1964, 1977): 1) develop of a phosphatase enzyme that acts in destroying these crystal poisons by hydrolizing them at the site of mineralization; 2) deposition of calcium phosphate in their wall. Bryozoa would appear to adopt the latter mechanism when the coelomic fluid loses its buffering properties with consequent rising in pH during the degeneration of polypide-like structures (Oakley, 1934). During the degeneration phase the zooecial microenvironment changes from oxydative to reducing conditions (negative Eh), as is proved by the abundance of pyrites in Sardinian specimens. In anoxic conditions, an increase in temperature and in pH was probably

EXPLANATION OF PLATE 11

Figs. 1-2 - *Anaphragma meneghinii* (Vinassa de Regny). 1a) Zoarial fragment showing the interzooecial budding pattern, IPUM 20171, Caletta di Portixeddu, × 100; 1b) Detail of the same specimen showing phosphatic walls, × 325; 2) Detail of phosphatic walls and of autozooecial phosphatic infillings, IPUM 21571, Caletta di Portixeddu, × 325.

Figs. 3, 7 - *Hallopora elegantula* (Hall). 3) Detail of a basal phosphatic diaphragm, IPUM 21448, Lago di Mulargia, × 160; 7a) Zoarial fragment displaying autozooecial and mesozooecial phosphatic walls, IPUM 21468, Caletta di Portixeddu, × 110; 7b) Detail of the same specimen showing the lumpy surface of the autozooecial phosphatic wall, × 1100.

Figs. 4-6 - *Graptodictya*, sp. 4) Zoarial fragment displaying the configuration of the autozooecia, IPUM 21544, Lago di Mulargia, × 45; 5) Detail of two autozooecial tubes and mesotheca (lateral view); note the wide gap between two autozooecia, occupied, before etching, by a thick extrazooecial calcareous skeleton IPUM 21542, Lago di Mulargia, × 70; 6) Two autozooecial tubes in frontal view, IPUM 21525, Lago di Mulargia, × 55.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caused by the occurrence of ammonia or other alkaline substances. For instance, calcular deposits of calcium phosphates form in saliva (Mc Connell, 1965) by local increases in pH and temperature.

As a consequence of the changed zooecial microenvironmental conditions, the phosphatization of originally membranous structures very rich in phosphorus (peritoneum of the cryptocyst) occurred. Mineralization of calcium phosphate seems, in fact, to be favoured if it take place on a protein (collagen) organic matrix (Glimcher, 1984; Spjeldnaes, 1984). Amorphous hydrogels of calcium phosphate can be deposited in the soft parts of numerous organisms (polychetes, bivalves, gastropods, malacostraces) (Lowenstam, 1972). This deposition seems usually to occur in temperate or cold waters (Lowenstam, 1972); amorphous hydrogels are, then, gradually converted into cryptocrystalline apatite (Glimcher, 1984; Lowenstam & Weiner, 1985), like that of the zooecial walls of Sardinian Bryozoa. It is probable that the phosphatic skeleton can be analogous and acting as a substitute for the calcareous lining (never found together in our samples), when the above described chemical conditions took place.

This phosphatic deposition (conversion from amorphous hydrogels into cryptocrystalline apatite) seems to be occurred in the Sardinian specimens in relationship to environmental factors (climatic cooling) and/or unfavourable geochemical conditions (high concentration of phosphorus). As a consequence of the calcium phosphate deposition in the zooecial cavity, the microenvironment would become less toxic and would allow further growth and development of calcareous zooecial walls (formerly inhibited by the high amount of phosphorus), starting off a successive regeneration cycle.

The frequent occurrence of phosphorite events after glacial episodes or in connection with transgressive phases stresses the relationship between calcium phosphate, plate tectonic, oceanic circulation, and glaciations (Sheldon, 1980). On the other hand, the existence of a climatic cooling in the Upper Ordovician is well proved for North Africa, SW Europe (Spjeldnaes, 1981) and, probably, Sardinia (Vai, 1982). It may be possible that, since the Lower Palaeozoic, Bryozoa had been able to live in high phosphorus environments using a complex degeneration-regeneration mechanism which roled a particular excretory function in order to get rid of harmful substances. During regeneration phases, the membranous part of the cryptocyst (peritoneum) becomes very rich in phosphorus, which will be deposited, during degeneration phases, as a phosphatic skeleton.

It would be interesting to extend this kind of investigation to post-Palaeozoic Bryozoa (e.g. the Cretaceous ones, where an important phosphorite event occurred) in order to find if they were still able to secrete calcium phosphate in response to particular environmental conditions.

CONCLUSIONS

The occurrence of phosphatic remains in Bryozoa seems to be much more frequent than is commonly believed and this gets out also going through the literature.

The phosphatic skeleton and other phosphatic structures (brown bodies, pearl-like bodies, polypide remains) are, at least in the Sardinian specimens, of primary origin, that is deposited during the zoarial life. The similarity between Sardinian phosphatic structures and those reported in literature led us to consider a primary origin also for most of the latter. Therefore it is probable that, at least during the Palaeozoic, Bryozoa were able to secrete a bimineralic (calcareous and phosphatic) skeleton in response to particular environmental conditions (high phosphorus contents).

The phosphatization of originally membranous structures (peritoneum of the cryptocyst), having an essential role during zoarial life, was caused by peculiar

EXPLANATION OF PLATE 12

Figs. 1-3 - *Graptodictya* sp. 1, 3) Oblique section displaying the configuration of the zooecial tubes and mesotheca, IPUM 19997, 19994, Caletta di Portixeddu, × 35; 2) Transverse section displaying the phosphatic walls and the cuticular structures, IPUM 19983, Caletta di Portixeddu, × 75.

Figs. 4, 6 - *Bithopora sardoa* (Vinassa de Regny). 4) Longitudinal section displaying the astogenetic pattern B1, IPUM 20085, Caletta di Portixeddu, × 15; 6) Longitudinal section, IPUM 21603, Lago di Mulargia, × 15.

Fig. 5 - *Anaphragma meneghinii* (Vinassa de Regny). Detail of the autozooecial phosphatic walls and acanthopores, IPUM 20047, Caletta di Portixeddu, × 160.

Figs. 7, 8 - *Hallopora elegantula* (Hall). 7) Longitudinal section displaying phosphatic autozooecial walls, IPUM 19965, Caletta di Portixeddu, × 150; 8) Longitudinal section showing phosphatic autozooecial walls and one communication pore, IPUM 20001, Caletta di Portixeddu, × 150.


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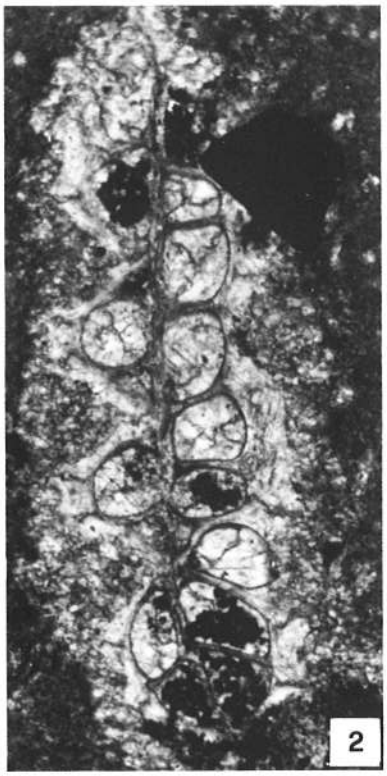
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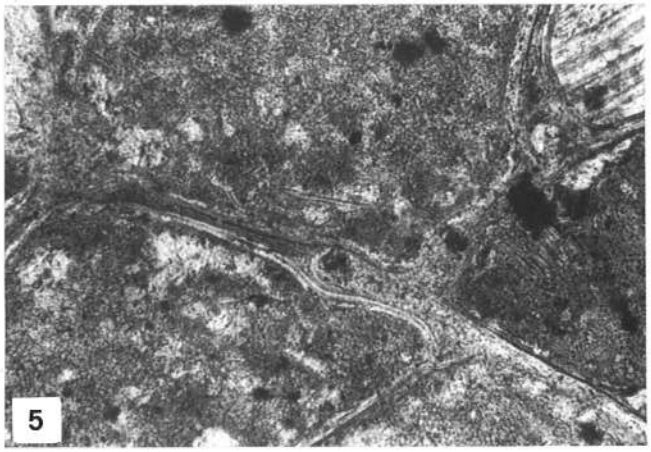
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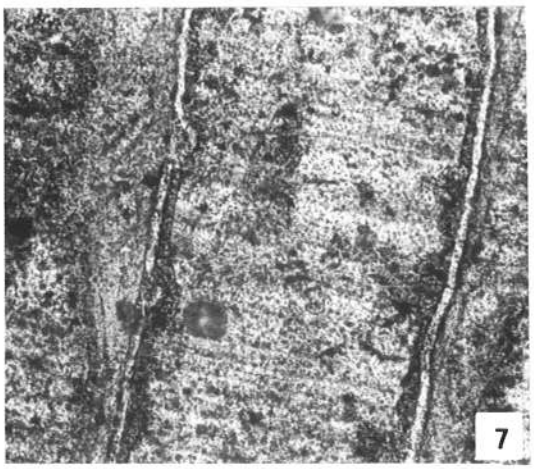
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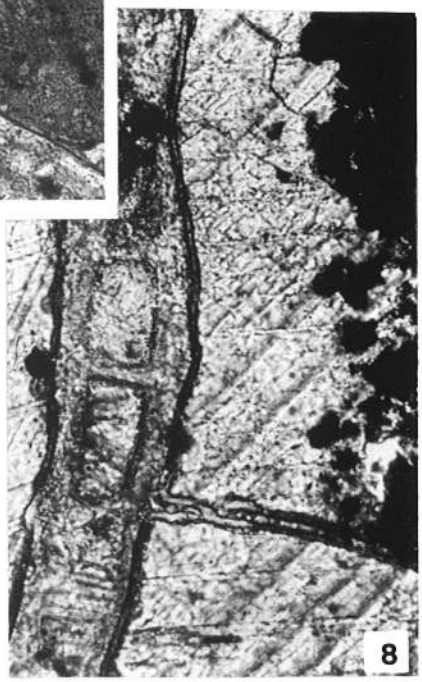
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chemical conditions inside the zooecial cavity during the degeneration phase. Once mineralized, these structures functioned as colonial supports.

High phosphorus concentrations rule out some palaeoecological considerations. Bryozoa with a bimineralic skeleton must have lived in shallow, brackish waters and/or on continental shelves characterized by upwellings. The authors want to outline an important relationship between the Sardinian climatic cooling occurred at the end of the Ordovician and oceanic circulation as well as calcium phosphate deposition.

We also hope that further research will be carried out on the spreading of calcium phosphate in Palaeozoic Bryozoa and on the connection between the proposed depositional pattern and their life environment.

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