A new interpretation of the anthozoan *Septodaeum* Bischoff, 1978 as a bryozoan

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ABSTRACT — *Taxonomically significant morphological and structural features of the Lower Palaeozoic genus* Septodaeum *Bischoff were discussed by the Authors in a short account in 1982 (IV International Symposium on the Ordovician System, held in Norway). At that time the Authors presented preliminary data indicating that the genus should be assigned to Bryozoa instead of a new subclass (Septodaearia) of the Anthozoa as supposed for Australian and Swedish specimens.*

The present paper gives detailed documentation and descriptions concerning the morphology, structure and budding of such tube-like enigmatic fossil compared with both Anthozoa and Bryozoa. The result is that Septodaeum, *without any doubt, is a trepostome bryozoan belonging to the genus* Hallopora *Bassler, 1911.*

RIASSUNTO — [Sulla posizione sistematica di *Septodaeum* Bischoff, 1978: dagli Antozoi ai Briozoi] — *Nel 1982 gli autori presentarono una nota preliminare al 4° Simposio Internazionale sull'Ordoviciano tenutosi in Norvegia, nella quale si sosteneva che il genere* Septodaeum, *forma singolare apparentemente assai diffusa nel Paleozoico inferiore dell'Australia e della Svezia, doveva essere attribuito ai Briozoi invece che a una nuova sottoclasse (*Septodaearia*) degli Antozoi. Sulla base di materiale fossilizzato in fosfato di calcio e quindi particolarmente ben conservato, proveniente dall'Ordoviciano superiore della Sardegna viene qui data una dettagliata descrizione e documentazione della morfologia di piccoli fossili tubiformi, apparentemente enigmatici, confrontandoli sia con gli Antozoi sia con i Briozoi. Lo studio, oltre a provare che* Septodaeum *Bischoff, 1978 appartiene senza alcun dubbio al genere* Hallopora *Bassler, 1911 (Briozoi Trepostomi), ha messo in evidenza sia la presenza di un apparato opercolare molto più complesso di quanto fino ad ora conosciuto sia un nuovo tipo di gemmazione esozonale.*

INTRODUCTION: THE SCIENTIFIC PROBLEM

Many years ago, one of us (E. Serpagli) sampled, in detail, slightly calcareous nodules for the recovery of conodonts in an Upper Ordovician siltitic sequence of southwestern Sardinia. Instead of conodonts, the nodules yielded a large number of microscopically small, tube-like fossils which chemical analyses revealed to be phosphatic. The shape of these « tubes » varied considerably: a) irregular pyramidal, b) irregular cylindrical, c) cup-like, d) contorted to irregularly flexuous and, e) cylindrical with a round disk-shaped cap with radial ridges. The small « tubes » were sometimes full of matrix and dark brown in color and sometimes empty and transparent; isolated or grouped in small colonies.

The first problem was that of establishing if these « tubes » were parts of a colonial organism or if each tube represented an individual, characteristic and well differentiated from the others. It quickly became clear that many of the isolated and fragment-ed « tubes » were perfectly identical to those constituting the individuals of the small colonies.

In the attempt to establish the systematic position of the seemingly problematic phosphatic or phosphatized fossils, various hypotheses were taken into consideration even if the possibility that these fossils were phosphatic linings of Bryozoa was studied with great care. Indeed, it was evident immediately that the « tubes » with an irregular pyramidal shape were analogous to those illustrated by Eisenack (1964) and Martinsson (1965) and which were interpreted by Martinsson as zooecial linings of Bryozoa.

In the meantime, studies were published regarding problematic phosphatic fossils from the Ordovician of Poland (Gorka, 1969) and from Voljnia, U.S.S.R. (Hynda, 1973); illustrated in these studies were both contorted «tubes» (*Labyrinthotuba*) and irregular pyramidal « tubes » (*Oxytuba*) similar to some of those found in Sardinia. These studies, however, made no contribution towards resolving the problem of the systematic position of such fossils.

In 1978, Bischoff published a study of some phosphatic « tubes » which he considered as phosphatized remains of originally organic thecae of Anthozoa. Bischoff's paper included a series of beautiful SEM photographs which showed clearly that the phosphatic tubes described by him were perfectly identical to the Sardinian ones which terminated in a disk-shaped cap with radial ridges.

In the association from the Sardinian Upper Ordovician, there also were present thecae with irregular pyramidal shapes and others with a cup-like shape which corresponded completely with i) those illustrated by Bischoff in Plates 1 & 2 which he considered as part of the colony of *Septodaeum siluricum* and ii) those previously described by Gorka (1969) as *Oxytuba* and *Phosphotesta*.

We were not satisfied as to the correctness of the systematic and functional interpretation of such thecae, considered by Bischoff as a new species (*Septodaeum siluricum*) representative of a new genus and a new subclass (Septodaearia) of Anthozoa.

All of the authors mentioned obtained the « tubes » by extracting them from the rock using the technique normally employed for recovering conodonts. It seemed quite clear, therefore, that phosphatic « tubes » very similar to those from the Upper Ordovician in Sardinia had been already described in the literature even though they were classified as belonging to questionable taxonomic units (Eisenack, 1964; Gorka, 1969; Hynda, 1973) or to a well-defined systematic group (Bischoff, 1978). At this point, it became ever more evident that we were involved with different pieces of a single puzzle.

When sampling more material in new outcrops of the same formation, we discovered that the tubes terminating in a disk-shaped cap with radial ridges were not exclusively found isolated in the sediments as it had seemed with the first samples cleaned with acetic acid. Instead, tubes with this shape were associated in colonies where they always occupied the most peripheral part (Pl. 2, fig. 1a; pl. 3, fig. 2).

Based on the fact that Bryozoa constitute the predominant part of the fauna in the Ordovician siltstones of southwestern Sardinia and that previous studies reported the presence of phosphatic linings in Bryozoa (McKinney, 1969, fig. 287; Boardman, 1971, pl. 4, fig. 2c; Wass, 1975, pl. 1), we began to take serious consideration of the hypothesis that the phosphatic « tubes » under study might well be none other than more or less complete zooecial linings belonging to colonies of Bryozoa. In fact, treatment of the colonies with acetic acid caused their calcareous portions and thus their continuity to be lost with their consequent fragmentation into isolated, phospatic remains.
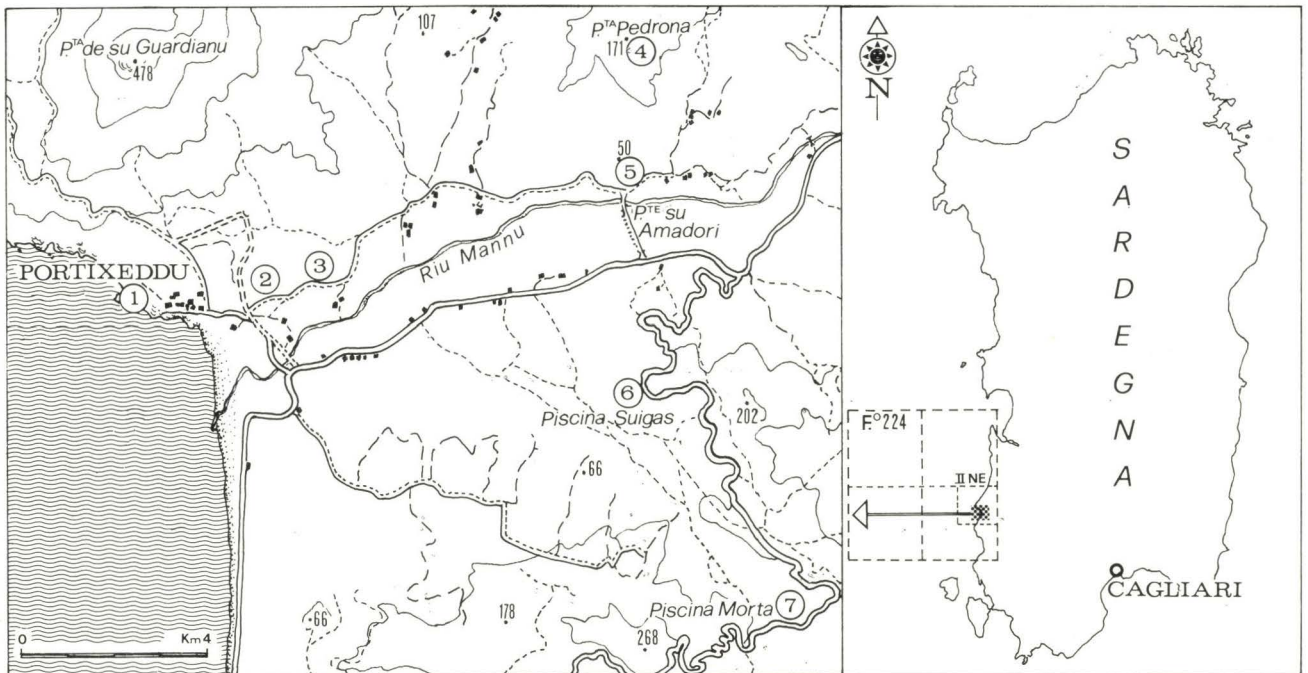
Text-fig. 1 - Detail map showing location of fossiliferous outcrops. 1, Caletta di Portixeddu; 2, Bunker; 3, Vasca anguille; 4, Punta Pedrona; 5, Ponte su Amadori; 6, Piscina Suigas; 7, Piscina Morta.

It was the study, in thin section, of the numerous colonies of Bryozoa which provided clear evidence that the «tubes» terminating with disk-shaped caps were not only autozooecia closed by a particular type of terminal diaphragm (opercular apparatus) (Pl. 3, fig. 1; pl. 4, fig. 1-4; pl. 5, 6) but also that they belonged to the Trepostomate genus *Hallopora* Bassler, 1911. In this genus, in fact, opercular apparati already had been illustrated both in tangential sections (Ulrich, 1890, text-fig. 5b; Bassler, 1906, pl. 26, fig. 12 - use a magnifying glass; Hennig, 1908, pl. 7, fig. 3, 7; Bassler, 1911, fig. 210f; Borg, 1965, p. 82, 83; Corneliussen & Perry 1973, pl. 7, fig. 7, 8 text-fig. 18) and longitudinal sections (Ross, 1969, pl. 43, figs. 3, 4, 7; Astrova, 1965, pl. 25, fig. 2b; Astrova, 1978, pl. 9, fig. 1b). These authors had illustrated longitudinal sections of such structures apparently without recognizing what they were.

The problem of the opercular apparatus and its functional morphology will be discussed in a future paper presently in progress.

A preliminar presentation of our data regarding such a new interpretation of the Lower Palaeozoic coelenterate *Septodaeum* Bischoff, 1978, was made at the IV International Symposium on the Ordovician System, held in Oslo, Norway (Serpagli & Conti, 1982). At that meeting, for the first time, we called attention to the fact that *Septodaeum,* was a bryozoan.

GEOLOGICAL SETTING

The southwestern part of Sardinia — the Iglesiente-Sulcis area — is geologically separated from the main part of the island by the « Campidano basin », a graben, the southwestern margin of which roughly follows a line from Cagliari through Guspini. The bed-rock of Iglesiente-Sulcis consists of sedimentary, metamorphic and plutonic Precambrian rocks (micaschists of Mt. Settiballas, orthogneiss of Mt. Filau, Bithia Formation), the thickness of which could be close to 2000 meters (Junker & Schneider, 1979).

The Cambrian sedimentary succession which follows the Bithia Formation with an apparently concordant contact (Minzoni, 1981) consists of 3 formations (Nebida, Gonnesa and Cabitza) each of which is subdivided into various parts. The Cambrian sequence, which is richly fossiliferous in several levels, has a total thickness of about 2300 meters.

After the deposition of these Early, Middle and (?) Late Cambrian strata, the area was affected by orogenic movements which are commonly referred to as the Sardic phase of the Caledonian orogeny. Later, possibly in the Arenigian, the sea transgressed

over the gently folded, partly eroded and deeply weathered area. As a result, above the Cambrian formations, lying with a net unconformity is a polygenic conglomerate with sandy-clayey cementing material, predominantly dark reddish-brown in color (« Puddinga ordoviciana ») which up until now has been the source of rare and doubtful phyllocarids (Taricco, 1922). In this complex, predominantly on the western side of the Iglesiente, calcareous olistolithes can be observed which are particularly large (some thousands of m³) and which probably are the result of synsedimentary tectonic activity (Brusca & Dessau, 1968). These large horizons are covered by sandstone, sometimes cross laminated, with silty-clayey intercalating material probably of Llandellian age (Cocozza & Leone, 1977).

The first horizon of the well-dated Post - Cambrian succession consists of silty and clayey shales with a low carbonate content and abundant fossil remains (bryozoans, brachiopods, cystoids, trilobites, conularids, chitinozoans, gastropods, ...) of Caradocian age. The earlier views regarding the age stated by old authors have been confirmed by new research on conularids (Serpagli, 1969) and chitinozoans (Laufeld, 1973). Also, according to Havlicek (1981), the brachiopods from the locality Portixeddu in southwestern Sardinia are most similar to those from the Montagne Noire and « may roughly be assigned to the shallow-water *Nicolella* community described by Pickerill & Brenchley (1979) from the Middle Caradoc of northen Wales ». The samples studied in the present work come from this level.

Another fossil bearing horizon, probably referable to the Upper Caradoc-Ashgill consists of clayey biocalcarenites and calcareous claystones, brick red in color and containing many fossils, especially at the base. The carbonate horizon, often substituted by siliceous layers derived from silicification of the carbonates, contains fauna very similar to those of the Caradocian but from which they differ in their lower variety of Bryozoa as well as in the presence of numerous small trolobites, not yet studied.

As for the remaining part of the Palaeozoic sequence of the Iglesiente-Sulcis area, it suffices in this regard to mention that:
— the transition between the Ordovician and the Silurian seems to be gradual through a rythmic sedimentation of sandstones, siltstones and claystones but it is never well exposed;
— the Silurian sequence is very thin, and consists of black graphitic shales in the upper part of which occur well-bedded black limestone with cephalopods, ostracods, bivalves, graptolites, conodonts, ... probably deposited in an epicontinental sea normally oxygenated close to the sur-

face but definitely toxic towards the bottom (Gnoli *et al.*, 1980); and

— the Lower-Middle Devonian sequence with which the sedimentary succession ends in the Iglesiente-Sulcis region, outcrops discontinuously along a narrow belt and consists mainly of clayey shales with thin calcareous intercalations and nodular limestones with tentaculites, crinoids and conodonts. Development of a *stromatactis*-bearing carbonate mud-mound (Gnoli *et al.*, 1981) of Late Pragian-Early Zlichovian age (Olivieri *et al.*, 1980) has been reported locally (Mt. Padenteddu).

SYSTEMATIC PALAEONTOLOGY

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 Palaeontology under the catalog numbers 19857 - 20234.

LOCALITIES, ABUNDANCE, TECHNIQUES

The specimens were collected in different outcrops (text-fig. 1). Consequently, their conditions of preservation are different, depending on more or less intensive phosphatization and diagenization of the local fossil community. Thus, for example, specimens from Caletta (Loc. 1) are particularly well preserved and the phosphatization is almost complete.

The specimens consist of around 4500 phosphatic thecae, numerous fragments of colonies separated from the sediments by various techniques and around 110 macroscopic samples.

Phosphatized thecae were either dissolved out of nodules with dilute acetic 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 miscroscope. The macroscopic samples, consisting of more or less complete colonies were cleaned using jets of compressed air, ultrasound and successively a weak detergent. Thin sections were made of some of the compact samples and were photographed with a Leica camera attached to a Leitz Orthoplan.

MAIN MORPHOLOGICAL TERMS

Terms used for the morphological description are those usually adopted by the bryozoologists plus some new terms introduced here chiefly for the features of the opercular apparatus. A comparison with the anthozoan terms used by Bischoff also is given.

Present work	Bischoff (1978)
opercular apparatus	oral disc
outer ring(opercular margin)	body wall
inner ring	stomodaeum
outer crest	mesentery
inner crest	stomodaeal mesentery
outer intercrestal membrane	intermesenterial membrane
inner intercrestal membrane	stomodaeal membrane
opercular membrane	intermesent.+stomodaeal membrane
opercular muscles	retractor muscles
branching muscles	branching muscles
opercular pores	fenestrae
opercular spine	incomplete mesentery
intercrestal budding	mesenterial budding
interzooecial budding	lateral offset
coelomatic cavity (body cavity)	gastrovascular cavity
cryptocystic peritoneum	gastrodermis
diaphragm	tabula
inner epidermis (ectoderm, hypostegal epithelium)	epidermis
zooecial apex	stolon
zooecial wall	thecal wall

Figs 1-7c - *Hallopora elegantula* (Hall).

  1, aboral view of the opercular apparatus showing no inner and outer crests continuing beneath it, x 120 (n. 20187).

  2, lateral view of an autopore closed distally by the opercular apparatus; the numerous pores are the casts of the intra-zooecial spines, x 110 (n. 20214).

  3, lateral view of another specimen showing the inner ring projecting distinctly above the opercular margin of the zooecium, x 120 (n. 20202).

  4, upper-lateral view where the inner crests are obscured; the pores are usually located in the uppermost part of the zooecial wall in no regular arrangement, x 120 (n. 20191).

  5a, upper view of a complete opercular apparatus showing 6 inner crests and 6 outer crests, x 140 (n. 20189).

  5b, detail of the inner ring of the same specimen, x 310.

  6, upper view of a complete opercular apparatus showing 7 inner crests and 8 outer crests, one of which is partly covered by a bud; note also in two intercrestal membranes the presence of bud scars, x 140 (n. 20220).

  7a, upper-lateral view of an autopore closed by the opercular apparatus; inner crests probably are obscured by remains of the budding platform, x 110 (20212).

  7b, detail of the same specimen showing the outer intercrestal membrane and some opercular pores arranged in rows on either side of two outer crests, x 550.

  7c, detail of 4 pores exposing a system of branching muscles; same specimen, x 1240.
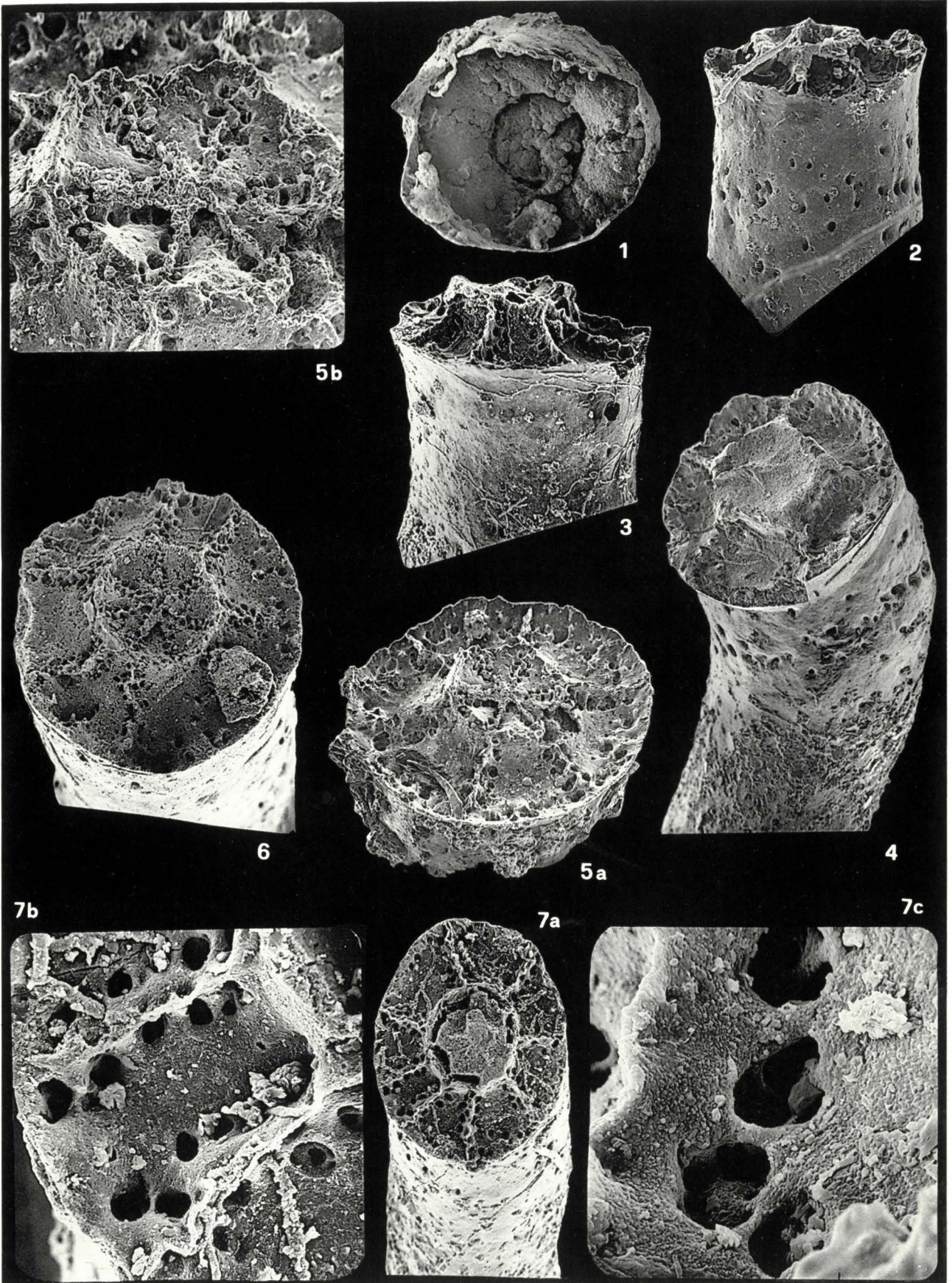
Class STENOLAEMATA Borg, 1926
Order TREPOSTOMATA Ulrich, 1882
Family HALLOPORIDAE Bassler, 1911
Genus HALLOPORA Bassler, 1911
*Type-species - Callopora elegantula* Hall, 1852

HALLOPORA ELEGANTULA (Hall, 1852)
Pls. 1-6; Text-figs. 2-7

1851 *Calopora elegantula* SILLIMAN *et al.,* p. 400;
1851 *Chaetetes fletcheri* EDWARDS & HAIME, p. 271;
1852 *Callopora elegantula* HALL, pp. 144-145, pl. 40, figs. 1a-m;
1973 *Hallopora elegantula* (Hall) - 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* (Hall) - ASTROVA, p. 69, pl. 9, fig. 1a-c;
1978 *Septodaeum 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.

External features — Zoarium erect, solid and ramose, dichotomous branching, with oval, elliptical or circular branches — maximum diameter ranging from 10.0 to 23.0 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 opercular apparatus consisting of two concentric rings linked by radial ridges (Pl. 2, fig. 1a-2; pl. 3, fig. 2; pl. 4, fig. 6). Above the opercular apparatus, new zooecia (mesopores and autopores) can develop by budding and are always located in the most peripheral part of the colony (Pl. 3, fig. 5; pl. 4, fig. 7). Medium length of zooecial tubes from 2 to 5 mm; occasionally a length of about 10-15 mm can be reached in the central part of the colony. Mesopores polygonal, elliptical, round and generally isolating adjacent zooecia (Pl. 2, fig. 6). Mesopore maximum width, approximately, less than 0.2 mm (average from 0.05 to 0.1 mm). Mesopore openings commonly restricted or covered at zoarial surface by concave diaphragms. Acanthopores absent.

Tangential section — Zooecial openings circular or elliptical. Zooecial walls most commonly amalgamate, composed of rather closely spaced concentric laminate microstructure arranged around zooecial openings. A fully developed dark-brown lining, running parallel to the zooecial wall, commonly present. Zooecial tubes may have asymmetrical cystiphragms and cystoidal diaphragms. Adjacent zooecia commonly not contiguous but separated by a series of mesopores (Pl.
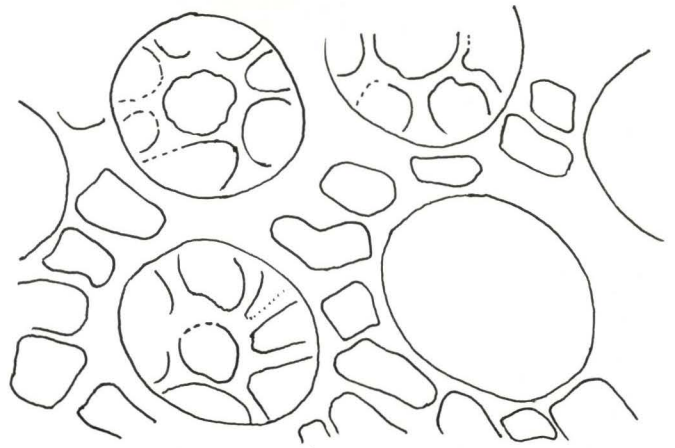

Text-fig. 2 : Diagrammatic and interpretative redrawing of the tangential section figured in plate 3, figure 6 for a better understanding of the structures, x 62, (n. 19963).

EXPLANATION OF PLATE 2

Figs. 1-9b - *Hallopora elegantula* (Hall).
     1a, branch of a colony: axial and peripheral regions distinct; an autopore showing the opercular apparatus located in the exozone, x 15 (n. 20176).
     1b, detail of the operculated autopore, x 62.
     2, zoarial fragment showing two autopores with the opercular apparatus, x 15 (n. 20178).
     3, zoarial fragment showing a budding platform linking several opercular apparati; a new zooecium rises above the platform, see also text-fig 7, x 30 (n. 20164).
     4, two zooecial tubes showing the opercular apparatus and a fragment of the budding platform, x 30 (n. 20159).
     5, upper view of an autopore whose opercular apparatus is obscured by the budding platform, x 140 (n. 20211).
     6, zoarial fragment showing two circular zooecia capped by the opercular apparatus and polygonal mesopores in between, x 40 (n. 20194).
     7, zoarial fragment showing two circular zooecia one of which is clearly capped by the opercular apparatus and polygonal mesopores; budding of new mesopores occurs above the opercular apparatus, x 62 (n. 20163).
     8, zoarial fragment showing a circular zooecium capped by the opercular apparatus, and polygonal mesopores; two new sets of mesopores arise above the opercular apparatus for intercrestal and interzooecial budding respectively, x 62 (n. 20157).
     9a, b, upper views of an autopore closed by the opercular apparatus; a bud arising from more intercrestal membranes is clearly visible and a fragment of a basal part of a second bud also is preserved, x 120 (n. 20160).
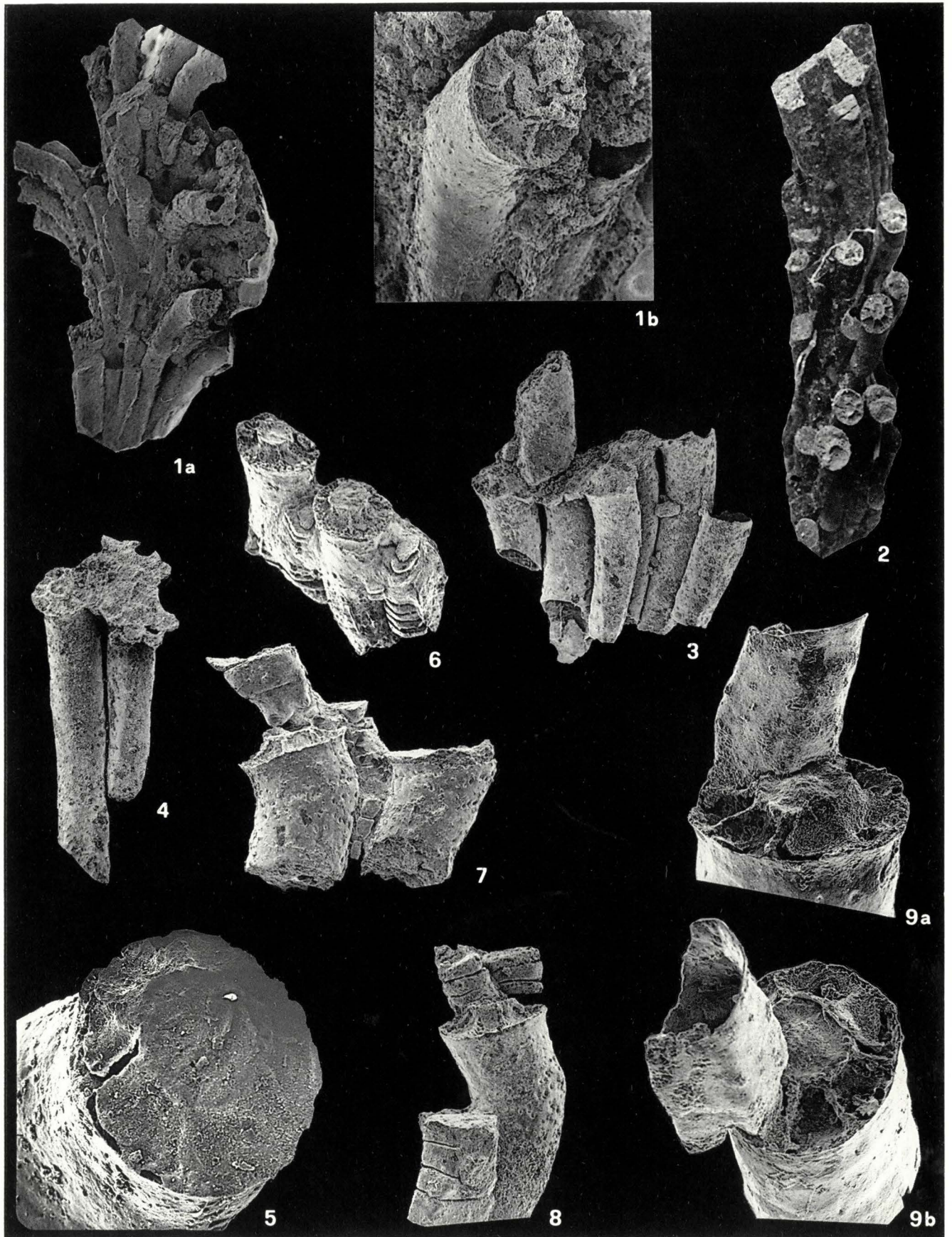
6, fig. 5). Mesopore shape very irregular, from polygonal to circular. Autozooecial/mesozooecial ratio about 1/4 to 1/5. Laminae closest to zooecial openings flexing outward into short peg-like mural spines, variable in number and distribution within zooecia (Pl. 6, fig. 5). Spines, noted only in a moderate number of zooecia, partially buried in zooecial linings. Enlarged circular zooecia may contain the opercular apparatus consisting of an inner and an outer ring joined by some spoke-like rods (crests) that may have been supported by mural spines (Pl. 3, fig. 6; text-fig. 2). This opercular apparatus is very common and below it, there are sometimes preserved soft parts of the lophophore (Conti, 1983).

Longitudinal section, exozone — Zooecia and mesopores curve gently to the periphery approaching the zoarial surface at right angles. Wall laminae run parallel to zooecia and mesopores before bending into the zooecial boundary. Zooecial boundaries not distinctly defined. Autozooecial diaphrágms rarely cystoidal; oblique, compound, concave, convex, curved diaphragms very abundant. Zooecial diaphragms crowded, from 1/4 to 1/2 to a full diameter apart. Zooecial walls gradually thicken, passing from subperipheral to peripheral region. Usually zooecial tubes show opercular apparati. Mesopore diaphragms laminated, 1/2 to 1/3 of the mesopore diameter apart, at base of exozone, but very closely spaced near the zoarial surface. Mesopore diaphragm-wall laminae form units that can be traced across several mesopores. Concentrations of mesopores near the surface very frequent. Mesopore diaphragms can be straight, oblique and cystoidal. Zooecial and mesopore-wall structures similar to leioclemid wall type described by Boardman (1960 p. 20). Zooecial diaphragms commonly very abundant near zoarial surface where their distance becomes similar to that of mesopore diaphragms (Pl. 4, fig. 4). Zooecial lining very common (Pl. 6, fig. 1). Mural spines short, stubby, concentrated only in the distal part of the autozooecia. Spines highly variable in number and in spacing, definitely composed throughout of inflected zooecial wall laminae (Pl. 5, fig. 7).

Brown bodies (cyst-like masses) very common in the autozooecia (Pl. 6, fig. 2). The exozonal/endozonal ratio is about 1/3. The mesozooecial number increases in the exozone because of the greater space available.

It is interesting to note that in the exozone, the passage from an autozooecial pattern to a mesozooecial pattern (the opposite of that in the endozone - pl. 6, fig. 4) often can be observed and this gradual change takes place in 3 different ways:

1) subdivision towards the top of a single autozooecial tube into 2 or 3 mesozooecia, via the insertion of more than one diaphragm;
2) step-wise tapering, localized at the point of intersection of the diaphragm, of a zooecial tube in a mesozooecium via marked thickening of the zooecial wall (Pl. 5, fig. 3);
3) mesozooecial budding above the opercular apparatus (Pl. 5, figs. 1, 2; text-figs. 3, 4).

These and other problems relative to intrazooecial polymorphism of the genus *Hallopora* will be dealt with further in a future publication.
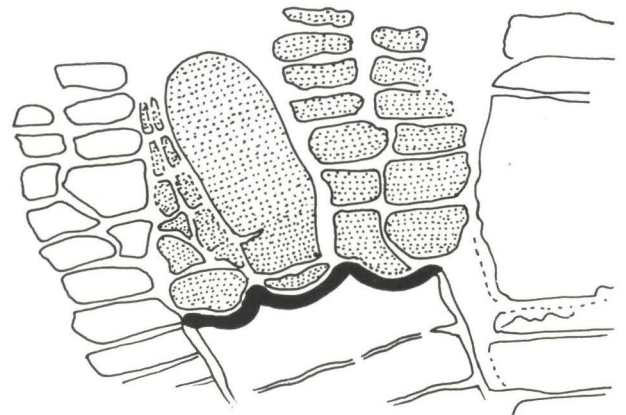
Text-fig. 3 - Diagrammatic redrawing of the longitudinal section figured in plate 5, figure 2 to show the outline of the opercular apparatus (black). Buds directly connected to the opercular apparatus are stippled, x 62, (n. 19968).

EXPLANATION OF PLATE 3

Figs. 1-6 - *Hallopora elegantula* (Hall).
    1, longitudinal section showing mesopore budding from an opercular apparatus; subperipheral region of the colony; see also text-fig. 4, x 62 (n. 19963).
    2, zoarial fragment displaying two circular zooecia capped by opercular apparati, x 18 (n. 19882).
    3a, b, cast of an opercular apparatus in the sediment surrounding the colony; internal moulds of 4 autopores and casts of mesopores also are visible; 3a x 30; 3b x 62 (n. 20175).
   4, aboral view of a budding platform with several partly preserved autopores capped by opercular apparati; in the lower right corner a new generation of autopores is visible, x 15 (n. 19958).
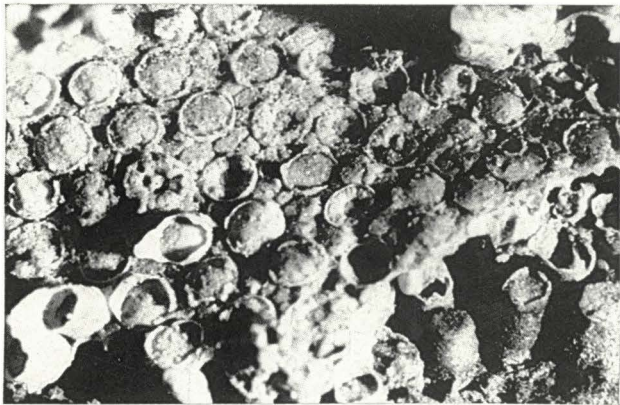   5, zoarial surface displaying many opercular apparati and the related intercrestal buds, x 10 (n. 19931).
    6, tangential section showing large circular zooecia each of which contain an opercular apparatus; see also text-fig. 2, x 62 (n. 19963).
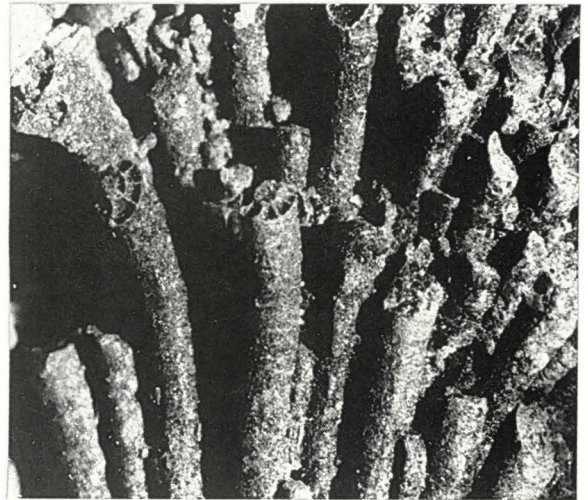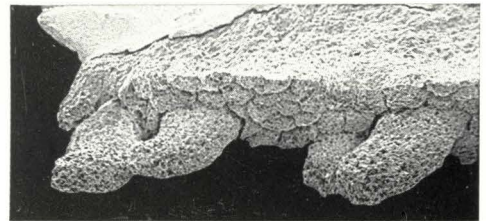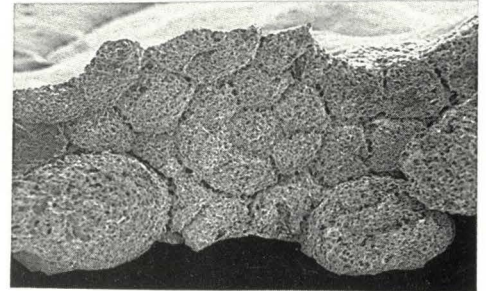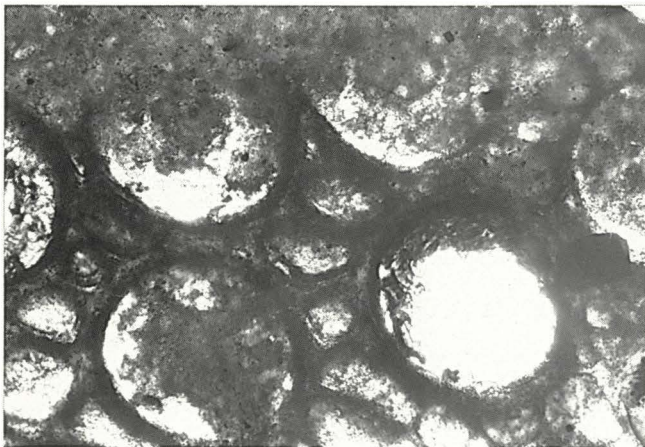
Longitudinal section, endozone — Zooecial diaphragms straight in axial zone, one tube diameter apart, then 2 or 3 diameters apart; in central tubes, diaphragms 7-8 diameters apart. In the elongate initial part of the tubes, characterized by very small cross sectional diameters, are closely spaced diaphragms (mesozooecial pattern) that are spaced progressively more widely where the zooecia have expanded to intermediate or nearly maximum diameter (autozooecial pattern). Interzooecial development of buds, as initial mesozooecia then changed to autozooecia, implies a subordinate function for the mesozooecial portions. Therefore mesozooecia must have functioned as space filling units that structurally bolstered the colony. Brown bodies, collected in cysts are very frequent in the zooecial tubes, especially near walls or diaphragms (Pl. 4, fig. 4). Brownish cuticular, collapsed tube-like structures are located in the zooecial tubes. Mesozooecia and autozooecia often display brown linings along diaphragms and walls. The mesozooecial/autozooecial ratio is commonly about 2 to 1.

Transverse section — Colonies display very distinct axial (endozone) and peripheral (exozone) regions (Pl. 4, fig. 1). Zooecial tubes have subcircular or polygonal shapes and their average diameter is always more than 0.2 mm. Round zooecial openings are fully isolated by rectangular and polygonal mesozooecia (Pl. 6, fig. 6). Zooecial walls, in the outer part of the endozone, begin to curve gradually towards zoarial surface. Lining parallel to zooecial laminae also is present (Pl. 6, fig. 7).

THE OPERCULAR APPARATUS OF H. elegantula

Generally, the opercular apparati of the Sardinian specimens are circular in shape. The average diameter is about 0.4 to 0.5 mm. They consist of two concentric rings linked by sinuous radial ridges (outer crests) that range in number from 5 to 10. Radial ridges (inner crests) also occur in the inner ring and number 5

to 7. The inner crests are only occasionally the prolongations of the outer crests (Pl. 1, figs. 5a, 5b, 6, 7a). Both sides of the crests have strong, equally well developed branches grading laterally into the intercrestal membrane. Between the branches, there are some oval-shaped to subcircular openings that we propose to call opercular pores instead of « fenestrae » (Bischoff, 1978). The pores are usually arranged in one or two rows on either side and along the entire length of the crests (Pl. 1, fig. 7b). In some specimens, irregularly scattered pores occur over the outer intercrestal membrane and near the opercular margin. In all
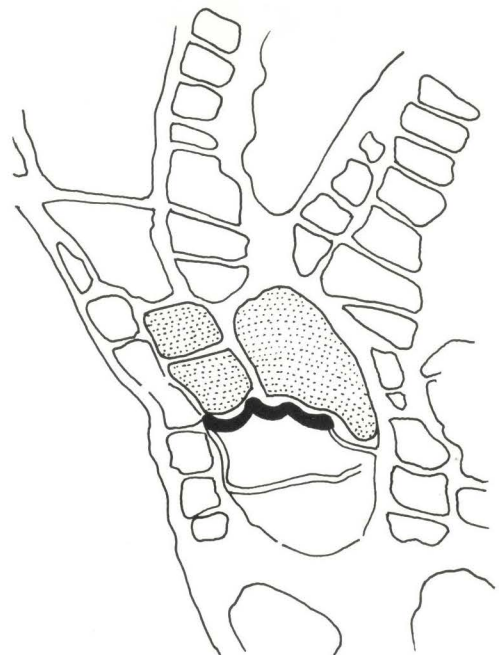
Text-fig. 4 - Diagrammatic redrawing of the longitudinal section figured in plate 3, figure 1 to show the outline of the opercular apparatus (black). Buds directly connected to the opercular apparatus are stippled, x 62, (n. 19963).

EXPLANATION OF PLATE 4

Figs 1-7 - *Hallopora elegantula* (Hall).

1, transverse section showing central axial bundle of large circular zooecia isolated by polygonal to irregularly subpolygonal mesopores; peripherally part of the exozone is visible, x 10 (n. 20003).

2, longitudinal section displaying configuration of zooecia and mesopores, x 10 (n. 19962).

3, sublongitudinal section showing the exozone of the colony with several autopores capped by opercular apparati, x 10 (n. 19963).

4, longitudinal section displaying configuration of zooecia and mesopores as well as interzooecial budding; note the sudden increase of mesopores toward the exozone, x 10 (n. 20004).

5, casts of many opercular apparati in the sediment surrounding the colony, x 10 (n. 19875).

6, zoarial surface displaying several autopores one of which is still capped by the opercular apparatus, x 22 (n. 19908).

7, zoarial surface showing many opercular apparati and the related intercrestal buds, x 35 (n. 19931).

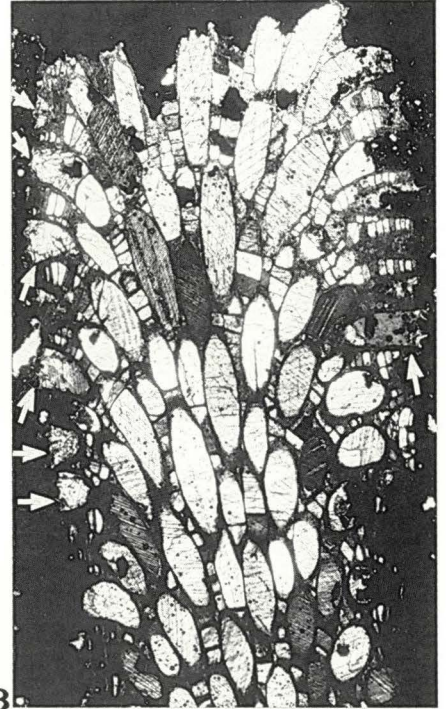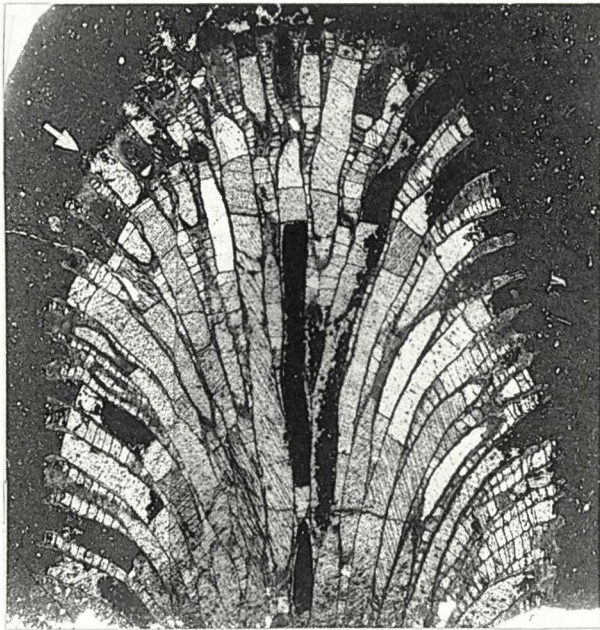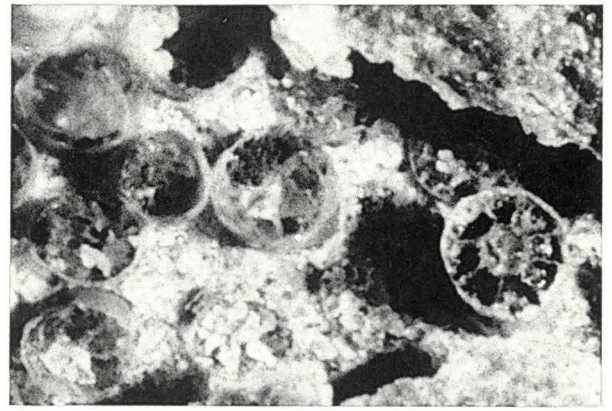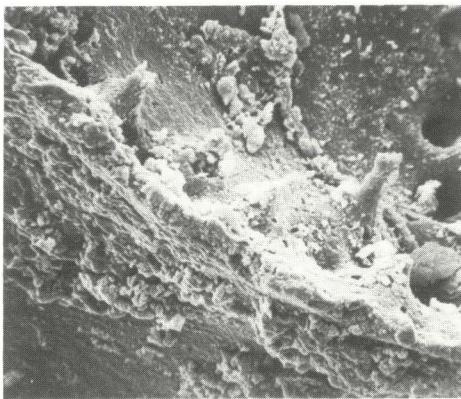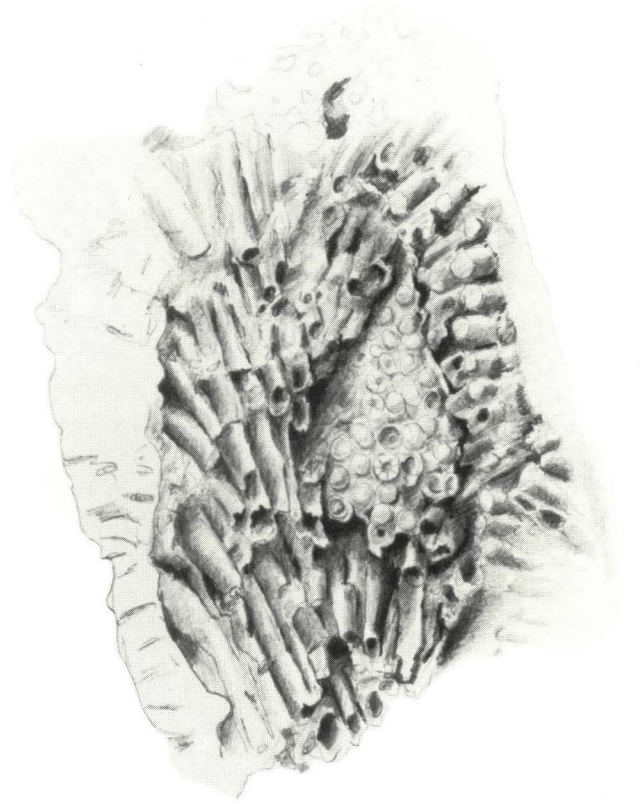The arrows in figures 2, 3, 4 point to autopores capped by opercular apparati.
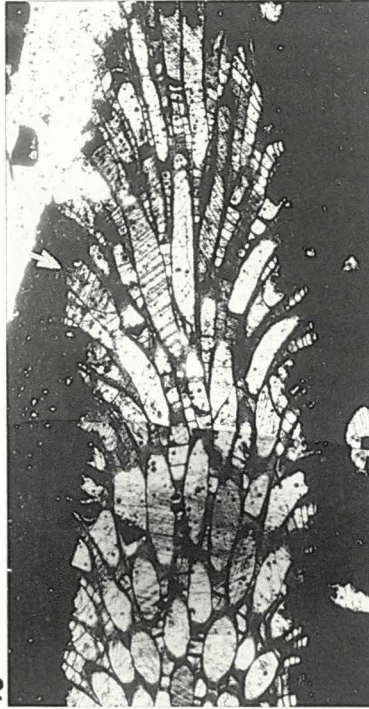
specimens, pores decrease in size towards the center of the structure. The pores always expose a system of branching muscles, extending to a moderate depth inside of the opercular membrane. The branching system of the crests is very complicated (Pl. 1, fig. 7c). The branches seem to subdivide into shorter and smaller stems. The thinning of the stems increases towards the inner side of the opercular membrane. As a result, the pores are subdivided into a labyrinth of many chambers. Figure 3 of plate 1 shows a lateral view of the inner ring projecting more or less distinctly above the opercular margin of the zooecia.

The presence of intercrestal buds is the most important feature of the opercular apparatus of the Sardinian *Hallopora* (Pl. 1, fig. 6; pl. 2, figs. 7, 8; text-figs. 3, 4). The buds are variable in shape, number and position. Some are located in the inner ring and others in the outer ring. They can occupy one or more intercrestal membrane (Pl. 2, figs. 9a, b). The buds can be directly connected to the opercular membrane or can be separated from it by a platform which linked and covered the opercular apparati of different autozooids (Pl. 2, figs. 3-5; text-figs 6, 7). In this last case, a total regeneration took place by the new buds. There could be more than one regeneration phase in the same

Text-fig. 6 - Diagrammatic drawing to show a large fragment of a colony in which is clearly visible part of the budding platform, x 10, (n. 19958).

colony (intracolony overgrowth) (Pl. 3, fig. 4; text-fig. 6). It is not clear if there was communication between the opercular pores and the buds but some specimens seem to exlude this possibility (Pl. 2, figs. 9a, b).

On the lateral surface of the zooids and near the opercular apparatus, there are many perforations in no regular arrangement (Pl. 1, figs. 2, 4). Probably they are the casts of the intrazooecial spines observed in many thin sections. Spine-like projections (opercular spines) also are located near the opercular margin (Text-fig. 5).

Text-fig. 5 - Detail of the opercular margin showing spine-like projections (opercular spines), x 310, (n. 20201).

EXPLANATION OF PLATE 5

Figs. 1-8 - *Hallopora elegantula* (Hall).

1, longitudinal section showing development of two intercrestal buds above the opercular apparatus; detail of fig. 2, pl. 4, x 62 (n. 19962).

2, longitudinal section displaying development of 4 intercrestal buds above the opercular apparatus; inside the bud, arising from the inner ring, brown cuticular structures also are visible; see text-fig. 3, x 62 (n. 19968).

3, longitudinal section showing concentration and step-wise tapering of mesopores; leioclemid-wall structure is evident, x 62 (n. 19968).

4, 6, longitudinal sections displaying several opercular apparati; details of fig. 3, pl. 4, x 62 (n. 19963).

5, longitudinal section showing a bud arising from the inner ring; detail of fig. 4, pl. 4, x 62 (n. 20004).

7, longitudinal section displaying zooecial lining and intrazooecial spines, x 62 (n. 19984).

8, longitudinal section displaying two opercular apparati, x 62 (n. 20003).
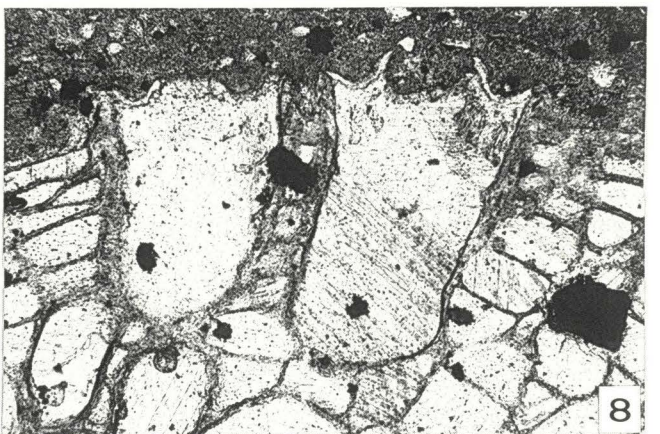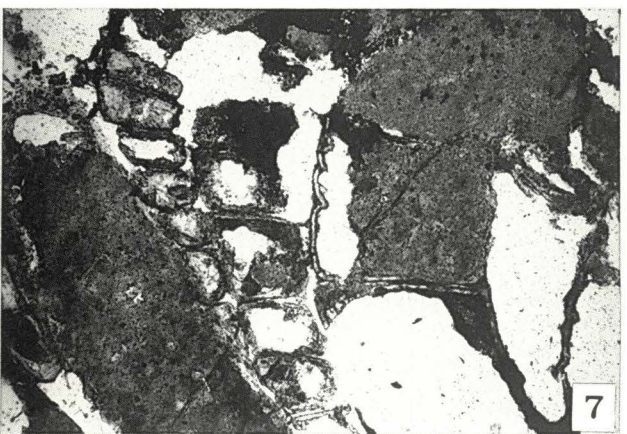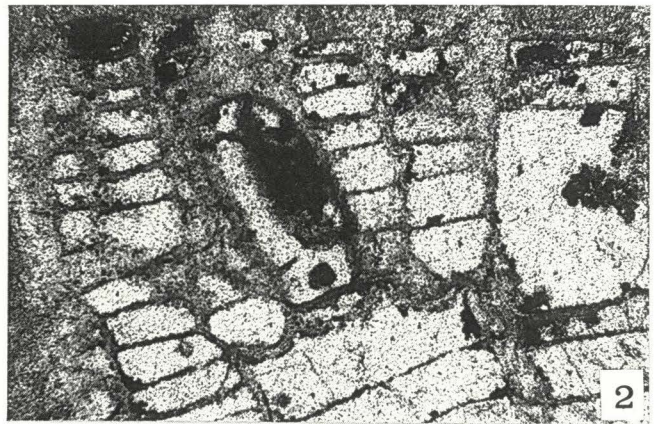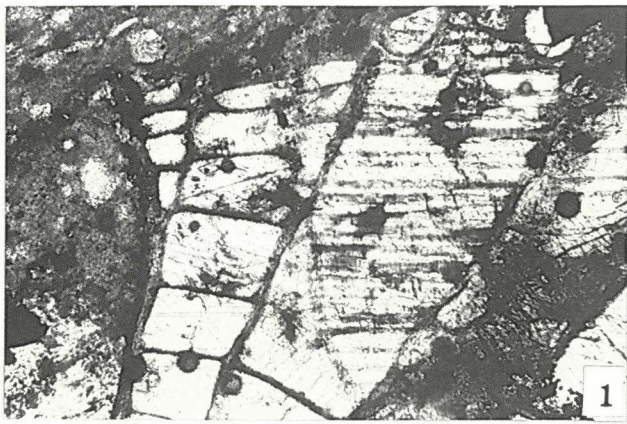
DISCUSSION

The Sardinian specimens have extensive analogies with *H. elegantula* as regards the general development of the colony, the number and insertions of the diaphragms and the mesopore/autopore ratio. The opercular apparatus of the Sardinian halloporas, however, occurs more frequently and most of the time has different levels of budding. In *Hallopora* type species only 8 external radial crests are observed and, apparently, internal radial crests are absent (Hall, 1852; Bassler, 1911). There also are close similarities with the forms illustrated by Ross (1969) as *Calopora elegantula* which have numerous mesopores in the peripheral region that surround autozooecia equipped at times with opercular apparati. In a longitudinal section illustrated by Ross (Pl. 43, figs. 3, 4, 7), there also is visible a layer of budding above the autopores and mesopores, all positioned at the same height, some of whose buds depart from the inner ring and others from the outer ring. The mesopores contain many cystoidal diaphragms and in the exozone is possible to observe the passage from an autozooecial pattern to a mesozooecial one, a feature completely identical with the Sardinian specimens. Budding of mesopores from autopores also can be seen in the specimens figured by Astrova (1965, 1973, 1978).

Even so, differences in certain structures are found when comparisons are made with the specimens of *H. elegantula* figured by Corneliussen & Perry (1973) and by Mc-Kinney (1977, pl. 2, fig. 3a), which show a high number of cystiphragms, something very rare in the Sardinian specimens.

Perry and Hattin (1960) speak of thick spines present in various layers of the colony of *H. elegantula* while in the Sardinian specimens, the spines are concentrated in the autopores, exclusively close to the zoarial surface.

A correspondence between intrazooecial spines and opercular apparati, often found in the autozooecia of *H. elegantula* from Sardinia, also has been found in *H. elegantula* from Tennessee (Corneliussen & Perry,

1973). In this work, the authors, using an hypothesis of Hennig (1908), suggested that the spines were the organs which supported the outer radial crests of the opercular appartus. It should be kept in mind that Corneliussen & Perry, just as all other preceeding authors, considered the opercular apparatus as being centrally perforated and completely similar to a basal diaphragm. The new facts which come to light from the study of the Sardinian samples are i) to have recognized the opercular apparatus, for the first time, in longitudinal section and ii) to have shown the existence of inner radial crests and of buds which depart from the top of the apparatus.

One final observation that should be mentioned here is that the species *Archaeocyathellus* (*Coscinocyathus*) *siluricus* Schouppé 1950, found in Caradocian beds of the eastern Alps and interpreted as being an archaeocyathid, is very close to our tube-like fossil remains. The only difference is that *A. siluricus* is two or three times bigger. Interestingly enough in that assemblage halloporids also are very common.

## CONCLUDING REMARKS ON THE SYSTEMATIC POSITION OF *SEPTODAEUM*

Bischoff (1978) published the first and sole description of *Septodaeum siluricum* which he based on more than 6800 phosphatized thecae and 12 complete specimens (the holotype and 11 paratypes). The study was done very carefully and every detail considered and investigated.

The presence of a « stomodaeum » in combination with the mode of asexual reproduction led the author to regard the new taxon as a representative of the Anthozoa. Furthermore he placed *Septodaeum siluricum* in a new subclass (Septodaearia) because of the unusual anatomical configuration of the « mesenteries », the mode of their insertion, the possession of « stomodaeal mesenteries » and the presence of « stomodaeal and intermesenterial membranes ».

EXPLANATION OF PLATE 6

Figs. 1-7 - *Hallopora elegantula* (Hall).
    1, longitudinal section showing zooecial lining, x 160 (n. 19966).
    2, longitudinal section displaying a large development of brown granular bodies, x 62 (n. 19971).
    3, longitudinal section showing an autopore capped by an opercular apparatus; detail of fig. 3, pl. 4, x 62 (n. 19963).
    4, longitudinal section displaying the passage from a mesozooecial pattern to an autozooecial pattern; endozone of the colony; brown granular bodies also are visible, x 62 (n. 19992).
    5, tangential section showing intrazooecial spines, x 62 (n. 19979).
    6, transverse section displaying zooecial lining and cuticular structures, interpreted as probably being remains of a membranous sac, x 62 (n. 19993).
    7, transverse section showing details of the phosphatic lining, x 160 (n. 19976).
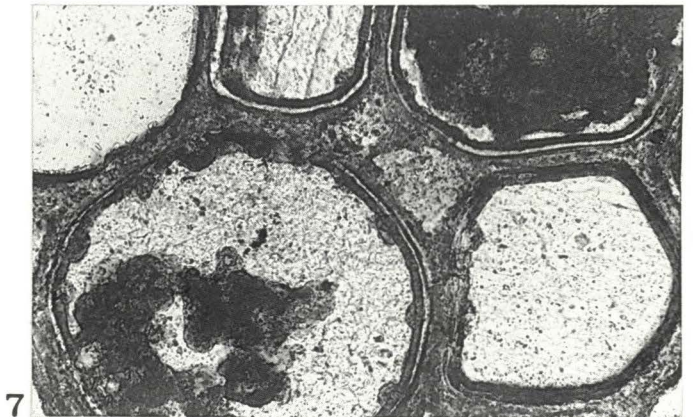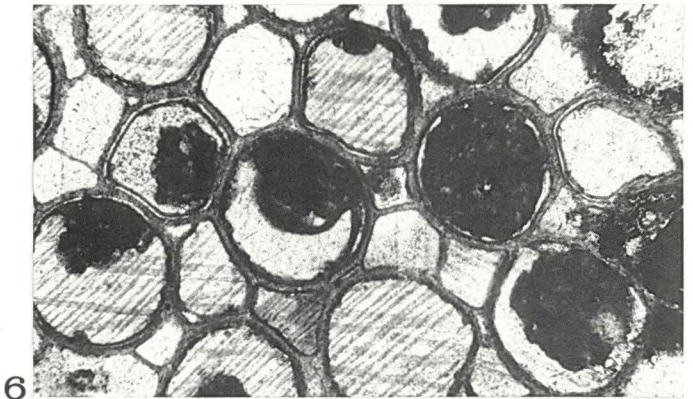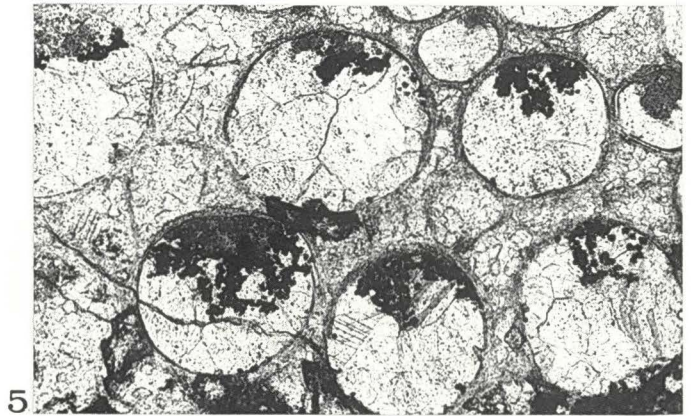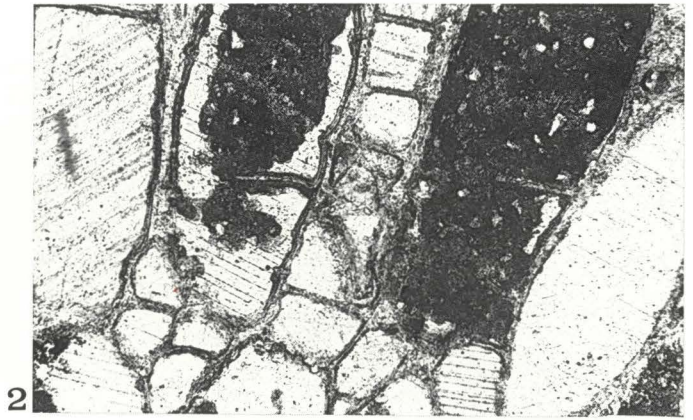
Interestingly enough, Bischoff must have realized that something was wrong in such a systematic assumption because he noted (p. 254) that « The generally accepted schemes of anthozoan development do not readily accommodate the Septodaearia n. subclass with their unusual combination of unique anatomical features ». So, he regarded the new subclass as an ancient, separate phyletic line of Anthozoa.

There are at least 5 principal reasons why *Septodaeum* cannot have been an anthozoan:

1 - Clear evidence for the presence of a true stomodaeum was never obtained.

2 - The presence of complete mesenteries was only inferred but not demonstrated.

3 - The occurrence of a system of « branching muscles » below the level of the intercrestal membrane (= stomodaeal membrane) was only speculative.

4 - The complete crests (= mesenteries) are inserted singly, never coupled nor paired.

5 - The opercular muscles (= retractor muscles) are equally developed on both faces of the crests.

As can be seen clearly either in the aboral view (Pl. 1, fig. 1) which shows the lower part of the opercular apparatus (= oral disc according to Bischoff) or in the longitudinal sections (Pl. 5, fig. 8; Pl. 6, fig. 3), no structural part of the opercular apparatus continues beneath it. Therefore, it is not possible to talk about stomodaeum, complete mesenteries or any system of branching muscles, prolongated to the interior of the coelomatic cavity (= gastrovascular cavity).
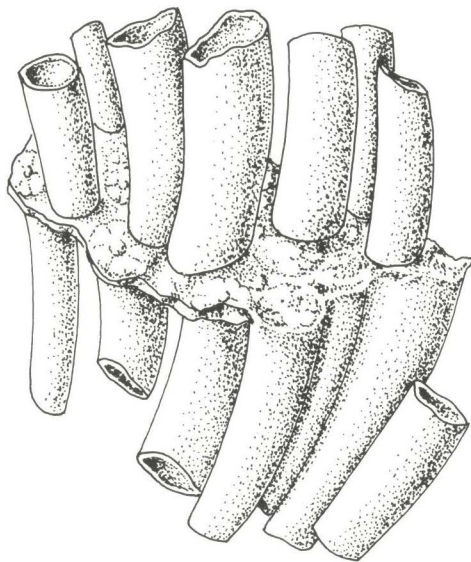
Text-fig. 7 - Interpretative redrawing of plate 2 fig. 3 to show the budding platform linking autopores and new generation of zooids, x 40, (n. 20164).

Another point of divergence between our opinion and that of Bischoff is that according to him these structures do represent exclusively soft parts and not skeletal elements secreted by the animal (p. 239). In reality, as can be seen clearly from the thin sections (Pl. 6, figs. 1, 7; pl. 5, fig. 7), such structures are also caused by the phosphatization of soft tissues which line the inside of calcareous skeletal elements secreted by the animal. The problem of phosphatic linings in Bryozoa is the subject of another study presently in progress.

The phosphatized thecae figured by Bischoff (Pl. 1, figs. 26-31; pl. 2, figs. 40-44) are very similar to those described by Eisenack (1964), Martinsson (1965), Gorka (1969) and Hynda (1973); based on our results, we believe, in agreement with Dzik (1981, p. 848), that such thecae can be attributed to isolated portions of phosphatized zooecial linings belonging to different colonies of Bryozoa. Today, there is much support for the necessity of revising the literature on such problematic phosphatic fossil remains.

As has been shown, budding is another peculiar aspect of « Septodaeum » and in light of this new interpretation, the two different types of asexual reproduction described by Bischoff (1978, pp. 246, 247) can be re-interpreted as follows:

1) The so-called « mesenterial budding » becomes non other than an episode of colonial regeneration or rejuvenation (zoarial overgrowth-Boardman, 1960), a very common phenomenon in the exozones of many bryozoans (text-figs. 6, 7).

2) The so-called « local offset » (Bischoff, pl. 5, fig. 52a), instead, is the typical « apparently disordered interzooecial budding» of mesozooecia (McKinney, 1977), characteristic of 11 genera of Bryozoa and in particular of the genus *Hallopora*. This type of budding, however, differs from that hypothesized by Bischoff in taking place without stolons.

Finally, as further evidence that the phosphatized thecae illustrated by Bischoff are non other than bryozoans of the genus *Hallopora*, it also is important to point out that:

1) Bischoff found in the same association a great abundance of other phosphatized fossil remains, among which are many bryozoans (p. 231);

2) The stratigraphic range of *Septodaeum* is exactly the same as that of *Hallopora*, i.e., from the Lower Ordovician to Early Devonian.

These, then, are the main reasons which justify the present statement that *Septodaeum* does not represent anything new but is simply a Trepostomate bryozoan belonging to the genus *Hallopora*.

ACKNOWLEDGMENTS

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