

## Microstructure and septal arrangement in a primitive Triassic Coral

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**ABSTRACT** — A research through optical and electron scanning microscope has been developed on more than 120 specimens of an Alpine Triassic single or phaceloid coral, here still named *Protoheterastraea leonhardi* (Volz) (pars). The specimens are still preserved in their original mineralogical composition (aragonite, with high strontium content) and structure.

Bilateral symmetry of septal insertion, peripheral insertion of septa two-by-two, absolute predominance of protosepta, no cyclic insertion of metasepta, are all characters more reliable to the late Paleozoic *Rugosa* than to the *Scleractinia*. On the other hand, no pinnate septal insertion occurs, as in *Rugosa*, and a theca is constantly present as an essential element of the skeleton.

Theca is given by aragonitic fibrolamellae, longitudinally finely folded. Contiguous, terminal surfaces of c-axes of aragonitic aggregates of contiguous fibrolamellae con knit together and give origin to a typical fibrous tissue.

Septa — discontinuous, frequently spiny and inwardly inclined — seem to have a fibrolamellar microstructure too: they seem to arise from a progressive infolding of thecal fibrolamellae. This structure cannot be relied either to the *Rugosa* or to the *Scleractinia*.

Further investigations are in course on the peculiar structure of *Protoheterastraea leonhardi* (Volz) (pars).

**RIASSUNTO** - [MICROSTRUTTURA E DISPOSIZIONE SETTALE IN UN CORALLO PRIMITIVO DEL TRIAS SUPERIORE] — Un'indagine morfologica e microstrutturale mediante microscopio ottico e a scansione è stata effettuata su 120 esemplari di una specie che per il momento viene ancora ascritta provvisoriamente a *Protoheterastraea leonhardi* (Volz) (pars). Altri 50 esemplari trovati di recente (R. Zardini racc.) convalidano le presenti deduzioni.

Un lavoro precedente, eseguito dall'A. e collaboratori, aveva dimostrato che lo scheletro di questa specie — come degli altri *Scleractinia* e di molte spugne provenienti dagli stessi affioramenti — è tuttora costituito da aragonite, con alto contenuto in stronzio, più o meno corrispondente allo stronzio contenuto in coralli ermatipici attuali. L'aragonite è in aggregati cristallini paralleli secondo l'asse z, casualmente disposti secondo gli altri due assi.

Lo studio morfologico e strutturale ha dato i seguenti risultati.

1. I setti sono rappresentati per lo più dai soli protosetti.
2. I protosetti hanno una disposizione spiccatamente bilaterale, con parametri costanti: setto cardinale più ridotto del controsetto, controalari più ridotti degli alari.
3. I setti hanno origine periferica.
4. I setti sono verticalmente discontinui, a volte ridotti a spine, a volte mancanti totalmente per lunghi tratti, lasciando la teca come unico elemento scheletrico.
5. I setti originano due a due, e non in numero di sei contemporaneamente, come è la regola. Qualunque sia il loro aspetto, essi immergono verso le regioni assiali.
6. I metasetti, quando presenti, sono irregolarmente distribuiti nei sestanti, cioè non hanno distribuzione ciclica né pinnata.

7. I setti hanno struttura fibrolamellare, non distinguibile dalla struttura tecale. Ciò appare alla scansione, a forte ingrandimento (8000-10000 x).

8. Strutture trabecolari vere e proprie non sono state finora osservate nei setti.

9. La teca, irregolare, fortemente rugosa, è costituita da una successione centripeta di sottili fibrolamelle ondulate, aventi le fibre disposte perpendicolarmente alla tangente al punto esterno di emergenza. L'ondulazione produce una fittissima solcatura longitudinale alle pareti esterna e interna della teca.

Tutti i caratteri elencati fanno di questa forma un tipo completamente aberrante sia rispetto a quanto si sa dei *Rugosa*, sia rispetto agli *Scleractinia*. Il significato filogenetico della specie è evidente, e la sua posizione sistematica verrà discussa nel prossimo lavoro.

## I. INTRODUCTION

Most part of the substance of the present paper was presented at the International Symposium on Coral Reefs, held on the Great Barrier Reef, Australia, on June 22nd - July 2nd, 1973, and will appear in the Proceedings of the Symposium.

Structural and paleobiogeochemical investigations have been developed by the writer and collaborators during the last few years on some peculiar genera of Coelenterata, collected from the lower Upper Triassic (Carnic) San Cassiano strata near Cortina d'Ampezzo, Dolomites, Italy. The absolute age is roughly 210 million years.

A monographic paper on the coral fauna of Cortina is in preparation.

A preliminary communication on the genera *Protobeterastraea* Wells, *Pinacophyllum* Frech and *Cassianastraea* Reuss was presented at the Second International Paleontological Symposium on Corals, held in Novosibirsk on 1971. It is supposed that the paper is still in press.

The present paper intends to give some informations and documentations on skeletal structure and septal arrangement in a large group of specimens recently collected, here provisionally still identified as *Protobeterastraea leonhardi* (Volz) (pars), concerning « aberrant » specimens figured by Volz (1896, pl. XI, fig. 24), and discussed by Schindewolf (1942, p. 228 pars, pl. 17).

In the far 1896 Volz described and illustrated two new species from the Triassic « Cassian » strata, and recognized that they pertained to a new genus, for which he

coined the name of *Hexastraea* Volz. He described first *Hexastraea fritschi* Volz, followed by *H. leonhardi* Volz. The Author, as usual at that time, did not designate either a type species or the holotypes of the two new species.

The generic name was subsequently invalidated by Wells (1937), because of homonymy. The new name was *Protobeterastraea* Wells (1937). As a type species, Wells selected the second species described by Volz, that is *P. leonhardi* (Volz), on the base of the three fragments previously studied by Volz. Wells did not illustrate any specimen of the type species.

During the second world war, the genus was almost contemporaneously mentioned from both sides of the barricade, respectively by Schindewolf (1942) in his volume on « Polycoelien und Plerophyllen » and by Vaughan and Wells (1943) in their fundamental « Revision on Suborders, Families and Genera of Scleractinia ».

Schindewolf was the first to point out the importance of the archaic septal insertion of *Protobeterastraea leonhardi* (Vols), working on 12 excellent thin section obtained from three poor original fragments. He stated that *Protobeterastraea leonhardi* (Volz) represents a document of phylogenetic connection between *Rugosa* and *Scleractinia* for its bilateral symmetry, arising of septa two-by-two, « incomplete » development of counter lateral septa. Moreover, he added (1942, pag. 237): « Die Verantwortung dafür, dass die beiden Arten Gattungsgleich sind, muss ich deren Bearbeiter W. Volz (1896, S. 90ff.) bzw. dem Be-

gründer des neuen Gattungsnamen *Protobeterastraea* J.W. Wells (1937, S. 75) überlassen ».

The statement of Schindewolf was first accepted (1956), then rejected by D. Hill (1960), who observed that Schindewolf based his statement on « aberration in the septal insertion in some Triassic Hexacorals (e.g. *Protobeterastraea*) ». This objection was quite pertinent, since the material available at that time was too scarce for such important statement, and no structural investigation had yet been approached.

Vaughan and Wells (1943) did not give any illustration of the type species selected by Wells: they report a text figure of *Protobeterastraea fritschi* (Volz) given by Volz to show « die Calicinalknospung unter Beteiligung eines Hauptseptums ».

Not even in Moore's « Treatise on Invertebrate Paleontology » 1956, vol. F) the type species of *Protobeterastraea* Wells is figured (Wells, 1956, pag. F396).

For the present investigation, more than one hundred and twenty specimens were available. The specimens were collected partly by the writer in the last few years, mostly

by Mr R. Zardini of Cortina d'Ampezzo (Dolomites, Italy) during half a century of fossil field collecting, chiefly on the outcrops near Cortina. Wonderful small pieces, preserved in their finest structures, were collected at Alpe di Specie (« Seelandalp ») and near the Misurina lake. In both localities, the corals — like all other abundant fossils — are imbedded in a pel-micritic gray-brown limestone, consisting of compact blocks of the most different sizes and weights up to dozens of tons, chaotically lying under a few decimetres of a debris marly deposit. When attacked by humic acids, the blocks let fossils become free and crop, shining white, out of the calcareous matrix.

For severe reasons of space, any general discussion on the still confused and controversial skeletal and sometimes « non-sense » terminology on corals cannot take place in the present paper. The most elementary terms are here provisionally adopted, at least until the skeletogenesis of this peculiar coral will be entirely understood. For example, the simple term « theca » is preferred to « eutheca », « pseudotheca », « syntheca », « peritheca », « paratheca », etc.; « stereome » — the

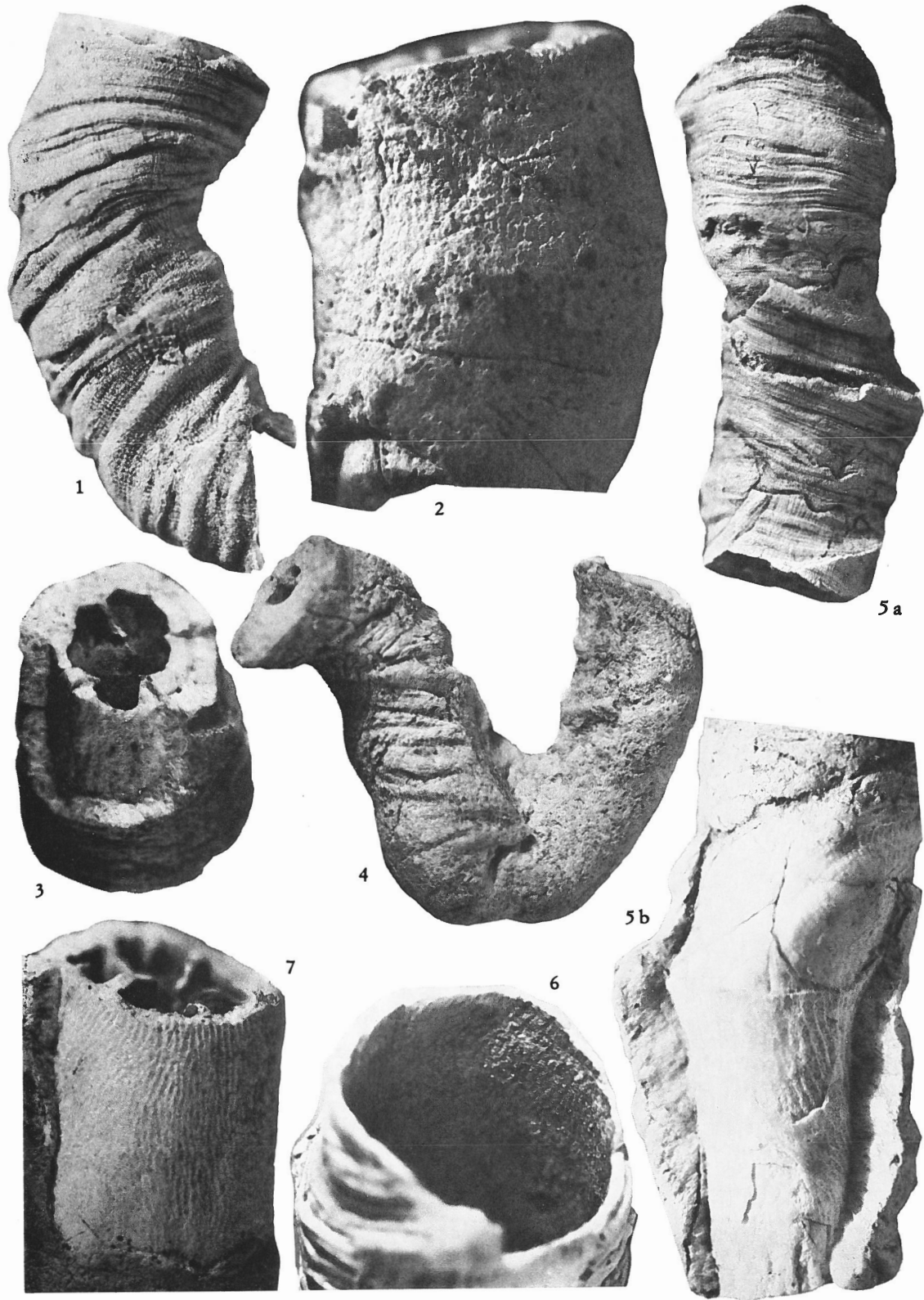
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PLATE 2

*Protobeterastraea leonhardi* (Volz) (pars) from lower Upper Triassic, San Cassiano Strata near Cortina (Dolomites, Italy).

- Fig. 1 - Ceratoid specimen: growth wrinkles and longitudinal thecal microridges, which are neither septocostae nor interseptal striae but thecal longitudinally folded fibrolamellae; 7x (spec. destroyed). Locality: Alpe di Specie (R. Zardini collected).
- Fig. 2 - Ceratoid specimen (incomplete) sparsely rugose, longitudinally ridged. See septal insertion at Pl. 2, figs. 1, 5, 7; 5x. Locality: Alpe di Specie (R. Zardini collected).
- Fig. 3 - Cylindric specimen; wall broken to show persistence of longitudinal microridges; protosepta 4, lacking of the two CL; 12x. Locality: Alpe di Specie (R. Zardini collected).
- Fig. 4 - Bigeminated corallite. Only a hollow theca is developed at the base of both individuals; and only 2 protosepta appear on the top calice; 7x. Locality: Misurina (E. Montanaro Gallitelli collected).
- Fig. 5 a-b - Subcylindrical specimen; growth wrinkles well developed, longitudinal microridges visible; 5a, 7x; 5b, other side of the same specimen, broken to show the « onion skin » structure of the wall and the longitudinal microridges (foldings) of the concentric fibrolamellae forming the wall. The direction of the ridges follows the growth irregularities, 10x. Locality: Alpe di Specie (R. Zardini collected).
- Fig. 6 - Absence of septa (11 similar specimens occur); microridges well visible on both internal and external surfaces of the thin theca, 10x. Locality: Alpe di Specie (R. Zardini collected).
- Fig. 7 - Thick wall broken to show the thecal structure, 10x. Locality: Misurina (Dolomites, Italy) (R. Zardini collected).

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Greek etymology of which (στερέωμα-ατος) does not have any other meaning but of « solid body » — will be rarely used; the term « fibrolamella » is decidedly preferred to « lamella », for the lamellae, even the thinnest ones, as the « flakes » of Wang (1951), mm. 0,001 thick, are obviously threedimensional, according to Ogilve (1897), Hill (1936), Kato (1963), and that during the skeletogenesis each lamella is formed by aragonite needles disposed perpendicularly to the outer margin.

The electron scanning investigations show now that the lamellae are in effect fibrolamellae.

For the same reasons of space, any historical review of the different interpretations given by the different authors to the skeletal structure of Scleractinia cannot be discussed here. The reader is suggested to consult the most authoritative contributions given on this subject during the last decades by many authors, among whom I want to cite Bryan and Hill (1941), Hill (1935-1973), Schindewolf (1942), Wang (1950), Vaughan and Wells (1943), Wells (1956), Kato (1963), Schouppé and Stacul (1955-1967), Goreau and Goreau (1959-1961).

I feel myself very indebted to Mr Zardini for the outstanding amount of specimens he collected for my study: to dr. A. Russo, dr. F. Russo, dr. M. Gnoli, Mrs N. Ferrari Pollacci and Mr G.C. Leonardi, all of the Institute of Paleontology of the University of Modena, respectively for the profitable discussion on general problems in scleractinian corals, for enthusiastic help and experience in performing electron scanning micrographs, for many good photographic prints, for typing the manuscript and for all the drawings of the present paper. My best thanks are given to dr. P. Kier, dr. A.G. Cooper, dr. W.J. Sando of the U.S. National Museum (Natural History) in Washington, D.C., for their assistance during my stay at the Museum on 1969. My husband, prof. P. Gallitelli of the Mineralogical Institute of the University of Bologna gave me all the assistance, as far as the mineralogical observations are concerned,

and prof. G.C. Parea gave me his sedimentological help. Last, but not least, I want to express my gratitude to M.J.P. Lehman, directeur de l'Institut de Paléontologie du Muséum d'Histoire Naturelle de Paris, who allowed the very capable technician M. Verbecke to prepare some excellent ultramicrosections for the investigation at polarized light. To M. Verbecke all my best thanks.

## II. ANALYTICAL RESULTS

### A. MINERALOGICAL AND CHEMICAL COMPOSITION.

Mineralogical and chemical composition was investigated by Morandi and Pirani (Montanaro Gallitelli, 1971, in press and Montanaro Gallitelli, Morandi and Pirani, 1973, in press) through X-ray (diffractometric method) and chemical spectrophotometric semiquantitative analyses, in order to verify possible occurrence and amount of aragonite and possible occurrence and amount of strontium in fifty five samples, mostly coelenterates of the San Cassiano strata. The representatives of the gen. *Protobeterastraea*, as well as all the other Triassic Scleractinia collected on the same outcrops, result composed of aragonite, with a high strontium content, that is an average of 7000-8000 parts per million, roughly corresponding to the strontium content in living Scleractinia. No traces of magnesium were found: and that could explain, according to Volz, the perfect preservation of the finest structures not only in *Protobeterastraea*, but in all the Scleractinia of the same outcrops. The calcareous matrix of the corals is entirely calcitic.

An X-ray Polanyi's analysis made by P. Gallitelli (personal communication) shows that the aragonite crystals are not single crystals but aggregates parallel to the c-axis, random to both a- and b-axes. This result, now obtained on corals as old as two hundreds of millions of years, coincides entirely with the data given by Wainwright (1964) for living corals.

A recrystallization of aragonite crystalline aggregates is improbable at normal conditions of temperature and pressure.

Bathurst (1971, p. 489) reports that Brown, Tebbutt and Shinn found that some skeletal aragonite structures of Jurassic bivalves and of Pleistocene bivalves and corals have been replaced by neomorphic sparry aragonite: the primary aragonitic structure seems to be distorted in the process. The electron scanning micrographs show that the crystal fibers are in the original position in the Triassic skeletons examined for the present paper.

## B. MORPHOLOGY AND MICROSTRUCTURE

### 1. General size and shape.

The specimens of *Protobeterastraea leonhardi* (Volz) (pars) are single individuals or probably elements of phaceloid colonies, or

simply bigeminated at the base (Pl. 1, figs. 1-7). Length between 4 and 18 mm., diameter between 3 and 6 mm. Wall thickness variable between 1/10 and 2/3 of the diameter.

Protosepta predominant, or exclusive, discontinuous, compact, either thin and rhopaloid or very thick and wedged-shaped; frequently spiny, all inwardly inclined. No dissepiments, no synapticulae; casual occurrence of rough, convex tabulae. Metasepta, when present, not pinnate, randomly distributed in all sextants. Text fig. 1 shows schematically the general shape and the calycinal characters of the coral.

### 2. The theca.

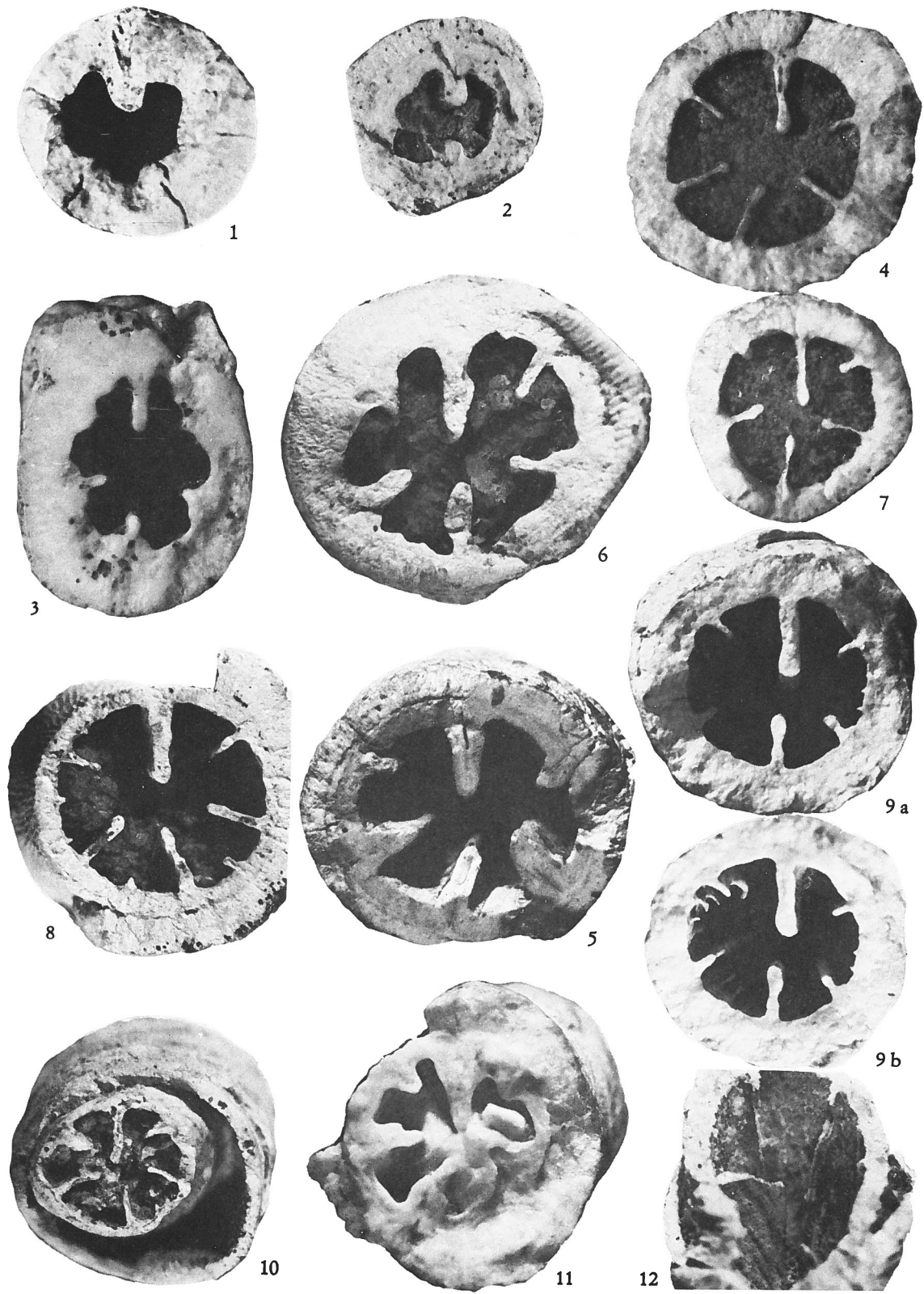
The wall is commonly thick; sometimes — when the discontinuous septa are lacking — it represents the only skeletal element (Pl. 2, fig. 6, text fig. 2). The wall

## PLATE 3

*Protobeterastraea leonhardi* (Volz) (pars) from Middle-Upper Triassic, San Cassiano strata near Cortina (Italy). Bilateral symmetry and septal arrangement.

- Fig. 1 a-b - Septal insertion; 1a, early stage: cardinal fossula, counter septum (this feature is visible in 18 specimens), 9x, same specimen of Pl. 1, fig. 2; 1b, complete settlement of 6 protosepta (wedged-shaped), 10x.
- Fig. 2 - Only two protosepta developed (3 more specimens have the same type of insertion), 15x.
- Fig. 3 - Four protosepta (C, K, 2A); 2CL forshadowed, 14x.
- Fig. 4 - The most common adult stage: six protosepta.  $K > C$ ,  $2A > 2CL$ ; bilateral symmetry evident and constant; septa rhopaloid, 12x.
- Fig. 5 - Wedged-shaped six protosepta; bilateral symmetry; on the thick wall, finely undulated traces (left) of fibrolamellar ridged sheaths of the theca are visible, 10x (same of Pl. 1, fig. 2 and Pl. 2, fig. 1).
- Fig. 6 - Normal bilaterally symmetrical arrangement of protosepta; two metasepta in CA sextant; internal ridged surface (right) of a broken external portion of the thick wall, 10x (spec. n. 26 IPUM).
- Fig. 7 - Rhopaloid protosepta, usual arrangement  $K > C$ ,  $2A > CL$ , 10x.
- Fig. 8 - Irregular insertion of metasepta, one on each alar sextant, two between A and CL, finely undulated trace (left) of the ridged wall, 10x (same of pl. 1, fig. 7), 8,5x.
- Fig. 9 a-b - Ridged thecal traces and septal insertion: still well visible traces of undulated single fibrolamellar sheaths of the wall, 9x; 9b shows the irregular character of the metaseptal insertion, 8,5x.
- Fig. 10 - Rejuvenescence, 14x.
- Fig. 11 - Abnormal growth of protosepta, 12x (same specimen figured at pl. 1, fig. 5a-b).
- Fig. 12 - Rejuvenescent specimen, broken in order to show 1) internal thecal longitudinal ridges as « loci » of septal insertion; 2) septal varices inward inclined, 10x (specimen destroyed for scanning analyses).

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is crossed by strong growth wrinkles (Pl. 2, figs. 1-5; text fig. 3). Epitheca rarely present. Indifferentiated, countless longitudinal thin ridges occur constantly; they are neither septal grooves nor interseptal striae. Internally (Pl. 3, figs. 6-12; Pl. 4, fig. 1) the wall has the same morphology and structure as outside (Pl. 3, fig. 12).

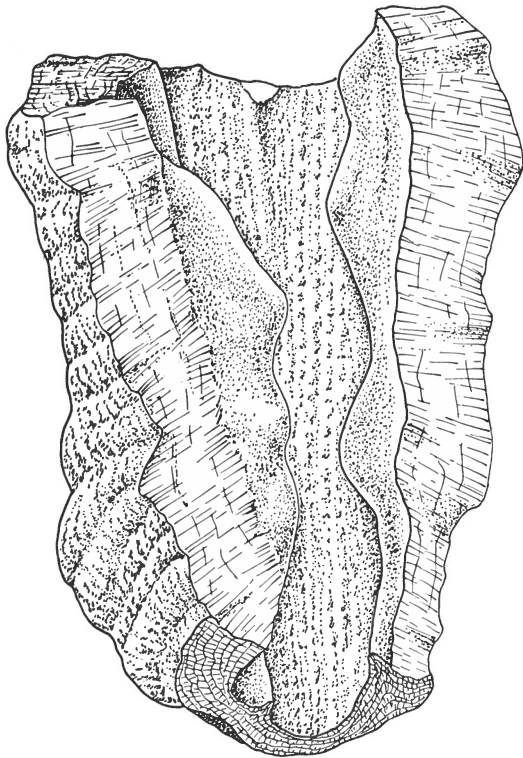
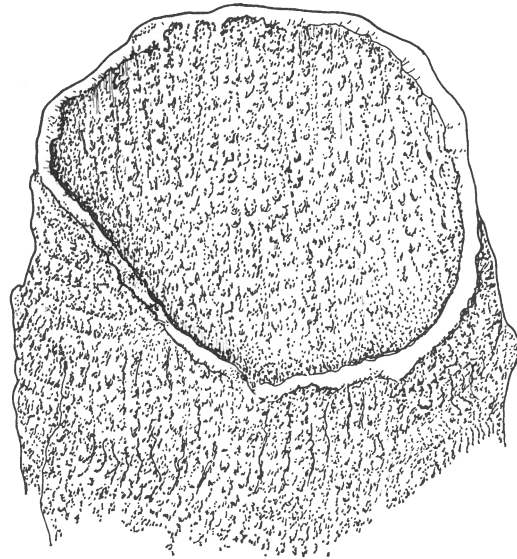


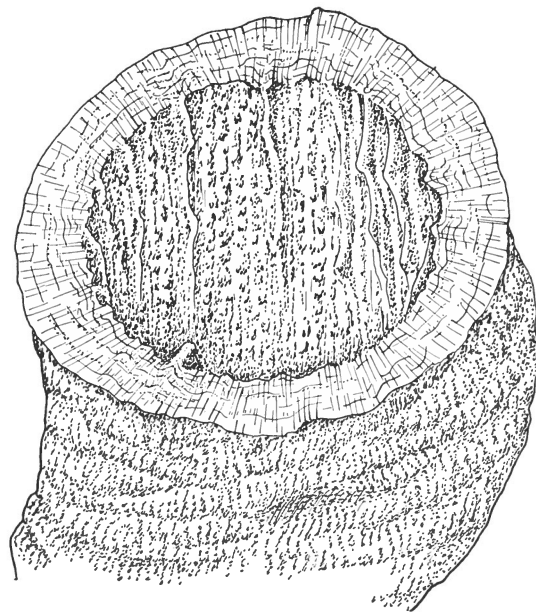
Fig. 1 - Schematic view of the general morphology of *Protobheterastraea leonhardi* (Volz) (pars): Thecal strong growth wrinkles, longitudinal ridges, septal morphology (discontinuity, inward inclination, swollen varices, etc.); about 15 x (G.C. Leonardi delin).

A series of concentric, often finely undulated traces visible at the upper view of the wall (Pl. 3, figs. 5, 9a), shows that the theca consists of a sequence of concentric fibrolamellae, the undulations of which correspond to the longitudinal ridges described above. The concentric lamellae, comparable to a sort of «onion skin» structure, is clearly shown at Pl. 2, figs. 5-7; Pl. 4, fig. 1, 2 and Pl. 6.

The structure of each lamella is fibrous. The fibers are aggregates of aragonite crystals.



Text-fig. 2



Text-fig. 3

Fig. 2, 3 - Hollow theca in *Protobheterastrea leonhardi* (Volz) (pars): 2, thickness reduced, inner longitudinal beaded ridges evident outside and internally, 15 x; 3, wall thick, fibrolamellar, growth wrinkles, abortive thecal spiny septa, 15 x (G.C. Leonardi delin.).

The c-axis of the crystals are roughly normal to the lamellar surface at the point of outcropping. Since the wall is irregular because of the strong transversal growth wrinkles, the fibers are only statistically parallel to each other, so that the aggregates can occasionally show a sort of a chevron structure (tufts), as shown on Plates 5 and 6. This is the most general and perhaps a rather simplistic explanation of the chevron structure observed and figured. A more satisfactory explanation would involve all the process of skeletogenesis and will be discussed later, at the end of the structural discussion. Here we have to take into account that the theca is the locus of septal insertion, which takes place along the longitudinal thecal ridges. When vertically discontinuous, one septum can reappear sometimes as a simple spine, but it arises always along the same longitudinal ridge. We have to add that the thecal tuft observed and figured at plate 4 is inward directed, i.e. with the axis of the possible trabecula horizontally arranged.

At the electron scanning microscope, the thecal ridges appear beaded (Pl. 4, figs. 1-3).

Pl. 4, fig. 1 shows the inner surface of a fibrolamella; fig. 2 shows the external surface of the internally contiguous fibrolamella. The latter appears as the mold of the first sheath, which is preceding in the skeletogenesis.

Terminal faces of crystal fibres of contiguous thecal fibrolamellae can knit together along the c-axis, while a knitting along a- and b-axes (which are randomly oriented in the aggregates) is improbable, because of the orthorhombic parameters. In other words, if there is a good contact between contiguous fibrolamellae (ocraceous or organic material can prevent the process) a transition from a fibrolamellar to a quite fibrous tissue can occur (Pl. 5, figs. 1a-d; Pl. 7) because of knitting of terminal surfaces of contiguous crystalline aggregates. Such a knitting must take place even during the skeletal growth. Plate 6 shows clearly the growth stages of the crystalline aggregates. The same fact is shown at higher magnification (10.000 x) on Pl. 4, fig. 3d. Such kind of crystalline knitting is supposed to be the rule in all carbonate fibrolamellar skeletons and shells,

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#### PLATE 4

##### *Protobeterastraea leonhardi* (Volz) (pars). Thecal structure.

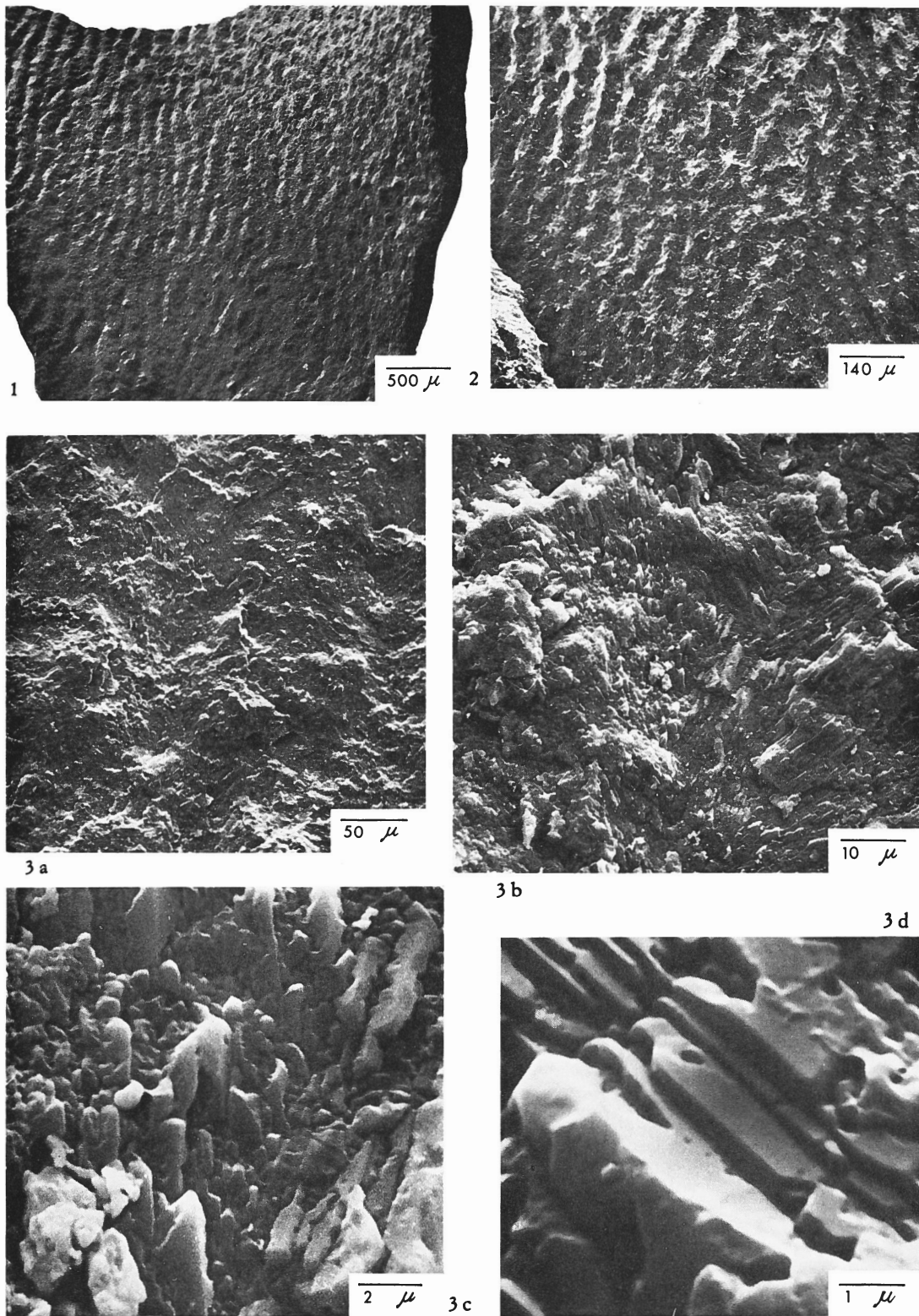
- Fig. 1 - Internal surface of a portion of thecal aragonitic fibrolamella, detached from the specimen figured at Pl. 2, fig. 7; its sculpture is the negative of the surface of the adjacent portion, see following figure, 20x.
- Fig. 2 - External surface of the decorticated wall of the specimen figured at Pl. 2, fig. 7, 70x.
- Fig. 3 a-d - Microstructure of the internal surface of the thecal fibrolamella of fig. 1; 3a, 200x; 3b tuft of crystalline aggregates of aragonite inward directed; in the middle of the cavity the tuft shows the mostly small terminal surfaces of the aggregates, which outcrop progressively more inclined and visible at the c axis as we move from the center to the periphery of the tuft (cf. Sorauf 1972), 1000x; 3c central portion of the same, 5000x; 3d, trigeminate aragonitic crystallites outcropping at the margin of the tuft; knitting of terminal surfaces of the crystal fibres is visible, 10.000x.

#### PLATE 5

##### *Protobeterastraea leonhardi* (Volz) (pars).

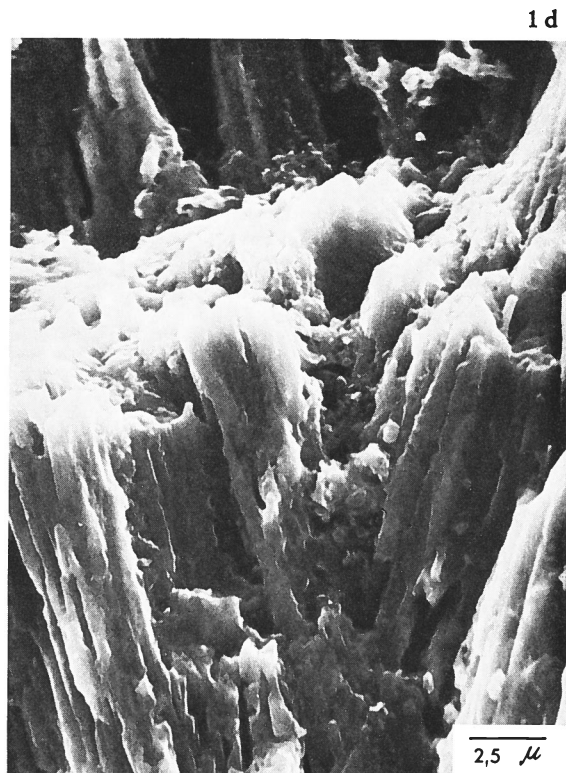
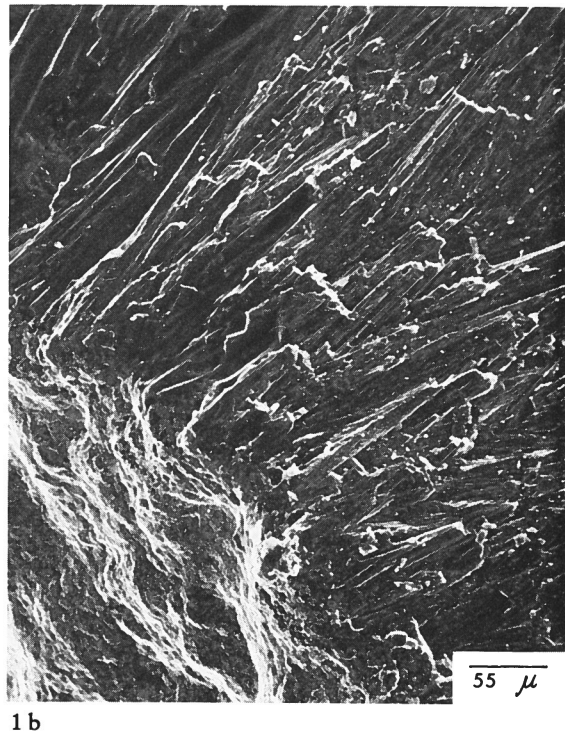
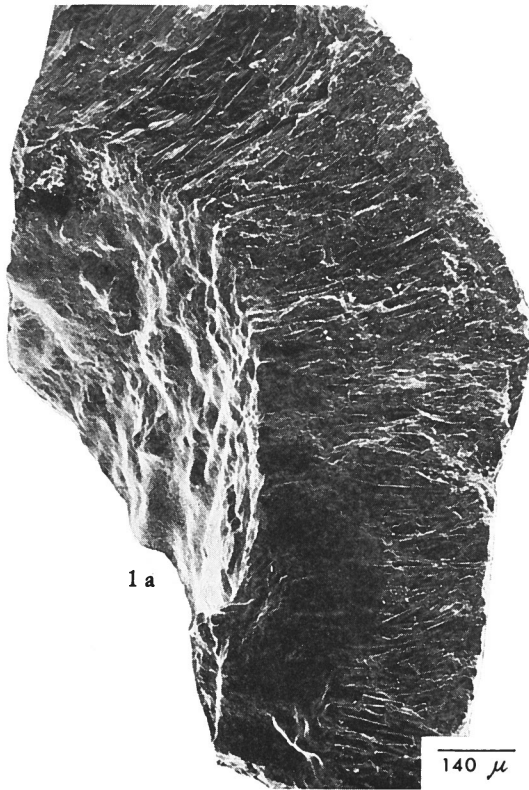
- Fig. 1 a-c - Fragment of the wall: 1a, internal surface ridged; transversal and longitudinal ruptures show the arrangement of the aragonite fibers normal to the tangent of the external surface at their outcropping, 70x; 1b, 190x; 1c, terminal surfaces of fascicles of aragonite aggregates corresponding to parallel cleavage surfaces, 250x; 1d, same, 4000x [see for comparison fibrolamellar structure of an otholite (*Gadus* cf. *elegans* Koken) Pl. 7, fig. 4].

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if the mineralogical composition is uniform, and if the crystals are isoriented along one axis. An example of a comparable modification is shown either by a thin section or by an electron scanning micrograph of two horizontal surfaces of a fish otholite (a sagitta of *Gadus* sp.) along the growth direction (Pl. 7, figs. 3-4).

Pl. 7, figs. 1-2 show two transversal thin sections of *Protobeterastraea leonhardi* (Volz) (pars) as far as the wall is concerned. We will see in the next paragraph that the lamellar tissue of the wall is the same of the septa (Pl. 10, fig. 2). The internally secreted finely lamellar tissue is commonly called stereome, and it is supposed not to have any relationship with the quite fibrous portion of the theca and of the septa (Bryan and Hill, 1941). Nevertheless, in the present species, even in the quite fibrous portions of the theca the original fibrolamellar tissue is in places recognizable, as shown on Pl. 7, figs. 1-2. When the undulated thecal fibrolamellae are still visible in the external portions of the wall thickness and can be easily cleft, (onion skin texture), this depends perhaps on a solution of continuity given by occurrence of extraneous material (cf. Pl. 2, figs. 2-3-5b-6-7).

Eighteen specimens among 120 have a hollow theca, because of septal atrophy. When the septa reappear, they arise along the same longitudinal ridge and in the same order.

### 3. Septa.

#### a. Morphology.

The septal apparatus is simple, neotenic, bilaterally symmetric. It is a unique example among post-Paleozoic corals.

Septa (mostly protosepta only) are either very thin and rhopaloid or thick, wedgeshaped, compact. They are vertically discontinuous, sometimes reduced to short and thick spines. When well developed, they are continuous, constantly inwardly inclined and commonly swollen and varicated. These characters are seen on Plate 3, fig. 12 and are

emphasized at text fig. 1. Lateral septal surfaces are commonly smooth, sometimes granulated, chiefly along the varices. No dissepiments, no endothelial vesicles. Rare and rough tabulae, highly convex.

#### b. Septal arrangement and order of insertion.

Among an amount of 120 specimens studied up to-day (50 more specimens have been recently found) — most of which opened also at the lowest surface because of basal lacking — only 25 individuals have more or less developed metasepta. Hollow calyces are observable too, either in mature stages — frequently connected with phenomena of rejuvenescence — or at the first stage of growth. A few specimens (four) have only one protoseptum and an opposite fossula (Pl. 3, fig. 1); ten specimens have only two protosepta (C and K) (Pl. 3, fig. 2), and a few more have only four protosepta (C, K, 2A) (Pl. 3, fig. 3). All the remaining specimens do not develop more than 6 protosepta.

The six protosepta, when entirely developed, have constant parameters, independently of their thickness or degree of length, as it is shown on Pl. 3, figs. 4-12. In the mature stage, the cardinal septum is constantly shorter than the counter septum, the counter lateral septa are constantly shorter than the alar septa.

No scleractinia have such a protoseptal arrangement.

Symmetry is thus decidedly bilateral. The order of septal insertion during the ontogeny requires a further investigation, when even more specimens will be available: but it is already clear that septa arise two-by-two. This character was previously noted by Schindewolf (1942).

No pinnate arrangement of metasepta has been observed, and not even cyclical insertion. Metasepta seem to arise irregularly and discontinuously in all sextants.

#### c. Structure.

At the present status of the investigations, the evidence seems to prove that



also the septa have a fibrolamellar structure. On Plate 8 and 9 some outstanding electron scanning micrographs at different magnifications show the structure of the axial edge of a rhopaloid septum, which was broken (Pl. 8, fig. 3) in order to let examine the inner structure. A fibrolamellar structure is evident (see also text fig. 4), followed at the inner edge by an apparent purely lamellar tissue (the well known stereome). At higher magnification (1600x to 8000x), even the internal stereome of the septal axial edge appears to be composed of a parallel series of fibrolamellae. The described structure is schematically sketched at Plate 9 and text figs. 4 and 5. Figs. 1-2 of Pl. 8 show the undulated median « dark line » in two different specimens: along the median plane the septa can be broken, showing the median surface entirely free and frequently undulated.

A lamellar internal structure seems evidenced also by the electron scanning micrographs of Pl. 11, but only at a low magnification. Here a septum (Pl. 11, fig. 1), broken along the line of thecal connection, shows countless vertical traces of lamellae (the black

spots are supposed to be borings of microorganisms). An inner view of the thecal surface (Pl. 11, fig. 3) shows the above described vertical ridges and the arising of the lamellar septal system. Pl. 11, fig. 3 shows a higher magnification of a spine and its lamellar tissue.

A knitting among isoriented crystal aggregates of contiguous lamellae is visible on Pl. 8, figs. 4-6. This « fibrillation process » has been described for the theca, and is a general process which must take place even during the skeletogenesis. On Pl. 10, fig. 3, an optical micrograph of a septal transversal thin section shows a fibrous structure — with fibres of each side of the dark line inwardly directed and parallel to each other — but is covered by a mantle of typical lamellar tissue (stereome). On the other hand, either in the thin section represented at Pl. 10, fig. 3 (left) or in the stereoscan pictures — chiefly at high magnification (see Pl. 8, fig. 6-7; Pl. 9 and text figs. 4-5) — transition from lamellar to fibrous tissue and, reversely, fibrous tissues with evident traces of a « lamellar » tissue are well visible. We see on the thin

#### PLATE 6

*Protobeterastraea leonhardi* (Volz) (pars). Transversal rupture of the theca.

Growth stages in the wall development, visible either along the c axis of the aggregates or on the free surfaces, normal to the long axis of crystallites and corresponding to « clivage » surfaces of fibrolamellar sheaths. See, for comparison, electron scanning micrograph of an horizontal rupture of an otholite (Pl. 6, figs. 3, 4) notoriously lamellar in structure: joining of crystal fibres of contiguous fibrolamellae gives, as a result, a typical fibrous texture, 4000x.

#### PLATE 7

Fig. 1, 2 - *Protobeterastraea leonhardi* (Volz) (pars); 1, transversal thin section of theca (polarized light). Internally (a) lamellar tissue (stereoma) actually given by overlapping of tiny fibrolamellae. Externally, (b) thick fibrous tissue; a few undulated dark concentric traces of the ridged fibrolamellae are still preserved; the thick fibrous tissue shows innumerable concentric broken lines corresponding to interruption of growth (cf. scanning micrographs, Pl. 4, and 5). The original fibrolamellar (« lamellar ») tissue is not yet modified to a quite fibrous tissue, because of an incomplete diagenetic knitting of the crystalline aggregates of contiguous fibrolamellae.

Fig. 3, 4 - Otholite. *Gadus* cf. *elegans* Koken (det. Bassoli): specimen selected for structural comparison; 3, horizontal thin section (polarized only), showing the well known fibrolamellar tissue, which is locally converted to a quite fibrous tissue, 40x; 4, scanning micrograph of another specimen, showing growth direction and knitting of fibers, traces of fibrolamellae along the « clivage » surfaces, 100x (cf. Pl. 4 and 5). Upper Miocene: Montegibbio (Modena, Northern Apennines).

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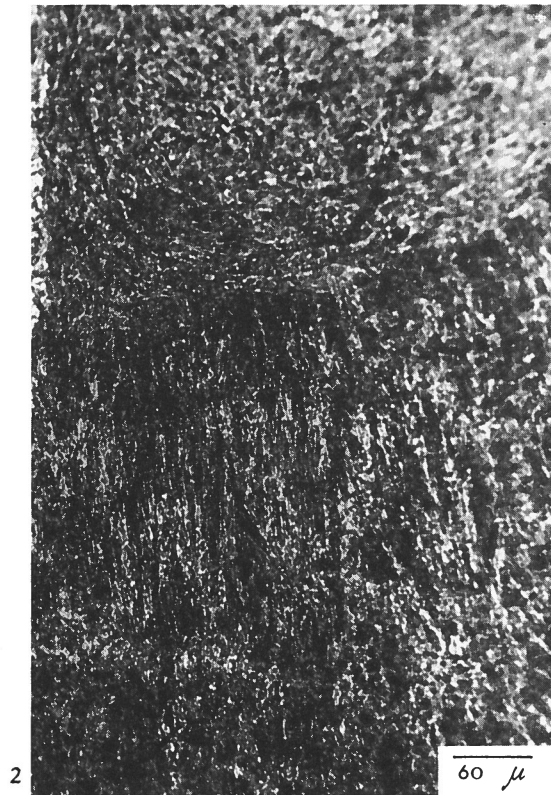




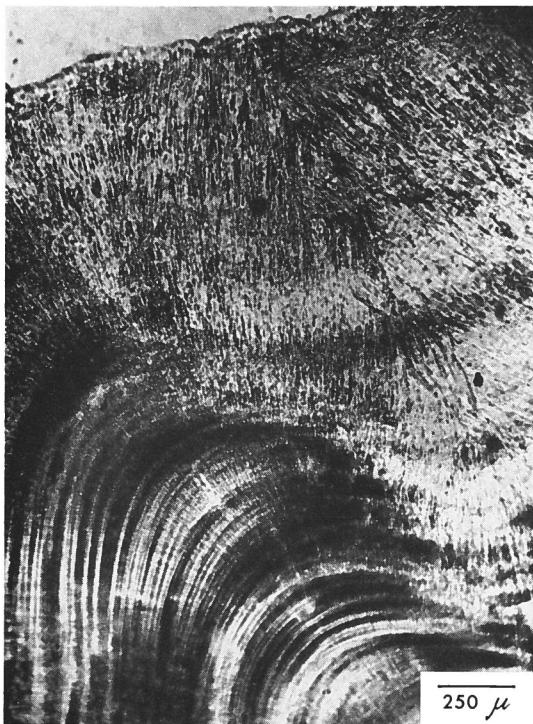
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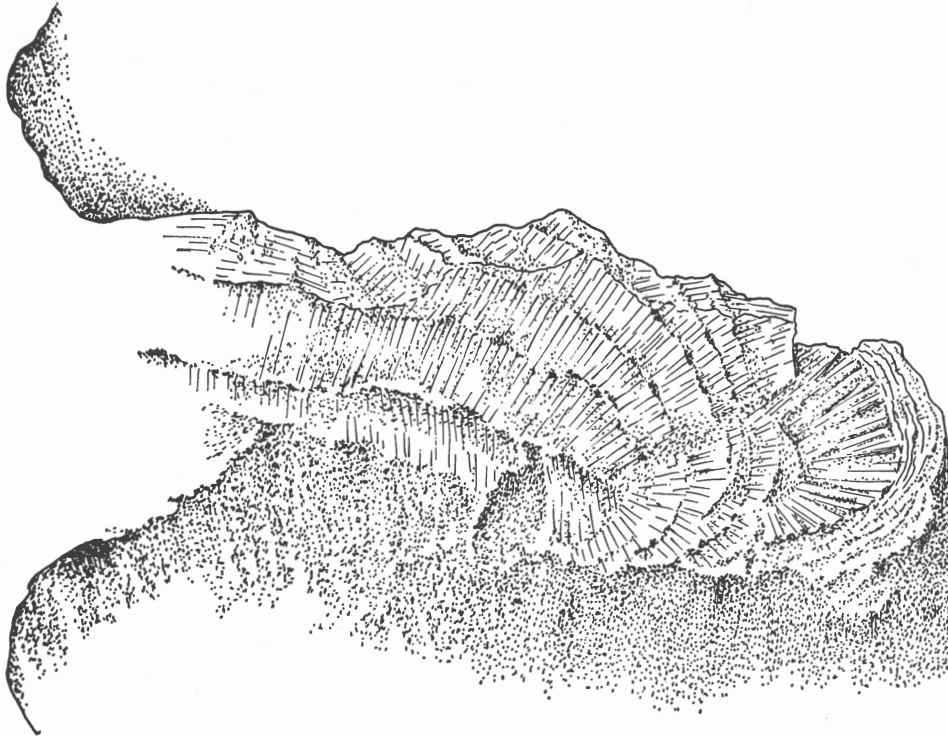


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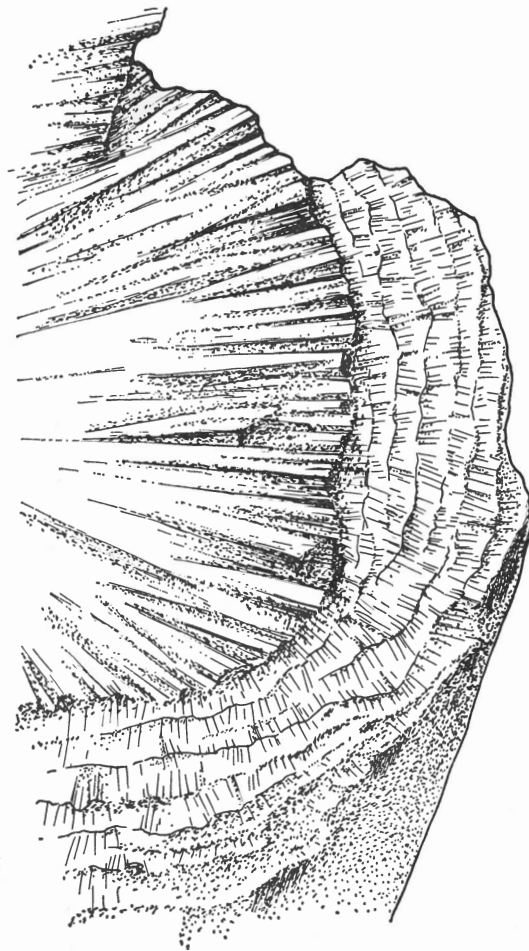
4





Text-fig. 4

Figs. 4, 5, Sketch of a septum, broken at the axial edge and along the median plane, cf. Pl. 8, 9; 4, fibrolamellar structure of the septum, involved internally by lamellar stereome, 550x; 5, lamellar stereome appears fibrolamellar too, at high magnification, about 8000x (G.C. Leonardi delin. from a scanning micrograph).



Text-fig. 5

section figured at Pl. 10, fig. 2 that, in spite of the relatively low magnification, a complete fibrous tissue is evident in all the course of the septum (fibres normal to the septal plane), except at the peripheral portion, at the joining with the theca, where a « lamellar » tissue is recognizable. Same view on Pl. 10, fig. 4, while fig. 1 seems to represent a simple lamellar tissue, except in the succeeding inner lamellar folding, where fibres are evident.

As far as the possible occurrence of a trabecular septal structure in *Protobeterastraea leonhardi* (Volz) (pars) is concerned, I have not yet found any evidence of it, and will continue the research chiefly through optical and scanning investigations.

Independently of further investigations and results, it seems that the geometric projection and representation of different trabecular and fibrolamellar structures was not always and entirely correct, or clear. If it is true, as it is, that trabeculae have centres of calcification, « from each of which fibrous crystals radiate toward those of neighbouring centers » and that « sclerodermites are more or less persistent vertically in the plane of the upfold from the basal disc of the polyp, and develop spines and rods called trabeculae » (Wells, 1956, F337), most of

the transversal sections of trabecular structures are not correctly figured from a geometrical point of view. A more detailed discussion on this subject will be presented elsewhere. As far as the persistent verticality or subverticality of septal growth is concerned, there are exceptions, and *Protobeterastraea leonhardi* (Volz) (pars) is among them. Here the discontinuous septa are often reduced to spines, which crop out of the inner thecal surface. Moreover such septa and spines are inwardly inclined (Schouppé and Stacul 1966 did carefully settle all kinds of septal directions in a very useful table): thus they cannot have but a peripheral origin. Septa of this Triassic species must have been developed from discontinuous lateral infolding of the calycolast layer, « comprising whatever parts of the ectoderm lie directly against the skeleton » (Wells, 1956, F331). If the inwardly inclined spines of this species are actually trabecular spines, as it was formerly stated but not yet demonstrated, a transversal thin section of the coral would give a septal view quite different from all other known septal thin sections.

A preliminary tentative approach to an explanation in terms of trabecular skeletogenesis can be attempted as follows. A regular vertical or subvertical trabecular septal

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#### PLATE 8

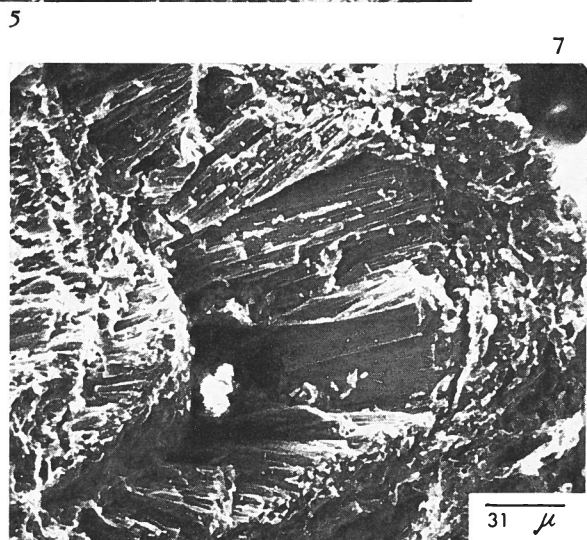
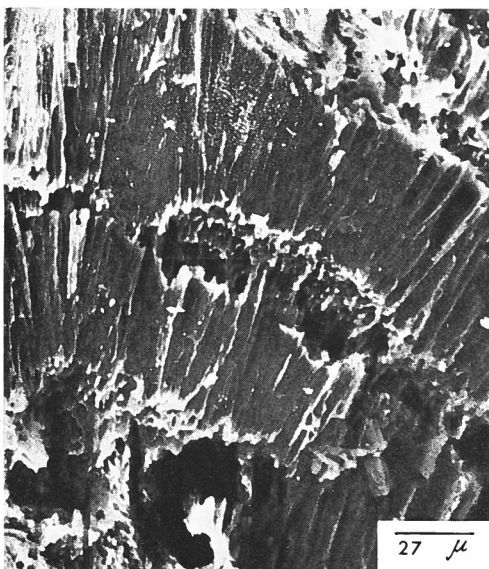
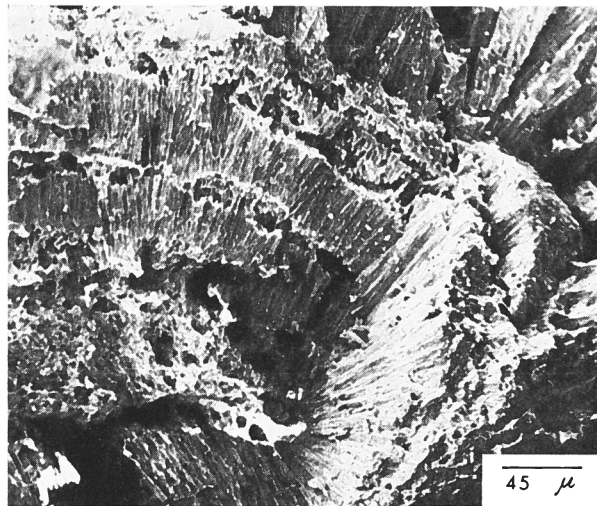
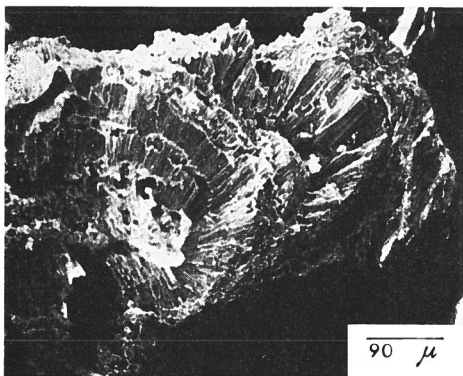
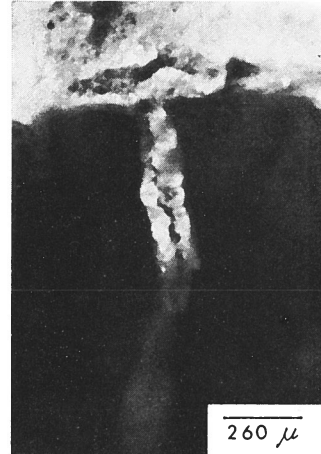
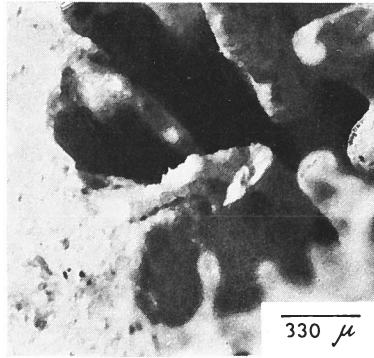
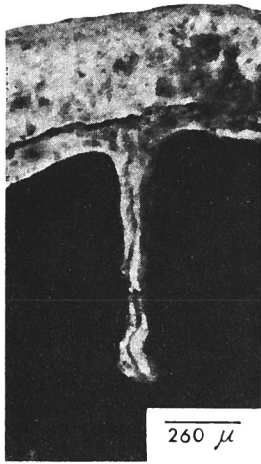
- Fig. 1, 2 - Optical micrograph of two rhopaloid septa, with undulated « dark line » trace of septal plane of symmetry, 38x.  
 Fig. 3-7 - A specimen with axial edge of a septum (K) broken in order to show the septal fibrolamellar structure; 3, optical micrograph of the calice (note irregular metasepta), 30x; 4, same structural detail at the electron scanning microscope; a sequence of some sheaths of overlapping fibrolamellae centripetally deposited by folded soft tissue; the last secreted portion of the septum (right) is still microfibrillar (stereome). The fibrolamellae are separated from each other by ocraceous material and seem to be bored by microorganism (left), 110x; 5, same, 220x; 6, portion of the same, 550x; 7, internal edge of the septum, with « lamellar stereome » (see following plate 9) at right.

#### PLATE 9

*Protobeterastraea leonhardi* (Volz) (pars).

- Fig. 1 a-d - Electron scanning micrographs of the « lamellar stereome » at the axial edge of the septum figured at Plate 7, figs. 3-7; 1a, the fibrolamellar structure is evident at 800x; 1b, 1600x; 1c, 3200x; 1d, 8000x. The crystal fibers of the « lamellar » region are less developed than the older region of the septum, but have identical habitus.

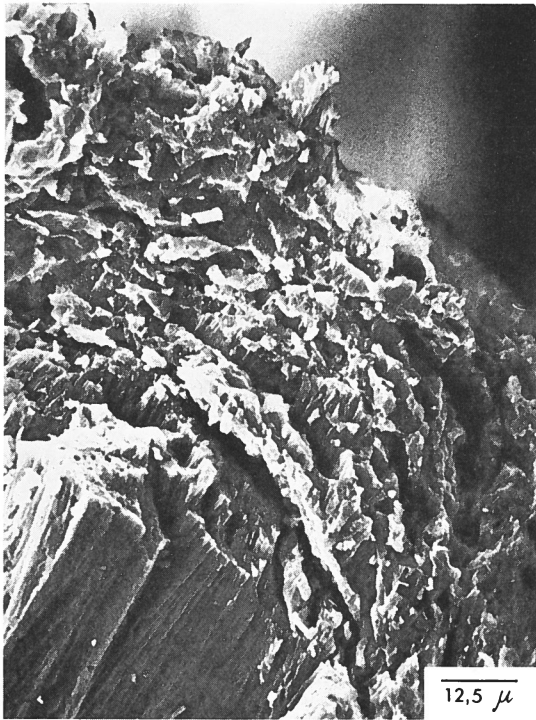
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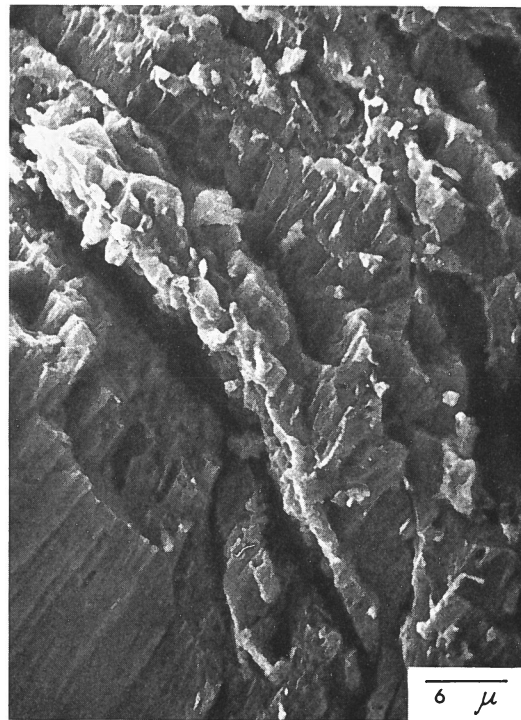




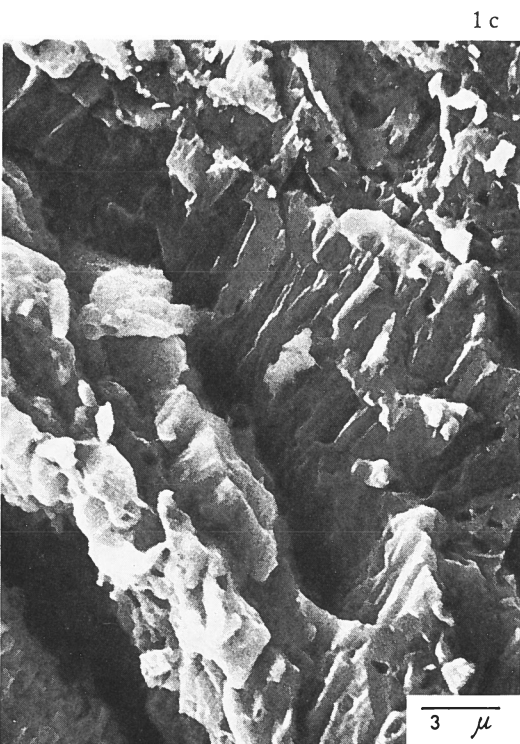
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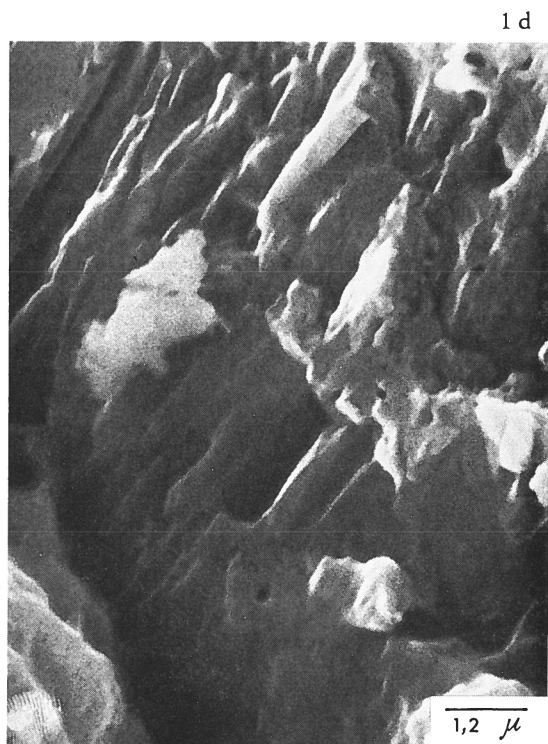
1 a



1 b



1 c



1 d



structure, as classically described, has not been observed in the Triassic studied type, still provisionally ascribed to *Protobeterastraea leonhardi* (Volz) (pars). A fibrolamellar growth of the skeleton is demonstrated for both septal and thecal structures. Nevertheless, some thecal structural features such as, for example, the clear crystalline tuft observed on the internal surface of a thecal fibrolamella and figured on Plate 4, leads to some considerations. This kind of tufts lies in the thickness of the theca, is inward directed, thus must originate from a centre of calcification situated along the lateral region of the polypal cup and develop centripetally, giving a resultant horizontal or subhorizontal axis of the possible trabecula. Discontinuity, spiny character and inward inclination of protosepta when developed, re-aring of each of them along the same vertical alignment of the thecal beaded ridges as tubercles and spines, all these features are further elements which allow to suppose that: a) all the surface of the polyp, not only a basal disc, was the situs of primary skeletal secretion; b) the predominant skeletal tissue was all over a fibrolamellar tissue; c) crystalline tufts could take origin from centres of calcification situated along precise intermesenterial positions of the polyp flanks (longitudinal thecal ridges) and generate discontinuous spiny or laminar, swollen septa. The lateral arising, accompanied by a rapid vertical growth and thickness of the thecal skeleton caused the inward inclination of the swollen septa.

This supposition, however, requires much more information, chiefly through multiple electron scanning micrographs of thecal surface and septal longitudinal axial features.

Thin sections and electron scanning micrographs show — at least at the present status of my work — that the septa do not give origin to a septotheca. The case of *Protobeterastraea leonhardi* (Volz) (typ.), *P. fritschi* (Volz), and of the coeve and not less primitive *Pinacophyllum* Frech is, for instance, quite different: here spiny septa occur as in *Protobeterastraea leonhardi* (Volz) (pars), but they appear indisputably trabecular in transversal calycinal thin sections (even

though with a peculiar direction of the tufts) and give origin to a typical and strong septotheca and even to strong and labyrinthic septocostae. And the septa in *Pinacophyllum* are never inwardly inclined.

I agree with Kato (1963) who states that theca and septa are mutually transformable from one into the other. Further investigations are in course.

### III. CONCLUSIONS

The present investigation has been developed on more than 120 specimens of a lower Upper Triassic (Carnic, San Cassiano strata) coral, which is provisionally still identified as *Protobeterastraea leonhardi* (Volz) (pars). Fifty more specimens have already been collected but have not yet been examined.

Previous work developed by the writer and collaborators demonstrated that the skeleton of *Protobeterastraea leonhardi* (Volz) (pars) is still composed of the original aragonite, with a high strontium content. Aragonite occurs in subparallel crystalline aggregates, developed along the c-axes, each of them roughly perpendicular to the tangent of the free surface at the point of outcropping.

The morphological and structural study gave the following results.

1. Septa are mostly represented by the only protosepta.

2. Protosepta have a distinct and constant bilateral symmetry, and constant parameters, with cardinal septum shorter than counter septum, counter lateral septa shorter than alar septa.

3. All septa have a peripheral origin.

4. Protosepta arise two-by-two, are compact, often varicated and constantly inwardly inclined.

5. Septa are vertically discontinuous, sometimes reduced to simple spines, sometimes even entirely lacking for long extension, thus

leaving a hollow theca as only skeletal element.

6. Metasepta, when present, are irregularly distributed. They are not pinnate; but, on the other hand, the investigation developed up to-day seems to demonstrate that they have not even a cyclic order of insertion but arise at random in all sextants.

7. Septa have a fibrolamellar structure, not distinguishable from the thecal structure. Fibers of contiguous lamellae can knit together at the terminal faces and give origin to a typical fibrous tissue (fibration process).

8. No sclerodermites have yet been recognized, not even in the swollen varices or in the spines, except one thecal tuft, which at present can only lead to some preliminary considerations.

9. The theca, irregular, strongly rugose, longitudinally ridged outside and inside, consists of a centripetal sequence of concentric fibrolamellar sheaths, as an onion skin succession, so that the fibrolamellar sheaths can easily be cleft, when a fibration process cannot be developed. Fibrolamellae are finely

undulated and give a finely ridged habitus to the thecal surfaces.

10. Thecal fibrolamellae, as in the septa, are frequently joint with one another along the c-axis because of fibration process, giving rise to a quite fibrous tissue. A solution of continuity among contiguous lamellae (given by occurrence of extraneous material which can prevent the joining of the aragonitic fibers) allows the cleavage of single thecal sheaths.

11. The theca can temporarily be the only skeletal process.

12. The theca is not a septotheca, and not even an amorph, secondary epitheca. All its thickness, at the electron scanning microscope, at high magnification, appears as a constant, homogeneous, centripetal range of undulated fibrolamellae, often transformed to a fibrous tissue.

All the described characters occur constantly in all specimens, which were collected in different localities of the San Casiano complex.

#### PLATE 10

##### *Protobeterastraea leonhardi* (Volz) (pars).

Fig. 1 - 4 - Thin transverse section (polarized light) of four septa. 1, microfibrilamellar structure in a portion of a thin rhopaloid septum; thin lamellae are observable and fibers appear only at the axial ends of progressive septal growth stages, 130x; 2, thick septum: fibers are normal to the « dark line »; at the peripheral portion of the septum, parallel thin lamellae (microfibrilamellae) take all the thickness of the septum, 125x; 3, fibrous short and thick protoseptum (A), imbedded in « stereome », shows fibers all inward directed and passing to « lamellar tissue » (cf. Pl. 7, 8) in the peripheral portion of the septum (low), 135x; 4, other thick mature septum, with fibers normal to the septal plane or slightly inward directed and hollow central trace corresponding to the so called « dark line », 135x.

#### PLATE 11

##### *Protobeterastraea leonhardi* (Volz) (pars).

Fig. 1 - Wall longitudinally broken at the distal (thecal) end of a septum (right): note the vertical microfibrilamellae (low magnif.) and the smooth surface (right) of the septum, 100x.

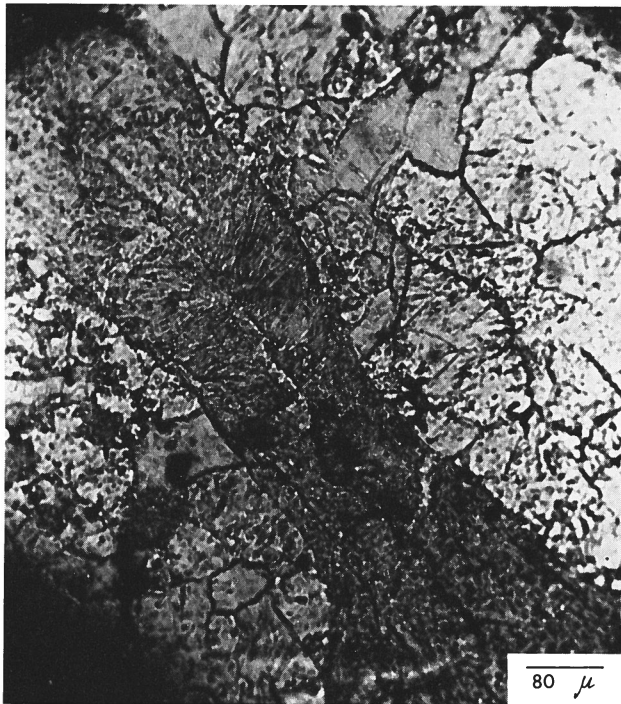
Fig. 2 - Internal surface of a wall with foreshadowed metasepta: visible a) vertical sequence of growth stages, b) inward inclination of septa, c) a spiny metaseptum, 95x.

Fig. 3 - Overview of a spiny metaseptum (sec. fig. 2), 474x.

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2



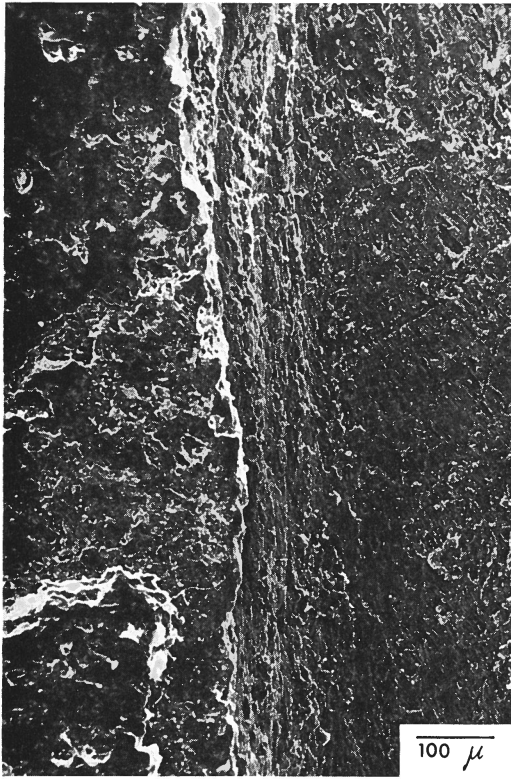
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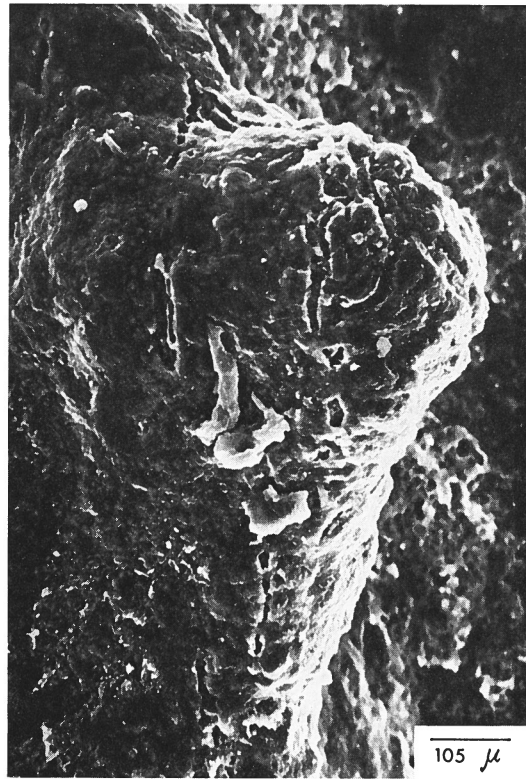
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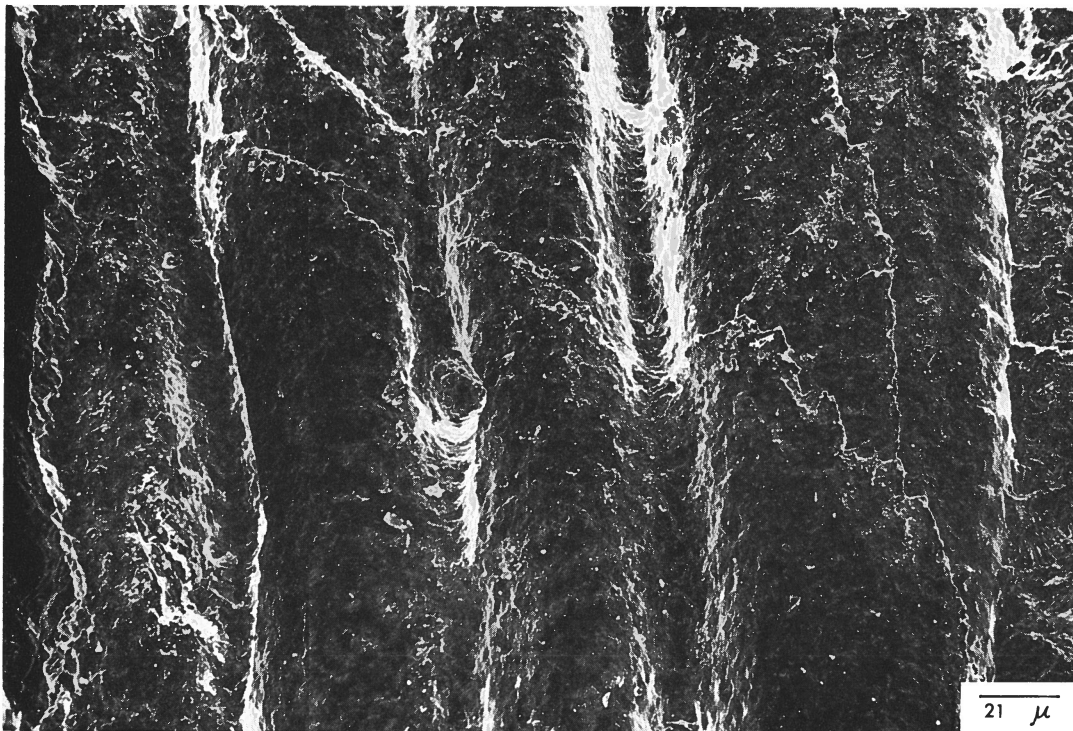
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2



3





According to Goreau and Goreau (1959), « the sclerenchime », or skeleton, consists of a succession of discontinuous layers held together by walls and partitions », and « the skeleton . . . is really composed by many separate lamellae ». Considering the fibrolamellar tissue of the skeleton in *Protobeterastraea leonhardi* (Volz) (pars), we can suppose an initial basal deposition, then a pallial deposition of successive laterally discontinuous lamellae and pallial discontinuous invaginations in the intermesenterial portions, with discontinuous deposition of fibrolamellar septa or simply septal spines, arising from the periphery.

In the peculiar, primitive coral here considered, both septa and theca seem structurally homologous, and a thecal fibrolamellar infolding to generate septal spines is evident. Moreover, septa arise with a constant order of insertion, bilaterally symmetrical, and the same position and order of insertion is respected after an interruption of septal growth.

If it is true that the septa, inwardly inclined, have a peripheral origin, if each pair of protosepta has a constant position and a constant relation with the others in spite of any discontinuity, we should search the septogenesis of *Protobeterastraea leonhardi* (Volz) (pars) in the microstructure of the ridged fibrolamellar theca. If crystalline tufts are distributed and regularly arranged in the theca, they could perhaps be interpreted as possible peripheral traces of septal trabeculae. But, up to-day, I have not yet seen any certain septal trabecula or a regular distribution of the tufts.

Further investigations are in course on this problem, on the systematic position of the species, on the general problem of skeletal fibration, and on the geometric prospective of skeletal structures.

What is certain at the present status of our knowledge, is that *Protobeterastraea leonhardi* (Volz) (pars) represents a conspicuous group of aberrant specimen, up to-day about 200, too abundant and too common in different outcrops of the Triassic

San Cassiano beds, to be neglected for a systematic and phylogenetic discussion. It can be connected to the latest Paleozoic Rugosa for bilateral symmetry, insertion of septa two-by-two, order of septal insertion and development, and, perhaps, fibrolamellar structure of the septa. On the other hand, the occurrence of a theca, the characters of the longitudinally parallel ridges, the lacking of pinnate metasepta are not peculiarities of the Rugosa, at least at the present status of our knowledge.

Avoiding to talk of transitional forms, we can only state that *Protobeterastraea leonhardi* (Volz) (pars) is neither a Rugosa nor a Scleractinia, in spite of many relations with both Paleozoic and Mesozoic corals. The systematic position of the present aberrant group will be discussed elsewhere.

The present paper was ready for printing, when I knew, just by chance, a publication on Triassic San Cassiano corals by J.P. Cuif, concerning also a discussion on *Protobeterastraea* Wells, issued at the end of 1972 on the Bull. Mus. Hist. Nat. Paris, ser. 3, 97. My first communication on some primitive genera of Triassic Scleractinia (among which *Protobeterastraea*) and on geochemical data about « aragonite and high strontium content in Triassic scleractinia » was presented at the International Paleontological Symposium on Corals, held in Novosibirsk on August 1971. M. Cuif was previously informed that I was since long working on Triassic Cassian corals. Unfortunately he did not even send me any reprint of his publication.

As far as *Protobeterastraea* Wells is concerned, at present it is only to be noted here that the 120 specimens of *Protobeterastraea leonhardi* (Volz) (pars) which are the object of the present paper, have nothing to do with the specimens of *Protobeterastraea leonhardi* (Volz) described by Cuif. A systematic statement and a critical review on this subject is ready and will be published soon.

## REFERENCES

- BRYAN, W. H. and HILL, D., 1941, Spherulitic crystallization as a mechanism of skeletal growth in the Hexacorals: Proc. R. Soc. Qd., 52, pp. 78-91.
- GOREAU, TH. F. and GOREAU, N. I., 1959, The physiology of skeleton formation in Corals; I. A method for measuring the rate of Calcium deposition by corals under different conditions: Biol. Bull., 116, pp. 59-75.
- , 1959, The physiology of skeleton formation in Corals; II. Calcium deposition by hermatypic corals under various conditions in the reef: Biol. Bull., 117, pp. 239-247.
- , 1960, The physiology of skeleton formation in Corals; III. Calcification as a function of colony weight and total nitrogen content in the reef coral *Manicina areolata* (Linnaeus): Biol. Bull. 119, pp. 416-427.
- HILL, D., 1935, British terminology for rugose corals: Geol. Mag., 72, pp. 481-519.
- , 1956, Rugosa: In Treatise on Invertebrate Paleontology (Ed. R. C. Moore), vol. F (Coelenterata), F233-324.
- , 1960, Possible intermediates between Alcyonaria and Tabulata, Tabulata and Rugosa, and Rugosa and Hexacorallia: Intern. Geol. Congr. Rep. XXI Sess. Norden, XXII, pp. 51-58.
- HYMAN, L. H., 1940, Protozoa through Ctenophora: In The Invertebrates (L. H. Hyman), pp. 509-521 (McGraw - Hill Publ. London).
- KATO, M., 1963, Fine skeletal structures in Rugosa: J. Fac. Sci. Hokkaido Univ., ser. IV, XI, pp. 571-630.
- MONTANARO GALLITELLI, E., 1971, Morphogenesis and structure of some primitive Triassic corals: problems of phylogeny: Transactions of the International Paleontological Symposium on Corals, Novosibirsk (in press).
- , Morandi, N. and Pirani, R., 1973, Aragonite and high strontium content in Triassic corals: Proc. II Intern. Symposium on Coral Reefs (in press).
- OGILVIE, M., 1897, Microscopic and systematic study of Madreporarian types of Corals: Phil. Trans. R. Soc., B, 187, pp. 83-345.
- SCHINDEWOLF, O. H., 1942, Zur Kenntnis der Polycilien und Pterophyllen: Abh. Reichsamts Bodenforsch., N. F. 204, pp. 1-324.
- SCHOUPPÉ, A. v. and STACUL, P., 1966, Morphogenese und Bau der Skelettes der Pterocorallia: Palaeontographica, Suppl. B. 11, I-II, pp. 1-186.
- SORAU, J. B., 1972, Skeletal microstructure and microarchitecture in Scleractinia (Coelenterata): Palaeontology, 15, I, pp. 88-107.
- TEICHERT, C., 1959, Cold and deep-water coral banks: Bull. Am. Ass. Petr. Geol., 42, 5, pp. 1064-1082.
- VAUGHAN, T. W. and Wells, J. W., 1943, Revision of the suborders, families and genera of the Scleractinia: Geol. Soc. Am. Spec. Pap., 44, pp. 1-363.
- VOLZ, W., 1896-97, Die Korallen der Schichten von St. Cassian in Süd-Tirol: Palaeontographica, 43, pp. 1-124.
- WELLS, J. W., 1937, New genera of Mesozoic and Cenozoic Corals: J. Paleont., XI, pp. 73-77.
- , 1956, Scleractinia: In Treatise on Invertebrate Paleontology (R. C. Moore ed.), vol. F. (Coelenterata), F328-444.