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SKELETOGENESIS OF NEWLY SETTLED PLANULAE OF THE HERMATYPIC CORAL *PORITES LUTEA*

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The early development of the exoskeleton of the hermatypic scleractinian coral *Porites lutea* has been established by scanning electron microscopy for 1 hour to 21 day old corallites. The initial deposits are dispersed small grain-like crystallites of calcium carbonate up to 6 µm in length and 0.5 to 3 µm in maximum width. These crystallites enlarge by syntaxial growth and in addition new ones may be nucleated on their surfaces to produce rosette-like aggregations. After 6 hours these aggregates fuse laterally to form the primary layer of the basal plate. At this stage the initial tufts of crystallites of the septal trabeculae are deposited in radial rows on the primary layer of the basal plate. In 24 hour old corallites the trabeculae are well developed and traces of 1, 2 or 3 orders of septa can be recognized. Subsequently (1—7 days), the trabeculae coalesce generating the radially arranged septa and the secondary layer of the basal plate is deposited in the interseptal areas. With further growth some trabeculae diverge laterally from the median plane of the septum to produce vepreculae which may fuse with those of adjacent septa to form synapticulae. After several orders of septa have been established, the basal plate may develop a peripheral epitheca.

K e y w o r d s: Scleractinia, development of exoskeleton, Recent.

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INTRODUCTION

Deposition of the calcareous skeleton of scleractinian corals is initiated soon after the planula settles on a suitable substrate. The understanding of the processes involved in this settling stage is essential in the study of calcification and skeletogenesis in corals. Various authors have described the rates and times of planulation, the morphology, cell structure, development and behaviour of planulae, and the mode of planular settlement (e.g. Haddon 1890; Durden 1904, 1905; Mavor 1915; Boschma 1929; Stephenson 1931; Marshall and Stephenson 1933; Abe 1937; Atoda 1947*a*, 1947*b*, 1951*a*, 1951*b*, 1951*c*, 1953; Harrigan 1972; Lewis 1974, Stimson 1978). Recent studies have provided ultrastructural details of the cells and their organization within the planula before and after settlement. and of the relationship of the epithelium to the skeleton in newly settled forms (Vandermeulen 1974, 1975; Hayes and Goreau 1976, 1977; Goreau and Hayes 1977; Johnston 1976, 1977, 1979). There is no data available on the actual mechanism which initiates the deposition of the skeleton. The initial mineral deposits of the skeleton have been described for the ahermatypic coral *Asteroides calycularis* by von Kock (1882), and the hermatypes *Pocillopora damicornis* by Wainwright (1963), Vandermeulen and Watabe (1973), Johnston (1977), *Porites lutea* by Jell (1974), and *Porites porites* by Goreau and Hayes (1977). Several studies of septal insertion and of corallum development after the initial mineralization phase are available for a number of reef corals but the most detailed study of the sequential skeletal growth stages immediately following settlement of the planula, is of *Pocillopora damicornis* during its first 22 days of growth (Vandermeulen and Watabe 1973).

The present study presents details of the development of the skeleton of *Porites lutea* Edwards et Haime during the first 21 days following settlement of the planula. The scanning electron microscope has been used to examine cleaned whole skeletons of corallites 1 hour to 21 days old. This has provided further data on the initial mineral deposits, the sequence of growth stages, the crystal units and their arrangement within the various skeletal elements, and the relationship of these elements to each other, in the early development of this hermatypic coral. Results of chemical and crystallographic analyses and examination of fractured and polished sections of the various skeletal elements will be published elsewhere.

MATERIAL AND METHODS

During January 1974 and December 1975/January 1976, live coralla of *Porites lutea* were collected in plastic buckets each day at low tide from the reef flat on Heron Reef, southern Great Barrier Reef, Australia. They were transferred as soon as possible into aquaria with open sea water circulating systems.

Planulae were collected by means of a pipette from the water in the buckets used to transport the colonies and from the aquaria at six hour intervals. The planulae were transferred to 2 litre plastic bowls in which glass slides and acetate film were arranged on the bottom and around the sides of the bowls. Some slides were frosted using fine grinding powder. The water in each bowl was gently aerated and was changed every morning and evening. The bowls were kept out of direct sunlight and little algal growth was observed. Planulae were considered settled when a gentle stream of water from a pipette did not dislodge them. The slides with the settled planulae were then numbered and transferred to a 5 litre glass bowl or an aquarium.

Slides, portions of acetate film, and pieces of the plastic bowls, with the various settled stages of the young corals were treated with warm 5% KOH, dilute 1:30 commercial sodium hypochlorite, or trypsin and then thoroughly washed in fresh water. This treatment removed the soft tissues leaving the bleached skeletons still adhering to the various substrates; no differences could be distinguished between the skeletons treated with the different reagents. The skeletons were coated under vacuum with aluminium before examination using a Model IA or a model S600 Cambridge Stereoscan scannnig electron microscope.

Acknowledgements. — The field work was based at the Heron Island Research Station and the help given by the Director and the staff is gratefully acknowledged. The electron microscopy was undertaken at the Electron Microscope Centre, University of Queensland and the Sedgwick Museum, University of Cambridge and the technical assistance received is greatly appreciated. The investigation was supported by an Advisory Committee on Research into Crown of Thorns Starfish Grant and a University of Queensland Research Grant.

OBSERVATIONS

Planulae

Following each collection trip, planulae were found in the water in which the colonies were transported back to the laboratory. During December and January extrusion of the planulae from the colonies in the aquaria was continuous, but was most active in a two to three day period just before the new moon. In general, more planulae were released if the colonies had been handled or the water circulation stopped for several hours.

The planulae are pyriform, range from 1 to 1.5 mm in length and 0.5 to 0.8 mm in maximum diameter, and are light brown in colour due to their contained zooxanthellae. They are completely and uniformably ciliated and swim actively rotating about their long axes in an aboral direction. Some settle within hours of extrusion especially those released just before the new moon, while others may float or swim for up to 10 days. However, if they do not settle within 6 days they generally never settle. Some settle and begin to flatten but will then move off resuming their normal form. As many settled on the plastic bowls as on the glass slides and there seems to have been no preference for normal or frosted glass, nor for the horizontal or vertical surfaces. Very few settled on the acetate film. Several fixed themselves to the underside of the slides lying on the bottom of the bowls and some adhered to the edges of the slides.

When finally settled, the planula flattens out and becomes an attenuated disc 1.0 to 1.5 mm in diameter with a slightly domed central area and a narrow transparent flat peripheral border devoid of zooxanthellae.

Skeletal development

Almost immediately the planulae settle they must begin to secrete a skeleton as even the youngest specimens (less than 1 hour old) examined possess some mineralized deposits. The deposition of the calcareous skeleton is continuous and no distinct stages of development are recognized. Considerable variation is found between individuals both in their rate of development and in the time and order of formation of the various skeletal elements. The following description of skeletal development is of the general sequence recognized and the time intervals used are arbitary.

1 to 6 hour old skeletons

The initial mineral deposits of the skeleton are small calcareous crystallites up to 6 μm in length and 0.5 to 3 μm in diameter. They are grain-like in shape and their surface texture suggests they are compound crystals (pl. 5: 6). The crystallites are relatively evenly distributed over a circular area 0.5 to 1 mm in diameter which is slightly less than that of the basal disc of the polyp (pl. 5: 1). With growth these crystallites may remain isolated and grow to 10 μm in length but more commonly other crystallites are nucleated on their surfaces so that small clusters begin to form (pl. 5: 7, 8). These clusters may further develop into rosette-like arrangements 10 to 20 μm in diameter (pl. 5: 2, 3).

After 5 to 6 hours this basal deposit begins to differentiate into a central area 0.35 to 0.4 mm in diameter and a peripheral area (pl. 5: 1). Further growth is by expansion of the peripheral area, the central area remaining approximately the same diameter. No regular incremental banding can be distinguished in this basal deposit.

6 to 24 hour old skeletons

The basal deposit expands laterally by nucleation of new crystallites at the periphery and usually attains its maximum diameter of 1.0 to 1.5 mm within 24 hours after settlement. The initial grains, clusters, and rosettes continue to grow so that the non-mineralized spaces become smaller (pl. 6: 1). Differentiation of the central area becomes more pronounced and the region of most rapid deposition is the inner peripheral area surrounding the central area (pl. 6: 1). The first septal deposits appear in this area of rapid mineralization. They occur as small isolated deposits radially arranged in six positions about the central area (pl. 6: 1). These initial septal deposits are spheritic aggregations of tufts of very fine crystallites (pl. 6: 5, 6) crystallographically distinct from the crystallites of the basal deposits on which they are based (pl. 6: 4). The spacing of these initial aggregates is 20 to 25 μm, centre to centre, which is the distance apart of the centres of trabeculae in the septa of older corallites. In the central area, spheritic aggregations (20 to 30 μm in diameter) of fine crystallites are deposited on the basal deposits in apparently random arrangement (pl. 6: 2, 3).

1 to 7 day old skeletons

The individual grains, clusters, and rosettes of the basal deposit continue to grow until they interfere with each other laterally. These form the primary layer of the basal plate. New bundles of fine crystallites are inserted between and over the initial deposits (pl. 7: 2). This additional material is of very fine crystallites aggregated into tufts with cross sectional diameters up to 2 μm. The tufts are arranged in parallel into bundles 5 to 10 μm in diameter and 10 to 20 μm in length. The bundles are arranged in a felted pattern over the initial basal deposits and form the secondary layer of the basal plate. Although the bundles are not arranged normal to the plane of the basal plate, the distal end of each bundle forms part of the irregular upper surface of the deposit. Occasionally small pits are developed on the upper surface of these deposits. Within 5 days, almost the entire area of the basal deposits is mineralized and forms the basal plate of the skeleton. It varies from 1 to 1.5 mm in diameter and 2 to 10 μm in thickness.

The incipient trabeculae of the protosepta grow centrifugally with the addition of layers of tufts of very fine crystallites so that the trabeculae grow upwards and outwards forming a row of isolated trabeculae. With further growth adjacent trabeculae interfere with one another and lateral growth ceases with the trabeculae fusing to form septa with strongly dentated distal edges (pl. 7: 1, 3). Upward growth produces tall cylindrical trabeculae 20 to 30 µm in diameter. The distal ends of the trabeculae are conical and show tufts of crystallites grouped into larger tufts normal to the surface of the trabeculae and with convex outwards distal surfaces (pl. 7: 4). The lower surface of the trabeculae shows the tufting more pronounced resembling small fascicles as seen in the septa of older corallites. The crystallites at the surface of the lower parts of the trabeculae are larger than those of the distal conical parts. The lower surfaces also show numerous pits (pl. 7: 5) which resemble the desmoidal process scars of *Pocillopora damicornis* (Wise 1970; Vandermeulen and Watabe 1973). Initially the trabeculae of the septa lie in a single plane with the tallest just to the outside of the central area of the basal disc (pl. 7: 1). Further development of the septa is by upward growth of the trabeculae, bifurcation of the trabeculae in the median plane so that the trabeculae become fanned, and insertion of additional trabeculae at the axial and peripheral ends of the septa (pl. 7: 5).

Shortly after the establishment of the six protosepta, second and third order septa (metasepta) are inserted cyclically. Their insertion is not always regularly cyclic. Within 7 days three orders of septa are generally well established.

In a seven day old specimen, a horizontal plate formed in the central area of the corallite with trabeculate spines projecting from its peripheral edges (pl. 7: 6).

7 to 21 day old skeletons

With further growth, the septa continue to grow upwards and some of the trabeculae diverge laterally to form lateral septal spines or vepreculae (pl. 8: 1, 2, 7). Vepreculae of adjacent septa may fuse into synapticulae uniting the septa (pl. 8: 7). Isolated trabeculae may develop between the peripheral edge of the septa and the outer edge of the basal plate (pl. 8: 7). The axial ends of the septa extend to the axis and fuse to generate axial structures.

In corallites as young as 7 days old and before the septa are fully developed, an epitheca may develop at or near the periphery of the basal plate (pl. 8: 1, 3—6). The external surface of the epitheca may show incremental growth banding parallel to its distal edge with each band approximately 10—20 µm in width and consisting of a series of bundles of fine crystallites directed upwards and outwards to the surface of the epitheca. In some specimens epithecal deposits are developed on the upper surface of the basal disc (pl. 8: 6) and in others where it is developed at the periphery, it is difficult to distinguish the initial band of the epitheca from the deposits of the basal plate (pl. 8: 5). The early deposits of the epitheca resemble the bundles of crystallites forming the secondary layer of the basal plate. In some corallites, the epitheca is only developed around part of the corallite and in others even as old as 21 days it is absent.

DISCUSSION

This study of the sequential skeletal growth stages of newly settled planulae of *Porites lutea* using scanning electron microscopic techniques supplements previous investigation of early skeleton development in other coral species. The similarities and differences are noted on the nature and structure of the basal plate, the relation of the septa to the basal plate, the early development of the epitheca and its relation to the basal plate, and the growth and modification of the septa.

As in other species, deposition of the skeleton commences soon after settlement of the planula with mineralization occurring between the epithelium of the flattened aboral end of the planula and the underlying substrate. These deposits form the primary layer of the basal plate and underlie all other skeletal elements such as the septa and epitheca. The mechanism of nucleation of the first formed crystallites remains unknown. The initial deposits are scattered, randomly orientated, small grain-like crystallites of similar size and form to the granules of the first formed deposits in *Pocillopora damicornis* described by Vandermeulen and Watabe (1973). The flattened spherulitic platelets distinguished by the latter authors have not been recognized in *Porites lutea*. However, they may be analogous to the rosette-like aggregations of crystallites of the primary layer as described herein. The rosettes appear to form by syntaxial and nonsyntaxial crystal growth from the initial seed crystals whereas no intermediate stages were observed between the granules and the platelets in *P. damicornis*. The mineralogy of these initial deposits is currently being investigated. Generally, the basal plate does not become completely mineralized until 5 days after settlement whereas in *Pocillopora damicornis* the entire area covered by the flattened polyp is calcified within 24 hours (Vandermeulen and Watabe 1973). The secondary layer of the basal plate consists of bundles of crystallites arranged in a felted or reticulated pattern similar to the reticulofasciculate pattern of fasciculi found in the basal parts of the septa of *Eusmilia fastigiata* (Wise 1972, pl. 8: 1, 2). Although the bundles are not orientated normal to the upper surface of the basal plate, the distal ends of the bundles are free and appear to have been adjacent to the basal epithelium of the polyp. Perhaps, this reticulofasciculated pattern is developed when the adjacent epithelium is not taut over the skeletal structure but is puckered so that instead of the crystals growing normal to plane of interface between the basal plate and the basal epithelium of the polyp, they grow normal to the small irregularities in the puckered tissue.

As in *Pocillopora damicornis* (see Vandermeulen and Watabe 1973) the basal plate does not show any evidence of being formed by a succession of concentric bands of crystalline material. Very early in the development of the basal plate it is differentiated into a central and a peripheral area with mineralization being most rapid in the region surrounding the central area. The surface of the basal plate shows pits similar to those of the basal plate of *P. damicornis* which have been considered scars of desmoidal processes to anchor the polyp to the skeleton. These scars are not as well developed or as numerous as in *P. damicornis*.

The initial deposits of the six protosepta appear to be laid down simultaneously on the initial deposits of the basal plate, within 6 hours of settlement of the planula. Metasepta are inserted in cycles between existing septa as is characteristic of the scleractinian corals but irregularities in the order of insertion are common. The trabeculae of the early septa are similar to those of older specimens except that the fasciculi and the individual tufts of crystallites are smaller. The small discrete spheritic aggregates of very fine crystals that are initially laid down on the basal plate are possibly similar to the aggregates of fine crystals that form the axes of trabeculae and have been referred to as centres of calcification (see Wainwright 1964).

Previously, epithecal deposits have not been described in the early development of the coral skeleton. The structure and the incremental growth banding on the external surface of the epitheca are similar to those of the epitheca of mature corallites as described by Barnes (1972). The epitheca does not appear to be simply the upturned edge of the basal plate as has been suggested previously. The initiation of the formation of the epitheca possibly corresponds to the development of a lappet at the edge of the basal disc of the polyp.

SUMMARY

1. The basal plate is the first skeletal element of the skeleton of *Porites lutea* to be calcified. It consists of a primary layer of grain-like crystallites, crystallite clusters and rosettes of crystals, and a secondary layer of fine crystalline fasciculi arranged in a reticulofasciculate pattern; spheritic aggregations of fine crystals occur randomly arranged in its central area.

2. The septa are based on the primary layer of the basal plate. Their initial deposits are isolated finely crystalline aggregations which in structure resemble the 'centres of calcification' of trabeculae. The trabeculae of the cyclically inserted septa are centred on these initial deposits and are similar to the trabeculae in more mature corallites except that their fasciculi are smaller.

3. Septal modifications such as vepreculae and synapticulae result from divergence of the trabeculae from the median plane of the septa.

4. The epitheca is initiated after 7 days and resembles the epitheca of mature corallites. It does not appear to be the upturned edge of the basal disc.

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EXPLANATION OF PLATES 5—8

All figures are of *Porites lutea* Edward et Haime reared from planulae collected from colonies from the reef flat of Heron Reef, southern Great Barrier Reef, Australia. The figures are all scanning electron micrographs of the skeletons after the soft tissue had been removed.

Plate 5

1—3. Six-hour skeleton; *1* — shows the initial deposits of the basal plate and the differentiation of the central area (arrows), ×80; *2* — rosette-like aggregations of crystallites in this initial deposit, ×1600; *3* — detail of the rosette-like aggregation, ×4000.

4—8. Six-hour skeleton; *4* — peripheral area of the initial deposits of the basal plate, ×300; *5* — enlargement of the periphery showing grain-like crystallites, ×1200; *6* — grain-like crystallite, ×6000; *7* — small aggregation of crystallites, ×6000; *8* — aggregation of crystallites, ×6000.

Plate 6

1—6. Twenty-four hour skeleton; *1* — showing the initial development of the 6 protosepta (arrows) and the differentiation of the central area, ×80, *2* — spherical aggregates of central area, ×660; *3* — central area, ×180; *4* — initial deposits of a protoseptum (arrows), ×900; *5* — enlargement of the initial deposits of the septum, ×3000; *6* — central part of the initial deposits of the septum, ×5000.

7,8. Two day old skeleton; *7* — showing the primary layer of the basal plate and the initial deposits of the protosepta and the second order metasepta ×70; *8* — enlargement of central area, ×140.

Plate 7

1—3. Five day old skeleton; 1 — protoseptum showing trabeculae fused at the base but separated distally, ×280; 2 — part of basal plate between septa showing arrangement of crystallites of secondary layer and parts that are not calcified (arrow), ×1200; 3 — basal plate and 3 orders of septa, ×50.

4—5. Seven day old skeleton; 4 — structure of distal tip of trabecula of first order septum, ×2250; 5 — trabeculae of second order septum showing bifurcation and fanning of trabeculae and scars of desmoidal processes (arrow), ×500.

6. Nine day old skeleton showing the basal plate, three orders of septa and a central tabula, ×33.

Plate 8

1—2. Twelve day old skeleton; 1 — showing basal plate, several orders of septa and epitheca, ×50; 2 — part of septum showing trabeculae diverging laterally from the median plane of septum, ×300.

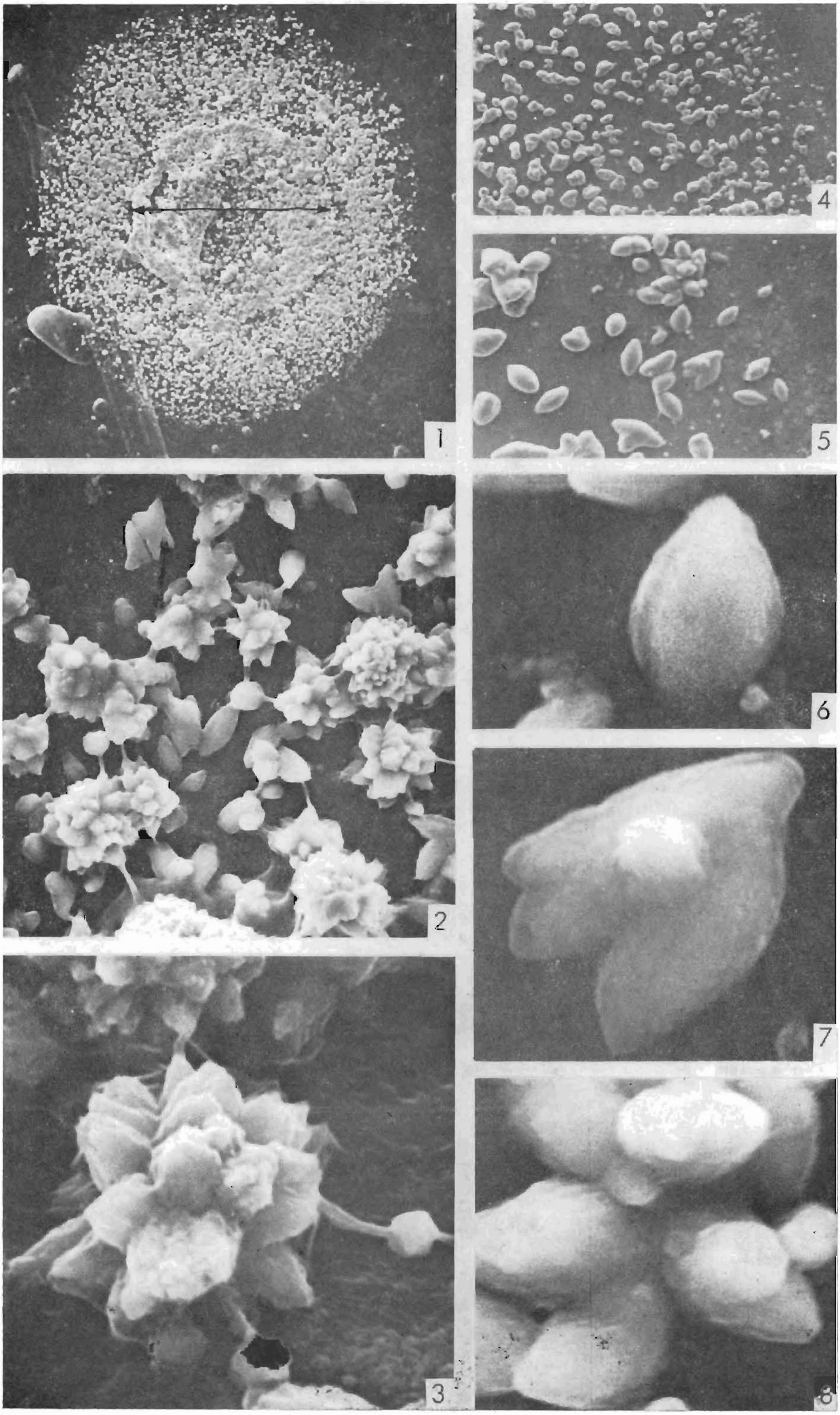
3—4. Fourteen day old skeleton; 3 — corallite with well developed epitheca, ×65; 4 — epitheca showing growth bands, ×300.

5. Eighteen day old skeleton; epitheca developed at extreme edge of basal plate, ×600.

6. Eighteen day old skeleton; epitheca developed inside the periphery of the basal plate, ×600.

7. Twenty-one day old skelton; well developed septa showing lateral spines and in places fusing, trabeculae developed peripherally to the septa; ×40.

8. Aggregation of 3 skeletons, ×20.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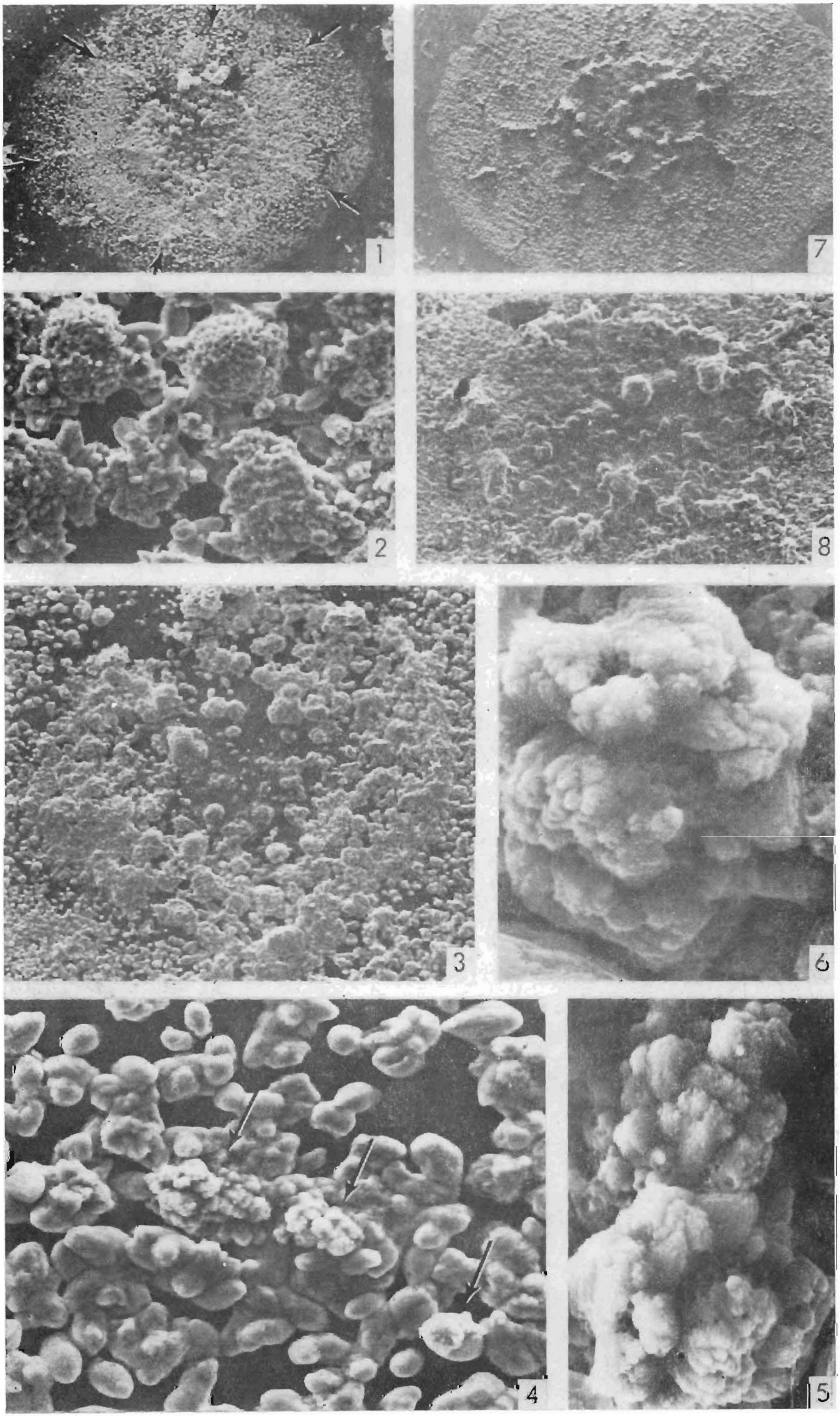

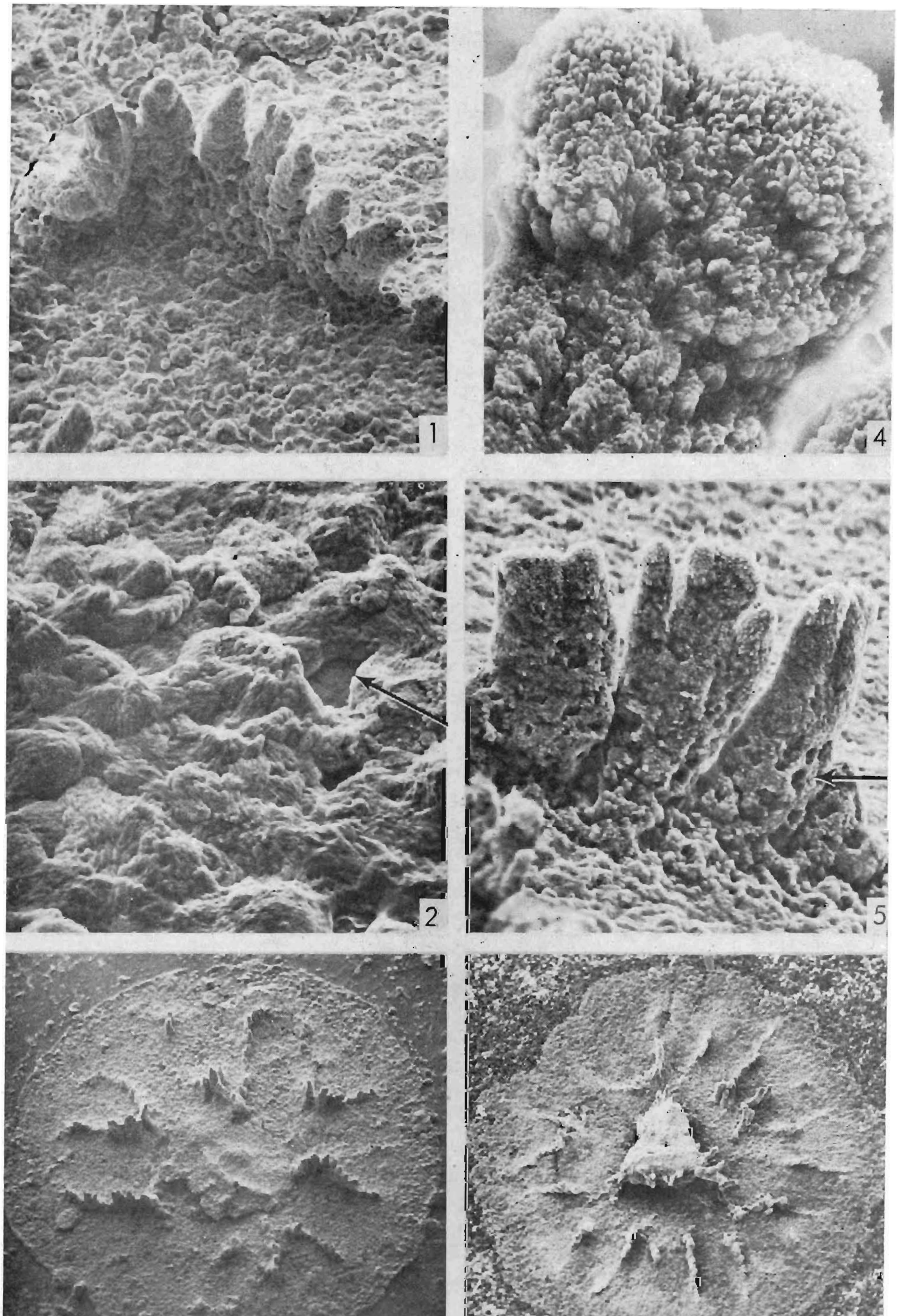
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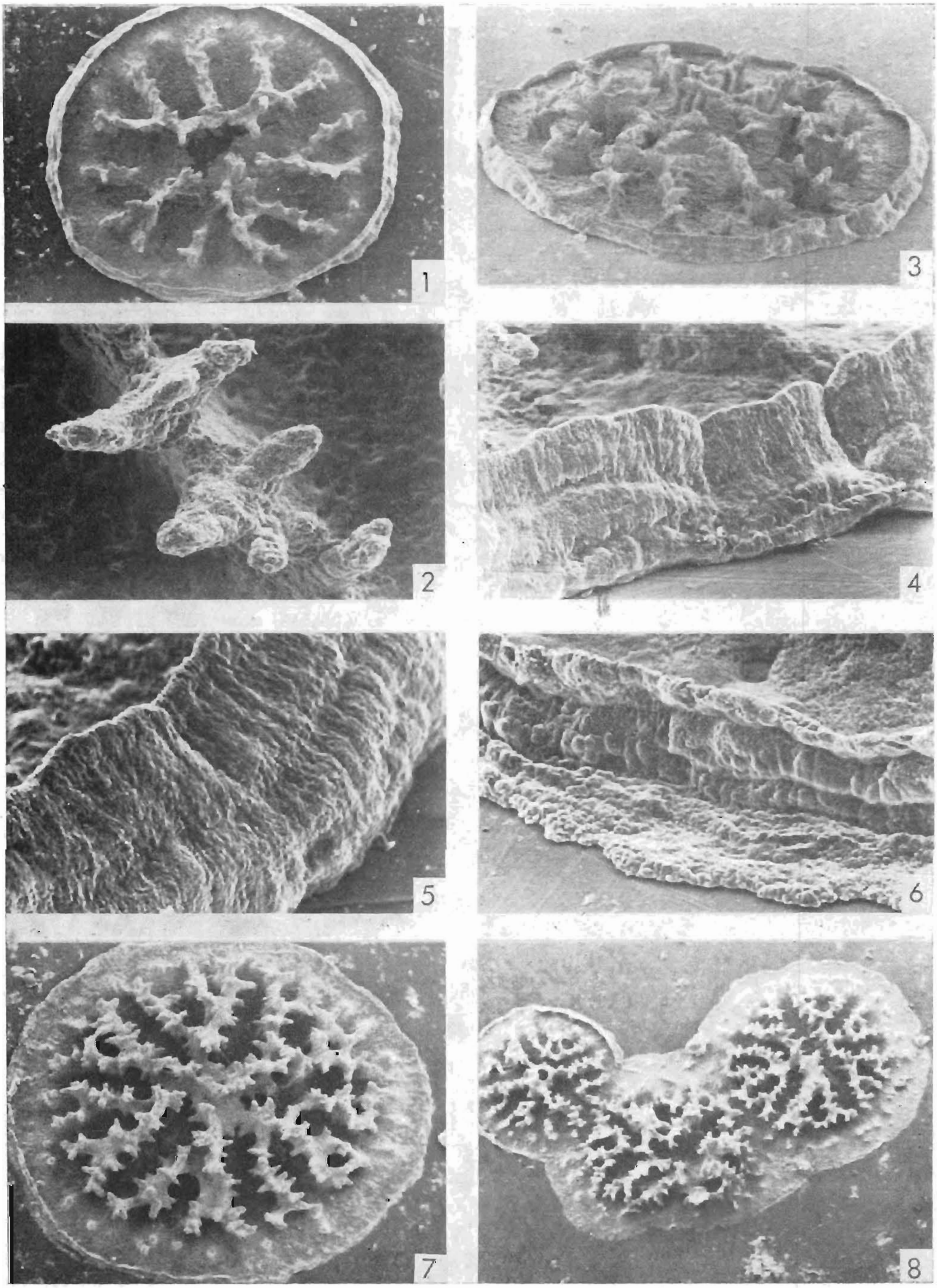
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