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THE FULTURAE ("COMPOUND SYNAPTICULAE"), THEIR
STRUCTURE AND RECONSIDERATION OF THEIR SYSTEMATIC
VALUE

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The study of the structure of fulturae in Recent *Cycloseris cyclolites* and various species of *Fungia* reveals an upward growth of fibers gradually diverging from the centre outwards. The distal end of each fultura is rounded and rhythmic secretion leaves a succession of horseshoe figures on the outer surface. In their structure, the fulturae differ basically from "simple" synapticalae and from the design which had been ascribed to them in literature. The twofold notion of synapticalae ("simple" and "compound"), until now considered as fundamental distinctive character for the suborder Fungiida, should be abandoned. The suborder Fungiida, as delineated in recent classifications, seems to include at least two apparent, non-related groups: one common in Tertiary and Recent forms which bear fulturae and show a septal structure similar to the *Montlivaltia* type (e.g. *Cycloseris*) and the other including pennular corals (mainly Mesozoic) with or without "simple" synapticalae.

Key words: Hexacoralla, Fungiidae, skeletal microstructure.

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INTRODUCTION

The currently used and most recent classifications of the order Hexacoralla (or Scleractinia) are those proposed by Vaughan and Wells (1943), Alloiteau (1952) and Wells (1956). Vaughan and Wells and then Wells subdivided the order into five suborders, whereas Alloiteau has recognized eight. Numerically dominant by far are the two suborders Fungiida and Faviida, common to all three classifications. In the recognition of Fungiida, two main criteria have been proposed: A. septal perforation and B. presence of synapticalae—simple or compound (coalescent after Alloiteau).

It seems that a series of misunderstandings have accompanied the observation and interpretation of the synapticalae since the very beginning of their study. The so-called "compound synapticalae" do not seem to be derived from, or have a common origin with the "simple" synapticalae. The fulturae ("compound synapticalae") which

in places unite laterally adjacent septa, occur essentially within *Fungia*, *Cycloseris* and other related Tertiary to Recent genera. Studies on some of these genera (Gill 1977) have allowed the recognition of a structure different from the one presumed for the "compound synapticalae" in the past. This leads to a re-examination of the validity of the criteria used to differentiate the Fungiida.

The term *fultura* (buttress in Latin) was first introduced by Gill 1977, (unpubl. thesis to Pierre and Marie Curie Univ. Paris 6, pp. 92—99); it has also been briefly discussed by Gill and Coates (1977).

HISTORICAL COMMENTS

The term "synapticula" was first introduced by Milne Edwards and Haime (1857, 1: 35, 65—66) to designate "bars formed by fusion of grains of the lateral surface of septa with those of contiguous septa". On p. 35 the authors state: "The lateral surfaces of the septa often present granulations or small conical points. A certain number of these grow sometimes to a point as to join those of neighbouring septum, giving as a result transverse prolongations, being a sort of interseptal bars which we have named synapticales (synapticulae)". On pp. 65—66 it follows: "The presence of these solid bars, which we call synapticales, characterizes the family of the Fungides, and as yet has not been discerned in any other group of the Class of Corals. It is in the genus *Fungia* that the synapticales have the greatest development as they extend sometimes in form of arched, nearly continuous lines, from down the interseptal chamber up to a small distance off the free edge of the septa".

Thus defined, Milne Edwards and Haime introduced the concept still generally accepted, that the continuous structures which they named synapticalae are merely a coalescence of bar units formed in turn by fusion of opposing granules originating from two contiguous septa. At the same time, these authors clearly state that the synapticalae were observed exclusively in the family Fungiidae.

An important illustrated account on synapticalae in *Fungia*, *Herpolitha* and *Halomitra* is that of Duncan (1883) whose observations are reinforced by microscopic study. Many of the results exposed here correspond to Duncan's conclusions which may be headlined as follows:

- a. The *fulturae* may have a partially or fully free side.
p. 142 (*Fungia*)—"Very often the synapticula are attached to a large septum and only partly so to a very thin septum, a portion of some synapticula remaining free". p. 161—"The synapticula may be seen on the side of a large septum in series, yet without a thin septum adhering to their flat free extremity; and hence the synapticulum may develop prior to one of the septa to which it will eventually attached".
- b. The *fulturae* are not issued from septal granulations.
p. 142 (*Fungia*)—"but the synapticula... are independent of and are not modified granular ornamentation". p. 145 (*Fungia*)—"the ... ornamentation ... is seen between the synapticula; and it is evident that they are different things". p. 147 (*Fungia*)—"The synapticula are not hypertrophied granulations, from which they differ in shape, position and structure".
- c. The *fulturae* do not follow trabecular directions.
p. 152 (*Fungia*)—"The ornamentation has not the same direction as the synapticular structures".
pp. 161—"this ornamentation differs in its direction from the synapticula, and maybe seen between them..."
- d. To a certain extent the formation of the *fulturae* may be regarded as independent of that of the septa.
p. 161—"the fibrous structure of the corals ... is discontinuous here and there between septa and synapticula; and these last are often formed independently of the septa".

e. Fenestration in *Fungia* is due to young incomplete stage of growth.

p. 144 — "It is evident that the fenestrate condition of the smallest septa is not permanent, and is due to incomplete development".

Duncan believed as well that the characters observed in the Fungiidae cannot be used as criteria for taxonomic units higher than family.

These observations of Duncan do not seem, however, to have influenced, as they should, future considerations concerning the fulturae.

Other 19th century authors have added various definitions and interpretations to elements considered to be synapticalae. The present comments will be restricted to some observations proposed by Ogilvie (1896) because they seem to have had a major influence on current prevailing views regarding the fulturae.

Ogilvie (1896) described synapticalae in different genera. She followed Pratz (1882) by considering "true" synapticalae to have independent centres of calcification (p. 170, p. 177 fig. 41) and "false" synapticalae to be an outward continuation of fascicles without calcification centres. Ogilvie's fig. 37 (1896: 172 and fig. 1 here) contributed perhaps most to the concept of "compound synapticalae". This figure shows a lateral side of a septum in *Fungia* bearing 28 fulturae. The surfaces of both septum and fulturae are covered with regularly spaced, identical granulations. The caption for this figure states (p. 173): "It may be observed that granulations are scattered alike over the septal surface and the synapticular bars. The granulations on the synapticalae can only be *actually seen* at their upper parts, where coalescence has not yet taken the place of the synapticalae on the adjacent faces of the septa. In fig. 37, the granulations are for the sake of *uniformity* carried out along the whole synapticular bar". (italics are mine).

This "sake of uniformity" made Ogilvie illustrate granulations where she had not actually observed them! Without referring to Ogilvie's text, her fig. 37 has been reproduced by Vaughan and Wells (1943: pl. 15: 5) and by Wells (1956: fig. 242C) to illustrate "compound synapticalae" and other skeletal elements. Ogilvie's fig. 37 thus became a sort of a modern graphical confirmation of the structural conception of „compound synapticalae".

Although Ogilvie believed that "Independent centres of calcification are present in the synapticalae" (p. 177) she recognized two origins for them (p. 185): "the synapticalae of *Fungia* ... are formed partly as septal outgrowths, partly as an *interseptal continuously-growing calcareous bar*". She also noticed that the synapticalae form after the septum (p. 225): "On the other hand, in the Fungiidae and their allies, the radial structures (continuous septa and costae) are *first* formed, and they determine the *subsequent* development of synapticalae". (italics are mine).

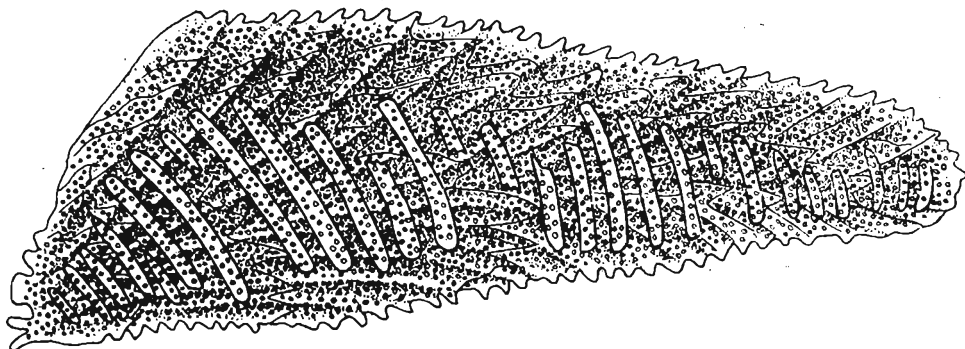


Fig. 1. Reproduction of Ogilvie's text-fig. 37 (Ogilvie 1896) illustrating a septum of *Fungia*. The 28 figured fulturae bear granulations identical to those spread over the septal surface. Ogilvie mentions, nevertheless, that granulations on the fulturae ("synapticular bars") were drawn "for the sake of uniformity".

The conception of fulturae being a union of many centres of calcification may be followed in recent works. Sorauf (1972: 103—106) maintains the distinction of simple and compound synapticalae. He observes that the simple synapticalae originate by the junction of granulations on opposing septal flanks. In *Siderastrea*, "the bars of simple synapticalae are aligned along a single septal trabecula. They apparently result from the enlargement and lateral growth of a trabecula ... and are not much different from septal granulations when small ... Since they are the result of the outgrowth of a single large, simple trabecula, they are simple synapticalae" (p. 104). Sorauf (1972: pl. 15: 1) gives a SEM view of septal flank in *Siderastrea radians*. The synapticalae are visible parallel to a trabecula. Their oval section is much bigger (4 to 8 times) than those of nearby granulations which do not seem to be associated with their formation.

To explain the origin of the "compound synapticalae" as in *Fungia*, Sorauf proposes the lateral outgrowth of a compound trabecular bundle, composed of a number of trabeculae. In *Fungia*, according to this author, synapticalae are formed of a multiplicity of trabeculae. In the micrograph of *Fungia scutarea* Sorauf discerns more than ten trabecular centres in each synapticala (1972: pl. 23: 1).

The synapticalae in *Fungia* consist, according to Jell (1974: 311), "of the lateral extension of secondary trabeculae or fascicles from each septum". No other origin is proposed by Jell who adds: "There is no suggestion that trabeculae or fascicles other than those derived from adjacent septa are involved in the construction of synapticalae". Two SEM micrographs of synaptical microstructure in sections are given in which (1974: fig. 6d) "cut axes of secondary trabeculae" are shown, and (1974: fig. 6f) whose orientation is not clearly explained.

DESCRIPTION

By removing an adult septum of *Cycloseris* or *Fungia*, a surface bearing fulturae is obtained. They start at the basal part of the coral and are set in a partially open fan-system pattern. The fulturae are straight at the median zone of the septum and more or less curved towards the coral axis in the axial zone, and outwards at the peripheral end (fig. 2; pl. 1: 1, 3; pl. 3: 1).

In *Cycloseris cyclolites* the width of the fulturae grows progressively upwards becoming more than doubled (150 μ at bottom, 400 μ at top). Within this species the distance between neighbouring fulturae increases upwards, as their number does not increase (or very rarely) during growth. In a given specimen this distance was 0.4 mm at the base reaching 1.0 mm at the top. Within a big *Fungia*, on the contrary, bifurcation of fulturae is frequent, keeping the distance between them constant (fig. 2; pl. 1: 1, 3; pl. 2: 2; pl. 3: 1, 3).

The fulturae do not reach either the axial edge or the upper end of the septum, leaving a clear uniform fringe devoid of fulturae. In *Cycloseris cyclolites* this fringe measures between 2 to 2.5 mm; in a big *Fungia* it may attain 1 cm (figs 1—3; pl. 1: 1, 3; pl. 3: 1).

Occasionally, portions of fulturae are oriented parallel to the trabeculae, yet in other places the angle between trabeculae and fulturae may vary from 0—90° and more (figs 1, 4; pl. 1: 3, 4; pl. 3: 1, 4; Duncan 1883: pl. 5: 1 and Sorauf 1972: pl. 23: 1).

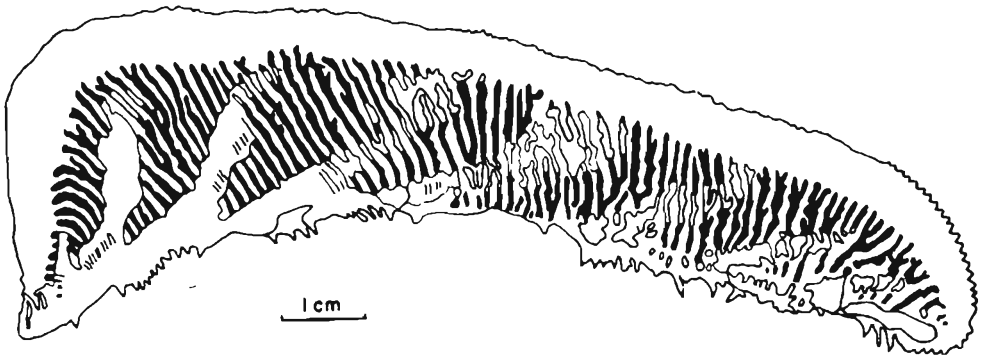


Fig. 2. Diagram of a loosened septal flank in *Fungia* sp. Recent, Pacific (after pl. 1: 1; pl. 3: 1). Some 90 fultriae (in black) frequently bifurcating, diverge with an angle of about 120° and curve outwards at the coral axial and peripheral ends. The free upper septal fringe and the hard bands (in white) crossing the surface occupied by the fultriae are shown.

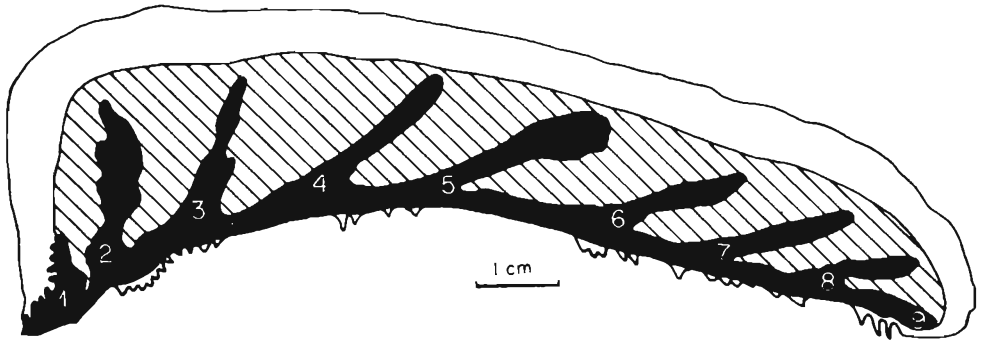


Fig. 3. Lay-out of the hard bands adherent to a loose septal face in *Fungia*. 9 bands uniformly distributed bend progressively from 1 to 9 (after specimen figured pl. 1: 1).

As already mentioned by Ogilvie, the secretion of fultriae takes place where the stereomic thickening of the septa has already occurred. In other words, for a given septal growth level the formation of fultriae is the final construction (pl. 1: 2—4; pl. 2: 1—3).

The fultriae often show a free interseptal side bearing arched growth wrinkles regularly superposed and slightly flattened. This external pattern of scales, with horseshoe outlines, successively secreted with their rounded side upwards, does not correspond to patterns figured in literature (pl. 1: 2; pl. 2: 1, 2; pl. 3: 3). Moreover, it does not seem compatible with an internal structure resulting from coalescence of a multitude of bars or trabeculae, the scheme classically formulated for the "compound trabeculae" since the time of Milne Edwards and Haime.

With increased proximity between an adult septum and a minor adjacent one, fusion of both septa takes place through portions of fultriae.

After loosening several entire septal flanks in *Fungia* by light hammer blows, there remained, very solidly attached, hard short bands of contiguous septa (fig. 3;

pl. 1: 1; pl. 3: 1). In all septa subjected to this procedure, the orientation of these hard bands was observed to be constant. Thus, near the coral centre the first band is vertical and parallel to the septal inner end (fig. 3: 1). Towards the periphery the bands progressively bend down with the last (fig. 3: 9) lying parallel to the coral lower face (figs 2, 3; pl. 1: 1). Apart from these bands, the fulturae are easily uncovered and their surfaces often appear free. This would mean that fusion between fulturae and adjacent septa is taking place in well defined zones.

The fulturae on either side of a septum may be placed in perfectly opposing or alternating positions without following any precise rule (Gill 1977: 84, fig. 6b).

Within *Cycloseris* and *Fungia* the summits of the fulturae are rounded (pl. 1:

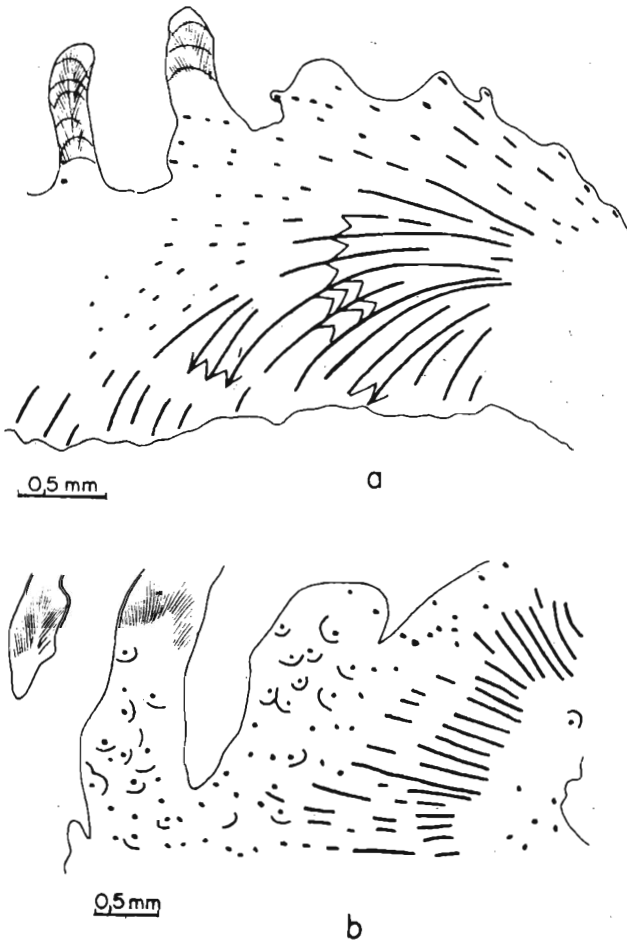


Fig. 4. Schematic presentation of longitudinal thin sections in septa showing traces of granulations at the basal parts of fulturae: *a* *Cycloseris cyclolites* Lamarck, Recent, Pacific. The section passes from the median part of the septum outwards; thus at the lower right side the trabeculae are seen in continuous lines. Above it they progressively pass into granulations which merge into the lower part of the fulturae. At the top the ascending fibrous structure of the fulturae is observed (after pl. 3: 4). *b* *Fungia scutarea*, Recent, Pacific. Orientation similar to that in *a* (after micrograph of thin section in Sorauf 1972: pl. 23: 1) (comp. p. 304).

2—4; pl. 2: 1, 2; pl. 3: 1—6), whereas the trabecular ends of the septa which bear them are pointed and when viewed laterally look like jig-saw teeth (pl. 2: 4). Traces of the pointed trabecular ends may be observed in longitudinal thin sections as parallel corrugated growth lines (pl. 2: 5). This geometrical difference between the upper ends of the trabeculae (angular) and the fulturae (rounded) seems to indicate separate origins.

In longitudinal sections parallel to the septal plane, the fulturae appear to have a continuous structure in which fibres diverge laterally and forwards from an axial area of divergence. Growth lines along the fulturae are arched and parallel to their rounded ends (fig. 4; pl. 3: 2, 4—6; pl. 4: 1—5). In transverse section, the semicircular radiating structure of the fulturae may be observed (pl. 2: 3).

To sum up, the structural pattern of a fultura may be regarded as a half of a trabecula with a rounded end and probably with secondary axes in case of bifurcation.

DISCUSSION AND CONCLUSIONS

How can the contradiction between the classically admitted structural conception of "compound synapticalae" and the view brought forth here be reconciled? Let us look again at some of septal flanks in *Cycloseris* and *Fungia* (pl. 1: 2—4; pl. 2: 1; pl. 3: 1, 3). The fringe between the upper ends of the fulturae and the septal upper end is dotted with strong granulations or spines arranged along or independent of the trabecular carinae. It is evident that the fulturae form posterior to these granulations. Since the secretion of the fulturae will inevitably progress over a certain number of granulations found along their way, these pre-existing granulations will remain embedded at the base of the new structure. The fulturae thus have their own composition of fibres in a diverging upward growth with arched growth lines and cover a variable number of granulations at their base.

Ogilvie was seemingly the only author in the past to have perceived a double composition in the synapticalae of *Fungia* (1896: 185 "... formed partly as septal out-growths, partly as an interseptal continuously-growing calcareous bar"). She failed to further clarify this just statement which finds itself masked by others of ambiguous or erroneous nature.

The presence of buried granulations at the side of the fulturae close to the septum explains how Sorauf, Jell and others could detect "centres of calcification" or "cut trabeculae" in sections of fulturae.

Some additional conclusions of this study are listed below:

1) The fulturae and the "simple synapticalae", none of which seem to originate from septal granulations, differ from each other basically. Some differing characters are:

a. "simple synapticalae" are punctual and isolated from each other by rather regular intervals — the fulturae are continuous structures;

b. "simple synapticalae" appear contemporaneous with the upper edge of the

septa and have an uniform distribution all across the septal surface — the fultracae upper ends lag behind the septal growth leaving a free upper margin;

c. "simple synapticalae" are oriented parallel to trabecular direction — fultracae are independent of trabecular direction;

d. "simple synapticalae" are always fused on both sides to adjacent septa — portions of fultracae do not traverse the interseptal chamber;

e. secretion of "simple synapticalae" is perpendicular to septal planes — fultracae are secreted parallel to the septal plane;

The combined notion of "simple" and "compound" synapticalae should not, therefore, be maintained anymore.

2) The structure of "simple" synapticalae has to be re-examined and re-defined before being proposed as an element of systematics. It seems already clear that "simple" synapticalae, for the most part at least, are not issued from septal granulations which have much smaller diameters.

3) Septal perforation in *Fungia* and *Cycloseris* is sporadic and due to lack of material in early stages of formation; it can not be compared to the structural perforation common in many pennular corals. The genus *Fungia*, provided with fultracae and sporadic perforation, can not, on the basis of these two elements, represent a suborder (Fungiida) which includes numerous genera that have been attributed because of the presence of "simple" synapticalae and structural septal perforation. The suborder Fungiida has therefore to be split and other systematic units, based on different characters, should be proposed to receive its genera.

4) The name "synapticala" has originally been given by Milne Edwards and Haime to the fultracae of *Fungia*. Having priority, with a better definition this term could have been preserved had it not been confused with other structures such as „simple" synapticalae, pseudosynapticalae etc. The detailed study of the fultracae will aid to better isolate structural groups.

Documentation concerning fultracae in fossils seems to be extremely rare. In a recent work Russo (1979: pl. 7: 1c, d, f) illustrates fultracae within *Paracycloseris vinassai* (Opp.) from the Upper Eocene "Blue Marls" of Possagno, Treviso, Italy.

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EXPLANATIONS TO THE PLATES 1—4

Plate 1

1. *Fungia* sp., Recent, Pacific. Septal flank showing the orientation of fulturae (about 90 in number), their uniform distribution due to bifurcation, the axial and upper fringe devoid of fulturae and the hard bands solidly adherent across the septum. $\times 0.9$.
2. Same specimen. Seven fulturae with their rounded upper ends aligned. On the surface, horseshoe-like growth wrinkles are set at parallel levels. The upper surface of the septum is uniformly covered by granulations. A hard band is seen at the lower part. $\times 6$.
3. *Cycloseris cyclolites* Lamarck, Recent, New Caledonia. Radial section in a coral. The fulturae, not bifurcating, are broader and more distant from each other at their tops. Diverging and bending, the fulturae have their orientation independent of the trabeculae. Sporadic perforation is seen in minor septa. $\times 5$.
4. Same specimen. SEM micrograph showing intersection (about 50°) of fultural and trabecular directions on a portion of septum. $\times 26$.

Plate 2

1. SEM view of three upper edges of fulturae in *Fungia* sp., Recent, Pacific. Granulations between them are faintly observed being partially masked by thickening on the fulturae sides. Above the fulturae granulations are well conspicuous. $\times 11$.
2. SEM view of bifurcating fultura in *Fungia* sp., Recent, Pacific. The fultura on the right shows abortive offshoots. $\times 17$.
3. Transverse thin section in septum of Recent *Cycloseris cyclolites* Lamarck, from New Caledonia. On the right, a section through a free fultura showing a radiating structure diverging from a centre at the level of the septal surface. The trabeculae in the septum have rhombic sections and are covered laterally by stereomic lamellar thickening. Such a structure is directly comparable with that of *Montlivaltia* and many other "faviid" genera (after Gill 1977). $\times 120$.
4. SEM view of septal marginal teeth in a Recent *Cycloseris cyclolites* Lamarck from New Caledonia. The granulations emerge from the carinae which run along the trabeculae. $\times 160$.
5. Thin section parallel to septal plane. View of a trabecular axis in a septum of Recent *Cycloseris cyclolites* Lamarck from New Caledonia. The angular growth lines (the fibres diverge from the axis at an angle of $35\text{--}55^\circ$) are marked by dark organic matter which leaves successive domes in the centre. $\times 500$.

Plate 3

1. *Fungia* sp., Recent, Pacific. (detail of pl. 1: 1). Septal flank at the axial zone showing the inclination of the fulturae towards the centre, their common bifurcation, the external free fringe covered with granulations, the discordance between the directions of fulturae and trabeculae and three adherent hard bands. $\times 2$.
2. *Fungia* sp., Recent, Pacific. Longitudinal thin section. The upper end of the fulturae showing bundles of fibres in ascending and diverging growth and arched, dark growth lines parallel to the upper limit. $\times 50$.
3. *Fungia* sp., Recent, Pacific. Granulations are well seen between the fulturae. SEM view. $\times 15$.
4. *Cycloseris cyclolites* Lamarck, Recent, New Caledonia. Longitudinal thin section at the base of the coral, slightly oblique to septal plane. On the right the section passes from the carinae (continuous) into the granulations (first elliptical, then circular). At the bases of the fulturae some granulations in continuity with the trabeculae are seen. At the upper ends of the fulturae, where the section is well off the septum, only the fibrous upgrowth of the fultura itself is seen. $\times 35$.
- 5, 6. Details of 4. In 5, the typical diverging structure of the fulturae with traces of arched growth lines. In 6, traces of granulations (above five) mingle with the microstructure of the fultura; the upper extremity is free of granulations. $\times 100$.

Plate 4

A longitudinal thin section taken parallel to a septum in *Fungia* sp., Recent, Pacific.

1. Fultura showing diverging upgrowth of fibres, arched growth lines and successive dark axial domes. $\times 40$.
2. Another fultura with same characteristics as in 1. $\times 100$.
3. Fibres in a portion of a fultura showing the continuous diverging upgrowth. $\times 100$.
4. Some of the arched growth lines are marked by dark organic matter which at the axial zone appears as successive domes. $\times 100$.
5. Detail of 4. $\times 250$.

