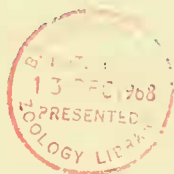# AN ACCOUNT OF A PATHOLOGIC STRUCTURE IN THE FAVIIDAE (ANTHOZOA): A REVISION OF *FAVIA VALENCIENNESII* (EDWARDS & HAIME) AND ITS ALLIES

BY

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AN ACCOUNT OF A PATHOLOGIC STRUCTURE IN THE FAVIIDAE (ANTHOZOA): A REVISION OF *FAVIA VALENCIENNESII* (EDWARDS & HAIME) AND ITS ALLIES

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CONTENTS

SYNOPSIS

The current concept of the coral *Favia valenciennesii* (Edwards & Haime) is reviewed and shown to include two groups of forms, the first similar to the type specimen, the second to the type of *Favia bertholleti* Edwards & Haime; these species have previously been regarded as synonymous. An important feature of the *F. valenciennesii* group is the unusual mode of corallite junction, taken in the past to be diagnostic of this species. This structure is seen in a number of dried (museum) specimens and is described here in detail for the first time. Evidence is presented for its occurrence in four different species and its diagnostic significance is accordingly doubted. Reasons are given for believing this structure to be pathologic. Specimens of the *F. bertholleti* group are regarded here as a growth-form of *Favia favus* (Forskål) and three principal intergradational facies are defined for this species.

I. INTRODUCTION

THE necessity for a revised systematic status for *Favia valenciennesii* was suggested in the first instance by Matthai's occasional difficulty in distinguishing each of the thin-walled facies he had described for *F. bertholleti* (= *valenciennesii* of later authors) and *F. favus*. One of his captions (1914, pl. 22, fig. 7) for instance, which shows one

of Forskål's types of *Madrepora favus*, refers it to " *?Favia bertholleti* (Val.)... Perhaps only a thin-walled *F. favus* ". A number of museum specimens however, some previously undescribed, provide evidence that the relationship of the two species is more complex, and additional species (with at least one other genus) are involved. Thus the problem of *F. valenciennesii* has wider implications that was realized at first. The ecological and geographical abundance of both the genus *Favia* and the species *F. favus* moreover, provided an added interest to the present study. The physiological significance of the very deep intercorallite grooves and associated features, customarily taken to be typical of one facies of *F. valenciennesii*, was an additional problem.

There has been virtually no consideration of any of these points in previous published work. Edwards & Haime (1848, 1849), in describing their type of *Phymastrea valenciennesii* provided the first description of the deeply grooved structure, but evidently thought it was simply another mode of junction of corallites that happened to be less common than most. Duncan (1883) added little detail of importance to their description and took the same view of the structure's significance. Quelch (1886) thought that the passage openings between the corallites of his new species *Phymastraea aspera* might be those of worm tubes; his figure of the structure is oversimplified. Although Matthai (1914 : 79) gave no description of the structure at all, he made it clear that, contrary to Edwards & Haime, he believed the particular mode of junction of the corallites had no generic significance; but it would seem from his remark that he perhaps did not appreciate the very unusual nature of the grooves. Vaughan (1918) agreed with Matthai. Crossland's (1952) only specimen of *Leptastrea bottae* exhibits what he called " beams connecting the thecal walls " and he suggested comparison of his figure showing a longitudinal section (Crossland, 1952 : pl. 2, fig. 2) with the similar sectional view given by Edwards & Haime of their *P. valenciennesii* (1848, pl. 9, fig. 3a). Both show the presence of " tubercles " uniting adjacent corallites. Crossland felt that *F. valenciennesii* was "difficult to define ", having also commented in his 1941 paper that Matthai seemed hardly certain of the distinction between *F. favus* and *F. bertholleti*, in certain instances. Apart from these relatively brief references, made largely in passing, very little discussion has arisen on this subject, though these few remarks make it clear that there were certain difficulties which deserved attention. There has in fact even been a lack of good descriptions and figures of the various features first noted by Edwards & Haime.

The subject has been considered in three parts. The first concerns problems of synonymy, as a result of which various authors' original concepts have seemingly become blurred. The second involves the precise nature of the intercorallite structure currently taken to be diagnostic of *Favia valenciennesii*, and hence its systematic significance. (Detailed description of this structure has been given at this point in the following account, rather than in the systematics section, for convenience of comparison.) The third part concerns the physiological significance of this structure, although further study is required before anything more than generalized speculation can be made. Only hard parts have been studied, there being no material available at the time that possessed soft parts. It is here, perhaps, that future work might best concentrate.

II. CURRENT CONCEPT OF *F. VALENCIENNESII*
(EDWARDS & HAIME)

Synonymy

A full synonymy based on the present currently accepted concept of the species *F. valenciennesii* is as follows:

?*Madrepora favus* Forskål, 1775 : 132 (part).

*Phymastrea valenciennesii Edwards & Haime, 1848 : plate 9, figs. 3, 3a; Edwards & Haime, 1849 : 124; Edwards & Haime, 1857 : 500; Duncan, 1883 : 408; Yabe, Sugiyama & Eguchi, 1936: 31, pl. 23, figs. 3–5, pl. 24, fig. 5.

Favia valenciennesii: Matthai, 1924 : 14, pl. 4, fig. 1, pl. 11, fig. 2 (also pl. 1, fig. 2[1] pl. 2, fig. 9); Faustino, 1927 : 133, pl. 27, figs. 1–3; Crossland, 1952 : 126; Wells, 1954 : 485; Nemenzo, 1959 : 89.

Favia (Phymastraea) valenciennesii: Umbgrove, 1939 : 28, pl. 28, fig. 2.

* *Prionastrea rousseaui* Edwards & Haime, 1849 : 131 (part).

* *Prionastrea halicora* Edwards & Haime, 1851 : 102 (part) (non *Astraea halicora* Ehrenberg, 1834); Edwards & Haime, 1857 : 517 (part).

* *Parastrea bertholleti* " Valenciennes, MS " Edwards & Haime, 1857 : 431.

* *Favia bertholleti* Edwards & Haime, 1857 : 431; Matthai, 1914 : 94, pl. 7, fig. 2, pl. 22, fig. 7, pl. 23, figs. 4, 6, pl. 24, fig. 1.

* *Prionastraea australensis* Edwards & Haime, 1857 : 520.

Phymastraea irregularis Duncan, 1883 : 409, figs. 1, 2.

* *Phymastraea aspera* Quelch, 1886 : 105, pl. 4, figs. 1–1b.

Taxa asterisked were brought together by Matthai (1914) under the name *Favia bertholleti* (Valenciennes). Duncan's paper (1883) included a shortened redescription of *P. valenciennesii* based on Edwards & Haime's account, not, it would seem, from relevant specimens of his own. His new species, *Phymastraea irregularis*, was believed by Matthai (1924) to be *Favia valenciennesi*. *Madrepora favus* Forskål has been added here because Matthai was of the opinion that one of Forskål's types was possibly *F. bertholleti*, although he did not place the species in his synonymy, (see his caption to pl. 22, fig. 7). Vaughan (1918 : 100) regrouped Matthai's species of *Favia* and in the course of his discussion pointed out that Valenciennes' name *bertholleti* was invalid, as it was only known from a manuscript. He suggested that the next available name be used instead, this being *Phymastrea valenciennesii* Edwards & Haime. *Phymastrea* was rejected as a genus, because Vaughan (and Matthai) agreed that the mode of junction of the corallites, regarded by Edwards & Haime as a distinguishing factor in separating "astraeid" genera, was of doubtful significance.

Prionastrea rousseaui, according to Matthai, consisted of eight specimens, five of which he referred to *F. favus*, including the types, and the remainder of which he identified as *F. bertholleti*. Edwards & Haime (1851) referred their *P. rousseaui* (1849) to an earlier species of Ehrenberg's, *Prionastrea halicora*, hence Matthai cited their use of this species, in part, also. The species name *bertholleti*, was made valid by Edwards and Haime (1857), when they redescribed it presumably from Valen-

[1] Plate printed upside down.

ciennes' original specimen. For reasons that will be clear below, it is convenient to continue to use this name as discussion is simplified. Two further species were included by Matthai in his synonymy, each consisting of one specimen only: *P. australensis* Edwards & Haime (with a query) and *Phymastraea aspera* Quelch.

Seven papers subsequent to Matthai (1914) have included descriptions or formal systematic reference to *Favia* (or *Phymastrea*) *valenciennesii*. This species name has always been used since Vaughan's revision in 1918, although Yabe, Sugiyama & Eguchi evidently did not agree with him on the use of the generic name. Apart from this change no revision has been suggested or implied by any other authors. It is clear from their synonymies that later authors' definitions of the species have always included Matthai's concept of *F. bertholleti*.

Skeletal morphology

Even though the valid name now in use is *F. valenciennesii*, consideration of Matthai's account of *F. bertholleti* shows that his concept of that species is based primarily on Edwards & Haime's specimen of the latter. It will be shown that the type of *F. valenciennesii* falls outside this delineation. From Edwards & Haime's type description, (a translation of which is given below under *F. favus* in the systematics section) and from Matthai's own account and specimens, the diagnostic characters of his *F. bertholleti* are the irregular or polygonal open calices, closely set corallites with adjacent walls united at the summits, or nearly so, weak columella and thin septa. Matthai divided the species into two facies or morphological forms (referred to by him as " varieties "):

" (1) in which the adjacent corallite-walls are fused, the intercalicinal walls thus formed being not more than 1 mm. in thickness, often thinner; over these the septa are continuous in arches, the septa being thin; (2) thicker-looking in which the corallite-walls are distinct, separated on the surface by intercorallite grooves at the margins of which the exsert ends of the septa stop; the septa are thicker and rougher."

It is concluded from the phrase, " at the surface ", that deeply grooved forms, like *Phymastrea valenciennesii* were not considered typical of either of Matthai's two varieties, which provides at least one reason for doubting the validity of including them as *F. bertholleti*. However, if, as here, it is thought that some of these deep-grooved forms might only be variants of for example, *F. bertholleti*, there is a second more important reason for separating at least several of them from *F. bertholleti*—in particular, the type of *Phymastrea valenciennesii*. Comparison of the two relevant type descriptions (below) shows that in contrast to *F. bertholleti*, *P. valenciennesii* has smaller corallites and good paliform lobes. Edwards & Haime also state in their description of the genus that *Phymastrea* has extracalicular budding.

Matthai was aware that *P. valenciennesii* possibly did not belong with *F. bertholleti*: " The single small type of *Phymastraea valenciennesii* (an edge of a colony...) perhaps belongs with the present species, it has deep intercorallite grooves and coarse septal sides and may therefore be only an extreme case of var. 2, described above,

but the principal septa have long teeth near their union with the columella." Had Matthai complemented his doubt in the text with a query in his synonymy, then Vaughan in making his revision, might conceivably have chosen the next available name after *P. valenciennesii* in Matthai's synonymy, this being appropriately *F. bertholleti* Edwards & Haime. The change would then only have required different authorship.

Further evidence that the deeply grooved forms are to be thought of as atypical within Matthai's *F. bertholleti* rather than typical, is given by the fact that apart from *P. valenciennesii* itself, only two other specimens in both Matthai's own material and that referred to in his synonymy exhibit these deep groves, as far as is known. The first of these is Quelch's type of *Phymastraea aspera* (" . . . which in all probability belongs here "), the second is a small fragment from Ceylon, which he figured (pl. 23, fig. 6, lower left). By reason of the change of name made by Vaughan, *valenciennesii*-forms have however become typical of the species, and *bertholleti*-forms atypical, so effecting a reversal of the previous situation.

Matthai's original two " varieties " were thought by him to intergrade, and his specimens and figures support this view. But subsequent authors have mistaken forms bearing deep grooves for his " var. 2 ", and it is here that intergradation has yet to be demonstrated. It is therefore convenient in the first instance to divide the current concept of *F. valenciennesii* into two groups of species: the first includes specimens which correspond to *F. bertholleti*, and the second, specimens which exhibit a similar structure to that of the type of *P. valenciennesii*. For the sake of brevity, the latter will be referred to here as " groove-and-tubercle forms " this term being based on Edwards & Haime's original description and has more implication than " deeply grooved ". A list of each group is given at the end of this section. Details of specimens examined are given in Table I.

As will be discussed in the systematics section, all gradation occurs between *F. bertholleti*-forms and specimens of *F. favus*. Since the latter name has priority, the former may be regarded as a facies of *F. favus*. This provides a solution to Matthai's difficulty in distinguishing the two species. Groove-and-tubercle forms however exhibit so wide a range of calicinal characters that affinity with any single species alone is improbable. Relevant museum material suggests that at least four species and two genera are involved, which is the principal reason for believing that the characteristic structure is not only of doubtful generic value, but of doubtful specific value also. This is further explained in the following section.

Forms broadly similar to *F. bertholleti* Edwards & Haime:

> *Madrepora favus* Forskål, 1775 (part).
> *Favia bertholleti* Edwards & Haime, 1857; Matthai, 1914 (non pl. 23, fig. 6, lower left).
> *Prionastrea rousseaui* Edwards & Haime, 1849 (part); Edwards & Haime, 1857 (part).
> *Prionastraea australensis* Edwards & Haime, 1857.
> *Favia valenciennesii*: Faustino, 1927; Crossland, 1952; Wells, 1954.

TABLE I

Details of specimens examined.

Groove-and-tubercle structure absent

Specimens more or less form morphological series in this order

PRESENT IDENTIFICATION	SPECIMEN No. (B.M. Register and Great Barrier Reef Expedition)	LOCALITY	PREVIOUS IDENTIFICATIONS	REFERENCES AND FIGURES	REMARKS
Favia favus (Forskål)	1927.5.4.89	Ceylon	Favia bertholleti (Valenciennes)	Matthai, 1914	—	Facies 3. Corallites small (c. 7 mm. diam.) and very close; rather smooth—spinules and prominent teeth absent.
Favia favus (Forskål)	1927.5.4.165	Long Island, Seychelles	Favia bertholleti (Valenciennes)	Matthai, 1914	—	Facies 3. See description in text. Pl. 5, fig. 2; Pl. 6, figs. 2, 4.
Favia favus (Forskål)	1927.5.12.6	Aldabra	Favia bertholleti (Valenciennes)	Matthai, 1914 pl. 24, fig. 1	Facies 2–3. On old label "F. favus" has been struck out and "F. bertholleti" substituted
Favia favus (Forskål)	1927.5.12.49	Aldabra	Favia bertholleti (Valenciennes)	Matthai, 1914	—	Facies 3
Favia favus (Forskål)	1927.5.12.67	Long Island, Seychelles	Favia bertholleti (Valenciennes)	Matthai, 1914	—	Facies 2–3
Favia favus (Forskål)	1934.5.14.128 (GBRE 163)	Great Barrier Reef	Favia valenciennesi (Edwards & Haime)	Crossland, 1952	—	Facies 2–3
Favia favus (Forskål)	1927.5.12.167	Delft, Ceylon	Favia bertholleti (Valenciennes)	Matthai, 1914 pl. 23, fig. 6 lower R.	Facies 3
Favia favus (Forskål)	1927.5.12.165	Delft, Ceylon	Favia bertholleti (Valenciennes)	Matthai, 1914 pl. 23, fig. 6 upper R.	Facies 3
Favia favus (Forskål)	1927.5.12.164	Point Pedru, Ceylon	Favia bertholleti (Valenciennes)	Matthai, 1914 pl. 23, fig. 6 upper L.	Facies 2–3
Favia favus (Forskål)	1927.5.12.166	Delft, Ceylon	Favia bertholleti (Valenciennes)	Matthai, 1914 pl. 23, fig. 6 lower L.	Pl. 5, fig. 3

Groove-and-tubercle structure present

Favia ?favus (Forskål)	1898.12.1.12	Singapore	Favia bertholleti (Valenciennes)	(previously undescribed) determined by?	Groove-and-tubercle structure present in most of colony, but transition to normal exothecal development. Corallites rather small for F. favus (see text) Pl. 8.
Favia speciosa (Dana)	1892.12.1.362	Great Barrier Reef	Favia bertholleti (Valenciennes)	(previously undescribed) "teste G.M." (label)	Compare corallites with those of B.M. 1895.10.9.133 (Pl. 7, fig. 1).
Favia speciosa (Dana)	1892.12.1.594	Great Barrier Reef	Favia bertholleti (Valenciennes)	(previously undescribed) "fide G.M." (label)	Compare corallites with those of B.M. 1895.10.9.133 (Pl. 7, fig. 1) Pl. 7, fig. 2.
Plesiastrea? valenciennesii (Edwards & Haime)	1886.12.9.151	Banda	Phymastraea aspera / Favia bertholleti (Valenciennes)	Quelch, 1886 pl. 4, figs. 1-1b; Matthai, 1914 —	See text Pl. 4, figs. 1-3.
Leptastrea bottae (Edwards & Haime)	1934.5.14.444 (GBRE 407)	Great Barrier Reef	Leptastrea bottae (Edwards & Haime)	Crossland, 1952 pl. 1, fig. 4 pl. 2, figs. 2, 3	See text
Favia favus (Forskål)	1934.5.14.166 (GBRE 166)	Great Barrier Reef	Favites aspera (Verrill)	Crossland, 1952 pl. 5, fig. 1	Facies 3. Originally identified by Matthai as ?Favia bertholleti and also Favites parvimurata, according to labels. Walls absent in places.
Favia favus (Forskål)	1927.5.4.158	Long Island, Seychelles	Favia favus (Forskål) "var. 1"	Matthai, 1914 pl. 20, fig. 2	Facies 2 (cavernosa-facies) Pl. 5, fig. 1; pl. 6, figs. 1, 3.
Favia speciosa (Dana)	1895.10.9.133	Roebuck Bay, N.W. Australia	Favia clouei (Valenciennes)	(previously undescribed) determined by?	Compare Vaughan's Pl. 36, fig. 1 (1918) of Dana's type of Astraea speciosa. Pl. 7, fig. 1.

Forms broadly similar to *P. valenciennesii* Edwards & Haime (i.e. Groove-and-tubercle forms):

Phymastrea valenciennesii Edwards & Haime, 1848, 1849, 1857; Yabe, Sugiyama & Eguchi, 1936.

Favia valenciennesi: Matthai, 1924; Nemenzo, 1959.

Favia (Phymastrea) valenciennesii: Umbgrove, 1939.

Phymastraea profundior Edwards & Haime, 1849, 1857.

Phymastraea irregularis Duncan, 1883.

Phymastraea aspera Quelch, 1886.

Favia bertholleti: Matthai, 1914 (part) pl. 23, fig. 6 lower left only.

also:

Leptastrea bottae: Nemenzo, 1959; Crossland, 1952.

III. NATURE OF THE GROOVE-AND-TUBERCLE STRUCTURE AND ITS SYSTEMATIC SIGNIFICANCE

Description

A translation of Edwards & Haime's description of *Phymastrea valenciennesii* in which this structure is described, is given below under *Plesiastrea? valenciennesii*. Duncan (1883) also described it for his species *Phymastraea irregularis*, later referred by Matthai (1924) to *Favia valenciennesi*. Duncan's description of the species, together with his further remarks are too lengthy to be quoted here in full, but those sections relating to groove-and-tubercle structure are given below.

There are six relevant specimens in the British Museum (Natural History), all of them Faviids. Three have not previously been described in any published account: B.M. (N.H.) Register Nos. 1892.12.1.362, 1892.12.1.594 and 1898.12.1.12. A fourth specimen (1886.12.9.151) has been described in some detail and figured by Quelch as his type of *Phymastraea aspera*; its unusual structure was only briefly referred to, however. A fifth, (1934.4.14.444), was figured and given a short description by Crossland as *Leptastrea bottae*; and the last specimen Matthai figured as an example of *Favia bertholleti* (1927.5.12.166).

Phymastraea irregularis Duncan[1] (= ? *Favia favus*). " The larger costae have nodules on their free edge placed in linear series, and often extending over an inter-costal space and smaller costae to the next large one. These nodules join those of approximated costae of neighbouring corallites, and form short processes. Junction-processes occasionally do not correspond to costae. An epitheca exists over each corallite, especially low down; it covers the costae and inter-costal spaces and laps round the junction-processes; it is membranous-looking and has a few transverse and other ridges. A small amount of exotheca exists between the costae. . . .

" There is considerable distance between the corallites at the surface, amounting to 1 millim. and more, and this is crossed by the junction-processes. These are very variable in their size and distribution; some do not reach across, and others are constricted in the middle. Very broad ones are exceptional."

[1] The section of Duncan's paper (1883) entitled " Remarks on the structure of *Phymastraea profundior* " should really refer to his own species *P. irregularis*. The list of contents of the paper, as well as its context indicate that the use of this name was a lapsus.

Favia speciosa B.M. (N.H.) Register No. 1892.12.1.594. At the margins of the corallum, corallites are up to 3 mm. apart, or more, and the intercorallite groove is, for the most part, a superficial feature as seen in most species of *Favia*. Occasionally however, small tubular passage openings are present, rising more or less vertically from the surface of the groove for about 0·5 mm., their diameter being somewhat less. The exothecal dissepiments in this part of the corallum are frequently more blistery and thinner than elsewhere, and bear fine lines, which are broadly concentric to the margins of the individual plates making up each dissepiment. In several instances, tubes may be seen rising up directly from these dissepiments; the fine lines on the plates do not continue up on to the outside of these tubes (Pl. 1, fig. 1).

Apart from the tubes, the structure is close to that typical of *Favia*, but the larger part of the corallum differs considerably, with gradations between the two conditions present within the same colony. In detail, the difference is essentially one of degree. For most of the corallum the intercorallite groove is up to 4 or 5 mm. deep, and, except at the uppermost margins of the corallites, about 1–1·5 mm. wide. The groove completely separates adjacent corallites: the costae of neighbouring corallites do not meet in the groove, although their spines may be united. At a depth greater than 5 mm., the groove continues downward at intervals, between which the coral-lites are united partially by exothecal material. Seen from above, the exothecal material, which is not solid, alternates with tube-like openings, similar to those already mentioned, but more frequent (1A, Text-fig. 1, and as in Pl. 4 which is a different specimen). The rims of the tube openings project above the level of the highest exothecal material by about 0·5 mm. (1C, Text-fig. 1). The openings them-selves are often circular and generally less than 0·5 mm. in diameter. More often they are elongated along the length of the groove, though in many such instances, the openings may be seen passing downwards into more than one tube (1Bc, Text-fig. 1). In all examples, the openings may either be turned inwards or outwards, (1B, 1C, Text-fig. 1) or even both, being the surface expression of a system of passages which surrounds each corallite. The walls of the tubes which are thin, bear very fine circumferential lines on the inside; but not, apparently, on the outside, though it is difficult to verify their external absence. The spacing of the openings along the grooves is irregular, as is the variation in their elongation.

Since this specimen is a complete colony, there are no longitudinal sections to be seen.

Structures in the grooves between new and parent corallites, differ from those already described and are taken to represent an early development of the latter. Until a complete partition is formed within the parent corallite, no visible difference can be seen between this and the same feature in corals without groove-and-tubercle structure. In instances where the new partition is complete, and the separated corallites have begun to develop exsert corallite margins on either side of the partition, the features shown in columns 3–6 of Text-fig. 1 may be observed. A sequence is inferred as follows:

(1) small plates form up to about 0·25 mm. in diameter, sometimes larger; these bear very fine, broadly concentric lines; the plates are generally concave uppermost. (Pl. 1, fig. 2, extreme right). In some instances, where a tube opening is situated

near the end of a new intercorallite groove, the actual opening develops a rim which becomes extended along the groove; this is also concave along its length, and bears concentric lines. (Pl. 2, fig. 1). These features are shown diagrammatically in column 3, Text-fig. 1.

(2) Continued growth of the plates and extended rims results in their becoming fused, (column 4, Text-fig. 1, and Pl. 1, fig. 2) to form trough-like plates.

(3) The margins curl upward and close over in part as in columns 5, 6 and 7. Points where the tubes are closed often correspond to positions of costae, particularly where costal spines are strongly developed (Pl. 2, fig. 1). Where the troughs remain only partly closed over, continued upward growth takes place at the margins of these openings so becoming vertical tubes (7D, 8D in Text-fig. 1). The tubes give the appearance of " finding their way " round the costal spines, and form a continuous system which is essentially rectilinear. Further details are better seen in the longitudinal sections found in other specimens, below.

Favia speciosa B.M. (N.H.) 1892.12.1.362. This specimen is not greatly different from that above, and again does not provide a sectional view, being a complete colony.

FIG. 1.   Diagram showing sequence of development of groove-and-tubercle structure around newly formed corallites of *Favia*. The sequence is given by each successive column, as below.

Rows: A—general view of corallites; B—details (plan view) of structures in intercorallite grooves; C—longitudinal sections through corallites at right angles to newly formed corallite wall; D—longitudinal sections along newly formed corallite wall.

COLUMNS 1—A—corallite and neighbours before division, showing tube openings. Compare Pl. 4. B—details of tube openings. Unshaded areas are the outsides of tubes; areas with growth lines are the insides; black areas represent the insides of the tubes at a depth too great for details to be seen. C—section through corallite and exotheca; the tube system appears discontinuous because of its pattern (section at right angles to those seen in Pl. 3). Note the united costal spines and two different modes of tube opening corresponding to 1Ba and 1Bb.
2—Earliest formed partition is no different from that seen in most specimens of *Favia*.
3—First structures to appear are the plates, and extended rims of the existing tube openings. (Pl. 1, fig. 2 extreme right; Pl. 2, fig. 1)
4—Fusion of plates follows, forming troughs (Pl. 1, fig. 2, centre and left).
5—Longer margins of troughs curl upwards (out of the plane of the diagram in 5B, in which the unshaded area represents the underside, or outside of the trough).
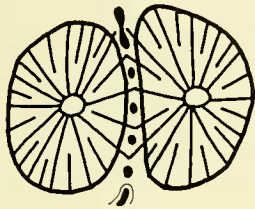6—Growth of exotheca obscures the outside of the trough and the structures now appear more like slots between the corallites.
7—Irregular upward growth results in the development of vertical tubes. 7C shows the original trough completely closed over beneath united costal spines. The position of this section corresponds to the first costa from left in 7D. 7D shows tubes " finding their way " round costal projections. View from above (7A) is now similar to that of parent corallite in 1A.
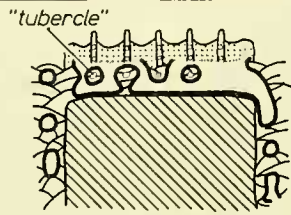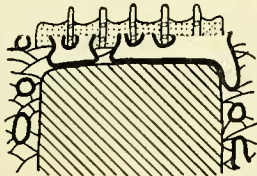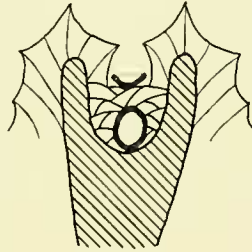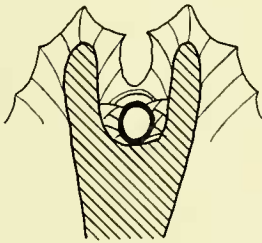8—Continued upward growth extends the tube system. 8C represents a section corresponding in position to the first costa at left in 8D. (Pl. 3, fig. 1).

	7	8
A		
B		
C		
D		"tubercle"

growth line
pattern in
tubes

Row/Column labels and annotations on the figure:

Columns: 1 2 3 4 5 6 7 8

Row A:
- tube opening
- extended rim
- plate
- trough
- trough almost closed over

Row B:
- a b
- c
- d
- growth lines

Row C:
- costa   septum   wall
- new intercorallite groove
- discontinuous exotheca with tubes
- new wall
- new wall
- new exotheca

Row D:
- new wall
- free limb of adjacent corallite
- costa
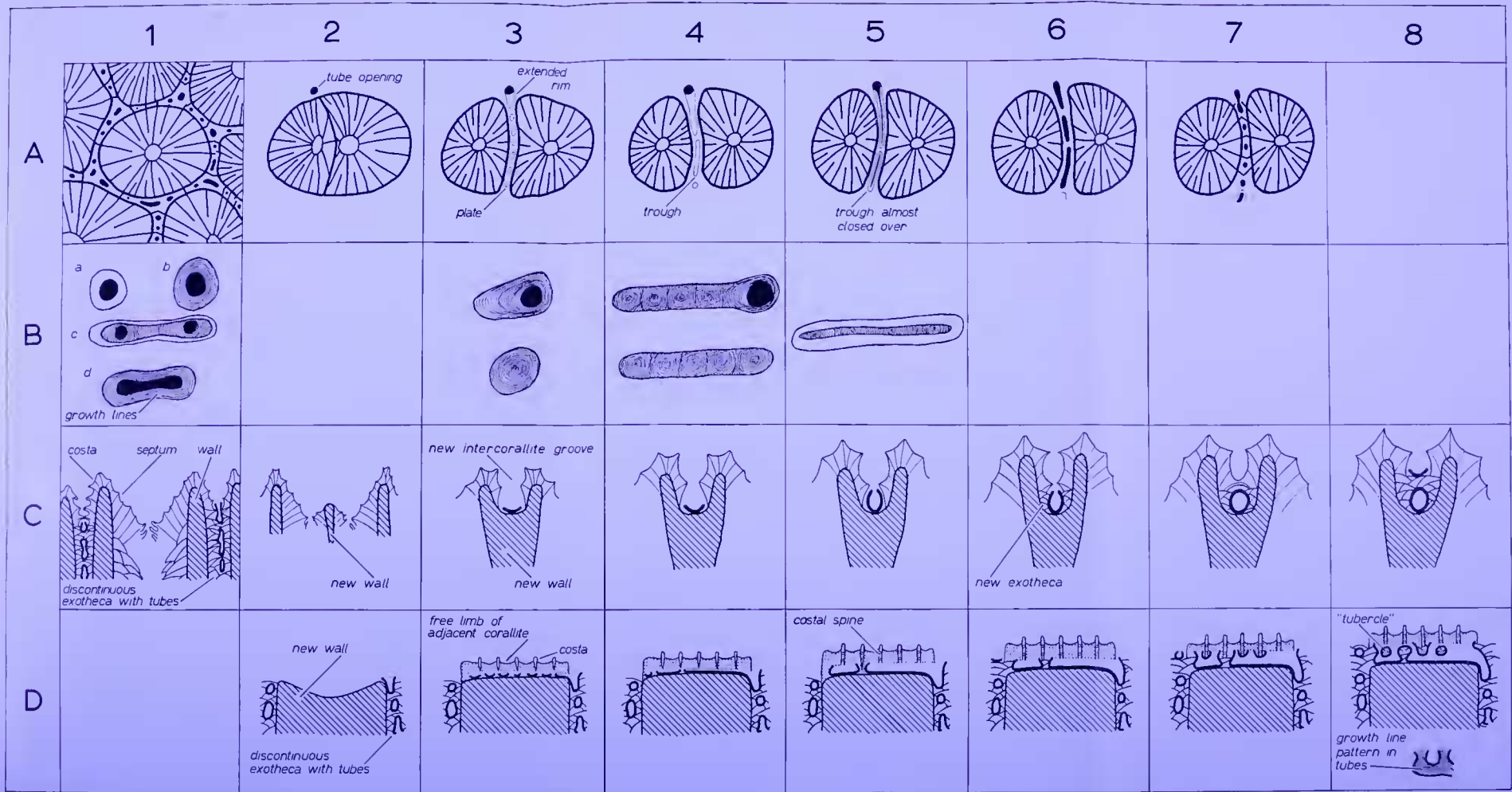- costal spine
- "tubercle"
- discontinuous exotheca with tubes
- growth line pattern in tubes

The stages seen in columns 4 and 5 of Text-fig. 1 are better seen than in the previous specimen. In one instance there is a trough, almost closed in, which surrounds the corallite concerned for about a third of its circumference; the floor of the trough can be clearly seen to consist of the fused plates noted in the previous specimen; at either end the floor passes downward into tubes. This example thus combines most of the features already described.

Favia favus B.M. (N.H.) 1927.5.12.166. The grooves in this specimen are shallower than in the previous specimen (about 1 mm.), but not in this sense superficial. Apart from this the details of intercorallite structure as seen from above, do not differ in any fundamental way from those examples previously described. The specimen does however provide sectional views, which enable further details to be elucidated.

The surface along which the specimen was broken both passes through corallites and between them, and the view so given may be compared with the figure given by Edwards & Haime of their type of *Phymastrea valenciennesii* (pl. 9, fig. 3a, 1848). Where corallites have been broken through, the view is more or less that shown diagrammatically in 1C, Text-fig. 1: between corallite walls, sections through tubes alternate almost regularly with those through bridges of exotheca; the exothecal material consists of stereome with some development of small dissepimental plates. The bridges are thus not solid. Where the plane of the break passes between corallites, the view (Pl. 3, fig. 1) is really an upward extension of the section shown in 8D, Text-fig. 1; the bridges of exotheca are mostly cut through at right angles to the previous section and are seen to be circular to oval in shape. The outside of the corallite walls therefore give the impression of being covered by "tubercles" as described by Edwards & Haime. In this case however, they are less symmetrically arranged (see type description below, under *Plesiastrea? valenciennesii*).

Whatever the disposition of any part of the tube system, the trend of the fine lines on its inner surface is always broadly parallel to the surface of the corallum; in the second section above, the tubes are, of course, split along their length and so resemble discontinuous, rather curled epitheca; the lines are very fine and could not be counted—they are probably of the order 30–50 per mm. The tubes reach 0·5 mm. in diameter though they are often narrower; tubercles are wider, there being about 10 per cm. along the length of the corallite; they may be elongated circumferentially with respect to the corallites up to 5 mm. or so. The tube system remains entirely outside individual corallites; nowhere was there seen any hole or tube passing through a corallite wall. As already observed, tubercles seem to consist of stereome and some dissepimental plates; the stereome is often concentrated around the margins of the tubercle. Costal material is also taken to be contributory, particularly costal spines. Many tubercles seem to have formed around united costal spines of adjacent corallites (7C and D, 8C and D in Text-fig. 1), which would follow from the feature already noted, where the tubes give the appearance of "finding their way" between united costal spines. The overall pattern of the tubes and tubercles is reasonably regular.

In addition to the tubes which emerge between the corallites, there are several instances where larger tubes are to be found within them. Some of these are almost

certainly serpulid tubes, (Pl. 5, fig. 3, extreme lower left) but in two adjacent corallites in the centre of the specimen, they more closely resemble the intercorallite tubes (Pl. 2, fig. 2). Both tubes are offset from the centre of the calices and become progressively wider upwards; they bear very faint circumferential lines on their inner surfaces and are about 3 mm. in diameter at the opening.

Favia ?favus B.M. (N.H.) 1898.12.1.12. The intercorallite grooves are about 3 mm. deep and the openings of tubes and slots somewhat narrower than in any of the above examples. Tubercles typically measure 0·5 mm. (vertical) × 1·5 mm., and as in the previous specimen, are approximately 10 per cm. In several places, the tubercles are much larger and can be seen to consist of rather irregularly arranged exothecal elements. There is further transition from this state to parts of the colony where the exotheca is almost continuous with only an occasional horizontal tube every 5 mm. or so along the corallite length (Pl. 3, fig. 2). The size of the tubes seems to remain constant. In yet other regions of the colony the tubes are absent.

Plesiastrea? valenciennesii B.M. (N.H.) 1886.12.9.151. This specimen shows no important differences from those already described. There is a larger proportion of exothecal material between the tubes than in most of the above specimens and the tubes, though frequent, seem to be more often vertical than horizontal.

Leptastrea bottae B.M. (N.H.) 1934.5.14.444. From above, the corallites are rounded and project irregularly; there is a narrow groove between them up 0·5 mm. across and 2 mm. deep. At a depth greater than 2 mm. adjacent corallites are seen to be united by discontinuous exothecal material. In contrast to all of the previous examples however, the spaces between the exothecal material are not occupied by tubes; that is, although the intervening spaces do constitute a tube system very similar to that described, the thin-walled, finely-lined tubes themselves are not present. A sectional view (Crossland, 1952 : pl. 2, fig. 2) shows the exothecal bridges to be the equivalent of the tubercles above; but here, they are solid, or very nearly so. They are more obviously circular, and measure 0·5–1·0 mm. in diameter. There are 10 per cm. Between these tubercles can be seen the slightly rough walls of the corallites themselves.

SUMMARY OF DESCRIPTIONS. In all specimens, the corallites are separated at the surface by a groove, often narrow and rather deep. An impression of greater depth is given by the exotheca being discontinuous. With a single exception, tubes are present in the intervening spaces and open into the grooves of all of the specimens and form a very broadly rectilinear intercommunicating system. If two adjacent corallites are broken apart the tubes are seen to be finely lined more or less horizontally, and the broken section of exotheca in between is found to correspond to Edwards & Haime's " tubercles ". The fine lines are similar to those seen on epitheca, and these broken sections of tubes are evidently what these authors meant by " epitheca ". Contrary to the impression gained from their description it is the tubes rather than the " tubercles " which are the positive feature, except in the one instance where a specimen has no tube system at all. This same specimen differs from the others in that exothecal material is solid or very nearly so.

At one extreme, adjacent corallites are united for only about 50 % of the maximum;

there is then all gradation, through corallites united by almost continuous exotheca (i.e. large " tubercles ") with some tube development, to those between which there are no tubes at all.   The diameter of the tubes remains broadly constant throughout. This complete gradation is seen in only one specimen here, although Professor J. W. Wells also possesses an example in his own collection (personal communication).

From observing the details of grooves between newly-formed and parent corallites, a sequence in the development of the groove-and-tubercle structure can be inferred. This is summarized in Fig. 1.

Discussion

Edwards & Haime and Duncan believed that groove-and-tubercle structure was an essential part of the coral skeleton, diagnostic of the genus *Phymastrea*.   Quelch was the only author to have stated the possibility of another organism being responsible, by suggesting that the openings along the grooves might be those of worm tubes.   Since Matthai's revision of the " Astraeidae ", the structure has always been taken to be a variation associated with one particular species.   In a sense, all three of these views are, in part, taken here.

The tube openings certainly do have a superficial resemblance to serpulid tubes, but the intercommunicating, broadly rectilinear system which they form round each corallite, and the character of the lines (see below) make this interpretation unlikely.   Moreover, the " plates " and " troughs " described remain unexplained. The material of which the tubes consist resembles epitheca too closely for it to be likely that they were laid down by anything other than the coral itself.   If, however, any external agency has been involved then it seems more probable that its presence would have induced the coral to grow in the manner described rather than it being directly responsible for the structure.   If this interpretation is accepted that the structure is part of the coral skeleton, it is nevertheless an insufficient criterion for recognizing a distinct taxon or taxa if species are to be defined and recognized on a truly biological, rather than merely morphological basis.   The evidence for believing this structure is induced is provided by at least two known specimens with complete gradation within their respective coralla from parts in which groove-and-tubercle structure is present, to parts where it is absent.   Both Matthai and Vaughan considered that the structure had no generic significance and the evidence provided by these specimens not only corroborates their conclusion but also extends it as now it follows that it has no specific significance either.   In addition there is the evidence that certain specimens exhibiting groove-and-tubercle structure may be identified with established species of *Favia* which lack this structure.

The tube material resembles epitheca as Edwards & Haime and Duncan pointed out.   In particular, it bears very fine lines on a scale similar to the epithecal growth lines described and figured by Wells (1963) and Scrutton (1965).   These lines within the tubes, seen also on the plates and troughs, are therefore taken to be growth lines. The direction of growth they indicate corresponds exactly with the sequence of groove-and-tubercle development inferred on other grounds.   On the other hand, the apparent presence of epitheca around individual corallites in corals of plocoid habit, clearly requires explanation.   Professor J. W. Wells has pointed out that

dissepiments, when newly formed, exhibit growth lines (personal communication), an
an observation borne out by Pl. 1, fig. 1.   Rather than attempting to explain the
structure in terms of true epitheca, it might be simpler, therefore, and more
accurate, to regard the tube system as modified exothecal dissepiments particularly
as in this same figure, the tube and dissepiment are seen to be entirely continuous.

By analogy, in specimen No. 1927.5.12.166, the presence within the corallites
of two tubes similar to, but larger than those found surrounding the corallites, might
equally represent unusual endothecal development.   However, No. 1934.5.14.444,
by possessing no tubes at all, may at first seem to provide conflicting evidence.   But
Crossland identified the latter specimen as *Leptastrea* (confirmed here) and the
exothecal character of this genus is dense, consisting mostly of stereome without
visible dissepiments.   The absence of tubes is therefore to be predicted if the present
interpretation is correct, and the Crossland specimen supplements, rather than
contradicts the evidence.

The possibility of this structure reflecting phylogenetic divergence by reason of
its great difference from all other features seen in this group of Scleractinia, has
already been discussed as being improbable.   On the other hand, to regard such a
striking feature simply as a variation seems insufficient, though not necessarily
incorrect if " variation " is understood in a wide sense.   The possibility of there
being a pathologic cause is discussed in the next section.   If this proves to be the
case, then it may be concluded that Edwards & Haime were right in believing the
tubes to be part of the coral skeleton; Quelch was right in thinking another organism
(or agency) might be involved; and Matthai and Vaughan correct in doubting the
systematic significance of the structure.

IV. PHYSIOLOGICAL SIGNIFICANCE OF THE GROOVE-AND-TUBERCLE STRUCTURE

Adequate discussion of the physiological significance of this structure is not entirely
valid without a study of the polyps, both preserved and living.   It is convenient
however, to discuss several points very briefly, in this section.

It is suggested above that the structure is essentially a modified dissepimental
growth.   With the possible exception of Matthai's figured specimen, it is the exo-
thecal dissepiments that are involved, from which it may be taken that the
coenosarc rather than the polyps themselves are affected.   Perhaps the coenosarc
in affected specimens does not form a continuous layer, as it usually does, and the
material of the tubes is laid down at the edges of holes.   Since these would be analo-
gous to edge zone margin (Wells, 1956 : Fig. F 228), material similar to epitheca
would be deposited.   The earliest formed plates in new intercoralliate grooves
could, in this way, correspond to the earliest formed holes in the coenosarc between
new and parent polyps, each growth line marking successive stages in their deposition.
Continued growth would then lead to the enlargement, and eventual coalescence of
the holes in the coenosarc, reflected by the circumferential growth of the plates and
their lateral fusion to form troughs.   Subsequent upward growth would cause the
material of these structures to be built up vertically, and the tube system would

develop in the form observed according to the way in which the holes expanded and contracted, fused and separated, or generally changed their relative position during upward growth. That the direction of growth is always essentially upward, and not consistently parallel to the length of the tubes, is demonstrated by the attitude of the growth lines (alternatively another interpretation of the fine lines is necessary). A different explanation might be that instead of the coenosarc being absent in places, the cause might lie within it. For instance, the calicoblast layer may be incomplete or diseased. Anything more widespread within the coral, would not in the first place seem to explain the highly localized nature of the abnormal feature.

None of the foregoing provides any explanation of the prime cause of the structure, which may be a disease or the indirect result of an association with another organism. There is some evidence that the living corals were adversely affected in their overall growth which would be expected if they were diseased or hosts to a parasite. In the case of Crossland's *Leptastrea bottae*, the septal cycles are fewer and the general character less spinulose than is usual in this species; both features point to inhibited growth. The specimen figured by Matthai as *Favia bertholleti* also gives the same impression; but here the numerous serpulid worms which were evidently present in the living colony cannot be excluded as a possible cause affecting structure during growth. (They might equally be the result, having taken advantage of a coral colony made unhealthy by whatever caused the groove-and-tubercle structure.)

Whether a disease or an association is involved, and whatever the nature of the latter, it seems that some species are more prone than others. One species, here referred to as *Plesiastrea? valenciennesii* is known only from affected specimens, while *Favia favus* is occasionally affected, and *Leptastrea bottae* has provided just the single example so far. Obviously future work is likely to modify this picture, so that for instance unaffected *Plesiastrea? valenciennesii* specimens may be found.

V. SYSTEMATIC DESCRIPTIONS

The diagnoses given below are intended to outline only those characters which serve to distinguish the species from others within the genus. Supraspecific characters and diagnoses followed here, are to be found in Wells (1956) and Vaughan & Wells (1943). The taxonomic state of certain species is such that accurate diagnoses are difficult to provide.

<div align="center">

Order SCLERACTINIA Bourne, 1900

Suborder FAVIINA Vaughan & Wells, 1943

Superfamily **FAVIICAE** Gregory, 1900

Family **FAVIIDAE** Gregory, 1900

Subfamily **FAVIINAE** Gregory, 1900

Genus *PLESIASTREA* Edwards & Haime, 1848

TYPE SPECIES. *Astrea versipora* Lamark, 1816 (by monotypy).

</div>

REMARKS. Two species are doubtfully referred to this genus. These correspond to Edwards & Haime's genus *Phymastrea*, which, according to these authors, shows extratentacular budding. In other respects specimens of the first of the species below are similar in appearance to *Favia* and they therefore seem to be positioned between the two genera. Duncan (1883) pointed out that Edwards & Haimes' description of the genus *Phymastrea* in their 1857 work, differed from those they gave previously, with respect to the nature of corallite increase. He concluded that the 1857 description ("calicular and submarginal") was incorrect, the true mode of increase being " extracalicular and subapical ". Quelch's specimen of *P. aspera*, (pl. 4, fig. 3) which closely resembles Edwards & Haime's *P. valenciennesii*, exhibits both methods, which might explain the " mistake ".

Plesiastrea? valenciennesii (Edwards & Haime, 1848)

(Pl. 4, figs. 1–3)

Phymastrea valenciennesii Edwards & Haime, 1848 : pl. 9, figs. 3, 3a, and 1849 : 124; Edwards & Haime, 1857 : 500 ; Duncan 1883 : 408 ; Yabe, Sugiyama & Eguchi, 1936 : 31, pl. 23, figs. 3–5, pl. 24, fig. 5.

Favia valenciennesii : Nemenzo, 1959 : 89, pl. 5, fig. 1.

Phymastraea aspera Quelch, 1886 : 105, pl. 4, figs. 1–1b.

Leptastrea bottae : Nemenzo, 1959 : 110, pl. 14, fig. 1 (non *Cyphastrea? bottae* Edwards & Haime, 1849).

MATERIAL. See accompanying table.

DIAGNOSIS. Corallites irregular, small to medium in size (5–10 mm.), strong costae, innermost septal teeth directed upwards as irregular, rounded paliform lobes.

DESCRIPTION.

B.M. (N.H.) Register No. 1886.12.9.151. (Type of *Phymastraea aspera* pl. 4, figs. 1–3).

Quelch's description of this specimen is excellent; it is quoted in full below:

" Corallum massive, heavy, irregularly convex. Calicles rather large, very unequal and deep, polygonal, circular, oval or elongated, greatest width from about 9 to 11 mm., many calicles less, about 4 to 5 mm. deep; furrows between the calicles well marked, very narrow, with deep spaces between the connecting portions occupied by small tubes—apparently worm tubes—which preserve the inter-calicinal spaces and keep them open during the growth of the colony; costae unequal, denticulate, those of opposite cups often coalescing. Septa not perforated, of five cycles, the last being very rudimentary, the fourth being small; those of the three first cycles are subequal, large and rather thick, much exsert, and roughly, unequally, and bluntly toothed; the innermost teeth are very distinct, large, long and paliform, not divided, surrounding a distinct deep and narrow depression, at the bottom of which is a small, subtrabeculate or papillose columella which is almost absent in a transverse section. Texture of the corallum very dense and hard."

The only important information lacking in this description concerns the mode of corallite increase. This and some additional details are given below:

One corallite near the margin of the corallum looks as if it has a new partition forming within it, suggesting unequal intratentacular budding (Pl. 4, fig. 3, left centre). Another has given rise to a young corallite which is circular and 1·5 mm. in diameter; the wall shared with the adult corallite is surprisingly substantial for an early growth stage of a corallite formed by intratentacular budding and is therefore thought to be extratentacularly formed (Pl. 4, fig. 3, upper right centre). Budding in such instances evidently takes place very close indeed to the corallite margin. Other corallites also give the impression of extratentacular formation, the only evidence of a partition forming within a calyx being the example already cited.

The corallum measures 7 × 5 × 3 cm. and is almost complete. It has at some time been partially killed off, but subsequently spread a new encrusting growth over most of the dead area.

The smallest corallites are usually completely united to adjacent (parent) corallites along their common wall, separated only by a superficial intercorallite groove 1 mm. or so deep, in which the low costae meet or almost meet. Between mature corallites, the intercorallite grooves are more prominent, the costae themselves do not meet, and the tube openings already described are seen along them.

On the free limb of the corallites, costae are about the same width as the septa in the theca, and bear one to three rough irregular teeth. They are exsert over the margin by about 2 mm. (i.e. relatively exsert); crests are rough and more or less horizontal. The upper half of the septal margins bear two to three rough, slightly lobate, spinulose teeth, of which the upper one to two are directed inwards, while the last is stronger and directed upwards as a rounded paliform lobe. The margin below the lobe is rough. The septa are thick in the theca (one half to one third of the width of the interseptal loculi) and taper towards the columella.

The groove-and-tubercle structure is described in a previous section.

DISCUSSION. Of the species included in the synonymy which were not actually examined, the figure given by Nemenzo of his *Leptastrea bottae* shows that his specimen is very close indeed to that described above, even in the details of new corallite formation. The same is true of the specimens figured by Yabe, Sugiyama & Eguchi.

The type specimen itself was not seen, but Edwards & Haime's figures and description suggest that Quelch's specimen above is very similar. Quelch, however, thought otherwise, believing his specimen to differ

"... by its convex mode of growth, by its more distinct and prominent calicles, which are also quite deep, by the much greater development of the septa, which are more exsert, numerous, and closely spaced, not perforated, with non-bifurcated and large paliform teeth, and by the slight development of columella".

He also stated, on the other hand, that round the outer part of the corallum, "the cups become rather shallow and approach very closely to the form of those of *Phymastraea valenciennesii*". Re-examination of Edwards & Haime's type is clearly desirable. For reference, a translation of their type description is given below. (Compare with that of *Favia bertholleti*, given under *F. favus*, below). Duncan's description is the only other in English and seems to be a shortened translation after Edwards & Haime.

" Corallum encrusting, (upper surface) subplanar.   Calices penta- or hexagonal, separated by very pronounced grooves, where deep holes may be seen (from place to place) by which the intercalicinal spaces communicate with the exterior.   (Fossa very slightly deep.)   Columella well developed, dense in texture and subpapillose at the surface.   Four complete cycles, but the last cycle is rudimentary in most systems.   Septa close, subequal, slightly exsert, slightly thick; the faces bear numerous unequal granulations projecting only a little; the teeth are rather numerous and very strong, particularly the innermost one which is usually bifurcated and upright.   In broken septa, small channels can be seen between the two septal plates.   In longitudinal section, epitheca is seen to cover the entire walls.   Each prism face of the corallites usually bears 2 vertical series of large verrucose tubercles, almost entirely solid in texture, rounded and elongated transversely, strongly uniting neighbouring corallites; the tubercles of one series alternate with those of the other series, and they are all covered by epitheca. The walls are thick.   The septa are wide and are perforated only near the free edge.   The columella is formed of upright trabeculae, very long, and very close. Dissepiments slightly irregular, very close together, but unevenly so, very slightly inclined, rather ramifying.   Larger diameter of corallites, from 8 to 10 mm. (their depth scarcely 2)."

Passages in parentheses in the above translation denote those omitted from Edwards & Haime's 1857 work.

The species seems to be represented only by specimens with groove-and-tubercle structure, a point already discussed.

OCCURRENCE.   Banda; Honsyû, Sikoku, Kyûsyû, and Taiwan (after Yabe, Sugiyama & Eguchi); Philippines (after Nemenzo).

Plesiastrea? profundior (Edwards & Haime, 1848)

Phymastrea profundior Edwards & Haime, 1849 : 125 ; Edwards & Haime, 1857 : 500 ; Duncan 1883 : 408.

MATERIAL.   Not seen (one specimen in Museum National d'Histoire Naturelle, Paris).

DESCRIPTION.   (*Translation of type description*): " Corallum encrusting, convex overall.   Calices polygonal: in the deep grooves which separate them, tubercles may be seen which unite their walls, and which are slightly granulose.   (Calicinal fossa deep.)   Columella poorly developed.   In general three cycles, but some systems have just the three, while others sometimes have a further septum of a fourth cycle.   Septa slightly close, slightly exsert, narrow above, rather thickened over the walls, thin within, at the edges unevenly divided.   There is normally one tooth much stronger than the others adjacent to the columella.   Secondary septa are almost equal to the primaries.   Larger diameter of calyces 8 to 10 mm.; (their depth 5 or 6). "

Passages in parentheses are those omitted from Edwards & Haime's 1857 work.

DISCUSSION.   The affinities of this taxon are not known as it was not seen, has never been figured as far as is known and has not been included by another author

in a synonymy. The presence of a strong tooth near the columella perhaps indicates affinity with *P.? valenciennesii* above. Duncan's description was taken from Edwards & Haime; he stated that *P. profundior* differed from *P. valenciennesii* " by having deeper and smaller calices, a smaller columella, a lower septal number and slender junctions."

OCCURRENCE. Not known.

FAVIA Oken, 1815

TYPE SPECIES. *Madrepora fragum* Esper, 1795 (subsequent designation Edwards & Haime, 1848).

Favia favus (Forskål, 1775)

(pl. 5, figs. 1–3, pl. 6, figs. 1–4, ?pl. 8.)

Madrepora favus Forskål, 1775 : 132.
Favia favus : Wells, 1954 : 458 (synonymy).
Parastrea bertholleti " Valenciennes MS," Edwards & Haime, 1857.
Favia bertholleti Edwards & Haime, 1857 : 431 ; Matthai, 1914 : 94, pl. 7, fig. 2, pl. 22, fig. 7 (= *M. favus* Forskål type), pl. 23, fig. 4 (= *F. bertholleti* Edwards & Haime type), fig. 6, pl. 24, fig. 1.
Prionastraea halicora : Edwards & Haime, 1857 : 517 (synonymy : non *Astraea halicora* Ehrenberg, 1834).
Prionastraea australensis Edwards & Haime, 1857 : 520.
Phymastraea irregularis Duncan, 1883 : 409, figs. 1, 2.
Favia valenciennesi : Matthai, 1924 : 14, pl. 4, fig. 1, pl. 11, fig. 2 (also pl. 1, fig. 2[1], pl. 2, fig. 9) Faustino, 1927 : 133, pl. 27, figs. 1, 2, ?3; Crossland, 1952 : 126; Wells, 1954 : 458; (non *Phymastrea valenciennesii* Edwards & Haime, 1848).
Favites aspera : Crossland, 1952 : 132 (part), pl. 5, fig. 1 only (non *Goniastrea aspera* Verrill, 1866).

MATERIAL. See accompanying table.

DIAGNOSIS. Corallites medium to large in diameter (10–15 mm. typical); rims only slightly exsert if at all; intercorallite areas very variable in width; fission equal to subequal. Septa rough and irregularly dentate.

DESCRIPTIONS.
B.M. (N.H.) Register No. 1927.5.4.165 (pl. 5, fig. 2, pl. 6, figs. 2, 4).
Corallum measures 17 × 12 × 9 cm., massive, rounded, complete colony.
Corallites rounded to irregular, open, 1 mm. apart, diameter 10–12 × 5–8 mm., depth 5mm.
Calicular margins fine, exsert 1 mm., often united. Intercorallite area less than 1 mm. across, or absent; costae continue across intercorallite area.
Twenty-five to thirty septa of which about half reach the columella; some rudimentaries are present. Septa may curve to unite before reaching columella, but rarely more than in two's, thin (about one quarter, or less, width of the interseptal loculi), narrow for the upper one half to two thirds benched, and broader below.
Costae more or less equal; usually continue directly into costae of adjacent corallite, but may also end abruptly against neighbouring corallite margin; exsert over theca by about 0·5 mm., or less, rarely more than 1 mm.; margins horizontal and virtually entire, but may slope inwards. Septa poorly or irregularly toothed or lobed

[1] Plate printed upside down.

above bench (up to 5); sometimes low rounded lobe on bench; a few slight teeth below bench. Septal faces covered with fine conical spinules.

Columella loose, trabecular, one quarter diameter of calice.

Fission intratentacular, subequal.

B.M. (N.H.) Register No. 1927.5.12.166 (pl. 5, fig. 3)

Fragment 4·5 × 5 × 4 cm. consisting of about twenty-five corallites only.

Corallites polygonal, 1 mm. apart, up to 13 mm. long and 7 mm. wide, 5 mm deep; margins rounded, 0·5 mm. thick, slightly exsert. Distinct intercorallite groove, narrow (less than 1 mm.), passing downwards into groove and tubercle system as described above.

About thirty septa of which twelve or so reach columella; some rudimentaries, thick in theca where they are of the same width as interseptal loculi, thinning just within; narrow for upper half, widening below to form a bench above columella.

Costae on free limbs often united by spines across intercorallite grooves, but spines usually limited to only one or two on each costa. Costae thick, separated only by narrow grooves; may alternate with rudimentary costae, slightly exsert over calicular margin where they are rough and generally without teeth or spines; up to six teeth on septal margins, often more pronounced above, sometimes poorly developed as lobes; bench usually marked by one or two larger lobes; two or three smaller teeth below bench; septal faces and costae bear fine spinules, often long and almost bristle-like.

Columella rudimentary, loose, one fifth to one quarter diameter of the calyx.

Fission not seen (intratentacular?).

Development of endothecal dissepiments gives corallites shallow appearance.

B.M. (N.H.) Register No. 1898.12.1.12 (identified here as *F. ?favus*) (pl. 8.)

Corallum measures 12 × 8 × 4 cm., almost complete.

Corallites rounded to slightly polygonal, up to 10 × 7 mm. in diameter, rarely less than 5 mm., 2–3 mm. apart, up to 5 mm. deep.

Free limb of corallites descends steeply or vertically to grooves 3 mm. deep, which pass downwards into groove-and-tubercle system described above, though not throughout the colony—absent in places, where groove is superficial.

Thirty-five to forty septa, of which fourteen usually reach the columella; some rudimentaries present. Septa are thick in theca, but otherwise thin (one third or less width of interseptal loculi), narrow above, upper two thirds either sloping towards centre or tracing concave outline to bench; lower one third vertical to columella or nearly so.

Costae equal in size, thicker than septa, but increase in thickness to meet thickened septa in theca; do not meet across intercorallite groove, bear seven or so good teeth with transversely flattened, upward-directed teeth which may either be pointed or slightly rounded, and occasionally unite with costal teeth of adjacent corallites to form arch over intercorallite groove; crests entire, sometimes with two or three smaller teeth, exsert above corallite margin by 1 mm. or so. Septal margins above bench bear up to eight usually five, inward-directed, irregular teeth, often stronger

above; below bench, two or three more teeth, usually less pronounced, also inward-directed.   The bench gives slight effect of palial crown, but no good lobes present.
Septal faces finely spinulose.

Columella loose, poor, approximately one fifth diameter of calyx.

Fission seen in one corallite is unequal.   In two others, nearer to subequal.   New corallites at margins of corallum formed by unequal fission.

DISCUSSION.   The first of the above described specimens, like most of those referred by Matthai to *F. bertholleti* differs in no fundamental way from the very large suite of specimens he identified as *F. favus*.   The principal differences are essentially superficial, with all transitions from these specimens to those of *F. favus*, mostly consisting of narrower intercorallite areas and rather smoother less dentate septa. Matthai's difficulty in distinguishing the two species has already been referred to (p. 325).   For comparison a figure is also given here of one of Matthai's specimens of *F. favus*, collected from the same locality (pl. 5, fig. 1, pl. 6, figs. 1, 3). This author describes two facies for each of the species *F. favus* and *F. bertholleti*— " thick-walled " and " thin-walled ".   Allowing for the apparent confusion that has arisen by which thick-walled forms of the latter have been mistaken for *Phymastrea valenciennesii*, and *vice versa* (see above) it is possible to define a broad morphological series thus: *F. favus* " var. 2 " (thick-walled)↔*F. favus* " var. 1 " (thin-walled)↔ *F. bertholleti* " var. 2 " (thick-walled)↔*F. bertholleti* " var. 1 " (thin-walled).   The usefulness of being able to distinguish such forms in the genus *Favia* seems open to doubt (see, for example, Wells' remarks on *F. pallida*; 1954 : 458), but it might prove to be helpful in the future.   The above series is accordingly regrouped, as follows:

(1) thick-walled, with enclosed corallites.   e.g. Matthai's pl. 22, fig. 4 (one of Forskål's types), Matthai's pl. 20, fig. 4, Vaughan's (1918) pl. 39. figs. 1, 1a (Verrill's type of *F. danae*).   This facies might referred to as " *danae*-facies ", and is the equivalent of Matthai's *F. favus* " var. 2 " (Wells, 1954).

(2) walls thinner—up to 3 mm. with calyces more open.   Septa often benched and corallites often bear a resemblance to *F. speciosa* (i.e. Dana's type). e.g. Matthai's pl. 20, fig. 2, pl. 22, fig. 5 (Forskål's type of the synonym *Madrepora cavernosa*). This facies might be referred to as " *cavernosa*-facies ", and is the equivalent of Matthai's *F. favus* " var. 1 " and *F. bertholleti* " var. 2 " together.

(3) walls of adjacent corallites closely united to summits, or nearly so; septa often rather fewer, thinner and less rough.   e.g. Matthai's pl. 22, fig. 7 (one of Forskål's types of *F. favus*).   It would be convenient to refer to this facies as " *bertholleti*-facies " but the type of the species seems to fall within the above category, to judge by Matthai's figure of it (pl. 23, fig. 4); it is the equivalent of Matthai's *F. bertholleti* " var. 1".

Forskål's type of *F. favus* range across the facies and there is therefore no " typical " form in the strict sense, if the above division is made.

In addition to the three specimens above, all those that Matthai (1914) referred to *F. bertholleti*, and the single specimen of *F. valenciennesi*, Crossland, 1952 were examined, together with several others.   With the exception of *Phymastraea aspera* Quelch, they are all referred here to *F. favus*. *Favites aspera*: Crossland

belongs here also. Of species known only from the literature, two of the four included by Matthai in his synonymy of *F. bertholleti* are included here, those omitted being *Phymastrea valenciennesii* Edwards & Haime and *P. aspera* Quelch, as discussed above. Edwards & Haime's *Prionastrea rousseaui* (later *halicora*) was divided by Matthai between *F. favus* and *F. bertholleti*; none of the eight specimens could have displayed groove-and-tubercle structure or these authors would surely have referred them to their genus *Phymastrea*. Matthai's grounds for dividing this species are taken to be that some of the specimens had very narrow walls. Edwards & Haime do not often seem to have referred a group of specimens to one species, where most later authors have recognized several; more often the reverse has been true. Edwards & Haime's *Prionastraea australensis*, according to Matthai consists of one specimen only, whose corallites have " a meandering tendency ", but otherwise " resemble those of *F. bertholleti* ". *F. valenciennesii*: Faustino corresponds to facies 3 above, in the specimen figured in pl. 27, figs. 1 and 2; the third figure might belong elsewhere. *F. valenciennesii*: Wells would appear to be facies 3 also, from the description given, but there is no figure.

Duncan's species, *Phymastraea irregularis* was reidentified by Matthai (1924) as *F. valenciennesi* [sic], though he omitted it from his synonymy.

Two of the specimens described above exhibit the pathologic (?) groove-and-tubercle structure. B.M. (N.H.) 1927.5.12.166 has corallites which differ in no fundamental way from normal specimens of *F. favus*. The fragments given by Matthai in his same figure, do not possess this same structure, but otherwise are very close. B.M. (N.H.) 1898.12.1.12 likewise exhibits groove-and-tubercle, but it is less easy to be certain of the affinities of the corallites: they are somewhat small, and the fission seems to be unequal; the costae are noticeably dentate. The specimens figured by Matthai in his 1924 paper as *F. valenciennesi* also seem to be groove-and-tubercle forms of *F. favus*.

For convenience of reference, a translation of Edwards & Haime's type description of *F. bertholleti* is given below. The differences between this and that of their *Phymastrea valenciennesii* have already been stressed:

"Corallum convex. Calices very close, rectangular, margins usually united or only separated by a weak groove. Columella very reduced. From 24 to 30 exsert septa, rather unequal, rather close, very thin within, with quite long teeth; the principals are thick near the wall. There are no distinct lobes. Size of calices 8 to 10 mm."

OCCURRENCE. Widespread Indo-Pacific species. "Red Sea and Indian Ocean eastward to the Fiji Islands, and Fanning Island." (Wells, 1954).

Favia speciosa (Dana, 1846)

(Plate 7, Figs. 1, 2.)

Astraea speciosa Dana, 1846 : 220, pl. 11, figs. 1–1d.
Favia speciosa : Wells, 1954 : 457, pl. 174, fig. 2 (synonymy).

MATERIAL. See accompanying table.

DIAGNOSIS. Distinct corallite margins; numerous thin fine septa, evenly dentate; fission subequal to unequal.

DESCRIPTIONS.

B.M. (N.H.) Register No. 1892.12.1.594 (pl. 7, fig. 2).

Corallum measures 9 × 8 × 6 cm., massive, hemispherical; complete.

Corallites polygonal, sometimes elongated or slightly rounded separated by deep intercorallite grooves 1 mm. in width. Mature corallites 10 × 15 mm. diameter, 7–10 mm. deep.

Groove between corallites up to 4 mm. deep. Free limbs of corallites bear spinulose costae which alternate regularly with rows of granulations which sometimes become rudimentary costae. Principal costae exsert up to 0·5 mm. relative to free limb surface. At a depth greater than 4 mm., most corallites are partially united by discontinuous exotheca, between which tube openings can be seen; margins of corallum tend to exhibit corallites joined more continuously, or even completely, by exotheca.

Forty to fifty septa of which about half reach the columella; some rudimentaries, which, together with slightly larger septa correspond to rows of granulations, or in some instances, rudimentary costae, between the main costae. Septa thin (one half to one third width of interseptal loculi), taper towards columella; narrow above, broadening out for lower one third to give bench.

Margins of costae bear numerous well developed spinulose teeth, lobed, sometimes forked, directed slightly upwards; absent over calicular margins, where costal margins are entire or irregular and horizontal. Septal margin vertical, concave, or convex to bench; up to twelve teeth which may be similar to costal teeth, or, when fewer than six, just irregular lobes; in some instances, comb-like set of very closely small teeth just below costal crest; septal teeth generally directed very slightly upwards; below bench, up to six teeth similar to those higher up; margin descends from bench vertically or nearly so. The septal bench gives slight appearance of palial-crown, but good lobes not developed. Septal faces finely granulose.

Columella loosely trabecular or spongy, up to one third diameter of calice.

Fission unequal to subequal.

B.M. (N.H.) Register No. 1892.12.1.362

Corallum measures 13·5 × 7 × 10 cm., massive, rounded, complete. Character of corallites virtually identical to specimen above, except that the general appearance is somewhat coarser. The thickening of septa over the calicular margin is more pronounced.

DISCUSSION. The principal difference between these specimens and most specimens of *F. speciosa* is in the presence of the groove-and-tubercle structure, identical to that seen in *Plesiastrea? valenciennesii*. For reasons already discussed, this feature is not believed to be of specific value. Comparison of the calicinal characters of these two specimens with those of a third Museum specimen without groove-and-tubercle structure, shows them to be very similar. (Pl. 7, fig. 1). This third specimen, not described at all before, is one of several that compare well with Vaughan's figure of Dana's type of *Astrea speciosa* (1918, pl. 36, fig. 1). It is on this basis that the present identification was made.

OCCURRENCE. Widespread Indo-Pacific species. " Red Sea generally eastward to Fanning Island northward to Honsyû " (Wells, 1954).

Subfamily **MONTASTREINAE** Vaughan & Wells, 1943

Genus *LEPTASTREA* Edwards & Haime, 1848

TYPE SPECIES. *Leptastrea roissyana* Edwards & Haime, 1848; subsequent designation Edwards & Haime, 1850.

Leptastrea bottae Edwards & Haime, 1848

Cyphastrea? bottae Edwards & Haime, 1849 : 115.
Leptastrea bottae : Vaughan, 1918 : 94, pl. 31, figs. 3, 4 (synonymy) ; Faustino, 1927 : 121, pl. 21, figs. 1–3; Wells, 1950 : 49; Crossland, 1952 : 116, pl. 1, fig. 4, pl. 2, figs. 2, 3.
Baryastrea solida Edwards & Haime, 1849 : 144.
Leptastrea solida : Matthai, 1914 : 69, pl. 17, figs. 8, 9, pl. 18, figs. 3–6, 8, pl. 19, figs. 5, 6 (synonymy).
non *Leptastrea bottae* : Yabe, Sugiyama & Eguchi, 1936 : 27, pl. 30, fig. 1 (= *Cyphastrea* sp) ; Nemenzo, 1959 : 110, pl. 14, fig. 1 (= *Plesiastrea? valenciennesii*).

MATERIAL. See accompanying table.

DESCRIPTION.

B.M. (N.H.) Register No. 1934.5.14.444.

Crossland's description of this specimen is as follows:

" In the small crowded calyces of the more usual size, only the six thick primary septa reach the columella, or the secondaries may reach it deep down in the calyx, but generally they are small; tertiaries are just visible or are absent, but their costae, low and rounded like those of the other series, are generally present. Columella greatly reduced, but may bear vertical points, and septa often bear paliform lobes. As seems to be usual in this species, giant corallites are present; in these, numerous septa reach the tuberculated columella, which seems to block the bottom of the theca. Comparison with the other species and with an intermediate specimen in the København museum, indicates that these " giant " calyces are, in fact, nearer the normal form, and the more numerous and smaller being the farthest from the ancestral type.

" A longitudinal section of this species has not yet been figured; it is remarkable for the beams[1] connecting the thecal walls, some solid, some hollow . . . Compare Milne Edwards and Haime's (1848) pl. 9, fig. 3a (for *Phymastrea valenciennesii*) ".

Additional information is as follows:

Corallum measures 6 × 5 × 4 cm., rounded, massive, not complete. Corallites circular, walls relatively thick (0·5 mm.); mature corallites 3 mm. diameter, 0·5–1·0 mm. apart; giant corallite 5·5 mm. diameter; separated by groove up to 1 mm. deep in which the corallites can be seen only partially united.

Giant corallite has one cycle of septa more than other corallites. Septa thick in theca where they are almost as wide as the interseptal loculi; taper fairly abruptly towards columella; broad; depending on cycle, exsert over calicular margin up to

[1] Footnote by A. K. Totton in Crossland's text: " visible also at surface."

1 mm. Septal margin horizontal or sloping slightly inwards over calicular margin for about half the distance to the columella; entire at this point; sharp angle before margin descends vertically or nearly so to fossa, then sharp angle again and margin horizontal to columella. Septal faces spinulose.

Columella formed of upstanding lobes corresponding to each septum of the first cycle, joined by a few horizontal elements to form a crude circle; sometimes a few additional horizontal elements.

Extratentacular budding.

DISCUSSION. The reduced columella, and less spinulose character would suggest some intergradation between *L. bottae* and *L. immersa*, the latter as described by Vaughan (1918 : 96, pl. 31, figs. 2–2b). Crossland believed that his sectional view of the specimen would be similar to that of other specimens of *L. bottae*, but this is not the case: in most instances, corallites are united by continuous exotheca, consisting almost entirely of stereome, as far as can be seen. The tubercles of his specimen are, moreover, not both solid and hollow, as he stated, but almost always solid: an illusion of their being hollow is given when the plane of the section passes slightly into the corallite wall, so allowing a view into the corallite cavity. Crossland's specimen has been interpreted here as abnormal by virtue of the discontinuous exotheca. It has been suggested above that it is essentially a groove-and-tubercle specimen, in which the absence of tubes seen in specimens of other species is explained by the absence of visible exothecal dissepiments in normal growth. The cause of this abnormality may be linked in some way with the cause of the rather atypical calicinal characters.

Nemenzo has described a specimen attributed by him to this species. In his figure, small tube openings can be seen in the intercorallite grooves. The calicinal characters are however totally different from those of *L. bottae* and the specimen is probably closer, if not the same as *Plesiastrea? valenciennesii* above.

OCCURRENCE. Maldives, Chagos, Red Sea, Great Barrier Reef. French Somaliland, Cocos-Keeling, South and Central Philippines, Hawaii (after Vaughan).

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ADDENDUM

Genus *BARABATTOIA* Yabe & Sugiyama, 1941

TYPE SPECIES. *Barabattoia mirabilis* Yabe & Sugiyama, 1941.

DISCUSSION. Yabe and Sugiyama described two species of this genus, *mirabilis* and *goroensis*, each represented by one specimen but *B. goroensis* is possibly only an example of *B. mirabilis* in a rather poor condition. None of the differences between the two original descriptions is usually found to be really significant in distinguishing other Faviid species. The nature of these differences is of the same order as those found for example, in the different facies of *Favia favus* as given above.

Barabattoia mirabilis Yabe & Sugiyama, 1941

Barabattoia mirabilis Yabe & Sugiyama, 1941 : 72, pl. 61, figs. 1–1c.

DIAGNOSIS. Columella well developed, pseudo-pallial crown present, septa alternating.

MATERIAL. B.M. (N.H.) 1894.6.16.37 (King's Sound, Northwest Australia; W. Saville Kent's Collection).

DISCUSSION. Yabe and Sugiyama's plates of the type specimen show clearly that groove-and-tubercle structure is absent. This is the only feature by which the present specimen differs from the type. Tube openings are not seen round every corallite however, nor are they as regularly developed as in some of the other described examples. Thus the specimen shows transition from one condition (taken to be normal) to the other (taken to be pathologic), the significance of which has been discussed above. The tubes themselves are not in any way significantly different from those already described.

This specimen is of great interest although it has been previously overlooked in the collections of the British Museum (Natural History). It was provisionally

labelled "*Stylophora*" because, according to the label inscription, it bore a small encrusting growth of that genus 2 mm. in size but the supposed *Stylophora*, in fact, appears to be a bryozoan growth.   The main body of the specimen, hitherto unidentified, is a small, complete colony of *Barbattoia mirabilis* Yabe & Sugiyama.   It is almost certainly the only representative of this taxon in the collections of the British Museum (Natural History), and seems to be the first record of this rare genus and species since the type description.   Of greater interest still in the present context, it exhibits groove-and-tubercle structure, so providing still further evidence that the occurrence of this feature is not restricted to either one species or one genus.   The number of different genera in which groove-and-tubercle is known to occur is now 3 (possibly 4), all Faviids.   It is therefore seems more than likely that still other related genera and species, both fossil and recent, may prove to be represented by such colonies.

OCCURRENCE.   Yap Island in Palau Islands, King's Sound in Northwest Australia.

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Fig. 1. View from above of an exothecal dissepiment in an intercorallite area near the margin of the corallum, showing growth lines on the dissepiment and a tube rising up from it. The tube is completely continuous with the dissepiment, and the growth lines are absent on the outside of the tube.   × 80.

Specimen No. B.M. (N.H.) 1892.12.1.594, *Favia speciosa* (Dana) (B.M. (N.H.) negative No. 46286).

Fig. 2. View from above of a newly formed intercorallite groove showing (extreme right) a plate, and (centre and left) troughs.   The pattern of the growth lines on the latter marks the original plates of which they are formed, now fused together.   The longer margins of the trough are beginning to curve upwards.   × 30.

Specimen No. B.M. (N.H.) 1892.12.1.594, *Favia speciosa* (Dana) (B.M. (N.H.) negative No. 46284).

Bull. Br. Mus. nat. Hist. (Zool.) 16, 8

PLATE 1

1

2

FIG. 1. View from above of a tube opening in an intercorallite groove, whose rim is extended along the groove. The margins are beginning to close over beneath pronounced costal projections. ⋅ 60

Specimen No. B.M. (N.H.) 1892.12.1.504 *Favia speciosa* (Dana) (B.M. (N.H.) negative No. 46281).

FIG. 2. View from above of a tube opening, within a corallite, similar to those found around corallites along grooves, but somewhat larger. This possibly represents an analogous structure to the latter which are more common. The two corallites in this specimen which contain tube openings may be seen in the centre of Pl. 5, fig. 3. ⋅ 27.

Specimen No. B.M. (N.H.) 1927.5.12.166, *Favia favus* (Forskål) (B.M. (N.H.) negative No. 46283).

1

2
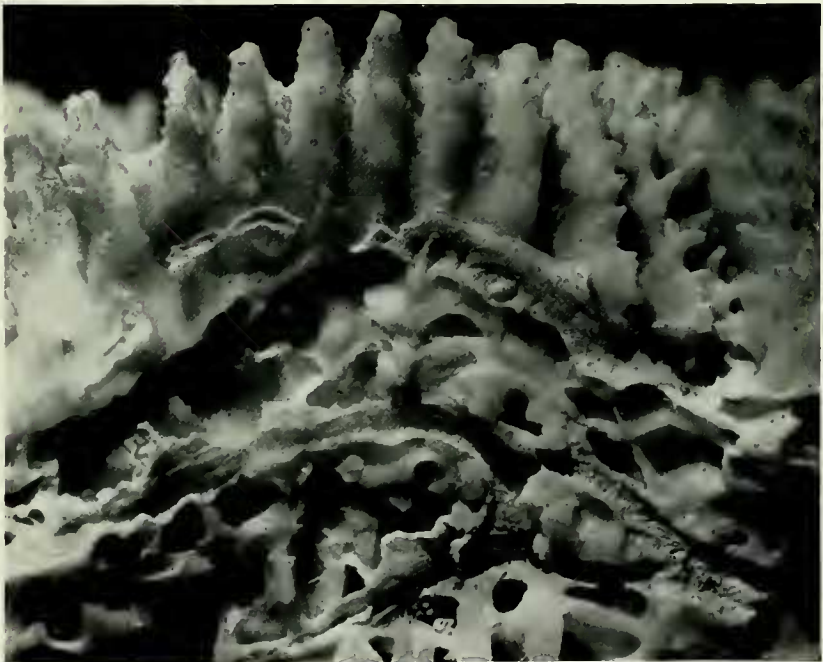
FIGS. 1–3. *Plesiastrea? valenciennesii* (Edwards & Haime). Quelch's type of *Phymastraea aspera*. The intercorallite grooves contain tube openings. Note mode of corallite increase. (see text p. 341). · 8, × 8, × 4.6.

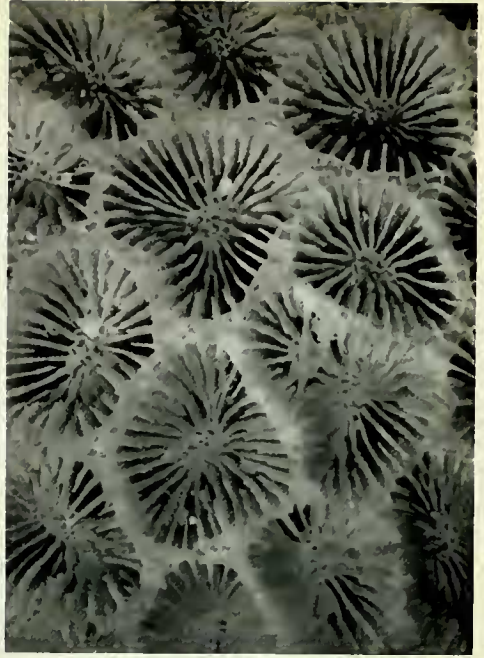Specimen No. B.M. (N.H.) 1886.12.9.151. (B.M. (N.H.) negative Nos. 47572/29b, c, a).
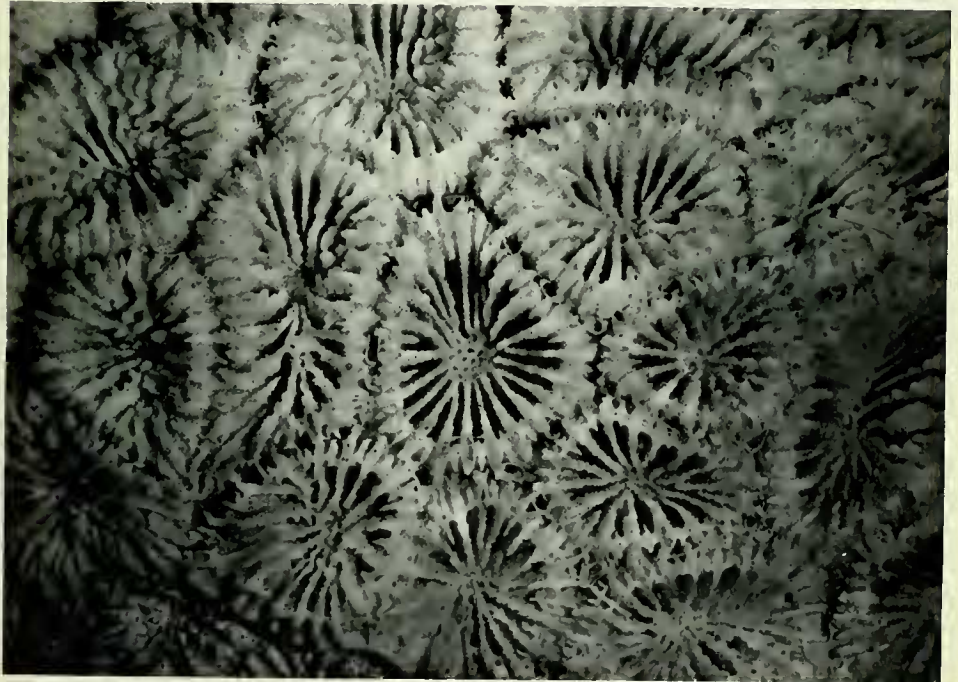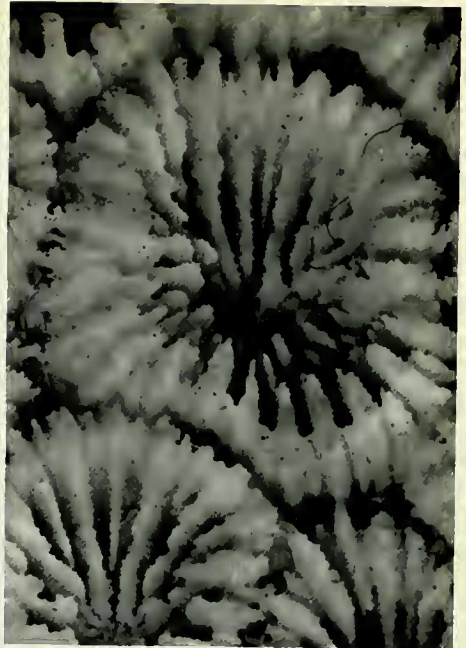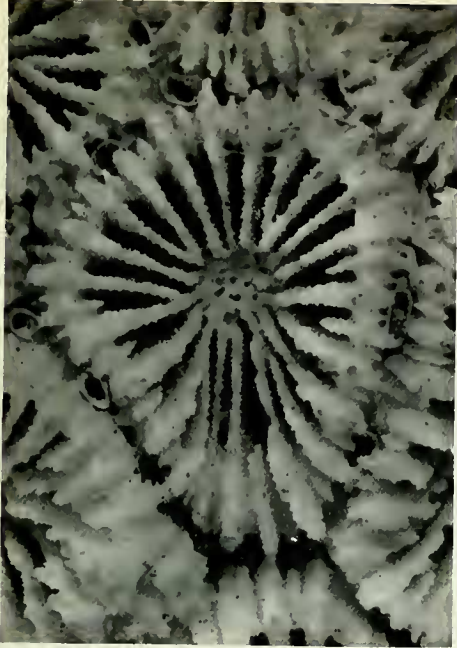
PLATE 4

Fig. 1. *Favia favus* (Forskål), *cavernosa*-facies. This specimen was also identified by Matthai as this species; compare with fig. 2, and pl. 6, figs. 2, 4 which he referred to *F. bertholleti* (Valenciennes). × 2.

Specimen No. B.M. (N.H.) 1927.5.4.158 (B.M. (N.H.) negative No. 47572/11a).

Fig. 2. *Favia favus* (Forskål), facies 3. This specimen was identified by Matthai as *F. bertholleti*; compare with fig. 1, and pl. 6, figs. 1, 3 which he referred to *F. favus* (Forskål) × 2.

Specimen No. B.M. (N.H.) 1927.5.4.165 (B.M. (N.H.) negative No. 47572/12a).

Fig. 3. *Favia favus* (Forskål) with groove-and-tubercle structure. For enlarged views of certain details see pl. 2, fig. 2, pl. 3, fig. 1. The tube within the extreme lower left corallite is that of a serpulid. The two tubes in each of two central corallites appear to be analogous structures to the tubes which surround the corallites, i.e., modified dissepiments. × 2.2.

Specimen No. B.M. (N.H.) 1927.5.12.166.
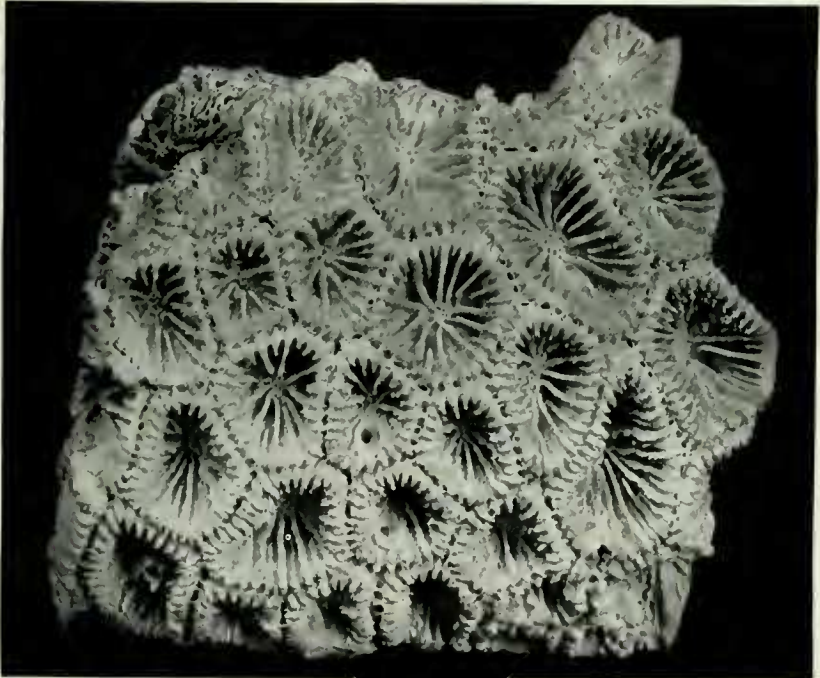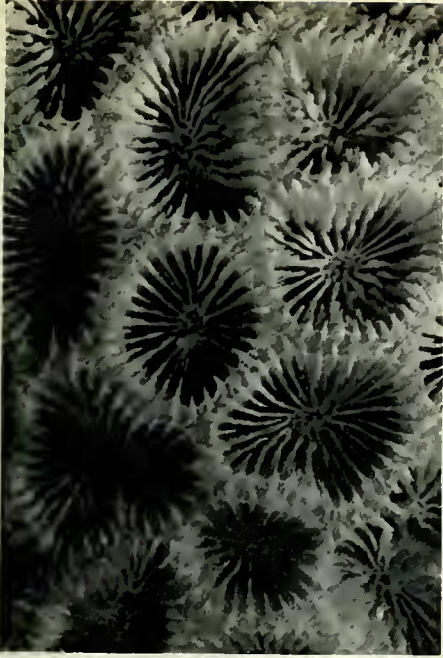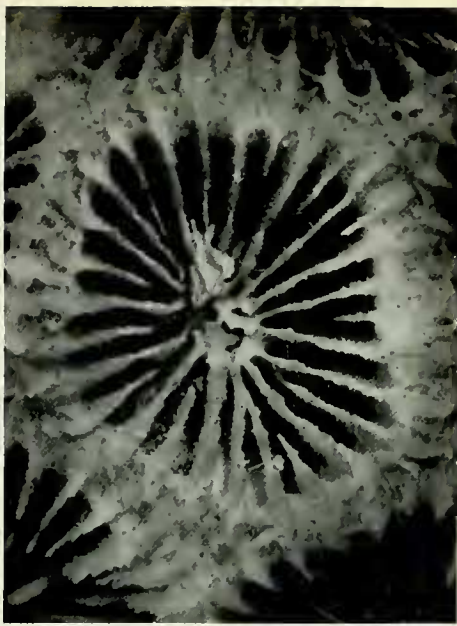
PLATE 6

FIG. 1. *Favia favus* (Forskål), *cavernosa*-facies. See caption to Pl. 5, fig. 1. × 6.
Specimen No. B.M. (N.H.) 1927.5.4.158 (B.M. (N.H.) negative No. 4757²/11b).

FIG. 2. *Favia favus* (Forskål), facies 3. See caption to Pl. 5, fig. 2. × 6.
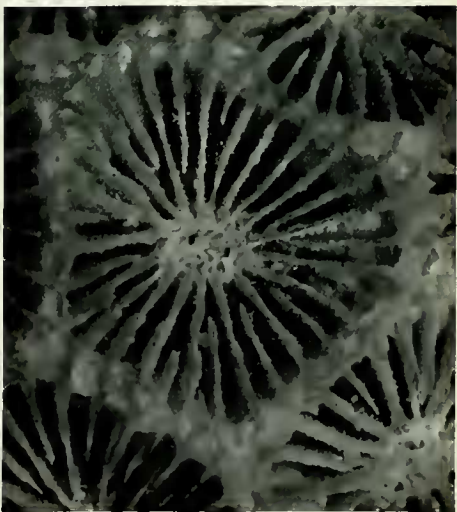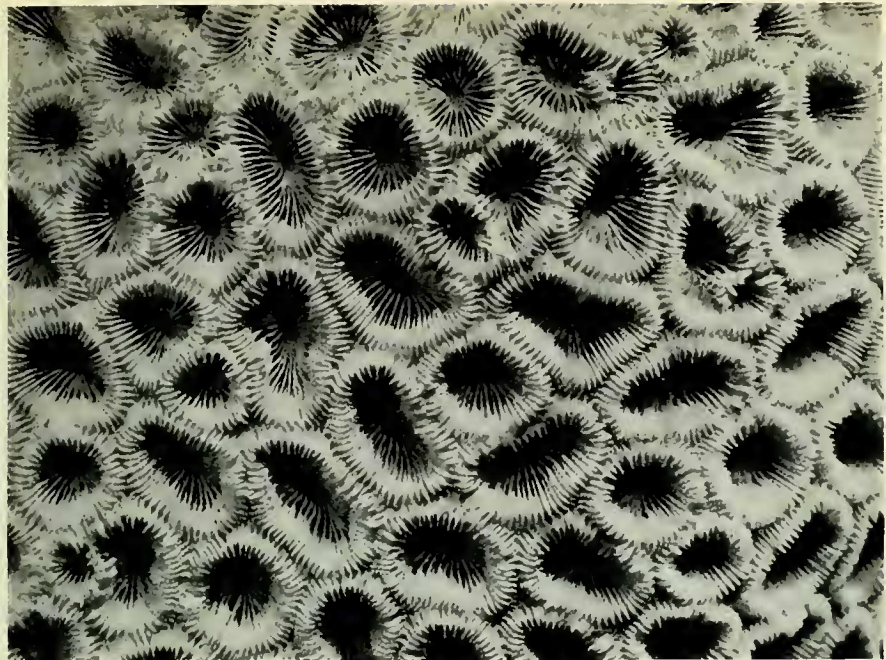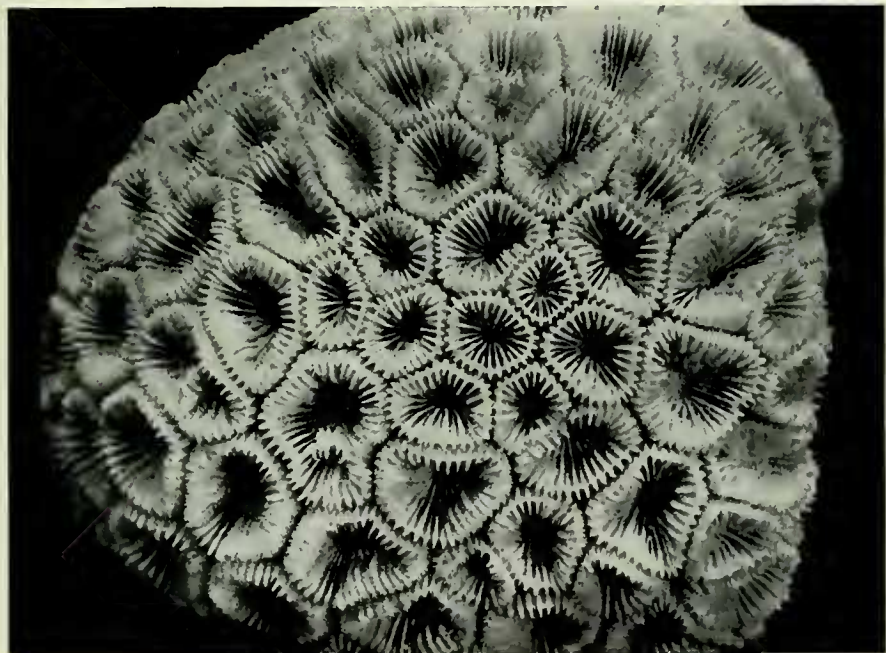Specimen No. B.M. (N.H.) 1927.5.4.165 (B.M. (N.H.) negative No. 4757²/12b).

FIG. 3. *Favia favus* (Forskål), *cavernosa*-facies. See caption to Pl. 5, fig. 1. × 6.
Specimen No. B.M. (N.H.) 1927.5.4.158 (B.M. (N.H.) negative No. 4757²/11c).

FIG. 4. *Favia favus* (Forskål), facies 3. See caption to Pl. 5 fig. 2. × 6.
Specimen No. B.M. (N.H.) 1927.5.4.165 (B.M. (N.H.) negative No. 4757²/12c).
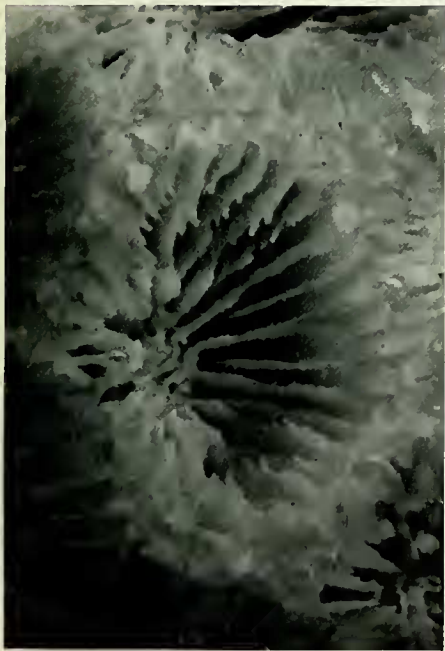
Bull. Br. Mus. nat. Hist. (Zool.) 16, 8

PLATE 6

1

2

Favia ?favus showing groove-and-tubercle structure (not visible in photograph). Corallites at the margins of the corallum (lower part of photograph) only partially exhibit the structure, as in Pl. 3, fig. 2, or do not do so at all. Elsewhere the structure is fully developed similar to that seen in Pl. 3, fig. 1. ⅹ 1.6.

Specimen No. B.M. (N.H.) 1898.12.1.12.