# INVESTIGATIONS ON STYLASTERIDAE

## *(HYDROCORALS)*

BY

HJALMAR BROCH

WITH 38 FIGURES IN THE TEXT AND 6 PLATES

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# Introduction

Various circumstances have delayed the completion of the present studies, lastly especially the war. Since the publication of Part I (1936)[1] Dr. W. K. FISHER in 1938 has issued his fundamental work "Hydrocorals of the North Pacific Ocean", and he has kindly placed at my disposal a series of specimens and photographs of the Pacific species. I wish here to express my sincere gratitude to Dr. W. K. FISHER. My thanks are also due to Dr. SYDNEY J. HICKSON who has facilitated my work with the intricate genus *Errina* by sending me some of his specimens for comparison.

Some time after the publication of Part I of the present studies, W. K. FISHER drew my attention to his paper on Californian Hydrocorals (1931) which had till then escaped my attention. In this paper FISHER, on the basis of *Errina pourtalesii* Dall, defines a genus *Errinopora* which is identical with the genus *Protoerrina* proposed by me in 1935. The proper name of the genus is accordingly *Errinopora* Fisher.

In his last paper FISHER (1938) in some cases holds views which to some degree diverge from mine. Thus regarding the question of a conservative adherence to the old use of *Stylaster* and *Allopora* as separate genera because of their being "time-honoured", and in spite of our acknowledgment that no traceable limit exists between them in nature. However, in spite of this continuity which in my opinion makes it impossible to keep them as separate genera, it is in most cases possible to range the single species within one of the two groups, and I cannot agree to the view that the sense of responsibility of conscientious scientists should be more lulled by using such groups or subgenera than by sticking to positively artificial "genera". — It is also a rather academic conservatism to stick to the axiomatic and exceedingly unpractical practice of using the generic name also as a designation of the central group (subgenus) containing the original type species without any prefix (or suffix) distinguishing it as a subgenus. Although it is not in full concordance with the unfortunate, academic practice of old in zoology, I prefer — like botanists in many

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[1] Untersuchungen an Stylasteriden (*Hydrokorallen*). T. 1. Skrifter utg. av Det Norske Videnskaps-Akademi i Oslo. I. 1936. No. 8.

cases — to use the prefix *Eu-* to emphasize the central group (subgenus) of a genus; in this way we can avoid misunderstandings and absurdities (a rather comical absurdity is illustrated e. g. by a common northern barnacle which should be named *Scalpellum (Scalpellum) scalpellum scalpellum* (Lin.); here genus, subgenus, species, and central race of one species, according to the axiomatic nomenclatorial rules, carry the same name!). But these questions are merely of academic interest.

A comparison with the details given by FISHER (1938) at once convinced me that the specimen from Snake Island, Strait of Georgia, identified as *Stylaster norvegicus* f. *pacifica* in Part I of my studies (1936 pp. 52 and 53), must be referred to *Stylaster (Allopora) verrilli* (Dall). — FISHER opines that all Alaskan specimens regarded by me as belonging to *Stylaster (Allopora) boreopacificus* Broch, should be referred to his extraordinarily varying species *Stylaster (Allopora) campylecus* (Fisher). I have in the present Part II of my studies used his specific name for these specimens, although I do not feel convinced that *Stylaster campylecus* and *Stylaster boreopacificus* really are specifically distinct, the morphologic differences falling well within the range of individual variations of several other species of *Stylaster*.

The present Part II of my studies i. a. gives systematic details of the subfamilies *Distichoporinae* and *Sporadoporinae* which have already been defined in Part I (pp. 7—8). — Also STECHOW (1921) has divided the Stylasteridae into three subfamilies which he characterizes in the following manner: "Fam. **Stylasteridae.** Diese Familie schließe ich eng an *Hydractinia* und *Clathrozoon* an. Zerfällt in drei Subfamilien: ***Erininae nov. subfam.***, ***Distichoporinae nov. subfam.*** und ***Stylasterinae nov. subfam.*** (Die Milleporidae gehören dagegen in die nächste Verwandtschaft der Corynidae)." No further details nor arguments have been given by STECHOW.

According to the definitions given in Part I, the *Distichoporinae* only contains the one genus, ***Distichopora***, whereas the *Sporadoporinae* comprises the genera *Sporadopora*, ***Pliobothrus***, ***Errina***, and a new genus described below, *Paraërrina*. Although *Errina* was the first described genus of this subfamily, it is more natural to name it after *Sporadopora* which already in its name gives the essential characteristic, viz. the irregular distribution of the pores in proportion to each other. To a certain degree the new species of *Pliobothrus* described below seems to break the rule owing to a serial occurrence of lateral dactylopores. On the other hand, however, there is also here no mutual regularity in the distribution of the other dactylopores and the gastropores, and no evident coordination between the gastropores and dactylopores can on the whole be traced.

MOSELEY (1878, 1881) came to the result that *Sporadopora* probably is the most primitive genus of the Stylasteridae. This view is in good accordance with a relationship between the Stylasteridae and Hydroids like *Hydractinia* and *Clathrozoon*, a suggestion already advanced in my report of the Danish Ingolf-Expedition (1914). On the other hand the distinct grouping of gastrozooids and dactylozooids in cyclosystems in the *Stylasterinae*, and in coordinate rows in *Distichoporinae*, must probably be considered a higher specialization. But the limits are in many ways rather vague between the three subfamilies as is demonstrated e. g. by *Errinopora*, and it is accordingly not justifiable to regard the three groups as anything more than subfamilies.

## Subfamily *Distichoporinae*.

### Genus *Distichopora* Lamarck.

The colonies are generally irregularly flabellate or dendritic with dichotomous or subdichotomous branching. The gastropores occur in rows, generally in more or less distinct sulci along the branches. The gastropore row is on both sides, or in rare cases only along one side, flanked by a row of smaller, often slit-like dactylopores. Quite exceptionally irregular cyclosystems are observed in very young colonies. The gastropolyp has tentacles and a well developed gastrostyle; the dactylozooids are finger-shaped and without dactylostyles. — The ampullae may be rather prominent or, in some cases, sunk into the coenosteum and hardly or not visible from without. They occur singly or, generally, in crowded groups on the more or less flattened anterior and posterior sides of the branches. Female ampullae commonly contain one gonophore, male ampullae more gonophores in different stages of development and generally seated round the basal part of a blastostyle. Exceptionally colonies or even ampullae may be hermaphroditic.

This very characteristic and distinctly limited genus was proposed by Lamarck (1816) for *Madreporaria violacea* Pallas 1766. Moseley (1881) in his summary of the literature enumerates 8 recent and 1 fossil species and adds a ninth recent species from the "Challenger" expedition. Later on Hickson and England (1909) have added one species from the Indian Ocean.

It is, however, in most cases impossible to reidentify the species on the basis of the dates given by the old authors, and we are greatly indebted to Fisher (1938) who, after painstaking studies of types and other specimens, has shown the way and furnished necessary details of some of the species mentioned by Gray, Verril, Dana, and Pourtalès.

The species of *Distichopora* are very closely related, and their morphological differences so slight that they can only be distinguished after minute examination. It is therefore in most cases impossible to rely on the old literature alone, and many names must be ranged with the "incertae sedes" until their types have been thoroughly re-examined and revised.

Useful systematic characters are in many cases the general features of the colony and its ramifications, and in some cases the gastrostyle and its structure may render service in the characterization of a species. But special attention should be paid to the surface structure of the coenosteum. In the following pages drawings are given which illustrate differences omitted by earlier investigators. Also here Fisher has shown the way in his description of *Distichopora borealis* Fisher (1938). In this species he furthermore draws attention to the structure of the gastropore wall, viz. to the bristles or spicules occurring here. In other species the wall may be smooth, the spicules converted into warty protuberances etc., features not paid heed to by previous investigators.

The present material contains no less than 7 species, and some of them are represented by several specimens. Their arrangement in a key will serve to give a better idea of the important taxonomic characters. This key can furthermore be filled in with other species as they are revised or discovered.

1 (12) Pore-rows lateral on branches and branchlets as two distinct longitudinal rows, one along each side. 2

2 (11) The gastropore-row flanked along both sides by complete dactylopore-rows. 3

3 (4) Sulcus very shallow, on larger branches commonly effaced. Surface of the coenosteum smooth or commonly covered by almost microscopical, small and crowded, round papillae. Gastropore wall smooth. *Distichopora violacea* (Pallas)

4 (3) Sulcus obvious, generally sharply defined especially on the branchlets. 5

5 (10) Sulcus of the same width as the larger gastropore openings. 6

6 (7) Surface of the coenosteum provided with flat, rounded warts and with rather obvious pores in the grooves between them. Transverse sections of the branches circular. Gastropore wall with spicules, in older pores forming one or two girdles near the brim. *Distichopora fisheri* n. sp.

7 (6) Transverse section of the branch oval or even more compressed, with sulci at the ends of the larger diameter. 8

8 (9) Surface of the coenosteum covered with rather coarse warts of irregular contours. No pores are seen between the warts under the lens. Gastropore wall with rather numerous, irregularly scattered warty protuberances. *Distichopora serpens* n. sp.

9 (8) Surface of the branchlets with irregular, vein-like longitudinal ridges and, especially in the furrows between them, obvious pores. Gastropore wall smooth, without spicules or warts. *Distichopora sulcata* Pourtalès.

10 (5) Sulcus conspicuously broader than the larger gastropores, generally twice as broad. Surface of the coenosteum with feebly prominent, rounded warts, the branchlets longitudinally irregularly veined. Gastropore wall with spicules, near the aperture more numerous and here crowded in a girdle. *Distichopora borealis* Fisher.

11 (2) The gastropore row is only on one side accompanied by a complete row of dactylopores. Sulcus lacking or very feebly developed. Surface of the coenosteum vermiculated, without obvious pores. *Distichopora foliacea* Pourtalès.

12 (1) Pore rows irregular, on all sides of the branches and branchlets, often branching. Sulci lacking or at most barely indicated. Transverse sections of branches and branchlets circular. Surface of the coenosteum vermiculated, without obvious pores. *Distichopora irregularis* Moseley.

## *Distichopora violacea* (PALLAS 1766) LAMARCK.

1766 *Madrepora violacea*, PALLAS, Elenchus Zoophytorum, p. 258.
1816 *Distichopora violacea*, LAMARCK, Histoire des Animaux sans Vertebres, t. II, p. 198.
1846 — *violacea*, DANA, Zoophytes, p. 704, pl. 60, fig. 3.
1860 — *violacea*, MILNE EDWARDS et J. HAIME, Histoire Nat. des Coralliaires, t. III, p. 451.
1860 — *coccinea*, GRAY, Description of a New Species of Distichopora.
1864 — *nitida*, VERRILL, Bull. Mus. Comp. Zool., Vol. 1, p. 46.
1878 — *violacea* + *coccinea* + *nitida*, MOSELEY, Structure of the Stylasteridae, p. 482.
1881 — *violacea* + *coccinea* + *nitida*, MOSELEY. Stylasteridae . . . . . "Challenger", p. 84—85.
?1892 — *violacea*, HICKSON, Scient. Proc. Roy. Dublin Soc., N. S., Vol. VII, p. 501, pl. XVIII and XIX.
1905 — *violacea*, HICKSON and ENGLAND. Stylasterina of the Siboga Exped., p. 20.
1938 — *violacea*, FISHER, Hydrocorals of the North Pacific Ocean, pp. 543—544.

### Forma *typica*.

(Pl. I, Fig. 1.)

Material: S. BOCK's expedition 1917: October 30, 1917, Jaluit, Marshall Islands, reef west of the southern entrance (CHR. HESSLE); two colonies. — Philippine Islands, San Bernardino Strait, 12° 27′ N., 134° 3′ E., 50—100 fathoms, bottom temperature 61° F. (SUENSON, Aug. 3, 1911); one small colony (Museum, Copenhagen). — Dried colonies: S. BOCK's expedition 1917: October 1917, Gilbert Islands, entrance reef; some few small colonies on a piece of dead coral. — October 24, 1917, Jaluit, Marshall Islands, southwestern strand of southwestern entrance (CHR. HESSLE); one small colony. — Eugenie-Expedition: Tahiti, Eimeo, outer reef, depth 3 feet; 6 small colonies (Riksmuseum, Stockholm). — Marshall Islands 1878 (ROSSKILDE) one colony and one fragment. Same locality 1880 (HARTMANN), 5 colonies (Museum, Copenhagen). — "Probably from the Pacific Ocean. Coll. HJALMAR STOLPE", 10 colonies and fragments (Riksmuseum, Stockholm).

Probably the large colony from Jaluit (Pl. I, Fig. 1) shows the most common exterior of the species, flabellate with rather irregularly subdichotomous ramification; the branches are almost cylindrical, a little flattened with their greater diameter in the main plane of the colony. This may be said to be the general type in the extensive material of the present collections. — The pore-rows follow the margin of the branches and branchlets, and the anterior and posterior, feebly flattened sides of the flabellum are generally devoid of pores.

The surface of the coenosteum is smooth, only with hints at small, rounded tubercles which, however, only are visible in somewhat oblique light and under a little greater enlargement. No pores are seen on the surface. — The color of the present colony (in alcohol) is a rather dark purple with somewhat lighter, more rosy or yellowish colored ends of the branchlets; the pore-rows are, especially on the branchlets, intensively coral red. — A small colony from Jaluit, also in alcohol, has the same deep purple color, but its three branchlets are yellowish white.

A comparison with the large collections of dried specimens at hand, and mostly originating from the same parts of the Pacific Ocean, is interesting. Newly collected specimens, like the new Form described below, coincide with the alcohol-preserved specimens from Jaluit. In most other cases, however, the color more or less pronouncedly approaches the carmine which ought to be characteristic of *Distichopora coccinea* of Gray (1860) which was described after specimens collected at the Marshall Islands, and one or two of the present colonies might probably be considered as representatives of this form. Altogether, however, the present colonies show all possible shades of coloring from a rather dark blueish purple through carmine and vermilion to apricot or orange yellow or even all but white branchlets, and there is no reason to regard the color-variants as separate varieties or forms.

In dried specimens the surface even under the lens exhibits a minutely granular surface. The very small, rounded tubercles, however, are not so obvious under the microscope with somewhat greater enlargment, and no pores are seen even in colonies, the organic tissues of which have been removed by sodium hypochlorite.

Several small colonies from three feet depth at Eimeo (Tahiti) are at first sight rather puzzling because of their low, broad and irregular growth and their extraordinarily dark purplish blue color. The colonies are partly covered by algae, sand grains etc., and cleaning with sodium hypochlorite shows that the color of the coenosteum is in reality only little darker than the darkest parts of the small colony from Jaluit mentioned above, although only few of the terminal branchlets are lighter colored than the stems and bases in the Eimeo colonies. The low and broad shape of the flabellums, and the spreading of the basal part over the substratum (dead coral), are

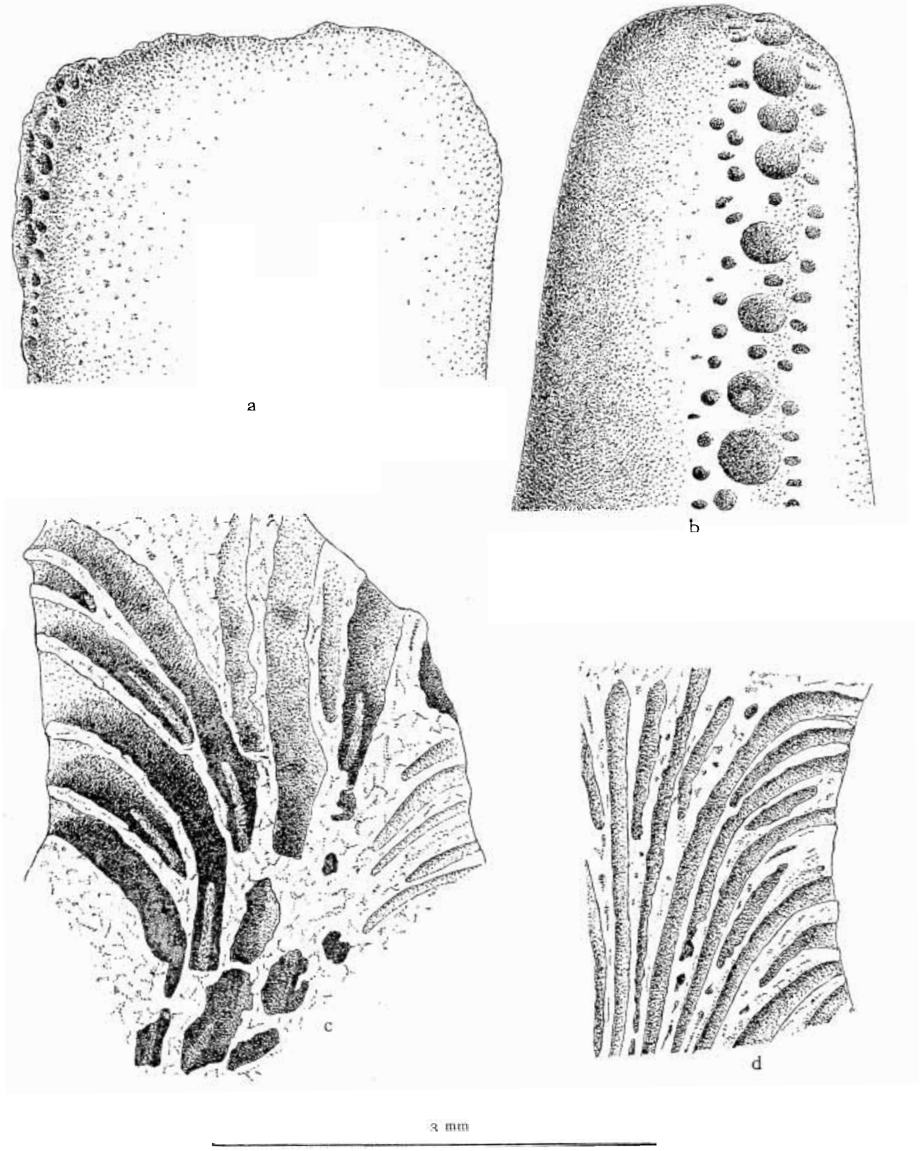


Fig. 1. *Distichopora violacea* form *typica*. Jaluit, Marshall Islands, taken by a diver. — a end of a branchlet from the flat side. b pore-row terminally on a branchlet in side view. c median section of a branchlet showing gastropores in longitudinal section. d section parallel with c through the dactylopores.

probably due to the physical conditions of the remarkably shallow habitat on a reef exposed to intensive movements of the sea.

It has already been mentioned above that the pore-rows are placed along the lateral, somewhat narrower sides of stem and branches (Textfig. 1). The large material shows that gastro- and dactylopores are normally absent on the generally somewhat flattened anterior and posterior sides of the colonies. In some very few cases, however, quite short rows may be found here; but in these cases they are placed on a more or less prominent eminence, an incipient new branchlet. — The gastropores are generally seated in a very shallow sulcus which, however, in many cases entirely fades away.

The gastropores (Textfig. 1 b, c) at the opening attain a diameter of 0.2—0.3 mm when fully developed. During the growth of the colony the gastropore becomes constantly deeper, but no trace of tabulae have been observed, and the polyp evidently holds its position during the life of its part of the colony. New gastropores are gradually formed in the peripheral walls between older gastropores, and are, on account of the peripheral growth of the coenosteum, in their turn sunk deeper and deeper into the branch. — The wall of the gastropore is smooth without protuberances or spicules. The gastrostyle is slender, cylindrical and rather needle-like.

The dactylopores (Textfig. 1 d) are placed in a single row on each side of the gastropore-row. They are formed and develope in the same way as the gastropores. No communication exists between dactylopores and gastropores, and there is no hint at dactylotome projections or dactylotomes. The dactylopores are somewhat irregularly placed, generally two or three at each side of a gastropore. Dactylostyles are lacking.

The ampullae are rather deeply immersed into the coenosteum and occur in groups on the posterior and anterior sides of the colony at the basis of small branchlets and, as far as the present material is concerned, never on the thicker main stems. In some cases the ampullae may be so deeply immersed that they are almost invisible; but generally they are seen as low, mostly rather well limited swellings which, however, do not disturb or influence the pore-rows in any way. The groups of ampullae are often so closely packed that they form a solid cake; this especially seems to be the case in male colonies.

An investigation of the soft parts reveals that the gastrozooid has four to seven small, though well developed tentacles. Smaller zooids have four, the largest ones seven tentacles. Probably new tentacles are added during the growth of the zooid also after the mouth opening has broken through; definitive evidence could not be given on the basis of the present material. — The fingershaped free part of the dactylozooid at all events reaches the length of the gastrozooids. The zooid is attached to the side wall of the dactylopore by a small adhesive part from the middle of which the free part arises.

Male ampullae generally contain one, in some cases two, or exceptionally even three conical blastostyles round the bases of which four to eight gonophores are found, each in different stages of development. Female ampullae only seem to contain one large gonophore at a time. — According to

ENGLAND (1926) the colonies of *Distichopora violacea* are exceptionally hermaphroditic, and in rare cases even one single gonophore may exhibit hermaphroditism.

The synonymy of the species has been given by FISHER (1938). — The identity of HICKSON's specimens from the Torres Strait (1892) is not quite certain; some of the drawings on his plates rather point in the direction of *Distichopora irregularis* Moseley.

### Forma *cornuta* nov.

(Pl. I, Fig. 2.)

Material: S. BOCK's expedition 1917: October 1917, Gilbert Islands, Aranuka. Several dried colonies from entrance reef.

Although the present colonies in their finer details correspond to the typical colonies of *Distichopora violacea*, the general shape as well as the strongly compressed and often rather acute branchlets which moreover in great numbers emerge from one ("anterior") side of the flabellum give them a so aberrant appearance (Pl. I, Fig. 2), that the only correct course at present is to keep them apart as representatives of a special forma *cornuta*. The color is an intense carmine, and the specimens might therefore also have been referred to the var. *coccinea* (Gray) of FISHER (1938). The latter, however, is based on the color which is a rather problematic systematic character in the present species which exhibits such varying coloring on the whole. The forma *cornuta* has on the other hand been singled out on the basis of its growth features.

The aberrant shape and ramification are probably due to milieu factors, and it seems natural to presume that the colonies have grown in a locality exposed to rather rough movements of the water; in so far we are reminded of the small colonies of forma *typica* from Eimeo. The present colonies, however, have a more erect growth, and this feature again indicates less rough conditions than those of the Eimeo-colonies. It is difficult with our present knowledge of the Stylasteridae and their relations to milieu conditions, to see the reason, why the flabellate colony in the present form exhibits a pronounced tendency to develope new branchlets perpendicularly to the plane of the fan, and here merely on one side (the "anterior") which so to say is covered by quite small incipient branchlets. At first sight this feature may even give the impression of a *Stylaster* much more than a *Distichopora*.

This feature also evidently to some degree influences the occurrence of the ampullae. In most places they occur in the same way as in the forma *typica*, although the assemblies of ampullae are found mostly on the "anterior" side of the fan. But in relation to the rudimentary branchlets of the "anterior" side, single ampullae in many cases are observed especially on the stem or main branches near the transition to the incipient branchlet.

The labels do not give further details as to depth or other conditions of the habital which might give hints as to special milieu factors possibly connected with the development of the present, special form of *Distichopora violacea.*

### *Distichopora fisheri* n. sp.

(Pl. II, Fig. 3.)

**Material:** S. Bock's expedition 1917: June 16, 1917, Fiji Islands, Viti Levu, Namuka; the barrier reef; one colony. — Western coast of Sumatra, Pulo Pasu, 1891 (further details lacking) (C. Aurivillius); one small colony (Riksmuseum, Stockholm).

The colonies are small, the type specimen from Namuka (Pl. II, Fig. 3) about 3 cm high and 2 cm broad, the specimen from Pulo Pasu only 1.3 cm high and 2.2 cm broad. The specimens are subdichotomously branched, more or less distinctly flabellate, and slightly concave on one (the "anterior") side. The pore-rows are almost entirely restricted to the lateral sides of the branches, whereas the ampullae are found in groups on the anterior and posterior sides of the branches, evidently normally not causing any disturbance of the pore-rows.

Owing to slight dactylotome projections, the contours of the end branchlets are feebly serrate. The surface of the coenosteum (Textfig. 2 a) is covered by rounded, flat tubercles or warts, and in parts treated with sodium hypochlorite rather obvious pores are seen in the depressions between these tubercles. Otherwise no finer vermiculation or coarser "veins" are observed. Transverse sections of the branches and branchlets are almost quite circular, although the pore-rows show a remarkably, strictly bilateral course along them. — The type specimen from Namuka is (in alcohol) greyish blue with a faint lilac hue; the colony from Pulo Pasu (also in alcohol) is light brown or yellowish, its branch ends mostly almost white.

The gastropore-row is seated in a deep sulcus which is rather clean cut (Textfig. 2 a, b); its breadth is about 0.35 mm and coincides with the diameter of the apertures of the larger gastropores. The **gastropores** (Textfig. 2 c) are somewhat curved. Their walls carry several small spicules, the bulk of which is gathered in one or two girdles a little below the aperture of the larger (older) gastropores. The gastrostyle is needle-shaped, but comparatively compact and robust; the distal half of it is closely covered with spicules which, however, are not bristling.

The **dactylopores** are placed at comparatively regular distances. In transverse section they are oval, and at the inner side an obvious dactylotome is present. The side walls of the aperture are slightly raised, and against the sulcus the wall accordingly ends in a clean cut and rather prominent tooth which is especially obvious against the sulcus in oblique projection (Textfig. 2 b).

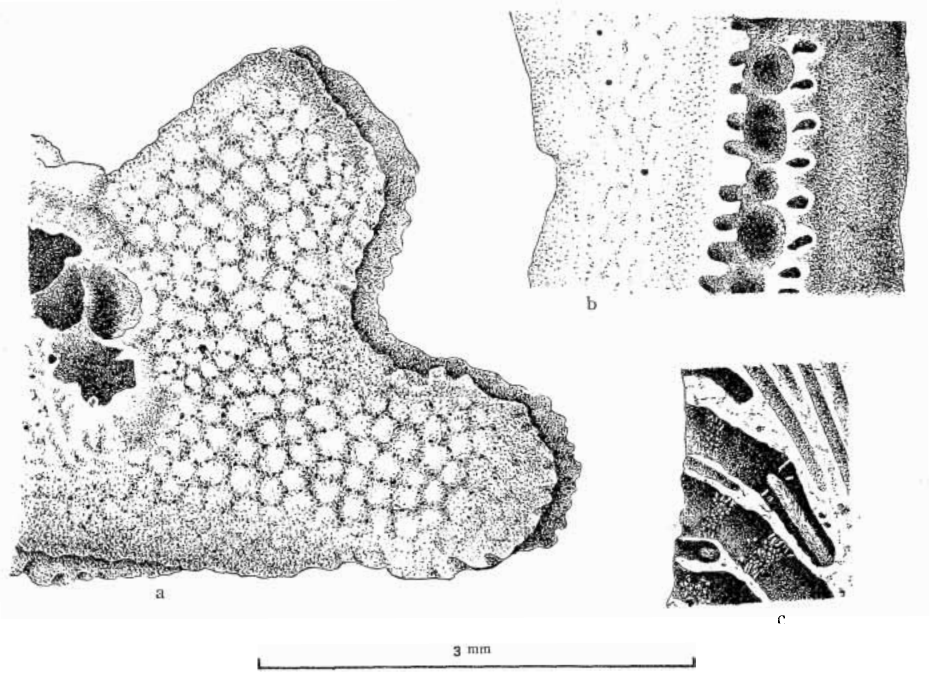


Fig. 2. *Distichopora fisheri.* Fiji Islands, Viti Levu, Namuka; barrier reef. — a end of a branch seen from the flat side (to the left a few ampullae, the roofs of which have been ruptured). b branch in lateral view showing the pore-row with its distinct sulcus. c section showing the gastropores, their style and inner wall.

Groups of ampullae are found on branchlets and smaller branches between the pore-rows, i. e. on the anterior and posterior sides of the flabellum. In the type specimen, a male colony, each elevation contains several small chambers (ampullae), although it may protrude as a uniform eminence comprising about one fourth of a sphere. In many places, however, these elevations again fuse into somewhat larger cakes covering greater parts of the branches from one pore-row to the other. — In the specimen from Pulo Pasu (probably a female colony) each such rounded eminence only contains one chamber, and even though the eminences also here mostly gather into large, closely packed groups, each ampulla (single eminence) in external view retains its individual contour.

The surface of the ampulla has especially in the Pulo Pasu colony the same structure as the coenosteum elsewhere in the colony. It is covered with low, rounded papillae. In the type specimen the eminences containing the ampullae also often have the same structure as the surface of the coenosteum elsewhere; but in many places the low tubercles of the roofs of the eminences tend to merge into a network or a vermiculation.

In spite of the rather obvious pores between the tubercles, i. e. the surface openings of the canal meshwork, the coenosteum is remarkably hard and compact; it does not give the spongy impression which is characteristic e. g. of *Distichopora sulcata* and *Distichopora irregularis.*

A small piece of the type colony was sacrificed for an examination of the soft parts. Serial microtome sections reveal that the gastrozooids have six almost rudimentary small tentacles, the endodermal core of which almost without exception consists only of some five or six cells. — The dactylozooids are slenderer than the gastrozooids, although they attain about the same length. The long, fingershaped free part is attached to the middle of a basal part adherent to the wall of the dactylopore on the side farthest away from the gastropores. The adhesive, basal part is rather short, only some five or six times as long as the breadth of the fingershaped free part at its source.

Male ampullae contain four or five gonophores in different stages of development seated round the base of a small, conical blastostyle.

The specimens might at first sight be taken for variants of *Distichophora violacea,* their surface structure also to some degree recalling this species, although it is in the present specimens somewhat coarse. However, the features of the pore-rows are very different. The sulcus of *Distichopora violacea* has almost faded away, whereas it is extraordinarily distinct and obvious in the present colonies. To this the spicules of the gastropore wall must be added which have only been found in one other species of the genus, viz. *Distichopora borealis.* Another feature which, however, generally must be characterized as subordinate, but which in the present case must be allotted a supplementary weight, is the circular transverse section of the branchlets. In all other species with strictly lateral pore-rows the branchlets, and especially their terminal parts, are decidedly anterior-posteriorly compressed, so that the larger diameter of the oval or elliptical transverse section coincides with the main plane of the flabellum.

It has not been possible to identify the present species with any of the earlier described ones, and I have named it after Dr. W. K. Fisher of the Hopkins Marine Station who has broken new ground in the study of Stylasteridae.

## *Distichopora serpens* n. sp.

(Pl. II, Fig. 8.)

Material: August 3, 1911, Philippine Islands, San Bernardino Strait, 12° 77′ N., 124° 3′ E., 50—100 fathoms, temperature at the bottom 61° F. (Suenson); several fragments and quite small colonies (Museum, Copenhagen).

The specimens display a distinctly dichotomic ramification (Pl. II, Fig. 8), and larger colonies evidently do not show pronounced differences in the dimensions of main stem and branches. The branches and the terminal branchlets are rather strongly compressed and have their pore-rows along the narrower, lateral margins. Owing to the dentiform projections at the

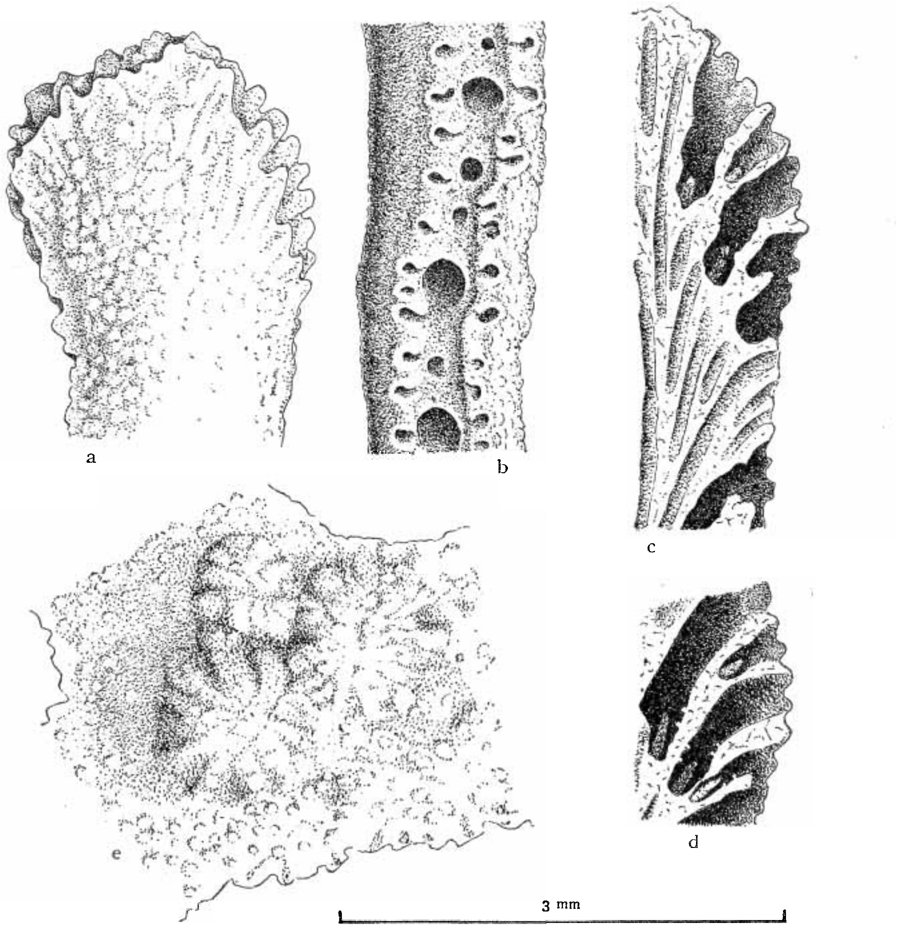


Fig. 3. *Distichopora serpens.* San Bernardino Strait, Philippine Islands, depth 50—100 fathoms. — a terminal part of a branchlet from the flat side. b side view of a branch showing details of the pore-row. c part of a branchlet ground down almost to the plane of the gastropores, slightly oblique so that also much of the dactylopores is visible. d Four neighbouring gastropores, in the largest two only the upper part of the gastrostyles is seen. e a group of three ampullae.

outer side of the dactylopores, the branchlets under the lens show a serrate contour in anterior or posterior aspect (Textfig. 3 a). The gastropores are seated in a comparatively deep and regular sulcus. The surface of the coenosteum (Textfig. 3) is distinctly and rather coarsely warty, but no pores are seen between the warts at lower magnifications, and neither vermiculation nor veins have been observed. The color (in alcohol) is a yellowish orange.

The gastropores (Textfig. 3, b–d) attain a diameter at the opening of 0.25—0.30 mm and have a comparatively short, feebly conical gastrostyle. In the deeper parts of the gastropore the walls especially in older pores carry rather numerous, small and irregularly warty protuberances, but no spicules are present.

The dactylopores are arranged at somewhat irregular intervals and show no distinct relation to the gastropores (Textfig. 3 b). A dactylotome connects the inner part of the oval dactylopore with the sulcus, whereas the side walls, and especially the outer wall of the pore opening, are elevated to form a low tooth which is more prominent on the terminal part of the branchlet.

The female ampullae are rather superficially placed on the flattened sides of the branches, and protrude like somewhat larger globe segments. Their surface is rather coarsely warty, and in most cases they are radially grooved, especially in their peripheral parts (Textfig. 3 e). The ampullae may occur singly, but in most cases they appear in small groups. They do not influence the regular configuration of the pore-rows.

The coenosteum of the present species is rather densely constructed with narrow coenenchym canals. It is on the other hand not copiously developed, and the colonies are accordingly rather slender, and slender in comparison with other species of *Distichopora*.

The zooids of the present species are large, especially in consideration of the slenderness of the branches. The gastrozooids have five or six well developed tentacles in a whorl a little below the mouth, which, in the present, in alcohol preserved specimens is found on the summit of a cone. — The dactylozooids are almost of the same size as the gastrozooids and have their base attached far down into the dactylopore. No special basal, adhesive part is differentiated in the dactylozooid, the fingershaped zooid thus, so to say, directly originating from the stolones. The endoderm is simply scalariform in spite of the remarkably large dimensions of the dactylozooid; a central lumen is lacking, although the dactylozooid otherwise very much recalls that of *Pliobothrus symmetricus* (cf. BROCH 1914).

Female ampullae contain one gonophore, but no trace was found of a blastostyle. When the ovum is ripe, the spadix is by and by reduced, till it at last, when the cleavage of the egg cell commences, is reduced to a small central cone at the inner wall of the ampulla. At the summit of this cone a new propagative cell now appears, indicating the development of a secondary gonophore. The latter is already developed to an advanced stage, when the planula larva of the primary gonophore escapes from the ampulla.

## *Distichopora sulcata* POURTALÈS 1868.

(Pl. II, Fig. 6.)

1868 *Distichopora sulcata*, POURTALÈS, Bull. Mus. Comp. Zoöl., Vol. I, p. 117.
1871 — *sulcata*, POURTALÈS, Deep-Sea Corals, p. 38; Pl. IV, Fig. 14, Pl. VII, Fig. 7.
1878 — *sulcata*, MOSELEY, Structure of the Stylasteridae, p. 482.
1879 — *sulcata*, POURTALÈS, Bull. Mus. Comp. Zoöl., Vol. V, p. 210.
1881 — *sulcata*, MOSELEY, Stylasteridae . . . . . "Challenger", p. 85.
1938 — *sulcata*, FISHER, Hydrocorals of the North Pacific Ocean, p. 545.

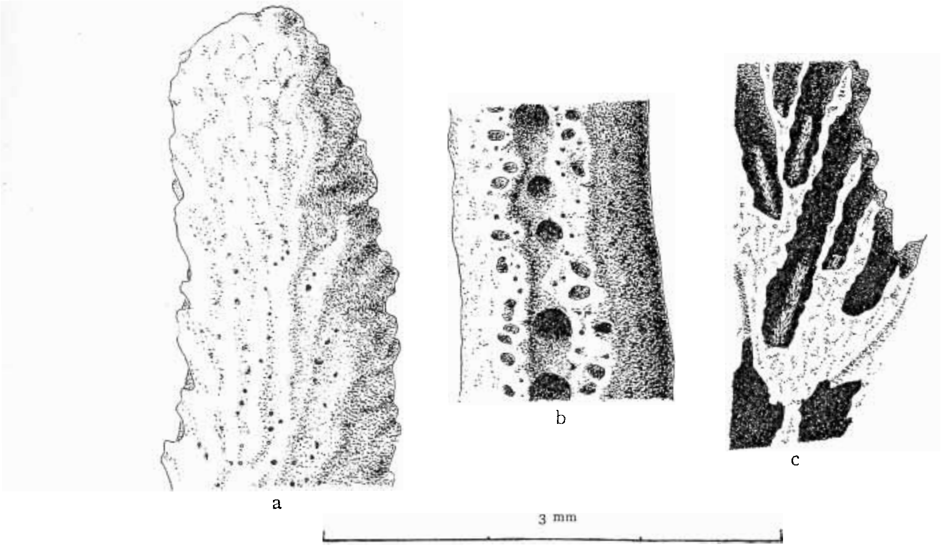


Fig. 4. *Distichopora sulcata.* 30 Miles N. E. of Cozumel Island, depth 130 fathoms. — a branchlet seen from the flat side. b branch in side view showing the pore-row. c section through the gastropores showing the gastrostyles.

Material: "Albatross", 30 miles N. E. of Cozumel Island, 130 fathoms depth; a few, up to about 1 cm high, dried fragments (Riksmuseum, Stockholm).

The small fragments (Pl. II, Fig. 6) give the impression of dichotomously branching colonies of a comparatively delicate construction. The colonies are evidently flabellate with pore-rows running along the narrow lateral sides of the branches, leaving the rather flat anterior and posterior sides bare of zooids. On account of the small projections generally developed at the outer side of the dactylopore, the contours of the branch are feebly serrate (Textfig. 4 a). The surface of the branchlet is obviously longitudinally veined with conspicuous pores, especially in the furrows between the "veins" or ridges. The surface is otherwise neither warty nor armed with spicules or spines. — The color of the fragments is a greyish white with a faint touch of lilac.

The pore-rows are very conspicuous, the gastropores being placed in a comparatively very deep sulcus between the prominent edges, which are furthermore emphasized by the tooth-shaped projections at the outer side of the dactylopores. — Fully developed gastropores have a diameter of 0.20—0.5 mm at the opening, or about the same width as the sulcus in general. The gastropore is straighter than in most other species (Text-fig. 4 c). Its walls are rugged, but generally without pronounced warts or spicules. The gastrostyle is needle-shaped, rather long with well developed bristling spicules on its distal parts.

The dactylopores exhibit an oval transverse section and their opening is often rather slit-like with its greater diameter approximately perpendicular to the sulcus (Textfig. 4 b). No dactylotome is observed, but the outer side of the dactylopore wall is almost always raised into a low, two-topped tooth.

No ampullae are present in the fragments.

In good accordance with the conspicuous pores between the ridges or veins of the surface, which are openings of the canal meshwork, the coenosarcal canals are comparatively wide. Grindings also show that the coenosteum is unusually spongy because of the richly developed canal meshwork. On the other hand the skeletal substance itself is rather hard.

Fisher (1938) points to the close relationship between the present Atlantic species and the Pacific species, *Distichopora borealis*. The latter, however, has a much coarser build and a more roughened surface, the coenosteum being moreover armed with small spicules in the typical, Aleutian form. Fisher furthermore points out differences in the ampullae. This feature shall not be discussed here, as ampullae are lacking in the present fragments.

## *Distichopora borealis* Fisher 1938.

1938 *Distichopora borealis*, Fisher, Hydrocorals of the North Pacific Ocean, p. 543, Pl. 70, Fig. 3, Pl. 71, 72, and 73.

### Forma *japonica* nov.

(Pl. II, Fig. 5.)

Material: Dr. Th. Mortensen's Pacific expedition 1914—16: June 11, 1914, Okinose, Sagami Sea, depth 60 fathoms, hard bottom; three specimens.

The largest specimen is with its height of 5.5 cm and its breadth of 3.5 cm evidently only a branch of a larger colony, whereas the next specimen seems to be a complete colony, although it is only 3.4 cm high, and 4.7 cm broad. A third colony has a height of 3.5 cm consisting of an erect stem with only one small branch near its upper end. — The specimens are dichotomously or subdichotomously branched, a little irregularly flabellate. In the specimen number 2 the fan has a tendency to curve in to one (the anterior) side, so that the flabellum here is a little concave; this tendency to concavity is most pronounced in the distal parts of the branches.

Owing to the development of tooth-shaped dactylotome-projections at the outer side of the dactylopores, the side contours of the branches are finely serrate. The branches are in transverse section anterior-posteriorly strongly compressed, and the pore-rows are strictly confined to the narrow, lateral sides. The surface of the coenosteum (Textfig. 5 a) is roughened by

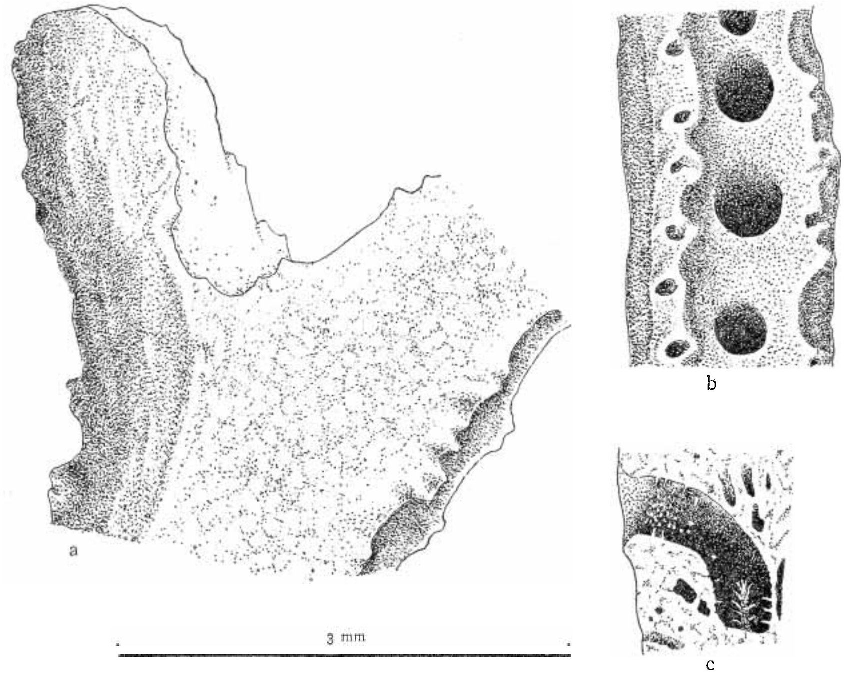


Fig. 5. *Distichopora borealis* forma *japonica.* Okinose, Sagami Sea, depth 60 fathoms. — a part of a branch with a branchlet seen from the flat side. b branch in side wie showing the pore-row with its broad and deep sulcus. c section through a gastropore; only the terminal part of the gastrostyle is visible.

small rounded warts or papillae which, however, in many places fuse into a vermiform reticulation. In the distal parts the branches are also longitudinally veined; but neither here nor elsewhere are pores observed under the lens. No microscopic spicules could be observed on the surface of the coenosteum. — Specimens preserved in alcohol have a light yellow color, whereas dried specimens are almost white, in most parts with a distinct lilac hue.

The sulcus is astonishingly broad (Textfig. 5 b) and distinctly limited. Owing to its great width (generally 0.7—0.8 mm) one might at first sight judge it as rather shallow; but in comparison with most other species the sulcus must in the present species be designated as comparatively fairly deep. The gastropores attain at the opening a diameter of about 0.53 mm, and are thus much narrower than the sulcus. The inner wall of the gastropore is furnished with scattered small, needle-shaped spicules which are especially numerous near the opening, and which here generally form a girdle of spines (Textfig. 5 c), evidently serving as a kind of sifting apparatus against smaller bodies (detritus) which are thus prevented from penetrating into the interior of the gastropore. — The gastrostyle is long and slender, needle-shaped, and armed with extraordinarily long, bristling spicules.

The dactylopores are usually separated from the sulcus by a low wall. Indications of a dactylotome have only been observed in a few cases. The bordering wall of the sulcus is slightly elevated at each side of the dactylopore as a distinct, though rather blunt point, and between these two denticles the outer wall of the dactylopore aperture is feebly carved out, so that the mouth part of the dactylopore in side view projects a little like a two-topped tooth on the contour of the branch.

No ampullae could be found in the present specimens.

The colonies no doubt belong to *Distichopora borealis* exhibiting the specific characters especially emphasized by FISHER (1938). However, some small differences of subordinate importance must also be noted, and as long as we do not know the features of the ampullae, it is preferable to look upon the Japanese specimens as representatives of a special forma *japonica*. Further investigations must settle whether the small differences from the Aleutian specimens described by FISHER are constant or only more casual features.

The gastropores of the Japanese specimens with their opening diameter of 0.53 mm attain greater sizes than the Aleutian specimens with diameters of 0.25—0.425 mm, and the surface of the coenosteum lacks the microscopic small spicules which are characteristic of FISHER's specimens, although the characteristic spiculation of the gastropores described by him is also present in the Japanese specimens and is here evidently more copiously developed. The color (FISHER's specimens are buff) is of subordinate value, but must also be noted in this connection. These small differences do not suffice for a specific separation, but may possibly justify a distinction between to different forms of the species.

## *Distichopora foliacea* POURTALÈS 1868.

(Pl. II, Fig. 7.)

1868 *Distichopora foliacea*, POURTALÈS, Contributions to the Fauna of the Gulf Stream, p. 137.
1871 — *foliacea*, POURTALÈS, Deep-Sea Corals, p. 38, Pl. IV, Fig. 12 and 13.
1878 — *foliacea*, MOSELEY, Structure of the Stylasteridae, p. 482.
1881 — *foliacea*, MOSELEY, Stylasteridae . . . . . "Challenger", p. 85.
1938 — *foliacea*, FISHER, Hydrocorals of the North Pacific Ocean, p. 545.

Material: Gulf Stream Exploration. From Mus. Comp. Zoöl. Depth 100—200 fathoms; one dried fragment of a colony about 2 cm high (Riksmuseum, Stockholm).

Only one small fragment is at hand (Pl. II, Fig. 7). It gives the impression of a subdichotomous, in part approximately pennate branching, coinciding with the characteristic drawing given by POURTALÈS (1871). The branches are extraordinarily strongly flattened, and in some places where the terminal part of a branchlet is about to divide, the apical part of the end branchlet may be a little broader than its proximal part. Pore-

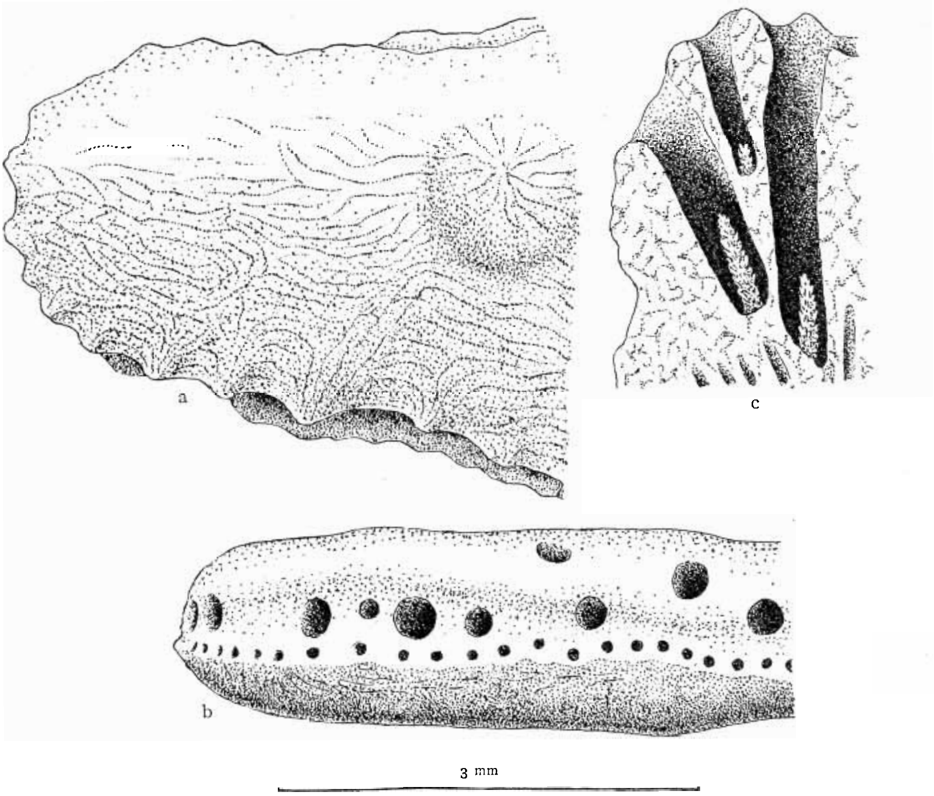


Fig. 6. *Distichopora foliacea.* Gulf Stream Exploration, depth 100—200 fathoms. —
a terminal part of a branchlet from the flat side, to the right an ampulla.
b a branchlet in lateral view showing the somewhat irregular pore-row
with its rudimentary sulcus and its single row of dactylopores.
c section through the gastropores exhibiting their gastrostyles.

rows run along the sharp, lateral edges of the branches, and the small dactylopores commonly open on the summits of small conical elevations, so that the contours of the branches are serrate (Textfig. 6 a). Only one of the dactylopore-rows is fully developed and at the same time a little raised above the plane of the gastropore-row. The edge of the branch is thus extraordinarily narrow, and the gastropore-row forms more or less of a ledge, mostly only with indications of a sulcus. The other row of dactylopores may in some places be indicated by a few straggling pores, sometimes even combined with indications of denticulations; but in most parts of the branches this second row of dactylopores has entirely disappeared. In some few places it also looks as though the pores of the rudimentary dactylopore-row have been closed secondarily.

The surface of the coenosteum is vermiculate, but neither warts nor thorns nor spicules are present. — The color of the fragment is a pale orange pink.

The pore-rows are very aberrant in comparison with all other species of *Distichopora*. A sulcus is lacking or may at most be feebly indicated; but one side of the pore-row, viz. that of the complete dactylopore-row, projects a little as a narrow, slightly serrate edge. Fully developed gastropores attain at the opening a width of 0.30—0.35 mm (Textfig. 6). The gastropore is generally rather feebly arched with smooth walls devoid of warts and spicules. The gastrostyle (Textfig. 6 c) is long and slender, needle-shaped or rodlike, and covered all over by minute, though not bristling spicules.

The dactylopores have the same circular openings as the gastropores, and in spite of the elevation of the mouth part of many of them in the shape of marginal denticles of the branch, no trace of dactylotomes are present.

Numerous ampullae are present on one side of the flabellum, whereas only few are seen on the other. The (female?) ampulla protrudes above the surface of the coenosteum like about 1/4 of a sphere and has a somewhat rugged surface, the vermiculation of the surface of the coenosteum also being present on the ampulla; generally the configuration of the ampulla roof is even more prominent than on the coenosteum elsewhere. The diameter of the ampulla amounts to about 1 mm.

Although the canal mesh-work of the coenosteum is not especially developed or conspicuous, the skeletal substance on grinding nevertheless gives the impression of being comparatively loose and rather brittle.

## *Distichopora irregularis* Moseley 1878.

(Pl. II, Fig. 4.)

1878 *Distichopora irregularis*, Moseley, Structure of the Stylasteridae, p. 502.
1881 — *irregularis*, Moseley, Stylasteridae ..... "Challenger", p. 80; Pl. XII, Fig. 8, 8 a.
?1892 — *violacea* pars, Hickson, Scient. Proc. Roy. Dublin Soc., Vol. VII, p. 501, Pl. XVIII, XIX.
1908 *Sporadopora providentiæ*, Hickson and England, The Stylasterina of the Indian Ocean, p. 349, Pl. 44, Fig. 1—3.

**Material:** Dr. Th. Mortensen's Pacific expedition 1914—16: March 17, 1914, Philippine Islands, off Jolo, depth about 25 fathoms, sand and coral; three colony fragments.

The largest fragment is 4.6 cm high and 2 cm broad, the second 2.7 cm high and 2.6 cm broad; the third fragment is only a small branch. — Already at first sight the fragments diverge characteristically from all other species of *Distichopora* on account of their coarse and heavy build, and they may at first glance easily be taken for colonies of *Sporadopora* or *Pliobothrus* which, in most cases, exhibit the same general appearance. However, the characteristic pore-rows on closer examination disclose the typical *Distichopora*.

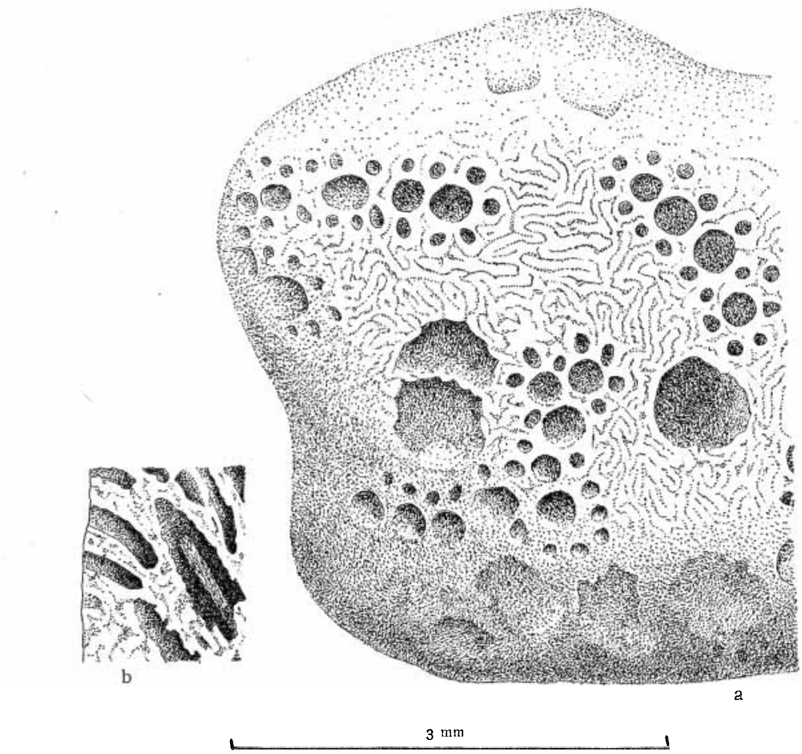


Fig. 7. *Distichopora irregularis.* Off Jolo, Philippine Islands, depth about 25 fathoms. -- a terminal part of a branch; the roofs of several ampullae have been ruptured. b somewhat oblique section through a pore-row, one gastrostyle is visible.

The aberrant impression given by the colonies (Pl. II, Fig. 4) as well as their cylindrical, not flattened branches and branchlets evidently depends upon the quite irregular course of the pore-rows, which are in no way confined to the lateral sides of the branches, but which traverse the sides in all directions in the way described by MOSELEY (1881). Neither evident dactylotome projections nor teeth nor spines accompany the pore-rows, and a sulcus is generally only very feebly developed, or in many cases even absent. The surface of the coenosteum (Textfig. 7 a) has a peculiar and very characteristic, finely vermiculated structure. — The colonies (in alcohol) are yellowish colored with a distinct lilac hue, especially evident at the ends of the branches. Broken branches show a rather vividly colored, lilac central part, and the same color is also observed here, when the soft parts have been removed with sodium hypochlorite.

The ramification of the present species (Pl. II, Fig. 4) is more decidedly dichotomous than in most other species of the genus, but no main branches or stems are especially accentuated. On the other hand the colonies are not so fan-shaped as is usual in other species of *Distichopora*; branches often diverge from the main plane of the fan.

As mentioned above, the pore-rows run irregularly on all sides of the branches, and the sulcus is very shallow or even absent. The fully developed gastropores generally have a diameter of 0.30—0.35 mm at the opening. They are more strongly curved in their outer part, and the gastrostyle is deeply seated in old gastropores. The gastrostyle (Textfig. 7 b) is slenderly needle-shaped, its outer parts are covered with spicules which, however, do not bristle, but cover the style almost scale-like.

The dactylopores are somewhat irregularly placed in relation to the gastropores. At the end of a pore-row or in short, individual pore-rows, an attempt at formation of cyclosystems may be observed round some of the gastropores. — The dactylopore is, in transverse section, more or less distinctly oval. But there are no dactylotomes, and no trace of tooth-like projections at the margin of the dactylopore apertures.

Ampullae occur in closely packed groups on the outer branches between the pore-rows, but they do not cause any visible swellings or influence the pore-rows in the present material. However, the surface of the fertile branches often shows obvious, large cicatrizations, where the ampullae have been seated. Near the end of the branch (Textfig. 7 a) ampullae are often found in smaller numbers or even singly. Here as elsewhere the ampulla roof is evidently ruptured, when the ampulla contents are emptied.

It is rather probable that the marked cicatrization is in some way connected with the remarkable porousness of the coenosteum. Although no pores of the canal system are observed on the surface of the coenosteum under a lens, grindings display a more spongy skeleton than in most other species of Stylasteridae. Among the *Distichopora* species none can compete in this respect with *Distichopora irregularis*. In its extreme porousness the coenosteum is much more reminiscent of a *Sporadopora*.

An investigation of the soft parts reveals that the gastrozooids have four to six comparatively well developed tentacles. The dactylozooids are large, at all events as long as the gastrozooids, and fixed to the wall of the dactylopore by a short adhesive basal part from the proximal part of which the free, fingershaped part proceeds. Also in this respect the species thus seems to hold an aberrant place. — The investigated specimen has male gonophores. Although the ampullae are seated closely below the surface, they show no openings. They contain 4—6 gonophores each in different stages of development, seated round the basal part of a slenderly conical blastostyle which does not atrophy during the development of the gonophores.

The present colonies entirely coincide with the description given by MOSELEY (1881), and no dobt as to their identity exists. They also come from the same waters as the specimens of the "Challenger".

It is a question, whether some of the specimens mentioned by HICKSON (1892) from the Torres Strait under the name of *Distichopora violacea* should be referred to the present species. The irregular arrangement of the pore-rows in some of the specimens figured, differs strikingly from all specimens of the very large collection of *Distichopora violacea*, which has been examined by me, and coincides obviously with *Distichopora irregularis*. The colors of HICKSON's specimens agree with some colonies of *Distichopora violacea*; but this character is generally of more subordinate taxonomic value among the Stylasteridae, and whereas the variation of colors has been demonstrated by an extensive material of *Distichopora violacea*, only a very small collection of *Distichopora irregularis* has as yet been found, and the specimens moreover have arrived from geographically neighbouring localities. The habitat of the last named species is somewhat deeper, and the colors of deeper living Stylasteridae are generally lighter and less variable than those of shallow water species.

The species *Sporadopora providentiæ* described by HICKSON and ENGLAND (1908) from Providence Island north of Madagascar, is according to their drawings certainly no *Sporadopora* at all, but young colonies of *Distichopora irregularis*. In the text the investigators moreover emphasize the tendency towards a formation of cyclosystems which is especially evident in shorter pore-rows of the present species. The scattered occurrence of pores in *Sporadopora* in fact differs principally from the characteristic drawings of HICKSON and ENGLAND which leave no doubt as to its identity with the present species.

## Subfamily *Sporadoporinae*.

### Genus *Sporadopora* MOSELEY 1878.

(*Polypora*, MOSELEY 1876.)

The colonies are irregularly, generally subdichotomously branched, and the branching is commonly in one main plane, so that the colony is rather flabellate. In some cases, however, the colony may attain a more bushy appearance, the branches or branchlets diverging more or less from the main plane. Gastropores and dactylopores are irregularly scattered over stem and branches, with simple circular apertures. Gastropores with gastrostyles fixed to the deeper part of the wall by hairfine, radiating bridges or tabulae. Dactylopores more numerous, without dactylostyles. Ampullae deeply immersed below the surface of the coenosteum, not visible externally. — The gastrozooids have well developed tentacles. Dactylozooids large, with well developed adhesive basal part. Female ampullae unknown, male with one to three gonophores, but without a blastostyle.

The genus was introduced by MOSELEY already in 1876 under the name of *Polypora* on the basis of a species dredged by the "Challenger" expedition off the mouth of Rio de la Plata in 600 fathoms depth. In 1878, however, he changed the name of the genus to *Sporadopora*, the name of *Polypora* having already been used. Since his day nobody has dealt with the genus. Only Hickson and England (1908) have described a new species which, however, according to the rather scanty details given is certainly a *Distichopora*.

*Sporadopora* is evidently closely related to *Pliobothrus*. The main difference is that the latter genus is devoid of gastrostyles. It should also be mentioned here that the coenosteum of *Sporadopora* is more spongeous owing to the larger dimensions of its coenenchym canals. Altogether no other genus examined has its coenosteum intersected by a meshwork of such coarse canals as *Sporadopora*, and its coenosteum is therefore more spongeous and brittle than in other Stylasteridae with the same dimensions. To this may be added that the gastropores very commonly penetrate into the central parts of the branches, and the primary ones evidently give rise to somewhat larger, irregular central and longitudinal canals like those earlier mentioned in *Pliobothrus* (see Broch 1914). The diameter of these canals does not generally surpass that of the gastropore.

In his definitions Moseley (1878, 1881) emphasizes that *Sporadopora* has no such tubular projections surrounding the dactylopore openings as *Pliobothrus*. It is, however, impossible to lay much stress on this feature. His own statement "The margins of the mouths of the dactylopores are often slightly raised above the general surface" already demonstrates that the character is variable.

Another point of likeness might seem to be the formation of tabulae in the gastropores (such have also been demonstrated by Broch 1914 in *Plibothrus*). Moseley speaks of more or less distinctly developed, although exceedingly delicately built tabulae in *Sporadopora dichotoma*. At first I believed there were traces of such tabulae in sections of the coenosteum through gastropores of *Sporadopora mortenseni*, where hairfine calcareous bridges now and again connect the basal part of the gastrostyle with the wall of the gastropore. Investigations of several fractures, however, where tubes and styles could be observed intact and in situ, revealed that real "tabulae" do not occur in this species. Generally the gastrostyle in longitudinal sections through the gastropores seems to be freely suspended in the middle of the pore (tube), and only occasionally can traces of false "tabulae" be observed. In fact the gastrostyle is attached to the walls of the gastropore by hairfine radiating bridges which emerge at slightly different heights from the lower part of the gastrostyle. Seen together from above or below, they radiate to all sides like the spokes of a wheel. — We can thus not maintain the "tabulae" as a characteristic of *Sporadopora*, and it is dubious, whether we are justified in considering this feature which has only been observed in some few species altogether, as evidence of a closer relationship between two genera, in the present case *Sporadopora* and *Pliobothrus*. Evidently there is much more in favour of a convergence caused by similar modes of growth in the different species in question.

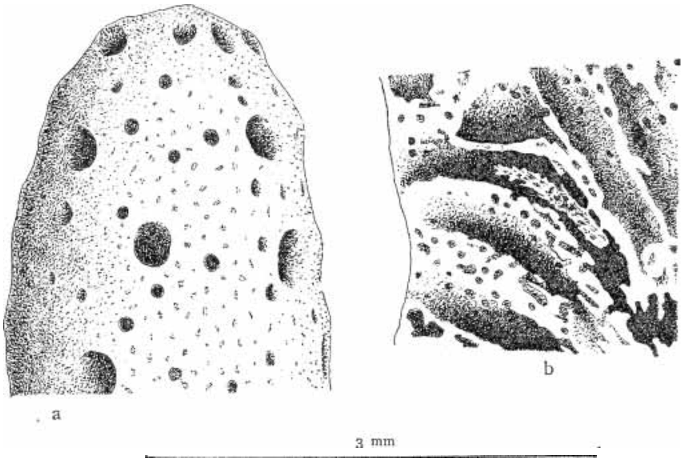


Fig. 8. *Sporadopora mortenseni.* Three Kings Island, New Zealand, depth 65 fathoms. — a terminal part of a branchlet. b section through the coenosteum of a larger branch with longitudinal sections of some of the gastropores; in the middle of the figure a gastrostyle is exposed in its entire length.

## *Sporadopora mortenseni* n. sp.

(Pl. III, Fig. 9.)

Material: Dr. Th. Mortensen's Pacific expeditions 1914—16: January 5, 1915, Three Kings Islands, New Zealand, depth 65 fathoms, hard bottom; several fragments of large colonies together with *Errina rubra.*

The largest fragments reach a height of 10 cm and 10.5 cm with a breadth of, respectively, 6.5 and 5.5 cm. In both specimens many of the peripheral branchlets have been broken off.

The colonies are quite irregularly branched, and although they must be said to have a rather flabellate shape, branches in many cases diverge from the main plane, and one of the largest fragments in which almost all branch ends have been broken off, holds an intermediate position between a flabellum and an entirely bushy ramification. All branches and stems have circular transverse sections, a compression of the branch is never observed. Gastropores and dactylopores are scattered quite irregularly over the surface of stems and branches, and in fragments treated with sodium hypochlorite numerous minute pores are also seen between them (Textfig. 8 a). These small pores are the openings of the canal system intersecting the coenosteum. Otherwise the surface of the coenosteum is quite smooth, and no trace is found of projections surrounding the mouth of the gastropores or dactylopores. The color (in alcohol) is a greyish white; after treatment with sodium hypochlorite the fragments are pearly white.

The gastropores at their circular opening attain a diameter of 0.4 mm or a little more. The pore is generally rather strongly arched, but in some cases the comparatively deeply placed gastrostyle is nevertheless dimly visible from without. The gastropores penetrate deeply into the branch and communicate with irregular central, longitudinal canals which evidently must be explained as primeval or fused gastropores. In most cases the gastrostyle does not sit at the bottom of the gastropore, but a little higher up (Textfig. 8 b), and it is attached to the gastropore wall by calcareous thin bridges. The latter are hairfine and exceedingly delicate, and it has not been possible to find one complete "tabula" in the many pores investigated. The gastrostyle itself is stout needle-shaped or rather like a slender fox-tail. Its basal part at or below the bridges is equipped with irregular, longitudinal spiny ridges and is solid, whereas its distal part is a filigree mesh-work of comparatively coarse structure; it is not so brushlike as in *Sporadopora dichotoma* (see MOSELEY 1878, Pl. 35, Fig. 1).

The dactylopores vary somewhat in size. They are quite irregularly scattered between the gastropores, and do not in any way seem to be coordinated to them in numbers or occurrence. In some parts of the branches the intervals between the gastropores are rather large, and the numbers of dactylopores as compared with the gastropores very high. In other places again, where gastropores occur more numerously, there may be comparatively rather few dactylopores.

The deeply immersed ampullae are not visible externally. — The canals of the coenosteum are in the present specimens extraordinarily wide, a feature coinciding with *Sporadopora dichotoma.* The dimensions of the canals decrease a little in the superficial layers of the coenosteum, and the inner parts are accordingly even more spongeous. Moreover a bundle of irregular longitudinal larger canals as mentioned above, appears in the centre of the branches. In the largest branches, however, this central bundle of canals is separated from the thick peripheral and slightly yellowish zone by a more whitish layer which is perforated by several gastropores, but which otherwise gives a more "dead" impression. Morphologically no other differentiations can be seen in fractions. — The main stems may reach a diameter of about 1 cm.

Although the material is preserved in alcohol, the structure of the soft parts indicates that the specimens have been dead some time, before they were preserved. Accordingly only few details concerning the soft parts could be stated with any certainty.

The gastropolyps are rather large. In one place a couple of well developed tentacles were observed, indicating that the polyps have tentacles which at all events are as large as those of *Sporadopora dichotoma.* In this species MOSELEY (1878) found four tentacles on the gastropolyps. — The dactylozooids are of different sizes, the largest ones in contracted state almost as large as the gastropolyps, but somewhat slenderer. The large, fingershaped free part of the dactylozooid is attached to the side wall of the dactylopore by an adhesive, basal part; the free part originates in the middle or distal half of the adhesive part. The base of the dactylozooid is placed deep down in the dactylopore.

MOSELEY (1878, 1881) found in *Sporadopora dichotoma* numerous nematophores irregularly scattered over the surface of the colony between the zooids. Such nematophores are also found in the present specimens, although only in small numbers. They are, however, very conspicuous in stained sections because of the intensive, dark blue coloring of the stinging capsules in hematoxyline.

The examined specimen has male ampullae. As far as could be made out, each ampulla only contains one gonophore. It is impossible to say, whether a "seminal duct" is formed or not. On the other hand half-ripe gonophores always have a more or less deeply bifurcate spadix. — In *Sporadopora dichotoma* MOSELEY (1878, 1881) describes the spadix as "cylindrical in form, with a rounded extremity". It does not seem very probable that a bifurcation should have escaped his careful examination. He also notes for his species that "Sometimes only one such body (i. e. gonophore) is present in an ampulla, sometimes two or three". The present specimen in all cases only shows one gonophore in the ampulla.

It is difficult to settle the specific identity of the present specimens. Previously only one certain species of the genus has been investigated, viz. *Sporadopora dichotoma* Moseley. The specimens were dredged by the "Challenger" expedition off the mouth of Rio de la Plata.

In spite of the great geographical distance the present specimens only show very small differences from the Atlantic species. MOSELEY (1881) describes the surface of the coenosteum as feebly undulated, whereas the present specimens have a quite even surface. In the present specimens there are no indications of such slightly raised mouth margins which MOSELEY mentions in *Sporadopora dichotoma,* and according to his studies, this species also has tabulae in the gastropores. Furthermore MOSELEY emphasizes that the branches as well as the upper part of the stem in his species are compressed in the plane of the fan "so as to be more oblong than oval in transverse section". Circular transverse sections characterize all stems and branches in the present specimens. Lastly MOSELEY also states that "The pores are usually more abundant on one face of the coral flabellum than on the other; indeed, large areas of what may be called the back of the stem are often devoid of pores altogether". In the present specimens the pores are throughout quite evenly distributed on all sides of stem and branches.

The differences here pointed out may seem slight and unimportant. However, the scarce material hitherto investigated of the genus, and the remote localities of the two finds warn us to be careful. We must moreover also pay heed to even such small differences, and at the present we must therefore look upon the specimens from New Zealand as representatives of another species than that obtained by the "Challenger". I have proposed to name the new species *Sporadopora mortenseni* after the collector, the well known Danish zoologist Dr. TH. MORTENSEN.

## Genus *Pliobothrus* POURTALÈS.

The colonies are flabellate, dichotomously or dendritically branched in one plane. Gastropores and dactylopores are irregularly scattered on all sides of the branches; but some of the dactylopores may also be arranged in single, longitudinal rows along the lateral sides of the branches. Cyclosystems are entirely lacking. The gastropores have simple openings, or a lip may be present at the lower side. The gastropores are of varying depths, in some cases the pore is distinctly limited, sometimes by one or more tabulae, in other cases it opens without distinct limits into irregular central canals of the branches. The dactylopores open on top of lower or higher tubular projections which in some species, owing to a slit in one side, may take the shape of horse-shoe-shaped collars. The gastropolyps are provided with well developed or rudimentary tentacles, or tentacles may even be entirely lacking. No gastrostyle is present. The dactylozooids are simply fingershaped and without styles; a basal adhesive part may be present or absent. — The ampullae are deeply imbedded and externally invisible, or they are superficially situated, prominent to semiglobular. Female ampullae contain a single gonophore (?), male ones more gonophores or a single gonophore composed of several "follicles" containing reproductive cells in different stages of development.

*Pliobothrus* was introduced into the literature by POURTALÈS (1869) for the Atlantic species, *Pliobothrus symmetricus* Pourtalès. The genus was again defined in his work "Deep-Sea Corals" (1871), and here he moreover also refers his *Heliopora tubulata* to the genus. In his diagnosis POURTALÈS also in this work emphasizes the lack of tentacles in the polyps in spite of the new species added which, according to his own statement, has well developed tentacles. In his paper POURTALÈS (1871) regards *Pliobothrus* as a Hydroid and ranges it with the family Milleporidae. — MOSELEY (1878, 1881) furnishes a more detailed study of the soft parts of specimens sent to him by POURTALÈS; he gives a somewhat revised diagnosis of the genus, however without observing the inconsequence concerning the tentacles.

HICKSON and ENGLAND (1905) described a new genus, *Steganopora* which, however, must be included in *Pliobothrus* (see BROCH 1914), the type species *Steganopora spinosa* Hickson and England being evidently very closely related to, or even identical with *Pliobothrus tubulatus* (Pourtalès). — A detailed study of *Pliobothrus symmetricus* and of the genus was again given by BROCH (1914) based on material from the Danish Ingolf-expediton fetched from the same waters as the specimens mentioned by DUNCAN (1874) from the "Porcupine"-expedition. Lastly some remarks concerning the same species have been given by DONS (1939) who had access to specimens from the Norwegian coast.

*Pliobothrus* is no doubt a very primitive genus and might on account of the absence of gastrostyles even seem to be more primitive than *Sporadopora.* In fact this is the only distinction between the two genera, all other main features coinciding in *Sporadopora* and *Pliobothrus symmetricus.*

On the other hand the new species *Pliobothrus seriatus* described below to some degree bridges the gap between *Pliobothrus* and *Errina* (the *Labiata*-group). In fact the species holds a so peculiar position on account of its serial arrangement of the lateral dactylopores that I was inclined to regard it as representative of a special genus. It is, however, very doubtful whether the character mentioned may be regarded as anything more than a specific one. — The same is the case with another character which, however, could not at present be studied in detail, partly because of the scarcity of material, partly also because the state of preservation is not quite satisfactory. The new species evidently exhibits a dimorphous development of its dactylozooids. The dactylozooids which are found more or less scattered between the gastrozooids on the anterior and posterior sides of the branches, have the usual, simple fingershaped form previously known in *Pliobothrus*; they are attached to the bottom of the dactylopore by a narrow base. These dactylozooids have no lumen, but a scalary endoderm; but this character depends evidently to some degree upon the dimensions of the zooid (or tentacle) and is thus of subordinate importance. The dactylozooids of the lateral rows are on the other hand attached to the proximal (lower) wall of the pores by a comparatively very long, basal adhesive part from the middle of which the finger-like, free part departs.

A study of living specimens is necessary to settle the importance of these anatomical differences, and anatomical studies of well preserved specimens are also needed to study the anatomical features in detail, before we can settle their taxonomic value. — In spite of the mentioned differences from earlier known species I have at present found it most correct to place the species in the genus *Pliobothrus* with which it agrees in all other essentials. With its "water-spout-like" dactylopores and the lower lip of the gastropore opening, the species links *Pliobothrus* to *Errina.*

## *Pliobothrus seriatus* n. sp.

(Pl. III, Fig. 10.)

Material: Dr. TH. MORTENSEN's Java—S. Africa-expedition 1929—30: September 27, 1929, off Tombeau Bay, Mauritius, depth about 150 fathoms, coral and sandy bottom; two colonies. — November 6, 1929, off Port Louis, Mauritius, depth about 130 fathoms, coral and mud; one branch of a colony.

Only one of the colonies (Pl. III, Fig. 10) is almost intact; it is attached to a small stony piece. The colony has a height of 5.5 cm and a breadth of 7.5 cm. The other specimen from the same locality is a branch, although of the same height, and has a breadth of 3.5 cm. Another branch was collected off Port Louis; it has a height of 3.8 cm and a breadth of 2.7 cm; this specimen is dried.

The colonies are strictly flabellate, the comparatively slender branches slightly tapering towards their distal ends. The branching is copious, side branches generally departing alternately on both sides, and the branches are in most cases a little zigzag with a side branch at the bend. This gives the colony a very characteristic aspect. — No difference is perceivable between an anterior and a posterior side of the flabellum, and transverse sections of stems and branches are quite circular. The slender build of the colony and the seriate arrangement of the lateral dactylozooids with their somewhat protruding apertures together with the glistening structure of the snowy white colony at first sight give a deceiving likeness with certain Bryozoans.

Gastropores and dactylopores are small and arranged in very characteristic manners. Most of the dactylopores are placed in a single row along both lateral sides of the branches and branchlets; on the anterior and posterior sides of the branches only few quite irregularly scattered dactylopores occur. On thicker main branches also additional, irregular short rows of dactylopores may sometimes be found beside the principal lateral rows. — Gastropores are on the other hand only found on the anterior and posterior sides and never, or at all events only in quite exceptional cases, among the lateral dactylopores. — The surface of the coenosteum (Textfig. 9 a) exhibits a delicate ornamentation with rather close longitudinal stripes connecting series of minute pores, the openings of canals of the coenosteum canal mesh-work.

The gastropores (Textfig. 9 b, c) have a transverse diameter seldom surpassing 0.35 mm. A lower (outer) lip makes the opening point obliquely upwards towards the apex of the branchlet. The gastropore is rather shallow, seldom deeper than 0.5 mm. Its axis forms an angle of nearly 45° with the axis of the branch. No gastrostyle is indicated.

Dactylopores occur on all sides of the branches, but they are rather scarce on the anterior and posterior sides and show here no regularity in their disposition. Laterally on the branches on the other hand, the dactylopores are arranged in one close, longitudinal row on each side. The aperture of the dactylopore is surrounded by a low collar which has the shape of a horse-shoe on account of a slit in the upper side turning against the end of the branch; the collars accordingly look like the low "water-spouts" occurring e. g. in *Errina cervicornis*. The collar is a little lower at the slit than at the opposite side.

The coenosteum has a compact structure with fine coenenchym canals; the skeletal substance is rather hard and semipellucid. No larger canals are

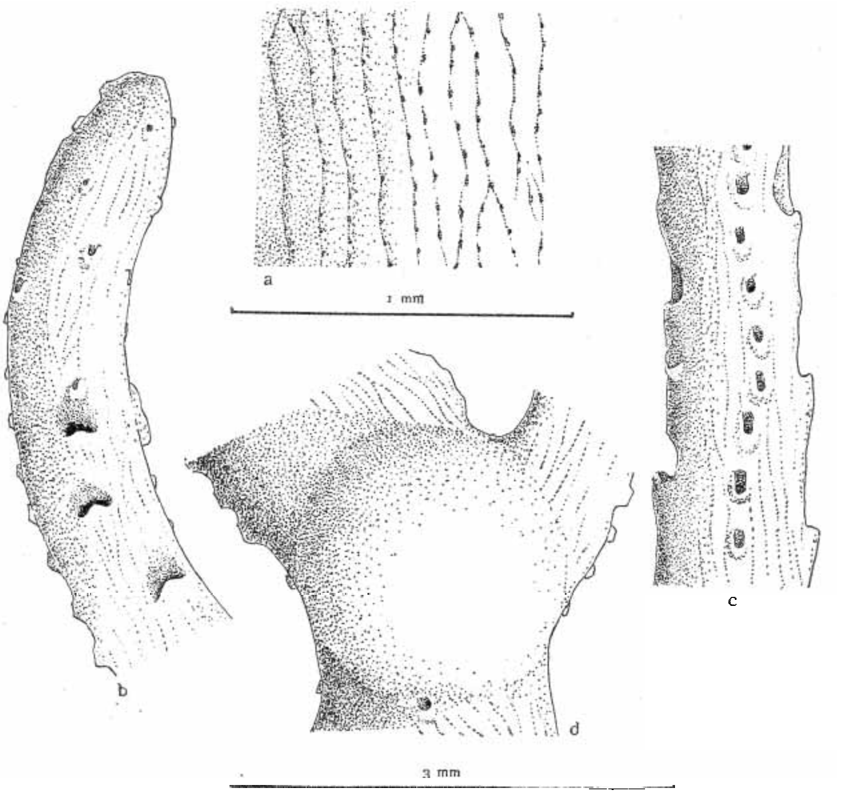


Fig. 9. *Pliobothrus seriatus.* Off Port Louis, Mauritius, depth 130 fathoms, — a surface of the coenosteum showing the rows of the openings of the coenenchym canals. b end of a branchlet seen from the flat side of the flabellum; three gastropore openings are visible. c branch in lateral view; the somewhat protruding "lip" of the gastropores is obvious in the contours. d ampulla at the basis of a branchlet.

indicated in the larger branches, and neither gastropores nor dactylopores can accordingly communicate with these as is the case in *Pliobothrus tubulatus* and more occasionally also in *Pliobothrus symmetricus* (see Broch 1914). In the present species both gastropores and dactylopores are well limited, and they do not show any formation of tabulae.

Female ampullae (Textfig. 9 d) are observed on the anterior and posterior sides of the colony. The large ampullae are in most cases found on the branch at the base of a branchlet, sometimes also in other places on somewhat thicker branches. The roof of the ampulla is quite smooth. Female ampullae may reach a diameter of 2 mm; nevertheless they only contain one gonophore.

The gastropolyps are devoid of tentacles or may have up to 6 (?) small tentacle rudiments quite irregularly placed.

The dactylozooids are evidently dimorphic. Those which occur scattered on the anterior and posterior sides are somewhat larger, simply fingershaped, and attached to the basal part of the pore by a narrow base. Although their central endoderm is scalariform and a central lumen is wanting, they must be said to belong to the same type as that previously known from the genus. The zooids of the lateral rows on the other hand are attached to the proximal (lower) side wall of the pore by a remarkably long basal part, and the finger-like free part is fixed to the middle of this adhesive part. Evidently the free part of the dactylozooid is comparatively very short and strongly contractile; in the investigated fragments it is always contracted to a small, conical wart. The free part of the dactylozooid points against the apical side of the pore, i. e. towards the slit in the horseshoe-shaped collar of the dactylopore opening.

As already mentioned above, the female ampulla only contains one gonophore. The yolk of the ovum exhibits a remarkably mosaic-like structure in sections of the specimen investigated. The cupshaped trophodisc embraces the lower third to one half of the large ripe ovum.

The species is very characteristic, and I was at first in doubt, whether it might be considered as a representative of a new genus on account of the seriate, lateral dactylopores and the dimorphism of the dactylozooids. However, the unsatisfactory state of preservation to some degree hinders a thorough investigation of the dactylozooids, and a closer examination of *Pliobothrus tubulatus* is also needed for a comparison. Under these circumstances it is at present the best course to range the species with the old genus *Pliobothrus*.

## Genus ***Errina*** Gray.

The colonies are more or less irregularly flabelliform, generally subdichotomously branched. Gastropores and dactylopores are irregularly scattered over the colony. The gastropores have simple, circular apertures, sometimes with a lip (or collar) at its lower (abaxial) side. Some or all dactylopores have one side of the opening prolonged into a grooved spine or nariform process; in many species dactylopores with simple openings also occur. Castrostyles are present, whereas dactylostyles are lacking. The gastropolyps may lack tentacles or have rudimentary or well developed tentacles. The finger-shaped free part of the dactylozooid is inserted on the side of a basal adhesive part or departs in a few cases from its upper end. — The ampullae are generally rather superficially seated and may give rise to swellings; they occur in groups in rare cases, but they are in some cases also so deeply immersed that they are externally invisible, although they also in these cases are found in the peripheral layers of the branches. Female ampullae generally contain one gonophore; in some cases also a young bud of a secondary gonophore may be present beside the ripe one. Male ampullae mostly contain several gonophores in different stages of development. In some of the species a blastostyle is present in male ampullae; the gonophores bud round the basis of this blastostyle.

The genus was introduced by GRAY as early as 1835 for the species *Millepora aspera* Linné 1767. The next to mention the genus, is POURTALÈS (1867); but later on he came to the result that the species investigated by him must be removed from *Errina*, and in "Deep-Sea Corals" (1871) he describes a closely related genus, *Lepidopora*, which, however, already MOSELEY (1878) again includes in *Errina*. On the other hand MOSELEY in the same paper introduces a related genus, *Spinipora*, for a species detected by the "Challenger"-expedition, and he also adds another related genus, *Labiopora*, for the old species *Porella antarctica* Gray 1872. — Little by little several species had been described by different authors, and in 1912 HICKSON published his revision "On the Hydrocoralline Genus, *Errina*." In this paper he maintains that both *Spinipora* and *Labiopora* must be included in the genus *Errina*.

Although HICKSON thus discards the previous genera as such, he nevertheless maintains them with some slight modifications as convenient groups (or subgenera). The limits must be designated as rather uncertain, and it is obvious that our present knowledge gives only a poor basis for a splitting up into more genera.

HICKSON, as mentioned, retains three groups. — viz. *Labiopora, Spinipora,* and *Errina* sensu strictiori — partly basing his classification on the orientation of the grooved spines (whether with their grooves turned away from or facing the end of the branch), and partly on the presence or absence of dimorphism among the dactylopores. If now v. MARENZELLER's interpretation (1903) should be right, that dactylopores with simple apertures are only young stages which later on develop grooved spines, HICKSON's fundamentum divisionis insofar fails. The present material in some cases speaks in favour of v. MARENZELLER's interpretation, in others again against it, and the details given by MOSELEY (1878) for *Spinipora* seem to indicate a real dimorphism which should defend a special group in this case. Having had no access to certain *Spinipora* species, I shall here leave this group out of consideration.

The study of the present extensive series of *Errina* species has revealed that we most naturally can distinguish between two groups, in the main coinciding with HICKSON's *Labiopora* and *Errina* groups. One group (*Labiopora* sensu HICKSON) has the grooves of the spines at least on the peripheral branchlets turned away from the branch ends. To this may be added that the surface of the coenosteum generally is reticulated or more seldom vermiculated, and in most cases the coenosteum under the microscope looks almost crystalline, reminding us of a lump of sugar.

The other group (*Errina* sensu HICKSON) has the grooves of the spines facing the branch ends. Here the surface of the coenosteum under the lens is almost glistening smooth with rows of fine pores, often placed in shallow and narrow, longitudinal furrows. The substance of the coenosteum here moreover seems dense and homogeneous, more milky pellucid than in the previous group.

A question turns up concerning the naming of the groups. In an appendix Hickson (1912) mentions that he has examined the type specimen of _Errina aspera_ (Linné) which is kept in the British Museum, and that this species must be referred to the _Labiopora_ group. As mentioned above this species is the type of Gray's genus _Errina_, and in accordance with nomenclatorial use the group containing the generic type ought to keep the name of the genus, or, as I have used it also here, it should be called _Eu-Errina_; at all events the name _Labiopora_ must be dropped. The _Errina_ group of Hickson must accordingly also have its name changed, and it seems here natural to use the specific name given by Moseley (1878) and call it the _Labiata_ group.

_Errina_ is linked to _Sporadopora_ by the closely related genus _Paraërrina_ described below. The latter genus seems also to hold an intermediate position between _Errina_ and _Errinopora_ (_Protoerrina_, Part I, p. 99), the type species of which latter genus was described by Dall (1884) under the name of _Errina pourtalesii_ (see Fisher 1938). One might indeed at first sight believe this species to belong to the _Eu-Errina_ group if it did not possess dactylostyles. The salient point of _Errinopora_, however, is that its dactylopores in their arrangement exhibit obvious coordination to the gastropores and in many places even show a tendency to a disposition into cyclosystems, whereas no such coordination can be traced in _Errina_, the pores of which are quite irregularly scattered all over the colony.

In spite of the obvious relations with the mentioned genera, _Errina_ is a rather well limited genus. On the other hand the limitation and identification of the different _Errina_ species is exceedingly difficult, and it is also impossible to reidentify most of the numerous earlier described species without a thorough examination of the type specimens. Almost more than elsewhere such subtle characters must be reckoned with as have not been mentioned in previous works nor emphasized in the drawings. In spite of the valuable revision of Hickson (1912) we must also today admit our insufficient knowledge of the _Errina_ species.

According to Hickson the following species belong to _Eu-Errina_: ("the _Labiopora_ group" of Hickson 1912).

*_Errina aspera_ (Linné) (=_Millepora aspera_ Linné 1767) Type species.
— _fissurata_ Gray.
* — _antarctica_ (Gray) (=_Porella antarctica_ Gray 1872).
— _moseleyi_ (Ridley) (=_Labiopora moseleyi_ Ridley 1881).
* — _novæ-zealandiæ_ Hickson.
* — _capensis_ Hickson.
— _gracilis_ v. Marenzeller.
— _dabneyi_ (Pourtalès) (=_Lepidopora dabneyi_ Pourtalès 1871).
* — _rubra_ n. sp.
* — _spongiosa_ n. sp.
? — _cochleata_ (Pourtalès) (=_Lepidopora cochleata_ Pourtalès 1871).
? — _glabra_ (Pourtalès) (=_Lepidopora glabra_ Pourtalès 1871).

(The only species belonging to the *Spinipora* group is *Errina echinata* (Moseley) = *Spinipora echinata* Moseley 1878.)

The species belonging to *Labiata* are:
("The *Errina* group" of Hickson 1912).
*Errina labiata* Moseley.
— *ramosa* Hickson and England.
— *horrida* Hickson and England.
* — *tenuistylus* n. sp.
* — *cervicornis* n. sp.
? — *carinata* Pourtalès.

Hickson with a query also places *Errina pourtalesii* Dall 1884 in this group; this is the type species of the genus *Errinopora* Fisher 1931.

Furthermore the species *Errina macrogastra* v. Marenzeller 1904 must be added which holds an intermediate position in so far as the orientation of the dactylopores and their grooved spines agrees with *Eu-Errina*, whereas the structure of the coenosteum is in better accordance with the *Labiata* group. The species should probably most naturally be placed among the *Eu-Errina* species.

The species marked in the list with an asterisk (*) have been studied, and detailed descriptions are found in the following. They have also been arranged in a key which is illustrative of the important taxonomic characters.

1 (12) Grooved spines on the terminal branches turned away from the apex (nariform). Coenosteum granular, with reticulated or vermiculated surface, without well-defined coenosteal pores. *Eu-Errina.* 2

2 (11) Grooved spines well developed. 3

3 (8) Surface of the coenosteum reticulated, structure under the microscope decidedly fine-crystalline (like a lump of sugar). 4

4 (7) Without a lower lip at the gastropore. 5

5 (6) Gastrostyle filigree-like, irregularly needleshaped, rather acute and with well developed spicules or bristles. *Errina aspera* (Linné)

6 (5) Gastrostyle compact, shaped like an acute, slender pine-cone, with almost rudimentary minute spicules. Surface structure of the coenosteum most obvious between the grooved spines. *Errina antarctica* (Gray).

7 (4) Gastropores with a small lower lip. Gastrostyle large, foxtail-like, compact and covered all over by short spicules. *Errina rubra* n. sp.

8 (3) Surface of the coenosteum more or less distinctly vermiculated. Structure not so obviously crystalline. 9

9 (10) The finely granulate surface structure generally most obvious on the grooved spines. No larger rounded warts between

the spines. No gastropore lip. Gastrostyle compact, robustly needleshaped with small spicules. Colonies extraordinarily robust and irregularly branched. ***Errina spongiosa*** n. sp.

10 (9) Surface of the coenosteum vermiculated, with numerous rounded warts between the pores and spines. A gastropore lip may be present or absent. Gastrostyle filigree-like, slenderly needle-shaped or conical, richly armed all over with small spicules. *Errina novæ-zealandiæ* Hickson.

11 (2) The grooved spines are almost rudimentary and horseshoe-shaped. Surface of the coenosteum coarsely rugged, especially at the brim of the gastropores also armed with small spines. No gastropore lip. Gastrostyle shaped like a pine-cone, with short bristles on its distal half. ***Errina capensis*** Hickson.

12 (1) Grooved spines on the terminal branches turned towards the apex (waterspout-like). Coenosteum hard and compact, perforated by well defined canals opening as pores or pore-rows on the surface. *Labiata.* 13

13 (14) Surface of the coenosteum under the lens longitudinally striped with stripes rather far apart. Gastropore without lip. Gastrostyle deeply seated, very slenderly needleshaped, armed with quite small spicules or all but smooth. ***Errina tenuistylus*** n sp.

14 (13) Pores of the coenosteum in rather closely placed, irregularly or often longitudinally running, shallow furrows. At the lower side of the gastropore a lip, when a dactylopore with its grooved spine is lacking here. Gastrostyle compact, conical, with numerous short spicules on its distal part. ***Errina cervicornis*** n. sp.

## *Errina (Eu-Errina aspera)* (Linné 1767).

(Pl. IV, Fig. 11.)

1767 *Millepora aspera*, LINNÉ, Systema Naturae ed. XIII.
1797 — *aspera*, ESPER, Pflanzenthiere, t. 1, p. 106, Pl. XVIII, Fig. 1–4.
1835 *Errina aspera*, GRAY. Trans. Zool. Soc., p. 85.
non 1867 *Errina aspera*, POURTALÈS, Bull. Mus. Comp. Zoöl., p. 116.
1871 *Errina aspera*, KENT, Proceed. Zool. Soc. London, p. 282.
1878 — *aspera*, MOSELEY, Structure of the Stylasteridae, p. 479.
1881 — *aspera*, MOSELEY, Stylasteridae . . . . "Challenger", p. 84.
1905 — *aspera*, HICKSON and ENGLAND, Stylasterina of the Siboga Exped., p. 18.
1912 — *(Labiopora) aspera*, HICKSON, On the Hydrocoralline Genus, *Errina*, p. 888, Pl. XCV, Fig. 6.
1912 — *(Labiopora) aspera*, HICKSON, Notes on some Stylasterina in the Museum d'Histoire Naturelle de Paris, p. 1 and 2.

Material: One small dried branch from the West Indies, further details concerning locality and collector are wanting (Riksmuseum, Stockholm).

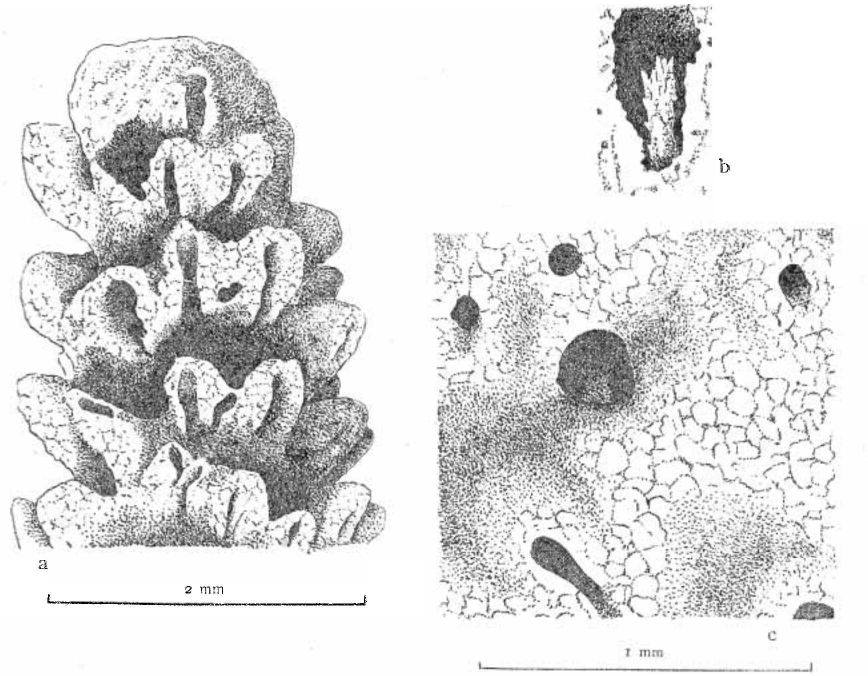


Fig. 10. *Errina (Eu-Errina) aspera.* West Indies. — a terminal part of a branchlet. b basal part of a gastropore with the gastrostyle. c surface of a part of the coenosteum; in the gastropore the top of the gastrostyle is dimly visible.

The branch (Pl. IV, Fig. 11) which is 2.5 cm high, gives evidence of a dichotomous or subdichotomous branching, and belongs evidently to a flabellate colony. No pronounced difference is seen between an anterior and posterior side of the branch, but a certain although feeble decrease in the numbers of pores and spines on one side indicates that older parts of the colony probably exhibit more obvious differences between the two sides of the flabellum. According to HICKSON (1912 a) this difference is very obvious in the type specimens, and he also emphasizes the pure white color of these. The present fragment is vividly salmon pink with whitish branch ends, and their identity might therefore seem questionable. The color is, however, a varying character in most other Stylasteridae, and all other features agree with previous descriptions of the species.

The branchlets terminate rather acutely and are comparatively slender. The surface of the coenosteum is reticulate, seemingly crystalline, and under a lens it exhibits almost the same structural picture as a lump of sugar, when it has been cleaned with sodium hypochlorite. The central part of the branches is rather compact, the surface layers (about 1 mm thick) more porous. Central canals are wanting, and the gastropores do not penetrate far into the coenosteum.

The gastropores have an opening diameter of some 0.24—0.25 mm and are mostly only little more than 1 mm deep. The opening is simple, without any lip. The deeply seated gastrostyle is only in few cases visible on an external examination. The gastrostyle (Textfig. 10 b) is remarkably irregularly needleshaped, in many cases with a more brushlike tip, in other cases rather acute; it is always covered by well developed spicules, and the style itself has a rather filigree-like build.

Only few small dactylopores are present, but on the other hand larger dactylopores are numerous and accompanied by prominent grooved spines (Textfig. 10 a) which in some places tend to an arrangement in longitudinal rows; on some of the terminal branchlets the spines also form indistinct transverse rows or whorls. In a few places a grouping of the spines is faintly indicated, but otherwise they occur quite individually and have their groove turned away from the apex of the branchlet.

Ampullae are present in great numbers in the peripheral, more porous layers of the branch and attain a diameter of at least 3/4 mm. They can nevertheless not be seen from without as they do not cause any swellings or disturbances among the pores.

The present specimen agrees well with the description given by HICKSON (1912 a), and seems to hold an intermediate position between the type specimen and the other colony described by him. In a following paper HICKSON (1912 b) mentions specimens from the deep sea near Cape Verde, but he does not add any particulars concerning the features of these colonies beyond a remark that they have longer grooved spines than previously examined colonies.

## *Errina (Eu-Errina) antarctica* (GRAY 1872).

1872 *Porella antarctica*, GRAY, Proceed. Zool. Soc.. p. 746, Pl. LXIV, Fig. 4.
1878 *Labiopora antarctica*, MOSELEY, Structure of the Stylasteridae, p. 476, 480.
1881 — *antarctica*, RIDLEY, Account of the Coelenterata . . . H. M. S. "Alert", p. 105.
1912 *Errina antarctica*, HICKSON, On the Hydrocoralline Genus, *Errina*, p. 887.
1912 — *antarctica*, HICKSON, Notes on some Stylasterina in the Museum d'Histoire Naturelle de Paris, p. 2 (462).

### Forma *typica*.

(Pl. IV, Fig. 12.)

Material: A small branch of HICKSON's specimen from Cape Horn (further details concerning the locality are wanting).

The branch (Pl. IV, Fig. 12) indicates a subdichotomic mode of branching. Previous descriptions do not especially mention this but at most speak of the colonies as flabelliform without anastomoses of the branches. According to earlier descriptions branches and stem have a rather circular transverse section, and also the branchlets are cylindrical, if an incipient bifurcation

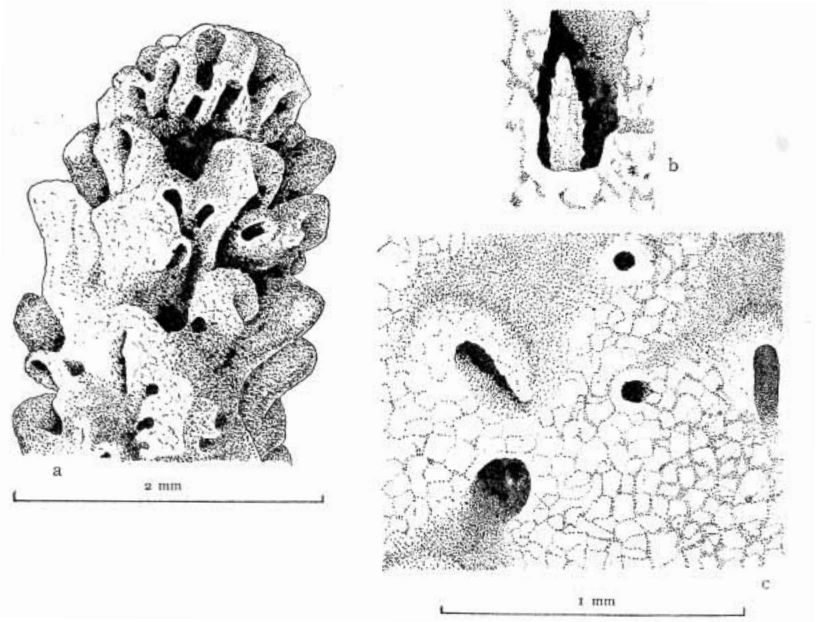


Fig. 11. *Errina (Eu-Errina) antarctica* forma *typica*. Cape Horn (Sydney J. Hickson). — a top of a branchlet. b basal part of a gastropore with the gastrostyle. c surface of a part of the coenosteum; in the gastropore the gastrostyle is dimly visible.

does not make the extreme end of it seem somewhat anterior-posteriorly compressed.

The present branch has an obvious anterior side with numerous, crowded gastropores and dactylopores, the larger dactylopores accompanied by a prominent grooved spine. On the posterior side of the main branch gastropores and dactylopores only occur in comparatively small numbers, and on this side especially few large dactylopores with prominent grooved spines are present. — Ampullae occur on all sides of the branches, but they are especially numerous where the zooids also are numerous. The ampullae are developed just below the surface of the coenosteum, and ripe ampullae protrude almost like hemispheres on the surface of the colony, in many cases carrying one to three grooved spines. The ampullae are the more obvious because they have a lighter hue than the other parts of the colony which are salmon pink.

After cleaning with sodium hypochlorite the surface of the coenosteum is finely reticulate and shows under the microscope a structure very much like that of a lump of sugar (Textfigs. 11 a and c). Sections reveal that the coenosteum is neither more porous nor more compact than in most other Stylasteridae, and the porousness is the same throughout the branch. The gastropores do not penetrate deeper into the branches, and no central canals are indicated.

The gastropores are comparatively rather small and do not generally surpass a diameter of 0.22 at their opening, but are commonly a little narrower. They are not very deep, and only seldom do they attain a length of more than 1 mm. No lip is indicated at the opening. — We can always discern the gastrostyle on external examination. The gastrostyle (Textfig. 11 b) has approximately the shape of a slender pine cone or the flame of a candle, and it is remarkably compact, not like the filigree construction of most other species.

The dactylopores show very varying features. In the terminal branchlets one might here agree with v. MARENZELLER (1903) who declares that the so-called "small dactylopores" without grooved spines are only young stages of the "large dactylopores" with grooved spines. In the terminal branchlets the growth obviously is most intensive, and the entire picture is here rather complicated and crowded. However, if we examine the posterior side of a main branch, we find that most of the dactylopores here belong to the small type, and in this case sometimes also an indication of grooved spines may be observed, generally in the shape of a low, horseshoe-shaped brim at the opening; but as often there is no indication of a spine at all. It must be remembered that the growth in this part of the branch probably is very slow, and that after all pores are here more likely to disappear than to arise. This makes the supposition of v. MARENZELLER somewhat problematic. Howsoever this may be, the present species exhibits extraordinarily numerous small dactylopores without grooved spines besides the characteristic larger dactylopores with their large grooved spines. The latter become extremely scarce on the posterior side of the main branches. The spines are not clustered, and their groove is turned away from the apex of the branch.

The ampullae protrude almost hemispherically on the surface. Although they in most cases are devoid of dactylopores and spines, it is by no means seldom to find one, two, or even three dactylopores with their adjoining spines on the ampulla roof. — The size of the ampullae with diameters up to 1 mm, seems to indicate a female colony. But the preservation of the soft parts did not allow any detailed study, and the skeleton was accordingly cleaned.

### Forma **kerguelensis** n. f.

Material: Two small, dried branchlets of about 1 cm length from Heard Island (south of the Kerguelen Island, about 53° S. and 73° E.), further details wanting (Copenhagen Museum, presented by D'ARCY THOMSON).

It is in most cases impossible to identify a species of *Errina* after a few such diminutive fragments. It is impossible to settle features like the arrangement of the pores on larger branches, or the shape of the colony, which are characteristics of some of the different species. In the present case, however, very much points in the direction of *Errina antarctica*, but

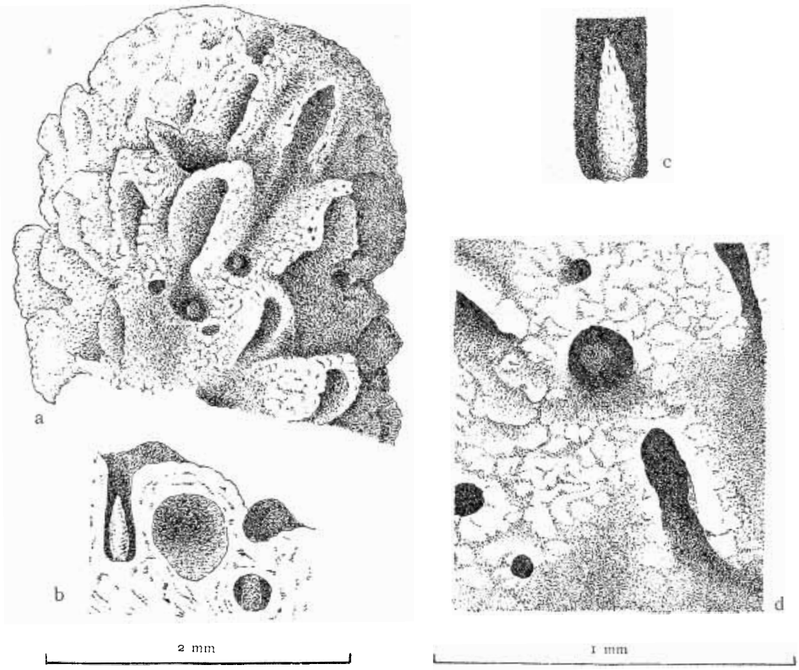


Fig. 12. *Errina (Eu-Errina) antarctica* forma *kerguelensis.* Heard Island. — a top part of a branchlet. b section through the coenosteum showing an ampulla (in the middle) and two gastropores with their styles. c gastrostyle. d surface of a part of the coenosteum; in the gastropore the gastrostyle is dimly visible.

some features differ so much from the Cape Horn specimen that it, at al events at present, is necessary to regard the specimen as representative of a special form or possibly even of a different species.

The surface structure of the coenosteum (Textfig. 12 d) is a trifle coarser than in the Cape Horn colony, and the surface is especially rough between the grooved spines, whereas the spines themselves are rather smooth. Moreover the structure is mostly more vermiculated than reticulated. It seems also as if the specimen from the Heard Island is more heavily built than the Cape Horn colony; this is also evident on a comparison of Textfigs. 11 a and 12 a. — There is also some difference in the color, the fragments from the Heard Island being yellowish orange with purely yellow branchlet tips.

The coenosteum shows the same, rather compact structure as in most other Stylasteridae, the peripheral layers of the branches being a trifle more porous than the central. There is no indication that the older gastropores penetrate to the centre of the branches or that central canals are developed.

The gastropores have diameters up to 0.25 mm at their opening and are rather shallow, generally not deeper than 1 mm, and the gastrostyles are accordingly readily visible on a superficial examination. The gastrostyle in detail agrees with that of the Cape Horn specimen and has the shape of an acute and slender although solid pine-cone (Textfig. 12 c). — The dactylopores are comparatively large. Between large pores with grooved spines also small, spineless pores are found in great numbers, but they are nevertheless not quite so numerous as in the typical *Errina antarctica* from Cape Horn. Pores and spines are crowded and evenly distributed on all sides of the branchlets.

Numerous ampullae occur. As the fragments are dried, the sex cannot be stated with certainty; the diameter of the ampullae is about 3/4 mm or even more. But the ampullae are not visible on the surface of the branchlet, although they are found in the superficial layers of the coenosteum. They cause no swellings of the surface.

Comparing with the Cape Horn specimen we can sum up the main differences as follows: The sculpturation of the coenosteum is heavier, rather more vermiculated than reticulated and does not give the obvious "sugar-like" impression of the typical form. The color is orange and yellow. The gastropores are a trifle larger with somewhat more obvious gastrostyles. Lastly, the ampullae are not visible on the surface of the branchlets, although they attain the same dimensions as in the typical form from Cape Horn.

### *Errina (Eu-Errina) rubra* n. sp.

(Pl. IV, Fig. 13.)

**Material:** Dr. Th. Mortensen's Pacific expeditions 1914—1916: January 5, 1915, Three Kings Island, New Zealand, depth 65 fathoms, hard bottom; several fragments together with a couple of quite small, intact colonies growing on Hydroids. — January 5, 1915, 10 miles N.W. of Cape Maria van Diemen, New Zealand, 50 fathoms, hard bottom; one fragment of about 2 cm height.

Although the branching must be characterized as dichotomous or subdichotomous, the colonies (Pl. IV, Fig. 13) exhibit a very irregular shape. Whereas the utmost branchlets are always slender and in most cases end acutely, the branches rapidly increase in dimensions, and a piece of a main branch (or stem) with a diameter of 7 mm has (secondary) side branches which at their source only have diameters of some 3 or 4 mm. Some of the smaller pieces give the impression of an irregular, bushy ramification, whereas others indicate a more flabellate development of the colony, and in some few cases a slight difference in the numbers of pores to all appearance indicates that an anterior and posterior side may be distinguished in some colonies. Otherwise transverse sections of the branches are almost always quite circular.

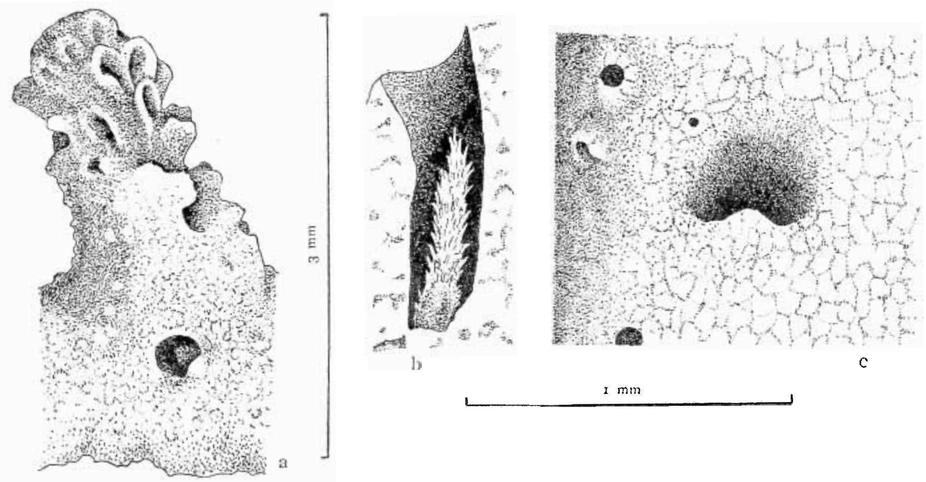


Fig. 13. *Errina (Eu-Errina) rubra.* Three Kings Island, New Zealand, depth 65 fathoms. — a branchlet of a small colony; on the mother branch a gastropore with its gastrostyle. b longitudinal section of a gastropore showing the gastrostyle. c structure of the surface of the coenosteum.

The colonies from Three Kings Island are intensely blood red with quite or almost quite white branch tips; the specimen from Cape Maria van Diemen is lighter red with white branch ends.

The surface of the coenosteum (Textfig. 13 c) is reticulated, and under the microscope the colony gives the impression of a lump of sugar. Although we get the same impression also of the thicker main branches, the surface structure may here tend a little to the vermiculated type. — The inner structure is the same as in most other species, neither more compact nor so spongy as f. inst. *Errina spongiosa.* In the thick fragment from the same locality the coenosteum is throughout blood-red colored with the exception of a small and generally very excentrically placed axial part which is quite white.

The gastropores are rather large, the largest of them attaining an opening diameter of 0.5 mm. On the other hand they are comparatively shallow, seldom surpassing a depth of 1 mm. In most cases a small lip is found at their lower (outer) side (Textfig. 13 a, c). The lip is prominent at the gastropores of the branchlets, and the aperture of the gastropores is accordingly here turned obliquely upwards against the apex of the branch. On the thicker branches on the other hand, the lip or the abaxial brim of the gastropore is less prominent, and on the main branches and stems the lip is, if at all, only very feebly indicated and the aperture of the gastropore simple, agreeing with the surface plane of the branch (stem). — Gastropores are also very numerous on the main branches.

Dactylopores occur crowdedly on the terminal branchlets, in comparatively smaller numbers on the thicker branches although always more numerous than the gastropores. "Small dactylopores" without spines are seldom met with, but the grooved spines are often more prominent along the lateral sides of the main branches than on the anterior and posterior sides, whereas they are of equal sizes on all sides of the terminal branchlets.

The ampullae are rather superficially placed in the coenosteum and may reach a diameter of 2/3 mm. In some cases they are seen externally as somewhat lighter spots which in exceptional cases are faintly protruding; in other cases again one cannot see the single ampulla externally, but comparatively small branchlets or branches of quite small colonies may give a somewhat irregular, rather inflated impression owing to the occurrence of ampullae. In this case the single ampulla does not show any special shade of coloring as against the other parts of the colony.

The state of preservation does not suffice for a study of the soft parts. It seems as though the gastrozooids have tentacles and the fingershaped, free part of the dactylozooids is rather large and fixed to the middle or just below the middle of a comparatively long adhesive part which is seated on the side wall of the dactylopore. It furthermore looks as though the female ampulla only contains one gonophore.

Although the present specimens have been dredged in New Zealand waters and belong to the *Eu-Errina* group, they differ markedly from *Errina novæ-zealandiæ* and represent an unknown species. The surface structure of the coenosteum, the lip of the gastropore, and the build of the gastrostyle differ so markedly in the two species that they even seem to be rather distantly related. Although the color in general only has a subordinate taxonomic value among the Stylasteridae, the present specimens indicate that a difference may also be present in comparison with all other species of *Errina*.

## *Errina (Eu-Errina) spongiosa* n. sp.

(Pl. IV, Fig. 16.)

Material: The Swedish Antarctic expedition 1901—1903: September 12, 1902, 53° 45′ S., 61° 10′ W., Burdwood Bank south of W. Falkland, depth 137—150 m, fractured shells and stones; several large fragments of large colonies.

The largest fragments are about 8 cm high, and the diameter of the thickest branches or stems may amount to 1.5 cm. — The extraordinarily robust specimens (Pl. IV, Fig. 16) show an entirely irregular ramification, and even quite small branchlets attain a diameter of about 5 mm or even more a little below the apex. Transverse sections of branches and stems are circular. The colonies are intensely salmon pink with almost white ends of the outer branches; the color is the same in dry colonies and in specimens preserved in alcohol.

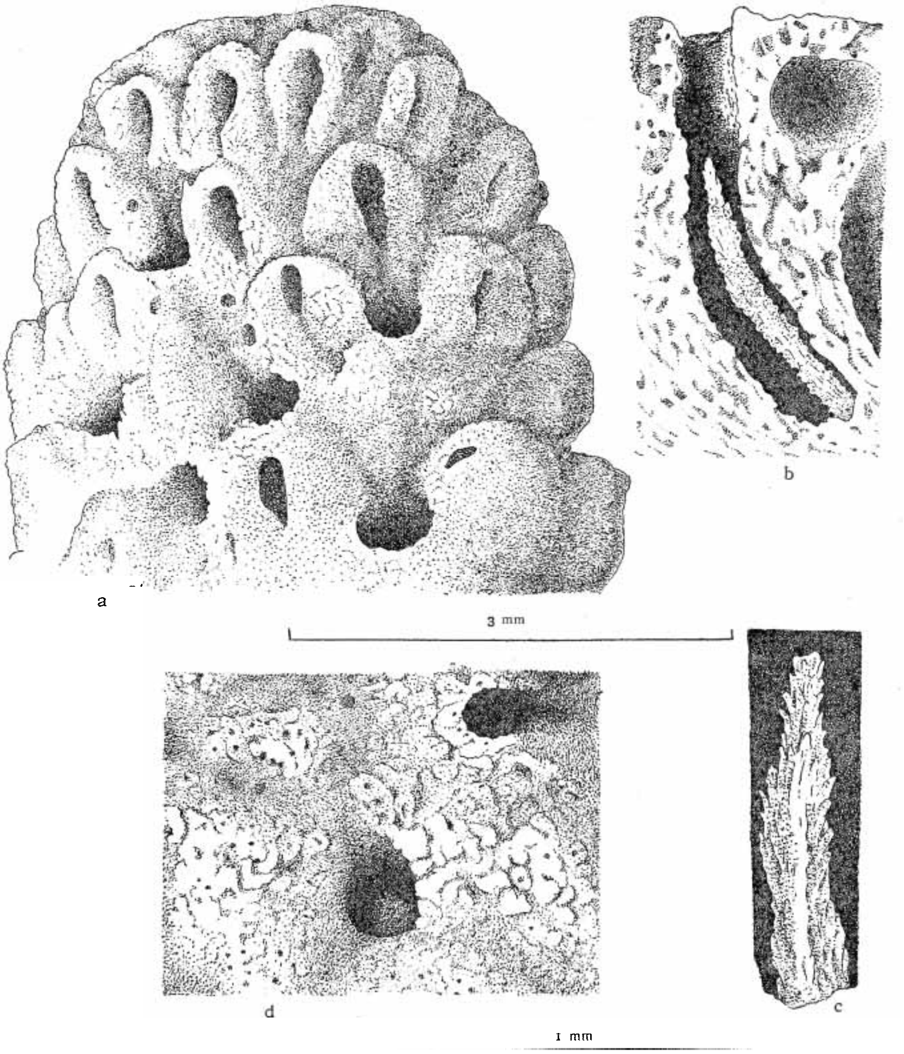


Fig. 14. *Errina (Eu-Errina) spongiosa.* Burdwood Bank S. of W. Falkland, depth 137—150 m. — a top part of a branchlet. b section showing a gastrostyle in its gastropore and (to the right) an ampulla. c top part of a gastrostyle somewhat more enlarged. d surface of the coenosteum.

Already at first glance the colonies give a peculiar, porous impression on account of their numerous, large pores and well developed although blunt and massive grooved spines (Textfig. 14 a). The surface of the coenosteum (Textfig. 14 d) is granular, but the granulation is a little more delicate than in *Errina antarctica*, and in the present species the granulation is as obvious or even more obvious on the grooved spines than between them, whereas the granulation in *Errina antarctica* is most prominent between the spines.

The central part of the branch is white, but the white axial part differs much in its dimension in comparison with the peripheral, pink layer. The structure of the coenosteum is remarkably porous or spongy and reminds us strikingly of *Sporadopora.* There is moreover a pronounced tendency to form tabulae in the gastropores in such a way that the older pore with its style is not directly continued into the younger, more superficial pore, but by a feeble displacement sideways limited from it. This is especially obvious in sections of thicker branches.

The gastropores (Textfig. 14 b, d) are in most cases deep with smooth walls, and the gastrostyle is so deeply set that it is often invisible from without. The diameter of the gastropore may at the opening reach 0.5 mm but is generally about 0.45 mm. The depth of the gastropore varies and is often about 3 mm or even more. The gastrostyle (Textfig. 14 b, c) is stout and needleshaped, but rather compact and covered with small spicules. The deeper gastropores of thicker branches are in many cases divided into two or three floors by irregular and incomplete tabula-formations.

Dactylopores are found in great numbers on all sides of the colony, and small dactylopores without grooved spines, or with more or less rudimentary spines are especially numerous between the larger pores with well developed spines. At the end of the branchlets the grooves are decidedly turned away from the apex (Textfig. 14 a), but on thicker branches there is no regularity in their orientation, and here we now and again observe a tendency in the spines to collect in clusters. An indication of arrangement in rows can on the whole not be traced.

Ampullae can in many cases be seen externally as whitish small spots, but they do not cause any other disturbances. In some cases, however, emptied ampullae may be observed on the surface as cicatrizations, circular grooves a little larger than the gastropores and without any trace of contents. Transverse fractures of branches show that ampullae occur throughout the colored parts of the coenosteum and attain a diameter up to 1 mm. In thicker branches more rows of ampullae are present, the deepest seated ones at the transition from the redcolored to the white central part of the coenosteum.

An investigation of the soft parts shows that the gastropolyp is generally furnished with six wart-like small tentacles or rudiments of tentacles; their endodermal core is seldom built up of more than four or five cells. In the present specimens the polyps are so contracted that the gastrostyle in most cases protrudes a little through the mouth. — The dactylozooids are simply finger-shaped, slightly obliquely inserted on a small adherent basal part fixed to the upper side wall of the dactylopore. The dactylozooids also are strongly contracted. — Comparatively large stinging capsules are very frequent in the coenenchym canals of the more peripheral parts of the branches.

Male ampullae generally contain three to five gonophores in different stages of development. Fully developed although not ripe gonophores have a three- or four-forked spadix which obviously recalls the tropodisc of a female gonophore (see Textfig. 28 c, p. 81). — Female ampullae can hardly be distinguished from male ones on external examination, the only difference being that the whitish spots are a trifle larger and sit a little more apart. Only one female colony is present in the material. Almost all ampullae are empty, but nevertheless intact, and in two cases quite small secondary gonophores are present. In one other ampulla one gonophore with ripe ovum was found filling the entire lumen of the ampulla; in this case no trace of a secondary gonophore was observed.

The dimensions alone of this giant *Errina* are so characteristic that it should not easily be mistaken. However, also qualitative characters separate it from its allies. The spines are more blunt than in other species and do not exhibit any regularity in their arrangement except at the end of the branchlets, and although the surface structure of the coenosteum comes very near to that of *Errina antarctica*, also here some differences may be noted in so far as the granulation in the present species is most prominent on the spines. Characteristic also is the remarkably spongy structure of the skeletal parts to which the name alludes.

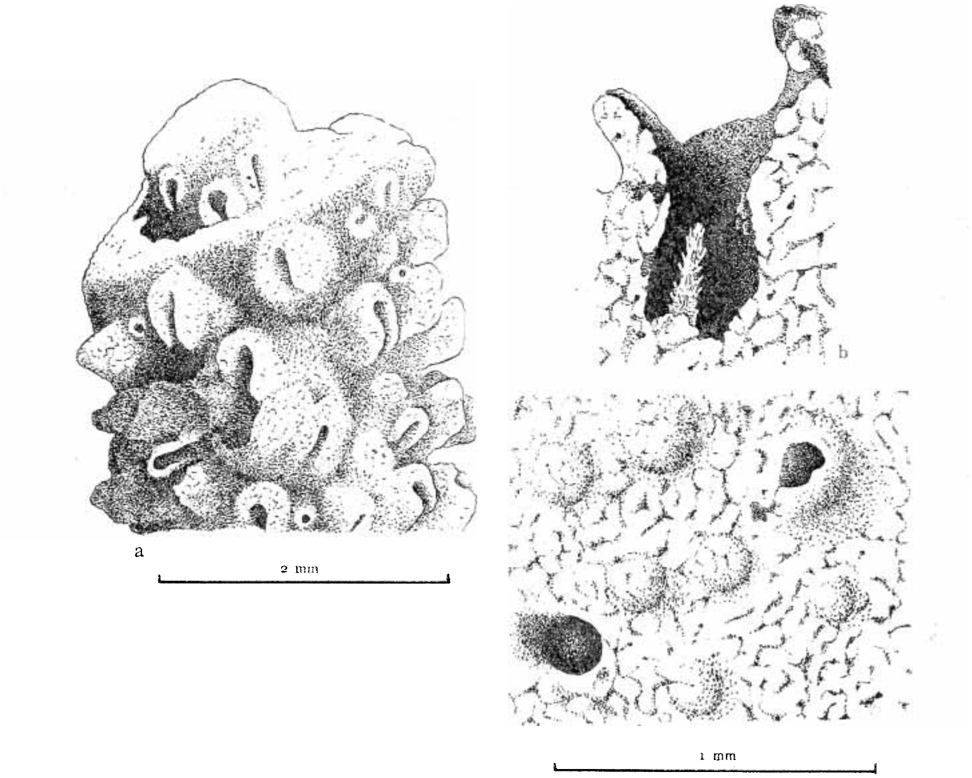
### *Errina (Eu-Errina) novæ-zealandiæ* Hickson 1912.

(Pl. IV, Fig. 14.)

1912 *Errina novæ-zealandiæ*, Hickson, On the Hydrocoralline Genus, *Errina*, p. 882, Pl. XCIV, Pl. XCV, Fig. 5, and Pl. XCVI, Fig. 9—14.

Material: Preservation Inlet, W. coast of South Island of New Zealand, depth about 3 fathoms; two about 2 cm long branches of the "Facies ramosa". — Cooks Strait, between the two Islands of New Zealand, depth not stated; eight 2—3 mm long splinters of the "Facies Cooki" (Hickson's original specimens).

According to the drawings reproduced by Hickson (1912) the colonies are subdichotomously branched and flabellate, or more irregularly branched, in the latter case tending more to a bushy form (subflabelliform). Pores and grooved spines are much more numerous on one (anterior) side of the branches than on the posterior side of the flabellum, and the characteristic surface structure (Textfig. 15 c) is here very obvious. The surface is vermiculated, and larger rounded warts are scattered between the pores and spines in considerable numbers. Hickson (1912) describes the structure as follows: "Surface minutely granular, substance of the coenosteum minutely reticulate." — The color is salmon pink or rosy, or pure white.



Figur 15. *Errina (Eu-Errina) novæ-zealandiæ* (*"facies ramosa"*). Preservation Inlet, New Zealand, depth 3 fathoms. — a terminal part of a branchlet. b section through a gastropore showing the gastrostyle. c structure of the surface of the coenosteum.

The gastropores reach a diameter of 0.27—0.28 mm at the opening. The aperture may be provided with a small (lower) lip, but is almost as often quite simple and without a lip. The gastrostyle is more or less dimly visible from without. When cleaned (Textfig. 15 b) it is obviously echinate, slenderly conical and composed of a rather loose-meshed latticework. — The dactylopores are in most cases combined with grooved spines which are more prominent in the peripheral parts of the colony, and which are rather closely crowded on the terminal branchlets. The grooves are in the main turned away from the branch apex. In numerous cases the spines may form clusters, and in such clusters the grooves are turned in different directions without any evident regularity.

The coenosteum is neither especially spongy nor compact but agrees with most other Stylasteridae. The ampullae are found just below the surface of the coenosteum and may in some cases protrude feebly like small and shallow segments of a sphere; generally, however, they are invisible on the surface of the branches.

The specimens have been dried so that no details can be given concerning their soft parts.

In his description HICKSON (1912) says under "Facies *ramosa*": "Groved spines (narial processes) numerous, arranged in rows, rarely in clusters." The two fragments at hand do not show any distinct serial arrangement of the grooved spines in most places. The character, however, is in the present species evidently of quite subordinate importance, and HICKSON also only uses it as a supporting feature in connection with his different "Facies" of the species. The same is true of the clustering of the grooved spines which in the present fragments is only seldom indicated, whereas it is said to be very frequently observed in the "Facies *Benhami*", and entirely lacking in the "Facies *Dendyi*". I have had no material of the two lastnamed forms.

The three mentioned "Facies" are salmon pink, whereas the fourth "Facies *Cooki*" is snowy white. Some few splinters, a couple of millimeters long could be studied of this form. They are, however, too small to give a basis for further details than those given above, and they give nothing new or aberrent as compared with the "Facies *ramosa*".

## *Errina (Eu-Errina) capensis* HICKSON 1912.

(Pl. IV, Fig. 15.)

1912 *Errina (Labiopora) capensis* HICKSON, On the Hydrocoralline Genus, *Errina*, p. 886, Pl. XCV, Fig. 7, Pl. XCVI, Fig. 15.

Material: Cape of Good Hope (further details concerning the locality are wanting); one 3.9 cm high branch of HICKSON's type specimen.

The branch (Pl. IV, Fig. 15) indicates a subdichotomic branching, and probably the colony is also flabellate and rather robust. Transverse sections of branches and branchlets are a little compressed anterior-posteriorly and accordingly ovate with the larger diameter in the plane of the flabellum. Gastropores and dactylopores are equally numerously distributed on all sides af the branches. — It is in the present species rather inadequate to speak of grooved "spines". Only a very faint, horseshoe-shaped ridge represents the grooved spine of other *Errina* species, and this ridge is moreover only obvious, because the elsewhere rugged structure of the coenosteum surface here fades away, so that the horseshoe appears as a smooth area round the greater part of the dactylopore. Elsewhere the surface of the coenosteum is extraordinarily rugged (Textfig. 16 a), partly also armed with minute spicules which are especially numerous at the mouths of the gastropores. HICKSON (1912) describes the surface as "coarsely granular" and the substance of the coenosteum as "coarsely reticulate." In spite of the remarkably rugged surface, however, the coenosteum is rather hard and compact, and it does not show any spongy features.

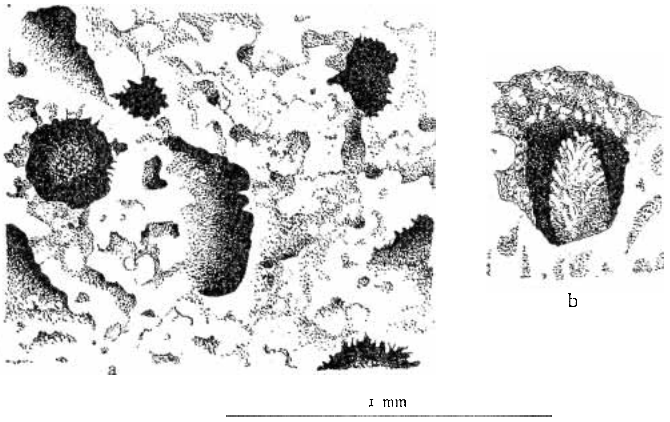


Fig. 16. *Errina (Eu-Errina) capensis.* Cape of Good Hope. — a surface of the coenosteum; the gastrostyle is distinctly seen in the gastropore. b section through a gastropore showing the gastrostyle.

The gastropores reach at their opening a diameter of about 0.3 mm and are always very shallow, a fact also emphasized by HICKSON in his drawing (l. c., Pl. XCVI, Fig. 15), but not mentioned in the text. The shallowness of the gastropore causes the comparatively large and prominent gastrostyles (Textfig. 16) to be very obvious when the colony is examined under the lens. Moreover, the gastropore opening under the microscope exhibits a finely denticulated brim owing to the calcareous spicules which are gathered in a girdle on the gastropore wall at the opening. — The dactylopores are comparatively large and obvious, although the "grooved spines" as already mentioned, must be said to be rather rudimentary.

Ampullae are not seen in the present fragment, nor does HICKSON give any details concerning them.

The species seems to be one of the most characteristic ones in its features and holds a rather isolated place in the genus. Its rudimentary "grooved spines", its shallow gastropores and rather rounded, robust gastrostyles are very characteristic.

## *Errina (Labiata) tenuistylus* n. sp.

(Pl. V, Fig. 17.)

Material: Dr. TH. MORTENSEN's Java—S. Africa-expedition 1929—1930: September 27, 1929, off Tombeau Bay, Mauritius, depth about 150 fathoms, sand and corals; several colonies. — November 5, 1929, off Tombeau Bay, Mauritius, depth about 130 fathoms, hard bottom; several colonies. — November 6, 1929, off Port Louis, Mauritius, depth about 130 fathoms, mud and corals; three colonies (dry).

The flabellate colonies (Pl. V, Fig. 17) which attain heights up to 5 cm with a breadth up to 7 cm, exhibit a rather irregular branching although

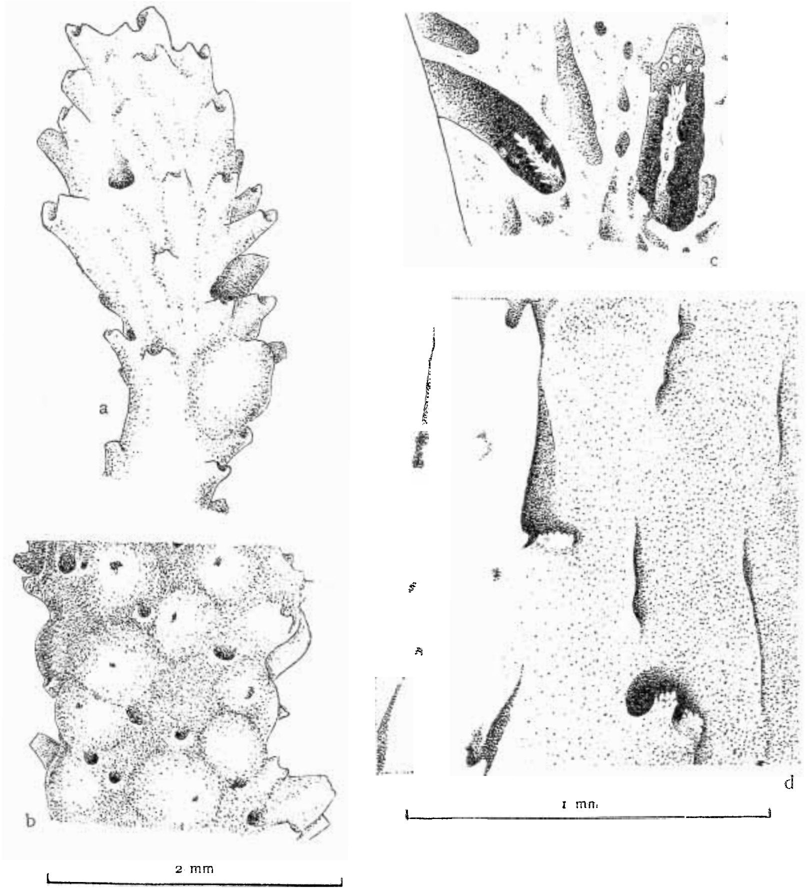


Fig. 17. *Errina (Labiata) tenuistylus.* Off Port Louis, Mauritius, depth about 130 fathoms. — a terminal part of a branchlet. b part of a branch with numerous ampullae. c section through two gastropores showing their gastrostyles. d surface of the coenosteum of a larger branch.

it generally must be designated as dichotomous or subdichotomous; but some of the main branches may again branch in a pennate manner with alternating or opposite secondary branches. Only in one case was an anastomosis observed in the present copious material.

The colonies are generally rough or, better, echinate owing to the numerous and comparatively slender, grooved spines. No difference is observed between an anterior and posterior side of the flabellum. On the other hand there are fewer zooids on the anterior and posterior sides of the branches than along their lateral sides, where the grooved spines moreover are larger, so that the outline of the greater branches is delicately serrate. Transverse sections of branches and stems are quite circular.

The dimensions of the branches increase only by slow degrees from the thin, terminal branchlets to the main branches or stems, and the diameter of the latter seldom surpasses 4 or 5 mm. Dried colonies as well as colonies preserved in alcohol are almost quite white, generally with a greyish purple flush caused by the coënenchyma. Cleaned in sodium hypochlorite the coenosteum is glistening white.

With moderate enlargement the surface of the coenosteum seems to be quite smooth (Textfig. 17 d); under the microscope, however, the surface is minutely granular. Fine pores of the canal meshwork open on the surface, generally in shorter or longer, narrow longitudinal slits or furrows. These small pores are placed in longitudinal rows on the branches, and the branch under the lens therefore gives the impression of being longitudinally striped.

The canal meshwork of the coenosteum is rather widely meshed, and to some degree it recalls that of *Sporadopora* and *Errina spongiosa*. On the other hand the skeletal substance itself is remarkably hard and resistant. The grinding of a branch therefore here demands comparatively more labour than in most species of the *Eu-Errina* group, the skeletal substance of which is looser, often also rather brittle. In accordance with its hard nature the skeletal substance of the present species is more milky semipellucid.

The gastropores have at their opening a diameter of 0.16 to 0.20 mm, and the deeply seated style is only with difficulty seen from without under a lens. The gastropore may be rather deep, and although its axis already at the aperture is inclined about 45° to the surface plane of the branch, and is somewhat arched so that the deeper part of the gastropore tends to be parallel with the branch axis, the gastropores nevertheless in smaller branches penetrate almost to the centre of the branch. No lip is developed at the opening, but in some few cases the gastropore is seated just at the upper side of a dactylopore, the grooved spine of which at first sight can be mistaken for a lip.

The internal wall of the gastropore is smooth (Textfig. 17 c), but generally one finds rather numerous round, warty small protuberances on the wall which in some instances are placed in the lower part of the gastropore round the gastrostyle, in others again mostly in the distal part of the pore. "Tabulae" are not developed. — The gastrostyle is very slenderly needleshaped, in some cases covered with small diverging spicules.

Only one kind of dactylopore is present, always accompanied by a prominent grooved spine turning its groove against the apex of the branch, and thus resembling a water-spout. On the terminal branchlets (Textfig. 17 a) the numerous dactylopores occur crowdedly on all sides. But on somewhat thicker branches (stems) the dactylopores are seated more distantly, and here the grooved spines are only feebly developed on the anterior and posterior sides, whereas they at all events retain their size along the lateral sides of the branches. They gives the branches a characteristic, finely serrate contour when the colony is regarded from the flat side. — The dactylopores show no tendency to gather into clusters but occur always singly and are always "waterspout-like".

Ampullae are found on all sides of the branch (Textfig. 17 a, b). Large female ampullae occur singly and may attain a diameter of 1 mm, protruding on the surface like one fourth of a globe, but nevertheles not causing any obvious disturbance in the arrangement of pores and spines. Male ampullae are smaller, not quite reaching a diameter of 0.5 mm; they are found in crowded assemblies on distal branchlets which in such places give the impression of beeing slightly vesicular, although one cannot say that the ampullae cause any disturbances in the arrangement of pores and spines. Also these small ampullae are visible as low prominences and have in most cases a small, centrally placed circular opening at the summit, whereas the large female ampullae show no such opening in the roof. Male and female ampullae are not found on the same colony.

The gastropolyp has four comparatively well developed tentacles. In the specimens investigated the polyps are strongly contracted, and the gastrostyle projects through the mouth opening. The projecting part of the style is longer than the contracted tentacles. — The dactylozooids have a very long basal adhesive part attached to the inner part of the groove of the spine and to the outer part of the adjoining wall of the pore. The fingerlike free zooid arises from the outer half of the adhesive part; it is strongly contractile, in the present specimens almost always only seen as a low, more or less conical wart on the adhesive part.

Female ampullae contain only one gonophore. Male ampullae have generally simultaneously three or two closely packed gonophores in different stages of development. No blastostyle is present.

The present, very characteristic species does not seem to exhibit any closer relationship with earlier known species of the genus.

### *Errina (Labiata) cervicornis* n. sp.

(Pl. V, Fig. 18.)

Material: Dr. Th. Mortensen's Pacific expedition 1914—16: January 2, 1915, 2 miles E. of North Cape, New Zealand, depth 55 fathoms, hard bottom; one small intact colony (height 3 cm) and 3 fragments of larger specimens.

The colonies (Pl. V, Fig. 18) are evidently branched in one plane, but the more or less dichotomous branching is rather straggling, and this in connection with the finely spinous surface makes the colony resemble miniature antlers of a stag. — No anterior side is discernible, the pores being equally numerous on all sides also of the larger branches. Pores are also numerous on the thickest branches. Grooved spines are well developed on all thicker branches as well as on the smaller ones, and their numbers are only slightly increased on the terminal branchlets. The colonies are robust, the thickest branches have a diameter between 6 and 7 mm; transverse sections of the branches are always circular.

The colonies (in alcohol) are white and attain a snowy white color when treated with sodium hypochlorite. The surface of the coenosteum (Textfig. 18 d) is glistening white and smooth with rows of small pores, openings of canals of the coenenchym canal meshwork. The pores of a row are connected by shallow, irregularly longitudinal furrows, and under the lens the branches therefore exhibit a somewhat irregular, longitudinal fine striation. In some places the course of the striation is so irregular that the structure must rather be characterized as a somewhat coarser vermiculation. — The canals of the interior meshwork of the coenosteum are comparatively wide, and the coenosteum is accordingly rather spongeous, the entire picture very like that of *Errina tenuistylus* as well as of *Errina spongiosa.* The calcareous substance is on the other hand hard and solid, although not quite so hard as in *Errina tenuistylus.*

The gastropores are of varying size and may at their opening attain a diameter of at least 0.75 mm. Their axis is almost straight and forms in the terminal branchlets an acute angle with the surface, whereas the angle in thicker branches amounts to some 60° as to the outer (lower) side of the branch surface. The gastropores are shallow, seldom deeper than 1 mm. The gastrostyle is therefore easily observed from without.

Gastropores are almost without exception seated at the distal side of a dactylopore, and a study of the coenosteum alone gives the impression that gastropores are secondarily developed from dactylopores at the distal side of the dactylozooid. Small gastropores can in fact only be distinguished from dactylopores by aid of the gastrostyle which in many cases might seem to have developed in a dactylopore. Such deceiving, small (young?) gastropores are connected with the largest gastropores by a continuous series of intermediate stages. — Quite exceptionally gastropores have been observed without the proximally seated dactylopore and its grooved spine. In these cases, however, the basal (proximal) side of the opening is slightly raised to a brim or an incipient "lip". In addition one or two cases have been observed where neither dactylopore (and spine) nor rudimentary lip were seen at the gastropore opening.

The gastrostyle (Textfig. 18 b) is well developed, slenderly conical, rather solid, and covered with minute spicules on its distal two thirds. With its base it is fixed to the bottom of the gastropore; on the other hand also some five or six rather robust "spokes" connect the style with the wall of the gastropore between the lower third and the middle of the gastrostyle. Seen from the opening of the gastropore these "spokes" seemingly form a bottom in the pore perforated by a circlet of five or six almost round holes.

Dactylopores are numerous all over the colony and are sometimes roughly arranged in longitudinal rows; as often however, the arrangement is quite irregular. — Only one kind of dactylopore is present. At the proximal side of the pore a grooved spine is seated with its groove

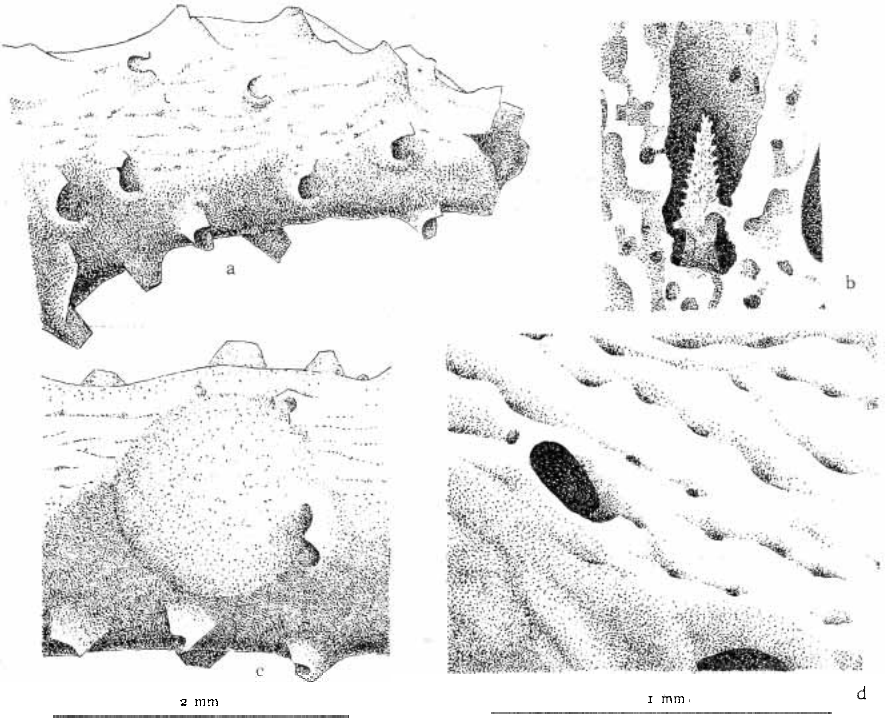


Fig. 18. *Errina (Labiata) cervicornis.* 2 Miles E. of North Cape, New Zealand, depth 55 fathoms. — a end part of a branchlet. c part of a branch with an ampulla. b section through a gastropore showing the gastrostyle. d surface of the coenosteum øf a thicker branch.

accordingly turned against the apex of the branch. In some cases the spine is rather prominent, generally however, it must be termed "medium sized" (Textfig. 18 a, c), and in rare cases only feebly developed. The majority of the spines are always so strongly developed that they give the colony an echinulate appearance.

Ampullae are found on all sides of the branches, but are evidently most numerous on the anterior and posterior sides of the flabellate colony. Although they do not directly form crowded assemblies, they are especially numerous on some parts of the branches, and in other parts numerous cicatrizations evince lively ampulla-formations of the past. — The (female) ampulla may attain a diameter of 1 mm and rises above the surface of the coenosteum almost like a hemisphere (Textfig. 18 c). Its surface is rugged or covered with small, low spines. The ampullae do not generally cause noteworthy disturbances in the arrangement of pores and spines which are commonly found along their periphery. Only in few cases were dactylopores observed some way up on the ampulla roof.

The several cicatrizations seem to indicate that the roof of the ampulla is ruptured when the larva breaks away, and that the surface of the coenosteum afterwards regenerates and reassumes its earlier "normal" appearance.

The preservation of the soft parts is very deficient. It has therefore not been possible to state with certainty, whether the gastrozooids have tentacles. The dactylozooids have no special adhesive, basal part, but are evidently fixed directly to the bottom of the dactylopore by the base of the fingershaped part. — Female ampullae develope one large planula, and no remainder of a spadix or indication of a secondary gonophore could be seen.

The present species also holds a rather isolated position in the genus, although it exhibits a remote likeness to *Errina macrogaster* v. Marenzeller 1904.

### Genus *Paraërrina* n. gen.

The flabellate colonies are irregularly dendritically or subdichotomously branched. Gastropores and dactylopores are irregularly scattered all over the stems and branches. The gastropores of the stem and main branches have simple, circular openings, whereas proximal collars may be found at their openings on the branchlets, so that the opening here is obliquely turned against the apex of the branchlet. The dactylopores of the end parts of the branchlets have in many cases low, almost rudimentary grooved spines at their margin with the groove facing the apex of the branch (waterspout-like). Elsewhere the openings of the dactylopores are simple, without spines. Well developed gastrostyles and dactylostyles are present, the latter fixed to the side wall of the dactylopore. Superficially seated ampulae give rise to prominent swellings; they occur singly. — The gastropolyps lack tentacles or have rudiments of tentacles. The dactylozooids have a short adhesive part. Female ampullae contain one gonophore and no blastostyle, male ones a large blastostyle carrying gonophores all over the surface.

The preliminary investigations of the only species was puzzling. Under the lens it at first seemed to be a slenderly built *Sporadopora*. But the utmost and very slender branch ends did not fit into the picture of this genus, and seemed to point much more towards the *Labiata* group of *Errina* on account of the rudimentary "water-spouts". Further investigations revealed well developed dactylostyles and thus seemed to indicate a connection with *Errinopora*. However, the last mentioned connection must be more remote, the structure of *Errinopora* in every respect otherwise indicating relations with the *Eu-Errina* group of *Errina*. Moreover this genus evidently exhibits a coordination of dactylopores and gastropores derived from cyclosystems (see Part I, p. 99 *Protoerrina*). *Paraërrina* on the other hand shows no trace whathever of such coordination, the features entirely agreeing with *Sporadopora*. But here again the occurrence of dactylostyles differs.

Moreover the finer structures of the colonies differ so markedly from the last named genus in so many details that a closer relationship between these two genera appears rather problematical.

The differences as against *Errina* (the *Labiata* group) may seem slight, and it is possible that future investigators will amalgamate the two genera. With our present knowledge, however, the *Errina* species otherwise form two so compact and inter se closely connected groups that it is natural to place the present rather isolated species in a genus of its own.

## *Paraërrina decipiens* n. sp.

(Pl. V, Fig. 19.)

Material: Dr. TH. MORTENSEN's Java—S. Africa-expedition 1929—30: September 27, 1929, off Tombeau Bay, Mauritius, depth about 150 fathoms, sand and corals; several colonies. — November 5, 1929, off Tombeau Bay, Mauritius, depth about 130 fathoms, hard bottom; several colonies. — November 6, 1929, off Port Louis, Mauritius, depth about 130 fathoms, mud and corals; a couple of colonies (dried),

The rich material from September 27 also contains one complete colony which has been selected as type (Pl. V, Fig. 19), although several other specimens evidently have been much larger. The mentioned colony is fanshaped, 5 cm high and 6.7 cm broad; the stem has at the base a diameter about 9 mm. — The largest fragment from November 5 is 5.5 cm high and 10 cm broad, and the basal diameter of the stem only 8 mm; the upper end of a broken main branch has a diameter of 3 mm. From the same locality one 6.5 cm long branch with a basal diameter of only 4.5 mm is present.

The colonies are flabellate, often a little concave along one side, and entirely irregularly branched; the branches are also often irregularly bent. The branching is almost always dense, but anastomoses have not been observed. Except for the concavity no difference is found between an anterior and a posterior side of the flabellum. Transverse sections of stems and branches are generally circular.

The surface of the coenosteum gives an almost velvetlike impression, and under the microscope a compatively large-patterned reticulation is observed with shallow furrows irregularly crossing each other in all directions (Textfig. 19 d). In the crossings fine pores are often observed. Grindings show the usual meshwork of the skeleton of the Stylasteridae, and the skeletal substance is not so semipellucid as in the *Labiata* group of *Errina* but much more in agreement with the *Eu-Errina* group. — The colonies (in alcohol) are ivory white, some dry specimens white with a touch of green (the depth of the localities indicates that this green hue cannot be caused by algae).

The gastropores are small with opening diameters generally up to some 0.2 mm; the apertures are simple and circular. Near the apex of the branchlets the lower (proximal) brim is usually slightly raised like an oblique collar, so that the aperture here is turned obliquely upwards. The gastropore has smooth walls and is remarkably shallow, generally not more than 0.5 mm deep, and accordingly no trace is observed of tabulae nor of larger canals in the deeper central layers of the branches communicating with the gastropores. Even a superficial examination reveals the well developed gastrostyles (Textfig. 19 b, d). The gastrostyle (Textfig. 19 c) has a short and broad conical or almost globular body distally armed with comparatively large, bristling and often branching spines.

Only one kind of dactylopore is present. On the distal part of the terminal branchlets the pore is accompanied by a low grooved spine or, better, its brim is raised to a low, horseshoe-shaped collar, the open side of which faces the apex of the branch ("water-spout" like). Further down the branchlet and on all stems and larger branches the openings of the dactylopores are simple with no trace of grooved spines. Dactylostyles are present and fixed to one side of the pore wall (see Textfig. 19 d).

It is necessary to emphasize that it is in many cases in the present species exceedingly difficult to distinguish small (young?) gastropores from dactylopores. Evidently new gastropores (and zooids) are incessantly formed in the colonies also on older branches, and as far as can be be seen, the young gastropores have the same dimensions as the dactylopores. In specimens cleaned with sodium hypochlorite the mark of distinction is only whether the style is centrally seated or fixed to one side of the pore; but also this feature is often rather intricate on an external examination alone.

Ampullae are formed on all sides of stem and branches. The female ones are found singly as obvious swellings attaining the shape of a hemisphere with a diameter up to 2 mm (Textfig. 19 b). The surface of the ampulla is smooth or, under the microscope, with the same openly-meshed reticular structure as the surface of the branches otherwise. In some cases the reticulation of the ampulla may be a little more obvious, its furrows being more accentuated. — Male ampullae are smaller, and so deeply immersed that they are almost quite invisible on superficial investigation.

In most cases the branches of the present species show several obvious swellings which at first may be taken for ampullae. Special caution is demanded here. In very many cases the swelling has a narrow elliptical slit at the summit, the larger diameter of which may amount to 1.5 mm. Such swellings are due to parasitic Cirripeds *(Lithoglyptes)* which evidently prefer *Paraërrina decipiens* as a residence, no such galls being found on the very numerous colonies of other species of Stylasteridae collected in the same localities (*Stylaster crassior* and *asper*, *Conopora tenuis* and *major*, *Pliobothrus seriatus* and *Errina tenuistylus*). It seems probable that

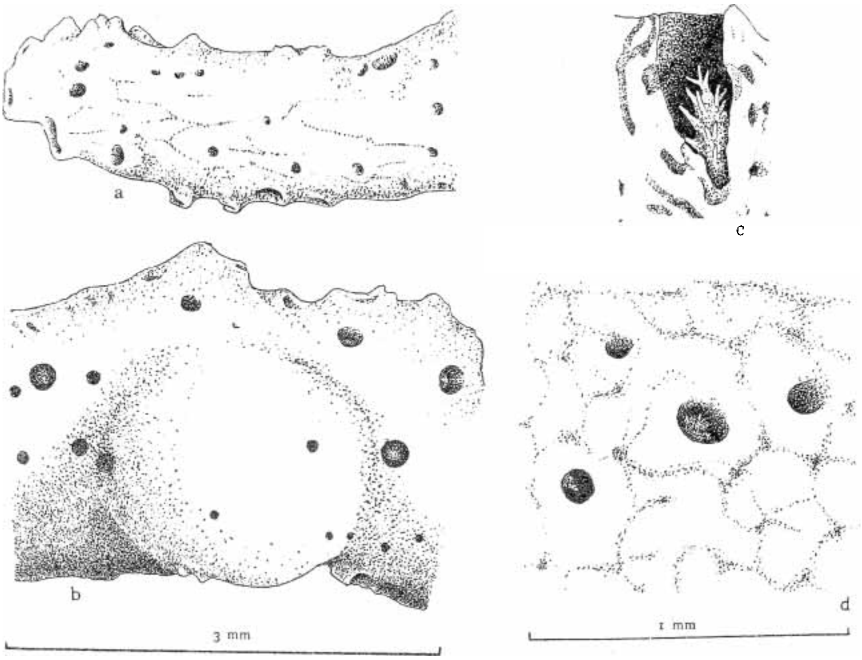


Fig. 19. *Paraërrina decipiens.* Off Port Louis, Mauritius, depth 130 fathoms. — a end part of a branchlet. b part of a branch with an ampulla. c section through a gastropore showing the gastrostyle. d surface of a branch showing the reticulate structure; styles are distinctly seen both in the central gastropore and in the dactylopore to the left.

we here face a commensalistic or symbiotic connection of the same kind as that between the *Conopora* species and their worm (see Part I, p. 86).

The gastrolyps are quite small and generally devoid of tentacles; but in some few cases microtome series indicate that one to four irregularly placed, rudimentary tentacles may be present. Also the dactylozooids are small and have a short and strongly contractile part originating from the middle of a short adhesive basal piece fixed to the side wall of the dactylopore.

Female ampullae only contain one gonophore, and no trace of a secondary gonophore could be discovered in gonophores with developing larvae. Male ampullae on the other hand contain a rather large blastostyle carrying a great number of gonophores all over its surface; the single gonophore is here small (see also Textfig. 29, p. 83).

## Zoogeographical remarks on the Stylasteridae

It has in earlier days been a general assumption that the Stylasteridae like the other Hydrocorals should be so to say altogether bound to the coral reefs. Towards the end of the last century, however, the marine explorations revealed that many of the species live far away from coral reefs and under quite different conditions, and through MOSELEY's reports of the "Challenger" results (1878, 1881) it was moreover demonstrated that several species of the Stylasteridae are mainly confined to deeper strata of the oceans, where coral reefs or banks are absent. Similar results had also previously been arrived at by the American Gulf Stream expeditions; but they had passed by rather unheeded, because they had been published in reports of POURTALÈS especially dealing with the stony corals of deeper waters on the whole.

Although Stylasteridae had already been masterly described from Norwegian waters by J. E. GUNNERUS (1767) and later on again been mentioned several times in Norwegian literature, it had also for long been assumed that the family must be looked upon as a special and characteristic component of the animal world of warmer, and especially of tropical seas. Little by little, however, different deep sea expeditions to some degree altered this point of view. Also now, it is true, we hold to the view that the majority of the Stylasteridae belong to temperate and warmer seas. But the numbers of species inhabiting colder parts of the oceans and their deeper strata have been increased remarkably by the investigations of later years, especially in the northern parts of the Pacific region.

During the sixties and seventies of the last century the American Gulf Stream explorations showed that the waters round Florida and Cuba are the home of several species of Stylasteridae, and that the Antillean region evidently must be characterized as the richest part of the Atlantic area. POURTALÈS (1871) mentions no less than 22 species alone from this region, whereas the rich collections brought home by the "Challenger" from all parts of the oceans according to MOSELEY (1881) only amounted to 15 species. — In 1905 HICKSON and ENGLAND mention as many as 23 species from the "Siboga" expedition in the Malayan archipelago, and this together with our previous knowledge of some more species from the same region was the basis of the assumption, that the Indo-Malayan waters should be the specifically richest area. But in 1938 FISHER published his report mentioning no less than 24 species from the northern parts of the Pacific Ocean to which numbers the present collections add two or three more, and it might thus seem as though we should here face the centre of the Stylasteridae and their greatest numbers of species in a limited region.

Howsoever this may be, we shall have to reckon with many alterations in the geographical details with increasing knowledge. Many parts of the oceans are all but unexplored at present, especially concerning the bottom fauna, and even in so thoroughly investigated territories as the western coast of Norway, surprising novelties may turn up like the unexpected find of *Pliobothrus symmetricus* Pourtalès made in recent years by Dons (1939). Nevertheless a survey of the available data is apt to give us some biogeographical main lines concerning the Stylasteridae on the whole.

A first glance at the accompanying charts shows us the obvious fact that no find of Stylasteridae has been reported from the strictly polar oceans. This cannot be an accidental circumstance, when we recall the intensive studies of the northern polar seas carried out during later years, especially by Russian expeditions which moreover have paid special heed to the animal world of the sea bottom.

The complete lack of Stylasteridae in the polar seas did not seem surprising as long as it seemed right to insist on the assumption, that the group should throughout belong to rather temperate and warmer living conditions. However, what today makes the phenomenon so puzzling, are the new data added to our knowledge by the northernmost Pacific waters, where more species of Stylasteridae even live in temperatures below 0° C. It is accordingly evident that the temperature alone does not account for their absence in the polar seas. They must be barred by other factors; but we cannot at the present discern by which. And although the genera forming the utmost outposts towards the northern and southern polar seas are different, the barriers most likely seem to be the same in both cases.

Starting with the Stylasterinae the extensive genus *Stylaster* is by far the most generally and widely spread genus of the Stylasteridae (Textfig. 20), and the gap in the distribution which seems to exist in the Indian Ocean, will probably be bridged by more detailed investigations of the fauna of the ocean floor of these waters. — The genus has evidently its main weight on the northern hemisphere. (It must here be noted that it has been impossible to give all the single finds and localities especially in the Malayan Archipelago and in the West Indies, and that also several finds in the Sagami Sea near Japan have been summarized in the chart.)

The *Eu-Stylaster* group has evidently its greatest numbers both of species and of individuals in the tropical seas, and probably a thorough investigation would reveal a rather common occurrence of the group on all Pacific coral reefs. In the Malayan Archipelago as well as in Australian waters species of the *Eu-Stylaster* group are seemingly the only representatives of the genus.

Bathymetrically the group shows a great elasticity, ranging from the lower limit of the tidal zone and at all events down to some 1900 m depth; but the majority of the species evidently prefer depths which do not surpass 1000 m. It is only in tropical waters that a few species of

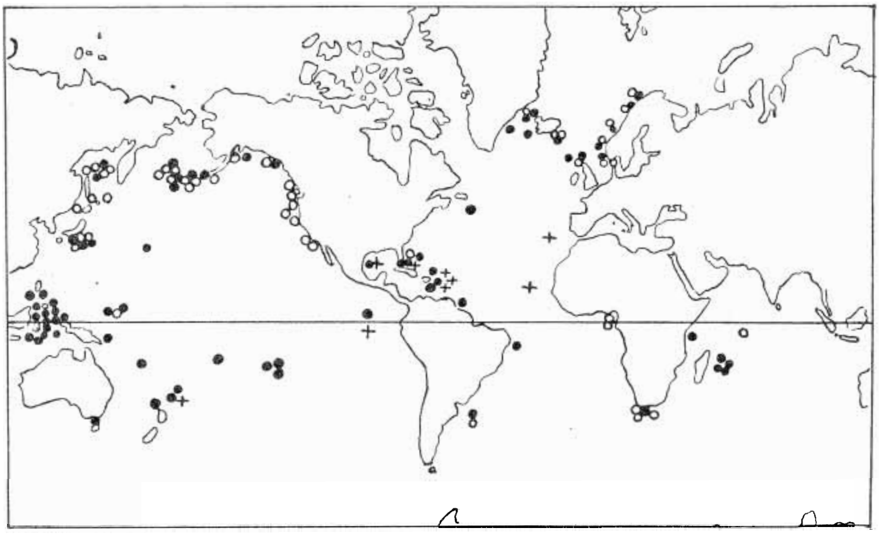


Fig. 20. Distribution of the Stylasterinae; the genus *Stylaster*.
● *Eu-Stylaster*. ○ *Allopora*. + *Stenohelia*.

*Eu-Stylaster* may live in the upper littoral zone bound to the coral reefs; but also here the bulk is met with somewhat deeper.

The species belonging to the northernmost parts of the Pacific Ocean have only been found in somewhat greather depths. Similar features are exhibited by the group in Atlantic waters also, as far as the present data indicate, but it seems only to count few and scattered representatives in the littoral strata of the Antillean region. On the other hand, the only representative met with to the north of the submarine ridges of the North Atlantic has its main habitat there between 150 and 4—500 m depth, and it seems thus to live a trifle shallower here than the representatives of the group in the northern Pacific Ocean. This must evidently be due to its preference of somewhat higher temperatures than its Pacific allies.

According to the available data the *Allopora* group must decidedly be characterized as mainly belonging to the northern hemisphere, although a few scattered representatives have also been met with in the southern Atlantic Ocean (off the mouth of Rio de la Plata, and at the coast of South Africa, see Textfig. 20). A survey of the species reveals that their majority belongs to the Pacific regions, and from the Antillean region and northwards in the Atlantic Ocean hitherto only one species has been observed, viz. *Stylaster (Allopora) norvegicus* (Gunnerus).

The bathymetrical range of the *Allopora* group is not quite so extensive as that of the preceeding group. The *Allopora* species live from the tidal zone and down to about 1400 m depth. But the great majority of them is met with in depths between 100 and 500 m. It is in this connection of interest to note that all the shallowest finding places are situated along the American coast of the Pacific Ocean from California to

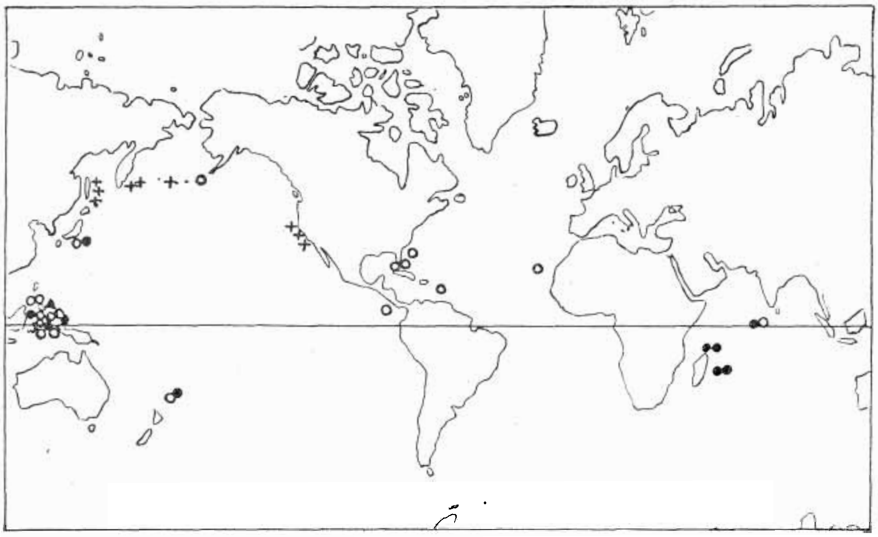


Fig. 21. Distribution of the Stylasterinae (except the genus *Stylaster*).
○ *Crypthelia*. ● *Conopora*. + *Errinopora*. ▲ *Astylus*.

Alaska; in these waters some of the species have even been found at the lower limit of the tidal zone. Also another, although slighter difference in comparison with the Atlantic Ocean is obvious. The only north Atlantic *Allopora* species may, in Norwegian waters, exceptionally be met with as shallow as in 80 m depth (DONS 1939); but its main occurrence is otherwise here as in the Antillean region below 150 m, and thus concordant with its habitat in the northern Pacific Ocean. — Contrary to the *Eu-Stylaster* group no *Allopora* species has been found in tropical waters in the uppermost littoral bottom region adjoining the tidal zone.

The *Stenohelia* group of *Stylaster* at last is evidently bound to somewhat deeper strata of warmer waters, the straggling finds ranging from 100 to 1100 m depth. Comparatively many finds are located in the tropical and warmer temperate parts of the Atlantic Ocean north of the equator; but two finds in the southern tropical and subtropical parts of the Pacific Ocean contradict an assumption, that the group should be exclusively Atlantic. — The remarkably discontinuous distribution of the group (see Textfig. 20) may possibly hold good. But it seems more probable that further investigations of the fauna of the sea bottom in corresponding depths of the entire tropical and subtropical region will result in a picture of a more continuous distribution of these evidently remarkably rare species.

A similar straggling occurrence seems to be characteristic also of other deeper living genera. Thus the related genus *Crypthelia* in many ways recalls *Stenohelia* (see Textfig. 21). According to the available data *Crypthelia* is the genus of the Stylasteridae which is bound to the deepest habitat. Its bathymetric range is from 240 to 3000 m depth, and most of the finding places are situated below 5 or 600 m. Until quite recently

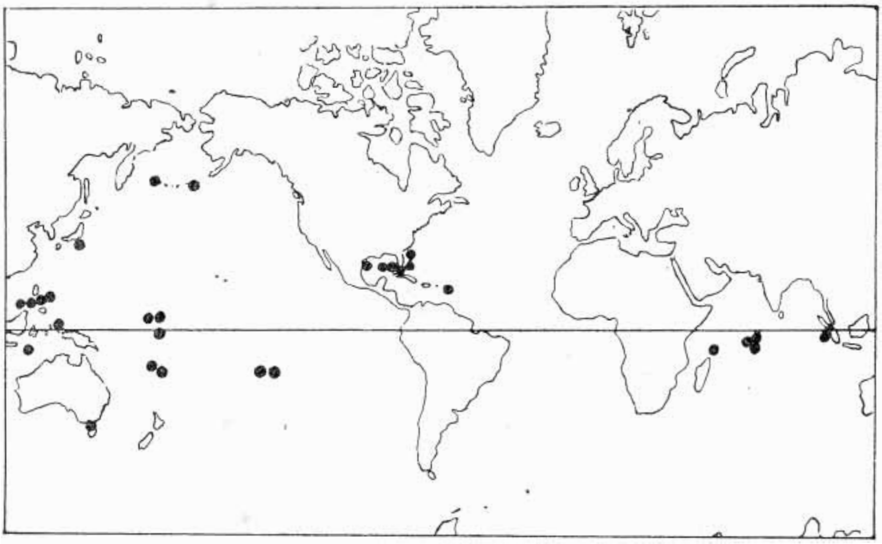


Fig. 22. Distribution of the Distichoporinae, genus *Distichopora.*

***Crypthelia*** has moreover been looked upon as an entirely tropical genus, and it was a great surprise when FISHER (1938) reported a species from the cold area at the Aleutian Islands. Otherwise the genus has a circumterrester occurrence; but according to the present data no continuity seems to exist between the Atlantic and Indo-Pacific habitats.

Zoogeographically nothing can be said concerning the genus *Astylus* which is only represented by one single find off the Meangis Island in some 1000 m depth. — *Conopora* has a bathymetrical range from 100 to 1000 m depth, although only three species have as yet been discovered. The map (Textfig. 21) shows that the genus is restricted to Indo-Pacific waters from Madagascar to Japan and the Kermadec Islands, but it has not been observed at the American side of the Pacific Ocean.

The genus *Errinopora* exhibits an even more restricted habitat; it has hitherto only been found in the cool waters of the northern Pacific Ocean (Textfig. 21). As yet four species have been found, and at all events two of them seem to be of rather common occurrence, one in northern Californian waters, the other in the Ochotsk Sea. Bathymetrically the genus has a comparatively narrow range from 50 to 550 mm depth. It is moreover remarkable that *Errinopora* must rather be characterized as a cold water genus. It prefers altogether lower temperatures than the other genera of the Stylasteridae, and three of the species even have their abode in temperatures below 0° C.

The only genus of the Distichoporinae, *Distichopora,* has its main occurrence in the tropical seas (Textfig. 22). The chart reveals a remarkable discontinuity in the distribution. The genus is continuously distributed in Indo-Pacific waters from the Providence Island (north of Madagascar) and

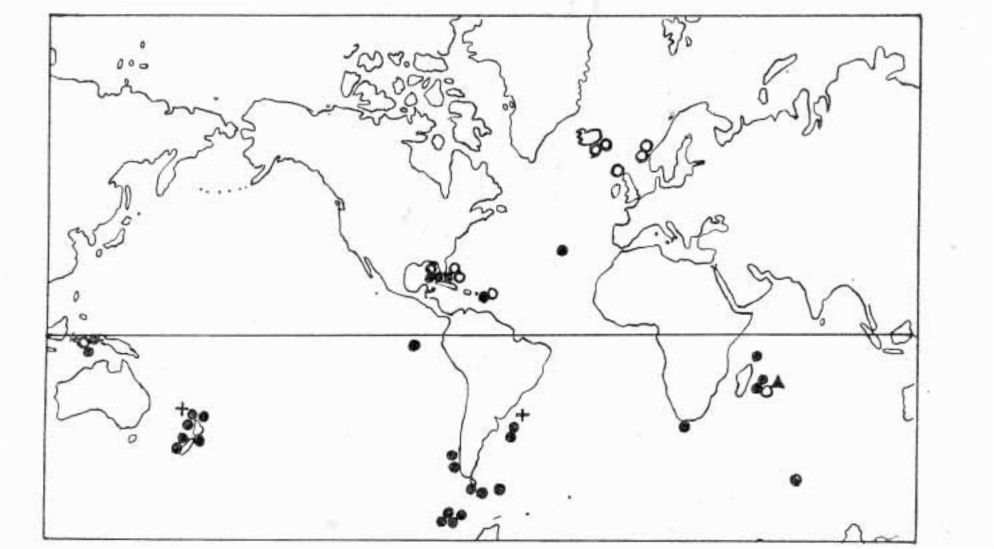


Fig. 23. Distribution of the Sporadoporinae.
● *Errina.* ▲ *Paraërrina.* + *Sporadopora.* o *Pliobothrus.*

eastwards through the entire Indo-Malayan Archipelago in the insular kingdom of coral reefs in the tropical Pacific Ocean, although detailed specifications as to the finding places at present are rather scarce. On the other hand we in many places in the literature find general remarks, that especially "*Distichopora violacea*" is generally met with on the Pacific coral reefs. — From this central field of distribution one species, viz. *Distichopora borealis* Fisher, has emancipated itself and occupied a habitat which at all events stretches from Japonese waters (Sagami Sea) to the Aleutian Islands, and in the last named region the species even penetrates into the cold area.

The above mentioned extensive and continuous Indo-Pacific area of distribution seems effectively isolated from the other, far more restricted habitat of the genus in the Central American, Atlantic region, where no less than 5 species have hitherto been recorded, none of them identical with any of the Indo-Pacific species. We shall not here try to enter into a theoretical discussion concerning the reason of this curious discontinuity, but only quite incidentally point out that it must be of very old date.

Bathymetrically *Distichopora* has an extensive range from the tidal zone and down to about 1100 m depth; but most of the finds have been recorded from depths of less than 500 m. Also in bathymetric respects we must note a difference between the two mentioned habitats. Whereas some of the species of *Distichopora* evidently are a rather constant feature of many Pacific coral reefs, no Atlantic species has been recorded from the littoral waters. On the other hand also most of the Pacific species live somewhat deeper, and it may be accidental that the deepest record as yet is from the Antillean region. In the Pacific Ocean the finding places at the Aleutian Islands show greater depths than most localities of the warmer parts of the ocean.

The Sporadoporinae exhibit on the whole a more straggling occurrence (Textfig. 23). We can here pass by the genus *Paraërrina* which has only been found once, viz. at Mauritius in a depth of 250 to 300 m. — The two single finds of *Sporadopora* are rather puzzling. Hitherto the Atlantic locality off Rio de la Plata in 600 fathoms depth stood quite isolated; but to this another finding place is now added near the northern point of New Zealand in only 65 fathoms depth. It is also with this genus more suitable to await further details before the zoogeography is discussed.

The genus *Pliobothrus* with its three species has a bathymetrical range from 80 to about 1100 m depth. The best known species, *Pliobothrus symmetricus* Pourtalès, is a characteristic inhabitant of the northern Atlantic Ocean from the Antillean region and to the Norwegian west coast, i. e. a characterform of the Atlantic current. The other species *Pliobothrus tubulatus* (Pourtalès) had also only been found in the Atlantic Ocean, and it was therefore surprising that the "Siboga" expedition brought home a small fragment from the Indo-Malayan region which seems to belong to this species. Now a third, rather aberrant species has in the present report been mentioned from the waters around Mauritius, and it seems thus rather probable that thorough investigations will reveal a yet greater habitat of the genus.

The genus *Errina* holds a zoogeographic position of its own in comparison with all other genera of the Stylasteridae. It is decidedly a southern genus, and the only one which penetrates southwards into the subantarctic parts of the oceans (Textfig. 23). Only in the Atlantic Ocean does the genus pass northwards over the equator, some few finds having been reported here from the Antillean region and one single find near the Azores. Judging from other genera alone we might have believed that the regions at the southern end of South America had been totally neglected by the investigators; but the numerous localities of *Errina* just here show that this "gap" of the other charts must really be due to the scarcity or even lack of other Stylasteridae in these waters, and in the same way we also find that *Errina* is almost the only genus occurring in the waters of New Zealand. Sporadically representatives of the genus have been met with in the Malayan Archipelago and in the neighbourhood of Madagascar; but the bulk of the species evidently builds a characteristic feature of the animal communities of southern temperate waters.

Bathymetrically *Errina* ranges from 4 or 5 m and down to depths of some 1100 m. It is of interest to note that the shallower localities are situated in the more southern parts of the habitat, i. e. around New Zealand, at the southernmost part of South America, and near the Kerguelen Island, whereas the localities situated in more tropical waters all over belong to the deeper half of the habitat.

A short review concerning the species of the Stylasteridae gives us at once a strong impression, that the overwhelming majority of them have rather limited habitats. In the deeper living species this may of course depend upon their special demands to living conditions. Evidently most of them prefer places where strong currents run over a hard bottom, i. e. places where dredging operations are difficult and only too commonly little successful. Many years experience with the dredge along the Norwegian coast with special aim at Hydrocorals has taught me that the colonies mostly occur in smaller assemblies in narrowly limited, straggling localities, and that the search after them thus is very much of a chance operation. Even in regions where the zoogeographer would designate the species as "common", the collector will accordingly register them as "rare". Altogether very many of the species have therefore only been found in one or very few localities.

On the other hand a few of the species have been collected in so many localities that we have a sufficient basis for geographical conclusions. And it is also then evident that most of the species must be regarded as forms characteristic of narrower limited areas. A few examples will illustrate this: It has already earlier been mentioned that *Pliobothrus symmetricus* Pourtalès is a characteristic species of the Atlantic current from the Antillean region to the west coast of Norway; *Stylaster roseus* (Pallas) has almost the same distribution, but does not penetrate into the North Atlantic Ocean north of the submarine ridges between Scotland and Iceland—Greenland. *Errinopora stylifera* (Broch) seems to be restricted to the Ochotsk Sea, and along the Pacific coast of North America *Errinopora pourtalesii* (Dall) and *Stylaster porphyra* (Fisher) are evidently characteristic species of the Californian region. *Distichopora violacea* (Pallas) is a characteristic and common partner of the coral reefs in all tropical Indo-Malayan waters, but does not seem to live outside of this region.

Although some of the genera have a more or less clearly pronounced circumterrester distribution, only very few species are common to the Pacific and Atlantic regions, and in a species like *Stylaster eximius* Kent which has been located in the Antillean region and is widely distributed in the Indo-Malayan waters, special races or forms have evidently developed in the two at present distinctly disconnected habitats.

The most interesting geographical features are probably those observed in *Stylaster gemmascens* (Esper) and *Stylaster norvegicus* (Gunnerus), both of which evidently belong entirely to the northern hemisphere. (A find of the first named species has been reported from the Indian Ocean; but the record seems very problematic and needs a careful revision of the specimens.) Disregarding the single doubtful record, we can say that the two species are characteristic of the northern Atlantic Ocean from the Antillean region and northwards to northern Norway; they are in other words character forms of the region of the Atlantic current. On the other hand both species are also distributed in the northernmost parts of the Pacific Ocean, and although they are here represented by races or forms which show some slight differences from the Atlantic stocks, they doubtless belong to identical species. The two at the present time disconnected habitats must accordingly in earlier times have been continuous, and at that time their habitats have probably also comprised parts of the northern polar seas, where the temperatures then must have been somewhat higher than in our time. These questions have been more thoroughly dealt with in earlier papers (Broch 1935 b, 1937).

## On the structure and development of the gonophores of the Stylasteridae.

Investigations of the gonophores of the Stylasteridae have first been published by Moseley (1878, 1881) in his fundamental works on the Hydrocorallinae of the "Challenger" expedition. In these publications he finally establishes the Hydroid nature of the Stylasteridae, and although he does not particularly state it, the gonophores also seem to play a part in the starting point of his reasonings. The simple structure of the male gonophores and the specialised spadix of the females, however, did not quite fit into the actual knowledge of his time concerning the Hydroid gonophores. Nevertheless, considering the technic of that time, his results are admirable and indeed fundamental, and he also contributed much to our knowledge of the development of male gonophores of *Astylus* and female gonophores of *Errina*, *Pliobothrus*, and *Crypthelia*.

The next studies of the gonophores were made by Hickson (1890, 1891, 1892) who after examinations of *Allopora*, *Distichopora*, and *Errina*, came to the result that the Stylasterid gonophores are peculiar and primitive formations and without any trace of an entocodon. Therefore he arrived at the conclusion, that they are not medusoid, and that they accordingly give no evidence of a relation to the Hydroids. Whereas Moseley speaks of a spadix in the gonophores, Hickson especially in the female gonophores speaks of a "trophodisc" judging it to be a special feature of the Stylasteridae not homologous with the spadix of the Hydroids. However, in a later paper (1915) he emphasizes that later investigators may come to other results, and tells us on this occasion also that his old master, Moseley, did not agree with him in his views concerning the gonophores of the Stylasteridae.

In a report of north Atlantic Stylasteridae, Broch (1914) gives some informations concerning the gonophores of *Stylaster* (both *Eu-Stylaster* and *Allopora*) and *Pliobothrus*, demonstrating the conformity with Hydroid gonophores except in the males of the last named genus which to some degree seems to hold a position of its own. However, the development of the gonophores is unknown in *Pliobothrus*.

Lastly the most important study of the gonophores of the Stylasteridae has been made by HICKSON's collaborator HELEN M. ENGLAND (1926). She investigated *Stylaster filogranus*, *Stylaster (Allopora) nobilis*, and *Distichopora violacea*. ENGLAND succeeded in finding also the earliest developing stages of the first- and lastnamed species and arrives at the conclusion that primary gonophores are always formed at the very surface of the colony and not, as HICKSON maintained, in coenosarcal canals below the surface. This primary formation is by ordinary growth of the corallum and by an especially rapid growth of the surrounding zone included in an "ampulla". Later on, secondary gonophores often bud in the same ampulla, but their development may to some degree differ from that of the primary one, although hardly principally. ENGLAND also gives a new interpretation of the apical formation of male gonophores which, according to HICKSON, gives rise to a "seminal duct". She explains it as an entocodon, and like BROCH she arrives at the conclusion that the Stylasterid gonophores principally fully agree with Hydroid gonophores. Also the "trophodisc" is a spadix.

A special interest is attached to ENGLAND's discovery of the formation of a blastostyle which in *Stylaster* is transformed into the gonophore itself (the name "blastostyle" is hardly proper in this case), but which in *Distichopora* remains as a separate formation from the basal part of which the gonophores bud, the primary as well as later gonophores. In this case a real blastostyle is thus present.

Additional investigations of the Stylasterid gonophores are thus desirable, and although the present material has not been collected for this purpose and in several cases is rather unsatisfactorily preserved, some information could be brought together. Most of the specimens which have not been dried, have only been put into alcohol. Some of these specimens nevertheless unfortunately also seem to have been halfway dried before they have been put into alcohol, but in other cases many details could be studied. Only in one case have Russian investigators fixed specimens of *Stylaster scabiosa* especially for histological purposes.

The details given in the following about each of the species which have been tolerably preserved, are based on series of microtome sections of decalcified specimens, often also supplemented by thicker celloidin sections. At the end of the chapter a short review is given of the present state of knowledge concerning the gonophores of the Stylasteridae on the whole.

## *Stylaster.*

Owing to the nature of the material only more casual observations could be made. It is best to commence with the male gonophores which are the most primitive ones.

*Eu-Stylaster*: In *Stylaster gracilis* gonophores of both sexes have been studied. In advanced stages of male gonophores, well developed entocodons are present which during the ripening of the sperm cells are transformed to efferent ducts opening into the coenenchym canals of the branches. — In *Stylaster profundiporus*, where young male ampullae normally contain two, older ampullae mostly four gonophores, the formation of an entocodon and a successive transformation of this into an efferent duct was again observed. Also here the duct opens into the surface canals of the branch.

Like most other species also *Stylaster asper* has several male gonophores in different stages of development in each ampulla (Textfig. 24 a). The gonophores, however, show no trace of an entocodon, and accordingly also no efferent duct is developed. Evidently the ripe gonophore rupture and empty into the ampulla which has a small aperture on the summit (see Part I, p. 37, Textfig. 9 d).

*Stylaster dentatus* again gives evidence of the function of the transformed entocodon as a seminal duct (Textfig. 24 b). The state of preservation was here so good that it is possible to discern the different cell layers with certainty. In this species there is generally no direct passage through the ampulla roof, but the duct usually communicates with neighbouring coenenchym canals of the branch.

*Allopora*: *Stylaster carinatus* has two or three gonophores in the remarkably small ampullae, and the gonophores therefore lie closely packed and attain varying shapes according to their site. Older gonophores have a distinct entocodon, and in almost ripe gonophores it protrudes faucet-like. The formation is here only exceptionally apical, generally more or less displaced along one side.

*Stylaster nobilis* has already been studied by ENGLAND (1926) who has given two drawings (l. c. Textfig. 10 and 11). She repudiates the interpretation of the apical formation as a seminal duct, although her Fig. 10 not only shows the entocodon clearly, but also demonstrates a central opening in the ectodermal supporting lamella. Fig. 11 has evidently been drawn after a somewhat oblique slide, no opening being indicated in the lamella through which the spermatozoans might escape into the canal; also the latter is without lumen in the drawing, and thus not hit centrally (or possibly insufficiently well prêserved). — Although the present material has only been preserved in alcohol, intermediate stages between the two figured by ENGLAND evidently demonstrate that the apical entocodon formation is transformed into the same efferent duct as in several other *Stylaster* species, leading into coenchym canals. Although no opening as yet is formed in the supporting lamella, the arrangement of the cells show the formation of a "stopple" like that observed in several *Eu-Stylaster* species just before the perforation (Textfig. 24 c). In the gonophore figured the spermatozoans are not yet quite ripe (although a little more advanced than in ENGLAND's Fig. 10), but the formation of the duct is already obvious.

In *Stylaster bocki* neither entocodon nor efferent duct are present. It is in this connection noticeable that the ampullae here lie quite superficially

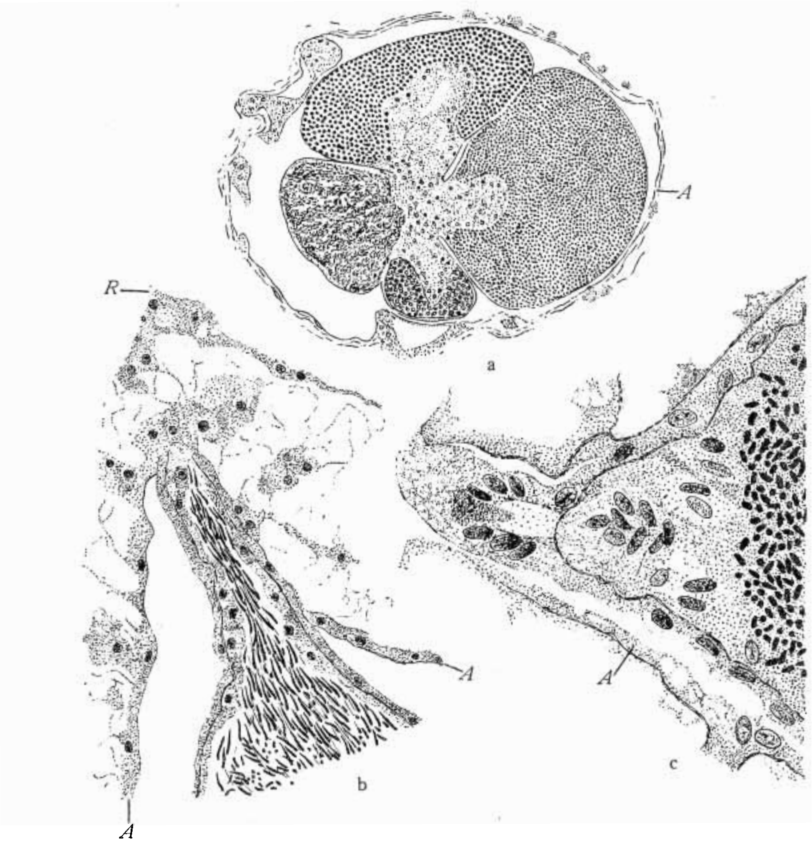


Fig. 24. Male gonophores of *Stylaster*. — a transverse section of an ampulla of *S. (Eu-Stylaster) asper* with four gonophores in different developmental stages. b apex of a ripe gonophore of *S. (Eu-Stylaster) dentatus*. c apical part of an almost ripe gonophore of *S. (Allopora) nobilis*; the arrangement of the nuclei of the entocodon seems to indicate the formation of a "stopple". (A ectodermal epithelium of the ampulla; R surface epithelium of ampulla roof. — a × 150, b × 540, c × 840.)

on the branches, the assemblies forming obvious "cushions" on the surface, and some of the ampullae show minute openings in the roofs. The features remind us of *Stylaster asper* (cf. above). — A well developed spadix is found in half-ripe gonophores here as elsewhere. The spadix is also in *Stylaster bocki* generally simple; in some cases, however, it forks into two branches reminding us of the spadix of male *Errinopora*.

Lastly well preserved *Stylaster scabiosa* have been studied. Here male gonophores show no trace whatever of an entocodon, and no duct seems to be formed. Although the ampullae here are found near the surface of the branch, no young gonophore was found at the very surface. It must be remarked, however, that quite small, primary gonophores were not observed with absolute certainty. — The young male gonophores of *Stylaster scabiosa* are of interest in comparison with the preceding species. The spadix

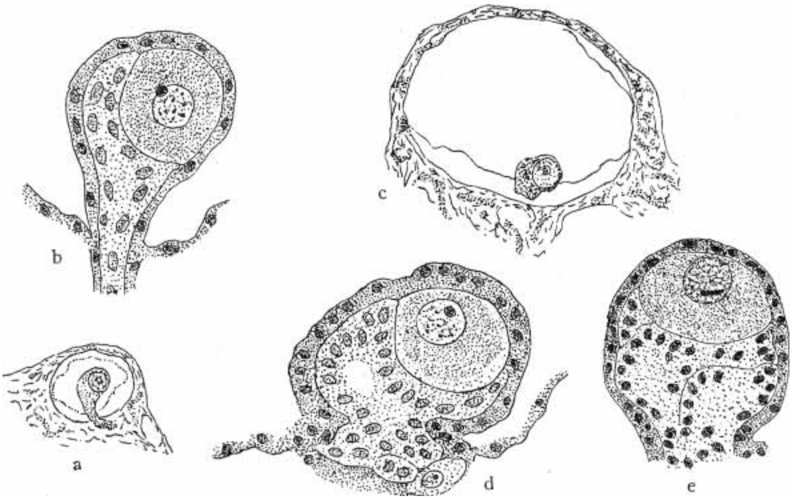


Fig. 25. Female gonophores of *Stylaster (Eu-Stylaster) gracilis* (a – d) and *S. (Eu-Stylaster) microstriatus* (e). — a primary ampulla with its gonophore. b the primary gonophore more enlarged. c old, emptied ampulla with a young, secondary gonophore. d the secondary gonophore strongly enlarged. e secondary, small gonophore. (a and c × 80, b, d, and e × 450.)

is here normally forked into two branches, the simple, unbranched spadix being the exception.

Female gonophores were observed in several species both of *Eu-Stylaster* and *Allopora*. — Only in *Stylaster gracilis* have primary female gonophores been found with certainty (Textfig. 25 a and b). The roof of the young ampulla is rather thick, and the gonophore is still so young that it seems doubtful that the ampulla should not have been formed till after the budding of the gonophore (cf. ENGLAND, 1926, *Stylaster filogranus* and *Distichopora violacea*). The present find does not absolutely preclude the possibility, that female gonophores primarily are formed superficially on the branches as maintaind by ENGLAND. But the observations point in direction that the apprehension of HICKSON (1890) at all events in some species (or cases) holds good, that gonophores and ampullae are formed in connection with peripherous coenenchym canals below the surface of the colony.

As well in *Stylaster gracilis* as in *Stylaster microstriatus* it is evident that the ampulla soon after the breaking away of the first larva again restores to shelter the secondary gonophore now developing (Textfig. 25 c, d, e).

In their young stages the female gonophores are decidedly "styloid", the oocyte lying between the single rowed ectoderm and entoderm layers of the gonophore bud. No difference is observed in so far between primary and secondary gonophores (cf. Textfig. 25). The cup-shaped spadix, however, later on grows out into lobes which in some species (i. a. *Stylaster roseus*,

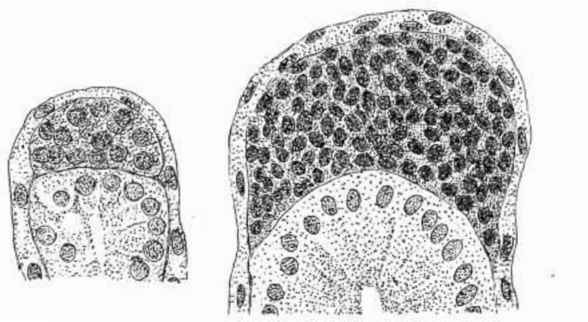


Fig. 26. Two young, male, secondary gonophores from an ampulla of *Conopora tenuis*. (×720.)

see Broch 1914, Pl. V, Fig. 47) also form a cup or, in other species, as finger-like anastomosing processes which form a hemispherical cushion on the flat, upper side of which the oocyte is deposited (e. g. *Stylaster gemmascens*, see Broch 1914, Pl. V, Fig. 46). It is evidently this secondary development of the spadix into the "trophodisc" which has prevented the acknowledgement of the styloid nature of the female gonophores of the Stylasteridae.

## Conopora.

Only male gonophores have been studied, and the material was also in this case rather scarce. In *Conopora major* the ampullae contain several gonophores at a time. This may also be the case in *Conopora tenuis* as demonstrated by a colony from Mauritius; but a male colony from shallower, Japonese waters has only three to six gonophores in each ampulla. Whether the numbers depend on the age of the specimen or on the conditions of the habitat, remains as yet an open question.

The gonophores of an ampulla are in different development stages, and beside quite ripe gonophores with fully developed spermatozoans, quite young stages of gonophores were also found (Textfig. 26). These secondary gonophores are quite typically styloid gonophores with propagating cells between the ectoderm and entoderm of the simple bud. Neither here nor in later stages have traces of an entocodon been found, and the ripe gonophores accordingly also show no trace of an efferent duct. Evidently the spermatozoans are emptied into the ampulla. — Primary gonophores were not observed with certainty; but there is no reason to assume that they should differ in any way from the secondary ones.

## *Errinopora* (= *Protoerrina*).

The youngest female gonophore observed holds an intermediate stage between those of *Stylaster filogranus* which England (1926) has illustrated in her Figures 7 and 8. It is already enclosed in a complete ampulla rather deeply below the surface of the branch. The spadix is as yet approximately hemispherical and unbranched, and the oocyte semiglobular and not ripe. According to the site of this young gonophore it seems questionable whether the female gonophore of *Errinopora stylifera* always originates at the surface of the branch. — During the succeeding development the spadix divides into a number of blind sacks or lobes forming a shallow cup in which the oocyte is deposited. The further development goes on in the ampulla until the planula is liberated and does not seem to differ from *Stylaster* in any way.

Also the smallest stages of primary male gonophores have been observed in completely closed ampullae, and there is no indication that they bave been formed at the surface of the branches and secondarily sunk into the coenosteum. — In quite young male gonophores the spadix forms a basal "cushion" both in primary and later formed gonophores (Textfig. 27 a). During the later development, however, the spadix grows out into two or three fingershaped branches (Textfig. 27 b, c), and these are again reduced during the ripening of the spermatozoans (Textfig. 27 d). The spadix reaches its greatest development just before the spermatozoans are formed, and the reduction evidently proceeds rather rapidly, until the spadix presents almost the same features as the spadix in a female gonophore at the escape of the planula larva.

England (1926) has observed male gonophores with bifurcate spadices in *Stylaster filogranus*, but explains it as "simultaneous formation of two gonophores". It must be noted that the bifurcate spadix in this case is an exception. In *Errinopora stylifera*, however, the spadix is always branched in two or three branches.

Early in the development of the gonophore an entocodon is observed at the apex in the form of an accumulation of cells; the inner accumulation of cells is distinctly limited from the outer ectoderm by a rather distinct basal membrane. The cells of the entocodon (Textfig. 27 f) soon become cylindrical, and in median sections their arrangement recalls the leaves of a bulb. At this time also the apical cells of the outer ectoderm become higher, cubic or cylindric.

It has not been possible to state the origin of the inner cells of the entocodon with certainty; but much seems to point in the direction that they are ectodermal and formed by delamination from the apical part of the gonophore ectoderm.

In *Errinopora stylifera* the entocodon formation attains its highest development, when the gonophore is filled with ripe spermatozoans. In the present, not too well preserved material, the orientation of the cells in ripe gonophores indicates the coming perforation (Textfig. 27 f), and a perforation of the supporting the lamella is clearly visible. — In ripe gonophores the apex is always orientated in such a way that the top of it is pushed into a coenenchym canal of the ampulla roof. It is obvious that

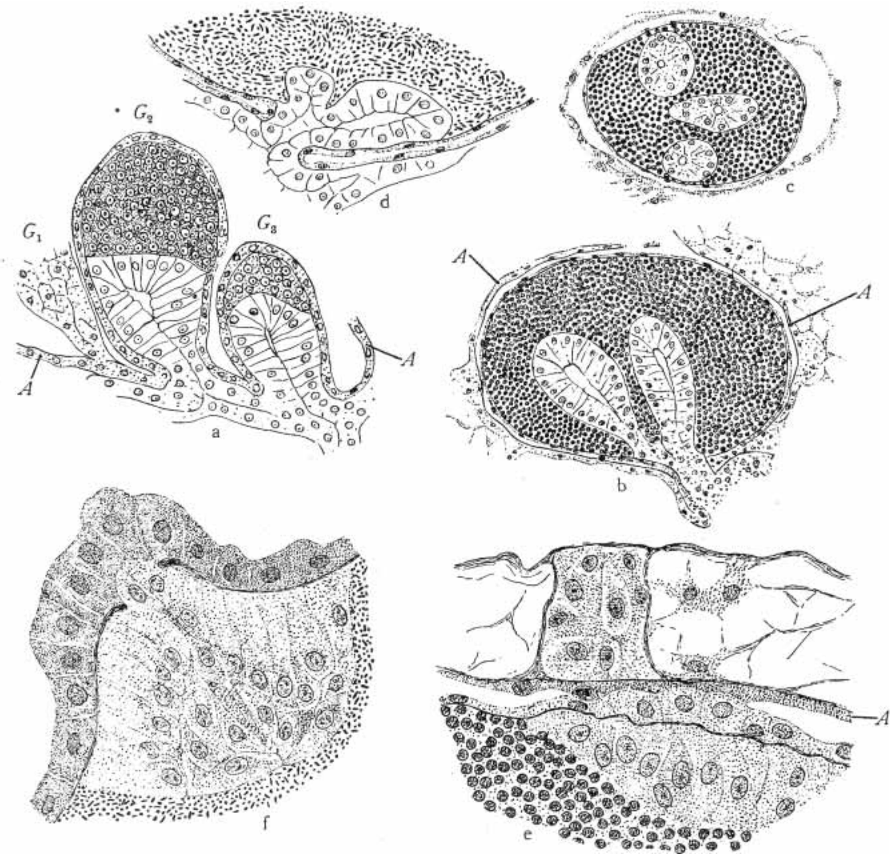


Fig. 27. Male gonophores of *Errinopora stylifera.* — a basis of a primary gonophore ($G_1$) and a secondary ($G_2$) and one still younger gonophore ($G_3$) of one ampulla. b half ripe gonophore showing two branches of the spadix. c transverse section showing the three branches of the spadix of a half ripe gonophore. d the strongly reduced spadix of an almost ripe gonophore. e apical part of a half ripe gonophore with its entocodon; in the ampulla roof an accumulation of cells shows the place, where later on the efferent opening breaks through. f apical part and entocodon of an almost ripe gonophore; an obvious central opening is seen apically in the thickened supporting lamella. (A epithelium of the ampulla wall. — a × 285, b, and c × 150, d × 340, e and f × 840.)

the seat of the eventual efferent canal of the ampulla roof has a determining influence on the localization of the entocodon formation. Young gonophores are often on this account compelled to develope quite obliquely with incipient entocodon displaced along one side. — The function of the efferent duct (the transformed entocodon) is stated by a couple of all but entirely emptied gonophores. The gonophore wall is here strongly contracted and in the cavity which is very much reduced, some few spermatozoans are still present. Instead of an entocodon we here find a rather wide, short tubular duct at the apex of the gonophore in which some spermatozoans are also present.

The histological structure seems to indicate that the entocodon is expelled like a stopple from the ripe gonophore, when it is emptied.

It has not been possible to state whether the primary male gonophore buds at the surface of the branches and is secondarily enclosed in an ampulla. On the other hand it could be stated with certainty that the ampulla is without an efferent canal as long as the primary gonophore is rather small. An efferent duct is not formed in the roof of the ampulla till the entocodon of the primary gonophore is rather obvious (Textfig. 27 e); at this time a number of cells accumulate like a tap right through the ampulla roof, and here the efferent duct of the ampulla later on breaks through. It is the position of this duct in proportion to the secondary gonophore which determines the position of the entocodon in the latter. The present material did not suffice to study the origin of the cells forming the tap through the ampulla roof or their further fate.

## *Errina.*

Of the *Eu-Errina* group only *Errina spongiosa* could be studied. The preservation is not quite satisfactory, but some facts concerning the male gonophores could be stated. — The first stages of primary gonophores (and ampullae) were found near the ends of the branchlets in the peripheral coenenchym canals, although not at the very surface of the branchlet. One of the youngest stages is figured in Textfig. 28 a. The blastostyle arises as a diverticulum in the wall of the canal, evidently at first as an accumulation of endodermal cells which by their rapid propagation force themselves and their ectodermal mantle away towards the superficial side of the branch. The diverticulum developes into a fingershaped blastostyle like that described by ENGLAND (1926) in *Distichopora violacea.* At the base of the blastostyle four gonophores are generally formed successively; they seem to arise in rather short time.

When these four primary gonophores are emptying themselves, secondary gonophores arise. Meanwhile the blastostyle is evidently reduced and disappears. It could not be traced in old ampullae. Such old ampullae often contain more than four, very commonly even up to six gonophores in different stages of development.

During the development of the gonophore the spadix undergoes a peculiar transformation. At first the spadix is low, cushion-like; but soon it grows out into three to five lobes which, however, do not push fingerlike into the assembly of spermatocytes like those of e. g. *Errinopora stylifera,* but which creep along the ectoderm of the gonophore wall thus forming a real, although simplified "trophodisc" (Textfig. 28 b and c). The bulk of propagative cells thus rests in a cup-like, primitive trophodisc. This trophodisc is again reduced during the ripening of the spermatozoans.

The gonophore empties its contents through an efferent duct into one of the canals of the ampulla roof (Textfig. 28 d). The investigation of

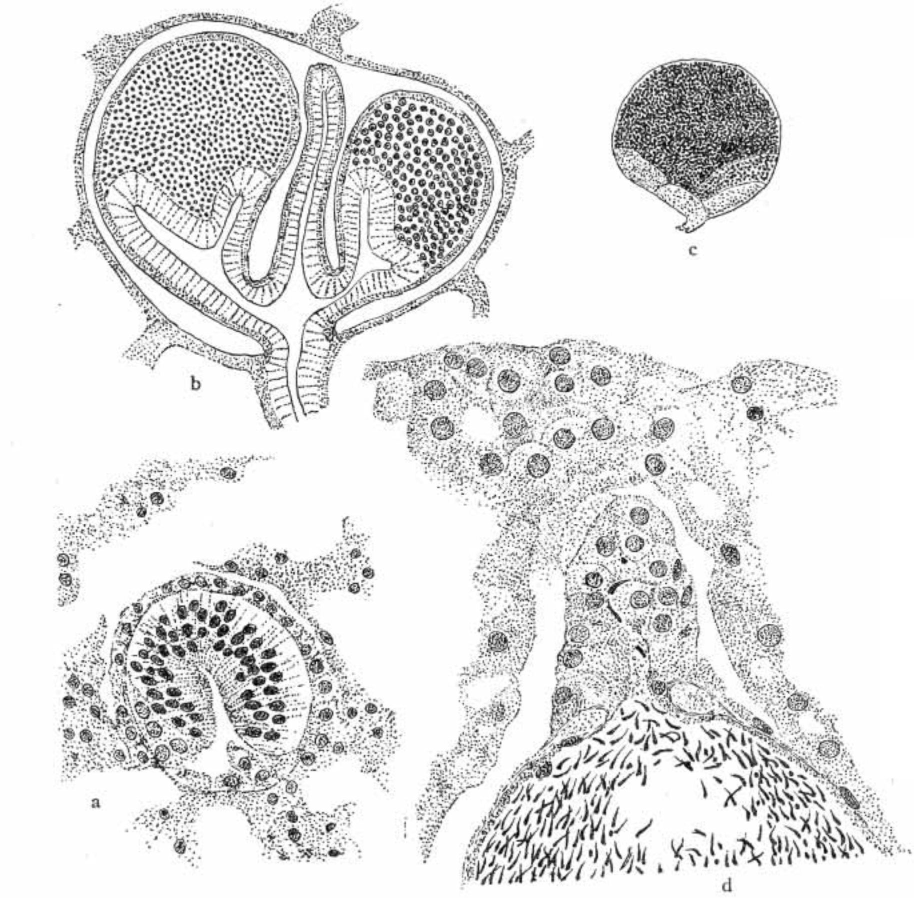


Fig. 28. Male gonophores of *Errina (Eu-Errina) spongiosa.* — a youngest stage of a blastostyle in an incipient ampulla developing in a coenenchym canal below the surface. b slightly diagrammatic section (drawing based on three sections à 10 μ) of two gonophores and the blastostyle; the spadix is forked. c half ripe gonophore; spadix with for "pouches". d apical part of a ripe gonophore on the verge of being emptied; the rather acute top part points into a niche of the ampulla roof, a central opening with swollen brim is seen apically in the supporting lamella. (a × 380, b × 160, c × 80, d × 720.)

several large series of microtome sections, however, did not reveal a real entocodon in this species. It has been impossible to trace an apical cell accumulation in earlier developmental stages of the gonophores; the apical faucet could only be observed so to say at the very moment when the gonophore is about to discharge its contents. Even though the preservation of the specimens is not first class, such earlier stages with entocodon or a group of specially developed cells so essentially different from the propagative cells should no doubt have been observed rather easily. It is therefore likely that an efferent duct is formed in the present species without any preceeding entocodon.

Among the *Labiata* only *Errina tenuistylus* could be studied. Here the male ampullae simultaneously contain two or, generally, three gonophores in different stages of development. Younger gonophores have a well developed and fingershaped, simple spadix which, however, again disappears during the later development of the propagative cells. Gonophores about to discharge their spermatozoans have no remaining trace of a spadix.

It is impossible to find any trace of a distal cell faucet in the gonophore when it is about to discharge its contents, and no efferent duct was found. On the other hand the apical end of gonophores just about to empty themselves is pointed or has a narrow, wart-like small protuberance at the apex turning towards the small opening in the centre of the ampulla roof. — In accordance with the above mentioned features, no trace of an entocodon has been found in earlier stages.

The male ampulla is very small, and the gonophores are therefore closely packed and have often a varying and rather irregular shape.

In the female ampulla only one gonophore is present. In many cases the ampullae contain fully developed planula larvae on the verge of escaping, but also in this case no trace of secondary gonophores has been observed. Nevertheless the roof of empty ampullae seem to indicate that no rupture takes place when the larva escapes.

The ripe oocyte exhibits a peculiar mosaic structure which is also observed in *Pliobothrus*. The "yolk cells" have a strongly eosinophile substance, but each of the polygonal "cells" contains a large, vesicular and round "vacuole" which is feebly basophile and accordingly seen as a light blue vesicle in the bright red yolk in sections coloured with hematoxyline and eosin. — The spadix of female gonophores has the usual cup-shape and is built up of several lobes; it is again reduced during the development of the ovum into a planula.

## *Paraërrina.*

Female ampullae of ***Paraërrina decipiens*** only contain one gonophore, and no secondary gonophore was observed even in ampullae with young planula larvae. On the other hand no quite young ampulla has been found, and it could not be stated with certainty in all cases whether the gonophore was a primary one or not.

Male ampullae contain numerous gonophores budding from a very large, central blastostyle (Textfig. 29 a). The single gonophore appears as a small wart on the surface of the blastostyle (Textfig. 29 b); the youngest stage observed indicates that the primary impulse is a primeval sperm mother cell which, coming from the endodermal side, pushes the supporting lamella out like a pouch, and this pouch is closed behind it, so that the propagative cells develope without any contact with an endodermal spadix (Textfig. 29 b and c). Far advanced stages of gonophores emancipate

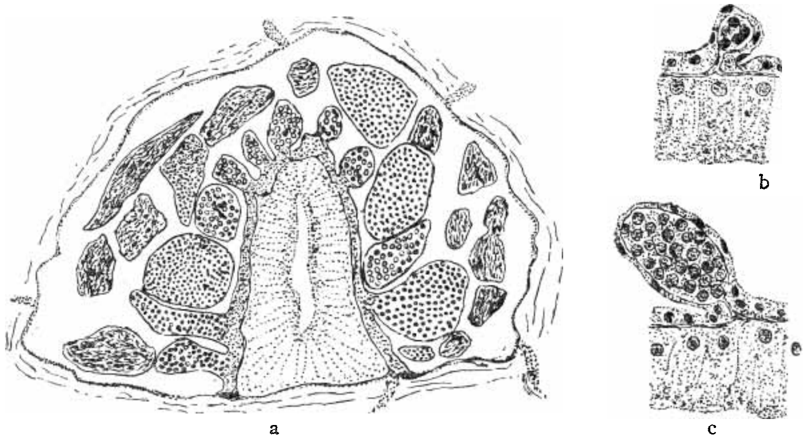


Fig. 29. *Paraërrina decipiens.* — a median section of male ampulla with its large blastostyle and numerous gonophores. b quite small gonophore showing the "pouch" formed by the supporting lamella. c somewhat older gonophore; also here every trace of an individual spadix is lacking. (a × 200, b and c × 450.)

themselves entirely from the blastostyle and are found isolated in the peripheral part of the ampulla lumen; they now consist of an ectodermal, closed sac in which the ripening of the spermatozoans is accomplished. Especially during the last phase of this process the freed "gonophores" attain quite irregular shapes according to the space left at their disposal. The ripe spermatozoans are evidently emptied into the ampulla. There is no trace of an entocodon or an efferent duct.

The male blastostyle and its gonophores are evidently of the same structure as in *Astylus*. MOSELEY (1878, 1881) does not speak of a blastostyle, and his descriptions seem to indicate that he did not get a clear conception of its structure and nature. Nevertheless his descriptions and drawings leave no doubt as to the conformity between the male apparatus of *Astylus* and *Paraërrina*.

The entire assembly is very different from that of *Conopora*. In this genus the blastostyle is reduced to a stalk, and it has accordingly never been mentioned as "blastostyle"; it has lost its importance as a "nutritive person", and each gonophore is provided with its individual endodermal spadix. In *Paraërrina* on the other hand, the blastostyle might be said to retain its rôle as a common spadix of all the gonophores of the ampulla.

## *Distichopora.*

Male gonophores have been studied in colonies of *Distichopora fisheri* and *Distichopora irregularis*. — The male ampullae of *Distichopora fisheri* are small and only seated in the thin, superficial layer of the branches. Each ampulla contains four or five gonophores round the basis of a conical blastostyle reminding us of that of *Errina spongiosa*. The gonophores of the ampulla are in different stages of development.

During the growth of the gonophore the spadix at first has the shape of a cushion and thus differs rather markedly from the generally finger-like spadices of most male gonophores of the family. Later on the spadix becomes disc-shaped or slightly excavated, like a saucer (Textfig. 30 a). The spadix is thus here a real "trophodisc" although of the simplest kind and without the distinct "pouches" which are developed in the trophodiscs of female gonophores. — During the later phases of the development of the spermatozoans the spadix is again little by little reduced, and it has entirely or almost entirely disappeared in gonophores about to discharge their contents.

In the last phase of the development of the gonophore a cell accumulation is observed near the apex and facing one of the coenenchym canals of the ampulla roof. The cell accumulation forms a "stopple" at the apex and is probably expelled or, possibly, transformed into the seminal duct which leads into the adjacent coenenchym canal. The inner cell accumulation is the entocodon, and it is not certain whether it gives rise to an inner cell layer of the efferent duct leading into the functioning efferent canal of the ampulla roof. No other, special or permanent opening seems to occur in the male ampulla.

Although the investigated fragment of *Distichopora irregularis* contained a great many male ampullae, only one or two quite young ones have been found. They are primary and here as yet only a blastostyle can be discerned. Nevertheless these primary and quite young gonophores have not been found at the very surface of the branch, but in the coenenchym canals a little below the surface.

Fully developed ampullae have four to six gonophores round the basal part of a blastostyle like that described by ENGLAND (1926) in *Distichopora violacea*, and new gonophores develope when the ripe ones are emptied and atrophy. Although the blastostyle is rather small in *Distichopora irregularis*, it retains its size during the period of propagation.

During the growth of the gonophore a rather large spadix developes. The spadix shows a varying shape. In some gonophores it retains a more cushion-like shape although generally more or less distinctly bilobed. In other gonophores it assumes a more pronounced finger-form and is then commonly bifurcate, and in this case the spadix is surrounded by the bulk of propagative cells. As usual the spadix is again reduced when the gonophore has reached its maximal size and the spermatozoans are maturing.

When the spadix has reached its greatest size or has already commenced to diminish, the first clear formation of an entocodon is observed (Textfig. 30 b). Although the preservation is not quite first class, it seems doubtless that the double ectodermal cell layer observed at the apex of the gonophore arises by delamination from the external ectoderm, and thus really represents a vestigial entocodon as maintained by ENGLAND (1926). Both the cells of the external and internal layer of the apical formation

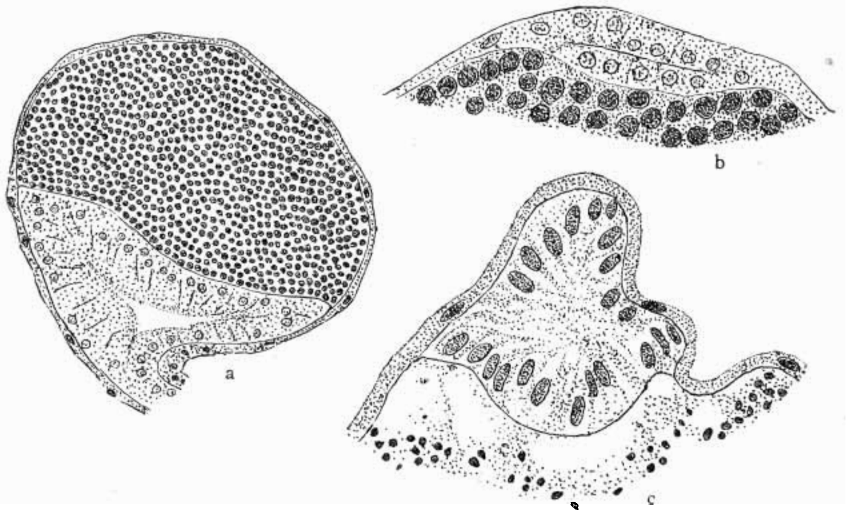


Fig. 30. Male gonophores of *Distichopora*. — a half ripe gonophore of *D. fisheri* with disc-shaped spadix. b youngest developmental stage of entocodon observed in *D. irregularis*. c. entocodon of an almost ripe gonophore of *D. irregularis*. (a × 450, b and c × 1120.)

are a little higher than the other cells of the gonophore ectoderm which generally form a low squamous epithelium.

During the later development the internal cell layer assembles into the shape of a globe, its bottom a little flattened, the distal part on the other hand feebly tapering towards the apex. It was in many cases observed that the cells of the lower part of the entocodon show a peculiar arrangement and shape almost like the leaves of an onion in sagittal section (Textfig. 30 c). The entocodon forms a stopple, and it seems in the present species probable that it is expelled when the spermatozoans are emptied; at this time the external ectodermal layer is transformed into an efferent duct leading into an adjacent coenenchym canal of the ampulla roof.

Female gonophores could only be studied in *Distichopora serpens*. The primary gonophore is here formed at or near the surface of the branch, where some of the coenenchym canals are somewhat more swollen than elsewhere. Whereas the finer structure of the coenenchym canal is elsewhere hardly discernible owing to a strong granulation which veils all cell limits, the cells of the small, globeshaped gonophore formation are rather clearly discernible, and the endoderm and ectoderm here show clear differentiations. The endodermal cells are rather large and devoid of granulations, and their nuclei form one rather distinct row, except in places where the growth is especially intensive; in such places the row of nuclei is irregular and seems double. The part of the gonophore bud turned against the branch surface is more conical and very soon developes into a narrow cone (Textfig. 31 a). In this stage the entire formation strongly recalls the blastostyle of *Distichopora violacea* described by ENGLAND (1926).

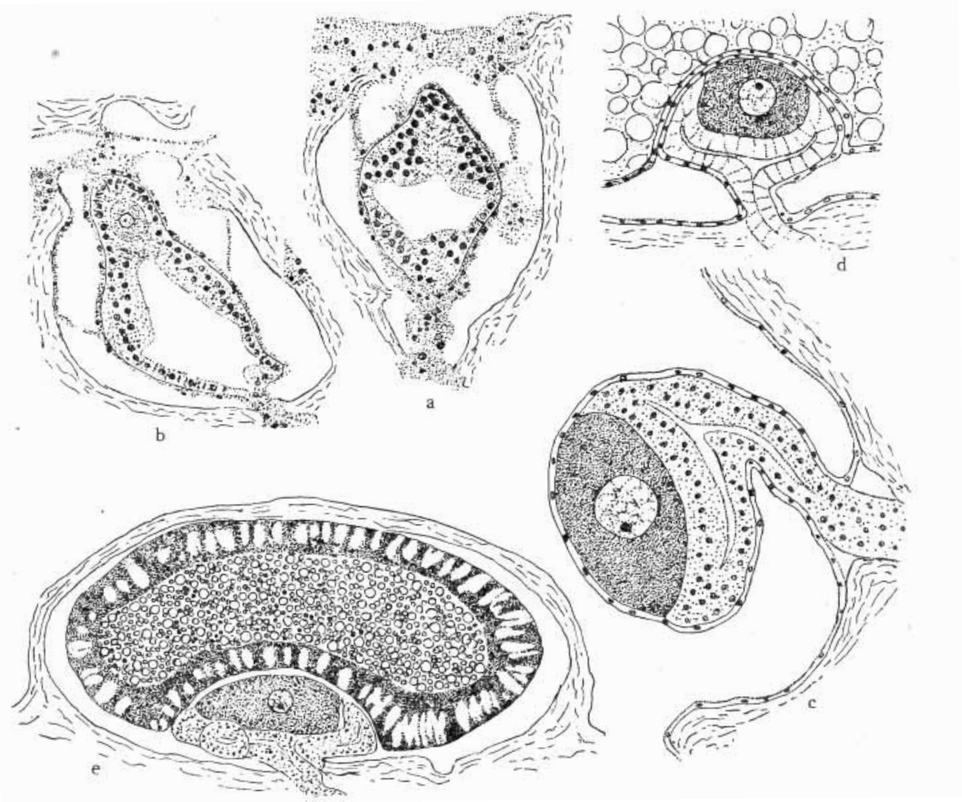


Fig. 31. Female gonophores of *Distichopora serpens*. — a youngest ampulla observed, blastostyle evidently as yet without oocyte; the blastostyle is formed in the end part of a coenenchym canal. b a slightly older blastostyle with apically placed oocyte; the ampulla is enclosed in the coenosteum. c much older, also primary gonophore in an open hollow on the surface of a branch. d quite young secondary gonophore of an ampulla with a ripe ovum (primary gonophore). e median section of an ampulla with planula larva about to depart; secondary gonophore well developed. (a—d × 340, e × 120.)

She always found it in this species at the very surface of the branch, whereas in the present species it has in most cases been found a short way below the surface, where at the same time a widening of the coenenchym canal forms the incipient ampulla round the "blastostyle". Probably, however, such "blastostyles" may also in *Distichopora serpens* be formed on the surface of the branch. At all events a somewhat older developmental stage of a gonophore (Textfig. 31 c) was found in a roof-less depression of the surface, and in this case the ampulla roof should certainly have developed later on by the outgrowth of the brim surrounding the depression.

The "blastostyle" does not quite correspond to the blastostyle of *Distichopora violacea*. In this species gonophores are formed from the basal part of the blastostyle, and the blastostyle remains otherwise unaltered beside the female gonophore for some time during the later development.

In *Distichopora serpens* on the other hand, the oocyte is deposed at the summit of the "blastostyle" (Textfig. 31 b) which thereupon is itself transformed into the covering ectoderm and the endodermal spadix of the primary gonophore. Already a stage like that reproduced in Textfig. 31 c shows no trace of the blastostyle.

During growth the oocyte has at first a rather homogeneous yolk. In later stages, however, spherical drops are formed in the yolk, and in ripe ova the yolk is filled by such smaller and larger "drops". — About this time, when the ovum is fertilized, the formation of a secondary gonophore is observed (Textfig. 31 d).

The spadix developes during the growth of the oocyte at first to a typical trophodisc with few and broad lobes. It has the shape of a cup or deep saucer. In gonophores with ripe ova the spadix has already passed its maximum size and is decreasing, till it at last only exists as a small wart in a niche of the inner side of the oocyte. At this time it seems as though the ectoderm is closed round the oocyte and isolated from a layer covering the reduced spadix; but the state of preservation is unfortunately not sufficient to give all such fine details with absolute certainty. — At the summit of the reduced spadix a new oocyte now appears (Textfig. 31 d), and the spadix again begins to develope into a trophodisc. As long as the development of the larva of the primary gonophore proceeds, the development of the secondary gonophore probably advances comparatively slowly, and when the planula larva is about to escape (Textfig. 31 e) the new oocyte is as yet rather small, although the spadix of the secondary gonophore has now assumed its cup-shape with several lobes adjoining each other.

Although no opening could be found in the ampulla roof, the roof is evidently not ruptured when the larva leaves the ampulla. How this comes to pass is as yet an open question.

## Summary

A survey of previous investigations and the results concerning the present material may give a fairly good impression of the gonophores of the Stylasteridae, their structure and development.

The gonophores of the Stylasteridae must in general be referred to the styloid type of the Hydrozoa. In several cases, however, the male gonophores show a vestigial entocodon linking them to reduced heteromedusoids. This may be taken as an indication that, taken together, the gonophores of the family are derived from heteromedusoids.

On the whole the male gonophores in their organisation hold the most primitive position. The main type is during its development furnished with a fingershaped spadix protruding into the bulk of the developing propagative cells; this spadix is again reduced during the ripening of the propagative cells. In some species like *Stylaster bocki* and *Stylaster filogranus* the

spadix is exceptionally bifurcate, and in *Stylaster scabiosa* and *Errinopora stylifera* the bifurcation is the normal feature. In the last named species moreover the spadix is equally frequently forked into three branches.

However, the spadix of male gonophores is not always fingershaped. In the varied gonophores of *Distichopora irregularis* the spadix may be fingershaped and bifurcate; but it may also remain cushion-like, although also in this case bilobed. In *Distichopora fisheri* the spadix metamorphoses from a cushion into the shape of a saucer without subdivision of the peripheral part into lobes, and in *Errina spongiosa* finally the peripheral part of a similar "saucer" consists of three to five pouches or broad lobes.

A comparison of the spadices in male and female gonophores shows that the simple saucer-shaped spadix of some male gonophores has the same shape and organisation as the most primitive "trophodiscs" of female gonophores; trophodiscs corresponding to the spadix of male *Errina spongiosa* are found in female gonophores of many species. And in species with more complex "trophodisc" the spadix during its development passes through stages like the saucer-shaped spadices of the above mentioned male gonophores. A subdivision of the primary peripheral lobes resulting in a greater number of blind pouches, leads up to the most common type of "trophodisc" which e. g. occurs in *Stylaster roseus* (see BROCH 1914, Pl. V, Figs. 47 and 48), and a further increase in the number of blindsacks also from the central parts of the spadix, and in some cases even anastomoses between the blindsacks finally results in such complicated "trophodiscs" as that of *Stylaster gemmascens* (see BROCH 1914, Pl. V, Figs. 46 and 49). There is thus no principal difference between the spadices of male and female gonophores, a trophodisc is merely a spadix consisting of several, more or less crowdedly placed endodermal blindsacks.

Returning to the male gonophores we must, according to the earlier statements, regard such gonophores as the most primeval ones which have kept an interior ectoderm at the apex or a rudimentary entocodon. Evidently this formation has some special function, where it has been kept. The origin of the entocodon in the Stylasteridae has not as yet been settled with absolute certainty. But such pictures as afforded by *Stylaster nobilis* (see ENGLAND 1926, Textfig. 9) and *Distichopora irregularis* (see Textfig. 30 b) indicate that it must after all probability be formed by a splitting of the ectoderm, by delamination from the apical ectoderm of the gonophore like the entocodon of other heteromedusoids.

It seems evident that the vestigial entocodon has been kept in gonophores which empty their contents into conenchym canals of the coenosteum, eventually of the ampulla roof, whereas it has disappeared in gonophores which empty their contents into the lumen of the ampulla. Where the roof of the ampulla has a distinct, rather large efferent opening for the propagative cells, no entocodon evidently appears in the male gonophores.

On the other hand, as far as can be observed, the entocodon only exceptionally partakes in the formation of the "seminal duct". The efferent duct is evidently formed by the surface ectoderm alone and of that part of it which covers the entocodon. The entocodon itself seems to play a part in the ejaculatory mechanism, and to be expelled when the gonophore empties its contents. Only in one or two cases (e. g. *Stylaster dentatus*) does the entocodon seem to partake in the formation of the duct which is here built of two cell layers; the internal layer arises after all probability from the entocodon.

The male gonophores hitherto mentioned must according to their structure be termed partly as heteromedusoids (with entocodon) and partly as styloid gonophores with somewhat variously constructed spadices. However, a still more reduced type is found in *Astylus* (see MOSELEY 1878, 1881) and *Paraërrina*,where no spadix at all is observed in any developmental stage of the gonophore. In *Paraërrina decipiens* the gonophore separates itself from the blastostyle during the last phase of the development of the propagative cells, and simply forms an ectodermal sac filled with developing spermatozoans. In these gonophore assemblies the strongly developed blastostyle evidently plays the part of common spadix to all the gonophores of the ampulla.

An enigmatic, composite male gonophore has been observed in *Pliobothrus symmetricus* (see BROCH 1914). However, the development is unknown, and the preservation of the investigated specimen has not been sufficient to settle the finer structure and the nature of this aberrant type.

Whereas the male gonophores thus show rather varied features, the female gonophores must be said to be remarkably uniform. They are throughout styloid, no trace of an entocodon or internal ectoderm has been discovered. On the other hand a spadix is always present, forming a trophodisc, the construction of which may vary to some slight degree.

The primary ampulla and its gonophore or gonophores are evidently in most cases found at the very surface of the colony (ENGLAND 1926); but they may also, as confirmed by the present material, be found in the peripheral coenenchym canals as supposed by HICKSON (1890).

The first foundation which ENGLAND (1926) quite universally terms a "blastostyle", is a more or less distinctly spherical cell assembly consisting of two cell layers, i. e. of ectoderm and endoderm. Although the origin of the propagative cells has not been stated with absolute certainty in the Stylasteridae, the earliest observed stages indicate that the common presumption of their endodermal origin is probably correct. The male gonophore buds of *Paraërrina decipiens* evidently support this presumption.

In most cases the entire primary formation develops into a gonophore, and it is in these cases hardly proper to speak of it as a "blastostyle".

On the other hand it is defensible to regard it as a reduced zooid as maintained by ENGLAND (1926); it must in so far be regarded as a parallel to other gonophores of the Hydroids.

In other cases again — *Distichopora violacea, Distichopora fisheri, Distichopora irregularis, Errina spongiosa* — real blastostyles are present, reduced polyps from the body of which the gonophores bud. This blastostyle may in some cases be reduced and disappear together with the primary gonophores as in *Distichopora violacea* (see ENGLAND 1926), or it endures as long as gonophores are produced in the ampulla; this is the case in male colonies of all the above named species.

In most of the investigated species where an ampulla contains several male gonophores on a short stalk, the common stalk might be parallelized with a "blastostyle" like the gonophore-carrying stalks of many Hydroids (e. g. *Tubularia*). It is, however, questionable whether this is defensible or not, as long as we do not know the development of the gonophore clusters and their stalks.

On the other hand an excessively developed blastostyle is found in *Astylus* (see MOSELEY 1878, 1881) and in *Paraërrina*. Here gonophores bud all over the surface of the blastostyle which must be said to function as a common spadix to the excessively reduced gonophores which lack individual spadices. It is accordingly not quite defensible to range this blastostyle side by side with the common stalk of the male gonophores observed in the ampullae of most other Stylasteridae.

The development of the single gonophore is the same as that in heteromedusoid or styloid gonophores of other Hydroids; this holds good both in primary and secondary gonophores. This fact effectively supports the view of MOSELEY, later on again defended by BROCH and by ENGLAND, that the Stylasteridae cannot be regarded as anything more than a family of the Hydroida.

## Structure and growth of the coenosteum (skeleton) of the Stylasteridae.

A study of the literature concerning the finer structures of the skeletal parts — the coenosteum — of the Stylasteridae gives only very meagre results. Some few hints concerning the "histological" structure of the hard parts are found in the fundamental monograph of MOSELEY (1878, 1881) and may be resumed here.

*Sporadopora*: "The tissue of the coenosteum is very like that of *Millepora* in histological structure, but appears somewhat more granular in texture, and less fibro-crystalline than it."

*Spinipora* (= *Errina* pars): "The substance of the coenosteum of *Spinipora echinata* is hard and compact in structure, and white."

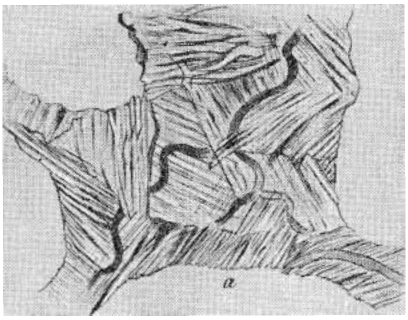


Fig. 32. Moseley's picture of the structure of the coenosteum of *Millepora* (1881, Pl. XIII, Fig. 8).

In the other species and genera treated by him Moseley does not give any particulars concerning the finer structures of the coenosteum. It is, however, in this connection necessary to recapitulate his statements concerning *Millepora* to which he alludes in his remark about *Sporadopora*. He writes as follows:

"In histological structure the hard tissue composing the coenosteum of *Millepora* seems to resemble closely that of the coralla of Heliopora and Anthozoa. It is composed of lamellae of fibro-crystalline calcareous matter (Pl. XIII, Fig. 8), the fibres of the supposed lamellæ crossing one another at all angles in the mass. In some places, in thin sections of the coenosteum, the appearance shown at *a* (Pl. XIII, Fig. 8) is clearly to be seen. The calcareous fibres of the hard tissue terminate towards a cavity in the coenosteum as a series of short points, seeming to show a composition of the hard tissue out of definite rod-like elements. Such an appearance is only to be met with sparingly, and possibly occurs at spots where the coenosteum was in active growth."

Later investigators of recent Stylasteridae usually give no information as to the finer structures of the coenosteum. An exception has Hickson made in his paper on *Errina* (1912) in so far as he on Pl. XCVI gives two rather diagrammatic drawings "intended to show the difference in texture between *Errina (L.) novæ-zealandiæ* (Fig. 14) and *Errina (L.) capensis* (Fig. 15), as seen in vertical section of the coenosteum". According to the drawings the calcareous matter between the canals is in *Errina novæ-zealandiæ* structureless and almost quite homogeneous, whereas in *Errina capensis* it ought to have a texture like that of *Millepora* as illustrated by the drawing of Moseley (see Textfig. 32).

A survey of the momentary state of our knowledge concerning the mineralogical composition of the skeleton of Hydrocorals has been given by Broch (1914). It had already earlier been stated that the skeletons of *Millepora* and *Stylaster* consist of aragonite, and by means of Meigen's reaction this was in 1914 also stated to be the case in the four north

Atlantic species of Sylasteridae, viz. *Pliobothrus symmetricus*, *Stylaster (Eu-Stylaster) gemmascens*, *Stylaster (Eu-Stylaster) roseus*, and *Stylaster (Allopora) norvegicus*. A survey of all Madreporarians and Hydrocorals investigated as to aragonite or calcite gave the interesting result that a skeleton of calcite is only a seldom exception in these groups, whereas a skeleton of aragonite seemed to be the general rule.

These data, however, have since especially puzzled me many times because all skeletons of the mentioned groups from the oldest geological periods consist exclusively of calcite. An eventually occurring aragonite must accordingly during the past millions of years have metamorphosed into calcite, and the hypothesis has also been proposed, that this metamorphosis might possibly be used as an indicator of time. In this connection, however, also another question arises: does the skeleton in all cases exclusively consist of aragonite, respectively calcite, or does not the possibility exist that the skeletons, at all events in some cases, contain both aragonite and calcite?

A chemical analysis gives only little information. The skeleton of *Sporadopora mortenseni* has been analysed (by my son, J. ANT. Z. BROCH). It consists of pure carbonate of calcium with traces of magnesium. The latter should always be present, when aragonite skeletons are formed (cf. BROCH 1914), but evidently nothing has been stated that it should be lacking in skeletons of calcite.

*Sporadopora mortenseni* has been chosen for the analysis, because this species has skeletons with an extraordinarily coarse, granular texture which might even be termed crystalline. Here an investigation by refraction also seemed possible, and I am greatly indebted to my colleague, Dr. TOM BARTH, who undertook the mineralogical analysis both of this species and of *Errina cervicornis* which, however, has a lamellous structure in places combined with an utmost fine granulation. An investigation by aid of Meigen's reaction gives in both species an indication of aragonite. In *Sporadopora*, however, the refraction gives certain indications of calcite.

These facts are of considerable interest and value. They show us, in the first place, that a "positive" result by aid of Meigen's reaction as to the occurrence of aragonite does not preclude a simultaneous presence of calcite, whereas a demonstration of calcite by aid of Meigen's reaction tells us that no aragonite is present (in other words: the colour-reaction of aragonite conceals that of calcite). It was on the other hand, because of the comparatively coarse, crystalline texture in *Sporadopora*, possible to demonstrate calcite by refraction, whereas the simultaneous presence of aragonite was hidden by this method.

The results concerning *Sporadopora* seem to indicate that the skeletal substance of the Stylasteridae at all events in most cases consists of an intermixture of both aragonite and calcite, and this is probably also the case in many of the Madreporarians.

Another question then again arises, to wit, the quantitative proportion between calcite and aragonite in each case. This, however, cannot be answered by the methods employed here; it demands a roentgenological investigation. — It might furthermore be a question, what bearing this proportion has on a time-bound metamorphosis of the skeleton into pure calcite. However, these questions lie a little outside of the scope of the present zoological investigations.

A study of the minute structures of the skeletons meets with rather great difficulties. It is necessary to have recourse to thin sections. As the coenosteum is intersected in all directions by fine coenenchym canals, and accordingly is rather brittle, the grinding of the slides is difficult and often comparatively hazardous. The drawings on the following pages and the accompanying Plate VI furthermore show that the finest details are only visible in a few places, and that the sections elsewhere only exhibit a "finely granulated" and otherwise rather homogeneous skeletal substance. However, in some places, when the slides have been most successful, a minute texture is observed which evidently gives us a glimpse of the "normal" structure connected with formation and growth of the skeleton. In such places the skeletal substance is on the whole a little more translucent than elsewhere, and here it has not the generally "finely granulated" appearance.

## *Stylaster.*

The present collections contain a copious material of the Stylasterinae, and a large series of sections of *Stylaster* have been examined. In their finer structure they exhibit rather great diversities.

Some slides of *Stylaster (Eu-Stylaster) asper* (Textfig. 33 a–c) demonstrate the influence of the varying thickness of the sections. In Textfig. 33 a the section is rather thick: this is also seen in the arrangement of the small spines of the free margin. We get here the impression that the calcareous substance is comparatively homogeneous, only intersected by coarse canals (the organic matter had not been removed before grinding, and the canals are accordingly filled with a "debris" which by transmitted light is seen in the slide as a dark mass); the irregular lines crossing the skeletal substance in different directions must be considered as chance "rupture lines". — The somewhat thinner section Textfig. 33 b exhibits a rather different picture. The "rupture lines" of the preceeding slide have disappeared, and the texture seems more regular. But also here the calcareous substance itself seems to be rather homogeneous, and at all events some of the observed stripes are probably artificial and caused by the process of grinding. — Finally, the very thin part of a transverse section reproduced in Textfig. 33 c renders quite another and clear picture of the structure. In this case we at once understand Moseley's term "calcareous fibres of the hard tissue."

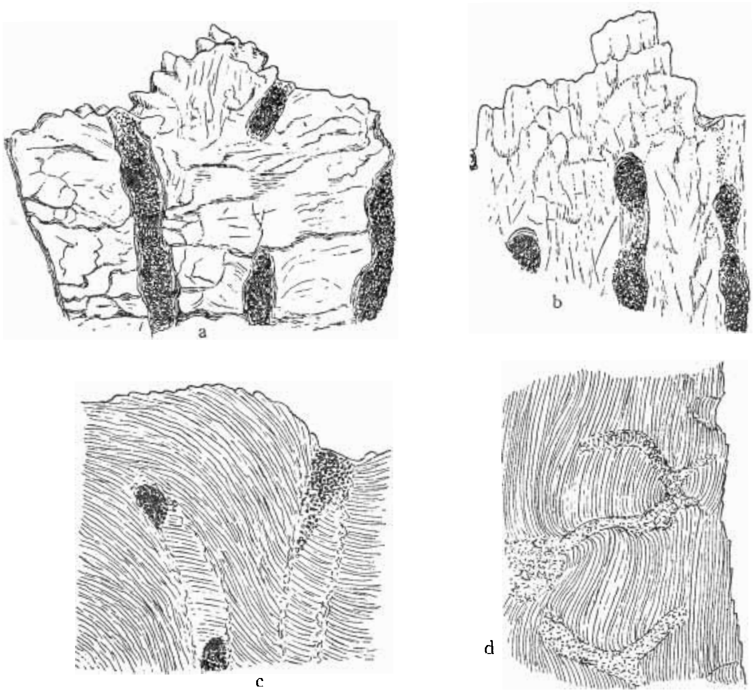


Fig. 33. Sections of the coenosteum of *Stylaster (Eu-Stylaster) asper.* — a from a thick, transverse section of a branch; note the conical thorns of the surface (upper margin). b part of a somewhat thinner slide. c peripheral part of a thin, transverse section of a branch; lamellae clearly seen. d peripheral part of a thin, axial longitudinal section of a branch; at the free margin the ledge-like ends of the lamellae are obvious. (× 120.)

A combination of the thin transverse section (Textfig. 33 c) and the structure as seen in a very thin radial and longitudinal section of a branchlet (Textfig. 33 d; in this preparation the organic tissues had been removed by aid of sodium hypochlorite before grinding) demonstrates that the calcareous substance of *Stylaster asper* should rather be characterized as lamellous than as fibrous. The coenosteum is evidently built up of more or less regularly superimposed, almost microscopically thin layers of calcareous matter which, as far as may be deduced from series of sections of decalcified specimens, evidently alternate with exceedingly thin laminæ of organic, though not cell-containing substance. The latter series of microtome sections furthermore show that the skeletal substance does not contain any cells between the canals or below the single-rowed epithelium covering the surface of the coenosteum and the walls of the pores. The calcareous lamellae are not orientated quite parallel with the surface of the coenosteum. The peripheral borders of the lamellae in the sections jut feebly out at the free margin (Textfig. 33 c, d) like minute points or ledges, and the lamella forms a very acute angle with the surface of the coenosteum, diving in under the next lamella. In some places lamellae later on again arch upwards and

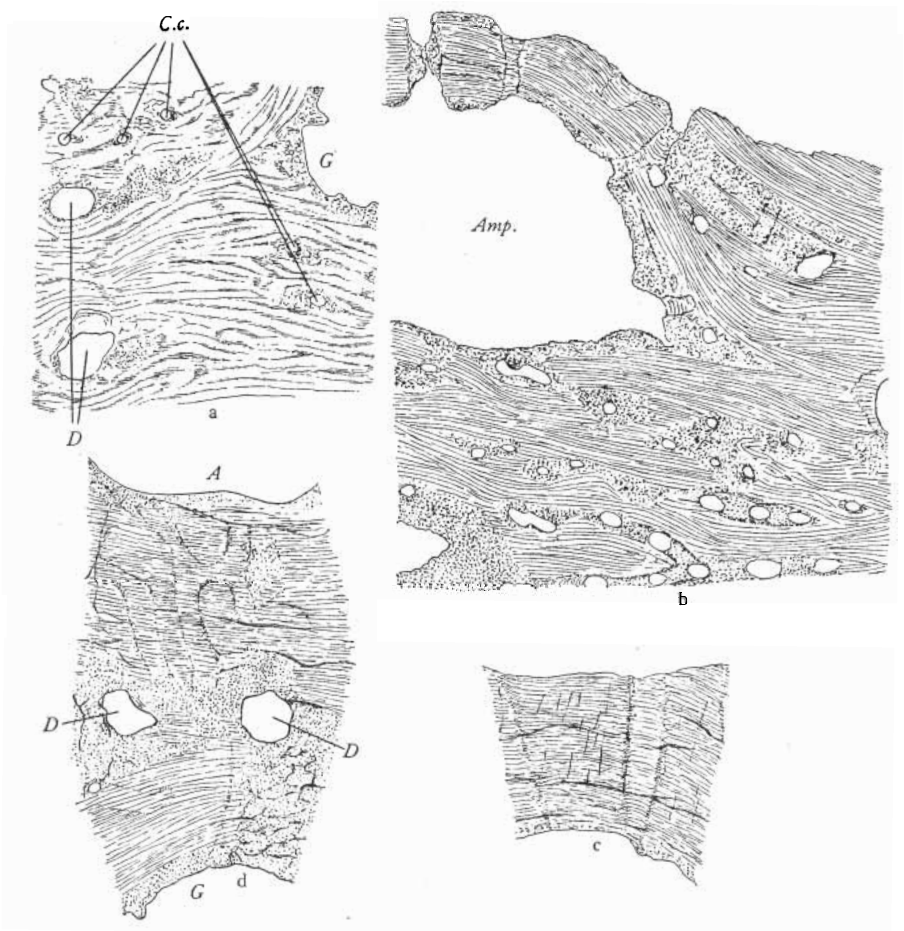


Fig. 34. *Stylaster (Eu-Stylaster) eximius.* — a from a somewhat thicker section of the coenosteum of a branch. b peripheral part of a thin, axial longitudinal section of a branch through an ampulla. c part of the ampulla roof from a thin transverse section of a small branch. d another part of the same transverse section. (A ampulla, G gastropore, D dactylopore, Cc coenenchym-canals. × 120.)

again terminate at the surface as similar ledges or broad teeth, now pointing slightly obliquely in the opposite direction of that of the other end of the lamella.

The same minute texture is observed in *Stylaster (Eu-Stylaster) eximius*, but the single calcareous lamellae are here even a little thinner. In transverse sections of the branchlets (Textfig. 34 b, c) the lamellae mostly seem to run parallelly with the surface of the coenosteum, although they are arranged parallel with the internal surface of the roof of the ampullae (Textfig. 34 b). This is even more obvious in an axial, longitudinal section of a branchlet (Textfig. 34 d), where the lamellae seemingly have been loosened from the inner part of the branch and bent upwards or, better,

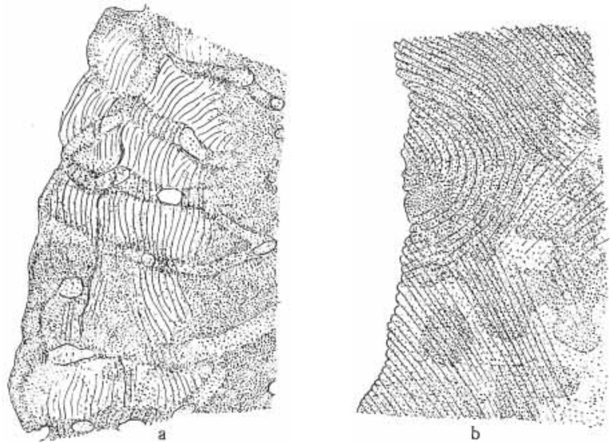


Fig. 35. *Stylaster (Eu-Stylaster) filogranus.* — a peripheral part of a thin transverse section of the coenosteum of a branch. b peripheral part of a thin axial longitudinal section of a branch showing the ledge-like ends of the lamellae on the surface. (× 120.)

bulged upwards to form the domeshaped roof of the ampulla. In the meantime new lamellae have only been added at the periphery of the bulging roof, where their free borders appear as the usual, here very minute, teeth or ledges.

In slightly thicker sections of *Stylaster eximius* (Textfig. 34 a) the stripes seem to collect into more or less obvious bands. Here somewhat more obvious limiting planes between some of the calcareous lamellae are placed more or less obliquely to the plane of the section and thus cause a moiré-like appearance.

Whereas the single calcareous lamellae of the two mentioned species are very thin, and the structure accordingly very delicate, *Stylaster (Eu-Stylaster) filogranus* exhibits a coarser texture with slightly thicker lamellae (Textfig. 35). Part of a transverse section (Textfig. 35 a), where the lamellous structure can be discerned clearly in comparatively great extent, shows us that the lamellae are in the main arranged rather parallel with the surface of the branch. However, in detail many aberrations and irregularities are observed on account of the intrusion of secondary (irregular) lamellae between the "regular" ones. Longitudinal axial sections of branchlets (Textfig. 35 b) show more irregular striations; in many cases the borderlines even cross at angles, often of about 90°. Closer examination, however, reveals that the lines in such cases are situated in different depths in the comparatively thick slide. — Sometimes some of the lamellae are curved in such a way that they form more or less of a semi-circle with its convexity turned into the branch and with both free ends terminating at the surface as minute points. Here as elsewhere the lamellae normally on the whole terminate at the surface of the coenosteum as diminutive, rounded

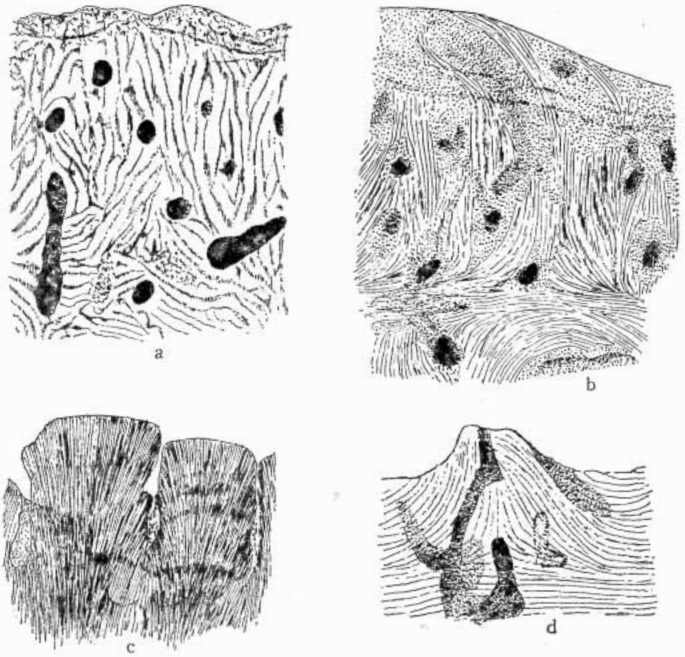


Fig. 36. — a peripheral part of a thin, transverse section of a branch of *Stylaster (Eu-Stylaster) profundiporus.* — b peripheral part of a thin, transverse section of a branch of *Stylaster (Allopora) dentatus.* — c thin section of the "papillae" in a tranverse section of a branch of *Stylaster (Allopora) nobilis.* — d median section of a wart of the surface of *Stylaster (Allopora) granulosus*; from an axial longitudinal section of a branch.
(a, b, and d × 120, c × 285.)

points or ledges. This is, however, not the case in strictly transverse sections of the branchlets (Textfig. 35 a), where the lamellae mostly taper towards their peripheral margin and fade gradually away, so that no tooth or ledge is to be seen.

In *Stylaster (Allopora) granulosus* an axial longitudinal section of the terminal part of a small branch shows almost the same, rather coarse structure as in *Stylaster filogranus*, and in some places also a great resemblance with Moseley's drawing of *Millepora* is obvious. This must at all events in many cases evidently be connected with the formation of the calcareous thorns or small warts of the surface of the coeosteum characteristic of this species. In places where the median plane of the wart coincides with the section (Textfig. 37 d), the lamellae converge at more or less acute angles towards the summit of the wart (or cone), and it is not till some distance below the surface of the branch that the lines again attain their usual orientation, more or less distinctly parallel with the surface of the branch. In places where the section passes obliquely through the median plane of the wart and its basal environs, the border-lines between the lamellae seemingly collect into short bundles meeting under varying angles in different places, thus giving rise to a picture like Moseley's drawing of *Millepora*.

The hitherto mentioned features clearly indicate that the texture should not here be designed as fibrous. The finer texture of the coenosteum must in these species be characterized as lamellous.

However, in many cases the texture seems to be much more irregular than in the above mentioned species; the lamellae have very different extensions and width, and they are interposed in different ways. Such irregularity is observed in e. g. *Stylaster (En-Stylaster) profundiporus* and *Stylaster (Allopora) norvegicus*. In the latter species the lamellae are exceedingly thin, and the structure accordingly very delicate; in fact the lamellae of this species in most places seem to be converted into fibres as mentioned below. — The more irregular arrangement of the lamellae in *Stylaster profundiporus* (Textfig. 36 a) gives an impression which in the main may be said to correspond to the drawing of *Millepora* given by Moseley (cf. Textfig. 32), and roughly also to Hickson's drawing of *Errina capensis* (1912 Plate XCVI, Fig. 15).

As far as has been discernible, the majority of the *Stylaster* species have a texture like that hitherto mentioned. However, one remarkable and obvious exception at once attracted the attention, viz. *Stylaster (Allopora) nobilis* (Textfig. 36 c). It should here be emphasized that the coenosteum of this species is intersected by an extraordinarily copious meshwork of very fine coenenchym canals, and the peripheral radiating canals of this meshwork debouch on the surface in such numbers and ways that the surface seemingly consists of closely packed, distally transversely cut calcareous papillae. These papillae, however, are so small and crowded that the surface with lower enlargement seems quite smooth (see Part I, p. 65, Textfig. 20). The substance of the single "papilla" exhibits only a fine, longitudinal striation, the stripes diverging feebly towards the distal end of the papilla (Textfig. 36 c). In this case it is defensible to speak of a fibrous texture. No trace can be detected of lamellae or finer lines more or less parallel with the surface which might be parallellized with the lamellae of the previously mentioned species.

To a certain degree we may say that the coenosteum of *Stylaster profundiporus* (Textfig. 36 a) represents a transitory stage in a line leading from *Stylaster eximius* to *Stylaster nobilis*. Principally the skeletal substance of *Stylaster nobilis* exhibits features of the same kind as that of *Stylaster profundiporus* although much finer. On the other hand, the structural lines seem to indicate that the lamellae in species like *Stylaster nobilis* metamorphose into fibres which between the coenenchym canals are combined into bundles tending to an orientation more or less distinctly perpendicular to the surface of the coenosteum. This transition from lamellae to fibres is more clearly demonstrated by a species like *Stylaster (Allopora) dentatus*

(Textfig. 36 b) the texture of which approaches *Stylaster nobilis* in its fine and narrow striation.

The intersecting canal meshwork of the coenosteum is in *Stylaster (Allopora) norvegicus* almost as copiously developed as in *Stylaster nobilis*. In the surface layers, however, the meshwork has slightly wider meshes, and in spite of the numerous radiating end canals, the surface of the coenosteum has the usual level character of most *Stylaster* species and not the papillous structure of *Stylaster nobilis*. However, the minute texture of the calcareous substance is much the same in both species. It looks fibrous with bundles of fibres generally almost entirely perpendicularly orientated to the surface of the coenosteum, i. e. parallel with the radiating canals of the branches.

It may thus seem as though a certain correlation exists between the finer texture of the coenosteum and the development of its canal system. A richer development of the canal system is evidently combined with the development of a finer texture of the calcareous substance, and seemingly the last phase of this development is a conversion of the lamellous texture into a more or less obviously fibrous texture.

Growth. In an earlier paper I have by aid of a diagram (Broch 1914, p. 5, Textfig. A) given the mode of growth of *Pliobothrus symmetricus*. In the same paper furthermore attention has been drawn to the formation of concentric layers in the coenosteum of *Stylaster gemmascens* and *Stylaster norvegicus*. As to the latter "the concentric layers, which indicate a periodic growth of the colony, are also distinct here on thin transverse sections of branches of the colony and are also readily seen in transverse series of sections of branches which are freed from their calcareous substance."

Even though it has not been directly stated in the above quoted paper, it is evident that the growth of the coenosteum has a priori been considered to be appositional and not intussusceptional. This of course holds good, even though canals sometimes secondarily may be filled up, or new canals formed in the more central parts of the coenosteum, especially in thicker branches.

"Growth zones" are observed in most Stylasteridae, and the present rich material has also been studied as to these features.

A glance at Plate VI at once shows us that the branches are built of concentric and comparatively pellucid layers of calcareous substance alternating with narrow zones of less transparency. Microscopical investigation of the calcareous substance has not revealed any structural differences of importance between the broader growth zones and the narrow "border zones" completing them. Possibly one might say that the border zone in some cases has a somewhat denser character, but generally it is also with greater enlargement impossible to detect clearly definable differences. On the other hand, similar zones are also observed in series of microtome sections of decalcified branches, and in this case the organic, structureless tissue is much more copiously developed and denser in the narrow border zone than in the broader part of the growth zone (generally only mentioned as the growth zone).

These features show us that it is defensible to use the terms as indicated. During the more intensive growth (or period of growth) a "growth zone" is built of almost pure calcareous substance which is rather pellucid. The approximate stagnation (or strong depression) of growth occurring at intervals, results in a "border zone", narrower zone with comparatively much organic matter interweaving the calcareous substance which accordingly is much less pellucid. In many cases the border zone may be rather broad, and in such cases the differences between the two zones are proportionally less pronounced. Here then, the different rate of growth has evidently been proportionally slight in different periods.

The growth zones may differ as to width and numbers in different colonies from one locality, or even in branches of the same colony in a way that we cannot surely assert that they are the results of certain yearly or other, regularly returning periods demonstrable at the present. But even though we cannot at present point out the cause of the periods, the zones of the coenosteum give us valuable information concerning the mode of growth of the colonies.

In the typical *Eu-Stylaster* colony one might be tempted to speak of a principally sympodial growth. Evidently the cyclosystem (which must here be treated as a whole, for example like one polyp of a Hydroid, e. g. *Laomedea*) buds at the very apex of the branch, and a new centre of growth arises at one side of the basis of the cyclosystem. In the *Eu-Stylaster* species the new centra of growth alternately arise laterally at the basis of the cyclosystems, and the terminal branchlets are therefore generally zigzag. Secondarily a centre of growth may later on arise at the other side of the basis of a cyclosystem; in this case a branching of the same kind as that of a composite sympodium is the result ("cymose growth").

In the *Stenohelia* group of *Stylaster* a similar budding and branching is observed. But here the new centre of growth is at one (the hind) side of the cyclosystem, only alternately slightly removed to one or the other side, so that the terminal branchlets also here attain a zigzag shape. New branches arise in the same way as in *Eu-Stylaster*, centres of growth coming into action on both postero-lateral sides of a cyclosystem.

The *Allopora* group of *Stylaster* may be said to have developed in the opposite direction. In slender species, or in species with slender terminal branchlets and branch-ends, principally the same mode of budding is observed, only that the new centres of growth may here arise at any side of the basis of the terminal cyclosystems. The latter accordingly have their openings irregularly turned towards all sides of the branchlets, and these do not exhibit the regularly zigzag shape more or less pronounced in *Eu-Stylaster* and *Stenohelia*.

During subsequent growth of the branches the appearance of the colony changes differently in different species of *Stylaster* on account of a varying proportionality between the longitudinal and the transversal growth of the branches. Many species like for instance *Stylaster (Eu-Stylaster) eximius*, *Stylaster (Eu-Stylaster) asper*, or *Stylaster (Stenohelia) complanatus* only exhibit a very slow additional transversal growth also in their older branches, and the colonies therefore throughout show a slender construction. In other species like for instance *Stylaster (Allopora) boreopacificus*, *Stylaster (Allopora) campyleca*, some colonies of *Stylaster (Eu-Stylaster) sanguineus* et al., the terminal branchlets are very slender; but already their mother branches have by rather intensive transversal growth attained much greater dimensions, and the thickness increases rapidly in older parts of the colonies. Thus a species like *Stylaster boreopacificus* shows pronounced and obviously thick main stems.

Some few *Stylaster* species on the other hand already exhibit a very pronounced and vivid growth of width in the end parts of the terminal branchlets which accordingly have a broadly rounded or more or less transversely cut end. This is especially obvious in *Stylaster (Allopora) solidus* and *Stylaster (Allopora) nobilis*. In *Stylaster solidus* the transversal growth seems to cease abruptly so to say directly at the end of the branchlet, and here all branches and stems accordingly have about the same dimensions. In *Stylaster nobilis* on the other hand a rapid transverse growth continues throughout the colony which therefore only has short terminal branchlets, obviously thick mother branches, and still stouter stems. The growth, however, is not homogeneous on all sides, but proceeds on a swifter scale laterally on stem and branches; in accordance herewith the growth zone along the anterior and posterior sides is narrower than laterally on the stem and the main branches. It is in this species also evident that the growth of the branch of course is superficial and terminal. On axial longitudinal sections of the branches, many gastropores with their gastrostyles have been embedded deep into the axial parts of the branches.

Also in *Stylaster campyleca* the growth as above mentioned is rather rapid. Here, however, the growth is rather homogeneous on all sides of the branch, and it is only near the offspring of a branch that the growth zones attain a more irregular aspect (see Pl. VI, Fig. 21). — *Stylaster (Allopora) norvegicus* and *Stylaster (Allopora) verrilli* which in their growth hold an intermediate position between *Stylaster campyleca* and *Stylaster solidus*, also show a generally homogeneous transversal growth (see Pl. VI, Fig. 20).

In extreme cases one might so to say expect that the terminal growth (the length growth) entirely ceases with the completed development of the cyclosystem, and that only a lateral extension (transversal growth) of the colony continues later on. This would then lead up to encrusting or "creeping" colonies like those of *Stylaster (Allopora) porphyrus* and its next allies (see Fisher 1931). However, I have not had sufficient material of such encrusting forms to analyse this working hypothesis critically.

The mode of growth and, in accordance with it, the configuration of the colony is more varying and manifold in the genus *Stylaster* with its numerous species than in any other genus of the Stylasteridae as far as is known at present. It is interesting to note the parallelism with other large groups of the Hydroids like for instance the Bougainvilliidae or the Campanulariidae. Also here we find "creeping" species which spread a more or less openly constructed meshwork of stolons over the surface of a substratum, or this meshwork may even *(Hydractinia)* be transformed into a continuous crust reminiscent of *Stylaster porphyrus* and its allies. Other species again have developed rhizocauloms *(Perigonimus muscoides* M. Sars, *Campanularia verticillata* (Lin.), *Clathrozoon)* which in many respects are allied to the colonies of the *Allopora* group (cf. also below, the Sporadoporinae), and in some cases lastly *(Laomedea)* a real hydrocaulus has developed which may even exhibit exactly the same "cymose sympodia" which evidently characterize the species of the *Eu-Stylaster* and the *Stenohelia* groups.

### *Errinopora.*

In the other genera of the Stylasterinae only *Errinopora stylifera* (= *Protoerrina stylifera,* Part I, p. 101) offered sufficient material for an investigation of the coenosteum. The coenosteum is here intersected by a very copious and fine-meshed meshwork of canals, and the skeletal substance exhibits a texture somewhat of the same character as *Stylaster nobilis.* In some places a longitudinally, very delicate and close striation may be observed; but in most places the texture is so delicate that the skeletal substance here seems almost entirely homogeneous and structureless.

The growth gives rise to rather obvious growth zones (Pl. VI, Fig. 22). These zones are on account of their course only faintly visible in transverse sections of the branches, whereas in longitudinal sections they are very obvious. The transversely cut ends of the branchlets evince an intensive, though very rapidly ceasing transverse growth, whereas the growth zones demonstrate an intensive and continued terminal (longitudinal) growth. The growth zones therefore fade away towards the periphery of the branch and almost disappear in transverse sections. It is also in accordance with this mode of growth that all branches of *Errinopora stylifera* have almost equal dimensions, and that the increase in thickness is very slow and gradual from the terminal branchlets to the main stems.

### *Distichopora.*

**Structure.** Turning now to the genera of the other sub-families we shall in accordance with the systematic part commence with the Distichoporinae. — The skeletal texture has been examined in five species, viz. *Distichophora violacea* forma *typica* and forma *cornuta, Distichopora fisheri, Distichopora serpens, Distichopora borealis,* and *Distichopora irregularis.* The structure of these species is remarkably uniform, also in the last named species which on external examination differs markedly from all other species of the genus.

It is in all species of *Distichopora* throughout defensible to speak of the texture of the calcareous substance as "fibrous", and the main direction of the fibres is always perpendicular to the surface of the branch (see Textfig. 37 a, b). The skeleton is in all directions intersected by the meshwork of coenenchym canals; but they do not in any way influence the structural striation. It has on the other hand been impossible to trace lines parallel with the surface which might indicate "growth lamellae". Probably the fibrous texture must be explained in the same way as in *Stylaster nobilis.*

In *Distichopora violacea* the walls between the pores af a lateral pore-row besides the delicate and close striation caused by the "fibres" also exhibit some somewhat coarser lines partly parallel with, partly crossing the fibres at varying angles and thus inducing another and somewhat wider structural network. This structure was also observed now and again in some places in slides of *Distichopora fisheri* and *Distichopora serpens.*

In very thin sections of the pore walls of *Distichopora violacea* (Textfig. 37 c) the calcareous substance seems to be composed of sclerites the limits of which are seen as serrulate, delicate lines. Although each "sclerite" so to say has its own system of fibrous striations, the structural lines of the entire wall (septum) nevertheless give the impression of one unit with longitudinal, towards the summit of the wall feebly diverging, "fibres". To a certain degree the features somewhat recall the pictures of skeletal elements in stony Corals given by OGILVIE (1896, see for instance Fig. 8 A—C). However, when we consider their dimensions and compare them with the cells of the tissues of *Distichopora* in decalcified specimens, it seems exceedingly questionable that they should really indicate calicoblasts.

In *Distichopora borealis* forma *japonica* a study of the finer details was rendered extraordinarily difficult by numerous, almost streak-like, straight canals crossing the skeletal substance in all directions. These canals are much narrower than the normal coenenchym canals of the coenosteum (their diameter measuring about $^1/_{10}$ of that of the coenenchym canals), and they might easily have been overlooked in smaller numbers, if they had not been filled by air and therefore appear like silvery threads in the slides. In some cases these fine canals branch, and the side branches

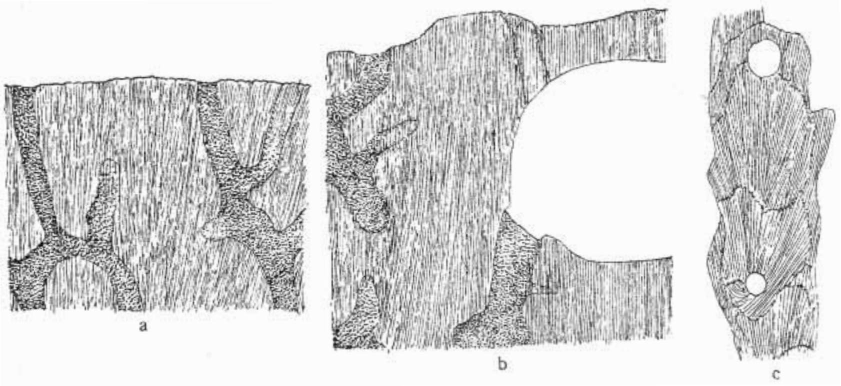


Fig. 37. *Distichopora violacea* f. *typica*. — a peripheral part from the polypless side of a transverse section of a branch. b peripheral part of a longitudinal axial section of a branch perpendicular to the plane of the pore-rows; to the right an ampulla. c part of the wall between two gastropores; from an axial section through the pore-rows of a branch. (× 135.)

emerge under rather acute angles from the mother canals. — Such fine and straight canals are also observed in slides of *Distichopora fisheri*, although in much smaller numbers. Probably the canals are caused by some parasitic micro-organisms boring in the calcareous skeletons. They have only been observed in the two mentioned species (the localities of the specimens are Okinose in the Sagami Sea, depth 60 fathoms, and the barrier reef of Namuka, Viti, Levu, Fiji Islands).

Growth. Under the lens, growth zones are easily observed. They are especially obvious in longitudinal axial sections of the branches perpendicular to the plane of the pore-rows (Pl. VI, Fig. 23). Evidently the zones evince a periodic rhythm in the growth. It is on the other hand also in this connection of interest to consider their relations to the pores (cf. Text-fig. 1—4). It is readily observed that new gastropores as well as dactylopores are formed at the periphery of the branch between the older pores, and that the depth-growth of a pore is caused by the addition of new calcareous substance at the mouth of the pore, i. e. at the surface of the branch, and not by an active growth of the pore deeper down into the older parts of the coenosteum. It may be added that the distinct zones of growth demonstrate that the terminal (length) growth of the branches of *Distichopora* is proportionally very rapid. On the other hand the slight differences in thickness of branchlets, branches, and stems in *Distichopora* evince a comparatively very slow transversal growth.

## *Sporadopora.*

Structure. Among the Sporadoporinae it is natural to commence with the primitive genus *Sporadopora*. The calcareous substance of *Sporadopora mortenseni* has a coarser crystalline texture than any other examined species, and it might therefore generally be designed as "coarsely granulate". The granulation is in fact so obvious that structural lines indicating lamellar or fibrous texture entirely fade away. Only in some few places do lamellae of growth seem to be indicated in transverse sections of small branches, and in such cases they are in the main orientated parallel to the periphery of the branch.

These features are of special interest in comparison with the statements of MOSELEY (1878, 1881) concerning *Sporadopora dichotoma*. Although he states that its "histological texture" coincides with *Millepora*, he emphasizes that it is more granular, and that its "fibrocrystalline" nature accordingly is less prominent. — The coenosteum of *Sporadopora* is intersected by an extraordinarily copious and close mesh-work of coenenchym canals. This should be noted here, because the general rule otherwise seems to be that the fibrous structure is more prominent in species with richly developed canal systems than in species with more scantily developed mesh-works of canals.

Growth. Transverse sections of thicker main branches show peculiarities in the arrangements of the coenenchym canals emphasizing the formation of broader zones of growth (Pl. VI, Fig. 24). The central part of the branch contains several wider, longitudinal canals (evidently prolonged pores of the primary gastrozooids) and therefore here exhibit an extraordinarily wide-meshed calcareous mesh-work which, however, rather abruptly changes into the more compact main parts of the branch. Here the skeletal substance dominates, and at the same time it seems to attain a more compact texture. The texture also little by little becomes slightly more compact towards the periphery, and the canal mesh-work more open, until we meet with a circle caused by a row of very closely placed canals parallel with the periphery of the branch. Outside of this circle the structural rhythm repeats itself until another circle is formed etc. Towards the periphery of the branch the single growth zones gradually become narrower, i. e. the growth proceeds more slowly.

The entire picture indicates a periodic growth with liveliest development of canals at the beginning of the period, and with gradually diminishing development of canals and increasing deposit of skeletal substance. Probably the growth is most intensive (rapid) at the commencement of this period. The older and thicker the branch is, the slower is evidently the growth; this is easily deduced from the diminishing dimensions of the single zones of growth.

## *Pliobothrus.*

The finer texture of *Pliobothrus seriatus* is extraordinarily delicate; evidently we should call it fibrous, but in most places it is so delicate that the calcareous substance exhibits a semipellucid, porcellaneous and almost entirely homogeneous aspect. — Axial longitudinal sections of the branches (Pl. VI, Fig. 25) give evidence of a proportionately intensive terminal (length) growth, whereas the transverse growth soon ceases. The colonies are accordingly also delicate with rather slender stems. — Seemingly the growth of *Pliobothrus symmetricus* is much more of the type of *Stylaster solidus* or *Errinopora stylifera.* Also here the terminal growth is probably rather rapid; but also the transverse growth is terminally very rapid and ceases thereupen abruptly, so that the stout branchlets are only slightly thinner than the main branches and the stems.

## *Errina.*

Structure. The finer texture of the coenosteum has been examined in three species of the *Eu-Errina* group. Sections of *Errina antarctica* and *Errina spongiosa* merely exhibit a uniform, minutely granular structure. Even in *Errina spongiosa* the skeletons of which in cleaned branches exhibit a striking resemblance with a lump of sugar, the single grains (crystals?) are exceedingly small and do not suffice for an investigation by refraction. The calcareous substance of these species is evidently very homogeneous and does not show any indications of lamellar or fibrous texture.

Also slides of *Errina rubra* in most cases show a similar, finely granulate texture. In some places, however, a fibrous structure corresponding to that of *Distichopora* is observed. This structure has been observed in a few places in transverse sections of thicker main branches, and also in a few places in an axial longitudinal section of a thin, peripheral branchlet. This fibrous structure can in *Errina rubra* only be seen in extraordinarily thin sections. The fibres are in the main radially orientated in a transverse section, i. e. they generally stand perpendicularly to the axis of the branch.

In the *Labiata* group *Errina cervicornis* exhibits a remarkably coarse and obvious lamellar structure (Textfig. 38). Here as elsewhere great parts of the sections only show a granular texture hiding finer structural lines; but the granulate parts are comparatively smaller in extent in the slides of *Errina cervicornis* than in most other investigated Stylasteridae.

It is easily seen in transverse sections of small branches (Textfig. 38 a) that the lamellae are fine layers, in the main parallel with the periphery of the section (branch). In the more central parts of the branches the course of the lines is seemingly more irregular and may here often agree more with the picture of *Millepora* given by Moseley (see Textfig. 32). Similar features may also be observed in longitudinal axial sections of the branches of *Errina cervicornis* (Textfig. 38 b), and in these sections we also observe the ledge- or point-like ends of the lamellae at the surface of the branch. The lamellar texture and the entire structure of *Errina cervicornis* thus entirely agrees with that of *Stylaster filogranus* and *Stylaster granulosus.*

In a slide of *Errina cervicornis* the complete axial section of a gastropore could be studied (Textfig. 38 c). Round the gastropore the lamellae

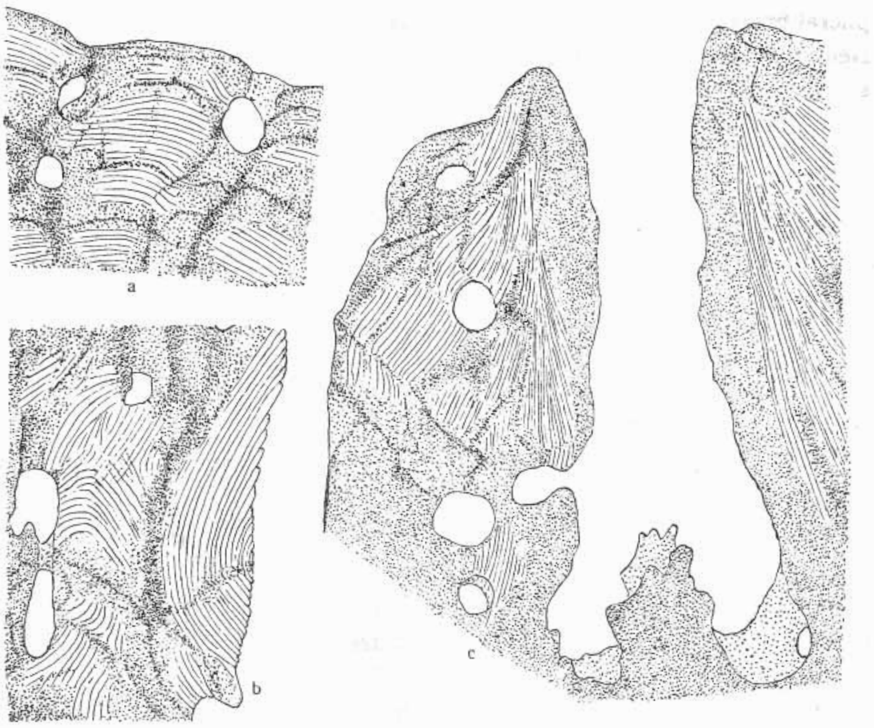


Fig. 38. *Errina (Labiata) cervicornis.* — a peripheral part of a thin transverse section of a branchlet. b peripheral part of a longitudinal axial section of a branch. c from a transverse section of a branch, at the same time axial section through a gastropore, and at the bottom of the latter its gastrostyle. (× 135.)

rise to a position almost parallel with the axis of the pore and converge steeply towards the summit of the "lip". The structural lines give the impression that the lamellae had been bent upwards by an internal pressure starting from the basal (primary or bottom) part of the pore.

Also the other species of the *Labiata* group, *Errina tenuistylus*, exhibits a lamellar texture which in its main features agrees with that of *Errina cervicornis*. But the layers are very much thinner: the structural lines are almost equally crowdedly placed as in *Stylaster eximius* or in the *Distichopora* species (see Textfig. 34 and 37). This very delicate structure is no doubt the cause of the rather semipellucid, porcellaneous impression of the entire coenosteum. Although the coenosteum also in *Errina cervicornis* is hard and not so sugar-like as in the species of the *Eu-Errina* group, it has not the semipellucidity of *Errina tenuistylus*.

Growth. The periodicity of growth demonstrated by the broader concentric growth zones in other species is remarkably feebly pronounced in the *Eu-Errina* species. In main branches of *Errina rubra* such zones are observed, although they are only faintly seen; they are here rather narrow and seem to indicate a comparatively slow growth. In the peripheral branchlets on the other hand, no such zones could be distinguished. — Neither in *Errina antarctica* nor in *Errina spongiosa* (Pl. VI, Fig. 26) have such structural growth zones been observed.

This is the more surprising in the last named species, because we here find series of older pores with their styles immersed in the central parts of thicker branches and thus probably have before us a species with especially rapid, periodical growth. In the systematic chapter it has been mentioned (p. 50) that the pores with their styles so to say occur in several floors, but that they do not form a direct continuation of each other, the new (successive) pore with its polyp arising at the side of the mouth of the old pore which here is closed by a "tabula". In this way the branches grow harmoniously and intensively in length and thickness. The pores give the impression that the formation of a new layer with all its pores proceeds spontaneously on a branch or on the branch and its branchlets, possibly even throughout the colony.

In the *Labiata* group no zones of growth could be seen in *Errina cervicornis*. It must, however, be kept in mind that only very few slides of this species could be examined. On the other hand transverse sections of somewhat thicker branches of *Errina tenuistylus* exhibit numerous extraordinarily distinct growth zones (Pl. VI, Fig. 27); but the narrowness of the zones at the same time indicates that the transverse growth must be rather slow. This also agrees well with the general impression of the colony; the stems and main branches are only very little stouter than the branchlets, and the construction of the colony is on the whole rather delicate. —

A few words may also be added here about the development and branching of the colonies in the Distichoporinae and Sporadoporinae.

The budding and growth of the branches in *Distichopora* obviously stand in relation to the pore-rows. Generally the new branch arises in the plane of the pore-row as a bulging out of the lateral side of the mother branch, and the young bud has an intensive apical growth, whereas no or all but no transversal growth is observed. In other words, the branch increases rapidly in length, whereas its diameter increases if at all, only with the utmost slowness. — In some cases, most frequently in *Distichopora violacea* forma *cornuta* (see Pl. I, Fig. 2), also small or incipient branches are found on the polypless anterior or posterior, flat sides of the colony. The new branch is here indicated by a short, linear, or in rare cases more cyclosystem-like group of pores, which little by little is elevated and grows out in the same way as the lateral branchlets.

Although the correlation between pore-rows and branch budding is not so obvious in *Distichopora irregularis*, the colonies here also bud mainly in one plane and are therefore flabellate.

In its principal features the budding and branching of *Distichopora* thus coincides with the *Eu-Stylaster* and *Stenohelia* groups of the genus *Stylaster*, although the colonies of *Distichopora* have a somewhat less regular shape, because the definite and regularly disposed cyclosystems of *Stylaster* here are merged into one coherent pore-row along the lateral sides of the entire branch. The budding is accordingly not limited to certain, narrowly circumscribed spots dependant on the site of the single cyclosystem.

In the genera of the Sporadoporinae the budding and shape of the colonies generally agree with those of the common type of the *Allopora* group of *Stylaster*. It is in most cases impossible to detect any regular correlation between the site of the polyps and the branching, excepted that the branch also here commences as a polyp-carrying bulge on the side of a mother branch. The buddings and branching are in most cases restricted to one plane, the colony on the whole therefore attains a flabellate shape. Only in rare cases *(Errina spongiosa, Sporadopora mortenseni)* does the branching proceed in all directions, so that the colonies here are quite irregular and bushy.

A somewhat more regular mode of branching is observed in *Pliobothrus*. The branching of *Pliobothrus symmetricus* is almost quite dichotomous, and the flabellum is accordingly very characteristic. The rather aberrant species *Pliobothrus seriatus* has zigzag branches giving rise to branchlets at almost every bend. The entire colony therefore reminds us of *Stylaster (Stenohelia) complanatus*. Nevertheless no regular correlation can be detected between the seat of the polyps and the budding of the branches, not taking into consideration the general rule that the branchlets arise laterally on the mother branches, i. e. in the lateral rows of dactylozooids.

On the whole the mode of growth of the Sporadoporina confirms the old assumption already advanced by MOSELEY (1878, 1881), that these genera must be looked upon as the more primitive and phylogenetic older ones among the Stylasteridae, an assumption at which MOSELEY arrived, based mainly on studies of the polyps and their relations. He is probably right in his opinion that *Sporadopora* is the oldest phylogenetically of the recent genera of the Stylasteridae, and it may be added that *Distichopora* and the *Stenohelia* and *Eu-Stylaster* groups of the genus *Stylaster* probably represent the summits of their two somewhat divergent lines of development.

A comparison of the skeletons of Stylasteridae and Madreporarian Corals reveals such differences that it should be possible to distinguish between them with certainty in most cases.

In her elaborate study Miss MARIA M. OGILVIE (1896) shares the old opinion of HEIDER (1886) that "the skeletal deposit forms, in the first place, within the calicoblast". In her drawing Fig. 8 (l. c.) this calcification is illustrated, and the drawings moreover give the impression that the calcareous substance is formed as thread-like fibres, often continuously through more calicoblasts in a radial direction to the centre of calcification (of growth). On the other hand the structural lines limiting the fine growth lamellae perpendicularly to the radiating fibres are explained by Ogilvie in the following way: "that the growth-lamellæ were originally layers of calicoblasts, and that their wavy outlines corresponded to the originally independent cells."

Only in the walls between the pores of *Distichopora violacea* have structural lines been observed which to some degree remind us of the calicoblasts of Madreporarian Corals with their serrulate (or "wavy") outlines. A comparison with the cells of decalcified specimens, however, shows us that the supposed "calicoblasts" are here many times as large as any cell of the coenenchym. Each of the scale-like elements must in *Distichopora* have been built up of several cells.

On the other hand the skeleton of the Stylasteridae may be fibrous or lamellar, although not in quite the same way as that of the stony corals. In these the structure is at the same time both "fibrocrystalline" with fibres radial to the centre of growth (calcification), and lamellar, with lamellae concentrically arranged around the above mentioned centre. Septae and thecae of stony corals moreover show regular systems of several obvious centres of calcification (growth centres).

Each branch or stem of a Stylasterid colony has only one centre of calcification, viz. the axis of the branch (stem), and this centre of growth is in most cases not especially accentuated in the structure or different from the calcareous substance elsewhere. In some cases the calcareous substance is throughout "granulate", consisting of such small grains or crystals that they are in most cases inaccessible for a crystal analysis by refraction. In other cases an obvious lamellar texture is present, and although the picture may be difficult to unravel in many cases, especially when oblique sections are examined, one can see that the lamellae in transverse sections of the branches are more or less distinctly parallel with the surface of the coenosteum. In longitudinal sections, however, the lamellae run slightly obliquely to the surface and terminate here as a feeble point or ledge. In some other species again (e. g. *Stylaster dentatus*) the thin lamellae have a more irregular orientation, and in many parts they take a rather radial course to the central axis of the branch. The structure is in such cases also so fine that it is proper to designate it as "fibrous". It leads over to the radially fibrous texture of species like *Stylaster nobilis*, *Distichopora*, et al.

The skeletons of the Stylasteridae are always permeated by a meshwork of fine canals. One might a priori suppose that the calcification to some degree might be regulated by this canal system, and that the structure accordingly should display some correlation to it. This, however, is not the case. It is clearly observed in all slides that the course of the structural lines is independent of the canals. The canals are evidently formed quite independently of the calcification, and in many cases one gets the impression that canals have made their way secondarily through the skeletal substance, or that the canals in other words, at all events in many cases, are formed by a secondary dissolution of the calcareous substance. Such dissolution is no doubt the cause of the large axial canals in the greater branches and stems of the *Sporadopora* species and of *Pliobothrus symmetricus*.

The features thus summed up should suffice to distinguish between the skeletons of Hydrocorals and real stony corals. They may be recapitulated in few words as follows:

The skeletons of Hydrocorals (Stylasteridae) have in most cases throughout or in part a finely granulate structure, or they exhibit partly or seldom throughout, lamellar or fibrous structure. The fibrous texture is derived from the lamellar; and accordingly fibres are not found together with and perpendicularly to the lamellae. Evident conspicuous centres of calcification (of growth) are lacking, and the skeleton is in all directions permeated by a mesh-work of fine canals which, however, do not influence the course of the structural lines of the skeletal substance.

In Madreporarian Corals regular systems of obvious centres of calcification (centres of growth) occur, and radiating from them, the calcareous substance seems composed of fine fibres which almost unbrokenly cross the parallel lines of concentric growth lamellae at right angles. Where the skeleton is perforated by finer canals (*Madrepora*, *Porites* et al.), several centres of growth are clearly visible in the walls between the pores, and the structure thus displays evident correlation to the canals (or "pores").

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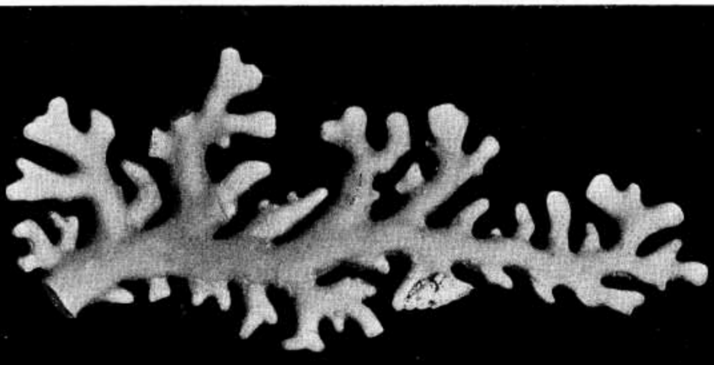
# PLATES

## Plate I

Fig. 1. *Distichopora violacea* forma *typica.* Specimen from Jaluit, Marshall Islands, entrance reef. — Nat. size.

Fig. 2. *Distichopora violacea* forma *cornuta.* Type specimen from Aranuka, Gilbert Islands, entrance reef. — Nat. size.



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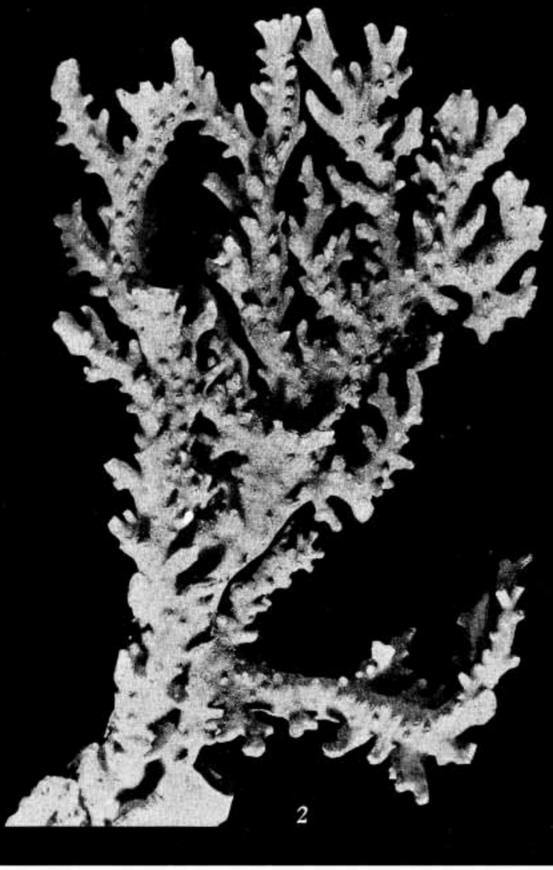

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*Olaf C. Bache photo.*

## Plate II.

Fig. 3. *Distichopora fisheri.* Type specimen from Viti Levu, Nanuka, Fiji Islands, barrier reef. — Nat. size.

Fig. 4. *Distichopora irregularis.* Off Jolo, Philippine Islands, depth about 25 fathoms. — Nat. size.

Fig. 5. *Distichopora borealis* forma *japonica.* Okinose, Sagami Sea, depth 60 fathoms. — Nat. size.

Fig. 6. *Distichopora sulcata.* „Albatross", 30 Miles N.E. from Cozumal Island, depth 130 fathoms. — Nat. size.

Fig. 7. *Distichopora foliacea.* Gulf Stream Exploration. depth 100—200 fathoms. — Nat. size.

Fig. 8. *Distichopora serpens.* Type specimen. 12° 27' N., 124° 3' E., San Bernardino Strait, Philippine Islands, depth 50—100 fathoms. — Nat. size.

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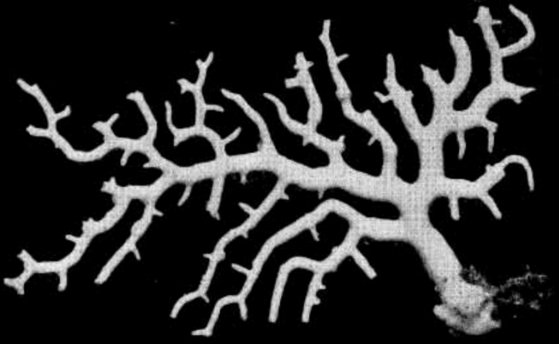
*Olaf C. Bache photo.*

## Plate III.

Fig. 9. *Sporadopora mortensenі.* Type specimen. Three Kings Island, New Zealand, depth 65 fathoms. — Nat. size.

Fig. 10. *Pliobothrus seriatus.* Type specimen, off Tombeau Bay, Mauritius, depth about 150 fathoms. — Nat. size.



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## Plate IV.

Fig. 11. *Errina* (*Eu-Errina*) *aspera*. **West Indies. — Nat. size.**

Fig. 12. *Errina* (*Eu-Errina*) *antarctica* forma *typica*. Cape Horn. — Nat. size.

Fig. 13. *Errina* (*Eu-Errina*) *rubra*. Above a fragment of a larger colony, below a small colony growing on a Hydroid. Three Kings Islands, New Zealand, depth 65 fathoms. — Nat. size.

Fig. 14. *Errina* (*Eu-Errina*) *novæ-zealandiæ*. Fragment of one of HICKSON's type specimens, Preservation Inlet, W. coast of South Island of New Zealand, depth about 3 fathoms. — Nat. size.

Fig. 15. *Errina* (*Eu-Errina*) *capensis*. Fragment of HICKSON's type specimen. Cape of Good Hope. — Nat. size.

Fig. 16. *Errina* (*Eu-Errina*) *spongiosa*. **Type specimen.** 53° 45′ S., 61° 10′ W., Burdwood Bank south of W. Falkland, depth 137—150 m. — Nat. size.

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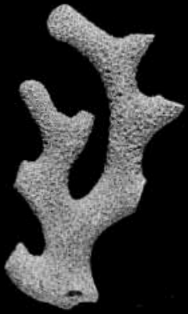

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## Plate V.

Fig. 17. *Errina (Labiata) tenuistylus.* Type specimen, off Tombeau Bay, Mauritius, depth about 150 fathoms. — Nat. size.

**Fig. 18.** *Errina (Labiata) cervicornis.* Type specimen. 2 Miles E. of North Cape, New Zealand, depth 55 fathoms. — Nat. size.

Fig. 19. *Paraërrina decipiens.* Type specimen, off Tombeau Bay, Mauritius, depth 130 fathoms. — Nat. size.

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## Plate VI.

Fig. 20. *Stylaster (Allopora) verrilli.* Transverse section of a branch with several obvious growth zones. x 10.

Fig. 21. *Stylaster (Allopora) campyleca* from Yukatat. Transverse section of a thick branch with numerous obvious growth zones. x 5.

Fig. 22. *Errinopora stylifera.* Axial section of the terminal part of a branch; the several obvious growth zones are hardly or not visible in transverse sections. x 5.

Fig. 23. *Distichopora violacea* forma *typica.* Axial section vertically to the plane of the pore-rows. The obvious growth-zones give evidence of an intensive terminal growth. x 5.

Fig. 24. *Sporadopora mortenseni.* Transverse section of a main branch. The rather broad growth zones are emphasized by the development of the canal system. x 5.

Fig. 25. *Pliobothrus seriatus.* Axial secton of a branch. Growth zones are observed with some difficulty and are in a few cases more distinct in transverse sections. The terminal growth is quite dominant. x 5.

Fig. 26. *Errina (Eu-Errina) spongiosa.* Transverse section of a branch; growth zones are not observed. x 5.

Fig. 27. *Errina (Labiata) tenuistylus.* Transverse section of a thicker branch with several, rather obvious growth zones (the slide is a little obliquely ground and comprises only about two thirds of the branch, the third to the right being ground away). x 10.


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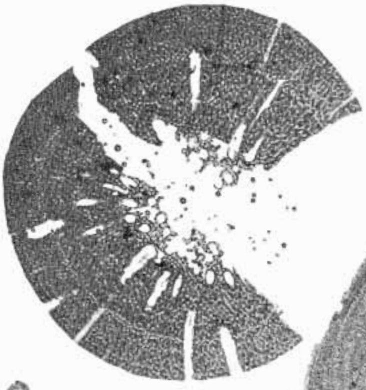
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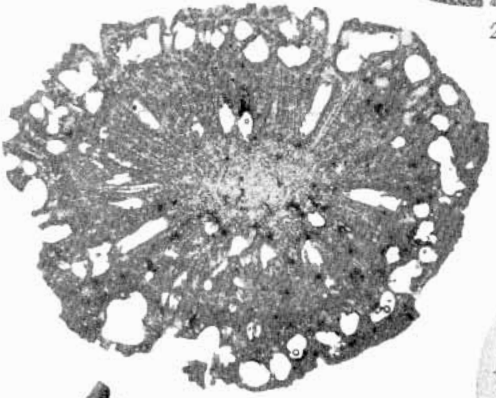
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