

II. "Preliminary Note on the Structure of the Stylasteridæ, a group of Stony Corals which, like the Milleporidæ, are Hydroids, and not Anthozoans." By H. N. MOSELEY, Naturalist on board H.M.S. 'Challenger.' Communicated by Professor WYVILLE THOMSON, F.R.S., Director of the Civilian Scientific Staff. Received May 5, 1876.

On 14th February, 1876, in lat. $37^{\circ} 17' S.$, long. $53^{\circ} 52' W.$, off the mouth of the Rio de la Plata, the trawl brought up from 600 fathoms a number of specimens of corals of the family Stylasteridæ (Gray *). The specimens included six genera of the family and seven species. They were all in most excellent preservation, notwithstanding the fact that they had been slowly raised from 600 fathoms, and all had their generative organs in full development. An opportunity which had long been desired was thus afforded for making a detailed examination of the structure of the soft parts of this family, which, in the structure of its coralla, shows so many points of variance from that of Zoantharian coralla. From observations made on a species of *Stylaster* obtained from 500 fathoms off the Meangis Islands, and on a *Cryptohelia*, a short account of which is given in the Royal Society's 'Proceedings,' vol. xxiv. p. 63, I had already been led to suspect that the Stylasteridæ might prove to be Hydroids, although I did not venture to express this opinion because the evidence was then insufficient. The examination of the series of forms obtained off the Rio de la Plata at once showed that the Stylasteridæ are true Hydroids.

Unfortunately the trawl came up rather late in the day, and hence a very short period of daylight was available for the examination of the animals in the fresh condition; but it sufficed for the sketching of the male gonophores of a new genus of Stylasteridæ (*Polypora*), with the stages of development of the spermatozoa, and of the female gonophores of *Cryptohelia*.

Portions of the corals were preserved by means of chromic acid, osmic acid, absolute alcohol, and glycerine; and they were subsequently examined in the usual manner by means of sections. In cutting the sections, a new method, described by Mihakowics, 'Arch. für mikroskopische Anatomie,' ii. Bd. 3 Hft. p. 386, was adopted, and found to yield most astonishingly successful results. The method seems to supply a want long felt of a means of cutting fine sections of structures the parts of which are very loosely held together, and where it is desirable to maintain the exact relations in position of parts which in the sections often become entirely disconnected from one another. Mihakowics used his method for sections of vertebrate embryos; it is certainly the best possible method for the investigation of decalcified tissues, such as those of Corals or Echinoderms. A strong jelly, composed of equal parts of glycerine and gelatine, is used as an imbedding substance; it permeates

* Ann. and Mag. Nat. Hist. vol. xix. (1847).

the tissues, and takes the place of the hard calcareous supporting structures which have been removed by the acid. The sections are mounted in glycerine, and the imbedding substance, which is left *in situ* in the sections, becomes perfectly transparent, in fact almost invisible in this fluid. I stain the decalcified corals with carmine, then soak them in glycerine, and then transfer them directly to the warm fluid jelly, instead of treating them first with absolute alcohol after staining, as does Miha-kowics. A teaspoon heated in hot water is a most convenient instrument for transferring the small masses of tissue, with the fluid jelly, to the cavities in the hardened liver used as an imbedding base. I have dwelt upon this method because it seems to me likely to be one which will prove of the greatest service in all kinds of difficult histological problems, such as Corti's organ, early stages of embryos, retina, &c. It is quite possible by the method to obtain sections of a single hydroid sporosac or planula.

The Stylasteridæ obtained off the Rio de la Plata comprised six genera, viz.:—*Stylaster*; *Cryptohelia*; *Allopora*; *Errina*; a new genus, *Polypora*; and a further new genus allied to *Errina*, which I propose to term *Acanthopora*. There is much confusion as to the determination of even the genera of the Stylasteridæ, and I have found it impossible to determine species in the absence of specimens for comparison. The *Stylaster* appears probably to be *S. erubescens* of Pourtales*. The *Cryptohelia* is the same as that obtained all over the world by the 'Challenger' in deep water, and apparently not specifically distinct from *C. pudica*†. Of the *Allopora* I cannot determine the species. There is one coral which appears to belong to the genus *Errina*, Gray‡, of which a further diagnosis is given from the type specimens by Saville Kent§, and one of the allied new genus *Acanthopora*. The whole of the classification of the Stylasteridæ will need revision on the more certain basis of the knowledge of the structure of the soft parts. In the older regions of its stem *Lepidopora* appears to assume the character of a *Stylaster*. The coral for the reception of which I form the new genus *Polypora* differs markedly from other members of the family; I at first took it to be a *Millepora* with unusually large zooids.

The genus may be thus characterized, as far as the hard parts are concerned :—

Genus POLYPORE.

Corallum pure white, composed of a finely reticular but compact cœnenchym. It forms single, stout, vertical stems, usually compressed from before backwards, so as to be oval in transverse section. The stem gives off a limited number of irregularly dichotomous branches, which

* Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College. No. IV. Deep-Sea Corals. By L. F. de Pourtales. Cambridge, Mass. 1871, p. 34.

+ Hist. Nat. des Coralliaires, par. MM. Milne-Edwards et J. Haime, t. ii. p. 127.

‡ Proc. Zool. Soc. 1835, p. 35.

§ Proc. Zool. Soc. 1871, p. 282.

are flattened like the stem from before backwards, and tend to coalesce by their lateral margins and assume a flabellate form, which is sometimes somewhat curved. The surface of the corallum is perfectly even and smooth, and pierced by deep calicular cavities, simply circular in outline, and of two kinds, large and small. The larger less numerous calicles are disposed at irregular intervals over the surface; they are very deep, reaching nearly to the centre of the axis of the branch or stem, and contain a deep-seated, very long, and slender style with a brush-like tip. The more numerous smaller calicles vary in size; they are thickly disposed between the larger ones; they have no style. Seated beneath the surface between the calicles are numerous ovoid cavities, the ampullæ, which in this genus do not project; at certain stages of development these communicate with the exterior by minute irregularly shaped pores, seated in small shallow pits on the surface of the corallum. The calicles are usually more abundant on one face of the corallum than on the other, especially in its older basal region.

Type of the genus *Polypora dichotoma*.

Dimensions of the specimen:—Height of the corallum from $1\frac{3}{4}$ to 1 inch; breadth of fan 6 inches; diameter of stem from $1\frac{3}{4}$ to 1 inch; diameter of the mouths of the larger calicles $\frac{1}{50}$ of an inch.

A further examination of the species of *Stylaster* obtained off the Meangis Islands was made in connexion with that of the corals referred to above. This *Stylaster* resembles *Cryptohelia* in every particular, excepting that it has not the peculiar lid in front of its calicles. It will have to be separated from the other *Stylasters*, and placed in the same genus as *Cryptohelia*.

Structure of the soft parts of the Stylasteridæ.

In all the *Stylasteridæ* examined there is present an abundant cœnosarc, made up, as in the *Milleporidæ*, of a network of anastomosing canals, composed of an endoderm and ectoderm, and ramifying in corresponding canals in the spongy trabecular calcareous cœnenchym. In *Polypora* the meshes of the network are comparatively close; in all the other genera examined far more widely open. In *Cryptohelia* and the *Stylaster* from off the Meangis Islands, in which the calicles appear as swellings seated upon slender connecting branches, bundles of larger canals traverse the axes of these branches, and connect the zooid groups of the several calicles with one another. A continuous layer of tissue, as far as has yet been seen without cellular structure, but containing thread-cells, covers the external surface of the cœnosarc in all the genera. In all the *Stylasteridæ* there are two kinds of zooids, as in *Millepora*; the larger and less numerous have mouths and a special layer of digestive cells lining their body-cavity. The more numerous smaller zooids have no mouths and no gastric cells. The alimentary zooids are short and cylindrical; the smaller or tentacular zooids long and tapering. The alimentary zooids in *Stylaster erubescens* have eight tentacles; in *Cryptohelia*, and in the

Stylaster so closely resembling it, they are devoid of tentacles. In *Allopora* they have twelve, in *Errina* four, in *Acanthopora* six, in *Polypora dichotoma* four. In *Polypora*, in which the tentacles of the alimentary zooid were examined in the fresh condition, the tentacles were seen to be clavate, the heads of the tentacles being somewhat elongate, not spherical as in *Millepora*. I am as yet uncertain whether these tentacles are clavate in the other genera. The point is difficult to determine in the extremely contracted condition of the organs in reagents. The tentacles of these alimentary zooids are very short; they are placed in a single whorl at the base of the broadly conical hypostome. In *Cryptohelia* and in the allied *Stylaster* the tentacleless alimentary zooids are flask-shaped, with a conical projecting hypostome, as seen by Sars *. The rounded bottoms of the zooids are blind and unconnected with the cœnosarcal canals; but a series of canals radiate upwards from the sides of the flask to branch and join the network above. The smaller zooids I have termed tentacular zooids, because, though invariably devoid of tentacles themselves, they have the form of the simple elongate tentacles, and evidently must perform a tentacular function. In *Polypora*, *Errina*, and *Acanthopora* these tentacular zooids are dispersed irregularly amongst the alimentary zooids; in *Cryptohelia*, *Stylaster erubescens*, and *Allopora* they are arranged in a circle around a centrally placed alimentary zooid in each so-called calicle of the corallum. The bases of these zooids communicate by large vascular offsets with the general network of the cœnosarc. The cavities of the alimentary zooids are four-rayed in transverse section, and in *Polypora* they divide at their base into four large vascular trunks, which subdivide to join the cœnosarcal meshwork. The cavities of the tentacular zooids are circular in transverse section. Both kinds of zooids are provided with strong circular and longitudinal muscles, which form wide conspicuous bands beneath the ectoderm. The alimentary zooids are situated on the summits of the styles of the corallum, where these are present. In *Polypora*, in the retracted condition of the zooids, the styles traverse the axes of the zooids from below for at least two thirds of their length. In *Polypora*, *Errina*, and *Acanthopora* the zooids of both kinds are retracted within long sacs, the cavities of which communicate with the surrounding network of the cœnosarc by a series of radially disposed canals, which canals in transverse sections of the zooids have at first sight exactly the appearance of a system of mesenteries. In *Cryptohelia* and the *Stylaster* so closely resembling it the alimentary zooids, lying as they do deep in the calicles, are probably never far protruded. The tentacular zooids are partly retracted between the pseudo-septa, partly doubled down within the calicles when the colony is in the retracted condition. In the other *Stylasters* and in *Allopora* the conditions are much the same. Two kinds of thread-cells are present, large and small: the large are of the slightly curved cylindrical form, and emit a thread with an elongate enlargement upon it near the sac, beset with a spiral of spines; these

* Forh. Selsk. Chr. 1872, p. 115.

larger cells are mostly gathered together in nematophores, which are disposed irregularly amongst the zooids in *Polypora*, regularly in the intervals between the tentacular zooids at the margins of the calices in *Cryptohelia* and the *Stylaster* resembling it. The smaller kind of thread-cells are of an ovoid form, slightly flattened on one side; they occur in the tentacles of the alimentary zooids, and form a closely set covering over the entire external surfaces of the tentacular zooids. No three-spined thread-cells, like those occurring in *Millepora*, exist in the Stylasteridæ. Reproduction takes place by means of adelocodonic gonophores, which are produced as buds from the cœnosarcal network without having any other connexion with the other zooids. They occupy in the corallum the ampullæ which in *Polypora* are concealed beneath the even external surface of the corallum, but in the other genera of Stylasteridæ show themselves as rounded prominences on the surface of the coralla, being specially prominent in *Errina* and *Distichopora*. The Stylasteridæ are all dioecious. Females only of *Errina* and *Cryptohelia** have been examined, and males only of the other genera. The generative elements of *Acanthopora* were not observed at all. In the males of *Polypora* the gonophores present the usual structures occurring in Hydroids; they are simple ovoid sacs, with an axially placed spadix, and resembling in all respects those, *e. g.*, figured by Allman from *Laomedea flexuosa*†. The gonophores are sometimes single in the ampullæ, sometimes in groups of two or three arising from a common base with their contents in various stages of development. The ripe spermatozoa are precisely similar in form to those of *Garveia nutans*‡. In *Allopora*, *Acanthopora*, and *Stylaster erubescens* the male gonophores have a similar structure. In the *Stylaster* allied to *Cryptohelia* the male elements are developed in a series of sacs, which encircle the calicle, often in a double row. The sacs spring from the cœnosarcal network; they contain numerous smaller globular cysts, attached to a common basal endodermal tissue. These cysts are some of them filled with ripe spermatozoa, others with spermatogenic cells in various stages. The female gonophores are, in *Errina*, simple, *i. e.* each ampulla contains only a simple ovum or embryo. In *Cryptohelia* large sacs are present at the sides of the calices, which contain ova and embryos in all stages of development. Only a single sac of the kind is developed in relation with each calicle. In both genera the spadix in its earliest stage is cup-shaped, the cup having fitted into it an ovum with germinal vesicle and spot well marked. The ova early lose the germinal vesicle and spot, and develop into very large planulæ, in the same manner as, *e. g.*, those in *Laomedea flexuosa*§. In *Errina* the planulæ are more ovoid in form than in *Cryptohelia*, in which they are long

* Off Japan last year a small fragment of what, at the time, I determined to be a male *Cryptohelia* was obtained by the dredge. I unfortunately cannot now refer to the specimen.

† 'A Monograph of the Gymnoblasic or Tubularian Hydroids,' by G. J. Allman, M.D. &c., Ray Soc. part 1, p. 65.

‡ *Ibid.* pl. xii. fig. 9.

§ Allman, *l. c.* p. 86.

and worm-like, measuring $\frac{1}{8}$ of an inch in length. They have a thick transparent ectoderm, abundantly supplied with the larger form of thread-cells. The spadix in both genera, as the development of the ovum proceeds, becomes divided at its margin into a series of lobes, which lobes subdivide and encroach over the surface of the ovum until more than half the proximal surface of the ovum is thus embraced by the cup of the spadix. The lobes of the margin of the spadix appear just like developing tentacles; and the spadix of *Cryptohelia* was at first supposed to be a developing actinula. The outer, thin, perforated calcareous walls of the ampullæ in *Errina* appear to get thinner as development of the embryo advances, until they fall away or are absorbed altogether, and give free exit to the planula. In *Cryptohelia* the planulæ probably escape through the mouths of the calicles. The endoderm, spadices, &c. are coloured red by a colouring-matter, soluble in spirit, insoluble in glycerine, in *Polypora*, *Cryptohelia*, and *Errina*. In the *Stylaster* resembling *Cryptohelia* the coloration is dusky green. The green colouring-matter is soluble in spirit, and yields an absorption-band in the spectrum. In *Polypora* the living layer of cœnosarc set free by decalcification is very thick, not merely a thin superficial film as in *Millepora*; indeed all but the most central axial regions of the branches of the corals are in active life. In the other genera the whole of the coral appears to maintain its vitality, there being no dead region represented by a cavity after decalcification.

Conclusions.

Since the observations of Prof. Sars* on the polyps of *Allopora oculina* it has been to some extent suspected that the Stylasteridæ were not Anthozoa, but possibly allied to the Milleporidæ, although the fact was not in any way demonstrated. Milne-Edwards long ago expressed himself extremely uncertain as to the affinities of *Distichopora*, and suspected that it might be an Alcyonarian†. In consideration of the facts now ascertained, there can be no doubt as to the hydroid affinities of the family. The Stylasteridæ appear to form a very natural family. They all possess two kinds of zooids. The tentacular zooids are closely similar in form in all the genera; and in the variations in the forms of the alimentary zooids all gradations are present. The thread-cells appear to be alike in form in all the genera. In all the gonophores are developed within ampullæ. The corals all bear, as far as has yet been ascertained, fixed sporosacs, as do, according to Allman, all deep-sea Hydroids‡. It is possible, however, that forms such as *Stylaster sanguineus* occurring in shallow water§ may bear planoblasts. There can be no doubt that *Distichopora* will prove closely allied to the other six genera of Stylasteridæ: its well-marked ampullæ and two kinds of pores are decisive in

* Sars, Forh. Selsk. Chr. 1872, p. 115.

+ MM. Milne-Edwards and Haime, *l. c.* t. iii., Appendice, p. 451.

‡ Allman, *l. c.* vol. ii. p. 155; also 'Nature,' Oct. 28th, 1875, p. 556.

§ Pourtales, *l. c.* p. 83.

the matter. *Pliobothrus* is said by Pourtales* to have "occasional round cavities in the centre of its branches filled with a yolk-like substance contained in a membrane." These cavities seem to be ampullæ; and if so, then *Pliobothrus* may prove to belong to the Stylasteridæ, and not to the Milleporidæ. In a specimen of *Pliobothrus* obtained by the 'Challenger' I have been able to detect neither ampullæ nor tabulæ. It will evidently be possible easily to form natural genera for the Stylasteridæ characterized by the number of tentacles of the alimentary zooids, grouping of the tentacular zooids around them, &c. This I propose to attempt when I have completed my study of the subject.

The Milleporidæ differ from the Stylasteridæ in having tabulæ, and in possessing neither styles nor ampullæ, as well as in having their mouthless zooids provided with numerous tentacles. The two families have, however, many points of alliance, and they should, provisionally at least, be referred to a special suborder of the Hydroidea, which may be termed the Hydrocorallinæ.

A most remarkable result of the present inquiry is the determination that the calicles of *Stylaster* and *Cryptohelia* are tenanted and formed by colonies of zooids, and not by single polyps, as was most naturally hitherto supposed to be the case. Prof. Verrill, in criticising Prof. Agassiz's relegation of the Rugosa to the Hydroidea†, dwells on the utter impossibility of Acalephs forming corals with distinct septa; yet in *Cryptohelia* and the *Stylasters* septa are present in the corallum, which in many cases so closely resemble those of Zoantharian corals that these corals were placed by Milne-Edwards in the Oculinidæ, and the septa were never suspected to be pseudo-septa until Sars‡ observed that in *Allopora oculina* the tentacles (tentacular zooids) were situate between the septa, and not upon them. I should not have detected the compound nature of the calicular groups in *Stylaster* had I not been led up to the fact by the examination of other genera of the family, in which the tentacular zooids are widely separated from the alimentary ones. The determination of the compound nature of the calicular groups at once explains the otherwise very anomalous arrangement of the pseudo-septa in many Stylasteridæ. The condition existing has been described§ as a "tendency of the septa to unite by their inner edges and enclose in the interseptal chamber thus formed the septa of a higher order." The real explanation of the matter is that the apparent interseptal chambers are the pores or calicles of the tentacular zooids. In those species in which the tentacles are removed from harm's way in the retracted condition of the coral by being bent inwards down into the wide cavity containing the alimentary zooid (calicular cavity), these pores have their walls incomplete on the side nearest to the calicle, and take the form at their mouths of elongate slits, in order to allow of this inward

* Pourtales, *l. c.* p. 57.

† Prof. A. E. Verrill, 'Ann. & Mag. Nat. Hist.' 1872, 4th ser. vol. ix. p. 358.

‡ Forh. Selsk. Chr. 1872, p. 115.

§ Pourtales, *l. c.* p. 33.

inclination of the contained tentacular zooid when at rest, or when feeding the deeply seated alimentary zooid. The supposed included septa of higher order are the styles of the tentacular zooids. In some forms of the family these styles are brush-like in shape, just like the central styles of the alimentary zooids; they have this form in *Allopora mineacea**, and less markedly in *Stylaster complanatus*, Pourt.† In some Stylasteridæ, as e. g. in *Stylaster amphihelioides*, S. Kent‡, there is no appearance at all of pseudo-septa. The pores of the tentacular zooids are simple circular-mouthed pits, arranged in a circle around the large pore of the alimentary zooid. In *Allopora subviolacea*, S. Kent§, the pores of the tentacular zooids are, in some zooid groups in the same specimen, mere pores; in others slits communicating with the cavity of the pore of the alimentary zooid. The irregularly scattered condition of the zooids existing in *Polypora* is to be regarded as the primitive one in genesis, from which that existing in *Stylaster amphihelioides* and that in *Allopora subviolacea* represent transitional stages towards the high specialization of the zooid groups found in *Cryptohelia* and other species at present termed *Stylaster*.

It has hitherto been a matter of regret that the Hydroidea were of such a structure as to be unsuitable || for preservation in the fossil state, and that thus we were almost, excepting as far as Graptolites are concerned, without direct evidence as to the forms which may have been presented by their remote ancestry. We have now two families excellently adapted for preservation as fossils, viz. the Milleporidæ and the Stylasteridæ. At present no members of these families appear to have been observed in rocks older than the tertiary deposits. A single species only, *Distichopora antiqua*, is known to occur in tertiary beds in France, at Chaumont and Valmondois ¶; but now that special attention will be directed to these corals, and their structure is better understood, no doubt allied fossil forms will be detected. It seems just possible that amongst Palæozoic corals such forms as *Cyathonaxia* may have been tenanted by a group of hydroid zooids with a large alimentary zooid situate upon the projecting style. *Cystiphyllum vesiculosum* has a crowd of small slit-like pits covering the inner surface of its calicle, which have all the appearance of having been tenanted by hydroid tentacular zooids. I cannot, however, now refer to specimens; indeed I have never seen any. Ampullæ seem to be absent in these corals; but in shallow-water forms, as in *Millepora*, they probably would be so. It is quite possible that the Millepores produce Medusæ.

Although the Milleporidæ take a very large part in the formation of coral reefs, the Stylasteridæ have very little share in the building up of these structures, being for the most part confined to the deep sea. A few

* Pourtales, l. c. pl. iii. fig. 15.

† Pourtales, l. c. pl. ii. fig. 17.

‡ Saville Kent, l. c. pl. xxiv. fig. 1 c.

§ *Ibid.* pl. xxv. fig. 2 a.

|| Allman, l. c. vol. ii. p. 231.

¶ MM. Milne-Edwards & Haime, l. c. t. iii., Appendice, p. 451.

species only occur in shallow water, and apparently not in great abundance. In deeper water, however, the Stylasteridæ are most luxuriant. Immense quantities of a large flabellate red *Distichopora*, brought from the Marquesas group, are sold to tourists at Honolulu. The corals are said to come from deep water. The results of the 'Challenger's' dredging off the Rio de la Plata in 600 fathoms showed that at that depth very considerable deposits of calcareous matter must be formed by these various genera of hydroid corals, growing associated as they do in masses and attached to one another. Large dead masses of *Polypora* brought up by the dredge were especially remarkable, weighing more than 1 lb., and forming bases of attachment for sponges and all kinds of other animals.

I am at present engaged in preparing a series of drawings illustrative of the anatomy of the Stylasteridæ, which I hope shortly to lay before the Royal Society, together with a more complete account of the structure of these corals.

South Atlantic,
March 24, 1876.

III. "On the Comparative Anatomy of the Auditory Ossicles of the Mammalia." By ALBAN H. G. DORAN, F.R.C.S. Communicated by Professor FLOWER, F.R.S. Received May 5, 1876.

(Abstract.)

The following observations have been made during the preparation of a series of the small ear-bones of the higher Vertebrata for the Museum of the Royal College of Surgeons of England, an undertaking which was commenced in the autumn of 1874, and is in the course of rapid enlargement up to the present date.

The foundation of the entire series was a small collection of the osseous auditory apparatus of the domestic and common indigenous animals of Germany, purchased by the College of Dr. Max Hübrich, of Munich, a few years since. Following the suggestions of the Conservator, Professor W. H. Flower, F.R.S., the author succeeded in removing from the crania of mammals in the College Museum a sufficient number of auditory ossicula to illustrate the characters of those bones in most of the important subdivisions of that class of vertebrated animals. Numerous additions from rare specimens have been obtained through the kindness of Sir Victor Brooke, Bart., Professor Parker, Professor A. H. Garrod, and other gentlemen.

These observations are now brought forward with the object of demonstrating how far the characteristics of the auditory ossicles of the different orders of the Mammalia accord with those distinctions throughout the whole organization which have assisted anatomists up to the present day in giving a definite position to each member of the class. Dr. Hyrtl has already published a well-known work on the Comparative