THE

CAMBRIDGE NATURAL HISTORY

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VOLUME I

PROTOZOA

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PORIFERA (SPONGES)

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COELENTERATA & CTENOPHORA

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ECHINODERMATA

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London

MACMILLAN AND CO., Limited

NEW YORK: THE MACMILLAN COMPANY

1906

And pitch down his basket before us,
    All trembling alive
With pink and grey jellies, your sea-fruit ;
    You touch the strange lumps,
And mouths gape there, eyes open, all manner
    Of horns and of humps.

BROWNING, *The Englishman in Italy*

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Class.	Order.	Sub-Order.	Family.	Sub-Family.
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Class.	Sub-Class.	Grade.	Order.	Sub-Order.	Family.
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				Fungiidae (p. 403)	
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Sub-Phylum.	Class.	Order.	Family.	
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COELENTERATA AND CTENOPHORA

BY

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CHAPTER X

COELENTERATA

INTRODUCTION—CLASSIFICATION—HYDROZOA—ELEUTHEROBLASTEA—MILLEPORINA—GYMNOBLASTEA—CALYPTOBLASTEA—GRAPTOLITOIDEA—STYLASTERINA

THE great division of the animal kingdom called COELENTERATA was constituted in 1847 by R. Leuckart for those animals which are commonly known as polyps and jelly-fishes. Cuvier had previously included these forms in his division Radiata or Zoophyta, when they were associated with the Star-fishes, Brittle-stars, and the other Echinodermata.

The splitting up of the Cuvierian division was rendered necessary by the progress of anatomical discovery, for whereas the Echinodermata possess an alimentary canal distinct from the other cavities of the body, in the polyps and jelly-fishes there is only one cavity to serve the purposes of digestion and the circulation of fluids. The name Coelenterata (κοῖλος = hollow, ἔντερον = the alimentary canal) was therefore introduced, and it may be taken to signify the important anatomical feature that the body-cavity (or coelom) and the cavity of the alimentary canal (or enteron) of these animals are not separate and distinct as they are in Echinoderms and most other animals.

Many Coelenterata have a pronounced radial symmetry, the body being star-like, with the organs arranged symmetrically on lines radiating from a common centre. In this respect they have a superficial resemblance to many of the Echinodermata, which are also radially symmetrical in the adult stage. But it cannot be insisted upon too strongly that this superficial resemblance of the Coelenterata and Echinodermata has no genetic significance.

The radial symmetry has been acquired in the two divisions along different lines of descent, and has no further significance than the adaptation of different animals to somewhat similar conditions of life. It is not only in the animals formerly classed by Cuvier as Radiata, but in sedentary worms, Polyzoa, Brachiopoda, and even Cephalopoda among the Mollusca, that we find a radial arrangement of some of the organs. It is interesting in this connexion to note that the word "polyp," so frequently applied to the individual Coelenterate animal or zooid, was originally introduced on a fancied resemblance of a *Hydra* to a small Cuttle-fish (*Fr.* Poulpe, *Lat.* Polypus).

The body of the Coelenterate, then, consists of a body-wall enclosing a single cavity ("coelenteron"). The body-wall consists of an inner and an outer layer of cells, originally called by Allman the "endoderm" and "ectoderm" respectively. Between the two layers there is a substance chemically allied to mucin and usually of a jelly-like consistency, for which the convenient term "mesogloea," introduced by G. C. Bourne, is used (Fig. 125).

The mesogloea may be very thin and inconspicuous, as it is in *Hydra* and many other sedentary forms, or it may become very thick, as in the jelly-fishes and some of the sedentary Alcyonaria. When it is very thick it is penetrated by wandering isolated cells from the ectoderm or endoderm, by strings of cells or by cell-lined canals; but even when it is cellular it must not be confounded with the third germinal layer or mesoblast which characterises the higher groups of animals, from which it differs essentially in origin and other characters. The Coelenterata are two-layered animals (DIPLOBLASTICA), in contrast to the Metazoa with three layers of cells (TRIPLOBLASTICA). The growth of the mesogloea in many Coelenterata leads to modifications of the shape of the coelenteric cavity in various directions. In the Anthozoa, for example, the growth of vertical bands of mesogloea covered by endoderm divides the peripheral parts of the cavity into a series of intermesenterial compartments in open communication with the axial part of the cavity; and in the jelly-fishes the growth of the mesogloea reduces the cavity of the outer regions of the disc to a series of vessel-like canals.

Another character, of great importance, possessed by all Coelenterata is the "nematocyst" or "thread-cell" (Fig. 124).

This is an organ produced within the body of a cell called the "cnidoblast," and it consists of a vesicular wall or capsule, surrounding a cavity filled with fluid containing a long and usually spirally coiled thread continuous with the wall of the vesicle. When the nematocyst is fully developed and receives a stimulus of a certain character, the thread is shot out with great velocity and causes a sting on any part of an animal that is sufficiently delicate to be wounded by it.

The morphology and physiology of the nematocysts are subjects of very great difficulty and complication, and cannot be discussed in these pages. It may, however, be said that by some authorities the cnidoblast is supposed to be an extremely modified form of mucous or gland cell, and that the discharge of the nematocyst is subject to the control of a primitive nervous system that is continuous through the body of the zooid.

There is a considerable range of structure in the nematocysts of the Coelenterata. In *Alcyonium* and in many other Alcyonaria they are very small (in *Alcyonium* the nematocyst is 0·0075 mm. in length previous to discharge), and when discharged exhibit a simple oval capsule with a plain thread attached to it. In *Hydra* (Fig. 124) there are at least two kinds of nematocysts, and in the larger kind (0·02 mm. in length previous to discharge) the base of the thread is beset with a series of recurved hooks, which during the act of discharge probably assist in making a wound in the organism attacked for the injection of the irritant fluid, and possibly hold the structure in position while the thread is being discharged. In the large kind of nematocyst of *Millepora* and of *Cerianthus* there is a band of spirally arranged but very minute thorns in the middle of the thread, but none at the base. In some of the Siphonophora the undischarged nematocysts reach their maximum size, nearly 0·05 mm. in length.

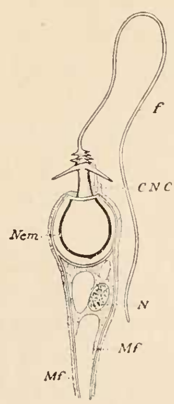

Fig. 124. — Nematocyst (*Nem*) of *Hydra grisea*, enclosed within the cnidoblast. *CNC*, Cnidocil; *f*, thread of nematocyst; *Mf*, myophan threads in cnidoblast; *N*, nucleus of cnidoblast. (After Schneider.)

When a nematocyst has once been discharged it is usually rejected from the body, and its place in the tissue is taken by a new nematocyst formed by a new cnidoblast; but in the thread of the large kind of nematocyst of *Millepora* there is a very delicate band, which appears to be similar to the myophan thread in the stalk of a *Vorticella*. Dr. Willey[1] has made the important observation that in this coral the nematocyst threads can be withdrawn after discharge, the retraction being effected with great rapidity. The "cnidoblast" is a specially modified cell. It sometimes bears at its free extremity a delicate process, the "cnidocil," which is supposed to be adapted to the reception of the special stimuli that determine the discharge of the nematocyst. In many species delicate contractile fibres (Fig. 124, *Mf*) can be seen in the substance of the cnidoblast, and in others its basal part is drawn out into a long and probably contractile stalk ("cnidopod"), attached to the mesogloea below.

There can be little doubt that new nematocysts are constantly formed during life to replace those that have been discharged and lost. Each nematocyst is developed within the cell-substance of a cnidoblast which is derived from the undifferentiated interstitial cell-groups. During this process the cnidoblast does not necessarily remain stationary, but may wander some considerable distance from its place of origin.[2] This habit of migration of the cnidoblast renders it difficult to determine whether the ectoderm alone, or both ectoderm and endoderm, can give rise to nematocysts. In the majority of Coelenterates the nematocysts are confined to the ectoderm, but in many Anthozoa, Scyphozoa, and Siphonophora they are found in tissues that are certainly or probably endodermic in origin. It has not been definitely proved in any case that the cnidoblast cells that form these nematocysts have originally been formed in the endoderm, and it is possible that they are always derived from ectoderm cells which migrate into the endoderm.

It is probably true that all Coelenterata have nematocysts, and that, in the few cases in which it has been stated that they are absent (e.g. *Sarcophytum*), they have been overlooked. It cannot, however, be definitely stated that similar structures do not occur in other animals. The nematocysts of the Mollusc *Aeolis* are not the product of its own tissues, but are introduced

[1] *Willey's Zool. Results*, pt. ii. 1899, p. 127.

[2] Murbach, *Archiv f. Naturg.* lx. Bd. i. 1894, p. 217.

into the body with its food.[1] The nematocysts that occur in the Infusorian *Epistylis umbellaria* and in the Dinoflagellate *Polykrikos* (p. 131) require reinvestigation, but if it should prove that they are the product of the Protozoa they cannot be regarded as strictly homologous with those of Coelenterata. In many of the Turbellaria, however, and in some of the Nemertine worms, nematocysts occur in the epidermis which appear to be undoubtedly the products of these animals.

The Coelenterata are divided into three classes :—

1. Hydrozoa.—Without stomodaeum and mesenteries. Sexual cells discharged directly to the exterior.

2. Scyphozoa.—Without stomodaeum and mesenteries. Sexual cells discharged into the coelenteric cavity.

3. Anthozoa = Actinozoa.—With stomodaeum and mesenteries. Sexual cells discharged into the coelenteric cavity.

The full meaning of the brief statements concerning the structure of the three classes given above cannot be explained until the general anatomy of the classes has been described. It may be stated, however, in this place that many authors believe that structures corresponding with the stomodaeum and mesenteries of Anthozoa do occur in the Scyphozoa, which they therefore include in the class Anthozoa.

Among the more familiar animals included in the class Hydrozoa may be mentioned the fresh-water polyp *Hydra*, the Hydroid zoophytes, many of the smaller Medusae or jelly-fish, the Portuguese Man-of-war (*Physalia*), and a few of the corals.

Included in the Scyphozoa are the large jelly-fish found floating on the sea or cast up on the beach on the British shores.

The Anthozoa include the Sea-anemones, nearly all the Stony Corals, the Sea-fans, the Black Corals, the Dead-men's fingers (*Alcyonium*), the Sea-pens, and the Precious Coral of commerce.

CLASS I. HYDROZOA

In this Class of Coelenterata two types of body-form may be found. In such a genus as *Obelia* there is a fixed branching colony of zooids, and each zooid consists of a simple tubular body-wall composed of the two layers of cells, the ectoderm and the

[1] G. H. Grosvenor, *Proc. Roy. Soc.* lxxii. 1903, p. 462.

endoderm (Fig. 125), terminating distally in a conical mound—the "hypostome"—which is perforated by the mouth and surrounded by a crown of tentacles. This fixed colony, the "hydrosome," feeds and increases in size by gemmation, but does not produce sexual cells. The hydrosome produces at a certain season of the year a number of buds, which develop into small bell-like jelly-fish called the "Medusae," which swim away from the parent stock and produce the sexual cells. The Medusa (Fig. 126) consists of a delicate dome-shaped contractile bell, perforated by radial canals and fringed with tentacles; and from its centre there depends, like the clapper of a bell, a tubular process, the manubrium, which bears the mouth at its extremity. This free-swimming sexual stage in the life-history of *Obelia* is called the "medusome."

It is difficult to determine whether, in the evolution of the Hydrozoa, the hydrosome preceded the medusome or *vice versâ*. By some authors the medusome is regarded as a specially modified sexual individual of the hydrosome colony. By others the medusome is regarded as the typical adult Hydrozoon form, and the zooids of the hydrosome as nutritive individuals arrested in their development to give support to it. Whatever may be the right interpretation of the facts, however, it is found that in some forms the medusome stage is more or less degenerate and the hydrosome is predominant, whereas in others the hydrosome is degenerate or inconspicuous and the medusome is predominant. Finally, in some cases there are no traces, even in development, of a medusome stage, and the life-history is completed in the hydrosome, while in others the hydrosome stages are lost and the life-history is completed in the medusome.

If a conspicuous hydrosome stage is represented by H, a conspicuous medusome stage by M, an inconspicuous or degenerate hydrosome stage by *h*, an inconspicuous or degenerate medusome stage by *m*, and the fertilised ovum by O, the life-histories of the Hydrozoa may be represented by the following formulæ:—

1.	O – H – O	(*Hydra*)
2.	O – H – *m* – O	(*Sertularia*)
3.	O – H – M – O	(*Obelia*)
4.	O – *h* – M – O	(*Liriope*)
5.	O – M – O	(*Geryonia*)

The structure of the **hydrosome** is usually very simple. It consists of a branched tube opening by mouths at the ends of the branches and closed at the base. The body-wall is built up of ectoderm and endoderm. Between these layers there is a thin non-cellular lamella, the mesogloea.

In a great many Hydrozoa the ectoderm secretes a chitinous protective tube called the "perisarc." The mouth is usually a small round aperture situated on the summit of the hypostome, and at the base of the hypostome there may be one or two crowns of tentacles or an area bearing irregularly scattered tentacles. The tentacles may be hollow, containing a cavity continuous with the coelenteric cavity of the body; or solid, the endoderm cells arranged in a single row forming an axial support for the ectoderm. The ectoderm of the tentacles is provided with numerous nematocysts, usually arranged in groups or clusters on the distal two-thirds of their length, but sometimes confined to a cap-like swelling at the extremity (capitate tentacles). The hydrosome may be a single zooid producing others asexually by gemmation (or more rarely by fission), which become free from the parent, or it may be a colony of zooids in organic connexion with one another formed by the continuous gemmation of the original zooid derived from the fertilised ovum and its asexually produced offspring. When the hydrosome is a colony of zooids, specialisation of certain individuals for particular functions may occur, and the colony becomes dimorphic or polymorphic.

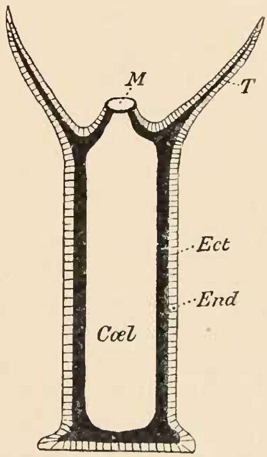

FIG. 125.—Diagram of a vertical section through a hydrosome. *Cœl*, Coelenteron; *Ect*, ectoderm; *End*, endoderm. Between the ectoderm and the endoderm there is a thin mesogloea not represented in the diagram. *M*, mouth; *T*, tentacle.

The **medusome** is more complicated in structure than the hydrosome, as it is adapted to the more varied conditions of a free-swimming existence. The body is expanded to form a disc, "umbrella," or bell, which bears at the edge or margin a number of tentacles. The mouth is situated on the end of a hypostome, called the "manubrium," situated in the centre of the radially symmetrical body. The surface that bears the manubrium is called oral, and the opposite surface is called aboral. The cavity partly enclosed by the oral aspect of the body when it is cup- or bell-shaped is called the "sub-umbrellar cavity."

In the medusome of nearly all Hydrozoa there is a narrow shelf projecting inwards from the margin of the disc and guarding the opening of the sub-umbrellar cavity, called the "velum."

The mouth leads through the manubrium into a flattened part of the coelenteric cavity, which is usually called the gastric cavity, and from this a number of canals pass radially through the mesogloea to join a circular canal or ring-canal at the margin of the umbrella.

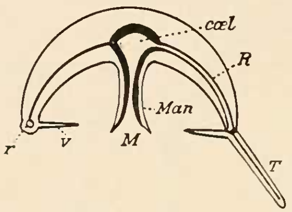

FIG. 126.—Diagram of a vertical section through a medusome. *coel*, Coelenteron; *M*, mouth; *Man*, manubrium; *R*, radial canal; *r*, ring or circular canal; *T*, tentacle; *v*, velum.

A special and important feature of the medusome is the presence of sense-organs called the "ocelli" and "statocysts," situated at the margin of the umbrella or at the base of the tentacles.

The ocelli may usually be recognised as opaque red or blue spots on the bases of the tentacles, in marked contrast to their transparent surroundings. The ocellus may consist simply of a cluster of pigmented cells, or may be further differentiated as a cup of pigmented cells filled with a spherical thickening of the cuticle to form a lens. The exact function of the ocelli may not be fully understood, but there can be little doubt that they are light-perceiving organs.

The function of the sense-organs known as statocysts, however, has not yet been so satisfactorily determined. They were formerly thought to be auditory organs, and were called "otocysts," but it appears now that it is impossible on physical grounds for these organs to be used for the perception of the waves of sound in water. It is more probable that they are organs of the static function, that is, the function of the perception of the position of the body in space, and they are consequently called statocysts. In the Leptomedusae each statocyst consists of a small vesicle in the mesogloea at the margin of the umbrella, containing a hard, stony body called the "statolith." In *Geryonia* and some other Trachomedusae the statolith is carried by a short tentacular process, the "statorhab," projecting into the vesicle; in other Trachomedusae, however, the vesicle is open, but forms a hood for the protection of the statorhab; and in others, but especially in the younger stages of development, the statorhab is not sunk into the margin of the umbrella, and resembles a short but loaded tentacle. Recent researches have shown that there is a complete series of connecting links between the vesiculate statocyst of the Leptomedusae and the free tentaculate statorhab of the Trachomedusae, and there can be little doubt of their general homology.

In the free-swimming or "Phanerocodonic" medusome the sexual cells are borne by the ectoderm of the sub-umbrellar cavity either on the walls of the manubrium or subjacent to the course of the radial canals.

Order I. Eleutheroblastea.

This order is constituted mainly for the well-known genus *Hydra*. By some authors *Hydra* is regarded as an aberrant member of the order Gymnoblastea, to which it is undoubtedly in many respects allied, but it presents so many features of special interest that it is better to keep it in a distinct group.

Hydra is one of the few examples of exclusively fresh-water Coelenterates, and like so many of the smaller fresh-water animals its distribution is almost cosmopolitan. It occurs not only in Europe and North America, but in New Zealand, Australia, tropical central Africa, and tropical central America.

Hydra is found in this country in clear, still fresh water attached to the stalks or leaves of weeds. When fully expanded it may be 25 mm. in length, but when completely retracted the same individual may be not more than 3 mm. long. The tubular body-wall is built up of ectoderm and endoderm, enclosing a simple undivided coelenteric cavity. The mouth is situated on the summit of the conical hypostome, and at the base of this there is a crown of long, delicate, but hollow tentacles. The number of tentacles is usually six in *H. vulgaris* and *H. oligactis*,[1] and eight in *H. viridis*, but it is variable in all species.

During the greater part of the summer the number of individuals is rapidly increased by gemmation. The young Hydras produced by gemmation are usually detached from their parents

[1] H. Jung, *Morph. Jahrb.* viii. 1881, p. 339.

before they themselves produce buds, but in *H. oligactis* the buds often remain attached to the parent after they themselves have formed buds, and thus a small colony is produced. Sexual reproduction usually commences in this country in the summer and autumn, but as the statements of trustworthy authors are conflicting, it is probable that the time of appearance of the sexual organs varies according to the conditions of the environment.

Individual specimens may be male, female, or hermaphrodite. Nussbaum[1] has published the interesting observation that when the Hydras have been well fed the majority become female, when the food supply has been greatly restricted the majority become male, and when the food-supply is moderate in amount the majority become hermaphrodite. The gonads are simply clusters of sexual cells situated in the ectoderm. There is no evidence, derived from either their structure or their development, to show that they represent reduced medusiform gonophores. The testis produces a number of minute spermatozoa. In the ovary, however, only one large yolk-laden egg-cell reaches maturity by the absorption of the other eggs. The ovum is fertilised while still within the gonad, and undergoes the early stages of its development in that position. With the differentiation of an outer layer of cells a chitinous protecting membrane is formed, and the escape from the parent takes place.[2] It seems probable that at this stage, namely, that of a protected embryo, there is often a prolonged period of rest, during which it may be carried by wind and other agencies for long distances without injury.

The remarkable power that *Hydra* possesses of recovery from injury and of regenerating lost parts was first pointed out by Trembley in his classical memoir.[3]

A *Hydra* can be cut into a considerable number of pieces, and each piece, provided both ectoderm and endoderm are represented in it, will give rise by growth and regeneration to a complete zooid. There is, however, a limit of size below which fragments of *Hydra* will not regenerate, even if they contain

[1] *Verh. Ver. Rheinland*, xlix. 1893, pp. 13, 14, 40, 41.

[2] For an account of the development and of the chitinous membrane see A. Brauer, *Zeitschr. f. wiss. Zool.* lii. 1891, p. 9.

[3] Trembley, *Mémoires pour servir à l'Histoire d'un genre de Polypes d'eau douce*, 1744.

cells of both layers. The statement made by Trembley, that when a *Hydra* is turned inside out it will continue to live in the introverted condition has not been confirmed, and it seems probable that after the experiment has been made the polyp remains in a paralysed condition for some time, and later reverts, somewhat suddenly, to the normal condition by a reversal of the process. There is certainly no substantial reason to believe that under any circumstances the ectoderm can undertake the function of the endoderm or the endoderm the functions of the ectoderm.

One of the characteristic features of *Hydra* is the slightly expanded, disc-shaped aboral extremity usually called the "foot," an unfortunate term for which the word "sucker" should be substituted. There are no root-like tendrils or processes for attach-

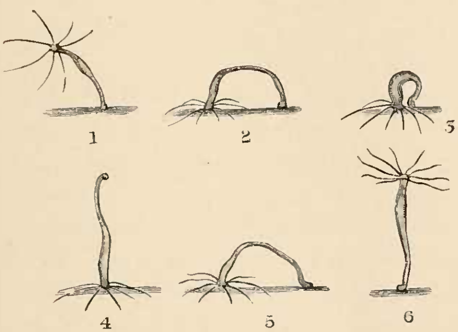

Fig. 127.—A series of drawings of *Hydra*, showing the attitudes it assumes during one of the more rapid movements from place to place. 1, The *Hydra* bending over to one side; 2, attaching itself to the support by the mouth and tentacles; 3, drawing the sucker up to the mouth; 4, inverted; 5, refixing the sucker; 6, reassuming the erect posture. (After Trembley.)

ment to the support such as are found in most of the solitary Gymnoblastea. The attachment of the body to the stem or weed or surface-film by this sucker enables the animal to change its position at will. It may either progress slowly by gliding along its support without the assistance of the tentacles, in a manner similar to that observed in many Sea-anemones; or more rapidly by a series of somersaults, as originally described by Trembley. The latter mode of locomotion has been recently described as follows:—"The body, expanded and with expanded tentacles, bends over to one side. As soon as the tentacles touch the bottom they attach themselves and contract. Now one of two things happens. The foot may loosen its hold on the bottom and the body contract. In this manner the animal comes to stand on its tentacles with the foot pointing upward. The body now bends over again until the foot attaches itself close to the attached tentacles. These loosen in their turn, and so the *Hydra* is again in its normal position. In the other case the foot is not detached, but glides along the support until it stands close to the tentacles, which now loosen their hold."[1]

Hydra appears to be purely carnivorous. It will seize and swallow Entomostraca of relatively great size, so that the body-wall bulges to more than twice its normal diameter. But smaller Crustacea, Annelid worms, and pieces of flesh are readily seized and swallowed by a hungry *Hydra*. In *H. viridis* the chlorophyll corpuscles[2] of the endoderm may possibly assist in the nourishment of the body by the formation of starch in direct sunlight.

Three species of *Hydra* are usually recognised, but others which may be merely local varieties or are comparatively rare have been named.[3]

H. viridis.—Colour, grass-green. Average number of tentacles, eight. Tentacles shorter than the body. Embryonic chitinous membrane spherical and almost smooth.

H. vulgaris, Pallas (*H. grisea*, Linn.).—Colour, orange-brown. Tentacles rather longer than the body, average number, six. Embryonic chitinous membrane spherical, and covered with numerous pointed branched spines.

H. oligactis, Pallas (*H. fusca*, Linn.).—Colour, brown. Tentacles capable of great extension; sometimes, when fully expanded, several times the length of the body. Average number, six. Embryonic chitinous membrane plano-convex, its convex side only covered with spines.

The genera *Microhydra* (Ryder) and *Protohydra* (Greeff) are probably allied to *Hydra*, but as their sexual organs have not been observed their real affinities are not yet determined. *Microhydra* resembles *Hydra* in its general form and habits, and in its method of reproduction by gemmation, but it has no tentacles. It was found in fresh water in North America.

Protohydra[4] was found in the oyster-beds off Ostend, and resembles *Microhydra* in the absence of tentacles. It multiplies by transverse fission, but neither gemmation nor sexual reproduction has been observed.

Haleremita is a minute hydriform zooid which is also marine.

[1] G. Wagner, *Quart. Journ. Micr. Sci.* xlviii. 1905, p. 589. [2] See p. 126.

[3] *Hydra pallida*, Beardsley, has been found to be very destructive to the fry of the Black-spotted Trout in Colorado, *U.S. Fish. Rep. Bull.* 1902, p. 158.

[4] For figures of *Protohydra* see Chun, Bronn's *Thier-Reich*, "Coelenterata," 1894, Bd. ii. pl. ii.

It was found by Schaudinn[1] in the marine aquarium at Berlin in water from Rovigno, on the Adriatic. It reproduces by gemmation, but sexual organs have not been found.

Another very remarkable genus usually associated with the Eleutheroblastea is *Polypodium*. At one stage of its life-history it has the form of a spiral ribbon or stolon which is parasitic on the eggs of the sturgeon (*Acipenser ruthenus*) in the river Volga.[2] This stolon gives rise to a number of small *Hydra*-like zooids with twenty tentacles, of which sixteen are filamentous and eight club-shaped. These zooids multiply by longitudinal fission, and feed independently on Infusoria, Rotifers, and other minute organisms. The stages between these hydriform individuals and the parasitic stolon have not been discovered.

Order II. Milleporina.

Millepora was formerly united with the Stylasterina to form the order Hydrocorallina; but the increase of our knowledge of these Hydroid corals tends rather to emphasise than to minimise the distinction of *Millepora* from the Stylasterina.

Millepora resembles the Stylasterina in the production of a massive calcareous skeleton and in the dimorphism of the zooids, but in the characters of the sexual reproduction and in many minor anatomical and histological peculiarities it is distinct. As there is only one genus, *Millepora*, the account of its anatomy will serve as a description of the order.

The skeleton (Fig. 128) consists of large lobate, plicate, ramified, or encrusting masses of calcium carbonate, reaching a size of one or two or more feet in height and breadth. The surface is perforated by numerous pores of two distinct sizes; the larger—"gastropores"—are about 0·25 mm. in diameter, and the smaller and more numerous "dactylopores" about 0·15 mm. in diameter. In many specimens the pores are arranged in definite cycles, each gastropore being surrounded by a circle of 5-7 dactylopores; but more generally the two kinds appear to be irregularly scattered on the surface.

When a branch or lobe of a Millepore is broken across and examined in section, it is found that each pore is continued as a

[1] *Sitzber. Ges. naturf. Freunde Berlin*, ix. 1894, p. 226.

[2] M. Ussov, *Morph. Jahrb.* xii. 1887, p. 137.

vertical tube divided into sections by horizontal calcareous plates (Fig. 129, *Tab*). These plates are the "tabulae," and constitute the character upon which *Millepora* was formerly placed in the now discarded group of Tabulate corals.

The coral skeleton is also perforated by a very fine reticulum of canals, by which the pore-tubes are brought into communica-

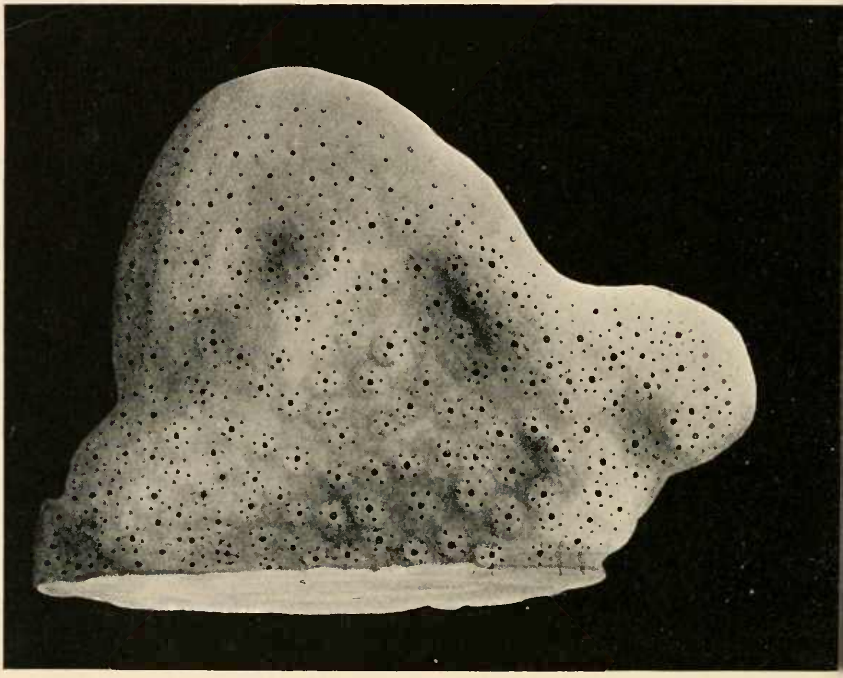

FIG. 128.—A portion of a dried colony of *Millepora*, showing the larger pores (gastropores) surrounded by cycles of smaller pores (dactylopores). At the edges the cycles are not well defined.

tion with one another. In the axis of the larger branches and in the centre of the larger plates a considerable quantity of the skeleton is of an irregular spongy character, caused by the disintegrating influence of a boring filamentous Alga.[1]

The discovery that *Millepora* belongs to the Hydrozoa was made by Agassiz[2] in 1859, but Moseley[3] was the first to give

[1] This organism is usually described as a fungus (*Achlya*), but it is probably a green Alga. See J. E. Duerden, *Bull. Amer. Mus. Nat. Hist.* xvi. 1902, p. 323.

[2] *Bibl. Univ. de Genève, Arch. des Sciences*, v. 1859, p. 80.

[3] *Phil. Trans.* cxlvii. 1876, p. 117.

an adequate account of the general anatomy. The colony consists of two kinds of zooids—the short, thick gastrozooids (Fig. 129, *G*) provided with a mouth and digestive endoderm, and the longer and more slender mouthless dactylozooids (*D*)—united together by a network of canals running in the porous channels of the superficial layer of the corallum. The living tissues of the zooids extend down the pore-tubes as far as the first tabulae, and below this level the canal-system is degenerate and functionless. It is only a very thin superficial stratum of the coral, therefore, that contains living tissues.

The zooids of *Millepora* are very contractile, and can be withdrawn below the general surface of the coral into the shelter of the pore-tubes. When a specimen is examined in its natural position on the reef, the zooids are usually found to be thus contracted; but several observers have seen the zooids expanded in the living condition. It is probable that, as is the case with other corals, the expansion occurs principally during the night.

The colony is provided with two kinds of nematocysts—the small kind and the large. In some colonies they are powerful enough to penetrate the human skin, and *Millepora* has therefore received locally the name of "stinging coral." On each of the dactylozooids there are six or seven short capitate tentacles (Fig. 129, *t*), each head being packed with nematocysts of the small kind; similar batteries of these nematocysts are found in the four short capitate tentacles of the gastrozooids. The nematocysts of the larger kind are found in the superficial ectoderm, some distributed irregularly on the surface, others in clusters round the pores. The small nematocysts are about 0·013 mm. in length before they are exploded, and exhibit four spines at the base of the thread; the large kind are oval in outline, 0·02 × 0·025 mm. in size, and exhibit no spines at the base, but a spiral band of minute spines in the middle of the filament. There is some reason to believe that the filament of the large kind of nematocysts can be retracted.[1]

At certain seasons the colonies of *Millepora* produce a great number of male or female Medusae. The genus is probably dioecious, no instances of hermaphrodite colonies having yet been found. Each Medusa is formed in a cavity situated above the last-formed tabula in a pore-tube, and this cavity, the "ampulla,"

[1] S. J. Hickson, *Willey's Zool. Results*, pt. ii. 1899, p. 127.

having a greater diameter than that of the gastrozooid tubes, can

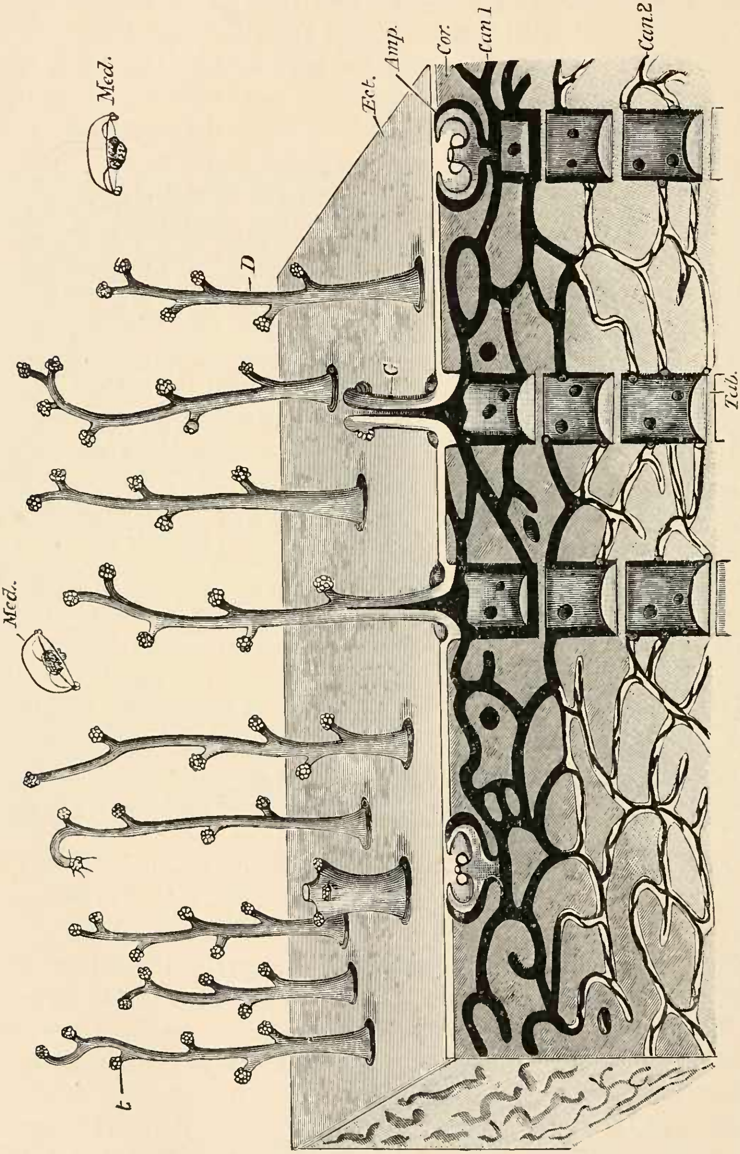

Fig. 129.—Diagrammatic sketch to show the structure of *Millepora*. *Amp*, an ampulla containing a medusa; *Can*.1, canal system at the surface; *Can*.2, canal system degenerating in the lower layers of the corallum; *Cor*, corallum; *D*, an expanded dactylozooid with its capitate tentacles; *Ect*, the continuous sheet of ectoderm covering the corallum (*Cor*); *G*, a gastrozooid, seen in vertical section; *Med*, free-swimming Medusae; *t*, tentacle; *Tab*, tabula in the pore-tubes. (Partly after Moseley.)

be recognised even in the dried skeleton. It is not known how frequently the sexual seasons occur, but from the rarity in the collections of our museums of Millepore skeletons which exhibit the ampullae, it may be inferred that the intervals between successive seasons are of considerable duration.

The Medusae of *Millepora* are extremely simple in character. There is a short mouthless manubrium bearing the sexual cells, an umbrella without radial canals, while four or five knobs at the margin, each supporting a battery of nematocysts, represent all that there is of the marginal tentacles. The male Medusae have not yet been observed to escape from the parent, but from the fact that the spermatozoa are not ripe while they are in the ampullae, it may be assumed that the Medusae are set free. Duerden, however, has observed the escape of the female Medusae, and it seems probable from his observations that their independent life is a short one, the ova being discharged very soon after liberation.

Millepora appears to be essentially a shallow-water reef coral. It may be found on the coral reefs of the Western Atlantic extending as far north as Bermuda, in the Red Sea, the Indian and Pacific Oceans. The greatest depth at which it has hitherto been found is 15 fathoms on the Macclesfield Bank, and it flourishes at a depth of 7 fathoms off Funafuti in the Pacific Ocean.

Millepora, like many other corals, bears in its canals and zooids a great number of the symbiotic unicellular "Algae" (Chrysomonadaceae, see pp. 86, 125) known as Zooxanthellae. All specimens that have been examined contain these organisms in abundance, and it has been suggested that the coral is largely dependent upon the activity of the "Algae" for its supply of nourishment. There can be no doubt that the dactylozooids do paralyse and catch living animals, which are ingested and digested by the gastrozooids, but this normal food-supply may require to be supplemented by the carbohydrates formed by the plant-cells. But as the carbohydrates can only be formed by the "Algae" in sunlight, this supplementary food-supply can only be provided in corals that live in shallow water. It must not be supposed that this is the only cause that limits the distribution of *Millepora* in depth, but it may be an important one.

The generic name *Millepora* has been applied to a great many fossils from different strata, but a critical examination of their structure fails to show any sufficient reason for including many of them in the genus or even in the order. Fossils that are undoubtedly *Millepora* occur in the raised coral reefs of relatively recent date, but do not extend back into Tertiary times. There seems to be no doubt, therefore, that the genus is of comparatively recent origin. Among the extinct fossils the genus that comes nearest to it is *Axopora* from the Eocene of France, but this genus differs from *Millepora* in having monomorphic, not dimorphic, pores, and in the presence of a minute spine or columella in the centre of each tube. The resemblances are to be observed in the general disposition of the canal system and of the tabulation. Whether *Axopora* is or is not a true Milleporine, however, cannot at present be determined, but it is the only extinct coral that merits consideration in this place.

Order III. Gymnoblastea—Anthomedusae.

This order was formerly united with the Calyptoblastea to form the order Hydromedusae, but the differences between the two are sufficiently pronounced to merit their treatment as distinct orders.

In many of the Gymnoblastea the sexual cells are borne by free Medusae, which may be recognised as the Medusae of Gymnoblastea by the possession of certain distinct characters. The name given to such Medusae, whether their hydrosome stage is known or not, is Anthomedusae. The Gymnoblastea are solitary or colonial Hydrozoa, in which the free (oral) extremity of the zooids, including the crown of tentacles, is not protected by a skeletal cup. The sexual cells may be borne by free Anthomedusae, or by more or less degenerate Anthomedusae that are never detached from the parent hydrosome. The Anthomedusae are small or minute Medusae provided with a velum, with the ovaries or sperm-sacs borne by the manubrium and with sense-organs in the form of ocelli or pigment-spots situated on the margin of the umbrella.

The solitary Gymnoblastea present so many important differences in anatomical structure that they cannot be united in a single family. They are usually fixed to some solid object by root-like processes from the aboral extremity, the "hydrorhiza," or are partly embedded in the sand (*Corymorpha*), into which long filamentous processes project for the support of the zooid. The remarkable species *Hypolytus peregrinus*[1] from Wood's Holl,

[1] *Quart. Journ. Micr. Sci.* xlii. 1899, p. 341.

however, has no aboral processes, and appears to be only temporarily attached to foreign objects by the secretion of the perisarc. Among the solitary Gymnoblastea several species reach a gigantic size. *Corymorpha* is 50–75 mm. in length, but *Monocaulus* from deep water in the Pacific and Atlantic Oceans is nearly 8 feet in length. Among the solitary forms attention must be called to the interesting pelagic *Pelagohydra* (see p. 274).

The method of colony formation in the Gymnoblastea is very varied. In some cases (*Clava squamata*) a number of zooids arise from a plexus of canals which corresponds with the system of root-like processes of the solitary forms. In *Hydractinia* this plexus is very dense, and the ectoderm forms a continuous sheet of tissue both above and below. The colony is increased in size in these cases by the gemmation of zooids from the hydrorhiza. In other forms, such as *Tubularia larynx,* new zooids arise not only from the canals of the hydrorhiza, but also from the body-walls of the upstanding zooids, and thus a bushy or shrubby colony is formed.

In another group the first-formed zooid produces a hydrorhiza of considerable proportions, which fixes the colony firmly to a stone or shell and increases in size with the growth of the colony. This zooid itself by considerable growth in length forms the axis of the colony, and by gemmation gives rise to lateral zooids, which in their turn grow to form the lateral branches and give rise to the secondary branches, and these to the tertiary branches, and so one; each branch terminating in a mouth, hypostome and crown of tentacles. Such a method of colony formation is seen in *Bougainvillia* (Fig. 130). A still more complicated form of colony formation is seen in *Ceratella,* in which not a single but a considerable number of zooids form the axis of the colony and of its branches. As each axis is covered with a continuous coat of ectoderm, and each zooid of such an axis secretes a chitinous fenestrated tube, the whole colony is far more rigid and compact than is usual in the Gymnoblastea, and has a certain superficial resemblance to a Gorgoniid Alcyonarian (Fig. 133, p. 271).

The branches of the colony and a considerable portion of the body-wall of each zooid in the Gymnoblastea are usually protected by a thin, unjointed "perisarc" of chitin secreted by the ectoderm; but this skeletal structure does not expand distally to form a cup-like receptacle in which the oral extremity of the zooid can be retracted for protection.

The zooids of the Gymnoblastea present considerable diversity of form and structure. The tentacles may be reduced to one (in *Monobrachium*) or two (in *Lar sabellarum*), but usually the number is variable in each individual colony. In many cases, such as *Cordylophora, Clava,* and many others, the tentacles are irregularly scattered on the sides of the zooids. In others there may be a single circlet of about ten or twelve tentacles round the base of the hypostome. In some genera the tentacles are arranged in two series (*Tubularia, Corymorpha, Monocaulus*), a distal series round the margin of the mouth which may be arranged in a single circlet or scattered irregularly on the hyposome, and a proximal series arranged in a single circlet some little distance from the mouth. In *Branchiocerianthus imperator* the number of tentacles is very great, each of the two circlets consisting of about two hundred tentacles.

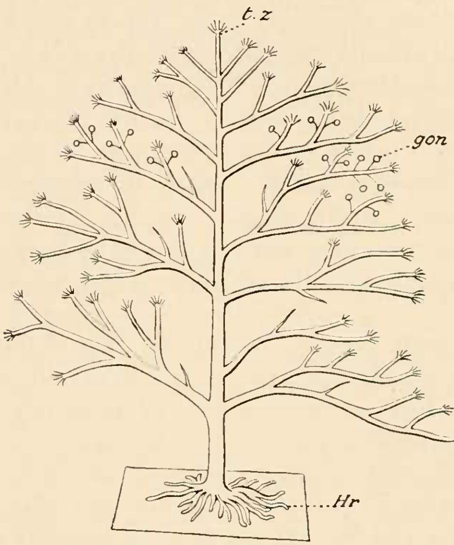

FIG. 130.—Diagrammatic sketch to show the method of branching of *Bougainvillia*. *gon*, Gonophores; *Hr*, hydrorhiza; *t.z*, terminal zooid.

The zooids of the hydrosome are usually monomorphic, but there are cases in which different forms of zooid occur in the same colony. In *Hydractinia*, for example, no less than four different kinds of zooids have been described. These are called gastrozooids, dactylozooids, tentaculozooids, and blastostyles respectively. The "gastrozooids" are provided with a conical hypostome bearing the mouth and two closely-set circlets of some ten to thirty tentacles. The "dactylozooids" are longer than the gastrozooids and have the habit of actively coiling and uncoiling themselves; they have a small mouth and a single circlet of rudimentary tentacles. The "tentaculozooids" are situated at the outskirts of the colony, and are very long and slender, with rudimentary tentacles and no mouth. The "blastostyles," usually shorter than the gastrozooids, have two circlets of rudimentary tentacles and a mouth. They bear on their sides the spherical or oval gonophores.

The medusome stage in the life-history of these Hydrozoa is produced by gemmation from the hydrosome, or, in some cases, by gemmation from the medusome as well as from the hydrosome. In many genera and species the medusome is set free as a minute jelly-fish or Medusa, which grows and develops as an independent organism until the time when the sexual cells are ripe, and then apparently it dies. In other Gymnoblastea the medusome either in the female or the male or in both sexes does not become detached from the parent hydrosome, but bears the ripe sexual cells, discharges them into the water, and degenerates without leading an independent life at all. In these cases the principal organs of the medusome are almost or entirely functionless, and they exhibit more or less imperfect development, or they may be so rudimentary that the medusoid characters are no longer obvious. Both the free and the undetached medusomes are gonophores, that is to say, the bearers of the sexual cells, but the former were described by Allman as the "phanerocodonic" gonophores, *i.e.* "with manifest bells," and the latter as the "adelocodonic" gonophores. The gonophores may arise either from an ordinary zooid of the colony (*Syncoryne*), from a specially modified zooid—the blastostyle—as in *Hydractinia*, or from the hydrorhiza as in certain species of *Perigonimus*. The free-swimming Medusa may itself produce Medusae by gemmation from the manubrium (*Sarsia*, *Lizzia*, *Rathkea*, and others), from the base of the tentacles (*Sarsia*, *Corymorpha*, *Hybocodon*), or from the margin of the umbrella (*Eleutheria*).

The free-swimming Medusae or phanerocodonic gonophores of the Gymnoblastea are usually of small size (1 or 2 mm. in diameter) when first liberated, and rarely attain a great size even when fully mature. They consist of a circular, bell-shaped or flattened disc—the umbrella—provided at its margin with a few or numerous tentacles, and a tubular manubrium bearing the mouth depending from the exact centre of the under (oral) side of the umbrella (Fig. 132, A). The mouth leads into a shallow digestive cavity, from which radial canals pass through the substance of the umbrella to join a ring-canal at the margin (Fig. 131).

The sense-organs of the Medusae of the Gymnoblastea are in the form of pigment-spots or very simple eyes (ocelli), situated at the bases of the tentacles. The orifice of the umbrella is guarded by a thin shelf or membrane, as in the Calyptoblastea, called the velum. The sexual cells are borne by the manubrium (Figs. 131 and 132, A).

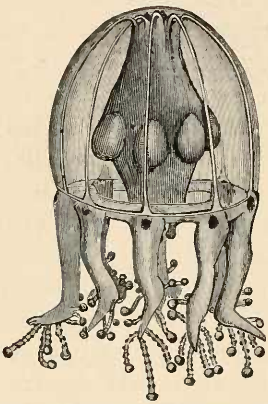

FIG. 131.—Medusa of *Cladonema*, from the Bahamas, showing peculiar tentacular processes on the tentacles, the ocelli at the base of the tentacles, the swellings on the manubrium that mark the position of the gonads, and the radial and ring-canals of the umbrella. (After Perkins.)

There are many modifications observed in the different genera as regards the number of tentacles, the number and character of the radial canals, the minute structure of the sense-organs, and some other characters, but they agree in having a velum, ocellar sense-organs, and manubrial sexual organs. The tentacles are rudimentary in *Amalthea*; in *Corymorpha* there is only one tentacle; in *Perigonimus* there are two; and in *Bougainvillia* they are numerous; but the usual number is four or six. The radial canals are usually simple and four in number, but there are six in *Lar sabellarum*, which branch twice or three times before reaching the margin of the umbrella (Fig. 132, B).

There can be no doubt that the Medusae of many Gymnoblastea undergo several important changes in their anatomical features during the period of the ripening of the sexual cells. Thus in *Lar sabellarum* the six radial canals are simple in the first stage of development (A); but in the second stage (B) each radial canal bifurcates before reaching the margin, and in the adult stage shows a double bifurcation. The life-history has, however, been worked out in very few of the Anthomedusae, and there can be little doubt that as our knowledge grows several forms which are now known as distinct species will be found to be different stages of growth of the same species.

The movements of the Medusae are well described by Allman[1] in his account of *Cladonema radiatum*:—"It is impossible to grow tired of watching this beautiful medusa; sometimes while dashing through the water with vigorous diastole and systole, it will all at once attach its grapples to the side of the vessel, and become suddenly arrested in its career, and then after a period of repose, during which its branched tentacles are thrown back over its umbrella and extended into long filaments which float, like

A

B

FIG. 132.—Two stages in the development of the Medusa of *Lar sabellarum* (*Willsia stellata*). **A**, first stage with six canals without branches; **B**, third stage with six canals each with two lateral branches. The developing gonads may be seen on the manubrium in **A**. (After Browne.)

some microscopic sea-weed in the water, it will once more free itself from its moorings and start off with renewed energy." The Medusa of *Clavatella*, "in its movements and mode of life, presents a marked contrast to the medusiform zooid of other Hydrozoa. The latter is active and mercurial, dancing gaily through the water by means of the vigorous strokes of its crystalline swimming-bell. The former strides leisurely along, or, using the adhesive discs as hands, climbs amongst the branches of the weed. In the latter stage of its existence it becomes stationary, fixing itself by means of its suckers; and

[1] "Gymnoblastic Hydroids," *Ray Society*, 1871, p. 359.

thus it remains, the capitate arms standing out rigidly, like the rays of a starfish, until the embryos are ready to escape."[1]

Among the Gymnoblastea there are many examples of a curious association of the Hydroid with some other living animals. Thus *Hydractinia* is very often found on the shells carried by living Hermit crabs, *Dicoryne* on the shells of various Molluscs, *Tubularia* has been found on a Cephalopod, and *Ectopleura* (a Corymorphid) on the carapace of a crab. There is but little evidence, however, that in these cases the association is anything more than accidental. The occurrence of the curious species, *Lar sabellarum*, on the tubes of *Sabella*, of *Campaniclava cleodorae* on the living shells of the pelagic Mollusc *Cleodora cuspidata*, and of a *Gorgonia* on the tubes of *Tubularia parasitica*, appear to be cases in which there is some mutual relationship between the two comrades. The genus *Stylactis*, however, affords some of the most interesting examples of mutualism. Thus *Stylactis vermicola* is found only on the back of an *Aphrodite* that lives at the great depth of 2900 fathoms. *S. spongicola* and *S. abyssicola* are found associated with certain deep-sea Horny Sponges. *S. minoi* is spread over the skin of the little rock perch *Minous inermis*, which is found at depths of from 45 to 150 fathoms in the Indian seas.

In many cases it is difficult to understand what is the advantage of the Hydroid to the animal that carries it, but in this last case Alcock[2] suggests that the *Stylactis* assists in giving the fish a deceitful resemblance to the incrusted rocks of its environment, in order to allure, or at any rate not to scare, its prey. Whether this is the real explanation or not, the fact that in the Bay of Bengal and in the Laccadive and Malabar seas the fish is never found without this Hydroid, nor the Hydroid without this species of fish, suggests very strongly that there is a mutual advantage in the association.

Cases of undoubted parasitism are very rare in this order. The remarkable form *Hydrichthys mirus*,[3] supposed to be a Gymnoblastic Hydroid, but of very uncertain position in the system, appears to be somewhat modified in its structure by its parasitic habits on the fish *Seriola zonata*. *Corydendrium*

[1] Hincks, *British Hydroid Zoophytes*, 1868, p. 74.
[2] *Ann. Mag. Nat. Hist.* (6) x. 1892, p. 207.
[3] Fewkes, *Bull. Mus. Comp. Zool.* xiii. 1887, p. 224.

parasiticum is said to be a parasite living at the expense of *Eudendrium racemosum*. *Mnestra* is a little Medusa which attaches itself by its manubrium to the Mollusc *Phyllirhoe*, and may possibly feed upon the skin or secretions of its host.

Nearly all the species of the order are found in shallow sea water. *Stylactis vermicola* and the "Challenger" specimen of *Monocaulus imperator* occur at a depth of 2900 fathoms, and some species of the genera *Eudendrium* and *Myriothela* descend in some localities to a depth of a few hundred fathoms. *Cordylophora* is the only genus known to occur in fresh water. From its habit of attaching itself to wooden piers and probably to the bottom of barges, and from its occurrence in navigable rivers and canals, it has been suggested that *Cordylophora* is but a recent immigrant into our fresh-water system. It has been found in England in the Victoria docks of London, in the Norfolk Broads, and in the Bridgewater Canal. It has ascended the Seine in France, and may now be found in the ponds of the Jardin des Plantes at Paris. It also occurs in the Elbe and in some of the rivers of Denmark.

The classification of the Gymnoblastea is not yet on a satisfactory basis. At present the hydrosome stage of some genera alone has been described, of others the free-swimming Medusa only is known. Until the full life-history of any one genus has been ascertained its position in the families mentioned below may be regarded as only provisional. The principal families are:—

Fam. Bougainvilliidae.—The zooids of the hydrosome have a single circlet of filiform tentacles at the base of the hypostome. In *Bougainvillia* belonging to this family the gonophores are liberated in the form of free-swimming Medusae formerly known by the generic name *Hippocrene*. In the fully grown Medusa there are numerous tentacles arranged in clusters opposite the terminations of the four radial canals. There are usually in addition tentacular processes (labial tentacles) on the lips of the manubrium. *Bougainvillia* is a common British zoophyte of branching habit, found in shallow water all round the coast. The medusome of *Bougainvillia ramosa* is said to be the common little medusa *Margelis ramosa*.[1] Like most of the Hydroids it has a wide geographical distribution. Other genera are *Perigonimus*, which has a Medusa with only two tentacles; and

[1] Hartlaub, *Wiss. Meeresunt. deutsch. Meere in Kiel* N.F.I. 1894, p. 1.

Dicoryne, which forms spreading colonies on Gasteropod shells and has free gonophores provided with two simple tentacles, while the other organs of the medusome are remarkably degenerate. In *Garveia* and *Eudendrium* the gonophores are adelocodonic, in the former genus arising from the body-wall of the axial zooids of the colony, and in the latter from the hydrorhiza. *Stylactis* is sometimes epizoic (p. 268). Among the genera that are usually placed in this family, of which the medusome stage only is known, are *Lizzia* (a very common British Medusa) and *Rathkea*. In *Margelopsis* the hydrosome stage consists of a single free-swimming zooid which produces Medusae by gemmation.

Fam. Podocorynidae.—The zooids have the same general features as those of the Bougainvilliidae, but the perisarc does not extend beyond the hydrorhiza.

In *Podocoryne* and *Hydractinia* belonging to this family the hydrorhiza forms an encrusting stolon which is usually found on Gasteropod shells containing a living Hermit crab. In *Podocoryne* the gonophores are free-swimming Medusae with a short manubrium provided with labial tentacles. *Hydractinia* differs from *Podocoryne* in having polymorphic zooids and adelocodonic gonophores.

A fossil encrusting a *Nassa* shell from the Pliocene deposit of Italy has been placed in the genus *Hydractinia*, and four species of the same genus have been described from the Miocene and Upper Greensand deposits of this country.[1] These are the only fossils known at present that can be regarded as Gymnoblastic Hydroids.

The Medusa *Thamnostylus*, which has only two marginal tentacles and four very long and profusely ramified labial tentacles, is placed in this family. Its hydrosome stage is not known.

Fam. Clavatellidae.—This family contains the genus *Clavatella*, in which the zooids of the hydrosome have a single circlet of capitate tentacles. The gonophore is a free Medusa provided with six bifurcated capitate tentacles.

Fam. Cladonemidae.—This family contains the genus *Cladonema*, in which the zooids have two circlets of four tentacles, the labial tentacles being capitate and the aboral filiform. The gonophore is a free Medusa with eight tentacles, each provided with a number of curious capitate tentacular processes (Fig. 131).

[1] Carter, *Ann. Mag. Nat. Hist.* (4) xix. 1877, p. 44 ; (5) i. 1878, p. 298.

Fam. Tubulariidae.—This important and cosmopolitan family is represented in the British seas by several common species. The zooids of the hydrosome of *Tubularia* have two circlets of numerous filiform tentacles. The gonophores are adelocodonic, and are situated on long peduncles attached to the zooid on the upper side of the aboral circlet of tentacles. The larva escapes from the gonophore and acquires two tentacles, with which it beats the water and, assisted by the cilia, keeps itself afloat for some time. In this stage it is known as an "Actinula."[1]

Fam. Ceratellidae.—The colony of *Ceratella* may be five inches in height. The stem and main branches are substantial,

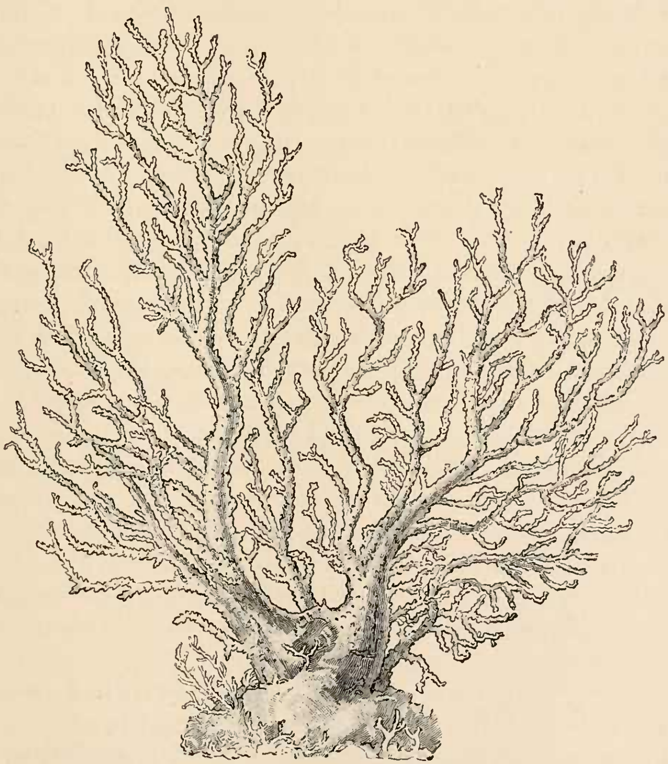

Fig. 133.—*Ceratella fusca.* About nat. size. (After Baldwin Spencer.[2])

and consist of a network of branching anastomosing tubes supported by a thick and fenestrated chitinous perisarc. The

[1] The aberrant genus *Hypolytus* (p. 262) may belong to this family.

[2] Spencer, *Trans. Roy. Soc. Vict.* 1892, p. 8.

whole branch is enclosed in a common layer of ectoderm. The zooids have scattered capitate tentacles. The Ceratellidae occur in shallow water off the coast of New South Wales, extend up the coast of East Africa as far as Zanzibar, and have also been described from Japan.

Fam. Pennariidae.—In the hydrosome stage the zooids have numerous oral capitate tentacles scattered on the hypostome, and a single circlet of basilar filiform tentacles. The medusa of *Pennaria*, a common genus of wide distribution, is known under the name *Globiceps.*

Fam. Corynidae.—In the hydrosome stage the zooids of this family possess numerous capitate tentacles arranged in several circlets or scattered.

In *Cladocoryne* the tentacles are branched. *Syncoryne* is a common and widely distributed genus with numerous unbranched capitate tentacles irregularly distributed over a considerable length of the body-wall of the zooid. In many of the species the gonophores are liberated as Medusae, known by the name *Sarsia*, provided with four filiform tentacles and a very long manubrium. In some species (*S. prolifera* and *S. siphonophora*) the Medusae are reproduced asexually by gemmation from the long manubrium. A common British Anthomedusa of this family is *Dipurena*, but its hydrosome stage is not known. In the closely related genus *Coryne* the gonophores are adelocodonic, and exhibit very rudimentary medusoid characters.

Fam. Clavidae.—This is a large family containing many genera, some with free-swimming Medusae, others with adelocodonic gonophores. In the former group are included a number of oceanic Medusae of which the hydrosome stage has not yet been discovered. The zooids of the hydrosome have numerous scattered filiform tentacles. The free-swimming Medusae have hollow tentacles.

Clava contains a common British species with a creeping hydrorhiza frequently attached to shells, and with adelocodonic gonophores. *Cordylophora* is the genus which has migrated into fresh water in certain European localities (see p. 269). It forms well-developed branching colonies attached to wooden gates and piers or to the brickwork banks of canals. Several Anthomedusae, of which the hydrosome stage is not known, appear to be related to the Medusae of this family, but are sometimes separated as the family **Tiaridae.** Of these *Tiara*, a very brightly coloured jelly-fish sometimes attaining a height of 40 mm., is found on the British coasts, and *Amphinema* is found in considerable numbers at Plymouth in September. *Turritopsis* is a Medusa with a hydrosome stage like *Dendroclava*. For *Stomatoca*, see p. 415.

Fam. Corymorphidae.—This family contains the interesting British species *Corymorpha nutans*. The hydrosome stage consists of a solitary zooid of great size, 50-75 mm. in length, provided with two circlets of numerous long filiform tentacles. The free-swimming Medusae are produced in great numbers on the region between the two circlets of tentacles. These Medusae were formerly known by the name *Steenstrupia*, and are noteworthy in having only one long moniliform tentacle, opposite to one of the radial canals.

The gigantic *Monocaulus imperator* of Allman was obtained by the "Challenger" at the great depth of 2900 fathoms off the coast of Japan. It was nearly eight feet in length. More recently Miyajima[1] has described a specimen from 250 fathoms in the same seas which was 700 mm. (27·5 in.) in length. Miyajima's specimen resembles those described by Mark from 300 fathoms off the Pacific coast of North America as *Branchiocerianthus urceolus* in the remarkable feature of a distinct bilateral arrangement of the circlets of tentacles. Owing to the imperfect state of preservation of the only specimen of Allman's species it is difficult to determine whether it is also bilaterally symmetrical and belongs to the same species as the specimens described by Mark and Miyajima. These deep-sea giant species, however, appear to differ from *Corymorpha* in having adelocodonic gonophores.

Fam. Hydrolaridae.—This family contains the remarkable genus *Lar*, which was discovered by Gosse attached to the margin of the tubes of the marine Polychaete worm *Sabella*. The zooids have only two tentacles, and exhibit during life curious bowing and bending movements which have been compared with the exercises of a gymnast. The Medusae (Fig. 132, A and B) have been known for a long time by the name *Willsia*, but their life-history has only recently been worked out by Browne.[2]

[1] *Journ. Coll. Sci. Tokyo*, xiii. 1900, p. 235 (with a beautiful coloured illustration).

[2] *Proc. Zool. Soc.* 1897, p. 818.

Fam. Monobrachiidae.—*Monobrachium*, found in the White Sea by Mereschkowsky, forms a creeping stolon on the shells of *Tellina*. The zooids of the hydrosome have only one tentacle.

Fam. Myriothelidae.—This family contains the single genus *Myriothela*. The zooid of the hydrosome stage is solitary and is provided, as in the Corynidae, with numerous scattered capitate tentacles. The gonophores are borne by blastostyles situated above the region of the tentacles. In addition to these blastostyles producing gonophores there are, in *M. phrygia*, supplementary blastostyles which capture the eggs as they escape from the gonophores and hold them until the time when the larva is ready to escape. They were called "claspers" by Allman. In some of the Arctic species Frl. Bonnevie[1] has shown that they are absent. Each zooid of *M. phrygia* is hermaphrodite.

Fam. Pelagohydridae.—This family was constituted by Dendy[2] for the reception of *Pelagohydra mirabilis*, a remarkable new species discovered by him on the east coast of the South Island of New Zealand. The hydrosome is solitary and free-swimming, the proximal portion of the body being modified to form a float, the distal portion forming a flexible proboscis terminated by the mouth and a group of scattered manubrial tentacles. The tentacles are filiform and scattered over the surface of the float. Medusae are developed on stolons between the tentacles of the float. They have tentacles arranged in four radial groups of five each, at the margin of the umbrella.

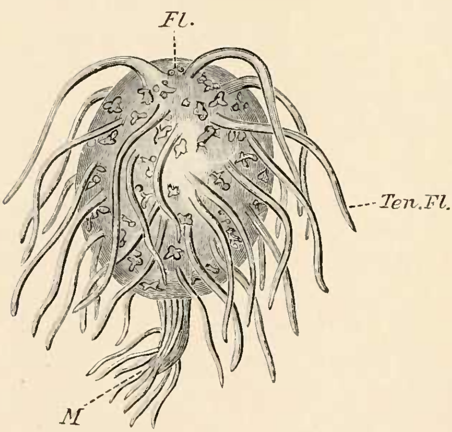

Fig. 134.—*Pelagohydra mirabilis*. *Fl*, The float; *M*, position of the mouth; *Ten.Fl*, filamentous tentacles of the float. (After Dendy.)

As pointed out by Hartlaub,[3] *Pelagohydra* is not the only genus in which the hydrosome floats. Three species of the genus *Margelopsis* have been found that have pelagic habits, and two

[1] *Zeitschr. f. wiss. Zool.* lxiii. 1898, p. 489.

[2] *Quart. Journ. Micr. Sci.* xlvi. 1902, p. 1.

[3] *Zool. Zentralbl.* x. 1903, p. 27.

of them have been shown to produce numerous free-swimming Medusae by gemmation; but at present there is no reason to suppose that in these forms there is any extensive modification of the aboral extremity of the zooid to form such a highly specialised organ as the float of *Pelagohydra.*

The affinities of *Pelagohydra* are not clear, as our knowledge of the characters of the Medusa is imperfect; but according to Dendy it is most closely related to the Corymorphidae. *Margelopsis* belongs to the Bougainvilliidae.

Order IV. Calyptoblastea—Leptomedusae.

The hydrosome stage is characterised by the perisarc, which not only envelops the stem and branches, as in many of the Gymnoblastea, but is continued into a trumpet-shaped or tubular cup or collar called the "hydrotheca," that usually affords an efficient protection for the zooids when retracted. No solitary Calyptoblastea have been discovered. In the simpler forms the colony consists of a creeping hydrorhiza, from which the zooids arise singly (*Clytia johnstoni*), but these zooids may give rise to a lateral bud which grows longer than the parent zooid.

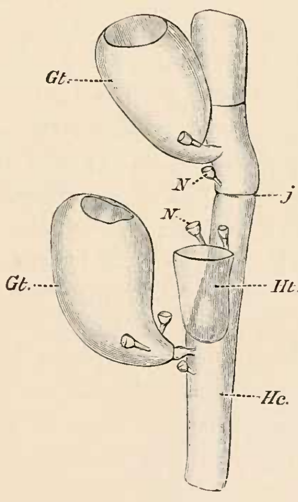

Fig. 135.—Part of a hydrocladium of a dried specimen of *Plumularia profunda.* *Gt*, Gonotheca; *Hc*, the stem of the hydrocladium with joints (*j*); *Ht*, a single hydrotheca; *N*, nematophores. Greatly enlarged. (After Nutting.)

The larger colonies are usually formed by alternate right and left budding from the last-formed zooid, so that in contrast to the Gymnoblast colony the apical zooid of the stem is the youngest, and not the oldest, zooid of the colony. In the branching colonies the axis is frequently composed of a single tube of perisarc, which may be lined internally by the ectoderm and endoderm tissues formed by the succession of zooids that have given rise to the branches by gemmation. Such a stem is said to be monosiphonic.

In some of the more complicated colonies, however, the stem is composed of several tubes, which may or may not be surrounded by a common sheath of ectoderm and perisarc, as they are in *Ceratella* among the Gymnoblastea. Such stems are said to be "polysiphonic" or "fascicled." The polysiphonic stem may arise in more than one way, and in some cases it is not quite clear in what manner it has arisen.[1]

In many colonies the zooids are only borne by the terminal monosiphonic branches, which receive the special name "hydrocladia." The gonophores of the Calyptoblastea are usually borne by rudimentary zooids, devoid of mouth and tentacles (the "blastostyles"), protected by a specially dilated cup of perisarc known as the "gonotheca" or "gonangium." The shape and size of the gonothecae vary a good deal in the order. They may be simply oval in shape, or globular (*Schizotricha dichotoma*), or greatly elongated, with the distal ends produced into slender necks (*Plumularia setacea*). They are spinulose in *P. echinulata*, and annulated in *P. halecioides*, *Clytia*, etc.

In some genera there are special modifications of the branches and hydrocladia, for the protection of the gonothecae. The name "Phylactocarp" is used to designate structures that are obviously intended to serve this purpose. The phylactocarp of the genera *Aglaophenia* and *Thecocarpus* is the largest and most remarkable of this group of structures, and has received the special name "corbula." The corbula consists of an axial stem or rachis, and of a number of corbula-leaves arising alternately from the rachis, bending upwards and then inwards to meet those of the other side above, the whole forming a pod-shaped receptacle. The gonangia are borne at the base of each of the corbula-leaves. There is some difference of opinion as to the homologies of the parts of the corbula, but the rachis seems to be that of a modified hydrocladium, as it usually bears at its base one or more hydrothecae of the normal type. The corbula-leaves are usually described as modified nematophores (*vide infra*), but according to Nutting[2] there is no more reason to regard them as modified nematophores than as modified hydrothecae, and he regards them as "simply the modification of a structure originally intended to

[1] For a discussion of the origin of the polysiphonic stem in Calyptoblastea see Nutting, "American Hydroids," *Smithsonian Institution Special Bulletin*, pt. i. 1900, p. 4.

[2] *Loc. cit.* p. 33.

protect an indefinite person, an individual that may become either a sarcostyle[1] or a hydranth.'

The other forms of phylactocarps are modified branches as in *Lytocarpus*, and those which are morphologically appendages to branches as in *Cladocarpus*, *Aglaophenopsis*, and *Streptocaulus*.

The structures known as "nematophores" in the Calyptoblastea are the thecae of modified zooids, comparable with the dactylozooids of *Millepora*. They form a well-marked character of the very large family Plumulariidae, but they are also found in species of the genera *Ophiodes*, *Lafoëina*, *Oplorhiza*, *Perisiphonia*, *Diplocyathus*, *Halecium*, and *Clathrozoon* among the other Calyptoblastea. The dactylozooids are usually capitate or filiform zooids, without tentacles or a mouth, and with a solid or occasionally a perforated core of endoderm. They bear either a battery of nematocysts (*Plumularia*, etc.), or of peculiar adhesive cells (*Aglaophenia* and some species of *Plumularia*). The functions of the dactylozooids are to capture the prey and to serve as a defence to the colony. In the growth of the corbula of *Aglaophenia* the dactylozooids appear to serve another purpose, and that is, as a temporary attachment to hold the leaves together while the edges themselves are being connected by trabeculae of coenosarc.

In a very large number of Calyptoblastea the gonophore is a reduced Medusa which never escapes from the gonotheca, but in the family Eucopidae the gonophores escape as free-swimming Medusae, exhibiting certain very definite characters. The gonads are situated not on the manubrium, as in the Anthomedusae, but on the sub-umbrellar aspect of the radial canals. The marginal sense-organs may be ocelli or vesiculate statocysts. The bell is usually more flattened, and the velum smaller than it is in the Anthomedusae, and the manubrium short and quadrangular. Such Medusae are called Leptomedusae.

Leptomedusae of many specific forms are found abundantly at the surface of the sea in nearly all parts of the world, but with the exception of some genera of the Eucopidae and a few others, their connexion with a definite Calyptoblastic hydrosome has not been definitely ascertained. It may be an assumption that time will prove to be unwarranted that all the Leptomedusae pass through a Calyptoblastic hydrosome stage.

[1] The term "sarcostyle" is usually applied to the dactylozooid of the Calyptoblastea.

Fam. Aequoreidae.—In this family the hydrosome stage is not known except in the genus *Polycanna*, in which it resembles a Campanulariid. The sense-organs of the Medusae are statocysts. The radial canals are very numerous, and the genital glands are in the form of ropes of cells extending along the whole of their oral surfaces. *Aequorea* is a fairly common genus, with a flattened umbrella and a very rudimentary manubrium, which may attain a size of 40 mm. in diameter.

Fam. Thaumantiidae.—The Medusae of this family are distinguished from the Aequoreidae by having marginal ocelli in place of statocysts. The hydrosome of *Thaumantias* alone is known, and this is very similar to an *Obelia*.

Fam. Cannotidae.—The hydrosome is quite unknown. The Medusae are ocellate, but the radial canals, instead of being undivided, as in the Thaumantiidae, are four in number, and very much ramified before reaching the ring canal. The tentacles are very numerous. In the genus *Polyorchis*, from the Pacific coast of North America, the four radial canals give rise to numerous lateral short blind branches, and have therefore a remarkable pinnate appearance.

Fam. Sertulariidae.—In this family the hydrothecae are sessile, and arranged bilaterally on the stem and branches. The general form of the colony is pinnate, the branches being usually on opposite sides of the main stem. The gonophores are adelocodonic. *Sertularia* forms more or less arborescent colonies, springing from a creeping stolon attached to stones and shells. There are many species, several of which are very common upon the British coast. Many specimens are torn from their attachments by storms or by the trawls of fishermen and cast up on the sand or beach with other zoophytes. The popular name for one of the commonest species (*S. abietina*) is the "sea-fir." The genus has a wide geographical and bathymetrical range. Another common British species frequently thrown up by the tide in great quantities is *Hydrallmania falcata*. It has slender spirally-twisted stems and branches, and the hydrothecae are arranged unilaterally.

The genus *Grammaria*, sometimes placed in a separate family, is distinguished from *Sertularia* by several characters. The stem and branches are composed of a number of tubes which are considerably compressed. The genus is confined to the southern seas.

Fam. Plumulariidae.—The hydrothecae are sessile, and arranged in a single row on the stem and branches. Nematophores are always present. Gonophores adelocodonic. This family is the largest and most widely distributed of all the families of the Hydrozoa. Nutting calculates that it contains more than one-fourth of all the Hydroids of the world. Over 300 species have been described, and more than half of these are found in the West Indian and Australian regions. Representatives of the family occur in abundance in depths down to 300 fathoms, and not unfrequently to 500 fathoms. Only a few species have occasionally been found in depths of over 1000 fathoms.

The presence of nematophores may be taken as the most characteristic feature of the family, but similar structures are also found in some species belonging to other families (p. 277).

The family is divided into two groups of genera, the Eleutheroplea and the Statoplea. In the former the nematophores are mounted on a slender pedicel, which admits of more or less movement, and in the latter the nematophores are sessile. The genera *Plumularia* and *Antennularia* belong to the Eleutheroplea. The former is a very large genus, with several common British species, distinguished by the terminal branches being pinnately disposed, and the latter, represented by *A. antennina* and *A. ramosa* on the British coast, is distinguished by the terminal branches being arranged in verticils.

The two most important genera of the Statoplea are *Aglaophenia* and *Cladocarpus*. The former is represented by a few species in European waters, the latter is only found in American waters.

Fam. Hydroceratinidae.—The colony consists of a mass of entwined hydrorhiza, with a skeleton in the form of anastomosing chitinous tubes. Hydrothecae scattered, tubular, and sessile. Nematophores present. Gonophores probably adelocodonic.

This family was constituted for a remarkable hydroid, *Clathrozoon wilsoni*, described by W. B. Spencer from Victoria.[1] The zooids are sessile, and spring from more than one of the numerous anastomosing tubes of the stem and branches. The whole of the surface is studded with an enormous number of small and very simple dactylozooids, protected by tubular nematophores. Only

[1] *Trans. Roy. Soc. Victoria*, 1890, p. 121.

a few specimens have hitherto been obtained, the largest being 10 inches in height by 4 inches in width. In general appearance it has some resemblance to a dark coloured fan-shaped *Gorgonia*.

Fam. Campanulariidae.—The hydrothecae in this family are pedunculate, and the gonophores adelocodonic.

In the cosmopolitan genus *Campanularia* the stem is monosiphonic, and the hydrothecae bell-shaped. Several species of this genus are very common in the rock pools of our coast between tide marks. *Halecium* is characterised by the rudimentary character of its hydrothecae, which are incapable of receiving the zooids even in their maximum condition of retraction. The genus *Lafoea* is remarkable for the development of a large number of tightly packed gonothecae on the hydrorhiza, each of which contains a blastostyle, bearing a single gonophore and, in the female, a single ovum. This group of gonothecae was regarded as a distinct genus of Hydroids, and was named *Coppinia*.[1] *Lafoea dumosa* with gonothecae of the type described as *Coppinia arcta* occurs on the British coast.

Perisiphonia is an interesting genus from deep water off the Azores, Australia, and New Zealand, with a stem composed of many distinct tubes.

The genus *Zygophylax*, from 500 fathoms off the Cape Verde, is of considerable interest in having a nematophore on each side of the hydrotheca. According to Quelch it should be placed in a distinct family.

Ophiodes has long and very active defensive zooids, protected by nematophores. It is found in the Laminarian zone on the English coast.

Fam. Eucopidae.—The hydrosome stage of this family is very similar to that of the Campanulariidae, but the gonophores are free-swimming Medusae of the Leptomedusan type.

One of the best-known genera is *Obelia*, of which several species are among the commonest Hydroids of the British coast.

Clytia johnstoni is also a very common Hydroid, growing on red algae or leaves of the weed *Zostera*. It consists of a number of upright, simple, or slightly branched stems springing from a creeping hydrorhiza. When liberated the Medusae are globular in form, with four radial canals and four marginal tentacles, but

[1] See C. C. Nutting, *Proc. U.S. National Museum*, xxi. 1899, p. 747.

this Medusa, like many others of the order, undergoes considerable changes in form before it reaches the sexually mature stage.

Phialidium temporarium is one of the commonest Medusae of our coast, and sometimes occurs in shoals. It seems probable that it is the Medusa of *Clytia johnstoni*.[1] By some authors the jelly-fish known as *Epenthesis* is also believed to be the Medusa of a *Clytia*.

Fam. Dendrograptidae.—This family includes a number of fossils which have certain distinct affinities with the Calypto-blastea. In *Dictyonema*, common in the Ordovician rocks of Norway, but also found in the Palaeozoic rocks of North America and elsewhere, the fossil forms fan-shaped colonies of delicate filaments, united by many transverse commissures, and in well-preserved specimens the terminal branches bear well-marked uniserial hydrothecae. In some species thecae of a different character, which have been interpreted to be gonothecae and nematophores respectively, are found.

Other genera are *Dendrograptus*, *Thamnograptus*, and several others from Silurian strata.

Order V. Graptolitoidea.

A large number of fossils, usually called Graptolites, occurring in Palaeozoic strata, are generally regarded as the skeletal remains of an ancient group of Hydrozoa.

In the simpler forms the fossil consists of a delicate straight rod bearing on one side a series of small cups. It is suggested that the cups contained hydroid zooids, and should therefore be regarded as the equivalent of the hydrothecae, and that the axis represents the axis of the colony or of a branch of the Calypto-blastea. In some of the forms with two rows of cups on the axis (*Diplograptus*), however, it has been shown that the cups are absent from a considerable portion of one end of the axis, and that the axes of several radially arranged individuals are fused together and united to a central circular plate. Moreover, there is found in many specimens a series of vesicles, a little larger in size than the cups, attached to the plate and arranged in a circle at the base of the axes. These vesicles are called the gonothecae.

The discovery of the central plate and of the so-called gono-

[1] E. T. Browne, *Bergens Museums Aarbog*, 1903, iv. p. 18.

thecae suggests that the usual comparison of a Graptolite with a Sertularian Hydroid is erroneous, and that the colony or individual, when alive, was a more or less radially symmetrical floating form, like a Medusa, of which only the distal appendages (possibly tentacles) are commonly preserved as fossils.

The evidence that the Graptolites were Hydrozoa is in reality very slight, but the proof of their relationship to any other phylum of the animal kingdom does not exist.[1] It is therefore convenient to consider them in this place, and to regard them, provisionally, as related to the Calyptoblastea.

The order is divided into three families.

Fam. 1. Monoprionidae.—Cups arranged uniserially on one side of the axis.

The principal genera are *Monograptus*, with the axis straight, curved, or helicoid, from many horizons in the Silurian strata; *Rastrites*, with a spirally coiled axis, Silurian; *Didymograptus*, Ordovician; and *Coenograptus*, Ordovician.

Fam. 2. Diprionidae.—Cups arranged in two or four vertical rows on the axis.

Diplograptus, Ordovician and Silurian; *Climacograptus*, Ordovician and Silurian; and *Phyllograptus*, in which the axis and cups are arranged in such a manner that they resemble an ovate leaf.

Fam. 3. Retiolitidae.—Cups arranged biserially on a reticulate axis.

Retiolites, Ordovician and Silurian; *Stomatograptus*, *Retiograptus*, and *Glossograptus*, Ordovician.

Fossil Corals possibly allied to Hydrozoa.

Among the many fossil corals that are usually classified with the Hydrozoa the genus *Porosphaera* is of interest as it is often supposed to be related to *Millepora*. It consists of globular masses about 10-20 mm. in diameter occurring in the Upper Cretaceous strata. In the centre there is usually a foreign body around which the coral was formed by concentric encrusting growth. Running radially from pores on the surface to the centre, there are numerous tubules which have a certain general resemblance to the pore-tubes of *Millepora*. The monomorphic

[1] Cf. Schepotieff, *Neues Jahrb. f. Mineralogie*, 1905. ii. pp. 79-98.

character of these tubes, their very minute size, the absence of ampullae, and the general texture of the corallum, are characters which separate this fossil very distinctly from any recent Hydroid corals. *Porosphaera*, therefore, was probably not a Hydrozoon, and certainly not related to the recent *Millepora*.

Closely related to *Porosphaera* apparently are other globular, ellipsoidal, or fusiform corals from various strata, such as *Loftusia* from the Eocene of Persia, *Parkeria* from the Cambridge Greensand, and *Heterastridium* from the Alpine Trias. In the last named there is apparently a dimorphism of the radial tubes.

Allied to these genera, again, but occurring in the form of thick, concentric, calcareous lamellae, are the genera *Ellipsactinia* and *Sphaeractinia* from the Upper Jurassic.

Another important series of fossil corals is that of the family **Stromatoporidae.** These fossils are found in great beds of immense extent in many of the Palaeozoic rocks, and must have played an important part in the geological processes of that period. They consist of a series of calcareous lamellae, separated by considerable intervals, encrusting foreign bodies of various kinds. Sometimes they are flat and plate-like, sometimes globular or nodular in form. The lamellae are in some cases perforated by tabulate, vertical, or radial pores, but in many others these pores are absent. The zoological position of the Stromatoporidae is very uncertain, but there is not at present any very conclusive evidence that they are Hydrozoa.

Stromatopora is common in Devonian and also occurs in Silurian strata. *Cannopora* from the Devonian has well-marked tabulate pores, and is often found associated commensally with another coral (*Aulopora* or *Syringopora*).

Order VI. Stylasterina.

The genera included in this order resemble *Millepora* in producing a massive calcareous skeleton, and in showing a consistent dimorphism of the zooids, but in many respects they exhibit great divergence from the characters of the Milleporina.

The colony is arborescent in growth, the branches arising frequently only in one plane, forming a flabellum. The calcareous skeleton is perforated to a considerable depth by the gastrozooids, dactylozooids, and nutritive canals, and the gastropores and dactylopores are not provided with tabulae except in the genera *Pliobothrus* and *Sporadopora*. The character which gives the order its name is a conical, sometimes torch-like projection at the base of the gastropore, called the "style," which carries a fold of the ectoderm and endoderm layers of the body-wall, and may serve to increase the absorptive surface of the digestive cavity. In some genera a style is also present in the dactylopore, in which case it serves as an additional surface for the attachment of the retractor muscles. The pores are scattered on all aspects of the coral in the genera *Sporadopora, Errina*, and *Pliobothrus*; in *Spinipora* and *Steganopora* the scattered dactylopores are situated at the extremities of tubular spines which project from the general surface of the coral, the gastropores being situated irregularly between the spines. In *Phalangopora* the pores are arranged in regular longitudinal lines, and in *Distichopora* they are mainly in rows on the edges of the flattened branches, a single row of gastropores being flanked by a single row of dactylopores on each side. In the remaining genera the pores are arranged in definite cycles, which are frequently separated from one another by considerable intervals, and have, particularly in the dried skeleton, a certain resemblance to the calices of some of the Zoantharian corals.

In *Cryptohelia* the cycles are covered by a lid-like projection from the neighbouring coenenchym (Fig. 136, *l* 1, *l* 2). The gastrozooids are short, and are usually provided with a variable number of small capitate tentacles. The dactylozooids are filiform and devoid of tentacles, the endoderm of their axes being solid and scalariform.

The gonophores of the Stylasterina are situated in large oval or spherical cavities called the ampullae, and their presence can generally be detected by the dome-shaped projections they form on the surface of the coral. The female gonophore consists of a saucer-shaped pad of folded endoderm called the "trophodisc," which serves the purpose of nourishing the single large yolk-laden egg it bears; and a thin enveloping membrane composed of at least two layers of cells. The egg is fertilised while it is still within the ampulla, and does not escape to the exterior until it has reached the stage of a solid ciliated larva. All the Stylasterina are therefore viviparous. The male gonophore has a very much smaller trophodisc, which is sometimes (*Allopora*) prolonged into a columnar process or spadix, penetrating the greater part of the gonad. The spermatozoa escape through a peculiar spout-like duct which perforates the superficial wall of the ampulla. In some genera (*Distichopora*) there are several male gonophores in each ampulla.

The gonophores of the Stylasterina have been regarded as much altered medusiform gonophores, and this view may possibly prove to be correct. At present, however, the evidence of their derivation from Medusae is not conclusive, and it is possible that they may have had a totally independent origin.

Distichopora and some species of *Stylaster* are found in shallow water in the tropics, but most of the genera are confined to

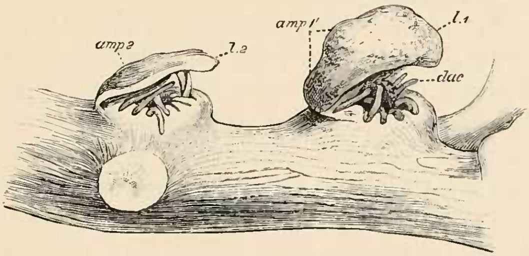

FIG. 136.—A portion of a branch of *Cryptohelia ramosa*, showing the lids *l* 1 and *l* 2 covering the cyclosystems, the swellings produced by the ampullae in the lids *amp*^{1}, *amp*^{2}, and the dactylozooids, *dac*. × 22. (After Hickson and England.)

deep or very deep water, and have a wide geographical distribution. No species have been found hitherto within the British area.

A few specimens of a species of *Stylaster* have been found in Tertiary deposits and in some raised beaches of more recent origin, but the order is not represented in the older strata.

Fam. Stylasteridae.—All the genera at present known are included in this family.

Sporadopora is the only genus that presents a superficial general resemblance to *Millepora*. It forms massive, branching white coralla, with the pores scattered irregularly on the surface, and, like many varieties of *Millepora*, not arranged in cyclosystems. It may, however, be distinguished at once by the presence of a long, brush-like style in each of the gastropores. The ampullae are large, but are usually so deep-seated in the coenenchym that their presence cannot be detected from the surface. It was found off the Rio de la Plata in 600 fathoms of water by the "Challenger."

In *Errina* the pores are sometimes irregularly scattered, but in *E. glabra* they are arranged in rows on the sides of the branches, while in *E. ramosa* the gastropores occur at the angles of the branches only. The dactylopores are situated on nariform projections of the corallum. The ampullae are prominent. There are several gonophores in each ampulla of the male, but only one in each ampulla of the female. This genus is very widely distributed in water from 100 to 500 fathoms in depth.

Phalangopora differs from *Errina* in the absence of a style in the gastropore; Mauritius.—*Pliobothrus* has also no style in the gastropore, and is found in 100-600 fathoms of water off the American Atlantic shores.

Distichopora is an important genus, which is found in nearly all the shallow seas of the tropical and semi-tropical parts of the world, and may even flourish in rock pools between tide marks. It is nearly always brightly coloured—purple, violet, pale brown, or rose red. The colony usually forms a small flabellum, with anastomosing branches, and the pores are arranged in three rows, a middle row of gastropores and two lateral rows of dactylopores on the sides of the branches. There is a long style in each gastropore. The ampullae are numerous and prominent, situated on the anterior and posterior faces of the branches. Each ampulla contains a single gonophore in the female colony and two or three gonophores in the male colony.

Spinipora is a rare genus from off the Rio de la Plata in 600 fathoms. The branches are covered with blunt spines. These spines have a short gutter-like groove at the apex, which leads into a dactylopore. The gastropores are provided with a style and are situated between the spines.

Steganopora [1] from the Djilolo Passage, in about 600 fathoms, is very similar to *Spinipora* as regards external features, but differs from it in the absence of styles in the gastropores, and in the wide communications between the gastropores and dactylopores.

Stylaster is the largest and most widely distributed genus of the family, and exhibits a considerable range of structure in the many species it contains. It is found in all the warmer seas of the world, living between tide marks at a few fathoms, and extending to depths of 600 fathoms. Many specimens, but especially those from very shallow water, are of a beautiful rose

[1] S. J. Hickson and H. England, *Siboga Exped.* viii. 1904, p. 26.

or pink colour. The corallum is arborescent and usually flabelliform. The pores are distributed in regular cyclosystems, sometimes on one face of the corallum only, sometimes on the sides of the branches, and sometimes evenly distributed. There are styles in both gastropores and dactylopores.

Allopora is difficult to separate from *Stylaster*, but the species are usually more robust in habit, and the ampullae are not so prominent as they are on the more delicate branches of *Stylaster*. It occurs at depths of 100 fathoms in the Norwegian fjords. A very large red species (*A. nobilis*) occurs in False Bay, Cape of Good Hope, in 30 fathoms of water. In this locality the coral occurs in great submarine beds or forests, and the trawl that is passed over them is torn to pieces by the hard, thick branches, some of which are an inch or more in diameter.

Astylus is a genus found in the southern Philippine sea in 500 fathoms of water. It is distinguished from *Stylaster* by the absence of a style in the gastropore.

Cryptohelia is an interesting genus found both in the Atlantic and Pacific Oceans at depths of from 270 to about 600 fathoms. The cyclosystems are covered by a projecting lid or operculum (Fig. 136, *l* 1, *l* 2). There are no styles in either the gastropores or the dactylopores. The ampullae are prominent, and are sometimes situated in the lids. There are several gonophores in each ampulla of the female colony, and a great many in the ampulla of the male colony.

CHAPTER XI

HYDROZOA (*CONTINUED*): TRACHOMEDUSAE—NARCOMEDUSAE—SIPHONOPHORA

Order VII. Trachomedusae.

THE orders Trachomedusae and Narcomedusae are probably closely related to one another and to some of the families of Medusae at present included in the order Calyptoblastea, and it seems probable that when the life-histories of a few more genera are made known the three orders will be united into one. Very little is known of the hydrosome stage of the Trachomedusae, but Brooks[1] has shown that in *Liriope*, and Murbach[2] that in *Gonionema*, the fertilised ovum gives rise to a *Hydra*-like form, and in the latter this exhibits a process of reproduction by gemmation before it gives rise to Medusae. Any general statement, therefore, to the effect that the development of the Trachomedusae is direct would be incorrect. The fact that the hydrosomes already known are epizoic or free-swimming does not afford a character of importance for distinction from the Leptomedusae, for it is quite possible that in this order of Medusae the hydrosomes of many genera may be similar in form and habits to those of *Liriope* and *Gonionema*.

The free border of the umbrella of the Trachomedusae is entire; that is to say, it is not lobed or fringed as it is in the Narcomedusae. The sense-organs are statocysts, each consisting of a vesicle formed by a more or less complete fold of the surrounding wall of the margin of the umbrella, containing a reduced clapper-like tentacle loaded at its extremity with a

[1] "Life-History of the Hydromedusae," *Mem. Boston Soc.* iii. 1885, p. 359.

[2] *Journ. Morph.* xi. 1895, p. 493.

statolith. This statocyst is innervated by the outer nerve ring. There appears to be a very marked difference between these marginal sense-organs in some of the best-known examples of Trachomedusae and the corresponding organs of the Leptomedusae. The absence of a stalk supporting the statolith and the innervation of the otocyst by the inner instead of by the outer nerve ring in the Leptomedusae form characters that may be of supplementary value, but cannot be regarded as absolutely distinguishing the two orders. The statorhab of the Trachomedusae is probably the more primitive of the two types, and represents a marginal tentacle of the umbrella reduced in size, loaded with a statolith and enclosed by the mesogloea. Intermediate stages between this type and an ordinary tentacle have already been discovered and described. In the type that is usually found in the Leptomedusae the modified tentacle is still further reduced, and all that can be recognised of it is the statolith attached to the wall of the statocyst, but intermediate stages between the two types are seen in the family Olindiidae, in which the stalk supporting the statolith passes gradually into the tissue surrounding the statolith on the one hand and the vesicle wall on the other. The radial canals are four or eight in number or more numerous. They communicate at the margin of the umbrella with a ring canal from which a number of short blind tubes run in the umbrella-wall towards the centre of the Medusa (Fig. 137, *cp*). These "centripetal canals" are subject to

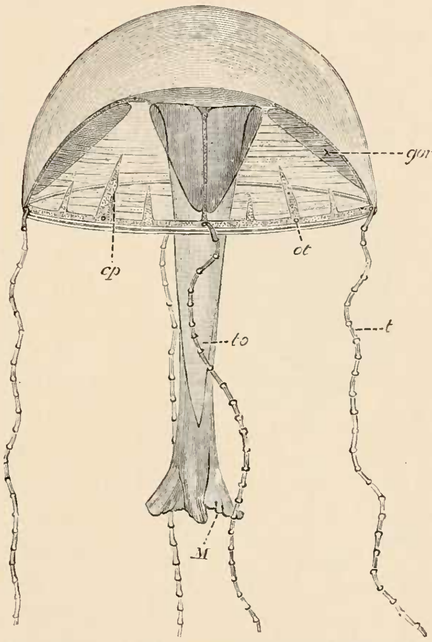

FIG. 137.—*Liriope rosacea*, one of the Geryoniidae, from the west side of North and Central America. Size, 15-20 mm. Colour, rose. *cp*, Centripetal canal; *gon*, gonad; *M*, mouth at the end of a long manubrium; *ot*, statocyst; *t*, tentacle; *to*, tongue. (After Maas.)

considerable variation, but are useful characters in distinguishing the Trachomedusae from the Leptomedusae. The tentacles are situated on the margin of the umbrella, and are four or eight in number or, in some cases, more numerous. The gonads are situated as in Leptomedusae on the sub-umbrella aspect of the radial canals.

In *Gonionema murbachii* the fertilised eggs give rise to a free-swimming ciliated larva of an oval shape with one pole longer and narrower than the other. The mouth appears subsequently at the narrower pole. The larva settles down upon the broader pole, the mouth appears at the free extremity, and in a few days two, and later two more, tentacles are formed (Fig. 138).

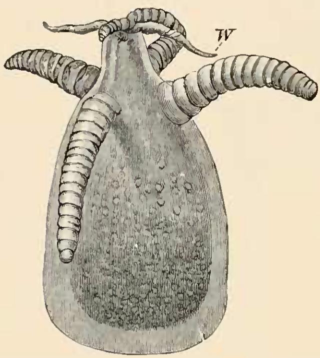

FIG. 138.—Hydra-like stage in the development of *Gonionema murbachii*. One of the tentacles is carrying a worm (W) to the mouth. The tentacles are shown very much contracted, but they are capable of extending to a length of 2 mm. Height of zooid about 1 mm. (After Perkins.)

At this stage the larva may be said to be *Hydra*-like in character, and as shown in Fig. 138 it feeds and lives an independent existence. From its body-wall buds arise which separate from the parent and give rise to similar *Hydra*-like individuals. An asexual generation thus gives rise to new individuals by gemmation as in the hydrosome of the Calyptoblastea. The origin of the Medusae from this *Hydra*-like stage has not been satisfactorily determined, but it seems probable that by a process of metamorphosis the hydriform persons are directly changed into the Medusae.[1]

In the development of *Liriope* the free-swimming larva develops into a hydriform person with four tentacles and an enormously elongated hypostome or manubrium; and, according to Brooks, it undergoes a metamorphosis which directly converts it into a Medusa.

There can be very little doubt that in a large number of Trachomedusae the development is direct, the fertilised ovum giving rise to a medusome without the intervention of a hydrosome stage. In some cases, however (*Geryonia*, etc.), the tentacles

[1] H. F. Perkins, *Proc. Acad. Nat. Sci. Phil.* Nov. 1902, p. 773.

appear in development before there is any trace of a sub-umbrella cavity, and this has been interpreted to be a transitory but definite Hydroid stage. It may be supposed that the elimination of the hydrosome stage in these Coelenterates may be associated with their adaptation to a life in the ocean far from the coast.

During the growth of the Medusa from the younger to the adult stages several changes probably occur of a not unimportant character, and it may prove that several genera now placed in the same or even different families are stages in the development of the same species. In the development of *Liriantha appendiculata*,[1] for example, four interradial tentacles appear in the first stage which disappear and are replaced by four radial tentacles in the second stage.

As with many other groups of free-swimming marine animals the Trachomedusae have a very wide geographical distribution, and some genera may prove to be almost cosmopolitan, but the majority of the species appear to be characteristic of the warmer regions of the high seas. Sometimes they are found at the surface, but more usually they swim at a depth of a few fathoms to a hundred or more from the surface. The Pectyllidae appear to be confined to the bottom of the sea at great depths.

The principal families of the Trachomedusae are:—

Fam. Olindiidae.—This family appears to be structurally and in development most closely related to the Leptomedusae, and is indeed regarded by Goto[2] as closely related to the Eucopidae in that order. They have two sets of tentacles, velar and exumbrellar; the statocysts are numerous, two on each side of the exumbrellar tentacles. Radial canals four or six. Manubrium well developed and quadrate, with distinct lips. There is an adhesive disc on each exumbrellar tentacle.

Genera: *Olindias*, *Olindioides*, *Gonionema* (Fig. 139), and *Halicalyx*.

As in other families of Medusae the distribution of the genera is very wide. *Olindias mülleri* occurs in the Mediterranean, *Olindioides formosa* off the coast of Japan, *Gonionema murbachii* is found in abundance in the eel pond at Wood's Holl, United States of America, and *Halicalyx* off Florida.

Two genera may be referred to in this place, although their

[1] E. T. Browne, *Proc. Zool. Soc.* 1896, p. 495.

[2] *Mark Anniversary Volume*, New York, 1903, p. 1.

systematic position in relation to each other and to other Medusae has not been satisfactorily determined.

Limnocodium sowerbyi is a small Medusa that was first discovered in the *Victoria regia* tanks in the Botanic Gardens, Regent's Park, London, in the year 1880. It has lately made its appearance in the *Victoria regia* tank in the Parc de la Bête d'Or at Lyons.[1] As it was, at the time of its discovery, the only fresh-water jelly-fish known, it excited considerable interest, and

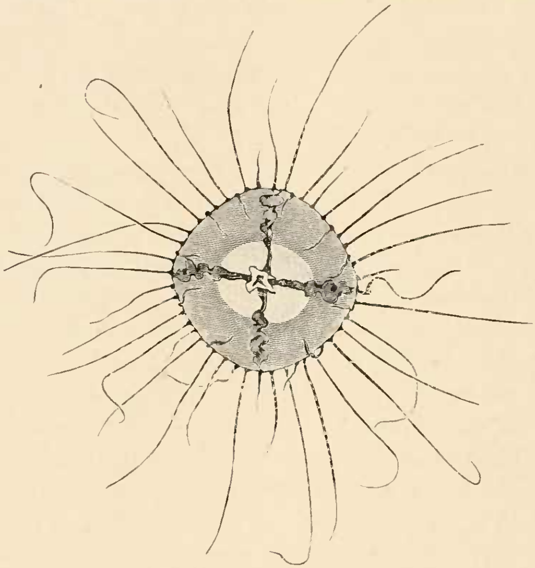

FIG. 139.—*Gonionema murbachii.* Adult Medusa, shown inverted, and clinging to the bottom. Nat. size. (After Perkins.)

this interest was not diminished when the peculiarities of its structure were described by Lankester and others. It has a rather flattened umbrella, with entire margin and numerous marginal tentacles, the manubrium is long, quadrate, and has four distinct lips. There are four radial canals, and the male gonads (all the specimens discovered were of the male sex) are sac-like bodies on the sub-umbrellar aspect of the middle points of the four radial canals. In these characters the genus shows general affinities with the Olindiidae. The difficult question of the origin of the statoliths from the primary germ layers of the embryo and some other points in the minute anatomy of the Medusa have

[1] C. Vaney et A. Conte, *Zool. Anz.* xxiv. 1901, p. 533.

suggested the view that *Limnocodium* is not properly placed in any of the other orders. Goto,[1] however, in a recent paper, confirms the view of the affinities of *Limnocodium* with the Olindiidae.

The life-history of *Limnocodium* is not known, but a curious Hydroid form attached to *Pontederia* roots was found in the same tank as the Medusae, and this in all probability represents the hydrosome stage of its development. The Medusae are formed apparently by a process of transverse fission of the Hydroid stock[2] similar in some respects to that observed in the production of certain Acraspedote Medusae. This is quite unlike the asexual mode of formation of Medusae in any other Craspedote form. The structure of this hydrosome is, moreover, very different to that of any other Hydroid, and consequently the relations of the genus with the Trachomedusae cannot be regarded as very close.

Limnocodium has only been found in the somewhat artificial conditions of the tanks in botanical gardens, and its native locality is not known, but its association with the *Victoria regia* water-lily seems to indicate that its home is in tropical South America.

Limnocnida tanganyicae is another remarkable fresh-water Medusa, about seven-eighths of an inch in diameter, found in the lakes Tanganyika and Victoria Nyanza of Central Africa.[3] It differs from *Limnocodium* in having a short collar-like manubrium with a large round mouth two-thirds the diameter of the umbrella, and in several other not unimportant particulars. It produces in May and June a large number of Medusa-buds by gemmation on the manubrium, and in August and September the sexual organs are formed in the same situation.

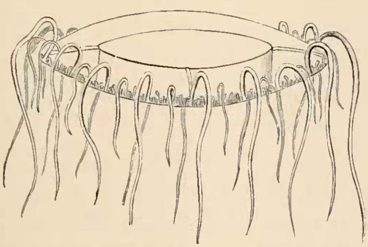

FIG. 140.—*Limnocnida tanganyicae.* ×2. (After Günther.)

The fixed hydrosome stage, if such a stage occurs in the life-history, has not been discovered; but Mr. Moore[4] believes that

[1] S. Goto, *l.c.* [2] G. H. Fowler, *Quart. Journ. Micr. Sci.* xxx. 1890, p. 507.

[3] *Limnocnida* has recently been discovered by Budgett in the river Niger. See Browne, *Ann. Nat. Hist.* xvii. 1906, p. 304.

[4] "The Tanganyika Problem," 1903, p. 298.

the development is direct from ciliated planulae to the Medusae. The occurrence of *Limnocnida* in Lake Tanganyika is supposed by the same authority to afford a strong support to the view that this lake represents the remnants of a sea which in Jurassic times spread over part of the African continent. This theory has, however, been adversely criticised from several sides.[1]

The character of the manubrium and the position of the sexual cells suggest that *Limnocnida* has affinities with the Narcomedusae or Anthomedusae, but the marginal sense-organs and the number and position of the tentacles, showing considerable similarity with those of *Limnocodium*, justify the more convenient plan of placing the two genera in the same family.

Fam. Petasidae.—The genus *Petasus* is a small Medusa with four radial canals, four gonads, four tentacles, and four free marginal statorhabs. A few other genera associated with *Petasus* show simple characters as regards the canals and the marginal organs, but as very little is known of any of the genera the family may be regarded as provisional only. *Petasus* is found in the Mediterranean and off the Canaries.

Fam. Trachynemidae.—In this family there are eight radial canals, and the statorhabs are sunk into a marginal vesicle. *Trachynema*, characterised by its very long manubrium, is a not uncommon Medusa of the Mediterranean and the eastern Atlantic Ocean. Many of the species are small, but *T. funerarium* has sometimes a disc two inches in diameter. *Homoeonema* and *Pentachogon* have numerous very short tentacles.

Fam. Pectyllidae.—This family contains a few deep-sea species with characters similar to those of the preceding family, but the tentacles are provided with terminal suckers. *Pectyllis* is found in the Atlantic Ocean at depths of over 1000 fathoms.

Fam. Aglauridae.—The radial canals are eight in number and the statorhabs are usually free. In the manubrium there is a rod-like projection of the mesogloea from the aboral wall of the gastric cavity, covered by a thin epithelium of endoderm, which occupies a considerable portion of the lumen of the manubrium. This organ may be called the tongue. *Aglaura* has an octagonal umbrella, and a manubrium which does not project beyond the velum. It occurs in the Atlantic Ocean and Mediterranean Sea.

[1] Cf. Boulenger. Presidential Address to Section D of the British Association (Cape Town, 1905).

Fam. Geryoniidae.—In this family there are four or six radial canals, the statorhabs are sunk in the mesogloea, and a tongue is present in the manubrium. *Liriope* (Fig. 137) is sometimes as much as three inches in diameter. It has a very long manubrium, and the tongue sometimes projects beyond the mouth. There are four very long radial tentacles. It is found in the Atlantic Ocean, the Mediterranean Sea, and the Pacific and Indian Oceans. *Geryonia* has a wider geographical distribution than *Liriope,* and is sometimes four inches in diameter. It differs from *Liriope* in having six, or a multiple of six, radial canals. *Carmarina* of the Mediterranean and other seas becomes larger even than *Geryonia,* from which it differs in the arrangement of the centripetal canals.

Liriantha appendiculata sometimes occurs on the south coast of England during September, October, or at other times.

Order VIII. Narcomedusae.

The Narcomedusae differ from the Trachomedusae in having the margin of the umbrella divided into a number of lobes, and in bearing the gonads on the sub-umbrellar wall of the gastral cavity instead of upon the radial canals. The tentacles are situated at some little distance from the margin of the umbrella at points on the aboral surface corresponding with the angles between the umbrella lobes. Between the base of the tentacle and the marginal angle there is a tract of modified epithelium called the "peronium." The manubrium is usually short, and the mouth leads into an expanded gastral chamber which is provided with lobular diverticula reaching as far as the bases of the tentacles. The marginal sense-organs are in the form of unprotected statorhabs. Very little is known concerning the life-history of any of the Narcomedusae. In *Cunoctantha octonaria* the peculiar ciliated larva with two tentacles and a very long proboscis soon develops two more tentacles and creeps into the bell of the Anthomedusan *Turritopsis,* where, attached by its tentacles, it lives a parasitic life. Before being converted into a Medusa it gives rise by gemmation to a number of similar individuals, all of which become, in time, Medusae. The parasitic stage is often regarded as the representative of the hydrosome stage reduced and adapted to the oceanic habit of the adult.

In *Cunina proboscidea*, and in some other species, a very remarkable method of reproduction has been described by Metschnikoff, called by him "sporogony." In these cases young sexual cells (male or female) wander from the gonad of the parent into the mesogloea of the umbrella, where they develop parthenogenetically into ciliated morulae. These escape by the radial canals into the gastric cavity, and there form a stolon from which young Medusae are formed by gemmation. In *C. proboscidea* these young Medusae are like the genus *Solmaris*, but in *C. rhododactyla* they have the form of the parent. In some cases the ciliated larvae leave the parent altogether and become attached to a *Geryonia* or some other Medusa, where they form the stolon.

This very interesting method of reproduction cannot be regarded as a primitive one, and throws no light on the origin of the order. It might be regarded as a further stage in the degeneration of the hydrosome stage in its adaptation to a parasitic existence.

The Narcomedusae have a wide geographical distribution. Species of *Aeginopsis* occur in the White Sea and Bering Strait, but the genera are more characteristic of warmer waters. Some species occur in moderately deep water, and *Cunarcha* was found in 1675 fathoms off the Canaries, but they are more usually found at or near the surface of the sea.

Fam. Cunanthidae.—Narcomedusae with large gastral diverticula corresponding in position with the bases of the tentacles. *Cunina* and *Cunoctantha*, occurring in the Mediterranean and in the Atlantic and Pacific Oceans, belong to this family. In *Cunina* the tentacles may be eight in number, or some multiple of four between eight and twenty-four. In *Cunoctantha* the number of tentacles appears to be constantly eight.

Fam. Peganthidae.—There appear to be no gastral pouches in this family. The species of *Pegantha* are found at depths of about 80 fathoms in the Indian and Pacific Oceans.

Fam. Aeginidae.—The large gastral pouches of this family alternate with the bases of the tentacles. *Aegina* occurs in the Atlantic and Pacific Oceans. *Aeginopsis*.

Fam. Solmaridae.—In this family the gastral pouches are variable, sometimes corresponding with, sometimes alternating with, the bases of the tentacles. The circular canal is represented in some genera by solid cords of endoderm. *Solmaris* sometimes appears in the English Channel, but it is probably a wanderer from the warmer regions of the Atlantic Ocean. It is found in abundance during November on the west coast of Ireland.

Order IX. Siphonophora.

In this order the naturalist finds collected together a number of very beautiful, delicate transparent organisms to which the general term " jelly-fish " may be applied, although their organisation is far more complicated and difficult to describe than that of any of the Medusae. In several of the Hydrozoa the phenomenon of dimorphism has already been noticed. In these cases one set of individuals in a colony performs functions of stinging and catching food and another the functions of devouring and digesting it. In many of the Siphonophora there appears to be a colony of individuals in which the division of labour is carried to a much further extent than it is in the dimorphic Hydrozoa referred to above. Not only are there specialised gastrozooids and dactylozooids, but also gonozooids, zooids for propelling the colony through the water (" nectocalyces "), protective zooids (" hydrophyllia "), and in some cases a specialised zooid for hydrostatic functions; the whole forming a swimming or floating polymorphic colony. But this conception of the construction of the Siphonophora is not the only one that has met with support. By some zoologists the Siphonophoran body is regarded not as a colony of individuals, but as a single individual in which the various organs have become multiplied and dislocated.

The multiplication or repetition of organs that are usually single in each individual is not unknown in other Hydrozoa. In the Medusa of the Gymnoblast *Syncoryne*, usually known as *Sarsia*, for example, there is sometimes a remarkable proliferation of the manubrium, and specimens have been found with three or four long manubria attached by a tubular stalk to the centre of the umbrella. Moreover, this complex of manubria may become detached from the umbrella and live for a considerable time an independent existence.[1]

If we regard the manubrium of a Medusa as an organ of the

[1] C. Hartlaub, *Verhandl. Deutsch. Zool. Ges.* 1896, p. 3.

animal's body, it might be thought obvious that the phenomenon observed in the Medusae of *Syncoryne* is a case of a simple repetition of the parts of an individual; but the power that the group of manubria possesses of leading an independent existence renders its interpretation as a group of organs a matter of some inconvenience. If we can conceive the idea that an organ may become detached and lead an independent existence, there is no reason why we should not regard the Medusa itself of *Syncoryne* as an organ, and we should be driven to the paradoxical conclusion that, as regards several genera and families of Hydrozoa, we know nothing at present of the individuals, but only of their free-swimming organs, and that in others the individual has degenerated, although one of its organs remains.

There is, however, no convincing argument to support either the conception that the Siphonophoran body is a colony of individuals, or that it is an individual with disjointed organs. These two conceptions are sometimes called the "Poly-person" and "Poly-organ" theories respectively. The difficulty is caused by the impossibility of giving any satisfactory definition in the case of the Hydrozoa of the biological terms "organ" and "individual." In the higher animals, where the correlation of parts is far more complex and essential than it is in Coelenterata, a defined limit to the scope of these terms can be laid down, but in the lower animals the conception of what is termed an organ merges into that which is called an individual, and no definite boundary line between the two exists in Nature. The difficulty is therefore a permanent one, and, in using the expression "colony" for the Siphonophoran body, it must be understood that it is used for convenience' sake rather than because it represents the only correct conception of the organisation of these remarkable Coelenterates.

Regarding the Siphonophora as polymorphic colonies, then, the following forms of zooids may be found.

Nectocalyces.—The nectocalyces are in the form of the umbrella of a medusa attached to the stolon of the colony by the aboral pole. They are provided with a velum and, usually, four radial canals and a circular canal. There is no manubrium, and the marginal tentacles and sense-organs are rudimentary or absent. There may be one or more nectocalyces in each colony, and their function is, by rhythmic contractions, to propel the colony through the water (Fig. 142, N).

Gastrozooids.—These are tubular or saccular zooids provided with a mouth and attached by their aboral extremity to the stolon (Fig. 142, G). In some cases the aboral region of the zooid is differentiated as a stomach. It is dilated and bears the digestive cells, the oral extremity or hypostome being narrower and more transparent. In some cases the mouth is a simple round aperture at the extremity of the hypostome, but in others it is dilated to form a trumpet-like lip.

Dactylozooids.—In *Velella* and *Porpita* the dactylozooids are similar in general characters to the tentacles of many Medusae. They are arranged as a frill round the margin of the colony, and each consists of a simple tube of ectoderm and endoderm terminating in a knobbed extremity richly provided with nematocysts.

In many other Siphonophora, however, the dactylozooids are very long and elaborate filaments, which extend for a great distance from the colony into the sea. They reach their most elaborate condition in the Calycophorae.

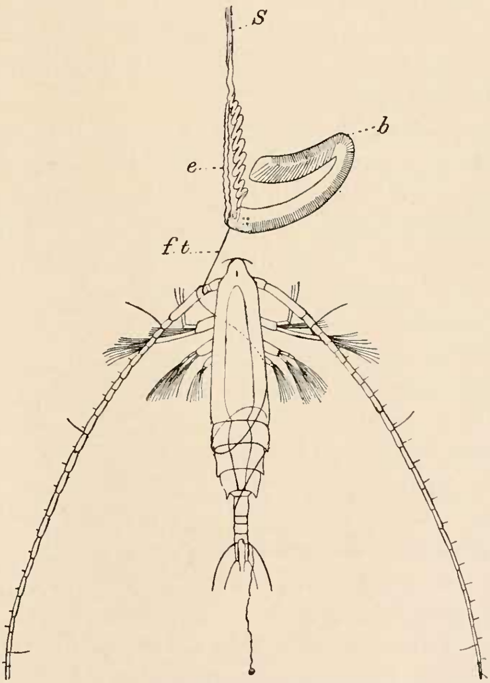

Fig. 141.—A small Crustacean (*Rhinocalanus*) caught by a terminal filament (*f.t*) of a battery of *Stephanophyes*. *b*, The proximal end of the battery with the most powerful nematocysts; *e*, elastic band; *S*, stalk supporting the battery on the dactylozooid. (After Chun.)

The dactylozooid in these forms has a hollow axis, and the lumen is continuous with the cavity of the neighbouring gastrozooid. Arranged at regular intervals on the axis is a series of tentacles (" tentilla "), and each of these supports a kidney-shaped swelling, the "cnidosac," or battery, which is sometimes protected by a hood. Each battery contains an enormous number of nematocysts. In *Stephanophyes*, for example, there are about 1700 nematocysts of four different kinds in each battery. At the extremity of the battery there is a delicate terminal filament. The action of the battery in *Stephanophyes* is, according to Chun,[1] a very complicated one. The terminal filament lassos the prey and discharges its somewhat feeble nematocysts at it (Fig. 141). If this kills it, the dactylozooid contracts and passes the prey to a gastrozooid. If the animal continues its struggles, it is drawn up to the distal end of the battery and receives the discharge of a large number of nematocysts; and if this also fails to put an end to its life, a membrane covering the largest and most powerful nematocysts at the proximal end of the whole battery is ruptured, and a final broadside of stinging threads is shot at it.

The larger nematocysts of these batteries in the Siphonophora are among the largest found in Coelenterata, being from 0·5 to 0·1 mm. in length, and they are frequently capable of inflicting painful stings on the human skin. The species of *Physalia*, commonly called "Portuguese Men-of-War," have perhaps the worst reputation in this respect, the pain being not only intense but lasting a long time.

Hydrophyllia.—In many Siphonophora a number of short, mouthless, non-sexual zooids occur, which appear to have no other function than that of shielding or protecting other and more vital parts of the colony. They consist of an axis of firm mesogloea, covered by a layer of flattened ectoderm, and they may be finger-shaped or triangular in form. In *Agalma* and *Praya* an endoderm canal perforates the mesogloea and terminates in a little mouth at the free extremity. In *Athoria* and *Rhodophysa* the hydrophyllium terminates in a little nectocalyx.

Pneumatophore.—In all the Siphonophora, with the exception of the Calycophorae, there is found on one side or at one extremity of the colony a vesicle or bladder containing a gas,[2] which serves as a float to support the colony in the water.

[1] *Abh. Senckenb. Ges.* xvi. 1891, p. 44.

[2] This gas is frequently called air. The gas contained in the pneumatophore of *Physalia* was analysed by Schloessing and Richard, *C.R.* cxxii. 1896, p. 615, and found to consist of CO_2 1·7 parts, O 15·1, nitrogen and argon, 83·2.

This bladder or pneumatophore is probably in all cases a much modified nectocalyx. It shows great variations in size and structure in the group. It is sometimes relatively very large, as in *Physalia* and *Velella*, sometimes very small, as in *Physophora*. It is provided with an apical pore in some genera (*Rhizophysa*), or a basal pore in others (Auronectidae), but it is generally closed. In the many chambered pneumatophore of the Chondrophoridae there are several pores.

In many forms two distinct parts of the pneumatophore can be recognised—a distal region lined by chitin,[1] probably representing the sub-umbrellar cavity of the nectocalyx, and a small funnel-shaped region lined by an epithelium, the homology of which is a matter of dispute. It is believed that the gas is secreted by this epithelium. In the Auronectidae the region with secretory epithelium is relatively large and of a more complicated histological character. It is remarkable also that in this family the pore communicates, not with the chitin-lined region, but directly with the epithelium-lined region.

There is no pneumatophore in the Calycophorae, but in this sub-order a diverticulum of an endoderm canal secretes a globule of oil which may serve the same hydrostatic function.

The *stolon* is the common stem which supports the different zooids of the colony. In the Calycophorae the stolon is a long, delicate, and extremely contractile thread attached at one end to a nectocalyx, and bearing the zooids in discontinuous groups. These groups of zooids arranged at intervals on the stolon are called the "cormidia." The stolon is a tube with very thick walls. Its lumen is lined by a ciliated endoderm with circular muscular processes, and the surface is covered with an ectoderm, also provided with circular muscular processes. Between these two layers there is a relatively thick mesogloea showing on the outer side deep and compound folds and grooves supporting an elaborate system of longitudinal muscular fibres. In many Physonectidae the stolon is long and filamentous, but not so contractile as it is in Calycophorae, but in others it is much reduced in length and relatively stouter. The reduction

[1] The chemical composition of the substance here called "chitin" has not been accurately determined. An analysis of two specimens of *Velella* bladders gave 9·71 and 10·35 per cent of nitrogen, which is higher than that of chitin and nearer to that of mucin.

in length of the stolon is accompanied by a complication of structure, the simple tubular condition being replaced by a spongy complex of tubes covered by a common sheath of ectoderm. In the Auronectidae the stolon is represented by a conical or hemispherical spongy mass bearing the zooids, and in the Rhizophysaliidae and Chondrophoridae it becomes a disc or ribbon-shaped pad spreading over the under side of the pneumatophore.

Gonozooids.—The gonozooids are simple tubular processes attached to the stolon which bear the Medusae or the degenerate medusiform gonophores. In the Chondrophoridae the gonozooids possess a mouth, but in most Siphonophora they have neither mouth nor tentacles. In some cases, such as *Anthophysa*, the colonies are bisexual—the male and female gonophores being borne by separate gonozooids—but in others (e.g. *Physalia*) the colonies appear to be unisexual.

As a general rule the gonophores of Siphonophora do not escape from the parent colony as free-swimming Medusae, but an exception occurs in *Velella*, which produces a number of small free-swimming Medusae formerly described by Gegenbaur under the generic name *Chrysomitra*. This Medusa has a velum, a single tentacle, eight to sixteen radial canals, and it bears the gonads on the short manubrium. The Medusa of *Velella* has, in fact, the essential characters of the Anthomedusae.

Our knowledge of the life-history of the Siphonophora is very incomplete, but there are indications, from scattered observations, that in some genera, at least, it may be very complicated.

The fertilised ovum of *Velella* gives rise to a planula which sinks to the bottom of the sea, and changes into a remarkable larva known as the *Conaria* larva. This larva was discovered by Woltereck [1] at depths of 600-1000 metres in great numbers. It is very delicate and transparent, but the endoderm is red (the colour so characteristic of animals inhabiting deep water), and it may be regarded as essentially a deep-sea larva. The larva rises to the surface and changes into the form known as the *Ratarula* larva, which has a simple one-chambered pneumatophore containing a gas, and a rudiment of the sail. In contrast to the *Conaria*, the *Ratarula* is blue in colour. With the development of the zooids on the under side of this

[1] *Zool. Jahrb. Suppl.* 1904, p. 347.

larva (*i.e.* the side opposite to the pneumatophore), a definite octoradial symmetry is shown, there being for some time eight dactylozooids and eight definite folds in the wall of the pneumatophore. This octoradial symmetry, however, is soon lost as the number of folds in the pneumatophore and the number of tentacles increase.

It is probable that in the Siphonophora, as in many other Coelenterata, the production of sexual cells by an individual is no sign that its life-history is completed. There may possibly be two or more phases of life in which sexual maturity is reached.

An example of a complicated life-history is found in the Calycophoran species *Muggiaea kochii*. The embryo gives rise to a form with a single nectocalyx which is like a *Monophyes*, and this by the budding of a second nectocalyx produces a form that has a remarkable resemblance to a *Diphyes*, but the primary nectocalyx degenerates and is cast off, while the secondary one assumes the characters of the single *Muggiaea* nectocalyx. The stolon of the *Muggiaea* produces a series of cormidia, and as the sexual cells of the cormidia develop, a special nectocalyx is formed at the base of each one of them, and the group of zooids is detached as an independent colony, formerly known as *Eudoxia eschscholtzii*. In a similar manner the cormidia of *Doramasia picta* give rise to the sexual free-swimming monogastric forms, known by the name *Ersaea picta* (Fig. 142). In these cases it seems possible that the production of ripe sexual cells is confined to the *Eudoxia* and *Ersaea* stages respectively, but it is probable that in other species the cormidia do not break off from the stolon, or may escape only from the older colonies.

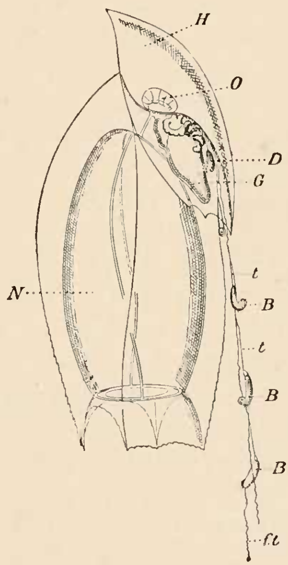

FIG. 142.—Free-swimming *Ersaea* group of *Doramasia picta*. *B*, *B*, batteries of nematocysts borne by the tentilla; *D*, dactylozooid; *G*, gastrozooid; *H*, hydrophyllium; *N*, nectocalyx; *O*, oleocyst; *f*, *t*, terminal filament of a battery; *t*, *t*, tentilla. The gonozooid is hidden by the gastrozooid. × 10. (After Chun.)

The Siphonophora are essentially free-swimming pelagic organisms. Some of them (Auronectidae) appear to have become adapted to a deep-sea habit, others are usually found in intermediate waters, but the majority occur with the pelagic plankton at or very near the surface of the open sea. Although the order may be said to be cosmopolitan in its distribution, the Siphonophora are only found in great numbers and variety in the sub-tropical and tropical zones. In the temperate and arctic zones they are relatively rare, but *Galeolaria biloba* and *Physophora borealis* appear to be true northern forms. The only British species are *Muggiaea atlantica* and *Cupulita sarsii*. *Velella spirans* occasionally drifts from the Atlantic on to our western shores, and sometimes great numbers of the pneumatophores of this species may be found cast up on the beach. *Diphyes* sp., *Physalia* sp., and *Physophora borealis* are also occasionally brought to the British shores by the Gulf Stream.

The Calycophorae are usually perfectly colourless and transparent, with the exception of the oil-globule in the oleocyst, which is yellow or orange in colour. Many of the other Siphonophora, however, are of a transparent, deep indigo blue colour, similar to that of many other components of the plankton.

Most of the Siphonophora, although, strictly speaking, surface animals, are habitually submerged; the large pneumatophores of *Velella* and *Physalia*, however, project above the surface, and these animals are therefore frequently drifted by the prevailing wind into large shoals, or blown ashore. At Mentone, on the Mediterranean, *Velella* is sometimes drifted into the harbour in countless numbers. Agassiz mentions the lines of deep blue Velellas drifted ashore on the coast of Florida; and a small species of blue *Physalia* may often be seen in long lines on the shore of some of the islands of the Malay Archipelago.

The food of most of the Siphonophora consists of small Crustacea and other minute organisms, but some of the larger forms are capable of catching and devouring fish. It is stated by Bigelow[1] that a big *Physalia* will capture and devour a full-grown Mackerel. The manner in which it feeds is described as follows:—"It floats on the sea, quietly waiting for some helpless individual to bump its head against one of the tentacles. The fish, on striking, is stung by the nettle-cells, and fastened probably by them to the tentacle. Trying to run away the fish pulls on the

[1] *Johns Hopkins Univ. Circ.* x. 1891, p. 91.

tentacle. The tension on its peduncle thus produced acts as a stimulus on apparently some centre there which causes it to contract. The fish in this way is drawn up so that it touches the sticky mouths of the squirming siphons [*i.e.* gastrozooids]. As soon as the mouths, covered as they are with a gluey substance and provided with nettle-cells, touch the fish they stick fast, a few at first, and gradually more. The mouths open, and their lips are spread out over the fish until they touch, so that by the time he is dead the fish is enclosed in a tight bag composed of the lips of a dozen or more siphon mouths. Here the fish is digested. As it begins to disintegrate partially digested fragments are taken into the stomachs of the attached siphons (gastrozooids). When they have become gorged they detach themselves from the remains of the fish, the process of digestion is completed in the stomachs, and the nutrient fluid is distributed. . . ."

In consequence of the very unsatisfactory state of our knowledge of the life-history of the Siphonophora the classification of the order is a matter of unusual difficulty.

Sub-Order I. Calycophorae.

The character which distinguishes this sub-order is the absence of a pneumatophore.

The colony usually consists of a long, slender, contractile stolon, provided at one end with one, two, or several nectocalyces. Upon the stolon are arranged several groups ("cormidia") of polymorphic zooids.

The nectocalyces have a well-developed velum, four radial canals, and a muscular umbrella-wall. A special peculiarity of the nectocalyx of this sub-order is a diverticulum (oleocyst) from one of the radial canals, containing a coloured globule of oil. The function of this oil-globule is probably similar to that of the pneumatophore, and assists the muscular efforts of the nectocalyces in keeping the colony afloat. One of the nectocalyces of each colony exhibits on one side a deep ectodermic fold, which is frequently converted into a pit. At the bottom of this pit is attached the end of the stolon, the whole of which with its numerous cormidia can be withdrawn into the shelter of the pit when danger threatens. The cormidia consist of at least four kinds of zooids: a gastrozooid with a trumpet-shaped mouth armed with nematocysts, a long dactylozooid provided with a series of tentilla, and a rudimentary gonozooid bearing numbers of male or female medusiform gonophores. These three kinds of zooids are partially covered and protected by a bent shield-shaped phyllozooid or hydrophyllium.

Each of the cormidia is unisexual, but the colony as a whole is usually hermaphrodite, the male and female cormidia regularly alternating, or the male cormidia being arranged on the nectocalycine half and the female cormidia on the opposite half of the stolon.

The families of the Calycophorae are:—

Fam. 1. Monophyidae.—In this family there is a single conical or mitre-shaped nectocalyx. The cormidia become detached as free-swimming *Eudoxia* or *Ersaea* forms.

Sub-Fam. 1. SPHAERONECTINAE.—The primary nectocalyx persists throughout life—*Monophyes* and *Sphaeronectes.*

Sub-Fam. 2. CYMBONECTINAE.—The primary nectocalyx is thrown off, and is replaced by a secondary and permanent nectocalyx—*Cymbonectes, Muggiaea,* and *Doramasia.*

Fam. 2. Diphyidae.—The primary mitre-shaped nectocalyx is thrown off and replaced by two secondary rounded, prismatic, or pyramidal, heteromorphic nectocalyces.

This family contains several sub-families, which are arranged in two groups: the Diphyidae Oppositae, in which the two secondary bells are opposite one another, and do not exhibit pronounced ridges; and the Diphyidae Superpositae, in which one of the two secondary nectocalyces is situated in front of the other, and each nectocalyx is provided externally with very definite and often wing-like ridges. In all the Diphyidae Oppositae the cormidia remain attached, whereas in most of the Diphyidae Superpositae they become free-swimming, as in the Monophyidae.

The sub-families of the **Diphyidae Oppositae** are:—

Sub-Fam. 1. AMPHICARYONINAE.—One of the two secondary nectocalyces becomes flattened above to form a shield, and at the same time its sub-umbrellar cavity is atrophied, and its radial canals reduced. *Mitrophyes,* Atlantic Ocean.

Sub-Fam. 2. PRAYINAE.—The colony exhibits a pair of large, obtuse nectocalyces, with a relatively small sub-umbrellar cavity. *Praya,* Mediterranean and Atlantic.

Sub-Fam. 3. DESMOPHYINAE.—The colony bears a large number of reserve or tertiary nectocalyces arranged in two rows. *Desmophyes*, Indian Ocean.

Sub-Fam. 4. STEPHANOPHYINAE.—There are four nectocalyces arranged in a horizontal plane. Each one of the cormidia bears a nectocalyx, which is periodically replaced. This sub-family is constituted for *Stephanophyes superba* from the Canary Islands. It attains a length of 25 cm., and is probably the largest and most beautiful of all the Calycophoridae.[1]

The group **Diphyidae Superpositae** contains the following :—

Sub-Fam. 1. GALEOLARINAE.—*Galeolaria.*

Sub-Fam. 2. DIPHYOPSINAE.—*Diphyes.*

Sub-Fam. 3. ABYLINAE.—*Abyla.*

These sub-families differ from one another in the character and shape of the nectocalyces and in other characters. They have a world-wide distribution, *Diphyes* and *Galeolaria* extending north into the Arctic Seas. *Diphyes* is British.

Fam. 3. Polyphyidae.—The nectocalyces are numerous, and superposed in two rows. The cormidia remain attached.

The family contains the genera *Polyphyes* and *Hippopodius*, both probably cosmopolitan in warm waters.

Sub-Order II. Physophorae.

In this sub-order the primary nectocalyx gives rise to a definite pneumatophore. There are four families.

Fam. 1. Physonectidae.—In this, the largest family of the sub-order, there is a monothalamic pneumatophore supporting a stolon, which in some forms is of great length, but in others is reduced to a stump or pad, on which there are usually found several nectocalyces, hydrophyllia, gastrozooids, gonozooids, and tentilla.

The principal sub-families are :—

AGALMINAE.—With a long stolon, bearing at the upper end (*i.e.* the end next to the pneumatophore) two rows of nectocalyces. The other zooids are arranged in cormidia on the stolon, each covered by a hydrophyllium. Dactylozooids with tentilla. *Agalma* and *Cupulita*, Mediterranean Sea.

APOLEMINAE.—Similar to the above, but without tentilla.

[1] C. Chun, *Abh. Senck. Nat. Ges. Frankfort*, xvi. 1891.

Apolemia—this genus attains a length of two or three metres. Mediterranean Sea. *Dicymba*, Indian Ocean.

PHYSOPHORINAE.—The pneumatophore larger in proportion than it is in the preceding families. The stolon is short, and bears rows of nectocalyces at the upper end. The gastrozooids, dactylozooids, and gonozooids are arranged in verticils on the lower expanded part of the stolon. Hydrophyllia absent. *Physophora*, cosmopolitan in the areas of warm sea water.

Fam. 2. Auronectidae.—The pneumatophore is large. The stolon is reduced to a spongy mass of tissue on the under side of the pneumatophore, and this bears numerous cormidia arranged in a helicoid spiral. Projecting from the base of the pneumatophore there is a peculiar organ called the "aurophore," provided with an apical pore. This organ has been described as a specially modified nectocalyx, but it is probably a specialised development of the epithelium-lined portion of the pneumatophore of other Physophorae. The Auronectidae are found only at considerable depths, 300 to 1400 fathoms, and are probably specially adapted to that habitat. *Rhodalia*, *Stephalia*, Atlantic Ocean.

Fam. 3. Rhizophysaliidae.—The pneumatophore is large, or very large, in this family. The zooids are arranged in horizontal rows on the under side of the pneumatophore (*Physalia*), or in a helicoid spiral on a short stolon (*Epibulia*). There are no nectocalyces nor hydrophyllia.

The genus *Physalia* is the notorious "Portuguese Man-of-War." The pneumatophore is a large bladder-like vesicle, sometimes attaining a length of 12 cm. One species described by Haeckel under the generic name *Caravella* has a pneumatophore 30 cm. and more in length, and dactylozooids attaining a length of 20 metres. It is a curious fact that only the male colonies of *Physalia* are known, and it is suggested that the female may have quite a different form.[1] *Epibulia* has a much smaller bladder than *Physalia*. Both genera have a cosmopolitan distribution at the surface of the warm seas.

Fam. 4. Chondrophoridae.—This family stands quite by itself in the sub-order Physophorae, and is placed in a separate division of the sub-order by Chun, who gives it the name TRACHEOPHYSA. The essential distinguishing characters of the family are

[1] Brooks and Conklin, *Johns Hopkins Univ. Circ.* x. 1891, No. 88.

the large polythalamic pneumatophore and the single large central gastrozooid.

The colony is disc-shaped, and has a superficial resemblance to a Medusa. On the upper side is the flattened pneumatophore, covered by a fold of tissue continuous with that at the edge of the disc. In *Velella* a vertical triangular sail or crest rises from the upper side, but this is absent in *Porpita*.

The mouth of the gastrozooid opens into a large digestive cavity, and between this and the under surface of the pneumatophore there is a glandular spongy tissue called the liver. The liver extends over the whole of the under side of the pneumatophore, and sends processes round the edge of the disc into the tissues of its upper surface. Intimately associated with the liver, and penetrating its interstices, is an organ which appears to be entirely composed of nematocysts, derived from the ectoderm, and called the central organ. At the margin of the disc there is a fringe of simple digitiform dactylozooids, and between the dactylozooids and the centrally placed gastrozooid are numerous gonozooids. Each of the gonozooids is provided with a distinct mouth, and bears the gonophores, which escape before the ripening of the gonads as the free-swimming Medusae called *Chrysomitra*. The pneumatophore consists of a number of annular chambers arranged in a concentric manner round the central original chamber formed from a modified zooid. These annular chambers are in communication with one another, and have each two pores (pneumatopyles) opening above to the exterior. The most remarkable feature, however, of the system is a series of fine branching tubes (" tracheae "), which pass from the annular chambers of the pneumatophore downwards into the hepatic mass and ramify there.

There are two well-known genera: *Velella* with a sail, and *Porpita* without a sail. They are both found at the surface of the warmer regions of the great oceans and in the Mediterranean. *Velella* sometimes drifts on to British coasts from the Atlantic.

The genus *Discalia* has a much more simple octoradial structure. It was found at depths of 2600 and 2750 fathoms in the Pacific Ocean.

CHAPTER XII

COELENTERATA (*CONTINUED*): SCYPHOZOA = SCYPHOMEDUSAE

CLASS II. SCYPHOZOA = SCYPHOMEDUSAE

The Scyphozoa are jelly-fishes, usually found floating at or near the surface of the sea. A few forms (Stauromedusae) are attached to rocks and weeds by a stalked prolongation of the aboral region of the umbrella. With this exception, however, they are all, in the adult stage, of the Medusa type of structure, having a bell-shaped or discoid umbrella, from the under surface of which depends a manubrium bearing the mouth or (in Rhizostomata) the numerous mouths.

Although many of the species do not exceed an inch or a few inches in diameter, others attain a very great size, and it is among the Scyphozoa that we find the largest individual zooids of the Coelenterata. Some Discophora have a disc three or four feet in diameter, and one specimen obtained by the Antarctic Expedition of 1898-1900 weighed 90 lbs.[1] The common jelly-fish, *Aurelia*, of our coasts belongs to a species that appears to be very variable in general characters as well as in size. Specimens obtained by the "Siboga" in the Malay Archipelago ranged from 6 to 64 cm. in diameter. The colour is very variable, shades of green, blue, brown, and purple being conspicuous in many species; but a pale milky-blue tint is perhaps the most prevalent, the tissues being generally less transparent than they are in the Medusae of the Hydrozoa. The colour of the Cubomedusae is usually yellow or brown, but *Charybdea xaymaeana* is colourless and transparent. The deep-sea species, particularly the Periphyllidae, have usually an opaque brown or dark red colour. The surface-swimming

[1] C. E. Borchgrevink, "First on the Antarctic Continent," 1901, p. 227.

forms, such as the common *Aurelia*, *Pelagia*, *Cyanaea*, are usually of a uniform pale milky-blue or green colour. Generally the colour is uniformly distributed, but sometimes the surface of the umbrella is freckled with irregular brown or yellow patches, as in *Dactylometra* and many others. There is frequently a special colour in the statorhabs which renders them conspicuous in the living jelly-fish, and the lips, or parts of the lips, of the manubrium have usually a different colour or tone to that of the umbrella.

There is no reason to believe that the general colour of any of these jelly-fishes has either a protective or a warning significance. Nearly all the larger species, whether blue, green, or brown in colour, can be easily seen from a considerable distance, and the colours are not sufficiently bright or alarming to support the belief that they can serve the purpose of warning either fish or birds of the presence of a dangerous stinging animal. It is possible, however, that the brighter spots of colour that are often noticed on the tips of the tentacles and on the lips may act as a lure or bait in attracting small fish and Crustacea.

Some of the Scyphozoa are phosphorescent, but it is a singular fact that there are very few recorded observations concerning the phosphorescence or the absence of it in most of the species. The pale blue light of *Pelagia noctiluca* or *P. phosphora* can be recognised from the deck of a ship in the open ocean, and they are often the most brilliant and conspicuous of the phosphorescent organisms.

The food of the Scyphozoa varies a good deal. *Charybdea* and *Periphylla*, and probably many others with large mouths, will capture and ingest relatively large fish and Crustacea; but *Chrysaora isosceles*[1] apparently makes no attempt to capture either Copepoda or small fish, but preys voraciously upon Anthomedusae, Leptomedusae, Siphonophora, Ctenophora, and pelagic worms. Very little is known about the food of the Rhizostomata, but the small size of the mouths of these forms suggests that their food must also be of minute size. The frequent association of small fish with the larger jelly-fish is a matter of some interest that requires further investigation. In the North Sea young whiting are the constant guests of *Cyanaea capillata*.[2] Over a

[1] M. J. Delap, *Irish Naturalist*, x. 1901, p. 27.

[2] E. W. L. Holt, *Report on the Sea and Inland Fisheries of Ireland for 1902*, pt. ii. 1903, p. xvi.

hundred young horse-mackerel (*Caranx trachurus*) may be found sheltering under the umbrella of *Rhizostoma pulmo*. As the animal floats through the water the little fishes hover round the margin, but on the slightest alarm dart into the sub-umbrella cavity, and ultimately seek shelter in the sub-genital pits.[1]

Two species of fish accompany the American Medusa *Dactylometra lactea*, one a Clupeoid, the other the young of the Butter-fish (*Stromateus triacanthus*). According to Agassiz and Mayer[2] this is not an ordinary case of mutualism, as the fish will tear off and devour fragments of the tentacles and fringe of the Medusa, whilst the Medusa will in its turn occasionally capture and devour one of the fish.

A great many of the Scyphozoa, particularly the larger kinds, have the reputation of being able to sting the human skin, and in consequence the name Acalephae[3] was formerly used to designate the order. Of the British species *Aurelia aurita* is almost harmless, and so is the rarer *Rhizostoma pulmo*; but the nematocysts on the tentacles of *Cyanaea*, *Chrysaora*, and *Pelagia* can inflict stings on the more delicate parts of the skin which are very painful for several hours, although the pain has been undoubtedly greatly exaggerated in many popular works.

The soft structure of the Medusae does not favour their preservation in the rocks, but the impressions left by several genera, all belonging apparently to the Rhizostomata, have been found in Cambrian, Liassic, and Cretaceous deposits.

There is reason to believe that many Scyphozoa exhibit a considerable range of variation in the symmetry of the most important organs of the body. Very little information is, however, at hand concerning the variation of any species except *Aurelia aurita*, which has been the subject of several investigations. Browne[4] has found that in a local race of this species about 20 per cent exhibit variations from the normal in the number of the statorhabs, and about 2 per cent in the number of gastric pouches.

The Scyphozoa are not usually regarded as of any commercial or other value, but in China and Japan two species of Rhizostomata (*Rhopilema esculenta* and *R. verrucosa*) are used as food.

[1] F. W. Gamble. See E. T. Browne, *Proc. Roy. Irish Acad.* 1900, p. 735.

[2] *Bull. Mus. Comp. Zool.* xxxii. 1, 1898.

[3] ἀκαλήφη = a nettle.

[4] *Biometrika*, i. 1901, p. 90.

The jelly-fish is preserved with a mixture of alum and salt or between the steamed leaves of a kind of oak. To prepare the preserved food for the table it is soaked in water, cut into small pieces, and flavoured. It is also stated that these Medusae are used by fishermen as bait for file-fish and sea-bream.[1]

In general structure the Scyphozoa occupy an intermediate position between the Hydrozoa and the Anthozoa. The very striking resemblance of the body-form to the Medusa of the Hydrozoa, and the discovery of a fixed hydriform stage in the life-history of some species, led the older zoologists to the conclusion that they should be included in the class Hydrozoa. Recently the finer details of development have been invoked to support the view that they are Anthozoa specially adapted for a free-swimming existence, but the evidence for this does not appear to us to be conclusive.

They differ from the Hydrozoa and resemble the Anthozoa in the character that the sexual cells are matured in the endoderm, and escape to the exterior by way of the coelenteric cavity, and not directly to the exterior by the rupture of the ectoderm as in all Hydrozoa. They differ, on the other hand, from the Anthozoa in the absence of a stomodaeum and of mesenteries.

The view that the Scyphozoa are Anthozoa is based on the belief that the manubrium of the former is lined by ectoderm, and is homologous with the stomodaeum of the latter; and that the folds of mesogloea between the gastric pouches are homologous with the septa.[2]

The Scyphozoa, notwithstanding their general resemblance to the Medusae of Hydrozoa, can be readily distinguished from them by several important characters. The absence of a velum in all of them (except the Cubomedusae) is an important and conspicuous character which gave to the class the name of Acraspeda. The velum of the Cubomedusae can, however, be distinguished from that of the Craspedote Medusae (*i.e.* the Medusae of the Hydrozoa) by the fact that it contains endodermal canals.

Sense-organs are present in all Scyphozoa except some of the Stauromedusae, and they are in the form of statorhabs (tentaculocysts), bearing statoliths at the extremity, and in many species,

[1] K. Kishinouye, *Zool. Jahrb. Syst.* xii. 1899, p. 206.

[2] For the discussion of this relationship the reader is referred to Goette, *Zeitschr. wiss. Zool.* lxiii. 1897, p. 360, and Carlgren, *Zool. Anz.* xxii. 1899, p. 31.

at the base or between the base and the extremity, one or more eyes. These organs differ from the statorhabs of the Hydrozoa in having, usually, a cavity in the axial endoderm; but as they are undoubtedly specially modified marginal tentacles, they are strictly homologous in the two classes. In nearly all the Scyphozoa these organs are protected by a hood or fold formed from the free margin of the umbrella, and this character, although not of great morphological importance, serves to distinguish the common species from the Craspedote Medusae. It was owing to this character that Forbes gave the name STEGANOPHTHALMATA, or "covered-eyed Medusae," to the class.

Another character of some importance is the presence in the coelenteric cavity of all Scyphozoa of clusters or rows of delicate filaments called the "phacellae." These filaments are covered with a glandular epithelium, and are usually provided with numerous nematocysts. They have a considerable resemblance to the acontia of certain Anthozoa, and are probably mainly digestive in function. These three characters, in addition to the very important character of the position and method of discharge of the sexual cells already referred to, justify the separation of the Scyphozoa from the Medusae of the Hydrozoa as a distinct class of Coelenterata.

The umbrella of the Scyphozoa varies a good deal in shape. It is usually flattened and disc-like (Discophora), but it may be almost globular (*Atorella*), conical (some species of *Periphylla*), or cubical (Cubomedusae). It is divided into an aboral and a marginal region by a circular groove in the Coronata. The margin may be almost entire, marked only by notches where the statorhabs occur, or deeply lobed as in the Coronata and many Discophora. Marginal tentacles are present in all but the Rhizostomata, and may be few in number, four in *Charybdea*, eight in *Ulmaris* (Fig. 143), or very numerous in *Aurelia* and many others. The tentacles may be short (*Aurelia*), or very long as in *Chrysaora isosceles*, in which they extend for a length of twenty yards from the disc.

The manubrium of the Scyphozoa is usually quadrangular in section, and in those forms in which the shape is modified in the adult Medusa the quadrangular shape can be recognised in the earlier stages of development. The four angles of the manubrium are of importance in descriptive anatomy, as the planes drawn through the angles to the centre of the manubrium are called "perradial," while those bisecting the perradial planes and passing therefore through the middle line of the flat sides of the manubrium are called "interradial."

The free extremity of the manubrium in many Scyphozoa is provided with four triangular perradial lips, which may be simple or may become bifurcated or branched, and have frequently very elaborate crenate edges beset with batteries of nematocysts. In *Pelagia* and *Chrysaora* and other genera these lips hang down from the manubrium as long, ribbon-like, folded bands, and according to the size of the specimen may be a foot or more in length, or twice the diameter of the disc.

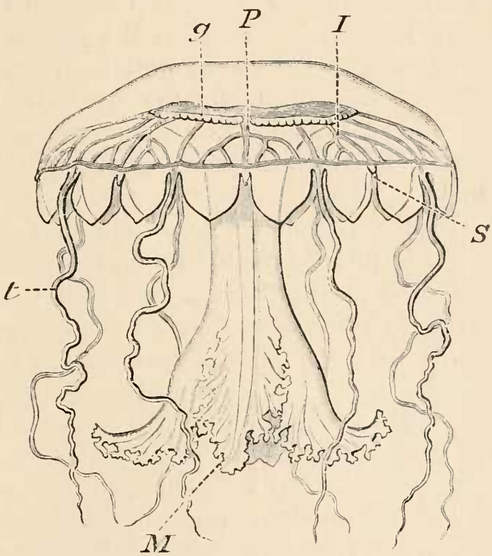

FIG. 143.—*Ulmaris prototypus.* *g*, Gonad; *I*, interradial canal; *M*, the fringed lip of the manubrium; *P*, perradial canal; *S*, marginal sense-organ; *t*, tentacle. × 1. (After Haeckel.)

In the Rhizostomata a peculiar modification of structure takes place in the fusion of the free edges of the lips to form a suture perforated by a row of small apertures, so that the lips have the appearance of long cylindrical rods or tubes attached to the manubrium, and then frequently called the "oral arms." The oral arms may be further provided with tentacles of varying size and importance. In many Rhizostomata branched or knobbed processes project from the outer side of the upper part of the oral arms. These are called the "epaulettes."

The lumen of the manubrium leads into a large cavity in the disc, which is usually called the gastric cavity, and this is extended into four or more interradial or perradial gastric pouches. The number of these pouches is usually four, but in this, as in other features of their radial symmetry, the jelly-fish frequently exhibit duplication or irregular variation of the radii.[1]

The gastric pouches may extend to the margin of the disc, where they are united to form a large ring sinus, or they may be in communication at the periphery by only a very narrow passage (Cubomedusae). In the Discophora the gastric pouches, however, do not extend more than half-way to the margin, and they may be connected with the marginal ring-canal by a series of branched interradial canals. Between the gastric pouches in these forms branched perradial canals pass from the gastric cavity to the marginal ring canal, and the system of canals is completed by unbranched "adradial" canals passing between the perradials and interradials from the sides of the gastric pouches to the ring-canal (Fig. 143).

In the Discophora there are four shallow interradial pits or pouches lined by ectoderm on the under side of the umbrella-wall. As these pits correspond with the position of the gonads in the gastric pouches they are frequently called the "sub-genital pits." In the Stauromedusae and Cubomedusae they are continued through the interradial gastric septa to the aboral side of the disc, and they are generally known in these cases by the name "interradial funnels." The functions and homologies of these ectodermic pits and funnels are still uncertain.

The Scyphozoa are usually dioecious, but *Chrysaora* and *Linerges* are sometimes hermaphrodite. The female Medusae can usually be distinguished from the male by the darker or brighter colour of the gonads, which are band-shaped, horse-shoe-shaped, or circular organs, situated on the endoderm of the interradial gastric pouches. They are, when nearly ripe, conspicuous and brightly coloured organs, and in nearly all species can be clearly seen through the transparent or semi-transparent tissues of the disc. The reproductive cells are discharged into the gastric cavity and escape by the mouth. The eggs are probably fertilised in the water, and may be retained in special pouches on the lips of the manubrium until the segmentation is completed.[2] Asexual reproduction does not occur in the free-swimming or adult stage of any Scyphozoa. In some cases (probably exceptional) the development is direct. In *Pelagia*, for example, it is known that the fertilised egg gives

[1] See note [4], p. 312.

[2] E. A. Minchin, *Proc. Zool. Soc.* 1889, p. 583.

rise to a free-swimming Medusa similar in all essential features to the parent.

In many species, however, the planula larva sinks to the bottom of the sea, develops tentacles, and becomes attached by its aboral extremity to a rock or weed, forming a sedentary asexual stage of development with a superficial resemblance to a *Hydra*. This stage is the "Scyphistoma," and notwithstanding its simple external features it is already in all essential anatomical characters a Scyphozoon.

The Scyphistoma may remain as such for some time, during which it reproduces by budding, and in some localities it may be found in great numbers on seaweeds and stones.[1]

In the course of time, however, the Scyphistoma exhibits a ring-like constriction of the body just below the crown of tentacles, and as this deepens the general features of a Scyphomedusa are developed in the free part above the constriction. In time this free part escapes as a small free-swimming jelly-fish, called an "Ephyra," while the attached part remains to repeat the process. In many species the first constriction is followed by a second immediately below it, then a third, a fourth, and so on, until the Scyphistoma is transformed into a long series of narrow discs, each one acquiring, as it grows, the Ephyra characters. Such a stage has been compared in form to a pile of saucers, and is known as the "Strobila."

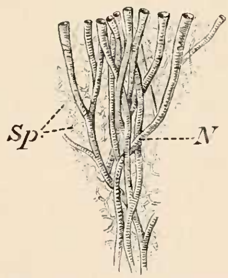

FIG. 144. — The perisarc tubes of a specimen of *Spongicola fistularis* (*N*) ramifying in the skeleton of the Sponge *Esperella bauriana* (Sp.), as seen in a macerated specimen. ×1. (After Schulze.)

The Ephyra differs from the adult in many respects. The disc is thin and flat, the manubrium short, the margin of the umbrella deeply grooved, while the statorhabs are mounted on bifid lobes which project outwards from the margin. The strobilisation of the Scyphistoma is a process of reproduction by transverse fission, and in some cases this is supplemented by gemmation, the Scyphistoma giving rise to a number of buds which become detached from the parent and subsequently undergo the process of strobilisation.

The Scyphistoma of *Nausithoe* presents us with the most

[1] For good illustrations of this see Sir J. Dalyell, "Rare and Remarkable Animals of Scotland," vol. i. 1847, pll. 13, 14, 18, 19, 20.

remarkable example of this mode of reproduction (Fig. 144), as it forms an elaborate branching colony in the substance of certain species of sponges. The ectoderm secretes a chitinous perisarc, similar to that of the hydrosome stage of many of the Hydrozoa, and consequently *Stephanoscyphus* (*Spongicola*), as this Scyphistoma was called, was formerly placed among the Gymnoblastea. It is remarkable that, although the Scyphozoan characters of *Spongicola* were proved by Schulze[1] in 1877, a similar Scyphistoma stage has not been discovered in any other genus.

Order I. Cubomedusae.

Scyphozoa provided with four perradial statorhabs, each of which bears a statolith and one or several eyes. There are four interradial tentacles or groups of tentacles. The stomach is a large cavity bearing four tufts of phacellae (Fig. 145, *Ph*), situated interradially. There are four flattened perradial gastric pouches in the wall of the umbrella which communicate with the stomach by the gastric ostia (*Go*). These pouches are separated from one another by four interradial septa; and the long leaf-like gonads are attached by one edge to each side of the septa. In many respects the Cubomedusae appear to be of simple structure, but the remarkable differentiation of the eyes and the occurrence of a velum (p. 313) suggest that the order is a highly specialised offshoot from a primitive stock.

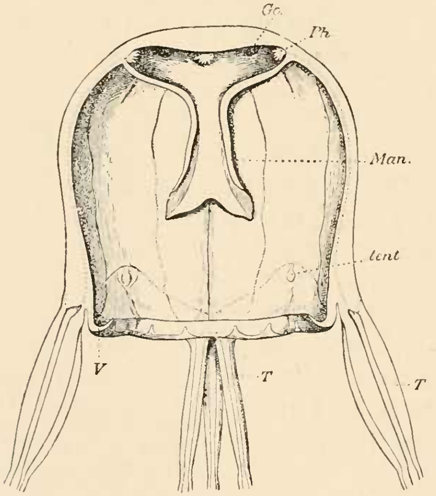

FIG. 145.—Vertical section in the interradial plane of *Tripedalia cystophora*. *Go*, Gastric ostia; *Man*, manubrium; *Ph*, group of phacellae; *T*, tentacles in four groups of three; *tent*, perradial sense-organs; *V*, velum. (After Conant.)

Fam. 1. Charybdeidae.—Cubomedusae with four interradial tentacles.

[1] *Archiv. Mikr. Anat.* xiii. 1877, p. 795.

Charybdea appears to have a very wide geographical distribution. Some of the species are usually found in deep water and come to the surface only occasionally, but others (*C. xaymacana*) are only found at the surface of shallow water near the shore. The genus can be easily recognised by the four-sided prismatic shape of the bell and the oral flattened expansion of the base of the tentacles. The bell varies from 2-6 cm. in length (or height) in *C. marsupialis*, but a giant form, *C. grandis*,[1] has recently been discovered off Paumotu Island which is as much as 23 cm. in height. The colour is usually yellow or brown, but *C. grandis* is white and *C. xaymacana* perfectly transparent.

"*Charybdea* is a strong and active swimmer, and presents a very beautiful appearance in its movements through the water; the quick, vigorous pulsations contrasting sharply with the sluggish contractions seen in most Scyphomedusae." It appears to be a voracious feeder. "Some of the specimens taken contained in the stomach small fish, so disproportionately large in comparison with the stomach that they lay coiled up, head overlapping tail."[2]

Very little is known of the development, but it is possible that *Tamoya punctata*, which lacks gonads, phacellae, and canals in the velum, may be a young form of a species of *Charybdea*.

Fam. 2. Chirodropidae.—Cubomedusae with four interradial groups of tentacles.

This family is represented by the genera *Chirodropus* from the Atlantic and *Chiropsalmus* from the Indian Ocean and the coast of North Carolina.

Fam. 3. Tripedaliidae.—Cubomedusae with four interradial groups of three tentacles.

The single genus and species *Tripedalia cystophora* has only been found in shallow water off the coast of Jamaica. Specimens of this species were kept for some time by Conant in an aquarium, and produced a number of free-swimming planulae which settled on the glass, and quickly developed into small hydras with a mouth and four tentacles. The further development of this sedentary stage is unfortunately not known.

[1] Agassiz and Mayer, *Mem. Mus. Comp. Zool.* xxvi. 3, 1902, p. 153.
[2] F. S. Conant, *Mem. Johns Hopkins Univ.* iv. 1, 1898.

Order II. Stauromedusae.

This order contains several genera provided with an aboral stalk which usually terminates in a sucker, by means of which the animal is temporarily fixed to some foreign object. There can be little doubt that this sedentary habit is recently acquired, and the wide range of the characteristic features of the order may be accounted for as a series of adaptations to the change from a free-swimming to a sedentary habit.

It is difficult to give in a few words the characters of the order, but the Stauromedusae differ from other Scyphozoa in the absence or profound modification in structure and function of the statorhabs. They are absent in *Lucernaria* and the Depastridae, and very variable in number in *Haliclystus*.

The statorhab of *Haliclystus* terminates in a spherical knob, which is succeeded by a large annular pad or collar bearing a number of glandular cells which secrete a sticky fluid. At the base of the organ there is a rudimentary ocellus. The number is very variable, and sometimes they are abnormal in character, being "crowned with tentacles." There can be little doubt that the principal function of these organs is not sensory but adhesive, and hence they have received the names "colletocystophores" and "marginal anchors," but they are undoubtedly homologous with the statorhabs of other Scyphozoa.

The tentacles are short and numerous, and are frequently mounted in groups on the summit of digitate outgrowths from the margin of the umbrella. They are capitate, except in *Tessera*, the terminal swelling containing a battery of nematocysts.

Very little is known concerning the life-history and development of the Stauromedusae.

Fam. 1. Lucernariidae.—Marginal lobes digitate, bearing the capitate tentacles in groups. *Haliclystus auricula* is a common form on the shores of the Channel Islands, at Plymouth, and other localities on the British coast. It may be recognised by the prominent statorhabs situated in the bays between the digitate lobes of the margin of the umbrella. Each of the marginal lobes bears from 15 to 20 capitate tentacles. It is from 2 to 3 cm. in length. The genus occurs in shallow water off the coasts of Europe and North America, extending south into the Antarctic region.

Lucernaria differs from *Haliclystus* in the absence of statorhabs. It has the same habit as *Haliclystus*, and is often found associated with it. *L. campanulata* is British.

Halicyathus is similar in external features to *Haliclystus*, but differs from it in certain important characters of the coelenteric cavities. It is found off the coasts of Norway, Greenland, and the Atlantic side of North America.

In *Capria*, from the Mediterranean, the tentacles are replaced by a denticulated membrane bearing nematocysts.

The rare genus *Tessera*, from the Antarctic Ocean, differs from all the other Stauromedusae in having no stalk and in having only a few relatively long non-capitate tentacles. If *Tessera* is really an adult form it should be placed in a separate family, but, notwithstanding the presence of gonads, it may prove to be but a free-swimming stage in the history of a normally stalked genus.

Fam. 2. Depastridae.—The margin of the umbrella is provided with eight shallow lobes bearing one or more rows of tentacles. Statorhabs absent.

Depastrum cyathiforme occurs in shallow water at Plymouth, Port Erin, and in other localities on the coasts of Britain and Norway. The tentacles are arranged in several rows on the margin of the umbrella. In *Depastrella* from the Canaries there is only one row of marginal tentacles.

Fam. 3. Stenoscyphidae.[1]—Stauromedusae with simple undivided umbrella margin. The eight principal tentacles are converted into adhesive anchors. Secondary tentacles arranged in eight adradial groups. *Stenoscyphus inabai*, 25 cm., Japan.

Order III. Coronata.[2]

The external surface of the umbrella is divided into two regions, an aboral region and a marginal region, by a well-marked circular groove (the coronal groove). The aboral region is usually smooth and undivided, but it is an elongated dome,

[1] Kishinouye, *Journ. Coll. Sci. Tokyo*, xvii. 7, 1902.

[2] A discussion of the classification of this order occurs in Vanhöffen, "Acrasped. Med. d. deutschen Tiefsee Expedition," iii. 1902, p. 49.

thimble- or cone-shaped, in marked contrast to the flattened umbrella of the Discophora. The margin is divided into a number of triangular or rounded lobes, and these are continued as far as the coronal groove as distinct areas delimited by shallow grooves on the surface of the umbrella. The tentacles arise from the grooves between the marginal areas, and are provided with expanded bases called the pedalia. The manubrium may be short or moderately long, but it is never provided with long lips.

Fam. 1. Periphyllidae.[1]—Coronata with four or six statorhabs.

In *Pericolpa* (Kerguelen) there are only four tentacles and four statorhabs. In *Periphylla*, a remarkable deep-sea genus from 700 to 2000 fathoms in all seas, but occasionally found at the surface, there are twelve tentacles and four statorhabs. The specimens from deep water have a characteristic dark red-brown or violet-brown colour. They are usually small Medusae, but the umbrella of *P. regina* is over 21 cm. in diameter. *Atorella* has six tentacles and six statorhabs.

Fam. 2. Ephyropsidae.—Coronata with eight or more than eight statorhabs.

Nausithoe punctata is a small, transparent jelly-fish, not exceeding 10 mm. in diameter, of world-wide distribution. Its Scyphistoma stage is described on p. 317. *N. rubra*, a species of a reddish colour found at a considerable depth in the South Atlantic and Indian Oceans, is probably an abysmal form. *Palephyra* differs from *Nausithoe* in having elongated instead of rounded gonads. *Linantha* and *Linuche* differ from the others in having subdivided marginal lobes.

Fam. 3. Atollidae.—*Atolla* is a deep-sea jelly-fish of very wide geographical distribution. It is characterised by the multiplication of the marginal appendages, but the number is very irregular. There may be double or quadruple the usual number of marginal lobes, or an indefinite number. There may be sixteen to thirty-two statorhabs, and the number of tentacles is quite irregular. Some of the species attain a considerable size, the diameter of the umbrella of *A. gigantea* being 150 mm., of *A. valdiviae* sometimes 130 mm., and of *A. bairdi* 110 mm.

[1] The Periphyllidae constitute Haeckel's order Peromedusae.

Order IV. Discophora.

This order contains not only by far the greater number of the species of Scyphozoa, but those of the largest size, and all those that are familiar to the seaside visitor and the mariner under the general term jelly-fish.

They may be distinguished from the other Scyphozoa by several well-marked characters. The umbrella is flattened and disc-shaped or slightly domed, but not divided by a coronary groove. The perradial angles of the mouth are prolonged into long lips, which may remain free (Semaeostomata) or fuse to form an elaborate proboscis (Rhizostomata).

Sub-Order I. Semaeostomata.

In this sub-order the mouth is a large aperture leading into the cavity of the manubrium, and is guarded by four long grooved and often tuberculated lips. The margin of the umbrella is provided with long tentacles.

Fam. 1. Pelagiidae.—Semaeostomata with wide gastric pouches, which are not united by a marginal ring sinus. *Pelagia*, which forms the type of this family, has eight long marginal tentacles. It develops directly from the egg, the fixed Scyphistoma stage being eliminated.[1] It is probably in consequence of this peculiarity of its development and independence of a shore for fixation that *Pelagia* has become a common and widespread inhabitant of the high seas. In the Atlantic and Indian Oceans *P. phosphora* occurs in swarms or in long narrow lines many miles in length. It is remarkable for its power of emitting phosphorescent light. In the Atlantic it extends from 50° N. to 40° S., but is rare or absent from the colder regions. *P. perla* is found occasionally on the west coast of Ireland. *Chrysaora* differs from *Pelagia* in the larger number of tentacles. There are, in all, 24 tentacles and 8 statorhabs, separated by 32 lobes of the margin of the umbrella. *C. isosceles* is occasionally found off the British coast. It passes through a typical Scyphistoma stage in development. *Dactylometra*, a very

[1] A stage in development before the formation of the sub-umbrellar cavity, but subsequent to the formation of the first tentacles, is regarded as homologous with the Scyphistoma stage of other Scyphozoa.

common jelly-fish of the American Atlantic shores, differs from *Chrysaora* in having sixteen additional but small tentacles arranged in pairs at the sides of the statorhabs.

Fam. 2. Cyanaeidae.—Semaeostomata with eight radial and eight adradial pouches, which give off ramifying canals to the margin of the umbrella; but these canals are not united by a ring-canal. The tentacles are arranged in bundles on the margin of the deeply lobed umbrella.

The yellow *Cyanaea capillata* and the blue *C. lamarcki* are commonly found on the British coasts.

Fam. 3. Ulmaridae.—The gastric pouches are relatively small, and communicate with a marginal ring-canal by branching perradial and interradial canals and unbranched adradial canals.

In *Ulmaris prototypus* (Fig. 143, p. 315) there are only eight long adradial tentacles, and the lips of the manubrium are relatively short. It is found in the South Atlantic.

Aurelia is a well-known and cosmopolitan genus, which may be recognised by the eight shallow lobes of the umbrella-margin beset with a fringe of numerous small tentacles.

Sub-Order II. Rhizostomata.

In this sub-order the lips are very much exaggerated in size, and are fused together by their margin in such a manner that the mouth of the animal is reduced to a number of small apertures situated along the lines of suture. Tentacles are absent on the margin of the umbrella. This sub-order contains some of the largest known jelly-fishes, and exhibits a considerable range of structure. The families are arranged by Maas[1] in three groups.

Group I. ARCADOMYARIA.—Musculature of the disc arranged in feather-like arcades. Oral arms pinnate.

Fam. Cassiopeidae.—There are no epaulettes on the arms. Labial tentacles present. *Cassiopea* is common in the Indo-Pacific seas, and extends into the Red Sea. It includes a great many species varying in size from 4 to about 12 cm. in diameter.

Group II. RADIOMYARIA.—Musculature arranged in radial tracts. Oral arms bifid.

Fam. Cepheidae.—The genera included in this family differ

[1] "*Siboga*" *Exped.* Mon. xi. 1903.

from the Cassiopeidae in the characters of the group. *Cephea* is found in the Indo-Pacific Oceans and Red Sea. *Cotylorhiza* is common in the Mediterranean Sea and extends into the Atlantic Ocean.

Group III. CYCLOMYARIA.—The group contains the majority of the Rhizostomata. Musculature arranged in circular bands round the disc. Oral arms primarily trifid, but becoming in some cases very complicated. The principal families are :—

Fam. Rhizostomatidae.—With well-marked epaulettes, and sixteen radial canals passing to the margin of the umbrella.

Rhizostoma pulmo (= *Pilema octopus*), a widely distributed species, is often found floating at the surface off the western coasts of Scotland and Ireland, and sometimes drifts up the English Channel into the German Ocean in the autumn. The umbrella is about two feet in diameter, and the combined length of the umbrella and arms is four feet. The colour varies considerably, but that of a specimen obtained off Valencia in 1895 was described as follows: "The colour of the umbrella was pale green, with a deep reddish margin. Arms bright blue."[1]

The family includes *Stomolophus*, of the Pacific and Atlantic coasts of America, in which the oral arms are united at the base, and *Rhopilema*, the edible Medusa of Japan and China.

Fam. Lychnorhizidae.—Here there are only eight radial canals reaching as far as the margin of the umbrella, and eight terminating in the ring-canal. There are no epaulettes, and the oral tentacles are often very long. The family includes *Lychnorhiza* from the coast of Brazil, *Crambione* from the Malay Archipelago, and *Crambessa* from the Atlantic shores of France and Spain and from Brazil and Australia. The last-named genus has been found in brackish water at the mouth of the Loire.

In the families **Leptobrachiidae** and **Catostylidae** there are eight radial canals reaching the margin of the umbrella, and between them a network of canals with many openings into the ring-canal. In a few of the Leptobrachiidae the intermediate canal-network has only eight openings into the ring-canal, as in the Lychnorhizidae.

[1] *Proc. Roy. Irish Acad.* 3rd ser. v. 1900, p. 735.

CHAPTER XIII

COELENTERATA (*CONTINUED*): ANTHOZOA = ACTINOZOA—GENERAL CHARACTERS—ALCYONARIA

CLASS III. ANTHOZOA = ACTINOZOA

AMONG the familiar objects included in this class are the Sea-anemones, the Stony Corals (Madrepores), the Flexible Corals, the Precious Coral, and the Sea-pens. With the exception of a few species of Sea-anemone, Anthozoa are not commonly found on British sea-shores; but in those parts of the tropical world where coral reefs occur, the shore at low tide is carpeted with various forms of this class, and the sands and beaches are almost entirely composed of their broken-down skeletons.

The majority of the Anthozoa are colonial in habit, a large number of individuals, or zooids as they are called, being organically connected together by a network of nutritive canals, and forming a communal gelatinous or stony matrix for their protection and support. Whilst the individuals are usually small or minute, the colonial masses they form are frequently large. Single colonies of the stony corals form blocks of stone which are sometimes five feet in diameter, and reach a height of two or three feet from the ground. From the tree or shrub-like form assumed by many of the colonies they were formerly included in a class Zoophyta or animal-plants.

But whether the individual polyps are large or small, whether they form colonies in the adult condition or remain independent, they exhibit certain characters in common which distinguish them not only from the other Coelenterata, but from all other animals. When an individual zooid is examined in the living and fully expanded condition, it is seen to possess a cylindrical body, attached at one end (the aboral end) to the common colonial matrix or to some foreign object. At the opposite or free extremity it is provided with a mouth surrounded by a crown of tentacles. In these respects, however, they resemble in a general way some of the Hydrozoa. It is only when the internal anatomy is examined that we find the characters which are absolutely diagnostic of the group.

In the Hydrozoa the mouth leads directly into the coelenteric cavity; in the Anthozoa, however, the mouth leads into a short tube or throat, called the "stomodaeum," which opens into the coelenteric cavity. Moreover, this tube is connected with the body-wall, and is supported by a series of fleshy vertical bands called the mesenteries (Fig. 146). The mesenteries not only support the stomodaeum, but extend some distance below it. Where the mesenteries are free from the stomodaeum their edges are thickened to form the important digestive organs known as the mesenteric filaments (*mf*). It is in the possession of a stomodaeum, mesenteries, and mesenteric filaments that the Anthozoa differ from all the other Coelenterata. There is one character that the Anthozoa share with the Scyphozoa, and that is, that the gonads or sexual cells (G) are derived from the endoderm. They are discharged first into the coelenteric cavity, and then by way of the mouth to the exterior. In the Anthozoa the gonads are situated on the mesenteries.

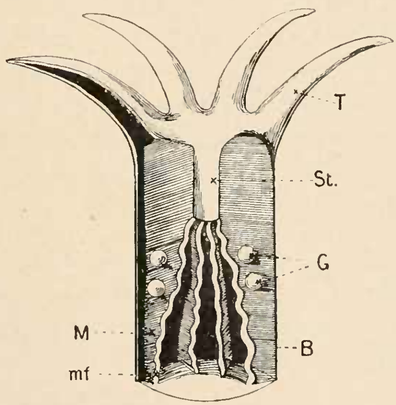

FIG. 146.—Diagram of a vertical section through an Anthozoan zooid. **B**, Body-wall; **G**, gonads; **M**, mesentery; **mf**, mesenteric filament; **St**, stomodaeum; **T**, tentacle.

Nearly all the Anthozoa are sedentary in habit. They begin life as ciliated free-swimming larvae, and then, in a few hours or days, they become attached to some rock or shell at the bottom and immediately (if colonial) start the process of budding, which gives rise to the colonies of the adult stage. Many of the Sea-anemones, however, move considerable distances by gliding over the rocks or seaweeds, others habitually burrow in the sand (*Edwardsia*, *Cerianthus*), and one family (the Minyadidae) are supported by a gas bladder, and float at the surface of the sea. The Sea-pens, too, although usually partly buried in the sand or mud, are capable of shifting their position by alternate distension and contraction of the stalk.[1] The Anthozoa are exclusively marine. With the exception of a few Sea-anemones that are found in brackish or almost fresh water in river estuaries, they only occur in salt sea water. The presence of a considerable admixture of fresh water, such as we find at the mouths of rivers, seems to interfere very materially with the development and growth of all the reef-forming Corals, as will be noticed again in the chapter on coral reefs. A few genera descend into the greatest depths of the ocean, but the home of the Anthozoa is pre-eminently the shallow seas, and they are usually found in great abundance in depths of 0-40 fathoms from the shores of the Arctic and Antarctic lands to the equatorial belt.

The only Anthozoa of any commercial importance are the Precious Corals belonging to the Alcyonarian family Coralliidae. The hard pink axis of these corals has been used extensively from remote times in the manufacture of jewellery and ornaments. Until quite recently the only considerable and systematic fishery for the Precious Corals was carried on in the Mediterranean Sea, and this practically supplied the markets of the world. In more recent times, however, an important industry in corals has been developed in Japan. In 1901 the value of the coral obtained on the coasts of Japan was over £50,000, the greater part of which was exported to Italy, a smaller part to China, and a fraction only retained for home consumption. The history of the coral fishery in Japan is of considerable interest. Coral was occasionally taken off the coast of Tsukinada in early times. But in the time of the Daimyos the collection and sale of coral was prohibited, for fear, it is said, that the Daimyo of Tosa might be compelled to present such precious treasure to the Shogun. After the Meiji reform, however (1868), the industry revived, new grounds were discovered, improved methods employed, and a large export trade developed.

There is evidence, however, in the art of Japan, of another

[1] Cf. Darwin, *Voyage of the Beagle*, chap. v.

coral fishery in ancient times, of which the history is lost. Coral was imported into Japan at least two hundred years ago, and used largely in the manufacture of those exquisite pieces of handicraft for which that country is so justly famous. On many of the carved "Netsukes" and other ornaments, however, the coral branches are represented as the booty of dark-skinned, curly-headed fishermen, "kurombo," and never of Japanese fishermen. The coral used in this art-work can hardly be distinguished from Mediterranean coral, and there are some grounds for believing that Japan imported coral from the far West in very early times. But this does not account for the "kurombo." The only coast-dwelling people of the type that is so clearly carved on these ornaments within the area of the Pacific Ocean at the present time are the Melanesians and Papuans, and the suggestion occurs that a coral fishery existed at one time in the Southern Pacific, which has since been lost [1]

The class ANTHOZOA is divided into two sub-classes:—I. ALCYONARIA; II. ZOANTHARIA.

In the Alcyonaria the fully developed zooids have always eight tentacles and eight mesenteries. In the Zoantharia the number of tentacles and the number of mesenteries in the fully developed zooids may be six, twelve, twenty-four, or an indefinite number, but individuals with eight mesenteries and only eight tentacles are not known to occur.

Sub-Class I. Alcyonaria.

This sub-class includes a large number of genera living in shallow sea-water and a few genera that extend down into deep water. With a few doubtful exceptions (Protoalcyonacea) they all form colonies composed of a large number of zooids. These zooids may be connected together by basal plates or a network of basal strands (stolons), or by stolons with additional connecting bars (*Clavularia viridis*, *Syringopora*) or by plates (*Tubipora*). In the majority of the genera the individual zooids are for the greater part of their length, from the base upwards, united together to form a continuous spongy, colonial mass, which determines the shape of the colony as a whole.

In this last-named group of genera there may be dis-

[1] Hickson, *K. Akad. Wet. Amsterdam*, 1905.

tinguished the free distal portions of the zooids bearing the mouths and tentacles (the "anthocodiae") from the common colonial mass perforated by the coelenteric cavities of the individual zooids. The coelenteric cavities are separated by a considerable amount of a substance called the "mesogloea," usually gelatinous in consistency but chemically more closely related to mucin than to gelatin, which is traversed by endodermal canals, rods of endoderm cells and a number of free amoeboid cells. In this substance, moreover, there are found in nearly all cases numerous spicules of carbonate of lime formed by the "scleroblasts" (spicule-forming cells) which have wandered from the superficial ectoderm of the common colonial mass. This common colonial mesogloea with its spicules, endoderm cells, and superficial covering of ectoderm is called the "coenenchym." The form assumed by the colonies is very varied. In some species of *Clavularia* they form encrusting plates following the irregularity of the rock or stones on which they grow, in *Alcyonium* they construct lobed masses of irregular form, in *Sarcophytum* they are usually shaped like a mushroom, in *Juncella* they are long whip-like rods, in most of the Gorgonacea they are branched in all directions like shrubs or in one plane to form fan-shaped growths, and in many of the Pennatulacea they assume that graceful feather form which gives the order its name.

The consistency and texture of the colonies also varies considerably. In some cases where the spicules are few or very small, the substance of the colony is soft to the touch, and frequently slimy at the surface, in other cases the great number of the spicules makes the colony hard but brittle, whilst in a few genera (*Sclerophytum*, *Heliopora*) the colony is so hard that it can only be broken by the hand with difficulty. In some genera (*Spongodes* and the Muriceidae) projecting spicules cause the surface to be rough or thorny, and in the Primnoidae the zooids and the surface of the general coenenchym are protected by a series of overlapping scales or plates.

In all the Alcyonaria the nematocysts are very minute, and although they can undoubtedly paralyse minute organisms they are unable to penetrate the human skin. None of the Alcyonaria have been described as stinging-corals except the Pennatulid *Virgularia rumphii.*

Zooids.—The fully formed zooids of the Alcyonaria exhibit a remarkable uniformity of structure. They have eight intermesenteric tentacles containing a cavity continuous with the coelenteron. Each of these tentacles bears at least two rows of simple pinnules, and they are therefore said to be "pinnate" tentacles. In some species of *Xenia* the tentacles may have three or four rows of pinnules, which give them a much more feathery appearance than is usually the case. In the great majority of species a single row of from eight to fourteen pinnules is found disposed laterally on each side of the tentacle. The mouth is usually small and slit-like with a slight rounded gape at the ventral extremity. The stomodaeum is usually very short, but in *Xenia* and in the autozooids of some Pennatulids it is relatively much longer. It is not known how far the stomodaeum is of importance in the digestion of the food. In *Xenia*[1] it has probably some importance, as shown by its unusual length and the numerous large goblet cells (mucus cells) which it exhibits, associated with the fact that the mesenteric filaments are relatively very small. In *Alcyonium* and other Alcyonaria gland cells also occur in the stomodaeum, and it is probable that they secrete a fluid capable of digesting to some extent the food as it passes through. The most important part of the digestion, however, is performed by the six "ventral" mesenteric filaments.

Attention has already been drawn to the fact (p. 330) that two regions of the zooids of the colonial Alcyonaria can be recognised. At the oral end there is a region, which in the fully expanded condition consists of a crown of eight tentacles surrounding the mouth, and a body-wall free from its immediate neighbours. This region is called the "anthocodia." The anthocodia is continuous with a region which forms a part of the common colonial mass. Some genera seem to have very little power of contracting the tentacles or of withdrawing the anthocodiae. The zooids of *Stereosoma*, of *Xenia*, of *Umbellula*, and of a few other genera may be described as non-retractile. In many cases, however, the tentacles can be considerably contracted, bent over the mouth, and withdrawn into the shelter of the subjacent body-wall. In such a condition the surface of the colony exhibits a number of tubular, conical, or convex protuberances, called "verrucae," and the colony is said to be partially retractile. In many genera, however, the whole of the

[1] J. H. Ashworth, *Proc. Roy. Soc.* lxiii. 1898, p. 443.

anthocodiae can be withdrawn below the general surface of the coenenchym, so that the position of the zooids in the colony is indicated only by star-like holes, or simple key-hole slits in the superficial coenenchym. Such colonies are said to be completely retractile (Fig. 147).

It is often very difficult to determine whether a particular species is or is not completely retractile, unless observations can be made upon the living colony; and there are many instances of confusion in the work of systematists due to a species being described as partially retractile in one instance, and completely retractile in another. The complete retraction of the anthocodiae

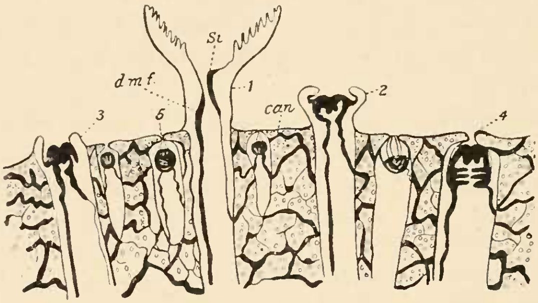

FIG. 147.—Diagram of a vertical section of a portion of a lobe of *Alcyonium* to show the mode of retraction of the anthocodiae. 1, Anthocodia of a zooid fully expanded; 2, in the first stage of retraction: 3, in the second stage; 4, in the third stage, leaving a shallow prominence or "verruca" on the surface; 5, final stage, the verruca flattened down and the coenenchym closed. *can*, Canal system; *d.m.f*, dorsal mesenteric filament of a zooid; *si*, siphonoglyph.

may be effected very slowly, and after continuous irritation only. If the colony is killed too quickly, the anthocodiae remain in a state of partial retraction. An example of this may be found in the common British *Alcyonium digitatum*. Specimens of this species which are put into a bucket of sea water and allowed to roll about with the movements of a small boat in a rough sea, undergo complete retraction; but if the same specimens be allowed to expand in the aquarium, and then plunged into spirit, or allowed to dry in the sun, they will die in a condition of partial retraction.

The phenomenon of dimorphism occurs in some Alcyonaria. A certain number of the zooids of a colony are arrested in their development, and are known as the "siphonozooids." They may be distinguished from the fully formed zooids, which, in these cases, are called the "autozooids," by the absence of tentacles, by the absence of the six ventral and lateral mesenteric filaments, and by the incomplete development of the muscles on the mesenteries, and of the mesenteries themselves. They are, moreover, frequently distinguished by the greater development and extent of the ciliated groove or siphonoglyph on the ventral side of the stomodaeum.

It is often difficult to distinguish between true siphonozooids and young autozooids, and consequently dimorphism has been attributed to some genera in which it almost certainly does not occur. Simple dimorphism undoubtedly occurs in the genera *Heteroxenia, Sarcophytum, Anthomastus, Lobophytum, Acrophytum,* and *Paragorgia.* It has also been said to occur in *Corallium* (Moseley and Kishinouye), *Melitodes* (Ridley), and some species of Dasygorgiidae.

The Pennatulacea are trimorphic. The main shaft of these colonies is the much modified first formed or axial zooid, adapted for the support of all the other zooids. It usually exhibits no mouth, no tentacles, and only four of the original eight mesenteries. It has no mesenteric filaments and no stomodaeum, and bears no sexual cells. The other zooids of the colony are similar in structure to the autozooids and siphonozooids of the dimorphic Alcyonaria.

There are eight **mesenteric filaments** in all Alcyonarian zooids. They have the appearance of thickenings of the free edges of the mesenteries. Two of them, called the "dorsal" mesenteric filaments, are straight when the anthocodia is expanded, and extend from the edge of the stomodaeum for a long distance down into the coelenteron of the zooid; the other six, called the "ventral" mesenteric filaments (*i.e.* the ventral and ventro-lateral and dorso-lateral), are usually short and are almost invariably slightly convoluted. The dorsal filaments are built up of columnar cells provided with long cilia, and have usually no gland cells, the others may show a few cilia but are principally composed of non-ciliated gland cells. When the bolus of food has passed through the stomodaeum it is seized by these ventral filaments and rapidly disintegrated by the secretion of its cells. The function of the dorsal mesenteric filaments is mainly respiratory. During life their cilia produce a current which flows towards the stomodaeum. On the ventral side of the stomodaeum itself there is a groove called the "siphonoglyph" composed of a specialised epithelium bearing long powerful cilia. But the current produced by the siphonoglyph flows from the mouth downwards into the coelenteric cavity and is thus in the opposite direction to that produced by the dorsal mesenteric filaments. It is very probable that these two currents on the opposite sides of the zooids maintain the circulation of water in the deep-seated parts of the colony which is necessary for the respiration of the tissues.

On each of the eight mesenteries there is a longitudinal ridge due to the presence of a band of retractor muscles. The position of these muscles on the ventral surfaces of the mesenteries only is one of the characteristic features of the sub-class (Fig. 148, and p. 329).

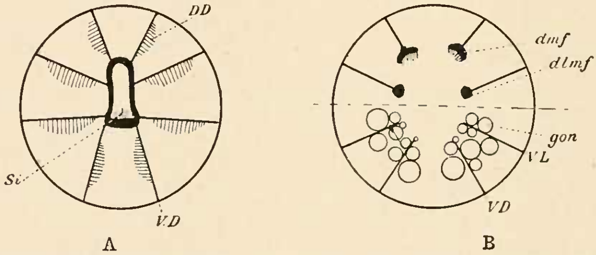

FIG. 148.—Diagrammatic transverse sections of an Alcyonarian. **A**, through the stomodaeum; **B**, below the level of the stomodaeum. *DD*, Dorsal directive; *dlmf*, dorso-lateral mesenteric filament; *dmf*, dorsal mesenteric filament; *gon*, gonad; *Si*, siphonoglyph; *V.D*, ventral mesentery; *V.L*, ventro-lateral mesentery. The upper half of the section in **B** is taken at a higher level than the lower half.

They vary considerably in thickness and extent according to the power of retractility possessed by the zooids, but they never vary in their position on the mesenteries.

The **skeleton** of Alcyonaria may consist of spicules of calcium carbonate, of a horny substance frequently impregnated with calcium carbonate and associated with spicules of the same substance, or in *Heliopora* alone, among recent forms, of a continuous crystalline corallum of calcium carbonate.

The spicules constitute one of the most characteristic features of the Alcyonaria. They are not found in *Cornularia*, *Stereosoma*, in a recently discovered genus of Gorgoniidae (*Malacogorgia*), in certain Pennatulacea and in *Heliopora*; and it is probable that they may be absent in some local varieties of certain species of *Clavularia*.

The spicules of Alcyonaria consist of an organic matrix supporting a quantity of crystalline calcium carbonate. In some cases (*Xenia*) the amount of inorganic salt is so small that the spicule retains its shape after prolonged immersion in an acid; but generally speaking the relative amount of calcium carbonate is so great that it is only by the careful decalcification of the spicules in weak acetic acid that the delicate fibrous organic matrix can be demonstrated.

The spicules vary in size from minute granules to long spindles 9 mm. in length (*Spongodes*, sp.). They exhibit so many varieties of shape that an attempt must be made to place them in groups. The most prevalent type perhaps is that called the spindle. This is a rod-shaped spicule with more or less pointed extremities. They are usually ornamented with short simple or compound wart-like tubercles (Fig. 149, 5). Spicules belonging to this type are found in all the principal subdivisions of the group except the Pennatulacea.

In the Pennatulacea a very characteristic form of spicule is a long rod or needle marked with two or three slightly twisted ridges, frequently a little knobbed or swollen at the extremities. In the same group, in *Xenia* and *Heteroxenia* among the Alcyonacea, and in the family Chrysogorgiidae the spicules are in the form of minute discs or spheres, and in some genera the discs may be united in couples (twins) or in threes (triplets) by short connecting bars (Fig. 149, 10). More irregular calcareous corpuscles of minute size are found in some genera of Pennatulacea.

Other characteristic spicules are the warted clubs of *Juncella*, the torch-like spicules of *Eunicella* (Fig. 149, 3), the clubs with irregular leaf-like expansions at one extremity ("Blattkeulen") of *Eunicea*, and the flat but very irregular scales of the Primnoidae. There are also many genera exhibiting spicules of quite irregular form (Fig. 149, 8).

In the greater number of cases the spicules lie loosely in the mesogloea and readily separate when the soft tissues of the colony decay or are dissolved in a solution of potash. In a few noteworthy examples the spicules become in their growth tightly wedged together to form a compact skeleton, which cannot subsequently be disintegrated into its constituent elements. In the Precious corals (Coralliidae) the spicules of the axial region fuse together to form a solid mass of lime almost as hard and compact as the substance of a pearl. In *Paragorgia* and some other closely related genera the spicules of the axis of the colony also become tightly wedged together, but the core thus formed is far more porous and brittle than it is in the Coralliidae. In

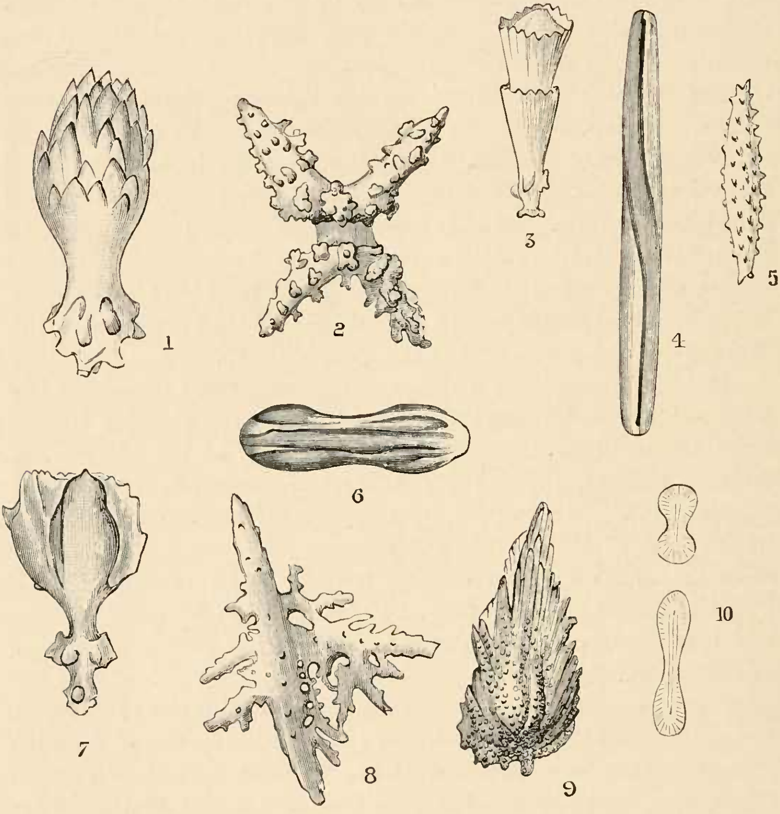

Fig. 149.—Spicules of Alcyonaria. 1, Club of *Juncella*; 2, warted cross of *Plexaurella*; 3, torch of *Eunicella*; 4, needle of *Renilla*; 5, warted spindle of *Gorgonella*; 6, spicule of *Pennatula*; 7, foliate club of *Eunicea*; 8, irregular spicule of *Paramuricea*: 9, scale of *Primnoa*; 10, spicules of *Trichogorgia*. (5 and 10 original, the remainder after Kölliker.)

Tubipora (the organ-pipe coral) and in *Telesto rubra* the spicules of the body-walls of the zooids fuse to form perforated calcareous tubes. In some species of *Sclerophytum* the large spicules of the coenenchym become so closely packed that they form dense stony masses, almost as hard as a Perforate Madreporarian coral. The horny substance, allied chemically to keratin, plays an important part in the building up of skeletal structures in many Alcyonaria. In *Clavularia viridis* and in *Stereosoma* a change in the chemical character of the mesogloea of the body-walls of the polyps leads to the formation of a horny tube, which in the former case is built up of interlacing fibres, and in the latter is formed as a homogeneous sheath. In many of the Alcyonacea which have a compact axial skeleton the spicules are cemented together by a horny matrix.

In the Gorgonellidae and some others the hard axis is formed of a horny substance impregnated with a crystalline form of calcium carbonate; but in the Gorgoniidae, many of the Pennatulacea and some other genera very little or no carbonate of lime is found in the horny axis.

The skeleton of the genus *Heliopora* differs from that of all the other Alcyonaria in its development, structure, and form. In the words of Dr. G. C. Bourne,[1] "the calcareous skeleton of *Heliopora* is not formed from spicules developed within cells but is a crystalline structure formed by crystallisation of carbonate of lime, probably in the form of aragonite, in an organic matrix produced by the disintegration of cells which I have described as calicoblasts." It is further characterised by its blue colour. A peculiar form of the axial skeleton (Fig. 155), consisting of alternate nodes mainly composed of keratin, and internodes mainly composed of calcium carbonate, is seen in the families Isidae and Melitodidae. In the Melitodidae the nodes contain a considerable number of loose spicules, and the internodes are mainly composed of spicules in close contact but firmly cemented together by a sparse horny matrix. In the Isidae the scanty calcareous substance of the nodes, and the bulk of the substance of the internodes, is formed of amorphous crystalline limestone.

The Alcyonaria exhibit a great variety of **colour**. Very little is known at present of the chemistry of the various pigments found in the group, but they may conveniently be arranged in two sections, the soluble pigments and the insoluble pigments. To the former section belong various green and brown pigments found in the anthocodiae and superficial coenenchym of many genera. These are related to chlorophyll, and may be very largely the product, not of the Alcyonarians themselves, but of the

[1] *Quart. Journ. Micr. Sci.* xli. 1899, p. 521.

symbiotic "Algae" (cf. p. 261) they carry. A diffuse salmon-pink colour soluble in spirit occurs in the living *Primnoa lepadifera* of the Norwegian fjords, and a similar but paler pink colour occurs in some varieties of the common *Alcyonium digitatum*. Gilchrist[1] states that when he was preserving specimens of *Alcyonium purpureum* from Cape waters a considerable quantity of a soluble purple pigment escaped.

But the predominant colour of Alcyonarians is usually due to the insoluble pigments of the calcareous spicules. These may be of varying shades of purple, red, orange, and yellow. The colours may be constant for a species or genus, or they may vary in different specimens of one species, or even in different parts of a single colony. Thus the skeletons of *Tubipora musica* from all parts of the world have a red colour, the species of the genus *Anthomastus* have always red spicules. On the other hand, we find in *Melitodes dichotoma* red and yellow varieties in the same locality, and in *M. chamaeleon* some of the branches of a colony are red and others yellow. In *Chironephthya variabilis* the colour of the spicules in any one specimen varies considerably, but in a collection of several specimens from a single locality a kaleidoscopic play of colours may be seen, no two specimens being exactly the same in the arrangement of their colour pattern. The influences that determine the colour of the spicules is at present quite unknown, and in view of the great variability that occurs in this respect, colour must be regarded as a most uncertain guide for the determination of species. The blue colour of the genus *Heliopora* is due to a peculiar pigment which shows characteristic bands in the spectrum.[2]

Phosphorescence.—A great many Alcyonaria are known to be phosphorescent. Moseley says that "All the Alcyonarians dredged by the 'Challenger' in deep water were found to be brilliantly phosphorescent when brought to the surface." The phosphorescence of the common British *Pennatula phosphorea* has attracted more attention than that of any other species, and has been well described by Panceri, Forbes, and others. Forbes[3] says, "The pen is phosphorescent only when irritated by touch; the phosphorescence appears at the place touched, and

[1] Quoted by Hickson, *Marine Investigations, S. Africa*, iii. 1904, p. 215.

[2] G. C. Bourne, *Phil. Trans. Roy. Soc.* clxxxvi. 1895, B. p. 464.

[3] Quoted by Marshall, *Oban Pennatulida*, 1882, p. 49.

proceeds thence in an undulating wave to the extremity of the rachis, but never in the opposite direction; it is only the parts at and above the point of stimulation that show phosphorescence, the light is emitted for a longer time from the point of stimulation than from the other luminous parts; detached portions may show phosphorescence. When plunged in fresh water, the *Pennatula* scatters sparks about in all directions—a most beautiful sight."

Panceri was of opinion that the mesenteric filaments were the organs of phosphorescence, but the whole question of the cause and localisation of the light in these colonies requires further investigation.

Food.—Very little is known about the food of Alcyonaria, but it is very probable that it consists entirely of minute larvae and other living organisms. When the coelenteric cavities of preserved Alcyonaria are examined, food is very rarely found in them, although fragments of Crustacean appendages have occasionally been seen in the neighbourhood of the mesenteric filaments. Experimenting upon *Alcyonium digitatum*, Miss Pratt [1] has found that the zooids seize and swallow various small organisms of a surface-net gathering, and that they will also swallow finely minced fragments of the muscle of fish, but that they reject many kinds of fish ova. In many tropical and some extra-tropical species the superficial canal systems and the inter-mesenterial spaces of the zooids contain a large number of Zooxanthellae, and their presence seems to be associated in some cases with a decided degeneration of the digestive organs. It has been suggested that these symbiotic "Algae" prepare food materials after the manner of plants, and that these are absorbed by the hosts, but it appears improbable that in any case this source of food supply is sufficient. It must probably be supplemented in some degree by food obtained by the mouth, and digested in the coelenteric cavity.

The question whether the Alcyonaria can form an important part of the dietary of fish or other carnivorous animals may be economically important. Fragments of the Pennatulid *Virgularia* have been found in the stomachs of cod and other fish, but with this exception there is no evidence that any genus is systematically or even occasionally preyed upon by any animal. With a very

[1] *Quart. Journ. Micr. Sci.* xlix. 1905, p. 327.

few exceptions Alcyonaria show no signs of having been torn, bitten, or wounded by carnivorous animals. It is improbable that the presence of nematocysts in the tentacles can account for this immunity, as it is known that some predaceous animals do feed upon Coelenterates provided with much larger nematocysts than any Alcyonarian possesses. All Alcyonaria, however, have a characteristic disagreeable odour, and it is possible, as in many other cases, that this is accompanied by an unpleasant taste. But if the Alcyonaria themselves are immune, it is possible that their large yolk-laden eggs may form a not unimportant source of food supply. In places where large colonies flourish, an immense number of eggs or embryos must be discharged into the water during the spawning season, and of these only a minute fraction can survive long enough to found a new colony.

Reproduction.—The formation of colonies by gemmation has frequently been mentioned above. The young buds of a colony arise from the endoderm canals in the body-wall of the zooids, in the general coenenchym, or in the stolon. They never arise from evagination of the coelenteric cavities of the zooids. There is no evidence that fission of a colony to form secondary colonies ever occurs. Gemmation leads to the increase in the number of zooids forming a colony, but not to an increase in the number of colonies.

Fission of the zooids is of extremely rare occurrence; a single case, however, has been recorded by Studer in the genus *Gersemia*. Sexual reproduction usually occurs once in a year; it is doubtful whether it ever occurs continuously. The colonies appear to be nearly always dioecious, only one case of hermaphroditism having yet been recorded.[1] The ova and sperm sacs are usually formed and matured on the six ventral mesenteries, rarely on the dorsal pair of mesenteries (Fig. 148, B) as well. The spawning season varies with the locality. *Alcyonium digitatum* spawns at Plymouth at the end of December, and somewhat later at Port Erin. The Pennatulid *Renilla* and the Gorgonid *Leptogorgia* spawn in the summer months on the coast of North America. In the Mediterranean *Alcyonium palmatum* spawns in September and October (Lo Bianco), *Gorgonia cavolinii* in May and June.

[1] *Corallium nobile* appears to be the exception to this rule, as it is stated that colonies and even individual zooids are occasionally hermaphrodite. Lacaze Duthiers, "Hist. Nat. du Corail," 1864, p. 127.

It is not known for certain when the fertilisation of the ova is effected, but in *Alcyonium digitatum,* and in the majority of the Alcyonarians, it probably takes place after the discharge of the ova from the zooids. A few forms are, however, certainly viviparous, the larvae of *Gorgonia capensis* being retained within the coelenteric cavity of the parent zooid until they have grown to a considerable size. The other viviparous Alcyonarians are *Corallium nobile* (de Lacaze Duthiers), the "Clavulaires petricoles," and *Sympodium coralloides* (Marion and Kowalevsky), and three species of *Nephthya* found at depths of 269 to 761 fathoms (Koren and Danielssen). The general features of the development are very similar in all Alcyonarians that have been investigated. The egg contains a considerable amount of yolk, and undergoes a modified form of segmentation. The free-swimming larva is called a "sterrula." It consists of an outer layer of clear ciliated ectoderm cells, surrounding a solid endodermic plasmodium containing the yolk. As the yolk is consumed a cavity appears in the endoderm, and the larva is then called a "planula" (Fig. 150). The mouth is subsequently formed by an invagination of the ectoderm at the anterior pole. The development of the mesenteries has not yet been fully described.

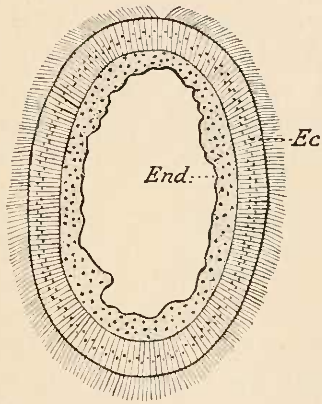

FIG. 150.—Ciliated "planula" larva of *Alcyonium digitatum.* *Ec,* Ectoderm; *End,* endoderm.

Classification.—The sub-class Alcyonaria may conveniently be classified as follows:—

Grade A. PROTALCYONACEA.
Grade B. SYNALCYONACEA.
Order 1. STOLONIFERA.
Order 2. COENOTHECALIA.
Order 3. ALCYONACEA.
Order 4. GORGONACEA.
Order 5. PENNATULACEA.

Grade A. Protoalcyonacea.

This Grade includes those genera which, like many sea-anemones, do not reproduce by continuous gemmation to form colonies.

Several genera have been described, and they have been placed together in one family called the **Haimeidae.**

Haimea funebris, M. Edwards, was found off the coast of Algeria; *H. hyalina*, Koren and Danielssen, in Norway; *Hartea elegans*, Wright, from the Irish coast; *Monoxenia darwinii*, Haeckel, from the Red Sea, and a large new species found by the "Siboga" Expedition in deep water off Ceram. All these species, however, are very rare, and there is no satisfactory evidence at present that they remain solitary throughout life.

Grade B. Synalcyonacea.

The sub-division of the Synalcyonacea into orders presents many difficulties, and several different classifications have been proposed. Only two orders of the five that are here recognised are clearly defined, namely, the Coenothecalia, containing the single living genus *Heliopora*, and the Pennatulacea or Sea-pens; the others are connected by so many genera of intermediate characters that the determination of their limits is a matter of no little difficulty.

Order I. Stolonifera.

These are colonial Alcyonaria springing from a membranous or ribbon-like stolon fixed to a stone or some other foreign object. The body-walls of the individual zooids may be free or connected by a series of horizontal bars or platforms (autothecalous); never continuously fused as they are in other orders (coenothecalous).

In the simplest form of this order, *Sarcodictyon catenatum* Forbes, the ribbon-like strands of the stolon meander over the surface of stones, forming a red or yellow network, from the upper surface of which the clear transparent anthocodiae of the zooids protrude. When retracted the anthocodiae are drawn down below the surface of the general coenenchym, and their position is indicated by small cushion-like pads on the stolon.

Sarcodictyon is found in depths of 10 to 22 fathoms in the Irish Sea, off the west coast of Scotland, the Shetlands, and off the Eddystone Lighthouse, South Devon.

Another very important genus is *Tubipora*, in which the tubular body-wall of each zooid is very much longer in proportion to its diameter than it is in *Sarcodictyon*, and the anthocodia is retracted not into the stolon, but into the basal part of the body-wall. The zooids are connected together by horizontal platforms on which new zooids are formed by gemmation. Both horizontal platforms and the body-walls of the zooids are provided with a skeleton of fused spicules of a red colour.

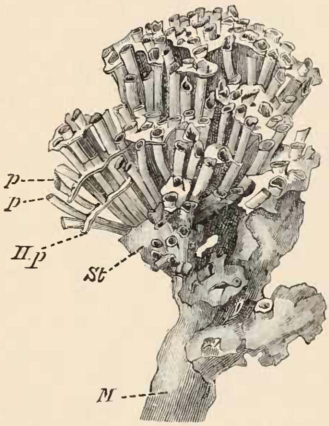

FIG. 151.—*Tubipora musica*, a young colony growing on a dead Madrepore branch (*M*). *Hp*, The connecting horizontal platforms ; *p*, *p*, the skeletal tubes of the zooids ; *St*, the basal stolon.

This genus is the well-known Organ-pipe coral, and is found sometimes in immense quantities on the coral reefs of both the old and new world.

It may be seen in pools on the edge of the reefs at low tides in colonies frequently a foot or more in diameter. The tentacles are often of a bright emerald green colour, and as the anthocodiae stand expanded in the clear water they contribute a brilliant patch of colour to the many beauties of their surroundings. When the coral is disturbed, or the water shallows and the anthocodiae are retracted, the dull red colour of the skeleton gradually takes the place of the bright green of the tentacles.

It is probable that this order of Alcyonaria was better represented on the reefs of some of the earlier periods of the world's history than it is at present. The fossil *Syringopora*, which is found abundantly in the carboniferous limestone and other strata, was probably an Alcyonarian belonging to this order. It resembles *Tubipora* in its mode of growth, but in place of the horizontal platforms connecting the zooids there are rods or bars from which new zooids spring (Fig. 152). Similar connecting bars are found in the recent *Clavularia* (*Hicksonia*, Delage) *viridis* of the East Indian reefs (Fig. 153). Other fossil forms belonging to the order are *Favosites*, a very abundant coral of the Upper Silurian rocks, and possibly *Columnaria*.

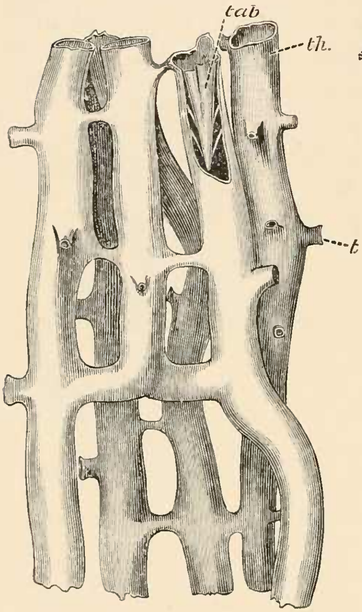

FIG. 152.—*Syringopora*, a fossil, showing autothecalous tubes (*th*), funnel-shaped tabulae (*tab*), and tubular cross-bars (*t*).

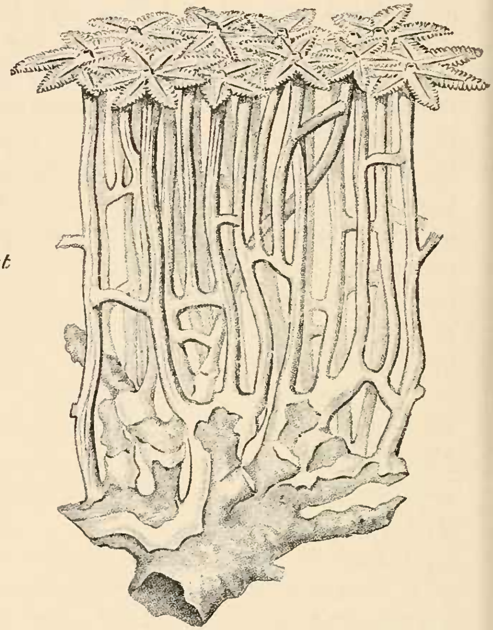

FIG. 153.—*Clavularia* (*Hicksonia*) *viridis*, with creeping stolon and transverse connecting tubes.

The principal families of the Stolonifera are:—

Fam. 1. CORNULARIIDAE. — Without spicules; *Cornularia*, Lamarck, Mediterranean; *Stereosoma*, Hickson, Celebes.

Fam. 2. CLAVULARIIDAE. — *Clavularia*, Quoy and Gaimard; *Sarcodictyon*, Forbes, British; *Sympodium*, Ehrb; *Syringopora*, Goldfuss, fossil.

Fam. 3. TUBIPORIDAE.—*Tubipora*, Linnaeus, tropical shallow water.

Fam. 4. FAVOSITIDAE. — *Favosites*, Lamarck; *Syringolites*, Hinde; *Stenopora*, King.

Order II. Coenothecalia.

This order contains the single genus and species *Heliopora coerulea* among recent corals, but was probably represented by a large number of genera and species in earlier periods.

It is found at the present day in many localities in the warm shallow waters of the tropical Pacific and Indian Oceans. It usually flourishes on the inside of the reef, and may form masses of stone five or six feet in diameter. The coral may easily be recognised, as it is the only one that exhibits a blue colour. This colour usually penetrates the whole skeleton, but in some forms is absent from the superficial layers.

The skeleton consists of a number of parallel tubes with imperforate walls, which are fused together in honey-comb fashion. On making a vertical section through a branch of the coral it is found that the tubes are divided into a series of chambers by transverse partitions or "tabulae." The soft living tissues of the coral, the zooids and coenosarc, are confined to the terminal chambers, all the lower parts being simply dead calcareous skeleton supporting the living superficial layer. Among the parallel tubes there may be found a number of larger chambers that seem to have been formed by the destruction of the adjacent walls of groups of about nineteen tubes. These chambers are provided with a variable number of pseudo-septa, and have a remarkable resemblance to the thecae of some Zoantharian corals. That *Heliopora* is not a Zoantharian coral was first definitely proved by Moseley, who showed that each of these larger chambers contains an Alcyonarian zooid with eight pinnate tentacles and eight mesenteries. The zooids arise from a sheet of coenosarc that covers the whole of the living branches of the coral mass, and this sheet of coenosarc bears a plexus of canals communicating on the one hand with the zooids, and on the other with a series of blind sacs, each of which occupies the cavity of one of the skeletal tubes as far down as the first tabula. The zooids of *Heliopora* are very rarely expanded during the day-time, and it has been found very difficult to get them to expand in an aquarium. The coral, however, is frequently infested with a tubicolous worm allied to the genus *Leucodora*, which freely expands and projects from the surface. So constant and so numerous are these worms in some localities that it has actually been suggested that *Heliopora* should be regarded as a Polychaete worm and not as an Alcyonarian. According to Mr. Stanley Gardiner, however, these worms do not occur in association with the *Heliopora* found on the reefs of the Maldive Archipelago.

There is very strong reason to believe that certain fossil corals were closely related to *Heliopora*; that *Heliopora* is in fact the solitary survivor of a group of Alcyonarian corals that in past times was well represented on the reefs, both in numbers and in species. The evidence is not so convincing that other fossil corals are closely related to *Heliopora*, and their true zoological position may remain a matter for surmise. The order may be classified as follows:—

Fam. 1. Heliolitidae.[1]—Coenothecalia with regular, well-developed septa, generally twelve in number, in each calicle.

Heliolites, Dana, Silurian and Devonian. *Cosmiolithus*, Lindström, Upper Silurian. *Proheliolites*, Klaer, Lower Silurian. *Plasmopora*, Edwards and Haime, Upper Silurian. *Propora*, E. and H., Upper Silurian. *Camptolithus*, Lindström, Upper Silurian. *Diploëpora*, Quenst, Upper Silurian. *Pycnolithus*, Lindström, Upper Silurian.

Fam. 2. Helioporidae.[2]—Coenothecalia with small irregularly arranged coenosarcal coeca, and a variable number of septa or septal ridges. *Heliopora*, de Blainville, recent, Eocene and Upper Cretaceous. *Polytremacis*, d'Orbigny, Eocene and Upper Cretaceous. *Octotremacis*, Gregory, Miocene.

The family **Coccoseridae** is regarded by Lindström as a sub-family of the Heliolitidae, and the families **Thecidae** and **Chaetetidae** are probably closely related to the Helioporidae.

Order III. Alcyonacea.

This order contains a large number of genera of great variety of form. The only characters which unite the different genera are that the body-walls of some groups of zooids, or of all the zooids, are fused together to form a common coenenchym penetrated by the coenosarcal canals, and that the spicules do not fuse to form a solid calcareous, or horny and calcareous, axial skeletal support.

The affinities with the order Stolonifera are clearly seen in the genera *Xenia* and *Telesto*. Some species of *Xenia* form flattened or domed colonies attached to stones or corals, with non-retractile anthocodiae and body-walls united for only a

[1] G. Lindström, *Handl. k. Svensk. Vet. Akad.* xxxii. 1899.

[2] J. W. Gregory, *Proc. Roy. Soc.* lxvi. 1899, p. 291.

short distance at the base. Young *Xenia* colonies are in fact Stolonifera in all essential characters. In *Telesto prolifera* we find a network of stolons encrusting coral branches and other objects after the manner of the stolons of many species of *Clavularia*, although the zooids do not arise from these stolons singly, but in groups, with their body-walls fused together for a certain distance. In *Telesto rubra* the spicules of the body-walls are fused together to form a series of perforated tubes very similar in some respects to the tubes of *Tubipora*.

A remarkable genus is *Coelogorgia*. Here we find a branching colony arising from a basal stolon, and the axis of the main stem and of each branch consists of a single very much elongated zooid bearing on its thickened walls the branches of the next series and other zooids. It is true that in this genus there is very little fusion of neighbouring zooids, and the amount of true coenenchym is so small that it can hardly be said to exist at all. Bourne[1] has united this genus with *Telesto* into a family Asiphonacea, which he joins with the Pennatulida in the order Stelechotokea; but their affinities seem to be closer with the Alcyonacea than with the Pennatulacea, from which they differ in many important characters.

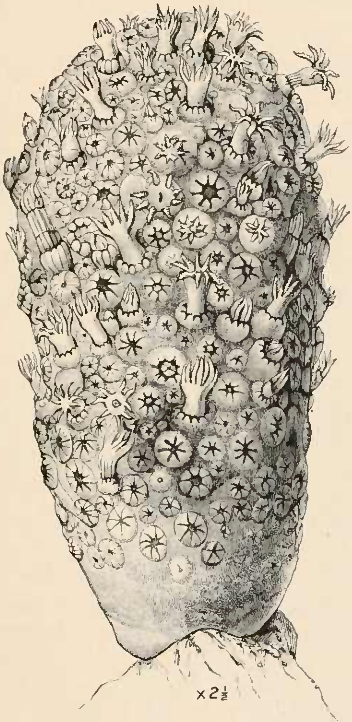

FIG. 154.—*Alcyonium digitatum*, a single-lobed specimen, with some of the zooids expanded.

The genus *Alcyonium* not only contains the commonest British Alcyonarian (*A. digitatum*), but it is one of the most widely distributed genera of all Alcyonaria that occur in shallow water.

The genera *Sarcophytum* and *Lobophytum* occur in shallow water in the tropics of the old world. The former frequently consists of huge toad-stool shaped masses, soft and spongy in

[1] G. C. Bourne, Lankester's *Treatise on Zoology*, pt. ii. 1900, "Anthozoa," p. 26.

consistency, of a green, brown, or yellow colour. On some reefs the colonies of *Sarcophytum* form a very conspicuous feature, and from their very slimy, slippery surface, add to the minor dangers of wading in these regions. Both genera are dimorphic. Some species of the genus *Sclerophytum*,[1] which occur in the Indian Ocean, are so hard and brittle that they might readily be mistaken for a Zoantharian coral. This character is due to the enormous number of tightly packed spicules borne by the coenenchym. Some of these spicules in *S. quereiforme* are 7 mm. × 1·7 mm.; the largest, though not the longest (*vide* p. 335) of any spicules occurring in the order.

Another very important genus occurring on coral reefs, and of very wide distribution, is *Spongodes*. This genus forms bushy and rather brittle colonies of an endless variety of beautiful shapes and colours. Arising from the neck of each anthocodia there are one or two long, sharp, projecting spicules, which give the surface a very spiny or prickly character.

The genera *Siphonogorgia* and *Chironephthya* form large brittle, branching colonies which might readily be mistaken for Gorgonians. The strength of the branches, however, is mainly due to the large, densely packed, spindle-shaped spicules at the surface of the coenenchym, the long coelenteric cavities of the zooids penetrating the axis of both stem and branches. *Siphonogorgia* is usually uniformly red or yellow in colour. *Chironephthya*, on the other hand, exhibits a great variety of colour in specimens from the same reef, and indeed in different branches of the same colony.

Fam. 1. Xeniidae.—Alcyonacea with non-retractile zooids. Spicules very small discs, usually containing a relatively small proportion of lime.

Xenia, Savigny; Indian Ocean and Torres Straits. *Heteroxenia*, Kölliker; Red Sea, Cape of Good Hope, and Torres Straits.

Fam. 2. Telestidae.—Colonies arising from an encrusting membranous or branching stolon. The erect stem and branches are formed by the body-walls of two or three zooids only, from which secondary zooids and branches of the next order arise.

Telesto, Lamouroux, widely distributed in warm waters of the Atlantic, Pacific, and Indian Oceans. The genus *Fascicularia*, Viguier, from the coast of Algiers, seems to be related to *Telesto*,

[1] E. M. Pratt, *Fauna and Geogr. Maldive Archip.* ii. pt. i. 1903, p. 516.

but the groups of zooids are short, and do not give rise to branches.

Fam. 3. Coelogorgiidae.—The colony arborescent, attached by stolon-like processes. The stem formed by an axial zooid with thickened body-walls. Branches formed by axial zooids of the second order, and branchlets by axial zooids of the third order, borne either on two sides or in spirals by the main stem. Genus *Coelogorgia*, Zanzibar.

Fam. 4. Alcyoniidae.—The colonies of this family are usually soft and fleshy, and the spicules, evenly distributed throughout the coenenchym, do not usually fuse or interlock to form a continuous solid skeleton. They may be unbranched or lobed, never dendritic in form. The principal genera are:—*Alcyonium*, Linnaeus, cosmopolitan, but principally distributed in temperate and cold waters. *Alcyonium digitatum* is the commonest British Alcyonarian. It is found in shallow water, from the pools left at low spring tides to depths of 40 or 50 fathoms, at most places on the British shores. It is stated by Koehler to descend into depths of over 300 fathoms in the Bay of Biscay. There are two principal varieties; one is white or pale pink in the living condition, and the other yellow. In some localities the two varieties may be found in the same pools. Another species, *Alcyonium glomeratum*, placed in a distinct genus (*Rhodophyton*) by Gray, and distinguished from the common species by its red colour and long digitate lobes, is found only off the coast of Cornwall. *Paralcyonium*, Milne Edwards; Mediterranean. *Sclerophytum*, Pratt; sometimes dimorphic, Indian Ocean. *Sarcophytum*, Lesson; dimorphic, principally tropical. *Lobophytum*, Marenzeller; dimorphic, tropical. *Anthomastus*, Verrill; dimorphic, Atlantic Ocean, deep water. *Acrophytum*, Hickson; dimorphic, Cape of Good Hope.

Fam. 5. Nephthyidae.—Colonies dendritic. Usually soft and flexible in consistency. *Nephthya*, Savigny; Indian and Pacific Oceans. *Spongodes*, Lesson; widely distributed in the Indian and Pacific Oceans.

Fam. 6. Siphonogorgiidae.—Colonies often of considerable size. Dendritic. Spicules usually large and abundant, giving a stiff, brittle consistency to the stem and branches. *Siphonogorgia*, Kölliker; Red Sea, Indian, and Pacific tropics. *Chironephthya*, Wright and Studer; Indian and Pacific Oceans. *Lemnalia*, Gray; Zanzibar. *Agaricoides*, Simpson;[1] Indian Ocean, 400 fathoms.

Order IV. Gorgonacea.

This order contains a very large number of dendritic and usually flexible corals occurring in nearly all seas and extending from shallow waters to the very great depths of the ocean. A large proportion of them are brightly coloured, and as the principal pigments are fixed in the spicules, and are therefore preserved when the corals are dead and dried, they afford some of the most attractive and graceful objects of a natural history museum.

The only character that separates them from the Alcyonacea is that they possess a skeletal axis that is not perforated by the coelenteric cavities of the zooids. The coelenteric cavities are usually short. The order may conveniently be divided into two sub-orders.

Sub-Order 1. Pseudaxonia.

The axis in this sub-order consists of numerous spicules tightly packed together, or cemented together by a substance which is probably allied to horn in its chemical composition. This substance may be considerable in amount, in which case it remains after decalcification as a spongy, porous residue; or it may be so small in amount, as in *Corallium*, that the axis appears to be composed of solid carbonate of lime. The statement is usually made that the axis is penetrated by nutritive canals in certain genera, but the evidence upon which this is based is unsatisfactory and in some cases unfounded. There can be no doubt, however, that in some genera the axis is porous and in others it is not, and this forms a useful character for the separation of genera.

Fam. 1. Briareidae.—The medullary substance consists of closely packed but separate spicules embedded in a soft horny matrix, which is uniform in character throughout its course. Nearly all the genera form dendritic colonies of considerable size.

The principal genera are:—*Solenocaulon*, Gray; Indian Ocean and North Australia. Many of the specimens of this genus have fistulose stems and branches. The tubular character of the stem and branches is probably caused by the activity of a Crustacean,

[1] *Zool. Anz.* xxix. 1905, p. 263.

Alpheus, and may be regarded as of the nature of a gall-formation.[1] *Paragorgia*, M. Edwards; Norwegian fjords, in deep water. This genus forms very large tree-like colonies of a ruby-red or white colour. It is perhaps the largest of the dendritic Alcyonarians. It is dimorphic. *Spongioderma*, Kölliker; Cape of Good Hope. The surface of this form is always covered by an encrusting sponge. *Iciligorgia*, Ridley; Torres Straits. The stem and branches are compressed and irregular in section.

Fam. 2. Sclerogorgiidae.—The medullary mass forms a distinct axis consisting of closely packed elongate spicules with dense horny sheaths.

Suberogorgia, Gray, has a wide distribution in the Pacific Ocean, Indian Ocean, and the West Indies. *Keroeides*, W. and S., comes from Japan.

Fam. 3. Melitodidae.—The axis in this family exhibits a series of nodes and internodes (Fig. 155), the former consisting of pads formed of a horny substance with embedded spicules, the latter of a calcareous substance with only traces of a horny matrix. The internodes are quite rigid, the nodes however give a certain degree of flexibility to the colony as a whole. Neither the nodes nor the internodes are penetrated by nutritive canals, but when dried the nodes are porous.

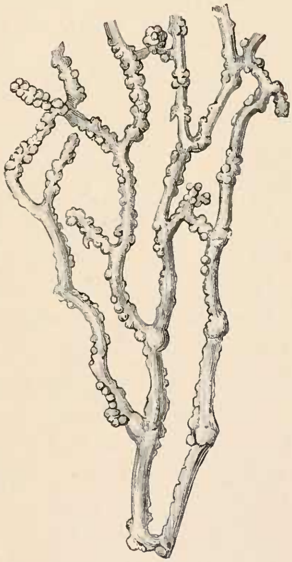

Fig. 155.—*Melitodes dichotoma*, showing the swollen nodes and the internodes.

The principal genera are:—*Melitodes*, Verrill; widely distributed in the Indian and Pacific Oceans, Cape of Good Hope, etc. This genus is in some localities extremely abundant and exhibits great brilliancy and variety of colour. The branching is usually dichotomous at the nodes. *Wrightella*, Gray. This is a delicate dwarf form from Mauritius and the coast of South Africa. *Parisis*, Verrill; Pacific Ocean from Formosa to Australia but not very common. One species from Mauritius. The branches arise from the internodes.

[1] S. J. Hickson, *Fauna and Geog. Maldive Archip.* ii. pt. i. 1903, p. 495.

Fam. 4. Coralliidae.—The axis is formed by the fusion of spicules into a dense, solid, inflexible, calcareous core.

Corallium, Lamarck. *Corallium nobile*, Pallas, the "precious coral," occurs in the Mediterranean, chiefly off the coast of North Africa, but also on the coasts of Italy, Corsica, Sardinia, and it extends to the Cape Verde Islands in the Atlantic Ocean. *C. japonicum*, Kishinouye, called Akasango by the fishermen, occurs off the coast of Japan, and *C. reginae*, Hickson, has recently been described from deep water off the coast of Timor.[1] The genus *Pleurocorallium*, Gray, is regarded by some authors as distinct, but the characters that are supposed to distinguish it, namely, the presence of peculiar "opera-glass-shaped spicules," and the occurrence of the verrucae on one side of the branches only, are not very satisfactory, The following species are therefore placed by Kishinouye[2] in the genus *Corallium*:—*C. elatius*, Ridley (Momoirosango); *C. konojoi*, Kishinouye (Shirosango); *C. boshuensis*, K.; *C. sulcatum*, K.; *C. inutile*, K.; and *C. pusillum*, K.,—all from the coast of Japan. Of the coral obtained from these species, the best kinds of Momoirosango vary in price from £30 per pound downwards according to the quality. The Shirosango is the least valuable of the kinds that are brought into the market, and is rarely exported.[3] Three species of *Corallium* (*Pleurocorallium*) have been described from Madeira,[4] and one of these, *C. johnsoni*, has recently been found in 388 fathoms off the coast of Ireland.[5] Other species are *C. stylasteroides*, from Mauritius; *C. confusum*, Moroff,[6] from Sagami Bay in Japan: and an undescribed species obtained by the "Siboga," off Djilolo. These corals range from shallow water to depths of 300-500 fathoms. *Pleurocoralloides*, Moroff, differs from the others in having very prominent verrucae and in the character of the large spindle-shaped and scale-like spicules. It was found in Sagami Bay, Japan. Specimens attributed to the genus *Pleurocorallium* have been found fossil in the white chalk of France, but *Corallium* has been found only in the tertiaries.[7]

[1] Hickson, *K. Akad. Wet. Amsterdam*, 1905.

[2] *Journ. Imp. Fish. Bureau*, Tokyo, xiv. 1, 1904.

[3] Kitahara, *Journ. Imp. Fish. Bureau*, Tokyo, xiii. 3, 1904.

[4] Johnson, *Proc. Zool. Soc.* 1899, p. 57.

[5] Hickson, *Nature*, lxxiii. 1905, p. 5.

[6] Moroff, *Zool. Jahrb. Syst.* xvii. 1902, p. 404.

[7] Ridley, *Proc. Zool. Soc.* 1882, p. 231.

Sub-Order 2. Axifera.

The axis in this sub-order may be horny, or horny with a core of calcium carbonate, or composed of horn impregnated with calcium carbonate, or of nodes of horn alternating with internodes of calcium carbonate. It may be distinguished from the axis of the Pseudaxonia by the fact that in no case have definite spicules been observed to take part in its formation. It has been suggested that as the Axifera represent a line of descent distinct from that of the Pseudaxonia they should be placed in a separate order. Apart from the character of the axis, however, the two sub-orders show so many affinities in their general anatomy that it is better to regard the two lines of descent as united within the Gorgonacean limit. It is very improbable that the two groups sprang independently from a stoloniferous ancestor.

Fam. 1. Isidae.—This family includes all those Axifera in which the axis is composed of alternate nodes of horn and internodes of calcareous substance.

There can be little doubt of the close affinities of many of the genera of this family with the Melitodidae among the Pseudaxonia. In both the coenenchym is thin and the coelenteric cavities short. No important differences have been observed between the structure of the zooids of the two families, and now that we know that the "nutritive canals" of *Melitodes* do not perforate the nodes there is no important difference left between the coenosarcal canal systems. The structure and method of calcification of the internodes of the two families are very similar. The main difference between them is that the nodes of the Isidae are purely horny, whereas in the Melitodidae the horny substance of the nodes contains calcareous spicules.

The principal genera are:—*Isis,* Linnaeus; Pacific Ocean. This genus forms substantial fan-shaped colonies with, relatively, a thick coenenchym, short stout internodes and black horny nodes. *Mopsea,* Lamouroux; Coast of Australia. The verrucae are club-shaped and are arranged in spiral rows round the stem. *Acanella,* Gray; principally found in deep water in the Atlantic Ocean but also in the Pacific. The internodes are long and the branches arise from the nodes. Most of the species occur in deep water, some in very deep water (*A. simplex,* 1600 to 1700 fathoms). In this and the following genera the coenenchym is thin and the zooids imperfectly or not retractile. *Ceratoisis*, Wright; Atlantic Ocean, extending from shallow to deep water. The branches arise from the nodes. *Chelidonisis*, Studer; deep water off the Azores. *Isidella*, Gray; Mediterranean Sea. *Bathygorgia*, Wright; off Yokohama, 2300 fathoms. This genus is unbranched, with very long internodes and short nodes. The zooids are arranged on one side only of the stem.

Fam. 2. Primnoidae.—This is a well-marked family. The axis of the colonies is horny and calcareous. The coenenchym and the non-retractile zooids are protected by scale-like spicules, which usually overlap and form a complete armour for the protection of the soft parts. On the aboral side of the base of each tentacle there is a specialised scale, and these fit together, when the tentacles are folded over the peristome, to form an operculum.

The principal genera are:—*Primnoa*, Lamouroux; Atlantic Ocean, occurring also in the Norwegian fjords. This genus is usually found in moderately deep water, 100 to 500 fathoms. *Primnoella*, Gray. This genus seems to be confined to the temperate seas of the southern hemisphere. It is unbranched. The zooids are arranged in whorls round the long whip-like stem. *Plumarella*, Gray; southern hemisphere, in moderately deep water. This is branched pinnately in one plane. The zooids are small and arise at considerable intervals alternately on the sides of the branches. *Stenella*, Gray; widely distributed in deep water. The zooids are large and are arranged in whorls of three situated at considerable distances apart. *Stachyodes*, W. and S.; Fiji, Kermadecs, Azores, in deep water. Colony feebly branched. Zooids in regular whorls of five. Other genera belonging to this group of Primnoidae are *Thouarella*, Gray, and *Amphilaphis*, Antarctic seas.

The following genera are placed in separate sub-families:—*Callozostron*, Wright; Antarctic Sea, 1670 fathoms. The axis is procumbent and the zooids are thickly set in rows on its upper surface. The zooids are protected by large imbricate scales, of which those of the last row are continued into long spine-like processes. *Calyptrophora*, Gray; Pacific Ocean, in deep water. The base of the zooids is protected by two remarkably large scales. *Primnoides*, W. and S.; Southern Ocean. The opercular scales are not distinctly differentiated and the calyx is therefore imperfectly protected.

Fam. 3. Chrysogorgiidae.[1]—The axis in this family is composed of a horny fibrous substance with interstratified calcareous particles, and it springs from a calcareous plate, which sometimes gives off root-like processes. It may be unbranched or branched in such a way that the branches of the second, third, and subsequent orders assume in turn the direction of the base of the main axis. The axis is frequently of a metallic iridescent appearance. The zooids usually arise in a single straight or spiral row on the branches, and are not retractile. The coenenchym is thin. The spicules vary considerably, but in a very large proportion of the species they are thin, oval, or hour-glass plates (Fig. 149, 10, p. 336).

By some authors this family is considered to be the simplest and most primitive of the Axifera; but the delicate character of the axis of the main stem and branches, the thinness of the coenenchym, the position of the zooids on one side of the branches only, and the tenuity of the calcareous spicules may be all accounted not as primitive characters, but as special adaptations to the life in the slow uniform currents of deep water.

The principal genera are:—*Lepidogorgia*, Verrill; Atlantic and Pacific Oceans, 300 to 1600 fathoms. Axis unbranched. Zooids large and arranged in a single row. *Trichogorgia*, Hickson; Cape of Good Hope, 56 fathoms. Colony branching in one plane. Zooids numerous and on all sides of the branches. *Chrysogorgia*, D. and M.; deep water. Axis branched. Spicules on the zooids always large. *Metallogorgia*, Versluys; Atlantic Ocean, 400 to 900 fathoms. Basal part of the stem unbranched (monopodial). *Iridogorgia*, Verrill. Spiral stem and branches. *Pleurogorgia*, Versluys. Axis branched in one plane. Coenenchym thick. *Riisea*, D. and M. Monopodial stem and thick coenenchym.

Fam 4. Muriceidae.—This is a large family, exhibiting very great variety of habit. The spicules are often very spiny, and project beyond the surface of the ectoderm, giving the colony a rough appearance. A great number of genera have been described, but none of them are very well known. The family requires careful revision.

The more important genera are:—*Acanthogorgia*, Gray; principally in deep water in the Atlantic Ocean. The calices are

[1] For a revision of this family, see Versluys, *Siboga Expeditie*, xii. 1902.

large, cylindrical, and spiny. *Villogorgia*, D. and M.; widely distributed. Delicate, graceful forms, with thin coenenchym. *Echinomuricea*, Verrill; *Muricea*, Lamouroux; *Paramuricea*, Köll; *Acamptogorgia*, W. and S.; *Bebryce*, Philippi.

Fam. 5. Plexauridae.—In this family we find some of the largest and most substantial Gorgonids. The axis is usually black, but its horny substance may be impregnated with lime, particularly at the base. The coenenchym is thick, and the zooids are usually completely retractile, and the surface smooth. The species of the family are principally found in shallow water in warm or tropical regions.

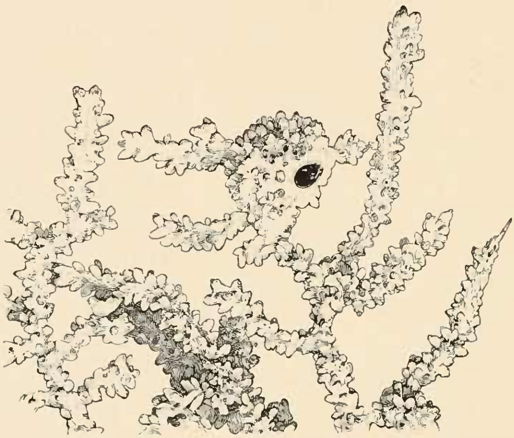

FIG. 156.—*Eunicella cavolini*. Some branches of a large dried specimen, showing a gall formed by a Cirripede.

The principal genera are:—*Eunicea*, Lamouroux. The calices are prominent, and not retractile. *Plexaura*, Lamouroux; *Euplexaura*, Verrill. *Eunicella*, Verrill. With an outer layer of peculiar torch-shaped spicules. The only British species of this order is *Eunicella cavolini* (formerly called *Gorgonia verrucosa*). It is found in depths of 10 to 20 fathoms off the coast of the English Channel and west of Scotland. Occasionally specimens are found in which a gall-like malformation with a circular aperture is seen, containing a Barnacle. Such gall formations, common enough in some species of Madreporaria, are rarely found in Alcyonaria.

Fam. 6. Gorgoniidae.—This family contains some of the commonest and best-known genera of the order. They usually form large flexible branched colonies with delicate horny axes and thin coenenchym. The zooids are usually completely retractile.

The principal genera are:—*Gorgonia*, Linn. This genus includes *Gorgonia* (*Rhipidogorgia*) *flabellum*, the well-known fan Gorgonia with intimately anastomosing branches, from the warm waters of the Atlantic Ocean. The genera *Eugorgia*, Verrill, and *Leptogorgia*, Milne Edwards, differ from *Gorgonia* in the character of the spicules. In *Xiphigorgia*, Milne Edwards, from the West Indies, the branches are much compressed, forming at the edges wing-like ridges, which bear the zoopores in rows. *Malacogorgia*, Hickson, has no spicules. Cape of Good Hope.

Fam. 7. Gorgonellidae.—In this family the horny axis is impregnated with lime. The surface of the coenenchym is usually smooth, and the spicules small. The colonies are sometimes unbranched (*Juncella*). In the branching forms the axis of the terminal branches is often very fine and thread-like in dimensions.

The principal genera are:—*Gorgonella*, with a ramified flabelliform axis; *Ctenocella*, with a peculiar double-comb manner of branching; and *Juncella*, which forms very long unbranched or slightly branched colonies, with club-shaped spicules. All these genera are found in shallow water in the tropical or semi-tropical regions of the world. *Verrucella* is a genus with delicate anastomosing branches found principally in the shallow tropical waters of the Atlantic shores. Like many of the Gorgonacea, with branches disposed in one plane (flabelliform) *Verrucella* frequently carries a considerable number of epizoic Brittle stars, which wind their flexible arms round the branches, and thus obtain a firm attachment to their host. There is no reason to suppose that these Brittle stars are in any sense parasitic, as a specimen that bears many such forms shows no sign of injury or degeneration, and it is possible they may even be of service to

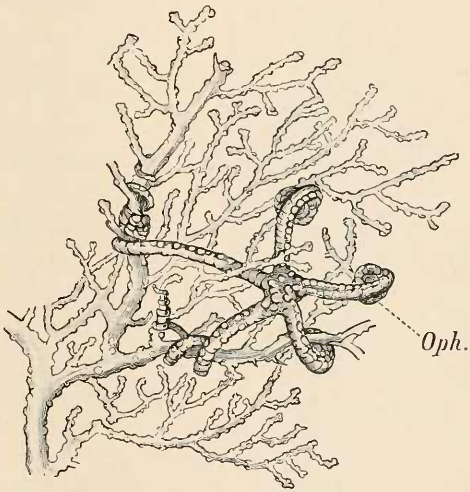

FIG. 157.—*Verrucella guadaloupensis*, with an epizoic Brittle star (*Oph.*) of similar colour.

the *Verrucella* by preying upon other organisms that might be injurious. An interesting feature of the association is that the Brittle stars are of the same colour as the host, and the knob-like plates on their aboral surface have a close resemblance to the verrucae (Fig. 157).

Order V. Pennatulacea.

The Sea-pens form a very distinct order of the Alcyonaria. They are the only Alcyonarians that are not strictly sedentary in habit, that are capable of independent movement as a whole, and exhibit a bilateral symmetry of the colony. No genera have yet been discovered that can be regarded as connecting links between the Pennatulacea and the other orders of the Alcyonaria. Their position, therefore, is an isolated one, and their relationships obscure.

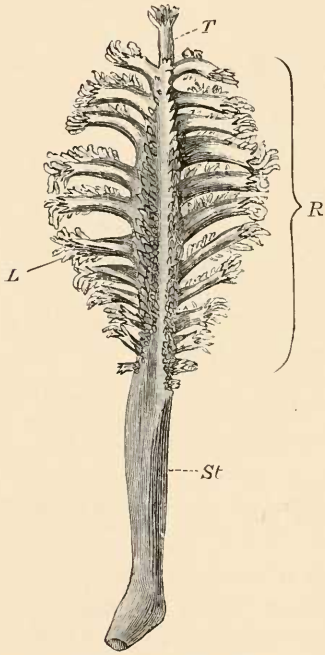

Fig. 158.—Diagram of a Sea-pen. *L*, leaves composed of a row of autozooids; *R*, rachis; *St*, stalk; *T*, anthocodia of the axial zooid, usually suppressed. (After Jungersen.)

The peculiarities of the order are due to the great growth and modification in structure of the first formed zooid of the colony. This zooid (Oozooid, Hauptpolyp, or Axial zooid) increases greatly in length, develops very thick fleshy walls, usually loses its tentacles, digestive organs, and frequently its mouth, exhibits profound modification of its system of mesenteries, and in other ways becomes adapted to its function of supporting the whole colony.

The axial zooid shows from an early stage of development a division into two regions: a distal region which produces by gemmation on the body-wall numerous secondary zooids, and becomes the rachis of the colony; and a proximal region which becomes the stalk or peduncle, and does not produce buds (Fig. 158). The secondary zooids are of two kinds:

the autozooids and the siphonozooids. The former have the ordinary characters of an Alcyonarian zooid, and produce sexual cells; the latter have no tentacles, a reduced mesenteric system, and a stomodaeum provided with a very wide siphonoglyph.

The arrangement of the autozooids and siphonozooids upon the axial zooid is subject to great modifications, and affords the principal character for the classification of the order. In the Pennatuleae the autozooids are arranged in two bilaterally disposed rows on the rachis, forming the leaves or pinnae of the colony (Fig. 158). The number in each leaf increases during the growth of the colony by the addition of new zooids in regular succession from the dorsal to the ventral side of the rachis[1] (Fig. 159). In other Pennatulacea the autozooids are arranged in rows which do not unite to form leaves (*Funiculina*), in a tuft at the extremity of a long peduncle (*Umbellula*), scattered on the dorsal side of the rachis (*Renilla*, Fig. 160), or scattered on all sides of the rachis (*Cavernularia*, Fig. 161). In those forms in which the autozooids are scattered the bilateral symmetry of the colony as a whole becomes obscured. The siphonozooids may be found on the leaves (*Pteroeides*), but more frequently between the leaves or rows of autozooids, or scattered irregularly among the autozooids. Usually the siphonozooids are of one kind only, but in *Pennatula murrayi* there is one specially modified siphonozooid at the base of each leaf,[2] which appears to have some special but unknown function.

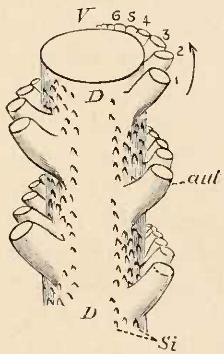

Fig. 159.—Diagram of a portion of a rachis of a Sea-pen. *aut*, The rows of autozooids; 1-6, the order of age of the autozooids composing a leaf; *D*, the dorsal side of the rachis; *Si*, the siphonozooids; *V*, the ventral side of the rachis. (After Jungersen.)

In *Umbellula gracilis* each siphonozooid bears a single pinnate tentacle, and in some other species of the same genus there is a tentacle which is not pinnate.[3]

[1] Jungersen (*Danish Ingolf Expedition*, Pennatulida, 1904) has shown that this is the correct nomenclature of the regions of the rachis. Nearly all other authors describe the dorsal side as ventral and the ventral as dorsal.

[2] S. J. Hickson, *Report British Association* (Southport Meeting), 1903, p. 688.

[3] Marshall, *Trans. Roy. Soc. Edinb.* xxxii. 1883, p. 143.

The zooids and coenenchym are usually protected by a crust of coloured or colourless, long, smooth, needle-like, calcareous spicules, situated principally in the superficial layer, so as to leave the subjacent tissues soft and spongy in texture. In some cases the spicules are smooth double clubs, rods, discs, or irregular granules, and in *Sarcophyllum*, *Chunella*, some species of *Umbellula* and others, there is no calcareous skeleton. The tuberculated spindles, so common in other Alcyonaria, are not found in any species. In most genera a horny, or calcified horny rod is embedded in the central part of the axial polyp, serving as a backbone or support for its muscles. It is absent, however, in *Renilla*, and reduced or absent in *Cavernularia*.

The sexual organs are borne by the mesenteries of the autozooids only, and each colony is either male or female. There is no record of hermaphroditism in the order. The eggs contain a considerable amount of yolk, and fertilisation is effected in the sea-water after their discharge. The segmentation is irregular, and the free-swimming ciliated larva (of *Renilla*) shows the rudiments of the first buds from the axial polyp before it settles down in the mud.

The Sea-pens are usually found on muddy or sandy sea-bottoms, from a depth of a few fathoms to the greatest depths of the ocean. It is generally assumed that their normal position is one with the peduncle embedded in the mud and the rachis erect. Positive evidence of this was given by Rumphius, writing in 1741, in the case of *Virgularia rumphii* and *V. juncea* at Amboina,[1] and by Darwin in the case of *Stylatula darwinii* at Bahia Blanca.[2]

"At low water," writes Darwin, "hundreds of these zoophytes might be seen projecting like stubble, with the truncate end upwards, a few inches above the surface of the muddy sand. When touched or pulled they suddenly drew themselves in with force so as nearly or quite to disappear."

It is not known whether the Pennatulids have the power of moving from place to place when the local conditions become unfavourable. It is quite probable that they have this power, but the accounts given of the Sea-pens lying flat on the sand do not appear to be founded on direct observation. The fable of

[1] Rumphius, *Amboinsche Rariteitkamer*, 1741, p. 64.
[2] Darwin, *Naturalist's Voyage round the World*, 1845, p. 99.

Pennatula swimming freely "with all its delicate transparent polypi expanded, and emitting their usual brilliant phosphorescent light, sailing through the still and dark abyss by the regular and synchronous pulsations of the minute fringed arms of the whole polypi," appears to be based on a statement made by Bohadsch in 1761, and picturesque though it be, is undoubtedly erroneous.

The brilliant phosphorescence of many species of Pennatulacea has been observed by many naturalists, and it is very probable that they all exhibit this property to some degree. The phosphorescence appears to be emitted by the mesenteric filaments of the autozooids, but it is not yet determined whether the phenomenon is confined to these organs or is more generally distributed.

The Pennatulacea are usually devoid of epizoites, but occasionally the parasitic or semi-parasitic Entomostracan *Lamippe* is found in the zooids. A small crab is also frequently found between the large leaves of species of *Pteroeides*. The most remarkable case of symbiosis, however, has recently been observed in the form of an encrusting Gymnoblastic Hydroid[1] living on the free edge of the leaves of a species of *Ptilosarcus*.

The order Pennatulacea is divided into four sections.

Sect. 1. Pennatuleae.—In this section the colony is distinctly bilaterally symmetrical, and the autozooids are arranged in rows with their body-walls fused to form leaves.

The genus *Pteroeides*, the representative genus of the family **Pteroeididae,** is a fleshy Sea-pen found in shallow sea water in the warm waters of the Pacific Ocean and in the Mediterranean. It has large leaves with long spiny, projecting spicules, and the siphonozooids are borne by the leaves. *Pennatula*, the representative genus of the family **Pennatulidae,** has a wider distribution in area and in depth. *Pennatula phosphorea* is a common British species, found in depths of 10 to 20 fathoms in many localities off our coasts. It is about 5 inches in length. There are several varieties of this species distributed in Atlantic waters. *Pennatula grandis* is a magnificent species found in Norwegian fjords, in the Faeroe Channel, and off the northern coasts of N. America, in depths of from 50 to 1255 fathoms. Specimens have been

[1] To be described in the forthcoming Report on the Pennatulidae of the "Siboga" Expedition.

obtained no less than $2\frac{1}{2}$ feet in length. *P. murrayi* and *P. naresi* are species of the genus found at depths of a few hundred fathoms in tropical seas.

The genus *Virgularia*, belonging to the family **Virgulariidae,** is represented in the British seas by *V. mirabilis*, a long slender Sea-pen found in many localities off the Scottish coasts.

Sect. 2. Spicatae.—This section includes those Sea-pens in which the autozooids are arranged bilaterally on the axial zooid in rows or more irregularly, but do not unite to form leaves. It is a large section and contains many widely divergent genera.

The family **Funiculinidae** is represented on our coasts by *Funiculina quadrangularis*, a long and slender Sea-pen 2 to 3 feet in length. The autozooids are arranged in oblique rows, and the siphonozooids are on the ventral side of the rachis. There is one point of special interest in this genus. The siphonozooids appear to change as the colony grows and to become autozooids. If this is the case it may be more correct to describe the genus as devoid of true siphonozooids.

The family **Anthoptilidae** contains the species *Anthoptilum grandiflorum*, which has a wide distribution in depths of 130 to 500 fathoms in the N. and S. Atlantic Ocean. It is perhaps the largest of all the Pennatulacea, specimens having been obtained from the Cape of Good Hope over 4 feet long with expanded autozooids, each more than half an inch in length.

The family **Kophobelemnonidae** contains a number of forms with remarkably large autozooids arranged in irregular rows on the two sides of the rachis. The siphonozooids are numerous and scattered, and their position is indicated by small papilliform calices on the coenenchym. The surface of these pens is usually rough, owing to the presence of numerous coarse projecting spicules. *Kophobelemnon* occurs in the Mediterranean in deep water, off the coasts of Ireland and Scotland, and in other regions.

The family **Umbellulidae** contains some of the most remarkable and interesting examples of the deep-sea fauna. The peduncle is very long and the rachis stunted and expanded. The autozooids are of great size, non-retractile, and arranged in a cluster or rosette on the terminal rachis. There is a wide structural range between the species. Some species have numerous large spicules, others have none. In some species the siphonozooids have a single pinnate or digitate tentacle, in others the siphonozooids are of the usual type. *Umbellula* appears to be a somewhat rare but cosmopolitan genus in deep water, extending from the Arctic to the Antarctic region in water ranging from 200 to 2500 fathoms.

The interesting genus *Chunella* was discovered by the German "Valdivia" Expedition at a depth of about 420 fathoms off the coast of E. Africa, and subsequently by the Dutch "Siboga" Expedition at a depth of about 500 fathoms in the Malay Archipelago. According to Kükenthal,[1] this genus with another closely allied genus *Amphianthus* should form a new section of Pennatulacea, the **Verticilladeae**. *Chunella* has a long and very delicate rachis and peduncle, and the former terminates in a single autozooid and has five or six whorls of three autozooids, situated at considerable distances from one another. Spicules are absent. The full description of this genus has not yet been published, but it is clear that it occupies a very isolated position in the order.

Sect. 3. Renilleae.—This section contains a single family **Renillidae** and a single genus *Renilla* (Fig. 160). The rachis

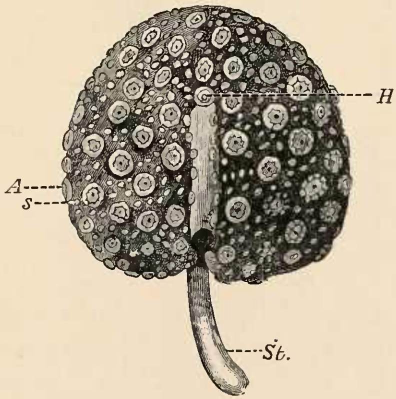

FIG. 160.—*Renilla reniformis*, a small specimen (34 mm.), showing the dorsal side of the expanded rachis. *A*, autozooid; *H*, the mouth of the axial zooid; *s*, siphonozooid; *St*, the short stalk. (After Kölliker.)

is expanded into a flattened cordate form set at an angle to the peduncle, and the zooids are confined to the dorsal surface, which is uppermost in the natural position of the colony. The peduncle is short and does not contain an axial skeleton. The colour of

[1] *Zool. Anz.* xxv. 1902, p. 302.

this Sea-pen is usually violet when dried or preserved. Specimens of *Renilla* are very abundant in shallow water in some localities on the Atlantic and Pacific coasts of N. America, but the genus has also been obtained from the Red Sea and the coast of Australia. A popular name for this genus is "Sea pansy."

Sect. 4. Veretilleae.—This section contains a number of genera in which the bilateral arrangement of the zooids is obscured by their gradual encroachment on the dorsal side of the axial polyp. The rachis and peduncle are thick and fleshy, and the autozooids and

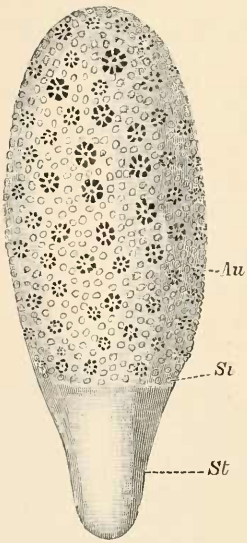

FIG. 161.—*Cavernularia obesa.* *Au*, autozooid; *Si*, siphonozooid; *St*, stalk. (After Kölliker.)

siphonozooids are irregularly distributed all round the rachis. The genus *Cavernularia* is not uncommonly found in moderate depths of water in the Indian and Pacific Ocean, and is distinguished from the other genera by the reduction of the skeletal axis. Other genera are *Veretillum*, Mediterranean and Atlantic Ocean, and *Lituaria*, Indian Ocean.

CHAPTER XIV

ANTHOZOA (*CONTINUED*): ZOANTHARIA

Sub-Class II. Zoantharia.

The Zoantharia exhibit a great deal more diversity of form and structure than the Alcyonaria. The sub-class is consequently difficult to define in a few words, and it may be taken to include all the Anthozoa which do not possess the typical Alcyonarian characters.

All the orders, with the exception of the Antipathidea and Zoanthidea, contain genera of solitary zooids, and the orders Edwardsiidea and Cerianthidea contain no genera that form colonies. In the Madreporaria, Zoanthidea, and Antipathidea, on the other hand, colonies are formed composed of a very large number of individuals which frequently attain to a very great size. The term "Sea-anemone" is commonly used in writing about the solitary Zoantharia which do not form any skeletal structures, and the term "Coral" is applied to all those Zoantharia which do form a skeleton.

In a scientific treatise, however, these popular terms can no longer be satisfactorily employed. The "Sea-anemones" exhibit so many important differences in anatomical structure that they must be placed in at least three distinct orders that are not closely related, and the organisms to which the term Coral has been applied belong to so many organisms—such as Alcyonaria, Hydrozoa, Polyzoa, and even Algae—that its use has become indeterminate.

Whilst these terms must disappear from the systematic part of Zoology, they may still be employed, however, in the description of a local fauna or coral reef to signify the soft solitary zooids on the one hand, and the organisms, animals or plants, which form large, massive skeletons of carbonate of lime, on the other.

The form of the solitary zooids and of the colony of zooids in the Zoantharia, then, may be very divergent. In the Actiniaria we find single soft gelatinous zooids of considerable size adherent to rocks or half-buried in the sand. Among the Madreporaria we find great branching colonies of thousands of zooids supported by the copious skeleton of carbonate of lime that they have secreted. Among the Antipathidea, again, we find a dendritic skeleton of a dark horny substance, formed by a colony of small zooids that cover it like a thin bark. The majority of the Zoantharia are, like other zoophytes, permanently fixed to the floor of the ocean. Where the embryo settles, there must the adult or colony of adults remain until death. Some of the common Sea-anemones can, however, glide slowly over the surface on which they rest, and thus change their position according to the conditions of their surroundings. Others (the Minyadidae) float upside down in the sea, and are carried hither and thither by the currents. Others, again (*Cerianthus*, *Edwardsia*, *Peachia*), burrow in the sand or mud at the sea-bottom.

The structure of the zooid varies considerably, but in the following characters differs from the zooid of the Alcyonaria. The **tentacles** are usually simple finger-like processes, and when they bear secondary pinnae these can readily be distinguished from the rows of secondary pinnules of the Alcyonarian tentacle. The number of tentacles is very rarely eight (young *Halcampa*), and in these cases they are not pinnate. The number of tentacles may be six (many Antipathidea and some zooids of *Madrepora*), twelve (*Madrepora*), some multiple of six, or an indefinite number. In the Thalassianthidae and some other families of Actiniaria the tentacles are plumose, but do not exhibit the regular pinnate form of the tentacles of Alcyonaria.

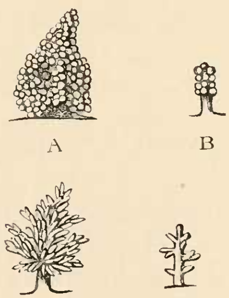

Fig. 162.—Large (A) and small (B) plumose tentacles of *Actinodendron plumosum*. Large (C) and small (D) plumose tentacles of *A. glomeratum*. (After Haddon.)

As regards the number of **mesenteries**, the Zoantharia exhibit very great variety. It has been shown that there is frequently a stage in their development during which there are only eight mesenteries. This stage is usually called the *Edwardsia* stage. These eight mesenteries are arranged in bilateral pairs as follows:—One pair is attached to the body-wall and reaches to the dorsal side of the stomodaeum, and is called the pair of dorsal directives; a corresponding pair attached to the ventral side of the stomodaeum is called the pair of ventral directives. The other two pairs are the lateral mesenteries. To these four pairs are added, at the close of the *Edwardsia* stage, two additional pairs, making in all twelve mesenteries (cf. Fig. 163).

These six primary pairs of mesenteries, conveniently called the "protocnemes" by Duerden, may be traced in the development and recognised in the adult of the majority of Zoantharia. But the number of the mesenteries is usually increased in the later stages by the addition of other mesenteries called the "metacnemes." The metacnemes differ from the protocnemes in that they usually appear in unilateral pairs, that is to say, in pairs of which both members arise on the same side of the stomodaeum, and the number is very variable throughout the group. The space enclosed by a pair of mesenteries is called an "entocoele," and the space between two pairs of mesenteries is called an "ectocoele."

The twelve protocnemes are usually complete mesenteries, that is to say, they extend the whole distance from the body-wall to the stomodaeum, while the metacnemes may be complete or incomplete; in the latter case extending only a part of the distance from the body-wall towards the stomodaeum.

We find, therefore, in making a general survey of the anatomy of the Zoantharia that there is no general statement to be made, concerning the number or arrangement of the mesenteries, which holds good for the whole or even for a considerable portion of the genera.

The bands of retractor muscles are, as in the Alcyonaria, situated on one face only of the mesenteries (except in the Antipathidea and Cerianthidea), but an important character of the Zoantharia is that the muscle bands on the ventral pair of directives are situated on the dorsal faces of these mesenteries, and not on the ventral faces as they are in Alcyonaria.

In the Edwardsiidea there are only eight complete mesenteries, but a variable number of other rudimentary and incomplete mesenteries have recently been discovered by Faurot.[1] In the Zoanthidea the mesenteries are numerous, but the order is remarkable for the fact that the dorsal directives are incomplete, and that, of the pairs of metacnemes that are added, one mesentery becomes complete and the other remains incomplete. In most of the genera of the Antipathidea there are only ten mesenteries, but in *Leiopathes* there are twelve, and as they bear no bands

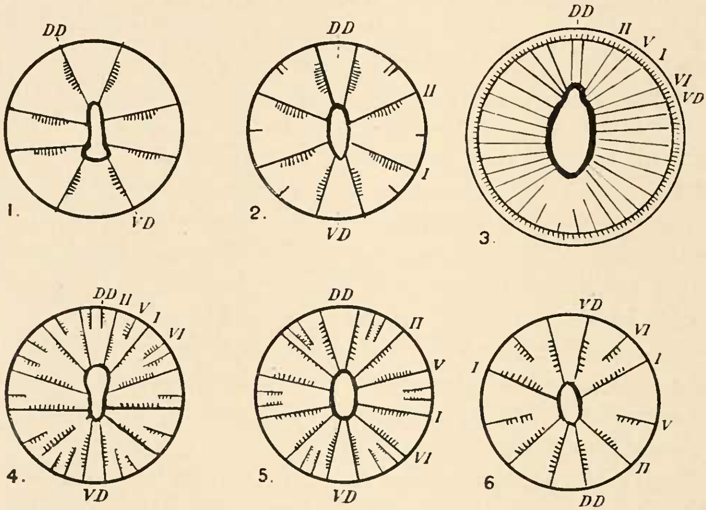

FIG. 163.—Diagrams of transverse sections of 1, Alcyonarian ; 2, *Edwardsia* ; 3, *Cerianthus* ; 4, *Zoanthus* ; 5, *Faria* ; 6, *Madrepora*. *DD*, the dorsal directive mesenteries ; *VD*, the ventral directives ; *I-VI*, the protocnemes in order of sequence.

of retractor muscles it is difficult to determine accurately their true relation to the mesenteries of other Zoantharia.

In the Cerianthidea the mesenteries are very numerous, and increase in numbers by the addition of single mesenteries alternately right and left in the ventral inter-mesenteric chamber throughout the life of the individual. These mesenteries do not bear retractor muscles.

In the Actiniaria and Madreporaria, with the exception of the genera *Madrepora*, *Porites*, and a few others, there are also very many mesenteries. The two pairs of directives are usually present, but they may not occur in those zooids that are produced

[1] Faurot, *Arch. Zool. Expér.* 3rd ser. iii. 1895, p. 71.

asexually by fission (see p. 388). The metacnemes are frequently formed in regular cycles, and in many genera appear to be constantly some multiple of six (Fig. 163, 5).

In *Madrepora* and *Porites*[1] the two pairs of directives and two pairs of lateral protocnemes are complete; the other two pairs of protocnemes are, however, incomplete; and metacnemes are not developed (Fig. 163, 6).

The stomodaeum is usually a flattened tube extending some distance into the coelenteric cavity and giving support to the inner edges of the complete mesenteries; in many of the Madreporaria, however, it is oval or circular in outline. In most of the Actiniaria there are deep grooves on the dorsal and ventral sides of the stomodaeum, but in Zoanthidea the groove occurs on the ventral side only and in the Ceriantlidea on the dorsal side only. In the Madreporaria these grooves do not occur or are relatively inconspicuous.[2] In the Alcyonaria the siphonoglyph exhibits a very marked differentiation of the epithelium (see Fig. 148, p. 334), and the cilia it bears are very long and powerful. It has not been shown that the grooves in the Zoantharia show similar modifications of structure, and they are called by the writers on Zoantharia the sulci. There is no difference in structure, and rarely any difference in size, between the dorsal sulcus and the ventral sulcus in the Actiniaria, and the use of the word—sulculus—for the former is not to be commended.

The mesenteries bear upon their free edges the mesenteric filaments. These organs are usually more complicated in structure than the corresponding organs of the Alcyonaria, and the dorsal pair of filaments is not specialised for respiratory purposes as it is in that group.

In many genera the mesenteric filaments bear long, thread-like processes—the "acontia"—armed with gland cells and nematocysts which can be protruded from the mouth or pushed through special holes (the "cinclides") in the body-wall.

The gonads in the Zoantharia are borne upon the sides of the mesenteries and are usually in the form of long lobed ridges instead of being spherical in form, and situated at the edges of the mesenteries as they are in the Alcyonaria.

[1] Duerden, *Mem. Acad. Washington*, 3rd Ser. viii. 1902.

[2] Duerden, *l.c.* p. 436.

Nearly all the zooids and even the colonies of the Zoantharia are unisexual, but some species, such as *Manicina areolata* (Wilson), *Meandrina labyrinthica* (Duerden), *Cerianthus membranaceus*, and others, are hermaphrodite. Mr. J. S. Gardiner has recently given reasons for believing that the genus *Flabellum* is protandrous.

Skeleton.—The soft tissues of the Zoantharian zooids may be supported or protected by hard skeletal structures of various kinds. In the Zoanthidea and the Actiniaria there are many species that have no skeletal support at all, and are quite naked. These seem to be sufficiently well protected from the attacks of carnivorous animals by the numerous nematocysts of the ectoderm, and perhaps in addition by a disagreeable flavour in their tissues. Anemones do not seem to be eaten habitually by any fish, but cases have been described of *Peachia hastata* being found in the stomach of the Cod, and of *Edwardsia* in the stomach of the Flounder.[1] On the Scottish coasts Anemones are occasionally used with success as a bait for cod.[2] The body-wall of *Edwardsia*, however, is protected to a certain extent by the secretion of a mucous coat in which grains of sand and mud are embedded. Some Anemones, such as *Urticina*, *Peachia*, and others, lie half-buried in the sand, and others form a cuticle, like that of *Edwardsia*, to which foreign bodies are attached.

Cerianthus is remarkable for constructing a long tube composed of a felt-work of discharged nematocysts mixed with mud and mucus, into which it retires for protection. In the Zoanthidea the body-wall is frequently strengthened by numerous and relatively large grains of sand, which are passed through the ectoderm to lie in the thick mesogloea.

In the Madreporaria a very elaborate skeleton of carbonate of lime is formed. In the solitary forms it consists of a cup-shaped outer covering for the base and column of the zooid called the "theca," of a series of radial vertical walls or "septa" projecting into the intermesenteric chambers carrying the endodermal lining of the coelenteric cavity with them, and in some cases a pillar, the "columella," or a series of smaller pillars, the "pali" projecting upwards from the centre of the base of the

[1] M'Intosh, "The Marine Invertebrates and Fishes of St. Andrews," 1875, pp. 37, 38.

[2] M'Intosh, "The Resources of the Sea," 1899, pp. 10, 129.

theca towards the stomodaeum. In the colonial forms the theca of the individual zooids is continuous with a common colonial skeleton called the "coenosteum." This is solid in the Imperforate corals, and it supports at the surface only a thin lamina of canals and superficial ectoderm. In the Perforate corals, however, the coenosteum envelopes and surrounds the canals during its formation, and thereby remains perforated by a network of fine channels. In the colonial Madreporaria the skeletal cups which support and protect the zooids are called the "calices."

The skeleton of the Antipathidea is of a different nature. It is composed of a horny substance allied to keratin. When it is old and thick, it usually has a polished black appearance, and is commonly termed "black coral." The surface of this kind of coral is ornamented with thorny or spiny projections, but it is never perforated by calices or canal systems. It forms a solid axis for the branches of the corals, and all the soft parts of the zooids and coenosarc are superficial to it.

It was formerly considered that this type of coral, which shows no trace of the shape and form of the living organisms that produce it, is of a different character to the calcareous skeleton which exhibits calices, septa, pores, and other evidence of the living organism, and it was called a "sclerobase" to distinguish it from the "sclerodерm" of the Madreporaria.

It is now known that both the sclerobasic skeleton and the sclerodermic skeleton are products of the ectoderm, and consequently these expressions are no longer in general use.

Asexual reproduction in the Zoantharia may be effected by continuous or discontinuous fission or gemmation.

In the Edwardsiidea, Actiniaria, and Ceriantbidea, that is to say in the animals popularly known as Sea-anemones, asexual reproduction does not commonly occur, but nevertheless a good many instances of it are now known in individual genera. In *Actinoloba* (*Metridium*), for example, Parker has described a case of complete longitudinal fission, and Duerden states that it occurs in the West Indian Anemones *Actinotryx* and *Ricordea*. A still more remarkable form of asexual reproduction known as transverse fission has been described in the genus *Gonactinia*.[1] In this case, the body of the Anemone becomes constricted in

[1] H. Prouho, *Arch. Zool. Expér.* 2nd ser. ix. 1891, p. 247.

the middle, a circlet of tentacles is formed below the constriction, and division takes place. The upper half floats away with the original tentacles and stomodaeum and becomes attached by the base in another place; the lower half remains behind and develops a new stomodaeum, mesenteric filaments, and sexual organs. In some of the Actiniaria another form of asexual reproduction occurs, known as "Pedal laceration." In the common British *Actinoloba*, for example, so often kept in aquaria, the pedal disc sometimes spreads on the glass or rock upon which the animal rests, in the form of a thin membrane or film of an irregular circular shape, nearly twice the diameter of the column. As the Anemone glides along, the film remains behind and breaks up into a number of hemispherical droplets, which in a few days develop tentacles, a mouth, mesenteries, and the other organs of a complete and independent Anemone. A similar method of reproduction has been observed in several species of *Sagartia*. A true process of discontinuous gemmation has also been observed in *Gonactinia*, in *Corynactis*, and in *Actinoloba*.

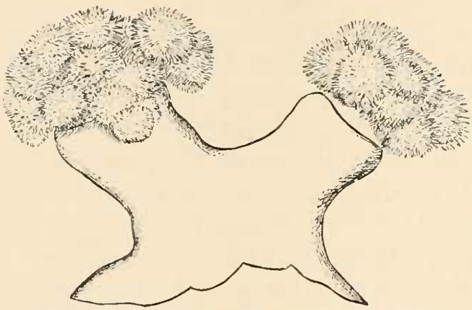

Fig. 164.—Longitudinal fission of *Actinoloba*. (After Agassiz and Parker.)

In the Madreporaria, Zoanthidea and Antipathidea, the usual method of reproduction to form the colonies is continuous gemmation. The new zooids that are added to the colony as it grows arise as buds, either from the superficial canals of the coenenchym, or from the base or body-wall of the older zooids. In these cases the young zooids acquire the same number of mesenteries, and the same characters of the stomodaeum as the original parent. Some further particulars of asexual reproduction in the Madreporaria are given on p. 387.

The **sexual reproduction** of a great many species of Zoantharia has now been observed. The eggs are, as a general rule, ripened in batches, and fertilisation is effected before their discharge from the body. In some cases the sexual condition is seasonal. In temperate climates the generative organs ripen in the spring and summer months, and remain small and relatively inconspicuous in the colder weather; but British Sea-anemones, when kept in an aquarium and regularly fed, will breed nearly all the year round. The corals of the tropics living in warmer water of a more regular temperature show considerable variety in their breeding habits. Thus Duerden found that colonies of *Favia*, *Manicina*, *Siderastraea* and *Porites* are fertile at nearly all times, whereas colonies of *Madrepora*, *Orbicella* and *Cladocora* were rarely so. In nearly all cases the fertilisation is effected, and segmentation of the ovum occurs within the body of the parent, the young Zoantharian beginning its independent life as an oval or pear-shaped ciliated larva.

There are a great many cases among the Actiniaria in which the embryos are retained within the coelenteron, or in special brood pouches of the parent (p. 379), until a stage is reached with twelve or more tentacles.

The oval or pear-shaped larva swims about for a few days or hours, and then settles down on its aboral end. In swimming, the aboral end is always turned forwards. In the larva of *Lebrunia coralligens* and *Rhodactis sancti-thomae*, a distinct sense organ has been observed upon the aboral extremity, and a similar but less distinct organ on the larva of *Actinia equina*. These organs are of considerable interest, as they are probably the only specialised sense organs known to occur in the Zoantharia.

The larvae of Zoantharia present, as a rule, very little variation from the type described, and live but a short time if they fail to find a suitable place for fixation. The colour is usually white and opaque, but in some species the endoderm may be coloured yellow by Zooxanthellae (cf. pp. 86, 125).

The larvae of the Ceriantliidea, however, are remarkable and exceptional. After the larva of these animals has passed through the gastrula stage, a certain number of mesenteries and tentacles are formed, and it rises in the water to live a pelagic life of some duration. This larva is known as *Arachnactis*, and is not unfrequently found in the plankton.

The character of the **food** of the Zoantharia varies with the size of the zooids, the occurrence of Zooxanthellae in the endoderm, and local circumstances; but in general it may be said to consist mainly of small living animals.

Sea-anemones kept in an aquarium will readily seize and devour pieces of raw beef or fragments of mussel that are offered to them; but they may also be observed to kill and swallow the small Crustacea that occur in the water. When a living animal of a relatively small size comes within range of the tentacles, it appears to be suddenly paralysed by the action of the nematocysts and held fast. The tentacles in contact with it, and others in the neighbourhood but to a lesser extent, then bend inwards, carrying the prey to the mouth. The passage of the food through the stomodaeum is effected partly by ciliary, and partly by muscular action, and the food is then brought to the region of the mesenteric filaments where it is rapidly disintegrated by the digestive fluids they secrete. Any unsavoury or undigested portions of the food are ejected by the mouth.

Very little is known concerning the food of the Madreporarian Corals. Many investigators have noticed that the zooids of preserved specimens very rarely contain any fragments of animal or plant bodies that could possibly be regarded as evidence of food. It is possible that many Corals derive a part, perhaps in some cases a considerable part, of their nourishment from the symbiotic Zooxanthellae (pp. 86, 125) which flourish in the endoderm; but it is improbable that in any case this forms the only source of food supply. The absence of food material in the cavities of the zooids may perhaps be accounted for by the fact that nearly all the Corals are fully expanded, and therefore capable of catching their food only at night. Corals are usually collected during the daytime, and therefore during the period of rest of the digestive organs.

It is true that nearly all Corals do exhibit Zooxanthellae in their endoderm, but there are some species from which they are nearly or wholly absent, such as *Astrangia solitaria* and *Phyllangia americana* on the West Indian reefs,[1] and the Pocilloporidae. The absence of any signs of degeneration in the tentacles or digestive organs of those corals with Zooxanthellae as compared with those without them suggests, at any rate, that the Zooxanthellae do not supply such a large proportion of the food necessary for the support of the colonies as to warrant any relaxation of the efforts to obta n food by other means. Mr. Duerden found that when living Annelids are placed upon the

[1] Duerden, *Mem. Acad. Was ington*, viii. 1902, p. 437.

tentacles of a living *Siderastraea*—a genus with Zooxanthellae, the tentacles at once close upon them and prevent their escape. The general conclusion seems to be, therefore, that the Madreporarian Corals feed upon small animals in much the same way as the Sea-anemones, whether they have Zooxanthellae or not, but that in general they feed only at night.

Age.—It is known that Sea-anemones kept in an aquarium and regularly fed will live for a considerable number of years without showing signs of weakness or failing health. Dalyell kept in an aquarium a specimen of *Actinia mesembryanthemum*, which lived for sixty-six years and then died a natural death; and specimens of *Sagartia*, still living, are known to be about fifty years old.[1] The unnatural conditions of life in an aquarium may have favoured the longevity of these specimens, and it would not be reasonable to conclude from these records that the average life of a full-grown Anemone on the rocks is more than thirty or thirty-five years, and perhaps it is a good deal less.

As regards the Madreporarian Corals, we know but little concerning their duration of life. An examination of any living coral reef is sufficient to convince an observer that the power of asexual reproduction of the colonial forms is not unlimited; that colonies, like individuals, have a definite span of life, and that they grow old, senile, and then die a natural death if spared in their youth from accident and disease. Mr. Gardiner has calculated that the duration of life in solitary Corals like *Flabellum* is about twenty-four years, in colonial forms such as *Goniastraea*, *Prionastraea*, *Orbicella*, and *Pocillopora*, from twenty-two to twenty-eight years.

Order I. Edwardsiidea.

This order contains only a few genera and species of small size living in shallow water in various parts of the world. In external features they closely resemble several genera of the Actiniaria, particularly those belonging to the family Halcampidae. The distinguishing character of the order is to be found in the system of mesenteries. In all the species only eight mesenteries are complete, namely, the first two pairs of protocnemes, and the two pairs of directives (Fig. 163, 2),

[1] Ashworth and Annandale, *Proc. Roy. Soc. Edinb.* xxv. 1904, p. 11.

and these usually support such large and powerful muscle-bands that they appear to be the only mesenteries present. A careful examination of transverse sections, however, reveals the fact that other mesenteries are present. The fifth and sixth pairs of protocnemes seem to be invariably represented, and two or three pairs of metacnemes can also be traced in some species.

The tentacles are variable in number. In *Edwardsia beautempsii*, for example, they may be 14-16 in number, arranged in a single row round the oral disc. In *E. timida* they vary from 20 to 24. The normal number appears to be eight tentacles of the first cycle, corresponding to the eight primary inter-mesenteric chambers, *plus* 6 or 12 tentacles, corresponding with the chambers limited by the more rudimentary mesenteries,—making a total of 14 or 20 tentacles; but by the suppression of the two primary dorso-lateral tentacles, or by the addition of tentacles of another cycle, the actual number is found to vary considerably. The Edwardsiidea are not fixed to the bottom, but are usually found deeply embedded in sand, the aboral extremity being pointed and used for burrowing purposes. The general colour of the body is yellow or yellowish brown, but it is partly hidden by a short jacket of mud or sand and mucous secretion. The oral crown frequently shows beautiful colours. De Quatrefages relates that in *Edwardsia beautempsii* the oral cone is golden yellow, and the tentacles, transparent for the greater part of their extent, terminate in opaque points of a beautiful yellowish red colour.

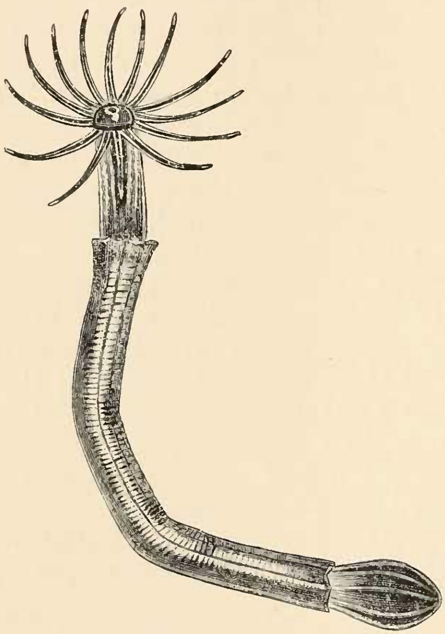

FIG. 165.—*Edwardsia beautempsii*. Nat. size. (After de Quatrefages.)

Fam. 1. Edwardsiidae.—Several species of this family have been found in the British area. They are very local in their distribution, but sometimes occur in great numbers.

Edwardsia beautempsii occurs in shallow water near the shores of the English Channel and has been found in Bantry Bay; and *E. carnea* and *E. timida* have also been found in the Channel. *E. tecta* is a recently described species from the S. Irish coast, and *E. allmani* and *E. goodsiri* are found in Scottish waters.

Fam. 2. Protantheidae.—This family, constituted for the reception of three remarkable genera, is now usually included in the order Edwardsiidea on the ground that not more than eight mesenteries are complete.

The genus *Gonactinia* exhibits the very exceptional character of having a thick layer of muscles in the body-wall (cf. Cerianthidea, p. 409), and it is also remarkable for the frequency with which it reproduces itself asexually by longitudinal and, more rarely, by tranverse fission. It has been found in Norway, the Mediterranean, and on the reefs of New Caledonia. The other genera of the family are *Oractis* from California, and *Protanthea* from the coast of Sweden.

Order II. Actiniaria.

This order contains nearly all the animals popularly known as Sea-anemones. They are usually found in shallow water, attached by a broad basal disc to shells, stones, or sea-weeds. In the Halcampidae, however, the aboral extremity ends in a blunt point as in the Cerianthidea and Edwardsiidea, and the animals live half-buried in sand or mud. The Minyadidae of the southern oceans are pelagic in habit, floating near the surface of the sea with the mouth turned downwards. They are supported in the water by a bladder, formed by an involution of the pedal disc, and filled with gas.

Many of the Sea-anemones are found in symbiotic association with other animals. The common *Adamsia* of the British coasts is found on whelk shells containing hermit crabs. The crab is probably protected from the attacks of some of its enemies by the presence of the Anemone, which in its turn has the advantage of securing some fragments of the food captured and torn to pieces by the crab. The association, therefore, seems to be one of mutual advantage to the messmates. It is a noteworthy fact that in these associations the species of Sea-anemone associated with a particular hermit crab is nearly always constant. Thus in the English Channel, *Adamsia palliata* is almost invariably found associated with *Eupagurus prideauxii*, and *Adamsia rondeletii* with *Eupagurus bernhardus*. But, perhaps, the most remarkable association of this kind is to be seen in the case of the little shore crab of the Indian Ocean, *Melia tesselata*, which invariably holds in each of its large claws a small Sea-anemone. Möbius, who originally described this case, relates that when the crab is robbed of its Anemone it appears to be greatly agitated, and hunts about on the sand in the endeavour to find it again, and will even collect the pieces, if the Anemone is cut up, and arrange them in its claw.[1]

Another very interesting association is that of certain fish and Crustacea with the large Sea-anemones of the tropical Australian coast.[2] Thus *Stoichactis kenti* almost invariably contains two or more specimens of the Percoid fish *Amphiprion percula*. This fish is remarkable for its brilliant colour, three pearly white cross-bands interrupt a ground plan of bright orange-vermilion, and the ends of the cross-bands as well as the fins are bordered with black. In another species a prawn of similar striking colours is found. These companions of the giant Anemones swim about among the tentacles unharmed, and when disturbed seek refuge in the mouth. It has been suggested that these bright and attractive animals serve as a lure or bait for other animals, which are enticed into striking distance of the stinging threads of the Anemone, but how the commensals escape the fate of the animals they attract has yet to be explained.

In a considerable number of Sea-anemones, such as *Actinoloba marginata* and *A. dianthus*, some species of *Sagartia*, *Actinia cari*, *Anemonia sulcata*, and *Calliactis parasitica*, the fertilisation of the eggs and their subsequent development take place in the sea water.[3] In a great many others, such as *Bunodes* (several species), *Cereactis aurantiaca*, *Sagartia troglodytes*, *Bunodactis*

[1] For recent experiments on this case, see a forthcoming paper by J. E. Duerden (*P.Z.S.*).

[2] Saville Kent, "Great Barrier Reef," London, 1893, p. 145.

[3] O. Carlgren, *Biolog. Centralbl.* xxi. 1901, p. 480.

gemmacea, etc., the embryos are discharged into the water from the body-cavity of the parent, at a stage with six or twelve tentacles. In the Arctic species of the genera *Urticina* and *Actinostola*, however, the embryos are retained within the body of the parent until several cycles of tentacles are developed, and in *Urticina crassicornis* the young have been found with the full number of tentacles already formed. In *Epiactis prolifera* from Puget Sound, the young Anemones attach themselves to the body-wall of the parent after their discharge, and in *Epiactis marsupialis*, *Pseudophellia arctica*, *Epigonactis fecunda*, and other species from cold waters, the young are found in numerous brood sacs opening in rows on the body-wall. It is not known for certain how these embryos enter the brood sacs, but it is possible that each sac is formed independently for a young embryo that has settled down from the outside upon the body-wall of the parent. The most specialised example of this kind of parental care in the Sea-anemones is seen in *Marsupifer valdiviae* from Kerguelen, in which there are only six brood sacs, but each one contains a great many (50-100) embryos.

The wonderful colours of our British Sea-anemones are familiar to most persons who have visited the sea-side. The common *Actinia mesembryanthemum* of rock pools, for example, is of a purple red colour. The base is usually green with an azure line. Around the margin of the disc there are some twenty-five turquoise blue tubercles. On each side of the mouth there is a small purple spot, and the numerous tentacles forming a circlet round the mouth are of a pale roseate colour. Nothing could be more beautiful than the snowy-white *Actinoloba dianthus* or the variegated *Urticina crassicornis.*

Similar wonderful variety and beauty of colour are seen in the Sea-anemones of other parts of the world. Thus Saville Kent[1] in describing a species of the gigantic *Stoichactis* of the Australian Barrier Reef says, "the spheroidal bead-like tentacles occur in irregularly mixed patches of grey, white, lilac, and emerald green, the disc being shaded with tints of grey, while the oral orifice is bordered with bright yellow."

The order Actiniaria contains a large number of families, presenting a great variety of external form and of detail in general anatomy. The definitions of the families and their

[1] Saville Kent, "The Great Barrier Reef," 1893, p. 144.

arrangement in larger groups have presented many difficulties, and have led to considerable differences of opinion; and even now, although our anatomical knowledge has been greatly extended, the classification cannot be regarded as resting on a very firm basis. The families may be grouped into two sub-orders:—

SUB-ORDER 1. ACTINIINA.—The tentacles are simple and similar, and there is one tentacle corresponding to each inter-mesenteric chamber (endocoel).

SUB-ORDER 2. STICHODACTYLINA.—The tentacles are simple and similar, or provided with teat-like or ramified pinnules. One or more tentacles may correspond with an endocoel, and there may be two kinds of tentacles (marginal and accessory) in the same genus.

Sub-Order 1. Actiniina.

Fam. 1. Halcampidae.—This family is clearly most closely related to the Edwardsiidea. There are, however, twelve complete mesenteries of the first cycle, and a second cycle of more or less incomplete mesenteries. The tentacles are usually twelve in number, but may be twenty or twenty-four. There is no pedal disc, but the base is swollen and rounded or pointed at the end.

The genus *Halcampa* includes a considerable number of small species occurring in the shallow waters of the temperate northern hemisphere, and of the Kerguelen Islands in the south. Three British species have been described, of which *Halcampa chrysanthellum* alone is common. The larva with eight tentacles and eight mesenteries has been found living on the Medusa *Thaumantias*.

Peachia is a genus containing Anemones of much larger size (10-25 cm.). It is remarkable for the very large siphonoglyph on the ventral side of the stomodaeum, prolonged into a papillate lip projecting from the mouth called the "conchula." The genera *Scytophorus* from 150 fathoms off Kerguelen and *Gyractis* from Ceylon, although showing some remarkable peculiarities of their mesenteric system, appear to be closely related to this family.

Ilyanthus mitchellii is a large Anemone with a vesicular base, forty-eight tentacles and mesenteries, occurring in the English Channel, but it is not very common. It is usually placed in a separate family, but is in many respects intermediate in character between the Halcampidae and the Actiniidae.

Fam. 2. Actiniidae.—This family contains some of the commonest British Sea-anemones. There is a large flat pedal disc by which the body is attached to stones and rocks. The body-wall is usually smooth, and not perforated by cinclides. The edge of the disc is usually provided with coloured marginal tubercles. There are no acontia.

Actinia.—This genus contains the widely distributed and very variable species *Actinia mesembryanthemum*, one of the commonest of the Sea-anemones found in rock pools on the British coast. The colours of this species are often very beautiful (see p. 379) but variable.

Anemonia is a genus with remarkably long tentacles which are not completely retractile. *A. sulcata* (sometimes called *Anthea cereus*) is very common in the rock pools of our southern coasts.

Bolocera tuediae is, next to *Actinoloba dianthus*, the largest of the British Anemones. It has very much the same colour as the common varieties of *Actinia mesembryanthemum*, but the body-wall is studded with minute, rounded warts. It is found between tide marks in the Clyde sea-area, but usually occurs in deeper water.

Fam. 3. Sagartiidae.—This family includes several genera with a contractile pedal disc, with the body-wall usually perforated by cinclides, and provided with acontia.

The genera may be arranged in several sub-families distinguished by well-marked characters. Among the well-known Sea-anemones included in the family may be mentioned:—

Sagartia troglodytes, a very common British species found in hollows in rocks. It is usually of an olive green or olive brown colour, and the upper third or two-thirds of the body-wall is beset with numerous pale suckers. *Adamsia palliata* has a white body-wall spotted with bright red patches, and is associated with the hermit crab *Eupagurus prideauxii*.

Actinoloba (frequently called *Metridium*) *dianthus* is considered the handsomest of all the British Sea-anemones. It has a lobed disc frilled with numerous small tentacles, and is uniformly coloured, creamy-white, yellow, pale pink, or olive brown. It lives well in captivity, and sometimes reaches a length of 6 inches with a diameter of 3 inches (Fig. 164).

Aiptasia couchii is a trumpet-shaped Anemone, found under stones at low-water mark in Cornwall and the Channel Islands, with relatively slight power of retraction.

Gephyra dohrnii is an interesting species with twelve tentacles, which was supposed at one time to form a connecting link between the Actiniaria and the Antipathidea. It is found attached to the stems and branches of various Hydrozoa and Alcyonaria, sometimes in such numbers and so closely set that it gives the impression of having formed the substance of its support. Haddon [1] has described specimens found on the stems of *Tubularia* from deep water off the south and south-west coasts of Ireland. It also occurs in the Mediterranean and the Bay of Biscay.

Fam. 4. Aliciidae.—The members of this family have a large flat contractile base and simple tentacles. The body-wall is provided with numerous simple or compound outgrowths or vesicles, usually arranged in vertical rows. *Alicia mirabilis* is a rare Anemone from Madeira with a very broad base, capable of changing its position with considerable activity, and of becoming free and floating upside down at the surface of the sea. Other genera of the family are *Bunodeopsis* and *Cystiactis*. The genus *Thaumactis*, described by Fowler,[2] from the Papeete reefs, has many peculiarities, but is probably capable of crawling rapidly and of floating at the surface like other members of the family. The remarkable Anemone *Lebrunia* from the West Indies may be included in this family.

Fam. 5. Phyllactidae.—These are distinguished by the presence of a broad collar of foliaceous or digitate processes outside the circle of tentacles. The processes have some resemblance to the foliaceous tentacles of the Stichodactylinae. They are found in the Mediterranean, Red Sea, and on the shores of the Atlantic Ocean, but have not yet been found in the British area.

Fam. 6. Bunodidae.—This family is characterised by prominent verrucae and tubercles of the body-wall. It contains several British species, of which *Bunodes gemmacea* found between tide marks on our southern shores is fairly common. The very common British species *Urticina* (*Tealia*) *crassicornis* is usually placed in this family, but exhibits some peculiarities which seem

[1] A. C. Haddon, *Trans. Roy. Dubl. Soc.* iv. 1889, p. 325.
[2] G. H. Fowler, *Quart. Journ. Micr. Sci.* xxix. 1888, p. 143.

to warrant its removal to another division of the Actiniaria. It is found in tide pools attached to rocks, but is usually partially hidden by adherent sand or small stones.

Fam. 7. Minyadidae.—This family contains a number of floating Anemones. The basal disc is folded over to form a gas bladder lined by a cuticular secretion. The species are principally found in the seas of the southern hemisphere.

Sub-Order 2. Stichodactylina.

Fam. 1. Corallimorphidae.—In this family the marginal cycle of tentacles and accessory tentacles are all of the same kind. The accessory tentacles are arranged in radial rows. All the tentacles are knobbed at the extremity. The musculature is weak. *Capnea sanguinea*, *Corynactis viridis*, and *Aureliania heteroecera* belong to the British fauna. They are all small Anemones of exquisite colours, but are not very common. The genus *Corallimorphus* is principally found in the southern hemisphere.

Fam. 2. Discosomatidae.—The tentacles are all of one kind and are very numerous. The mesenteries are also very numerous. The sphincter muscle is strong.

This family includes a rather heterogeneous assembly of forms, and will probably require some rearrangement as our knowledge increases. Nearly all the species are found in the shallow waters of the tropics, and among them are to be found some of the largest Anemones of the world. *Stoichactis kenti*, from the Barrier Reef, is from one to four feet in diameter across the disc. In the West Indies these Anemones do not attain to such a great size, but *Homostichanthus anemone* from Jamaica is sometimes 8 inches in diameter.

Fam. 3. Rhodactidae.—In this family the body-wall is smooth and the oral disc greatly expanded. The tentacles are of two kinds. On the margin there is a single cycle of minute tentacles, while on the disc there are numerous tuberculate or lobed tentacles. Many of the species of this family are quite small, but *Actinotryx mussoides* from Thursday Island has an oral disc 8 inches in diameter. The genera and species are widely distributed in the warm, shallow waters of the world.

Fam. 4. Thalassianthidae.—The tentacles are simple or ramified (Fig. 166), and in some cases very long (*Actinodendron arboreum*). Many of the specimens of *A. plumosum* and *Megalactis griffithsi* are of very large size, 8 to 12 inches in diameter. Of the former of these two species Saville Kent remarks: "The colours are lacking in brilliancy, being chiefly represented by varying shades of light brown and white, which are probably conducive to its advantage by assimilating it to the tint of its sandy bed. When fully extended the compound tentacles are elevated to a height of 8 or 10 inches, and bear a remarkable resemblance to certain of the delicately branching, light brown sea-weeds that abound in its vicinity." The same author calls attention to their stinging, which is "nearly as powerful as the ordinary stinging nettle."

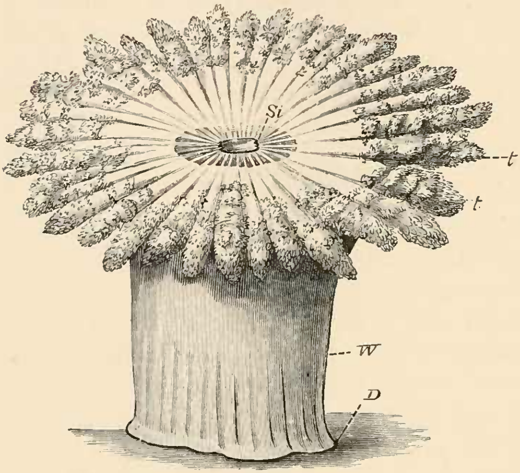

FIG. 166.—*Actinodendron plumosum*. *D*, disc of attachment; *Si*, siphonoglyph; *t*, *t*, lobes of the marginal disc bearing the tentacles; *W*, body-wall. Height of the column 200 mm. (After Haddon.)

Order III. Madreporaria.

The Madreporaria form a heterogeneous group of Zoantharia characterised by a single common feature, the formation of an extensive skeletal support of carbonate of lime. In a great many cases the skeleton exhibits cups or "calices" into which the zooids may be completely or partially retracted, and these calices usually exhibit a series of radially disposed vertical laminae, the "septa," corresponding with the inter-mesenteric spaces of the zooids. Calices and structures simulating septa also occur in *Heliopora*, which is an Alcyonarian, and in certain fossil corals which are probably not Zoantharians. The anatomy of the zooids of a great many Madreporaria is now known, and, although a great deal of work yet remains to be done, it may be said that the Madreporaria exhibit close affinities in structure with the Actiniaria. The chief points in the anatomy of the zooids are described under the different sub-divisions, but a few words are necessary in this section to explain the principal features exhibited by the skeleton.

There is no more difficult task than the attempt to explain upon any one simple plan the various peculiarities of the Madreporarian skeleton.[1] The authorities upon the group are not agreed upon the use of the terms employed, nor are the current theories

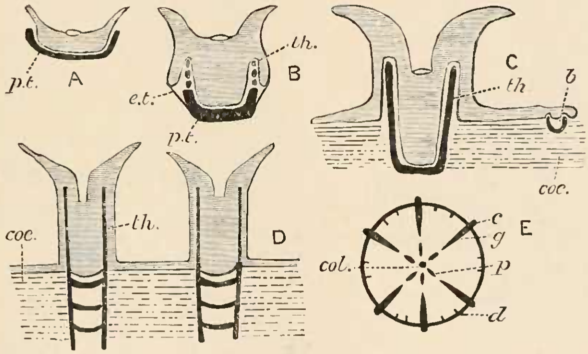

FIG. 167.—Series of diagrams to illustrate the structure of the Madreporarian skeleton. **A**, young stage of a solitary coral with simple protheca (*p.t*). **B**, solitary coral, with theca (*th*), epitheca (*e.t*), and prototheca (*p.t*). **C**, young stage of colonial coral, showing coenosteum (*coe*) and theca (*th*), and the formation of the theca of a bud (*b*). **D**, two zooids of a more advanced stage of a colonial coral. *coe*, Coenosteum ; *th*, theca. The black horizontal partitions are the tabulae. **E**, transverse section of a calyx. *c*, Costa ; *col*, columella ; *d*, dissepiment ; *g*, septum ; *p*, pali.

of the evolution of the skeleton consistent. It is necessary, however, to explain the sense in which certain terms are employed in the systematic part that follows, and in doing so to indicate a possible line of evolution of the more complicated compound skeletons from the simple ones.

There can be no doubt whatever that the whole of the skeleton of these animals is formed by the ectoderm, and is external to their bodies. If we could get rid of the influence of tradition upon our use of popular expressions we should call this skeleton a shell. There can be little doubt, moreover, that this skeleton is formed by a single layer of specialised ectoderm cells called the "calicoblasts."

[1] For a general account of the Madreporarian skeleton, cf. Ogilvie, *Phil. Trans. Roy. Soc.* clxxxvii. B. 1896.

The calicoblasts form, in the first instance, a skeletal plate at the aboral end of the coral embryo, which becomes turned up at the edges to form a shallow saucer or cup. This cup is called the "prototheca."[1] At this stage the body-wall of the living zooid may or may not overflow the edge of the prototheca. In the former case the growth of the rim of the prototheca is brought about by the calicoblasts of an inner and outer layer of epiblast, and the cup is then called the "theca." In the latter

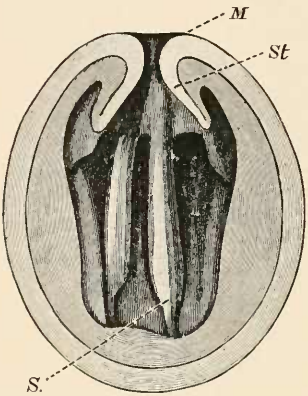

FIG. 168.—Diagram of a vertical section of a young *Caryophyllia*, showing the septa (*S*) covered with endoderm projecting into the coelenteric cavity. *M*, mouth; *St*, stomodaeum. (After G. von Koch.)

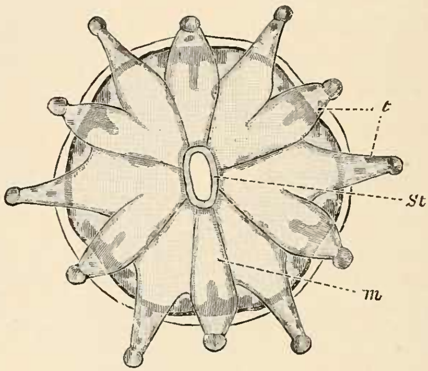

FIG. 169.—A young *Caryophyllia*, viewed from above, showing the tentacles (*t*) and the stomodaeum (*St*). The letter *m* points to a space between a pair of mesenteries, and the darker shading in this place shows a septum projecting radially from the wall of the theca. (After G. von Koch.)

case, the growth of the rim of the prototheca is continued by the calicoblasts of one layer of epiblast only, and it is called the "epitheca" (*Flabellum*). With the continued growth of the theca the tissues that have overflowed—the "episarc"—retreat from the base, and in doing so the ectoderm of the edge and, to some extent, the outer side of the episarc secrete a layer of epitheca which becomes more or less adherent to the theca. Thus the cup may have a double wall, the theca and the epitheca (*Caryophyllia*).

With the growth of the theca and epitheca a certain number of radially disposed laminae of lime rise from the walls and grow centripetally. These are the "septa." Additional ridges on

[1] H. M. Bernard, *Ann. Mag. Nat. Hist.* (7) xiii. 1904, p. 1.

the inner wall of the cup between the septa are called the "dissepiments." Corresponding with the septa there may be a circle of columns or bands rising from the basal parts of the prototheca—the "pali"; and from the actual centre a single column called the "columella." The longitudinal ridges on the outside of the theca, corresponding in position with the septa inside, are called the "costae" (Fig. 167, E, *c*).

We may imagine that in the primitive forms that gave rise to colonies, the episarc of the primary zooid overflowed on to the substance to which it was attached, and gave rise to successive layers of epithecal skeleton, which may be called the "coenosteum." The ectoderm at the base of the original prototheca is in some corals periodically dragged away from the skeleton, and forms another cup or platform of lime at a little distance from it—the "tabula." New zooids are developed at some distance from the primary one by a process of gemmation in the episarc, and independent thecae, septa, etc., are formed in it; the skeleton of the new zooid thus originated being connected with that of the primary zooid by the coenosteum.

There are many modifications of this simple description of skeleton formation to be considered before a thorough knowledge of coral structure can be understood, but sufficient has been said to explain the use of the terms that it is necessary to employ in the description of the families. When it is necessary to speak of the cup in which the zooid is situated without expressing an opinion as to the homology of its wall, it is called the calyx.

There are many forms of asexual reproduction observed in the Madreporaria. Of these the most frequent is gemmation. The buds are formed either on the episarc or on the canals running between zooids at the surface of the coenenchym. When the young zooids that have been formed by gemmation reach maturity they have the same characters as their parents. Fission occurs in the production of a great many colonies of Madreporaria. It occurs occasionally in such genera as *Madrepora* and *Porites*, where reproduction by gemmation prevails, but it is said that gemmation never occurs in those forms such as the Astraeidae Fissiparantes where fission is the rule. In fission a division of the zooid takes place in a vertical plane passing through the stomodaeum and dividing the zooid into two equal parts. In some cases these two parts become separated during the further growth of the coral. In other cases, however, further divisions of the stomodaeum occur before the separation of the zooids, and then elongated, serpentine polyps are produced (as in *Meandrina*, etc.), which consist of a number of imperfectly separated zooids, each with a distinct mouth and stomodaeum but with continuous coelenteric cavities. Two kinds of fission must be distinguished from each other. In *Madrepora* and *Porites* the plane of fission passes dorso-ventrally through the zooids, that is, between the dorsal and ventral pairs of directive mesenteries. In these cases the zooids produced by fission are similar to the parent form.

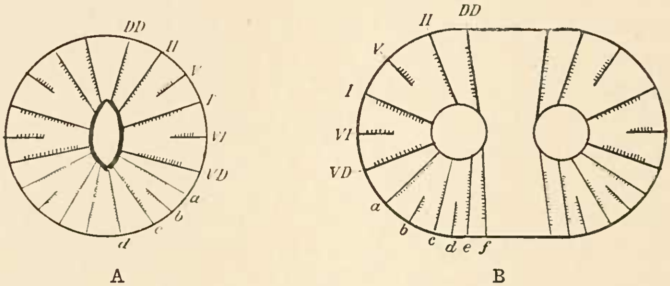

FIG. 170.—Diagrammatic transverse sections of *Porites* to illustrate the process of fission. **A**, before division; **B**, fission nearly completed. In **A** four bilateral pairs (*a*, *b*, *c*, *d*) of mesenteries have appeared in the entocoele of the ventral directives (*VD*). These are increased to six pairs and then fission commences as seen in **B**, the plane of fission passing through the entocoeles of the last pair of secondary mesenteries (*f*) and of the dorsal directives (*DD*). *I*, *II*, *V*, *VI*, the protocnemes in the order of their development. (After Duerden.)

In most Madreporaria, however, the plane of fission appears to be more or less at right angles to this, and the resulting zooids are unlike the original parent form in having either no directive mesenteries at all or only one pair of them.

The section Fungacea presents us with some exceptional and remarkable forms of asexual reproduction. The embryo *Fungia* gives rise to a conical fixed coral called a "trophozooid." The upper part of the calyx of this trophozooid expands and becomes disc-shaped. This is called the "anthocyathus," and after it has reached a certain size it breaks away from the rest of the trophozooid as an adult *Fungia*. Several anthocyathi may be formed in succession from one trophozooid. This may be described as a process of successive transverse fission. In *Diaseris* the disc divides into four quadrants, and each quadrant appears to be capable of acquiring the shape and size of the undivided parent.

Without doubt a process of sexual reproduction occurs in all Madreporaria. In some genera sexual reproduction appears to be almost continuous throughout the year; in others the sexual organs are formed only at periods separated by considerable intervals of sterility. According to the researches of Duerden the Madreporaria appear to be usually viviparous, the early stages of development are passed through within the body of the parent, and the young coral is discharged into the water as a free-swimming ciliated larva. The larvae are spheroidal, oval, or pear-shaped, but change their shape a good deal, and sometimes become elongated, straight, or spirally twisted rods. The larvae are at first dense and opaque, but subsequently they become distended by the absorption of water, and more nearly transparent. They swim about for one or two days, and then settle down by the aboral pole and become fixed. The tentacles are not formed, in any species that has yet been observed, during the free-swimming stage of existence.

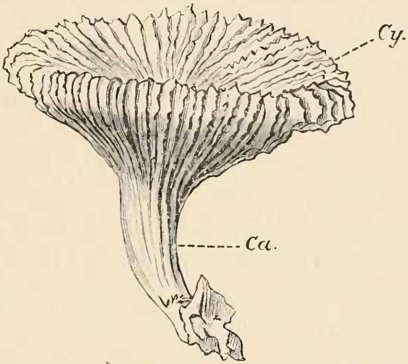

FIG. 171.—A fixed stage in the development of *Fungia*. The trophozooid has become differentiated into a discoid crown, the anthocyathus (*Cy*) and a pedicle, the anthocaulus (*Ca*). (After G. C. Bourne.)

Distribution of Reef Corals.—The principal reef-forming corals reach their greatest size and grow with greatest rapidity in the warm, shallow waters of the world, but they are not confined to this habitat. A species of *Madrepora* has been found in the very cold waters of Archangel, and *Manicina areolata* occurs in Simon's Bay, Cape of Good Hope, many degrees south of the region of the East African coral reefs. As regards the distribution of these corals in depth, very little is known at present. The face of the growing coral reef that is turned towards the open sea is so steep that it has been found impossible to determine to what depth the living reef corals actually extend.

The survey of the Macclesfield bank proved that a considerable number of reef corals are to be found alive at depths ranging from 30 to 50 fathoms.[1] To give one example:—In the dredging No. 50, depth 32 to 35 fathoms, living examples of the following genera of corals were obtained: *Madrepora*, *Montipora*, *Psammocora*, *Pavonia*, and *Astraeopora*.

Coral Reefs and Atolls.—In many regions of the tropical seas, banks and islands are found which are built up of blocks of coral, coral detritus, and altered or modified limestone. These are the famous coral reefs of which so much has been said and written during the last half-century. There can be little doubt that the superficial strata of these formations are entirely due to the action of coral-forming animals and plants living in warm, shallow sea-water.

Three classes of coral reefs are usually recognised: the "fringing reefs" which follow the contour of the coast at a distance of a few hundred yards, and are separated from the beach at low tide by sand flats or a shallow lagoon; the "barrier reefs," following the contour of the coast less regularly than the fringing reefs, but at a much greater distance, and separated from the beach by a lagoon of sufficient depth to serve as a harbour for ships of great size; and, finally, the "atolls," which are ring-shaped, or broken circlets of low islands enclosing a lagoon which is, in some cases, of considerable depth.

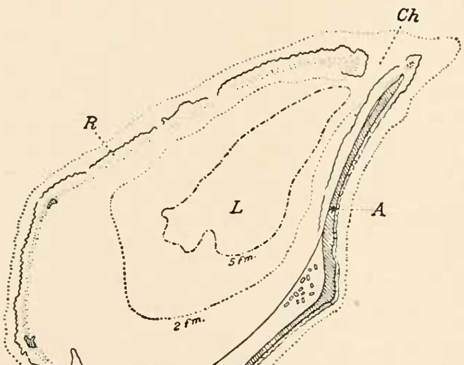

Fig. 172.—Plan of Minikoi Atoll in Laccadive Archipelago. *A*, the land elevated above the level of high-water mark; *Ch*, the boat channel; 5 *fm*, the five fathom line; 2 *fm*, the two fathom line; *L*, the lagoon with a maximum depth of 7 fathoms; *R*, the reef continuing the circle on the east side of the atoll, awash at high tides. (After Stanley Gardiner.)

It was observed by the early surveyors that in many cases the sea-bottom slopes downwards steeply or almost precipitously from the outer edge of the barrier reefs and atolls to very great

[1] "Report on the Results of Dredging on the Macclesfield Bank," *Admiralty Report*, 1894.

depths—to depths, in fact, at which reef-forming corals do not live.

It seems obvious, therefore, that the atolls and barrier-reefs are resting upon some stratum which could not possibly have been formed by reef-building organisms at the same relative position it has now, and the questions arose, What is the substratum and how was it formed?

If this stratum is a coral rock, it is clear that it must have been formed at a time when it was nearer to the surface of the sea than it is now, and that it must have subsided subsequently to greater depths. If, on the other hand, it is a primitive rock, we must assume that in such regions as the Indian Ocean and the South Pacific, where the archipelagoes of atolls extend for hundreds of miles, there are chains of mountain ranges with peaks reaching to a uniform level beneath the surface of the sea. "But we cannot believe that a broad mountain summit lies buried at the depth of a few fathoms beneath every atoll, and nevertheless that throughout the immense areas above named not one point of rock projects above the level of the sea. For we may judge of mountains beneath the sea by those on land, and where can we find a single chain, much less several such chains many hundred miles in length, and of considerable breadth, with broad summits attaining the same height from within 120 to 180 feet?"[1]

To account for the observed facts of the atolls and barrier-reefs, Darwin conceived and expounded the subsidence theory. According to this theory, the regions where atolls now occur were at one time dry land, or an archipelago of volcanic islands surrounded by fringing reefs of the ordinary type. A gradual subsidence of the land took place, and the area of the land diminished; but the area enclosed by the coral reefs did not diminish in a corresponding degree, and the young corals growing on the débris of the older ones as they sank continued the growth of the reef in a direction nearly vertical to the sea-bottom. The fringing reefs thus became barrier reefs, and they were separated from the land by a lagoon of considerable depth. Finally, when the mountain peaks disappeared beneath the waves, a ring-shaped reef or atoll was all that was left to mark the position of the former land.

The fundamental assumption in the subsidence-theory is that

[1] C. Darwin, *Coral Reefs*, 3rd edition, 1889, p. 125.

the substratum of the coral reefs and islands is coral-formed limestone. To test the truth of this assumption an expedition was sent out to obtain, by boring, evidence of the character of the substratum of a typical atoll. The island of Funafuti in the Ellice group of the Pacific Ocean was selected, and after several attempts a successful boring was made to a depth of 1114 feet. The material from the boring was found to consist of rocks or sands entirely derived from the calcareous skeletons of marine Invertebrate animals and calcareous Algae.[1] Moreover, in the cores from various depths down to the lowermost the fossilised

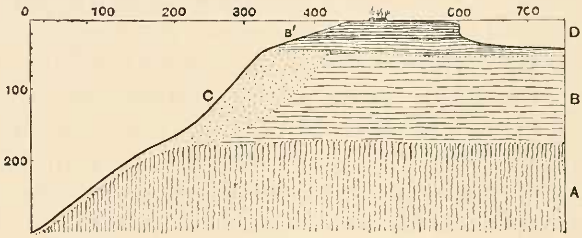

Fig. 173.—Section of the outer edge of one of the Maldive Atolls. **A**, foundation of primitive rock cut down by the currents ; **B**, upgrowth of the rim by the deep-sea-, intermediate depth- and (**B'**) reef-organisms ; **C**, extension outwards by means of the talus slope ; **D**, lagoon. Scale in fathoms. (After Stanley Gardiner.)

skeletons of the common genera of recent corals, and very few or no representatives of genera of corals now extinct were discovered.

These facts, therefore, prove the justice of Darwin's assumption as to the nature of the substratum—and give support to the subsidence-theory as applied to this particular island. A strong opinion has, however, been expressed by several authors of recent years that the subsidence-theory cannot account for the formation of all the atolls and barrier reefs that have now been investigated, and alternate hypotheses have been put forward to account for particular cases. The main chain of the Maldive Archipelago in the Indian Ocean, for example, presents special difficulties to the acceptance of the subsidence-theory as one of general application.[2] The main chain of these islands is more than 300 miles long, and lies at right angles to the monsoon currents of the

[1] For the details of these borings, see "The Atoll of Funafuti," *Royal Society of London*, 1904.

[2] For further information, see J. Stanley Gardiner, *The Fauna and Geography of the Maldive and Laccadive Archipelagoes*, vol. i. pt. ii. 1902, p. 172.

Indian Ocean. Here the action of the currents appears to have cut down a great tract of land to form a plateau more than 100 fathoms in depth. The outer rim of this plateau may have grown in height by the deposit of the skeletons of surface-swimming animals, and the skeletons of deep-sea corals, until it reached a level where reef-forming corals can thrive. A certain number of channels would be retained and even deepened as the rim grew up, and thus the coral would eventually reach the surface not as a single large atoll, but as a series of coral islands. When the coral reef has thus reached the surface and cannot grow farther in height, it spreads radially like a fairy ring on the talus formed by broken corals that have fallen down the slopes. The central parts, no longer protected by living organisms, are continually subject to the solvent action of the sea water penetrating the porous substratum, and sink to form the lagoon.

It is not only in the reefs of the Indian Ocean, however, but in many of the archipelagoes of the Pacific Ocean, where there is evidence of very extensive elevation of the land areas in the neighbourhood of atolls and barrier reefs, that the subsidence-theory does not satisfactorily account for all the observed facts. It appears probable, therefore, that although a gradual subsidence of the land may have been the primary cause of coral reef formation in some areas, similar reefs may have been formed in other areas by other natural methods.

Fossil Corals.—A great number of the genera of corals found in the newer Tertiary deposits, and a smaller number of those occurring in the older Tertiary and Cretaceous strata clearly belong to families now represented by recent corals. In the earlier strata, however, fossils are found which cannot be placed in our system with any degree of certainty. Attempts have been made from time to time to arrange these corals in their proper positions by the careful study and comparison of their skeletal features, but the reasons given are not convincing. The genus *Syringopora*, and the families Favositidae, Heliolitidae, and Coccoseridae have been noticed in the chapter on Alcyonaria (pp. 343-346). The family Zaphrentidae will be noticed when dealing with the order Zoanthidea.

Among the families of fossil corals of uncertain position which may still be included in the order Madreporaria, the more important are:—

Cyathophyllidae, a family of solitary and colonial corals with numerous radially arranged septa, extending from the Silurian to the Carboniferous limestone. It includes the genera *Cyathophyllum*, which was very abundant in Devonian times, and *Lithostrotion*, which, in the times of the formation of the Carboniferous limestone, occurred in continuous masses extending over great areas of the sea-bottom. The Cyathophyllidae may possibly be ancestral to the representatives of both Astraeidae and Fungiidae, which appeared in the Triassic strata.

The **Cyathaxoniidae** form a family of solitary turbinate or horn-shaped corals, with septa showing a regular, radial arrangement, and may have been the ancestors of the modern family Turbinoliidae. They have the same geological range as the Cyathophyllidae.

The **Cystiphyllidae.**—This family consists of solitary corals with very thin septa; the interseptal spaces are filled with an abundant vesicular substance called the "stereoplasm." The systematic position of this family is very doubtful, as the structure is evidently much destroyed, but by some authors it is supposed to be ancestral to the family Eupsammiidae.

These three families, together with the Zaphrentidae (p. 406), were formerly grouped together as the Tetracoralla or Rugosa.

Sub-Order 1. Entocnemaria.

Madreporaria forming perforate coralla, with calices that do not project above, or project only slightly above the surface of the coenosarc. The zooids of each colony are usually small and crowded. The mesenteries arise in bilateral pairs, and the increase in their number takes place in the chamber between the ventral or the dorsal pairs of directives. The corals included in this order are among the most important of the reef-builders. On many of the recent coral reefs they occur in enormous numbers and of great individual size. But although so prevalent upon recent reefs, they appear to have played a far less important part in the formation of the reefs of the early Tertiary times, and in the reefs of times antecedent to the Tertiary they were rare or absent.

Judging from the structure of the skeleton and the palaeontological history alone it might be thought that the Entocnemaria represent the most recent types of Madreporarian structure, but the anatomy of the zooids points to a contrary conclusion. The zooids are of very simple structure; the mesenteries are found only in bilateral pairs, and all the new mesenteries formed after the protocnemes originate in one of the directive chambers. These are characters indicating a very ancient history, suggesting affinities with the Edwardsiidea on the one hand, and some ancient type of Cerianthidea on the other. There can be little doubt that it was owing to the evolution of a porous skeleton of rapid growth that these corals have caught up and passed the Astraeidae and other more specialised forms in the struggle for predominance on the coral reefs.

Fam. 1. Madreporidae.—The calices of the corallum are small and contain a few perfectly distinct septa. The coenosteum is porous and contains a plexus of the coenosarcal canals, which connects the cavities of neighbouring zooids. This family is divided into a number of sub-families, but it is only necessary here to mention the peculiarities of a few of the well-known genera.

Madrepora.—This genus is represented by an immense number of forms on the coral reefs of both the old and new world. Attempts have been made at various times to divide these forms into specific groups, and a large number of species have been defined and named. The differences between these species, however, are such as may be due to varying conditions of life upon the reefs and not to characters transmitted from generation to generation by heredity. There can be no doubt that when our knowledge of the soft tissues of these corals is extended the number of species will be greatly reduced. There are, however, three principal forms of growth or *facies* in the genus.

1. The flabellate or palmate colonies with large flat or concave fronds, radiating from an encrusting base: *Forma palmata.*

2. Much branched colonies, several branches radiating obliquely from a common centre: *Forma prolifera.*

3. Large and more erect colonies, less branched except towards the periphery: *Forma cervicornis.*

On some reefs one of these forms of growth predominates, and for miles the reef seems to be built up mainly of corals of this shape. On other reefs two or sometimes all three of these forms may be found within a stone's throw of one another. Notwithstanding the difficulty of distinguishing the species, the genus itself is quite well defined. The calices project slightly from the surface of the branches and contain six septa, of which the pair that is parallel with the axis of the branch is the strongest. This strong pair of septa can usually be well seen when a slender branch of a Madrepore is examined by a lens by transmitted light. At the apex of each branch there is a terminal zooid and in the skeleton an apical calyx. The terminal zooid is (in some species at least) different from the lateral or radial zooids. The former is radially symmetrical and has six long equal digitiform tentacles, the latter have usually twelve tentacles, of which six are larger than the others. These tentacles alternate, but they are so arranged on the disc as to give a distinctly bilateral appearance to the zooids.

The colour of the West Indian Madrepores appears to be entirely due to Zooxanthellae (pp. 86, 125). They are lighter or darker shades of brown, sometimes becoming green, yellow, or orange. On the Australian barrier reef and other reefs of the eastern seas the growing points of the branches are variable and often brilliantly coloured, emerald green, violet, or red; giving some of the most wonderful colour effects for which the reef pools are famous. The cause of these brilliant apical colours has not yet been ascertained.

The genus is found in shallow water of all seas of the tropical belt except on the western side of the continent of America.

Montipora.—In this genus the calices are small and situated in depressions in the coenosteum, and there are six, sometimes twelve, septa of approximately equal size. There is no terminal calyx at the apex of the branches. This is a genus of very variable form and wide distribution in all tropical seas except on the shores of the Atlantic Ocean.

Turbinaria.—This genus is usually cup-shaped or foliaceous and twisted in form. The septa may be six to thirty in number. Some of the species of this genus attain to a very great size in favourable localities. There is a specimen in the British Museum that is 16 feet in circumference and weighed, when dried, 1500 lbs.

Fam. 2. Poritidae.—The corallum is usually encrusting, foliaceous, lobed or tufted, rarely dendritic. The whole skeleton is built up of a system of trabeculae and stout cross bars, and in section the limits of the calices are not well defined. The septa are represented by twelve trabeculae. The zooids are small and are usually provided with twelve tentacles. The most important genus is *Porites,* which is so abundant on many reefs that it may be said to rival *Madrepora* itself in the luxuriance of its growth. On the Australian barrier reef a species of *Porites* builds up coralla over twenty feet in length and as many in height. According to Saville Kent they are usually found on the outer side of the reef and form a basis of support for the high-level Madreporas and other corals.[1]

The colours of *Porites* are very variable and often beautiful. In Jamaica[2] the prevailing colours are bright blue, pale yellow, and yellowish green. In Australia the colours are less brilliant perhaps, but among the prevailing tints are light or bright lilac, a delicate pink, dark yellow, and brown. The genus *Porites* occurs in Eocene and Miocene deposits, and is now found on all the more important coral reefs of the world.

The genus *Alveopora* is usually placed with the Poritidae. According to Bernard,[3] however, its affinities with this family are remote, and it is more closely related to the Favositidae (see p. 344). The walls of the calices are contiguous and the septa are reduced to rows of spines, as in the Favositidae. It is found in shallow water in the Pacific, the Indian Ocean, and the Red Sea.

Sub-Order 2. Cyclocnemaria.

Madreporaria forming perforate or imperforate coralla. Solitary or colonial. The zooids have usually a large number of mesenteries arranged in two or more cycles. The mesenteries beyond the protocnemic pairs arise in unilateral pairs in chambers other than those between the directives.

Sect. 1. Aporosa.—Cyclocnemaria in which the theca and septa are not perforated. The zooids of the colonial forms may communicate by means of superficial canals of the coenosarc, or they may be in contact with one another only at their edges.

Several families are included in this section, of which the more important are :—

[1] Saville Kent, "Great Barrier Reef," 1893, p. 185.
[2] Duerden, *Mem. Ac. Washington*, viii. 1902, p. 550.
[3] H. M. Bernard, *Journ. Linn. Soc. Zool.* xxvi. 1897, p. 495.

Fam. 1. Turbinoliidae.—The corals included in this family are mostly solitary forms attached to foreign objects, or living partly embedded in sand. In some cases a small colony is formed by gemmation.

The genus *Flabellum* is a solitary coral of a compressed top shape. It has a large number of septa arranged radially on the cup-wall. This cup-wall is not a true theca but an epitheca. In some forms root-like tubes grow out from the sides of the cup near its base and may serve to support the coral on solid objects. In some remarkably fine specimens recently obtained from the Persian Gulf these tubes served to attach the coral to a telegraph cable. *Flabellum* seems to be cosmopolitan in its distribution. It is usually found in deep or moderately deep water, but some specimens have been dredged in water of 2 to 9 fathoms.

Caryophyllia is a conical coral fixed by a slightly expanded base. The cup-wall is a true theca covered below by an epitheca. There is a spongy columella surrounded by a single circle of pali. There is one British species, *C. smithii*. It is found attached to shells at a depth of about thirty fathoms near the Eddystone Lighthouse and in other localities in the English Channel. It also occurs between tide marks in the Scilly Islands, and is found off the Shetlands, on the west coast of Scotland, and the south-west of Ireland. The genus is widely distributed and extends from shallow water to depths of 1500 fathoms. *Caryophyllia* sometimes occurs in clusters which have the appearance of an incipient colony. This may be due to the embryos fixing themselves upon the epitheca of existing individuals and developing there. It is doubtful whether the species ever reproduce asexually either by gemmation or by fission. When the zooid is fully expanded it projects some distance above the corallum and shows a very transparent body-wall with a crown of some fifty tentacles. Each tentacle terminates in a globose head (Fig. 169) charged with nematocysts. The general colour is pale pink, and there is a broad brown circle

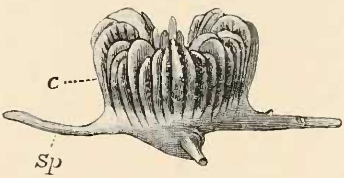

FIG. 174.—Side view of *Trochocyathus hastatus*, with exsert septa, well-marked costae (*c*), and with three spinous projections (*Sp*) at the base formed by outgrowths from primary costae. (After G. C. Bourne.)

round the mouth. Large specimens may be three-quarters of an inch in diameter.

Turbinolia is a common Eocene fossil genus found in England and France, and is stated to occur in the Caribbean Sea. The columella stands up like a stylet and the septa are "exsert," *i.e.* project above the rim of the theca.

Trochocyathus is a genus with well-marked "costae" occurring in tropical shallow water (Fig. 174).

Fam. 2. Oculinidae.—Colonial forms, dendritic or encrusting, with relatively large and rather prominent calices separated by considerable stretches of compact coenosteum. The zooids bear a crown of ten to forty-eight or more capitate tentacles.

Neohelia has a fistulose stem lined internally by a horny membrane. There seems to be some reason for supposing that this membrane is formed by the zooids themselves. A similar membrane is found in the fistulose stems of *Amphihelia* and perhaps other Oculinidae. If this membrane is really formed by the activity of the corals it forms an exception to the general rule that the skeleton of the Madreporaria is entirely calcareous. Others maintain, however, that this membrane is formed by the Chaetopod worms which are found in the tubes, and that the fistulose stem of the coral is formed by folding round and encrusting the horny tubes of the worm. *Neohelia* is found in the Pacific Ocean.[1]

Lophohelia is a genus forming dendritic colonies of considerable size. The calices have thick walls and are very deep. *Lophohelia prolifera* has been found in deep water off the island of Skye and in other localities off the west coast of Scotland. It is also not uncommon in some of the Norwegian fjords and in other parts of the world.

Oculina is another widely distributed genus found in the shallow tropical waters of the West Indies, the Indian and Pacific Oceans. It forms dendritic colonies of considerable size. The calices are usually arranged in a spiral manner on the branches. The colour of the West Indian species is stated to be light or dark brown when alive. The tentacles are arranged in three cycles, and are usually twenty-four in number. Asexual reproduction takes place by budding at the apex of the branches.

Fam. 3. Astraeidae.—This is a very large family, and

[1] E. M. Pratt, *Willey's Zoological Results*, pt. v. 1900, p. 591.

authorities are not agreed as to its limits or classification. Excluding the simple forms for the present, the family may be said to be distinguished by having the calices so closely crowded that there is little or no coenosteum between them. The corallum is compact and massive, unless bored and perforated by algae, worms, and other coral-destroying organisms.

The genera of Astraeidae that form colonies may be divided into two groups: the GEMMANTES and the FISSIPARANTES. In the group GEMMANTES asexual reproduction is effected by gemmation, and each zooid of a colony is a distinct individual with two pairs of directive mesenteries. Among the best known of recent corals included in this group may be mentioned *Galaxea*. In this genus there is a good deal more coenosteum between the calices than there is in most of the Astraeidae. The calices are long and project some distance above the coenosteum. The septa are exsert. In *Galaxea esperi* examined by Fowler[1] there are twelve septa, twelve pairs of mesenteries, and twenty-four tentacles, of which twelve are very small and twelve rather larger. The colour is green or brown. The genus is found in shallow water in the tropics of the old world.

In *Astrangia solitaria* the zooids are either isolated or more generally united by thin strands of perithecal tissue to form encrusting colonies. The septa are not exsert as in *Galaxea*. Six are prominent and belong to the first cycle, six smaller ones form a second cycle, and an incomplete third and fourth cycle may be seen. Corresponding with each septum there is a tentacle. The tentacles of the innermost cycle are the longest (3 mm. in length). All the tentacles terminate in a knobbed apex. The living zooids are colourless throughout, or display only very delicate tints within restricted areas.[2] This genus occurs principally on the coasts of the American continent, extending as far south as the Straits of Magellan. Other well-known genera of Astraeidae Gemmantes are *Orbicella*, *Cladocora*, *Phyllangia*.

In the group FISSIPARANTES asexual production takes place by fission without the production of morphologically complete zooids. The tentacles, mesenteries, and septa, when fission is established, are not arranged in regular hexameral cycles, and no

[1] G. H. Fowler, *Quart. Journ. Micr. Sci.* xxx. 1890, p. 410.
[2] J. E. Duerden, *Mem. Ac. Washington*, viii. 1902, p. 553.

new directive mesenteries arise. In some cases very large corals are formed, and, if our conception is correct, these must be regarded, not as a colony of zooids, but as a single individual zooid divided into a considerable number of incompletely separated parts. Among the well-known genera belonging to this group are *Euphyllia*, *Mussa*, *Meandrina*, *Coeloria*, *Favia*, and *Goniastraea*.

In such genera as *Euphyllia* the parts of the colony become separated by deep grooves, and have the superficial appearance of being distinct individuals; but in the Brain-coral *Coeloria* and others the surface of the coral presents a series of more or less bent or curved grooves, each with a row of slit-shaped mouths and bordered by rows of tentacles.

A number of genera of solitary corals united in the sub-family Trochosmiliacea are generally included in the family Astraeidae. The study of their skeletal characters has suggested[1] that they are more closely allied to the Turbinoliidae. The principal genera thus transferred would be *Trochosmilia*, *Placosmilia*, *Parasmilia*, and *Asterosmilia*. As these genera and their allies are nearly all extinct, and nothing is known of the structure of the living zooids, their removal from the Astraeidae may be regarded as not fully justified.

Fam. 4. Pocilloporidae.—The general anatomy of the zooids of this family of corals has some resemblance to that of the Entocnemaria, and it is possible that they will eventually find a place in our classification near to, if not actually within that group. The fact, however, that the skeleton is imperforate is sufficient for the present to justify the inclusion of the family in the section Aporosa. There are but two genera at present known, and in both of them the zooids have twelve tentacles, twelve mesenteries, and only two mesenterial filaments. The zooids are connected together by an elaborate system of canals running in the superficial coenosarc. The calices are bilaterally symmetrical, and in *Seriatopora* the septa which are parallel with the axis of the branch are united in the centre of the calyx, and are very much larger than the others, as in *Madrepora*. In all these characters the family shows affinities with the Entocnemaria. In the characters of the skeleton, which is imperforate and tabulate, the affinities are rather with the

[1] M. Ogilvie, *Trans. Roy. Soc.* clxxxvii. B. 1896.

Cyclocnemaria. The two genera are widely distributed on the coral reefs of the old world, and in some localities are very abundant. Neither genus is found in the West Indies. They are both of recent origin, but *Pocillopora* occurs in the Miocene. It is a remarkable feature of the family that both genera may be attacked by the gall-forming crab *Hapalocarcinus*. From some reefs nearly all the Pocilloporidae show crab-galls on a large number of their branches, whereas other Madreporaria are free from them.

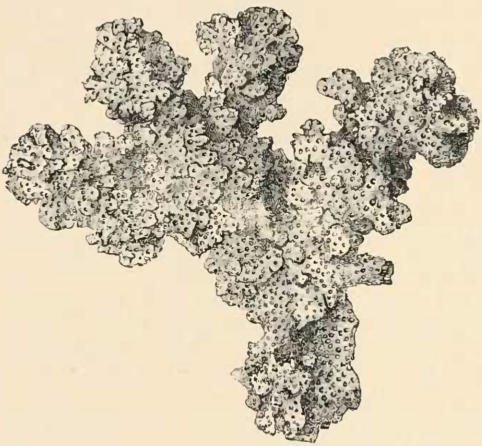

FIG. 175.—A portion of a colony of *Pocillopora* from the Maldive Archipelago.

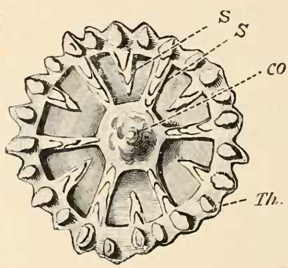

FIG. 176.—A single calyx of *Pocillopora septata*, showing *Co*, the columella; *S*, *S*, the septa; *Th*, the theca wall. (After Gardiner.)

Pocillopora is a coral that forms encrusting masses, rising into lobes or branches of considerable size, terminating in blunt apices. *Seriatopora* is much more slender and ramified, the branches terminating in sharp points.

SECT. 2. FUNGACEA.—This section of Cyclocnemaria contains a number of solitary and colonial corals of very varied form united in the possession of a number of cross-bars called "synapticula" connecting the septa, and thereby giving strength to the calyx apart from any increase in the thickness of the calyx-wall. The family Fungiidae shows many peculiarities which separate it very distinctly from both the Cyclocnemaria and the Aporosa. The Eupsammiidae, however, approach the Cyclocnemaria in many respects, and the Plesiofungiidae form a connecting link with the Astraeidae. It is very probable that this section had a dual origin, and therefore does not represent a single line of descent.

Fam. 5. Plesiofungiidae.—This family is related to the Aporosa in the possession of septa that are generally solid and imperforate, and to the Astraeidae in particular in the possession of dissepiments. They differ from them, however, in the presence of synapticula and in certain peculiarities of the tentacles.

The genus *Siderastraea* has recently been studied by Duerden.[1] The colony is usually massive and encrusting in habit. The zooids when expanded do not rise much above the level of the corallum. The tentacles are short and are arranged in irregular cycles on the disc. They terminate in knobbed extremities, and those of the inner cycles are bifurcated. The colour of *S. sideraea* is reddish-brown when alive. *Siderastraea* is found in shallow water on the coral reefs, and is widely distributed.

In *Agaricia* the colony is more foliaceous. The tentacles are rudimentary or small. The colour of the living zooids is very similar to that of *Siderastraea*. *Epistrelophyllum* is a solitary coral, from the Jurassic series, belonging to the family.

Fam. 6. Fungiidae.—*Fungia* is an unattached solitary coral of a flat disc-like shape with very numerous exsert imperforate septa. It is frequently of considerable size (six to twelve inches in diameter). On many of the coral reefs of the old world it is extremely abundant, and consequently it is one of the commonest corals of our collections. When alive the corallum is almost hidden by the disc, which is studded all over with very numerous long tentacles.[2] The colour varies in different species, but is usually brown. One species on the Australian barrier reef, *F. crassitentaculata*, is of a dark olive green colour, the tentacles terminating in white knobs.

The free adult Fungias are derived from a fixed stock called the trophozooid, from which the young Fungias are detached by transverse fission (see p. 388). The thecal wall of the young *Fungia* when detached from the trophozooid is perforated, but

[1] "The Coral *Siderastraea*," *Carnegie Inst.* No. 20, Washington, 1904.

[2] The reader is referred to the excellent photographs of living Fungias in Saville Kent's "Great Barrier Reef," 1893, pl. xxiv. p. 160.

the pores become largely filled up during the later growth of the coral.

There are several genera of colonial Fungiidae of less frequent occurrence, such as *Halomitra*, *Herpetolitha*, and *Cryptabacia*.

Fam. 7. Cycloseridae.—These are solitary or colonial Fungacea with an imperforate theca. *Bathyactis* occurs at great depths. *Diaseris*, shallow water on coral reefs.

Fam. 8. Plesioporitidae.—The septa in this family are trabeculate and perforate, resembling in this respect the septa of Poritidae. *Leptophyllia*, *Microsolena*, extinct.

Fam. 9. Eupsammiidae.—This family of perforate corals is usually placed with the Madreporidae and Poritidae in the old group Perforata. The researches of Fowler and Gardiner have shown that the arrangement of the mesenteries is that of the Cyclocnemaria, and the presence of synapticula connecting the septa suggests affinities with the Fungacea. The synapticula of the Eupsammiidae, however, are peculiar in being arranged, not in a vertical series, but alternately with one another or quite irregularly in position. The members of this family are solitary or colonial in habit.

Stephanophyllia is a flattened disc-shaped coral, with perforate and dentate septa, found in the Pacific Ocean and as a fossil in various strata since Cretaceous times.

In *Leptopenus*, from depths of about 1500 fathoms, the perforations are much larger than in the last-named genus, and the skeleton is reduced to a system of slender trabeculae.

Rhodopsammia has a conical shape, and gives rise by gemmation to a number of young zooids, which remain attached for some time to the parent form before becoming free.

Among the colonial genera are *Dendrophyllia*, *Coenopsammia*, and the well-known Mediterranean genus *Astroides*.

Order IV. Zoanthidea.

This order of Zoantharia consists of a number of solitary or colonial Anemones that do not form a skeleton of horn or carbonate of lime, and are distinguished from the Actiniaria by the peculiar arrangement of their mesenteries.

Fam. 1. Zoanthidae.—*Sphenopus* is a solitary coral and terminates aborally in a small sucker-like base, by which it may be attached to foreign bodies. The genera *Gemmaria* and *Isaurus* include solitary forms.

In the majority of the species of Zoanthids, however, a basal encrusting stolon is formed, which may be thick and fleshy or membranous, or may consist of a plexus of bands from which several zooids rise and on which the new buds are formed.

The tentacles are numerous, simple, usually short, and arranged in one or two circles on the margin of the disc. Most Zoanthidae are encrusted with sand, shell fragments, or sponge spicules, but *Zoanthus* and *Isaurus* are naked. The foreign particles that form the incrustation are firmly attached to the ectoderm, and as a rule many of them sink down into the mesogloea to give additional support to the body-wall. It is the presence of so much incorporated sand that frequently gives these Zoantharia such a very brittle character. The stomodaeum usually exhibits a well-marked ventral siphonoglyph. The mesenteries consist of a pair of complete ventral directives, a pair of incomplete dorsal directives, while of the remaining protocnemes the lateral mesenteries which are first and second in the order of appearance are complete, the sixth is incomplete, whereas the fifth is complete in the Macrocneminae and incomplete in the Brachycneminae. Duerden[1] has found in specimens of three species that the arrangement of the mesenteries is "brachycnemic" (the sixth protocneme imperfect) on one side and "macrocnemic" (the sixth protocneme perfect) on the other. The metacnemes appear in the spaces between the sixth protocnemes and the ventral directives in unilateral pairs, of which one becomes complete and the other always remains incomplete (Fig. 163, 4, p. 368).

The Zoanthidae are usually dioecious, but hermaphroditism undoubtedly occurs in the genera *Zoanthus* and *Isaurus*. Little is known of their development, but a larval form discovered by Semper off the Cape of Good Hope, of cylindrical shape, with an opening at each end and distinguished by a longitudinal band of cilia running from one end to the other, is probably the larva of a Zoanthid. It is commonly known as Semper's larva. Other larvae provided with a ring of cilia have also been attributed to this group.

A great many Zoanthidae are epizoic in habit. Thus several

[1] *Trans. Roy. Soc. Dubl.* (2) vi. 1898, p. 331.

species of *Epizoanthus* form colonies on the shells of Gasteropods inhabited by hermit crabs. *Parazoanthus tunicans* is found on the stem of a *Plumularia*; *Parazoanthus separatus*, from Jamaica, is associated with a sponge. The base of the bundle of long spicules of the Sponge *Hyalonema* (p. 204) is almost invariably sheathed by a colony of *Epizoanthus stellaris*.

The only genera occurring within the British area are *Epizoanthus* (with six species), *Parazoanthus* (with four species), and *Zoanthus sulcatus*.

Of the species of *Epizoanthus*, *E. incrustatus* is fairly common, in depths of twenty to eighty fathoms on all our coasts, and is frequently commensal with different species of hermit crabs, while *E. paguriphilus* is found in much deeper water off the west coast of Ireland and is always commensal with hermit crabs. *Parazoanthus anguicomus* is found at depths of a hundred fathoms off the Shetlands and west of Ireland, and is usually associated with various species of Sponges.

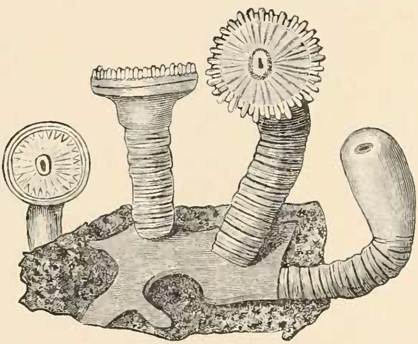

Fig. 177.—*Zoanthus macgillivrayi*, a small colony. The tentacles are shown somewhat contracted by the preservative. Each zooid is about 25 mm. in length. (After Haddon.)

Gerardia savalia is the largest "black coral" of the Mediterranean. The colony begins by encrusting the stem of one of the Gorgoniidae, but soon surpassing its support in growth, it forms a basal horny skeleton of its own and builds up very large branching colonies. A specimen in the British Museum,[1] from twenty fathoms off the island Negropont, is two metres high and two metres wide. The genus appears to be related anatomically to *Parazoanthus*.

Fam. 2. Zaphrentidae.—This family of Palaeozoic corals is usually placed with the Turbinoliidae or in the separate group Tetracoralla. Recently Duerden[2] has given reasons, based on the method of increase of the septa in *Lophophyllum*, for believing that their affinities lie rather with the Zoanthidae than

[1] F. J. Bell, *Trans. Zool. Soc.* xiii. pt. ii. 1891, p. 87.

[2] J. E. Duerden, *Ann. Mag. Nat. Hist.* (7) ix. 1902, p. 381.

with the Madreporaria. They are solitary turbinate corals, with numerous septa exhibiting a distinct bilateral symmetry in arrangement. *Zaphrentis, Lophophyllum.*

Order V. Antipathidea = Antipatharia.

The members of this order can readily be distinguished from all other Zoantharia by the presence of a horny axial skeleton (sclerobase) and the absence of any spicules of calcium carbonate. The skeleton is covered by a thin bark which consists of a number of simple, naked zooids united at their edges. The zooids bear six tentacles, or if there are more than six, six large prominent tentacles. In most genera there are but ten mesenteries, in others twelve. In *Cladopathes* only six mesenteries are found. The skeleton of the Antipathidea is simple in *Stichopathes* and *Cirripathes,* but in all other genera it is ramified. The ramification is usually profuse and irregular. The horny substance of which it is composed is free from any deposit or infiltration of lime. The surface of the younger branches is beset with numerous short spines, the number and arrangement of which are characters largely used in the determination of species. The basal parts of the main axis and the thicker branches are frequently bare, the zooids having died and become disintegrated. In these cases the spines wear away and the skeleton appears to be smooth. The presence of spines on some of the branches is, however, generally sufficient to enable the naturalist to distinguish a dried Antipathid from the axis of a Gorgonid, with which alone it might be confounded.

There are six complete mesenteries in each zooid, but as they bear no retractor muscles it is not certain that they represent the first six protocnemes of other Zoantharia. In a great many species the zooids are oval in shape, the longer diameter being parallel with the axis of the branch. The mouth and stomodaeum are compressed and at right angles to this diameter. It is usually assumed that the mesenteries attached to the angles of the stomodaeum are the directives, and that the remaining pair, which is axial in direction, corresponds with the first pair of protocnemes. The axial pair of mesenteries is frequently very well developed and alone bears the gonads. When other mesenteries are formed they always arise in bilateral pairs between the axial mesenteries and the directives. The tentacles correspond with the intermesenteric chambers. In some genera there is a constriction of the zooid between the pairs of the tentacles on each side of the axial mesenteries and the directive tentacles. This gives them the appearance of a division into three zooids with two tentacles apiece, one with a mouth and two without a mouth; and as the mouthless parts alone bear the gonads on the single axial mesentery, they have been called the "gastrozooids" and "gonozooids" respectively. This must not be regarded, however, as a case of true dimorphism, as the cavities of the so-called gastrozooid and gonozooids are continuous.

The Antipatharia are widely distributed in nearly all the great seas of the world. Some species are found in shallow water in the tropics, but most of them occur in depths of fifty to five hundred fathoms. The genus *Bathypathes* is only found at enormous depths ranging from 1070 to 2900 fathoms. Specimens of *Cirripathes spiralis*, *Antipathella gracilis*, and another species have recently been obtained in deep water off the west coast of Ireland,[1] but these are the only Antipatharia known to occur within the British area.

The very simple structure of the Antipatharia is usually attributed to degeneration. On this view the Antipathidae with only six complete mesenteries are the most modified, whereas the Leiopathidae with twelve mesenteries are more closely related to the ancestral forms, and *Gephyra dohrnii* (see p. 382) is a link connecting the order with the Actiniaria.

There is no reason, however, for supposing that *Gephyra* is specially related to this order, and, as pointed out recently by Roule,[2] the simple structure of the zooids of the Antipathidea is more easily explained if they are regarded as primitive forms.

Gerardia (p. 406), from the Mediterranean, forms a horny axial skeleton like that of the Antipathidea, but this genus is probably a Zoanthid.

Fam. 1. Antipathidae.—In this family the zooids have six tentacles and six or ten mesenteries. It includes nearly all the familiar genera, such as *Stichopathes*, *Cirripathes*, *Antipathes*, *Antipathella*, *Cladopathes*, and *Bathypathes*. *Schizopathes* and

[1] Hickson, *Nature*, lxxiii. 1905, p. 5.
[2] L. Roule, *Bull. Mus. Océanogr. Monaco*, 1904, p. 3.

its allies occurring in deep water are the forms regarded by Brook as dimorphic.

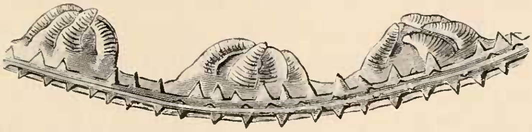

FIG. 178.—A portion of a branch of *Antipathes ternatensis*, showing three zooids and the horny axis beset with thorn-like projections. (After Schultze.)

Fam. 2. Leiopathidae.—This family includes the single genus *Leiopathes* of the Mediterranean Sea. It is distinguished from the others by the presence of twelve mesenteries.

Fam. 3. Dendrobrachiidae.—This family also consists of a single genus, *Dendrobrachia*, from 400 fathoms in the South Atlantic. It is distinguished by having pinnate retractile tentacles.

Order VI. Cerianthidea.

This order contains the remarkable Sea-anemone called *Cerianthus.* Two of the species have been placed in separate genera, but they do not appear to be of more than sub-generic rank. *Cerianthus* has a long cylindrical body with a double crown of numerous long tentacles at the oral extremity and tapering to a blunt point or rounded at the aboral extremity.

There are numerous mesenteries, which increase in number by the addition of bilateral pairs, arising only in the ventral inter-mesenteric space throughout the greater part, if not the whole, of the life of the zooid. The right mesentery of each young pair is always more advanced than the left, so that the mesenteries have the appearance of arising alternately right and left. None of the mesenteries bear conspicuous bands of retractor muscles. The movements of the body are effected by a thick band of longitudinal fibres lying between the ectoderm and the mesogloea in the body-wall.

The absence or very slight development of muscles on the mesenteries renders it difficult to recognise the homologues of the protocnemes of other Zoantharia in the adult. From the evidence of embryology, however, it seems certain that the six dorsal pairs of mesenteries represent the protocnemes (Fig. 163, 3, p. 368) and the others are metacnemes.

The stomodaeum exhibits a single long deep siphonoglyph, which is probably dorsal in position.

There are two tentacles to each inter-mesenteric space, one being marginal and the other circumoral. The gonads are borne upon alternate mesenteries, and both ova and spermatozoa are produced by the same individual.

The ectoderm of *Cerianthus* is remarkable for the immense number of nematocysts and gland cells. The latter secrete a

FIG. 179.—*Cerianthus membranaceus.* Colour pink, with tentacles annulated pink and brown. About 35 cm. in length. (After Andres.)

quantity of mucus which binds the threads of the discharged nematocysts into a sticky feltwork and this secures particles of sand and mud, the whole forming a long tube in which the animal freely moves. This tube is often of considerable thickness. It is tough and resistant, smooth inside but ragged and muddy outside. It is often many times the length of the animal's body.

The embryo of *Cerianthus* is set free before the completion of segmentation, and it gives rise to a floating pelagic larva known as *Arachnactis.* It has a variable number of tentacles and mesenteries according to its age, but when it reaches a size of about 15 mm. in length it has developed characters which are sufficient to determine its position as a Cerianthid.

The genus *Cerianthus* appears to be widely distributed. *C. membranaceus* is the common species in the Mediterranean Sea, but a smaller species has been described from Naples under the name *C. oligopodus* by Cerfontaine. *C. americanus* occurs on the eastern coasts of North America. The British and North European species is *C. lloydii*, but another species, *C. vogti*, has been found at a depth of 498 fathoms in the North Sea. *C. nobilis* is a gigantic species supposed to be about 1 foot in length when complete, from Torres Straits.

C. bathymetricus of Moseley, placed by Andres in the genus *Bathyanthus*, is a species of small size (25 mm.), obtained by the "Challenger" from a depth of 2750 fathoms in the North Atlantic. It exhibits a remarkable prolongation of the stomodaeum into the coelenteron in the form of a sack which contained food. Moseley described a species of *Cerianthus*, 6 inches long, living on the coral reef at Zebu in the Philippines fully expanded in the tropical sunshine.

Several species of *Arachnactis* larvae have been described. Of these *Arachnactis lloydii* appears to be undoubtedly the larva of *C. lloydii*. The adult forms of *Arachnactis albida* from various stations in the Atlantic Ocean and of *Arachnactis americana* are not known. The larva of *Cerianthus membranaceus* has been called *Dianthea nobilis*, and is characterised by the great length of the column, by the general opacity of all parts of the body, and by the precocious appearance of the median marginal tentacle. A considerable number of remarkable pelagic larvae have been described by van Beneden[1] from the Atlantic Ocean, and provisionally assigned by him to five different genera. The adult forms of these larvae are not known, but they are probably members of this order.

[1] E. van Beneden, *Les Anthozoaires de la Plankton Expédition*, Kiel, 1898.

CHAPTER XV

CTENOPHORA

The Ctenophora are spherical, lobed, thimble-shaped, or band-like animals, usually very transparent and gelatinous in structure. They are exclusively marine, and are found floating at or near the surface of the sea.

Although they are generally classified with the Coelenterata, they are regarded by some authors as having closer affinities with the Polyclad Turbellaria (cf. Vol. II. p. 7). They agree, however, with neither of these divisions in their essential characters, and the only way to indicate and emphasise their unique position is to place them in a separate Phylum.

They differ from all the Coelenterata in the absence of nematocysts, and in the presence in development of a definite mesoblast. The character from which they derive their name, Ctenophora, is the presence on the surface of bands of swimming plates. The plates are called the "combs" (κτείς, gen. κτενός = a comb) or "ctenophoral plates." They occur in all genera included in the Phylum except in *Coeloplana* (Fig. 183, p. 422).

Another peculiarity of all Ctenophora (except the Beroidae) is the presence, at some stage in the life-history, of two long and extremely contractile tentacles. There is also a well-developed sense-organ (statocyst) in the centre of the aboral area of the body.

The Ctenophora differ from the Turbellaria in the presence of the combs and of the two long tentacles, in the position and relative importance of the statocyst, and, with the exception of *Coeloplana*, in the general characters of the alimentary canal.

Shape.—Several of the Ctenophora are conical or spherical in shape, but exhibit at the pole where the mouth is situated

(Fig. 180, *M*) a slight conical projection, and at the opposite pole where the sense-organ is placed a slight depression (*Ab*). In others, the sides of the body are drawn out into a pair of wing-like lobes (Lobata), and the body is considerably flattened or compressed (Fig. 181). The Cestoidea have a long flattened ribbon- or band-shape (Fig. 182), and the Platyctenea (Fig. 183) are flattened in the oro-apical axis and exhibit a well-marked distinction between the dorsal and ventral surfaces. The shape of *Beroe* is that of a hollow cone or thimble.

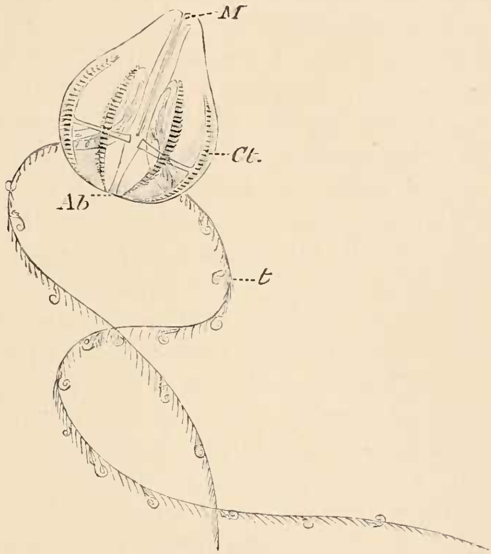

FIG. 180.—*Hormiphora plumosa.* *Ab*, position of the aboral sense-organ; *Ct*, rib of ctenophoral plates; *M*, mouth; *t*, tentacle, with two kinds of pinnae. (After Chun.)

Ctenophoral plates.—In many Ctenophora eight lines can be traced, like the lines of longitude on a globe, from the area of the sense-organ to the base of the mouth-cone or hypostome. In the course of these lines are situated the ctenophoral plates. In some species they extend along the greater part of these lines of longitude, but in others they are more restricted. That part of the line that bears the plates is called the "rib" or "costa." These plates or combs form the principal organs of locomotion of the Ctenophores. They consist of a row of cilia fused at the base (cf. p. 141) to form the plate, but free at the extremity where they form the comb-like edge. They are alternately raised, by a rapid contractile action, and then slowly flattened down again. The plates are raised in succession from the aboral to the oral end of each rib, and the appearance given to the bands in the living animal is that of a series of waves travelling down the lines of longitude from the sensory area towards the mouth. The effect of these rhythmic movements of the combs is to drive the animal slowly through the water with the oral cone forwards. In some Ctenophores the costæ are phosphorescent.[1]

Tentacles.—In all the Ctenophora, except the Beroidae and the adult stages of Lobata and Cestoidea, there is a single pair of tentacles. They are attached to the base of a blind funnel-shaped pit which opens to the exterior near the equator of the animal's body. The pits are on opposite sides of the body, and the plane which passes through them both vertically divides the body into approximately equal parts. It is called the "tentacular" or "transverse" plane (Fig. 180). The plane at right angles to this, which also passes through the mouth and statocyst, is called the "sagittal" plane.

The tentacles are solid, and in the Cydippidae, of considerable length. During life they are usually extended, and trail behind the animal as it progresses through the water. But they are extremely contractile, and when the animal is alarmed are suddenly withdrawn into the shelter of the tentacular pits. Each tentacle usually bears a row of short pinnae. The surfaces of the tentacles and of their pinnae are crowded with remarkable cells which carry little globules of an adhesive secretion, and are called the glue-cells or "colloblasts." These cells stick to any foreign body they touch, and may be drawn out some distance from the tentacle, but they remain attached to it by a long spiral thread which unwinds as the cell is pulled out. Although the colloblasts have the function of catching prey similar to that of the nematocysts of Coelenterata, they are true animal cells and are not therefore homologous with nematocysts, which are the cell products of the cnidoblasts.[2]

The Lobata and Cestoidea pass through a stage in development called the Cydippiform or *Mertensia* stage, when they possess a single pair of long tentacles similar to those described above. In the adult condition, however, these tentacles are absent, and their functions are performed by numerous small accessory tentacles or tentilla arranged in rows on definite lines along the body-wall.

Sense-organ.—At the aboral pole of the Ctenophore there is a hard granulated calcareous body, the "statolith." This is

[1] A. W. Peters, *Journ. Exper. Zool.* ii. (1) 1905, p. 103.

[2] Cnidoblasts are stated by Chun to occur on the tentacles of *Euchlora*; and batteries of "nettle cells" by Abbott on the tentacles of *Coeloplana*.

supported by four tufts of fused cilia, and is usually covered by a dome of delicate protoplasmic texture, which is believed to be formed by a fusion of cilia. The dome enclosing the statolith is called the "statocyst."

Supporting the statocyst there is a circular or oval area of ciliated epithelium which is usually supposed, but on insufficient evidence, to be specially sensory in function. Extending from this area in the sagittal plane there are two strips of ciliated epithelium called the "polar fields."

The aboral sense-organ of the Ctenophora is one of the most characteristic organs of the Phylum. The aboral pole of the Medusae of Coelenterata is usually devoid of any special modification of the ectoderm of the bell, and in the Tiarid genus *Stomatoca* the little tassel at the aboral pole of the Medusa cannot in any sense be regarded as a homologue of the sense-organ of the Ctenophore. If the aboral sense-organ of the Ctenophora can be compared with that of any other group of animals, it would be with the statocyst of many of the Turbellaria, such as that of *Convoluta*, but it is far more satisfactory to regard it as an organ peculiar to the Ctenophora and as having no true relationship with any sense-organ found in other animals.

Alimentary Canal. — The mouth of the Cydippiform Ctenophores opens into a sac-like chamber called the "stomodaeum," flattened in the sagittal plane and stretching from the oral pole as far as the centre of the body. The stomodaeum passes into a chamber flattened in the transverse plane called the "infundibulum." From the infundibulum a narrow tube passes in the direction of the aboral pole called the "intestine," and from the extremity of this four short tubes pass to the sides of the polar fields at the place where these fields join the sensory area. Two, or, in some cases, all four of these tubes open to the exterior; but they do not appear to serve the purpose of ejecting the undigested portions of the food, which usually pass to the exterior by the mouth as in Coelenterata and Turbellaria.

From the lateral extremities of the infundibulum four pairs of tubes pass to the equatorial region of the body, where each one joins a longitudinal vessel which runs immediately beneath the epithelium supporting the ribs. These are called the longitudinal or "sub-costal" canals. From the infundibulum there also passes a single pair of blind canals, the "paragastric canals," one on each side of the stomodaeum, to end in the oral cone.

In the Lobata the paragastric canals communicate with the longitudinal canals under the transverse costae,[1] and send long blind processes into the lobes. In the Cestoidea the arrangement of the canals is considerably modified in adaptation to the needs of the ribbon-like body. In the Beroidae the paragastric and longitudinal canals are in communication by a peripheral network of canals, and in the Platyctenea there is also a network of canals but without any definite longitudinal vessels.

Sexual Organs.—Most of the Ctenophora are undoubtedly hermaphrodite, but Willey was unable to find ova in some of his specimens of *Ctenoplana* that were producing spermatozoa. In the Cydippidea the ova are produced on one side of the longitudinal canal and the spermatozoa on the other. Each longitudinal canal therefore performs the functions of a hermaphrodite gland. When the sexual cells are ripe they escape into the infundibulum and are discharged by the mouth. In *Ctenoplana* there are definite and direct male genital ducts.

The ova are very small when discharged and undergo complete segmentation in the sea water. The development of the Cydippidea is really direct, but there is a stage passed through in which the tentacles are relatively very prominent and situated close to the aboral pole, and this stage is very different in appearance from the adult. In the Lobata and Cestoidea there is, however, a definite larval stage, of the general appearance of a *Mertensia*, and during this stage fertile eggs and spermatozoa are formed and set free.

Distribution. — Ctenophora are found at the surface of nearly all seas, and many of the genera have a cosmopolitan distribution. Some of the Lobata, the Cestoidea, and the Platyctenea are more commonly found in the warmer regions of the world. *Pleurobrachia pileus*, *Bolina infundibulum*, *Beroe ovata*, and *B. cucumis* occur off the British coast.

Most of the Ctenophora are from 5 to 20 mm. in diameter, but *Beroe* reaches the length of 90 mm., *Eucharis multicornis*

[1] The two costae that are seen in the middle when the Ctenophore is viewed in the transverse plane, as in Figs. 180 and 181, and the corresponding costae on the opposite side are called the "transverse" costae; the other four are called the "sagittal" costae.

a height of 250 mm., and *Cestus veneris* has been found no less than $1\frac{1}{2}$ metres from one extremity to the other.

Ctenophores usually go about in shoals, and in the case of *Beroe cucumis* and *Eucharis multicornis* the shoals may be of very great extent. *Pleurobrachia pileus* of the British coasts is often found at the end of the season (July) as a series of isolated individuals; but in June they occur in small shoals, swimming so close together that they will choke a tow-net in a very short space of time.

CLASS I. TENTACULATA

Ctenophora provided with a pair of tentacles in the larval stages only or in both larval and adult stages.

Order I. Cydippidea.

This order includes a number of spherical or oval Ctenophores, with a pair of tentacles retractile into deep tentacular pits in the adult stage.

Fam. 1. Mertensiidae.—The body is compressed in the transverse plane, and the ribs on the transverse areas are longer than those on the sagittal areas. The family includes the genus *Euchlora*, which occurs in the Mediterranean and in the northern part of the Atlantic Ocean. In *Charistephane* there are only two enormous ctenophoral plates in each of the longitudinal tracts. These plates are so broad that they almost meet laterally to form two continuous circlets round the body of the animal. This genus is found in the Mediterranean, but a few specimens have also been obtained in the Atlantic.

In *Tinerfe* the body is almost cylindrical, and there is a pair of kidney-shaped swellings at the sides of the aboral pole. It has a pale blue colour, and is found in the Guinea and south equatorial currents of the Atlantic Ocean.

The name *Mertensia* has been given to several forms that are undoubtedly the young stages of genera belonging to the Lobata, but Chun retains the name *M. ovum* for a species which is very abundant in the Arctic currents of the North Atlantic.

Fam. 2. Callianiridae.—Two or four wing-like processes, into which the longitudinal canals extend, are found at the aboral pole. *Callianira* has two of these processes arranged in the transverse plane, and *Lophoctenia* has four. *Callianira* is found in the Mediterranean and in the Atlantic from the Arctic to the Antarctic waters.

Fam. 3. Pleurobrachiidae.—The body is almost spherical in form, and the eight ribs are equal in length.

This family includes the genus *Pleurobrachia,* in which the ribs extend for a considerable distance along the lines of longitude of the spherical body, but do not reach either the oral or the aboral areas. *P. pileus* is the commonest British Ctenophore, and may be found in shoals in May, June, and July at the surface of the sea or cast up on the sand as the tide ebbs. It is widely distributed in the North Atlantic waters. *P. rhodopis* of the Mediterranean has rather shorter ribs than *P. pileus.* Two new species have recently been described from the Malay Archipelago.[1] *Hormiphora* (Fig. 180, p. 413) differs from *Pleurobrachia* in having much shorter ribs, and in possessing two kinds of pinnae on the tentacles, those of the ordinary kind and others much larger and sometimes palmate in character. This genus has a world-wide distribution.

In *Lampetia* and *Euplokamis* the body is more cylindrical in shape than it is in the other genera, but the ribs and subjacent longitudinal canals extend up to the margin of the aboral field. Both these genera occur in the Mediterranean, but *Lampetia* is also found in the Malay Archipelago.

Order II. Lobata.

The body is considerably flattened in the transverse plane, and the sagittal areas are extended into the form of two wide peristomial lobes. The oral ends of the areas between the transverse and sagittal ribs are extended to form four flaps, called the "auricles." There are no tentacles nor tentacle-sheaths of the ordinary kind in the adult form; but numerous tentilla, similar in some respects to the pinnae of the tentacles of other Ctenophora, form a fringe round the margin of the auricles and the peristome. A single pair of long, filamentous, non-retractile tentacles arise from the sides of the peristomium in *Eucharis*

[1] F. Mosser, "Ctenophoren der Siboga Expedition," Leiden, 1903.

multicornis. These tentacles have no sheaths, and do not bear pinnae. They are probably not homologous with those of other Ctenophora.

The characters that separate the families of Lobata are chiefly those of varying size, shape, and position of the peristomial lobes and auricles. In the Lesueuriidae the peristomial lobes are rudimentary; in the other families they are moderately or very large. In the Bolinidae the auricles are short, but in most of the other families they are long and ribbon-like. In *Eucharis* they can be spirally twisted in repose.

The modifications of the external form seen in the Lobata are accompanied by some modifications of the internal structure Among these, perhaps the most interesting is a communication between the transverse longitudinal and the paragastric canals, and the long convoluted tubes given off to the peristomial lobes by the sagittal longitudinal canals. Very little is known about the life-history and development of most of the Lobata, but Chun has shown that in *Eucharis* and *Bolina* there is a Cydippiform larval stage which produces ripe ova and spermatozoa. This is followed by a period of sterility, but when the adult characters are developed they become again sexually mature. To this series of sexual phenomena the name "Dissogony" is given.

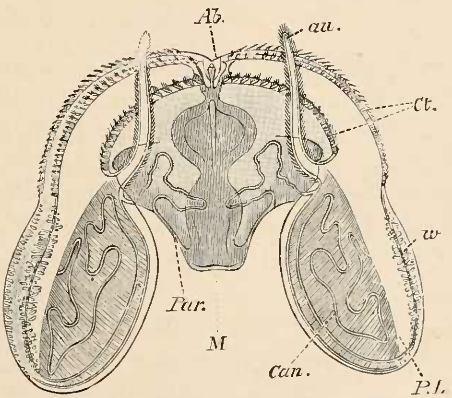

FIG. 181.—*Ocyroe crystallina*. *Ab*, aboral sense-organ; *au*, auricle; *Can*, diverticulum from the paragastric canal passing into peristomial lobe; *Ct*, costae; *M*, mouth; *Par*, paragastric canal passing outwards to join one of the transverse subcostal canals; *P.L.* peristomial lobe; *w*, wart-like tubercles on the lobe. (After Mayer.)

The order contains only fifteen genera, but they are usually arranged in the following eight families:—

1. **Lesueuriidae.** *Lesueuria.*
2. **Bolinidae.** *Bolina, Bolinopsis.*
3. **Deiopeidae.** *Deiopea.*
4. **Eurhamphaeidae.** *Eurhamphaea.*

5. **Eucharidae.** *Eucharis.*
6. **Mnemiidae.** *Mnemia, Mnemiopsis.*
7. **Calymmidae.** *Calymma.*
8. **Ocyroidae.** *Ocyroe.*

Most of these Ctenophores occur in the warm and tropical seas; but *Bolina* is found occasionally at Plymouth in the month of May, on the west coast of Ireland, and at other stations on the British coasts. *Eucharis* is regarded as one of the most beautiful of the Phylum. A swarm, some miles in length, of large specimens of *E. multicornis* was met by the Plankton Expedition in the south equatorial current of the Atlantic during the month of September.

Order III. Cestoidea.

In this order the body is so much compressed in the transverse plane and elongated in the sagittal plane that it assumes the shape of a long narrow band or ribbon. The tentacular sheaths are present but the tentacles are degenerate in the adult. The tentacular functions are performed by numerous tentilla situated in long grooves extending along the whole length of the oral side of the band-like body. The transverse ribs are reduced; the sagittal ribs extend along the whole of the aboral side.

Fam. Cestidae.—This is the only family of the order. *Cestus veneris*, the Venus's girdle of the Mediterranean Sea, is also found in the Atlantic Ocean, and specimens belonging to the

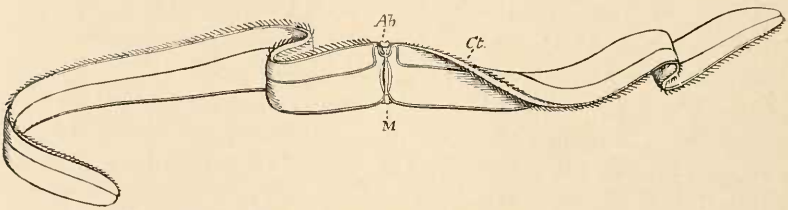

FIG. 182.—*Cestus pectenalis.* *Ab*, aboral sense-organ; *Ct*, the sagittal ribs; *M*, mouth. (After Bigelow.)

same genus, but probably to a different species, occur as far north as the White Sea. Some of the larger specimens are considerably over 1 metre in length.

C. pectenalis was found in abundance off one of the Maldive Islands,[1] and differs from *C. veneris* in having a large and pro-

[1] H. B. Bigelow, *Bull. Mus. Comp. Zool.* xxxix. 1904, p. 267.

minent orange patch at each end of the body. It is said to be extremely graceful in the water, moving with slow, ribbon-like undulations, and shining in the sunlight with a violet iridescence. *Vexillum,* from the Mediterranean Sea and Canary Islands, is rather more pointed at the extremities than *Cestus,* and differs from it in some important anatomical characters.

Order IV. Platyctenea.

This order has been constituted for two remarkable genera, in which the oro-apical axis is so much reduced that distinct dorsal and ventral surfaces can be distinguished.

There is a single pair of long milky-white tentacles capable of complete retraction into tentacular sheaths.

Fam. 1. Ctenoplanidae.—*Ctenoplana* was discovered by Korotneff in 1886 floating with the Plankton off the coast of Sumatra. In 1896 Willey[1] discovered four specimens on a cuttle-bone floating off the coast of New Guinea. To these authors we are indebted for the only accounts of this animal that have been published.

When the *Ctenoplana* is creeping on the bottom of a dish or with its dorsal side downwards on the surface film of the water, it has the form of a flattened disc with a notch on each side. On the upper or dorsal surface eight short rows of ctenophoral plates may be seen, and in a position corresponding with the two notches in the margin of the body are situated the two sheaths from which the long pinnate tentacles protrude. In the exact centre of the dorsal surface is situated the statolith, supported by stiff processes from adjacent cells; and forming a circlet round the statolith there is a row of short ciliated tentacles. These tentacles, however, when examined carefully in the living animal, are found to be arranged in two sets of about nine in each, separated by narrow gaps on each side, the gaps corresponding in position with the axis through the tentacles.

When the animal is swimming it assumes a helmet-shape by depressing the sides of the body like a pair of flaps on the tentacular axis, and then the ctenophoral plates come into play and produce the progressive movements of the animals. The pinnate tentacles are opaque white in colour, and have peculiar serpentine

[1] *Quart. Journ. Micr. Sci.* xxxix. 1897, p. 323.

movements. Very little is known at present concerning many details of the internal anatomy, but there is one point of considerable theoretical interest—namely, the presence of definite male genital ducts.

Three of Dr. Willey's specimens were mottled with a green pigment, whereas his fourth specimen and Korotneff's only specimen were mottled with a red pigment. It has yet to be determined whether the differences which have been observed in the individual specimens are of specific value.

Fam. 2. Coeloplanidae.—*Coeloplana* was originally discovered by Kowalevsky in the Red Sea, but has recently been found by Abbott[1] on the coast of Japan.

The Japanese species are found principally on encrusting Algae, *Zostera*, *Melobesia*, etc., which they resemble very closely in colour. The Red Sea species is, according to Kowalevsky, ciliated all over, but the Japanese species are ciliated only on the ventral surface. As in *Ctenoplana*, the body of *Coeloplana* is a flattened disc with a notch at each end of the tentacular axis, when creeping; but *Coeloplana* does not swim, nor at any time does it assume a helmet-shape. The tentacles are very long and of a chalky-white colour. They can be retracted into tentacle-sheaths. When the animal is excited it throws out the whole tentacle in a cloud of white filaments, "and to watch it at such a time, shooting out and retracting the tentacles, moving along the side of the aquarium like a battleship in action is truly a remarkable spectacle."[2] On the dorsal side of the body there is a series of processes which are called the dorsal tentacles. The statolith is very small, and is not surrounded by sensory processes as it is in *Ctenoplana*. There are no ctenophoral plates. The colours of the Japanese

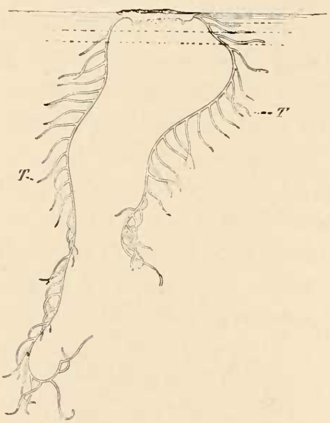

FIG. 183.—*Coeloplana mitsukurii*, floating at the surface of the sea with the dorsal side downwards. *T*, *T*, the tentacles expanded. (After Abbott.)

[1] *Annot. Zoolog. Japon.* iv. pt. iv. 1902, p. 103.
[2] Abbott, *l.c.* p. 106.

species are scarlet or carmine red and dirty brown or brownish yellow. They are from 1 to 2 centimetres in diameter.

CLASS II. NUDA

Ctenophora without tentacles.

Fam. Beroidae.—*Beroe*, the only genus of this family and class, differs from other Ctenophora in several important particulars. There are no tentacles, and the stomodaeum is so large that the body-form assumes that of a thimble with moderately thick walls. The infundibulum is small. The paragastric and longitudinal canals give rise to numerous ramifications which form a network distributed throughout the surface of the body. The statolith is unprotected by a dome, and the polar fields are bordered by a number of small branching papillae. The eight ribs extend for nearly the whole length of the body. *Beroe* is almost cosmopolitan, and is frequently found at the surface of the sea in great numbers. *B. ovata* is found off the Shetlands, Hebrides, and west coast of Ireland, but is rare on the east coast of the British Islands and in the English Channel. At Valencia it is common in August and September, and sometimes reaches the great size of 90 mm. in length by 50 mm. in breadth. It is usually of a pale pink colour.

Appendix to Ctenophora

Hydroctena salenskii has recently been discovered by Dawydoff[1] floating with the Plankton off the island Saparua in the Malay Archipelago. It is claimed to be a connecting link between the Ctenophora and the Medusae of the Hydrozoa.

In external features it is like one of the Narcomedusae, having a transparent jelly-like bell with a wide bell-mouth guarded by a velum (Fig. 184, *V*). There are only two simple but solid tentacles (*t*), provided with tentacle-sheaths, but inserted on opposite sides of the bell—not on the margin, but, as in the Ctenophore, at a level not far removed from the aboral pole. At the aboral pole there is a minute pore surrounded by a high ciliated epithelium bearing an orange pigment. This leads into

[1] *Zool. Anz.* xxvii. 1904, p. 223.

a short blind canal, which terminates in an ampulla bearing two statoliths supported by elastic processes from the ampullar epithelium.

The sub-umbrellar cavity extends for a distance of about one-half the height of the bell. The mouth (*M*), which opens into this cavity, leads into a wide cavity that gives off a short blind canal to the side of each tentacular sheath, and a straight tube that leads straight to the statocyst, where it also ends blindly.

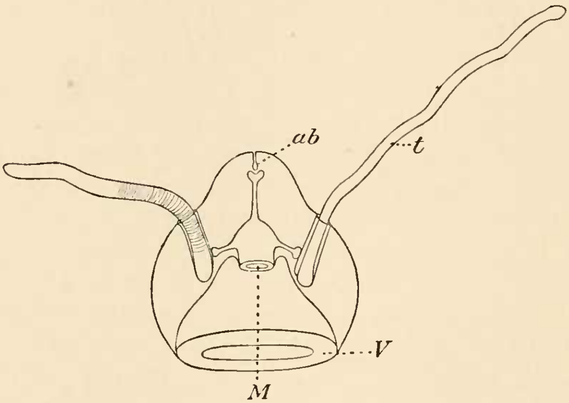

FIG. 184.—*Hydroctena salenskii.* *ab*, Aboral organ; *M*, manubrium; *t*, tentacle; *V*, velum. (After Dawydoff.)

There are no radial canals and no ring canal at the margin of the umbrella. There are also no ctenophoral plates. In the absence of any information concerning the position of the genital glands, the character of the epithelium of the tentacles and the development, we are not justified in regarding *Hydroctena* either as a Ctenophore or as a connecting link between the Ctenophora and the Hydromedusae. It may be regarded simply as a Craspedote Medusa, probably related to the Narcomedusae, with a remarkable aberrant aboral sense-organ.