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TEXT-BOOK OF EMBRYOLOGY

VOL. I
INVERTEBRATA

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CHAPTER IV

COELENTERATA

Classification adopted—

Hydrozoa	<div> <div>Hydrida</div> <div>Hydromedusae...</div> <div>Narcomedusae</div> <div>Trachymedusae</div> <div>Siphonophora</div> </div> <div> <div>Gymnoblastera</div> <div>Calyptriblastera</div> </div>
Scyphozoa	
Actinozoa	<div> <div>Alcyonaria</div> <div>Zoantharia</div> </div> <div> <div>Edwardsiae</div> <div>Hexactiniae</div> <div>Cereanthidae</div> <div>Zoanthidae</div> </div>
Ctenophora	<div> <div>Cydropidae</div> <div>Lobata</div> <div>Cestidae</div> <div>Platyctenea</div> <div>Beroidea</div> </div>

THE Coelenterata are considered by many zoologists to be closely related to the parent group from which the other groups of Metazoa have sprung. In simplicity of general organisation they rival the Porifera, since the bodies of the adult Coelenterates, like those of Porifera, are composed of two layers of cells with an intervening jelly. Ever since in 1859, Huxley compared these two layers in a Coelenterate to the two primary layers of the Vertebrate embryo, they have been termed **ectoderm** and **endoderm**.

The most interesting thing about the relationship between the Porifera and the Coelenterata is that whilst the earliest stages of development in the most primitive representatives of each group are strikingly similar, and whilst in both cases a two-layered adult condition is reached, yet the steps by which this goal is attained differ so totally in the two cases that the two layers cannot be regarded as corresponding to one another in the two groups.

I. HYDROZOA

TUBULARIA

The type which we select for special descriptions is the common hydroid *Tubularia*, species of which are abundant in shallower water on British, Mediterranean, and American coasts. We base our account on the careful work of Brauer (1891) who has worked out the development of the Mediterranean species of *Tubularia mesembryanthemum*.

The British *Tubularia indivisa* is found attached to the bottoms of old boats. The medusa in most species of this genus remains permanently attached and the young pass through the earliest stages of their development within the bell of the mother. In this respect, as in the permanent attachment of the medusae, *Tubularia* is far from exhibiting primitive or typical conditions, but the free-swimming medusae of any particular species cannot always be obtained, and the eggs of these can often only be reared through the earlier stages of development. In many cases the hydroid stage is unknown, and a picture of the complete development of a typical hydroid which produces free-swimming medusae, can only be made out by piecing together the only fragments of the life-histories of many species which are known. It is for this reason that, in spite of its manifest disadvantages, we choose *Tubularia* as a type.

The egg and early segmentation stages are found by examining transverse sections of the **gonophores** and by means of whole mounts. The gonophores are the rudimentary medusae which remain attached to the colony throughout life. On the manubria of these the eggs and sperm are produced. The eggs are dehiscid into the bell, in which they undergo practically the whole of their development, so that the bell is no longer a *locomotor organ* but a *nursery*. The eggs are amoeboid and appear to segment fairly regularly, but they are deformed by mutual pressure in the confined space in which they find themselves. Only two or three are dehiscid at one time.

The segmentation of the egg is somewhat irregular and leads, after about sixteen segments have been formed, to the formation of a hollow vesicle or **blastula**. It is, however, a remarkable circumstance that what appears to be an abnormal form of segmentation frequently occurs and leads also to the formation of a regular blastula. In this latter form of development the nucleus divides repeatedly before any division of the protoplasm occurs, and then subsequently the multi-nucleate mass is cut into cells. When we find that these two methods of development sometimes characterize different genera of the same class of the animal kingdom, we are apt to think of them as very different, but their occurrence side by side in the same species shows that the physiological difference separating them must be very slight.

The blastula stage is succeeded by a solid **morula** stage. This

word, which literally means "mulberry," is used to characterize a condition where the cells which constitute the embryo form a compact spherical mass. The morula stage is reached by the proliferation of cells from the walls of the blastula in sufficient number to fill up the interior. Whether these cells are budded from all parts of the blastula wall or only from a certain area of it, has not been made out. In the case of the eggs of the free-swimming medusae, however, it is beyond all question that these cells are budded only from one end of the blastula, and none of Brauer's figures are inconsistent with

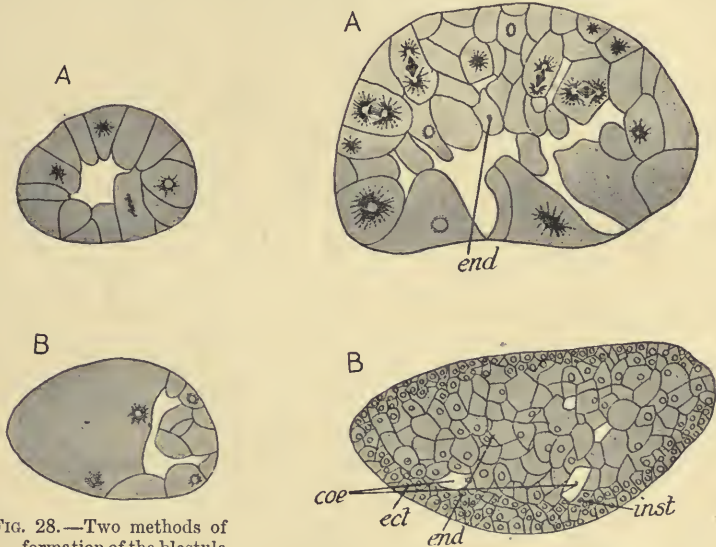


FIG. 28.—Two methods of formation of the blastula in *Tubularia mesembryanthemum*. (After Brauer.)

A, egg segmenting in normal method. B, egg segmenting in abnormal method.

FIG. 29.—Formation of endoderm in *Tubularia mesembryanthemum*. (After Brauer.)

A, budding of endoderm cells from blastula wall. B, morula stage. *coe*, spaces which will ultimately form the coelenteron; *ect*, ectoderm; *end*, endoderm; *inst*, interstitial cells.

the assumption that this is the case with the blastulae of *Tubularia* also. In any case a solid morula stage is soon reached in which the whole interior of the blastula becomes clogged up with a mass of cells.

This mass of cells constitutes the rudiment of the **endoderm** of the adult, whilst the original blastula wall forms the **ectoderm**. In the solid mass of endoderm spaces begin to appear owing to the absorption of some of the central cells. These spaces (*coe*, Fig. 29) eventually coalesce so as to form one cavity which is the gastral cavity or **coelenteron** of the adult. The embryo has now the form of a circular disc, and from its edges a series of blunt protuberances grow out. These are the rudiments of the **aboral tentacles** of the adult: they are bent towards the future aboral end of the body. At

the opposite or oral end is a spot where ectoderm and endoderm thin out, and there eventually the **mouth** will be formed by a perforation of both layers. The disc-shaped embryo grows rapidly in the direction of its

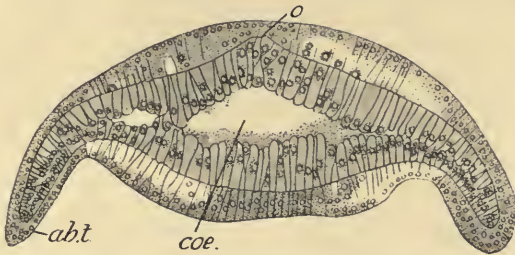


FIG. 30.—Section of embryo of *Tubularia mesembryanthemum* showing the formation of the aboral tentacles. (After Brauer.)

abt, aboral tentacle; *coe*, coelenteron; *o*, spot where the mouth will be formed.

principal axis and becomes cylindrical, and finally develops round its oral end a series of small protuberances which are the rudiments of the **oral tentacles** of the adult. By this time the mouth has been formed and the aboral tentacles have become long and slender (Fig. 31).

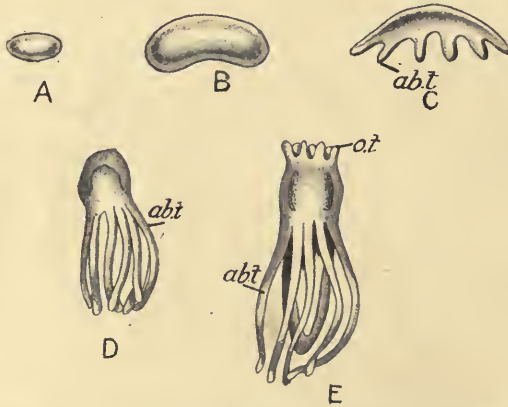


FIG. 31.—Five views of external features of different stages in the development of the embryo of *Tubularia indivisa*. (After Alliman.)

A, oval embryo. B, aboral concavity appears. C, rudiments of aboral tentacles. D, tentacles long; embryo becomes cylindrical. E, oral tentacles formed. *abt*, aboral tentacles; *o.t.*, oral tentacles.

The embryo is now called an **Actinula**, and is ready to leave the bell of the gonophore. It escapes from its nursery, and creeps about on the bottom of the sea with its mouth turned downwards, but finally it attaches itself by the aboral end. It then rapidly grows in height, and from its sides daughter persons are budded, so that it forms an upright shoot in the adult colony. From its base arise

creeping **stolons** which give rise at intervals to other upright shoots: Its lower part secretes a horny shell, the **perisarc**.

The adult colony, however, is still unripe sexually; full sexual maturity is only reached by the gonophores produced subsequently, and thus we have an **alternation of asexual and sexual generations**.

The development of these gonophores in the case of *Tubularia* (as well as in the case of many other genera) has been worked out by Götte (1907); we follow his account in what follows. From just above the region of the aboral tentacles, finger-like stolons grow out, and on these, lateral protrusions arise, which are the **medusa-buds**. At the tip of such a bud, the

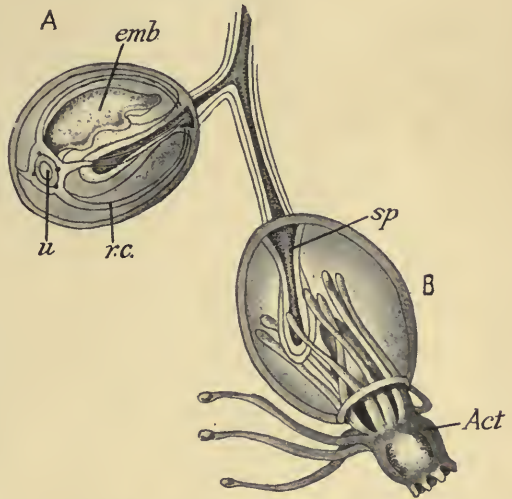


FIG. 32.—Two gonophores of *Tubularia indivisa* with developing embryos inside. (After Allman.)

A, gonophore with discoid embryo; opening of umbrella-cavity just formed; radial canals clear. B, gonophore with actinula larva just escaping; radial canals have disappeared. *Act*, actinula; *emb*, embryo; *r.c.*, radial canal; *sp*, manubrium or spadix; *u*, opening of umbrella-cavity.

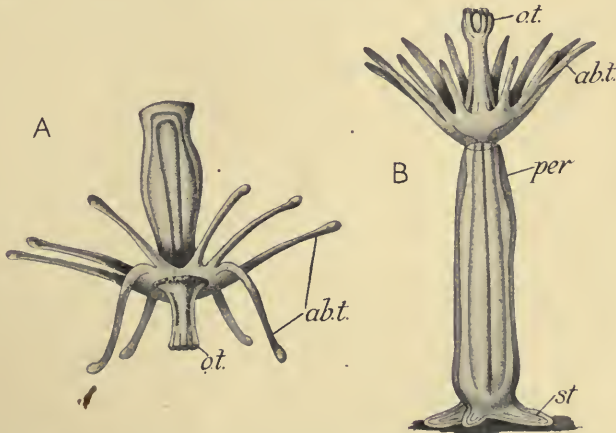


FIG. 33.—Stages in development of Actinula larva of *Tubularia indivisa*. (After Allman.)

A, creeping larva. B, first fixed form. *ab.t.*, aboral tentacles; *o.t.*, oral tentacles; *per*, perisarc; *st*, stolon.

ectoderm thickens to form a mass of cells, and in this mass a cavity develops, the future **umbrella-cavity**.

The mass is termed by German authors "**Glockenkern**," which we may translate "**bell-rudiment**"; it is crescentic in section with its concavity directed downwards. Into this concavity fits a protrusion of the endoderm of the medusa-bud; this is the "**spadix**," the rudiment of the future manubrium, so far as its endodermal portion is concerned. From the base of the spadix four hollow protrusions

of endoderm grow out as canals, and insinuate themselves between the ectoderm of the bud and the outer ectoderm of the bell-rudiment. The spots where these canals bud out are the interspaces between four vertical, solid ridges of endoderm called the **taeniolae**, which project into the gastric cavity of the spadix.

The canals are termed the **radial canals**, and they eventually push out short protrusions of the ectoderm which are the rudiments of the **medusa tentacles**. The radial canals flatten out and become fringed with flat extensions of endoderm. These extensions meet one another in the centre of the interradii, and so constitute continuous sheets of endoderm covering the interradii and forming the so-called **endoderm lamella** (Fig. 35, *en.l.*).

The apex of the medusa-bud consists only of the ectoderm of the bud and the outer ectoderm of the bell-rudiment closely pressed together. Absorption of these adpressed layers now takes place, and an opening is thus formed which places the cavity of the bell in connection with the exterior, and through this aperture the manubrium often protrudes. The thin ectoderm round the edge of the aperture forms the **velum**. In *Tubularia* the hollow

radial canals are transitory structures, and their lumina soon become crossed by cords of cells.

The **genital cells** are found in the ectoderm covering the lower part of the spadix. According to Brauer (1891) they originate as interstitial cells of the ectoderm in the early stages of development of the medusa-bud; they then migrate through the jelly into the endoderm, and finally into the ectoderm covering the spadix (Fig. 36).

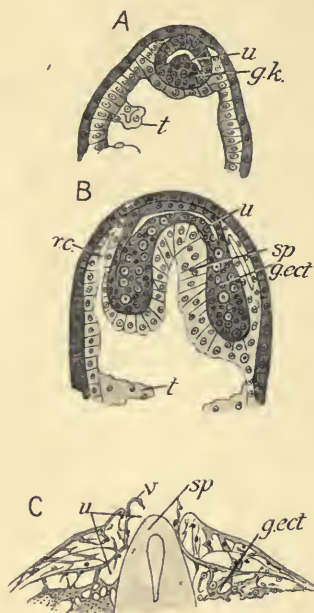


FIG. 34.—Three longitudinal sections through developing medusa-bud of *Tubularia mesembryanthemum*. (After Götte.)

In A, the youngest, the bell-rudiment is just formed. In B, the spadix and radial canals are differentiated. In C, the umbrella-cavity is open to the exterior. *gk*, bell-rudiment (*Glockenkern*); *g.ect*, genital ectoderm; *r.c.*, radial canal; *sp*, spadix; *t*, taeniola; *u*, umbrella-cavity; *v*, velum.

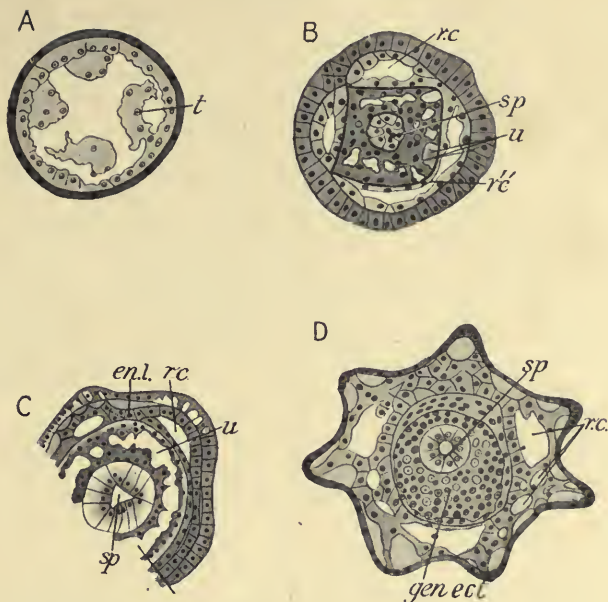


FIG. 35.—Four transverse sections through the developing gonophore of *Tubularia mesembryanthemum*. (After Götte.)



FIG. 36.—Longitudinal section through very young gonophore-bud of *Tubularia mesembryanthemum* to show the origin of the genital cells. (After Brauer.)

Letters as in Fig. 34. In addition: *gen*¹, genital cells originating in ectoderm; *gen*², genital cells which have penetrated into endoderm.

A, section through base of gonophore showing the four taeniolae; *t*, taeniola. B, section through upper part of older gonophore; *r.c.*, radial canal; *r'c'*, spot where two radial canals join; *sp*, spadix; *u*, spaces, portions of the irregular umbrella-cavity. C, section through still older gonophore; letters as before; *en.l.*, so-called endoderm lamella. D, section through almost mature gonophore. *r.c.*, remnants of cavity of radial canals; *gen.ect.*, generative ectoderm clothing the spadix.

FREE MEDUSAE

When we contrast with this development the life-history of the free medusae so far as it is known, we find many marked differences. Our principal source of information on this subject is Metschnikoff (1886), who captured the free medusae of *Tiara*, *Rathkea*, *Oceania*, *Clytia*, etc., and kept them in aquaria till they had deposited their eggs. He was then able to rear the embryos through the larval stages, until they produced young hydroid colonies.

In nearly every case he found that the egg underwent a very regular segmentation which led to the formation of a **blastula**; this was at first spherical but soon became

oval and ciliated, with an anterior broad and a posterior more pointed end, and which swam freely about in the water. At the pointed

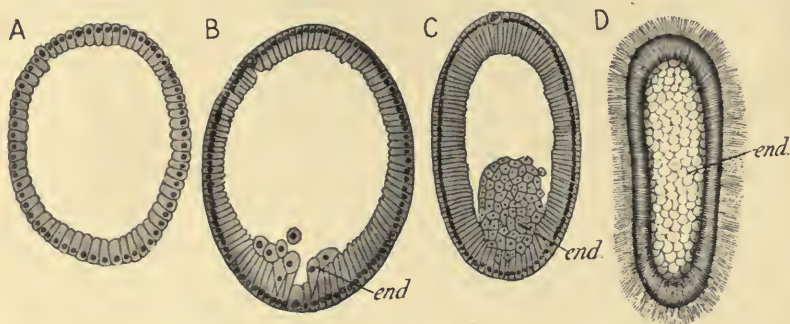


FIG. 37.—Four stages in the development of the planula of *Clytia*. (After Metschnikoff.)

A, blastula stage. B, formation of endoderm by immigration of cells of blastula wall at one pole. C, endoderm, a solid mass, half-filling the cavity of the blastula. D, free-swimming planula larva. end, endoderm.

end, and at this end alone, cells migrated inwards and formed a mass which rapidly increased in extent, owing, not only to the successive immigration of new cells, but also to the division of the immigrated cells *in situ*; and so the blastula was converted into what is termed a **planula**.

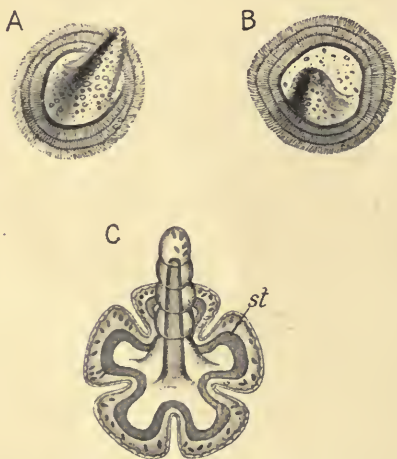


FIG. 38.—Three stages in growth of fixed planula of *Clytia*. (After Metschnikoff.)

A, at moment of fixation. B, a short time after. C, a day after. st, divisions of broad attached end which are the rudiments of stolons.

In the vast majority of Hydrozoa, and also in many Actinozoa, the organism enters on its free life in the "planula" stage. A planula is an oval larva covered with a layer of ciliated cells containing a solid mass of cells inside. Development within the bell of the parent medusa till the adult form is attained, such as occurs in *Tubularia*, is exceptional. Hence the planula is termed the typical larva of the Coelenterata. This planula, after a short free life, attaches itself to the bottom by the broad end, which flattens out. Then, and then only, absorption of the

central cells takes place, and a gastric cavity makes its appearance. The broad end becomes divided by indentations into lobes, each of

which constitutes one of the creeping stolons. The narrow end grows up and develops into the first polyp, the mouth and tentacles being formed as described in *Tubularia*. Metschnikoff's results have been confirmed in the most gratifying manner by Rittenhouse (1910), who studied the development of the eggs of the medusa *Stomatoca apicata*. The sole point in which he is inclined to differ from Metschnikoff is, that he regards the endoderm as arising by the budding of cells from the cells constituting the blastula wall, rather than from the migration of cells forming part of that wall into the interior. Thus we see that processes, which in the case of *Tubularia* are completed before the larva leaves the bell of the mother, do not occur in the case of the free medusae till long after the larva is fixed.



FIG. 39.—A young colony of *Clytia* reared from a planula in the aquarium.
(After Metschnikoff.)

bl, blastostyle ; g, rudiment of medusa ; per, perisarc.

A thorough study of the development of the medusae and gonophores has been made by Götte (1907). In the series of progressive modifications of development which can be constructed from the development of the forms which he describes, *Tubularia* and *Pennaria* (in which the medusae occasionally become free) take the second place. The most primitive type of development is found in forms like *Podocoryne*, in which the medusa regularly becomes a free-swimming organism, and swims about for a long time, and eats and grows before it develops genital cells.

In *Podocoryne*, after the medusa-bud has attained the stage just described for *Tubularia*, after the radial canals have been formed, they give rise to lateral outgrowths which meet those of adjacent radial canals, and in this way a circular canal is formed ; then the freely-projecting ends of the radial canals give rise to free tentacles. By the formation of flat solid extensions from the lateral walls of the radial canals, which meet each other, a continuous sheet of endoderm is formed which spreads over the whole extent of the bell. This is called the **endoderm lamella**. The manubrium attains a

mouth, and the whole medusa becomes free by the absorption of the stalk of the bud. Generative cells are only matured after a considerable period of free-swimming life.

On the other hand, according to Götte, in *Clava* the bell-rudiment is formed but the umbrella-cavity never opens to the exterior, nor are there any radial canals formed, and the whole bell-rudiment is absorbed before the germ cells are shed. In such forms as *Clava* the generative cells of at least one sex—in the case of *Clava* of both sexes—can be detected in the stalk of the person (**blastostyle**) which bears the gonophores. Their development in this genus has been described by Harm (1903). They appear to arise from amongst the interstitial cells of the ectoderm, but, as is also the case with the genital cells of *Tubularia*, they migrate early into the endoderm, where they grow. They reach the spadix when fully ripe, and burst through the ectoderm there (Fig. 42).

In *Cordylophora* the bell-rudiment remains a solid mass of cells, part of which is converted into generative cells.

In *Sertularia* the gonophore is a broad-based lateral swelling on the blastostyle, the bell-rudiment separates from the ectoderm and splits imperfectly, the vestigial umbrella-cavity being crossed by cell trabeculae; and finally, in *Halecium* no bell-rudiment at all is formed.

The last two forms belong to that division of Hydromedusae termed Calyptoblastea, which possess **hydrothecae**, and in which the mouthless person, or **blastostyle**, which bears the gonophores, is

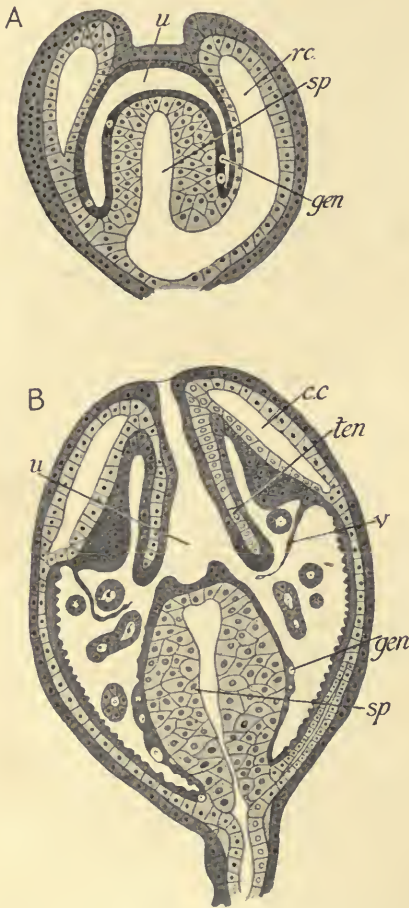


FIG. 40.—Two longitudinal sections through the developing medusa-bud of *Podocoryne carnea*. (After Götte.)

A, before umbrella-cavity is open to the exterior. B, after umbrella-cavity is open to the exterior. c.c, circular canal; gen, developing genital cells; r.c, radial canal; sp, (in A) cavity of the spadix; (in B) wall of the spadix; ten, tentacle; u, umbrella-cavity.

enclosed in a special case, the **gonangium**. This gonangium is secreted by a special outer layer of ectoderm, the **mantle layer**, which breaks away from the inner ectoderm covering the medusa-bud. In *Halecium* a set of endoderm tubes, like the radial canals, grow out from the blastostyle and ramify in the mantle.

Götte interprets the series of forms which he describes, as steps in the building up of the medusa out of what was originally nothing but a lateral swelling on a hydroid **person** (as the member of a Coelen-

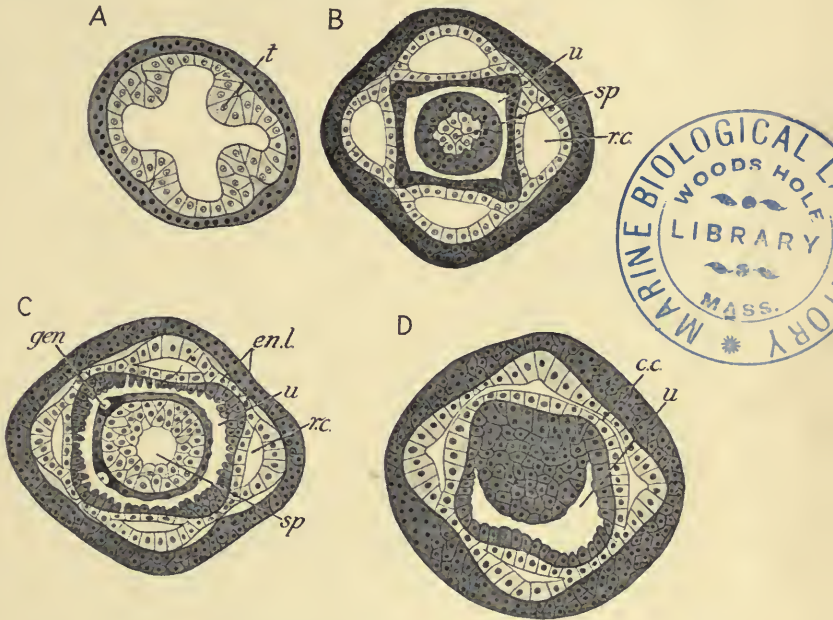


FIG. 41.—Four transverse sections through the developing medusa of *Podocoryne carnea* to show formation of circular canal and endoderm lamella. (After Götte.)

A, through base of young gonophore showing four taeniolae. B, through older bud showing four separate radial canals. C, through base of older bud showing the fringes growing out from the radial canals which form the endoderm lamella. D, through upper part of older bud showing circular canal. In this figure the roof of the umbrella-cavity is grazed. Letters as in previous figure; *en.l.*, endoderm lamella; *t*, taeniola.

terate colony is termed). This swelling is caused by the genital cells, and is therefore similar to the swelling produced by the ovary or testis of *Hydra*. The majority of zoologists, however, read the series in the opposite direction and, as it seems to us, with infinitely more justice. They regard the "gonophores" as degenerate forms of medusae, which once were perfectly developed and became free, but have ceased to be detached, and so the structures which a free medusa uses for swimming have become functionless in them. How else can the umbrella-cavity of *Clava*, which never opens and becomes completely resorbed, be interpreted?

At the same time Götte's results have thrown light on how a medusa was developed out of a hydroid form. It used to be held that a medusa was essentially a hydroid shortened in the direction of the mouth-foot axis. This shortening, it was thought, had caused the oral and aboral walls of the peripheral portions of the stomach of the hydroid to adhere to one another, and so to form a solid plate of endoderm, the so-called **endoderm lamella**; thus leaving the lumen only in the centre, in the extreme outer edge (the circular canal), and in four radiating lines (the radial canals).

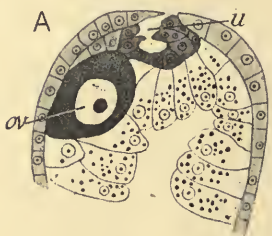


FIG. 42.—Two longitudinal sections through the developing gonophore of *Clava squamata*. (After Harm.)

A, young gonophore with rudimentary umbrella-cavity and unripe ovum embedded in endoderm. B, fully developed gonophore with ripe ovum. *ov*, ovum; *u*, umbrella-cavity.

But if we follow Götte we must imagine a simpler process of evolution. The bell of a medusa is, according to him, merely a web connecting the basal parts of the tentacles of a hydroid, and a medusa is related to a hydroid as a duck's foot is related to a hen's foot.

We may suppose, then, that originally the hydroid persons were separated from the mother, and crept about, as still happens in the case of the buds of *Hydra*, and that these persons eventually developed genital organs; but that a differentiation in these buds took place, so that some never separated, but remained permanently immature and asexual, whilst those that did separate developed a swimming web. In this way the **alternation of generations** so characteristic of Hydrozoa was developed.

SIPHONOPHORA

The Siphonophora are floating or swimming Hydromedusae. The most ingenious and plausible hypothesis as to their origin is that put forward by Korschelt and Heider (1890), who regard as most primitive those forms like *Physalia* and *Verella*, which float only, and are without those engines of propulsion known as **nectocalyces**. Korschelt and Heider (1890) suppose such forms to have been derived from larvae of ordinary Hydromedusae, which have fixed themselves to the surface film of the water.

That this is a possible and even probable contingency will be self-evident to any one who has watched young starfish walking upside down on the surface film, like flies on the ceiling of a room,

or who has seen some members of a swarm of Ascidian tadpoles thus fix themselves to the film. The surface film, although able to sustain the weight of a larva, would soon bend under the growing weight of the hydroid colony which developed from it, and this would lead to a cupping of the base. If we suppose this base to secrete mucus and to entangle bubbles of air, the elements of a float would thus be presented.

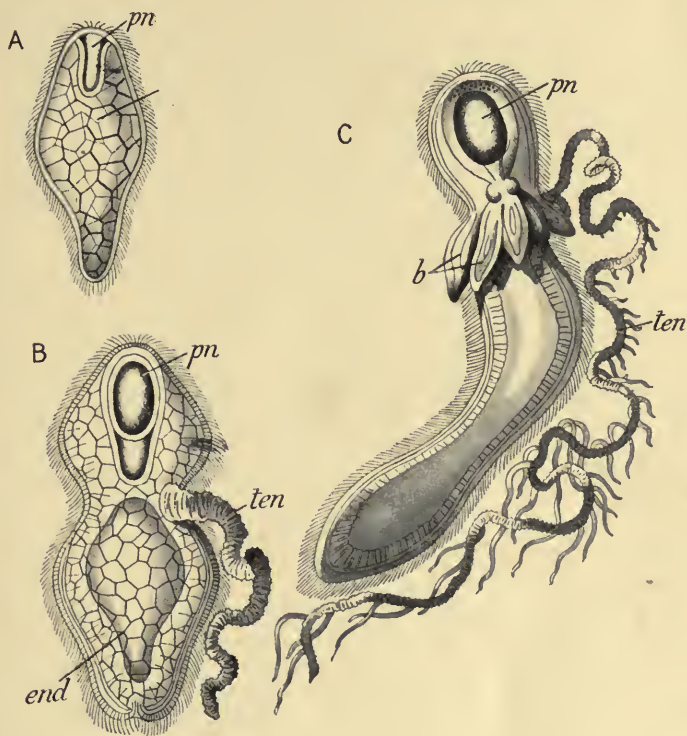


FIG. 43.—Three stages in the development of a Siphonophore (*Cystalia monogastrica*).
(After Haeckel.)

A, planula with float, an open invagination of the aboral ectoderm. B, Older larva, a single long tentacle formed. C, still older larva in which the definitive endoderm is formed, and in which buds of other persons have been formed. *b*, buds; *end*, endoderm; *pn*, float; *ten*, tentacle.

The earlier stages in the development of these Siphonophora have not been made out, but the planula larva is well known. The peculiarity of this larva lies in the fact that the large vacuolated internal cells which occupy its interior, are not directly converted into the endoderm of the adult, but that they bud off smaller cells on their outer sides, which form the definitive endoderm which persists throughout life.

As in other planulae, the narrow end lengthens and becomes

converted into the body of the first hydroid polyp, at the apex of which the mouth is formed; but the broad end develops an ectodermic invagination, the rudiment of the **float**, at the spot where the attached base would naturally be looked for if we were dealing with planulae of Hydromedusae. A single tentacle sprouts from the base of the polyp, and above this, *i.e.* nearer the float, is a **growing zone**, from which other polyps arise.

In many Siphonophora certain of the medusoid buds lose their genital cells, and even the manubrium, and become organs of locomotion merely. These organs arise in the part of the growing zone nearest the float, morphologically the most basal part. In one group the adult relies on these modified medusae (**nectocalyces**) alone for swimming, the float having disappeared; and in such cases, which we regard as the most modified of all, the endoderm cells in the base of the planula secrete oil drops, and the first definite organ to be formed in this region is a huge nectocalyx.

To this theory of Korschelt and Heider there are opposed two other theories, *viz.* the medusome theory of Haeckel (1888) and the theory of Chun (1887).

According to Haeckel, the whole Siphonophore colony is merely a medusa which budded, as some few medusae are known to do. Every person is supposed to be a modified medusa; the bells of the medusae are supposed to be represented by the translucent leaf-like bracts, termed **hydrophyllia**, which many species possess; and the hydroid-like persons are their "manubria," which are supposed to have migrated out from them through a slit in the bell. The violent dislocations required by this theory belong to the period of imaginative morphology.

Chun agrees with Korschelt and Heider in regarding the Siphonophore as a Hydromedusan colony, containing both hydroid and medusoid persons; but he regards the float as a modified medusa, in which air has replaced water. It is, however, very difficult, if not impossible, to picture a series of ancestors in which one of the medusa bells gradually replaced its contained water by air. In other words, Chun's hypothesis transgresses the law of **functional continuity**, which should be exemplified in any supposed phylogenetic change.

NARCOMEDUSAE AND TRACHYMEDUSAE

The Narcomedusae and Trachymedusae are usually stated to be Hydromedusae, in which the egg develops directly into a medusa without an intervening hydroid stage. A more correct statement of the case would seem to be that the egg develops into a modified hydroid person, which does not bud, but which, by the formation of a web, becomes directly transformed into a medusa. The fact that both these groups are pelagic in their habit has rendered the formation of a fixed budding colony of hydroids impossible. Therefore the development is hurried on, and the first

person develops into a medusoid, passing, in some cases at least, through a hydroid stage in the course of its development.

In the development of Geryonidae, a family of the Trachymedusae, it is usually stated that a spherical blastula is at first formed, and then that the inner vesicular portion of each cell of the blastula becomes detached from the outer end, and that these inner portions unite to form an endodermic vesicle. In this way, it is said, the two-layered condition is reached.

This view is founded exclusively on views of living segmenting eggs which, owing to their spherical character, could not be orientated; and on the assumption that this mode of the formation of endoderm and ectoderm actually occurs, it has been regarded as typical **delamination**, and as representing the primitive way in which a two-layered condition was arrived at.

Strong objections may be urged against this view. The development of the Trachymedusae and Narcomedusae is greatly modified as compared with that of the more normal Hydromedusae, on account of their mode of life; and further, when we consider how easily mistakes can be made as to the nature of a process, unless carefully orientated embryos are examined and cut into sections, we must regard it as very questionable whether the kind of delamination described in the Geryonidae does actually take place. It is possible that in this family we have to do with a proliferation of the cells forming the blastula wall, at one side of the blastula, but that the area of proliferation is of considerably greater extent, relatively to the whole surface of the blastula, than it is in the case of the blastulae of ordinary Hydromedusae. If this pole were turned towards the observer, he would receive the impression that he was looking at a sphere, from the whole of whose circumference cells were being budded inwards.



FIG. 44.—Embryo of a Geryonid (*Carmarina fungiformis*) in which endoderm cells are being budded off. (After Metschnikoff.)

end, endoderm.

II. SCYPHOZOA

AURELIA

If we now turn our attention to the great group of the Scyphozoa, we find that the development of the genus *Aurelia* has been fully worked out, the latest accounts being given by Hein (1900) and Friedemann (1902). These workers used a mixture of 100 parts concentrated solution of corrosive sublimate, with 2% acetic acid, to preserve the larvae of *Aurelia*.

This common jelly-fish swarms on both sides of the Atlantic. As in all Scyphozoa the genital cells are produced from the endoderm

of the stomach, and are discharged into its cavity,—where they are fertilized by spermatozoa of other individuals taken in with seawater. The fertilized eggs escape from the mouth but are retained for a considerable period in pockets of the inner surface of the oral arms.

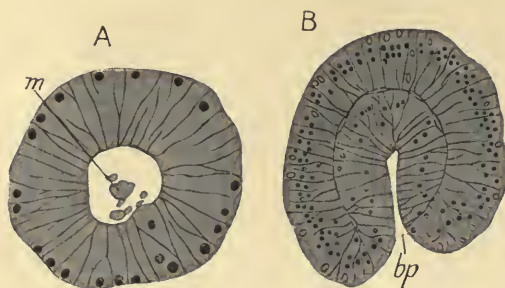


FIG. 45.—Early stages in the development of *Aurelia aurita*. (After Hein.)

A, blastula stage. B, gastrula stage. *bp*, blastopore; *m*, cells budded from the blastula wall which migrate into the interior and disintegrate.

parallel to their longitudinal axis. When such sections are examined it is found that the egg segments with great regularity, and that a spherical hollow blastula is formed. The cells forming the outer wall of this blastula bud off other cells which migrate into the interior, and it looks as if we were about to witness the formation of a solid planula; but the cells which thus migrate inwards break up into granules and are absorbed, thus serving as food for the rest. Then, at one end, the cells forming the wall of the blastula are *invaginated*, and in this way the single-layered blastula is converted into a hollow, double-layered structure termed a **gastrula**. The opening of the invagination is termed the **blastopore**. The conversion of a blastula into a gastrula is called the process of **gastrulation**.

The blastopore never closes and eventually forms the **mouth**, although it becomes contracted to the finest capillary dimensions. The yolk granules in the cells become absorbed, and the spherical gastrula becomes converted into an oval one, with a broad basal end

These pockets can be recognized in the surface view as opaque spots. If they are slit open by needles under sea water the embryos can be extracted.

The embryos can be preserved in corrosive sublimate and acetic acid, or in osmium acid, and mounted whole; or else embedded in celloidin, orientated, and cut into sections

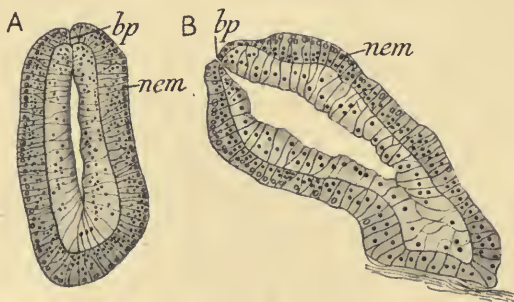


FIG. 46.—The fixation of the free-swimming larva of *Aurelia aurita*. (After Hein.)

A, free-swimming planula. B, stage just after fixation. *bp*, blastopore reduced to a mere slit. *nem*, nematocysts.

and a more pointed end where the mouth opens. Thus by a single process a stage is reached which, in the Hydromedusae, is attained first by a process of the immigration of cells, then by the absorption of the more central cells, and lastly by the formation of an aperture to the exterior.

The embryo now emerges from the maternal pockets and swims freely about by means of its cilia. The outer cells commence to show traces of the formation of nematocysts, whilst the inner cells develop large vacuoles, as in *Hydra*. It appears that, as in the blastula stage so also in the gastrula stage, cells migrate from the wall of the stomach into its cavity and are digested.

After swimming about for four or five days the larvæ attach themselves by their broad ends, the ectoderm cells of which secrete an

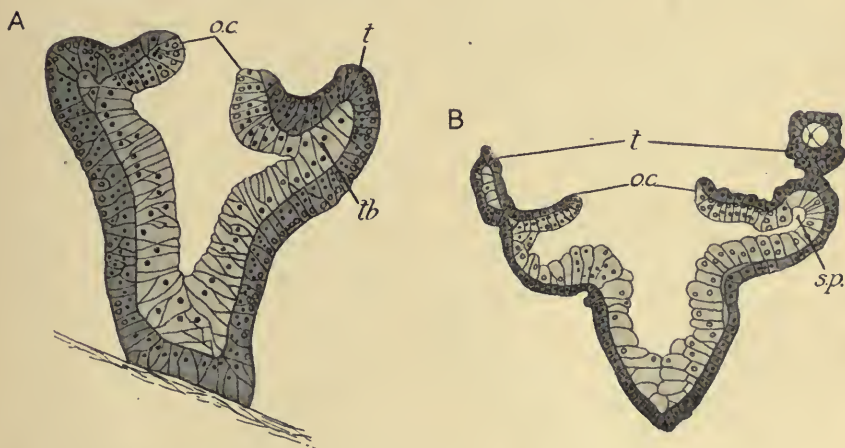


FIG. 47.—Two longitudinal sections through two *Hydra*-tubae of different ages.

A (after Hein), through a specimen with four tentacles. The section goes through the origin of a tentacle. B (after Friedemann), through a specimen with eight tentacles, showing the stomach pocket intervening between two taeniolae. *o.c.*, oral cone; *sp.*, stomach pocket; *t.*, tentacle; *t.b.*, tentacle bases of vacuolated endoderm.

adhesive secretion. The attached larva becomes gradually somewhat flattened, and passes from a cylindrical to a cup shape. The endoderm cells in the neighbourhood of the mouth multiply rapidly to form a slight elevation or **oral cone**. The ectoderm cells in this region do not multiply but become stretched so as to form a thin flattened layer. The almost obliterated blastopore becomes now widened so as to form the permanent mouth; it becomes indeed quite a gaping opening.

Immediately after this, four primary tentacles arise as warts surrounding the mouth. The interior of each is occupied by a solid cord of endoderm, and the ectoderm covering it becomes crowded with nematocysts. Alternating with these tentacles there arise four **taeniolae** or ridges of the endoderm projecting into the stomach

cavity. Each of these is produced by an inwardly-directed fold of the endoderm, between the limbs of which is jelly. These taeniolae are also termed **septa** (Fig. 48).

Then a circular depression appears in the ectoderm on the upper part of the larva, which marks off the oral cone from the bases of the tentacles, and just above the upper ends of the four endodermal folds this depression appears to be deeper. From the bottom of these deeper depressions, which are termed the **septal funnels**, ectoderm

cells are budded off and force their way into the jelly between the limbs of the taeniolar folds. These cells develop fine muscular fibrils on their external surfaces, which form the four longitudinal septal muscles. These muscles extend down to the base of the larva; they are exceedingly irritable and serve to contract it (Fig. 49).

The larva which is now provided with a flattened upper surface or oral disc, with four long tentacles with solid axes, with four endodermal septa, and four ectodermal septal muscles, is termed a **Hydra-tuba** or **Scyphistoma**. Four secondary tentacles alternating with the first four are soon added, and eventually eight tertiary ones, alternating with the primary and secondary, so that in all sixteen are formed.

As Sir J. Dalyell (1847), the first discoverer of this larva showed, lateral buds like those of a true *Hydra* can be formed,

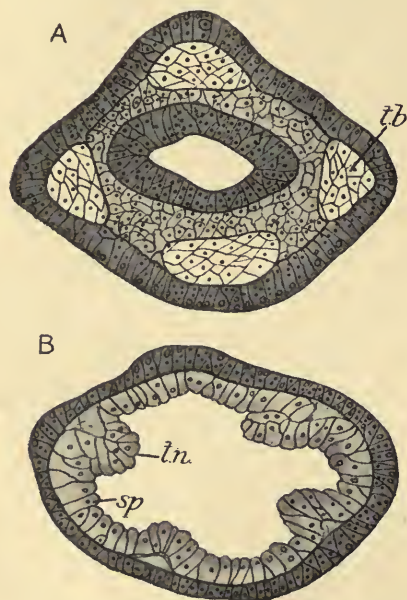


FIG. 48.—Two transverse sections through a Hydra-tuba with four tentacles. (After Hein.)

A, grazing the upper surface or oral disc. B, through the middle of the body. *s.p.*, stomach pocket; *t.b.*, endoderm cells forming the bases of the tentacle; *t.n.*, taeniolae.

which repeat the structure of the parent and eventually become detached, and stolons can grow out from the body wall just above the base, extending a short distance, and from them other hydra-tubae can be given off.

Friedemann (1902) takes up his account of the development where Hein left off. The eight-tentacled hydra-tuba grows in size as it captures more and more prey. Then eight new tentacles make their appearance alternating with the former, so that the animal now possesses sixteen tentacles. The number is then raised to twenty-four by the appearance of eight new ones, and with this number the hydra-tuba attains the maximum of

its development. The nematocysts on the tentacles increase till, by their aggregation, they form warts and finally garland-like thickenings.

Meanwhile, whilst the number of tentacles is increasing from sixteen to twenty-four, other changes supervene. Four new and larger invaginations of the ectoderm of the oral disc make their appearance, just in the positions occupied by the old septal funnels. These are the rudiments of the four **sub-genital pits** of the adult. Just under the oral disc a hole, the **ostium**, appears in each taeniola, so that this structure is transformed from a complete ridge into a pillar, and the four gastric pouches of the hydra-tuba become in this way converted into the so-called **ring-sinus** (Fig. 51).

The free edge of the taeniola thickens and grows out into two

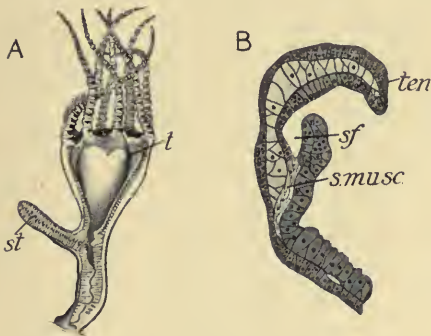


FIG. 49.—A, a Hydra-tuba with eight tentacles. (After Friedemann.) B, longitudinal section of a part of a similar specimen to show origin of septal funnels. (After Hein.)

s.f., septal funnel; *s.musc.*, septal muscles; *st*, incipient stolon; *ten*, tentacle; *t*, taeniola.



FIG. 50.—Oral view of Hydra-tuba with twenty tentacles. (The tentacles are represented as cut off.) (After Friedemann.)

sp, stomach pouch; *t*, taeniola.

diverging lips, which are the first rudiments of the **gastral filaments**, and these are covered in the adult with specially active digestive cells. From the oral side of the first eight tentacles there appear eight bud-like warts on the oral disc, which are the rudiments of the sense-organs of the adult. Beyond the ring-sinus eight lobes grow out; four of these, termed **per-radial**, are outpouchings of the original spaces between the taeniolae, whilst the other four, termed **inter-radial**, take their origin from those portions of the ring-sinus which have developed from the perforations in the taeniolae. Thus the oral disc becomes drawn out into eight lappets, and the tentacles are then thrown off. Each lappet contains one of the eight lobes which have grown out from the ring-sinus; the lappet is forked at its distal extremity, and in the re-entrant angle of each fork is the rudiment of the sense-tentacle.

The next process which occurs is the separation of the "head" or "crown" of the hydra-tuba from the stalk. This process is initiated

by the appearance of a groove in the stalk; it can take place, as Friedemann shows, at different stages in the development, either before or after the loss of the tentacles.

If food is scarce the crown separates as a free-swimming organism termed an **Ephyra**, and the stalk slowly regenerates a new crown; but if food is abundant the process of the formation of a new crown begins before the old crown has separated, and before it is well under way a second groove appears below it, and a third crown starts to develop; and by a repetition of the process the *Scyphistoma* comes to look like a pile of plates, and is called a **Strobila**. This process is known as **strobilization**, and in this way one hydra-tuba can give rise to multitudes of Ephyrae (Figs. 52, 53).

The just liberated Ephyra is about an $\frac{1}{8}$ inch across the disc. The wart-like sense-tentacles develop otoliths in their distal endodermal

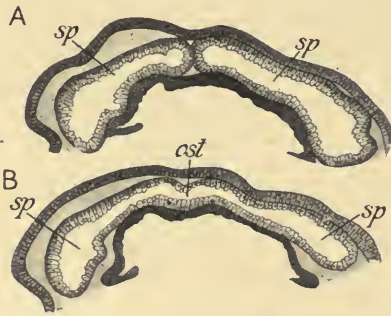


FIG. 51.—Two horizontal sections through the upper part of a Hydra-tuba, about as old as that represented in Fig. 50, to show the formation of the ostium connecting the stomach pockets. (After Friedemann.)

A, above the level of the ostium. B, at the level of the ostium; *ost*, ostium.

cells, and this distal mass of endoderm becomes separated from the rest. The Ephyra does not attain the characters of the adult *Aurelia* until it has grown to a size of at least $\frac{1}{8}$ inch in diameter. The change in its shape, which brings in the adult features, consists in the slow growth of **adradial cushions**, which are situated between the bases of the eight lobes of the Ephyra. These cushions, by their growth, gradually fill up the deep re-entrant notches in the disc of the Ephyra, and change its star-like outline into the rounded outline of the adult *Aurelia*.

As each of these cushions grows, a new endodermal pouch grows out from the ring-sinus and extends into it. At the same time each endodermal pouch, which already occupies a lobe of the Ephyra, becomes trilobed at its distal extremity. The median branch of these three-pronged forks goes to the wart developed from the base of the hydra-tuba tentacle once situated there. This wart develops into the sense-tentacle of the *Aurelia* (Fig. 55). The two lateral branches of the forks go into the two folds forming the forked extremity of the Ephyra-lobe. These forks persist in the adult as the curtains which eventually form a hood for the sense organ of the adult. The oral cone becomes more and more prominent and forms the manubrium of the adult.

The genus *Pelagia* goes no farther than this stage. Each adradial cushion develops a single long tentacle, and one only. But in *Aurelia*, just as is the case with the Hydromedusan

Podocoryne (see p. 61), the endoderm of the radial pouches flattens out so as to form plates which meet each other in the interspace between two adjacent pouches, and thus form the so-called **cathammal plates**, or, collectively, the **endoderm lamella**. In these plates branches of the radial pouches hollow themselves out. Some of these branches, at right angles to the pouches, form a circular canal just as happens in *Podocoryne*; others form branches of the per-radial and inter-radial pouches. The last formed adradial pouches do not branch. The numerous small tentacles which fringe the disc of the adult, arise as sprouts from the circular canal (Fig. 56).

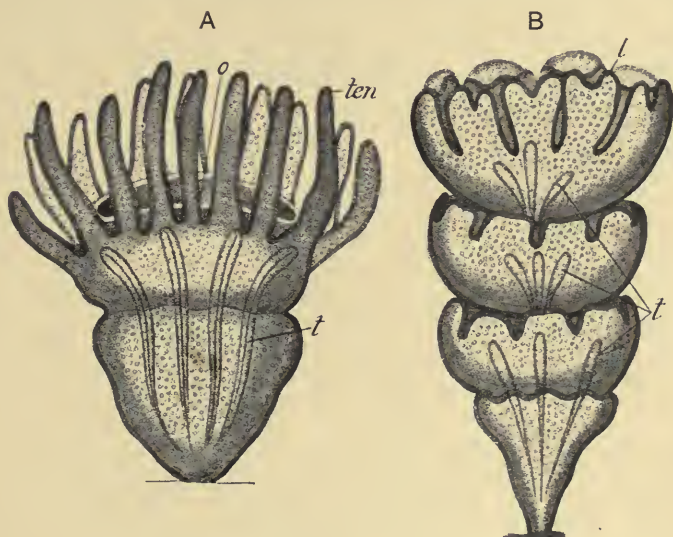


FIG. 52.—Two stages in the strobilization of the Scyphistoma of *Aurelia aurita*. (After Claus.)

A, the appearance of the first transverse groove. B, tentacles lost, four transverse grooves. *l*, lobe of Ephyra; *o*, oral cone; *t*, taeniola; *ten*, tentacle.

OTHER SCYPHOZOA

Hein (1903) has investigated the early development of another genus *Cotylorhiza*. It agrees very closely with *Aurelia*, but the original blastopore closes, and the mouth is formed later by the reopening of this orifice. The temporary closure and subsequent reopening of an orifice is to be noted as a phenomenon of very frequent occurrence in development; we interpret it as a sign that the orifice in question is no longer continuously functional.

Pelagia is an instance of a form modified for oceanic life; it develops a blastula like that of *Aurelia*, and a gastrula is formed by invagination as in that animal; but the original blastocoele persists in the aboral end of the larva since the endodermic sac remains

relatively small. This again is a feature which we find in many larvae which are adapted for continuous free-swimming life. The larva never fixes itself, and eventually the lobes of the Ephyra grow out in a circle round the mouth. The whole development is therefore modified along quite similar lines to those exhibited by the Geryonidae, the hydra-tuba being modified into a floating larva, just as is the hydroid stage of the Geryonidae.

When we review what we have learned of the development of Scyphozoa, we are struck at first by the great differences between their life-histories and those of the Hydrozoa. A deeper and closer analysis tends, however, to diminish the supposed differences very much. It has been shown that many Hydroid colonies periodically lose and regenerate the "polyps" (Allman, 1871-2), (*i.e.* the swollen distal ends or heads of the hydroids which carry the tentacles and genital organs), that during the winter the polyps are often absent, and that these are regenerated from the basal stumps in

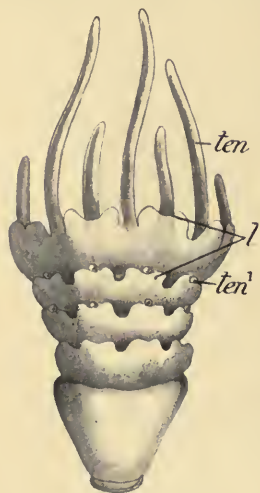


FIG. 53.—Astrobilized Scyphistoma of *Aurelia aurita*. (After Claus.)

l, forked lappet of edge of disc of Ephyra; *ten*, tentacles of Hydra-tuba degenerating; *ten¹*, rudimentary sense-tentacles of Ephyra.

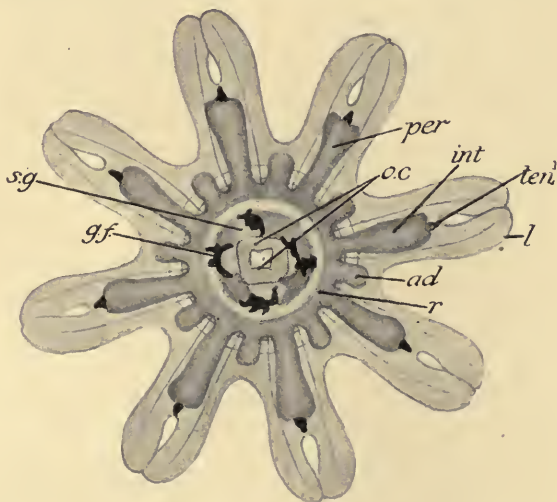


FIG. 54.—An Ephyra larva of *Aurelia aurita* just after liberation from the strobilized scyphistoma. (After Friedemann.)

ad, adradial lobe of ring-gut; *gf*, gastral filament; *int*, inter-radial lobe of ring-sinus; *l*, forked lappet of edge of disc; *o.c.*, oral cone; *per*, per-radial lobe of ring-sinus; *r*, ring-sinus; *sg*, sub-genital pit; *ten¹*, sense-tentacles.

the summer. This is very much the same phenomenon as the "strobilization" of the *Scyphistoma*, when the first "Ephyra-head" is budded off.

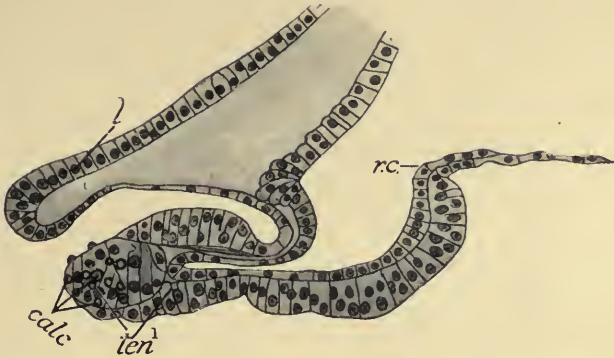


FIG. 55.—Longitudinal section through the sense organ of a young Ephyra.

calc, calcareous concretions in the sense-tentacle; *l*, lobe of disc of Ephyra; *r.c.*, wall of radial canal; *ten¹*, sense-tentacle.

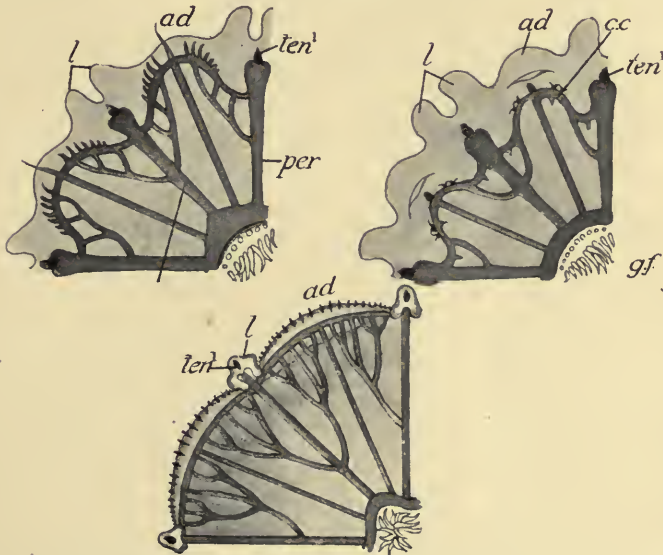


FIG. 56.—Three stages in the development of the Ephyra larva into the adult *Aurelia*.
(After Claus.)

ad, adradial cushion; *cc*, circular canal; *g.f.*, gastral filament; *l*, lobe sheltering sense tentacle; *per*, per-radial canal; *ten¹*, sense-tentacle. (The reference line without letter in the first figure points to an inter-radial canal.)

Then in both groups the sexually mature person is typically a person which breaks loose from the colony and develops a swimming-web. In Hydrozoa such a person breaks loose in such a way as

to leave practically no stump, but in Scyphozoa a stump is left which can regenerate a new head. This is what the only difference, often much emphasized, between the formation of a medusa by lateral budding and the formation of a medusa by transverse fission consists in.

The fact that the sexual cells of Scyphozoa are discharged inwards towards the stomach cavity, and not outwards as in Hydrozoa, is a real difference. But it must be remembered that it is confidently asserted that in many Hydrozoa with rudimentary gonophores the sexual cells originate in the endoderm; and it may be that they always have an ectodermal origin, but that in their first stages they are indistinguishable from ectodermal interstitial cells. Gastral filaments and septal muscles constitute, however, features in which Scyphozoan organization is higher than that of Hydrozoa.

III. ACTINOZOA

The great group of the Actinozoa, one of the four primary groups of the Coelenterata, is distinguished from the Scyphozoa by the replacement of the oral cone by an inturned tube of ectoderm, the **stomodaeum**.

The eggs of Actinozoa, like those of Scyphozoa, are developed in the endoderm and dehiscid into the coelenteron of the parent. In most Zoantharia the embryos pass through the first stages of their development within the body of the mother; but in a few Zoantharia and apparently in most Alcyonaria, the eggs are discharged through the mouth of the parent into the sea and fertilized there. In this case it is possible to obtain a great many specimens of the same age. But when development takes place within the coelenteron of the mother only a very few specimens of the earliest stages of development will be found in any one individual parent, since these stages are rapidly passed through. For this reason we select a Zoantharian (*Urticina crassicornis*), in which the eggs are discharged before fertilization, as a type for special study in order to illustrate the development of Actinozoa.

URTICINA CRASSICORNIS

Urticina crassicornis is a sea-anemone found on the British and Norwegian coasts and its development has been worked out by Appellöf (1900). This observer kept the adults living in tanks in the Bergen aquarium until they spawned; he kept the eggs in dishes of clean sea-water until the larvae hatched out, and these he was able to keep alive until they fixed themselves and metamorphosed into young sea-anemones. As preservative he used the mixture of corrosive sublimate solution and acetic acid described in Chapter II.

The egg of *Urticina* when discharged is surrounded by a gelatinous mass, through which presumably the fertilizing spermatozoon has to penetrate. After fertilization this gelatinous mass hardens into a firm capsule beset with spines, and within the shelter of this capsule the early stages of development are passed through. The egg is composed of a thin rind of relatively clear cytoplasm and an internal zone of cytoplasm loaded with large spheres of yolk. The kernel of the egg consists of a mass of material with sparse yolk spheres but with many granules, which appears to be reserve food material not cytoplasm.

The egg is thus of the type called **centrolecithal** in Chapter I., and its segmentation is a matter of considerable interest. The zygotic nucleus is situated in the outer clear layer of cytoplasm, and there it undergoes its first division. The daughter nuclei migrate into the deeper layer of yolky cytoplasm and here undergo repeated division until sixteen nuclei have been formed, which are distributed around the periphery of the egg in the yolky layer. Then and then only the cytoplasm begins to be divided into blastomeres, of which consequently sixteen are produced at once. At first (Fig. 57) the blastomeres are separated from one another only at their outer ends, but they soon become sharply defined over their whole surfaces; nevertheless, even when so defined, their inner ends are embedded in the mass of reserve material which forms the innermost core of the egg.

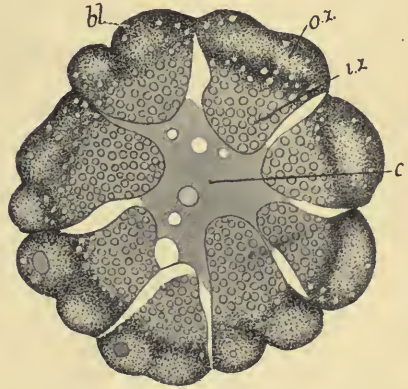


FIG. 57.—An egg of *Urticina crassicornis* dividing into sixteen blastomeres. (After Appellöf.)

bl, blastomeres; *c*, core of nutritive material in the centre of the egg; *i.z.*, inner zone of yolky cytoplasm; *o.z.*, outer zone of clear cytoplasm.

As segmentation proceeds a **blastula** is eventually formed, whose wall consists of a single layer of small cells, but in whose cavity there still remains the mass of "reserve-material" which formed the kernel of the unsegmented egg (Fig. 58).

The blastula is at first ellipsoidal, but one pole becomes flattened and in the centre of this pole an invagination takes place. The manner in which this occurs is of great interest. The borders of the patch which is to be invaginated bend in first, so that for a brief period its central part projects like a knob. As the process of invagination proceeds the centre is also carried downwards and inwards, and thus a two-layered organism—*i.e.* a **gastrula**, is produced. Occasionally the reserve material in the blastocoele persists in considerable quantity; it adheres to the centre of the area which is normally invaginated and thus impedes the process of invagination.

This plug which normally persists for only a short time, persists in this case much longer, and eventually the cells forming the borders of the area of invagination are carried in past it, so that the invaginated layer, or endoderm, is represented by a solid plug of material surrounded by a layer of cells. This plug is gradually

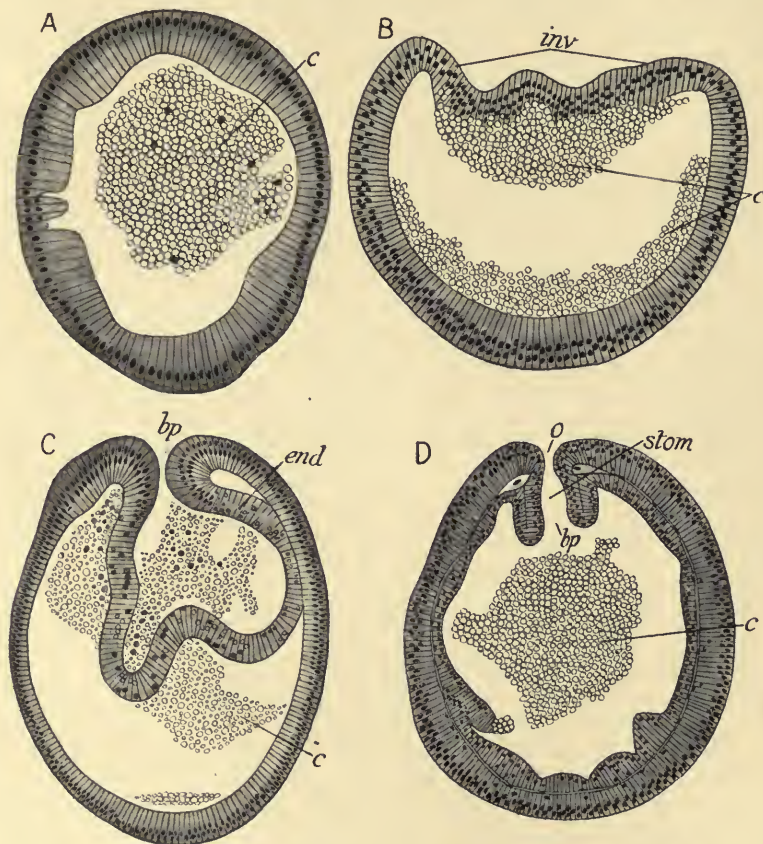


FIG. 53.—Four stages in the development of the egg of *Urticina crassicornis* as seen in longitudinal sections. (After Appellöf.)

A, blastula. B, blastula preparing to undergo invagination. C, invagination nearly complete, gastrula stage. D, formation of stomodaeum. *bp*, blastopore; *c*, remnants of the core of the egg; *end*, endoderm; *inv*, area of invagination; *o*, mouth; *stom*, stomodaeum.

digested by the surrounding cells and thus the hollow gastrula stage is reached.

The relation between the normal and abnormal methods of reaching the two-layered stage in this species is the same as the relation between the method of forming the planula larva in Scyphozoa and that in Hydrozoa. We may regard them as two varieties of **gastrulation**. The invaginated cells or endoderm,

form an inner sac which spreads till it completely displaces the food material in the blastocoele, which is used up in nourishing the growing cells. Both ectoderm and endoderm then co-operate in producing a gelatinous secretion, the so-called jelly, **mesogloea**, or **supporting lamella**. The cavity of the gastrula becomes the **coelenteron** of the adult.

When the opening of the invagination has become narrowed so as to form a slit-like blastopore, the ectoderm acquires cilia and the embryo rotates within the egg-capsule, which shrinks and becomes more transparent. A little later the embryo escapes from the capsule altogether and swims about as a larva, but the swimming is not very vigorous and the larvae do not rise far from the bottom.

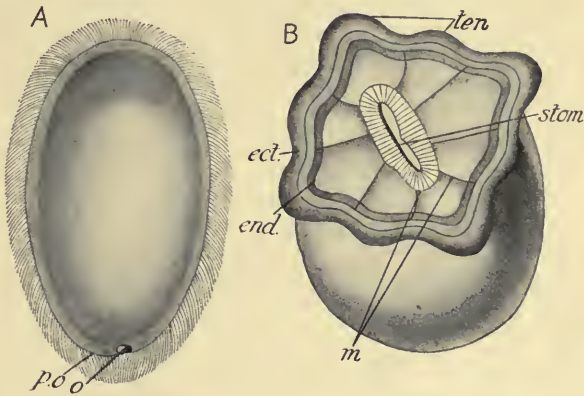


FIG. 59.—Two stages in the development of the larva of *Urticina crassicornis*.
(After Appellöf.)

A, free-swimming larva. B, stage just before fixation. *ect.*, ectoderm; *end.*, endoderm; *m*, mesenteries; *p.o.*, post-oral region; *o*, mouth; *stom.*, stomodaeum; *ten*, tentacles.

The larvae are of ovoid shape with a broad aboral and a pointed oral end. The aboral end is directed forwards in swimming, but the reduced **blastopore**, which persists as the **mouth**, is not situated actually at the oral end but a little to one side of it, so that there is a small **post-oral projection** of the body. The ectodermal lips of the blastopore grow inwards and form an inwardly-projecting tube which is the **stomodaeum** (Fig. 58, D).

The **mesenteries** now make their appearance. The eight so-called primary ones are formed about the same time. Each originates as a fold of the endoderm which projects inwards into the gastric cavity: the cavity between the limbs of the fold being occupied by a layer of supporting lamella secreted by the cells forming the fold. The mesenteries correspond exactly to the **taeniolae** which occur in the *Hydra-tuba* of the Scyphozoa, and which are irregularly developed even in the polyps of the Hydrozoa. The eight mesenteries are arranged in four pairs, or, as it is usual to term them in this case,

couples. Of these, one couple, which project into the post-oral prominence of the larva, are known as the **dorsal couple**; then follow **dorso-lateral**, **ventro-lateral** and **ventral couples**. The ventro-lateral couple develop more quickly than the others, they soon reach the stomodaeal wall with which they fuse, and thus divide the gastric cavity into a dorsal and a ventral chamber. They also extend farther towards the aboral pole of the larva than the others, but as development proceeds all eight fuse with the stomodaeum and reach equally far towards the aboral pole.

The chambers into which the coelenteron is divided by the eight mesenteries are arranged as follows. The **dorsal** chamber is a median chamber at one end of the long slit-like stomodaeum; then follow a pair of **dorso-lateral** chambers, then a pair of **lateral** chambers, then a pair of **ventro-lateral** chambers, and finally a median ventral chamber, making eight in all.

When the process of formation of mesenteries is complete, perforations take place in the septa, forming the so-called **mesenterial stomata**, and thus the cavities into which the coelenteron is divided by the mesenteries are placed in communication with each other. In *Urticina* there are two sets of these stomata, an inner set near the stomodaeum and an outer set near the outer body wall of the larva. Both sets arise in the same way; the supporting lamella becomes absorbed over a limited area and the two layers of cells which form the mesenterial

fold fuse with one another, and then in the centre of this area of fusion absorption of the cytoplasm begins, and so a perforation is made (Fig. 61). We may note that the taeniolae of the *Hydra-tuba* larva become perforated in exactly the same way.

After swimming for about six weeks the larvae begin to attach themselves to the substratum by the aboral pole; at first the attach-

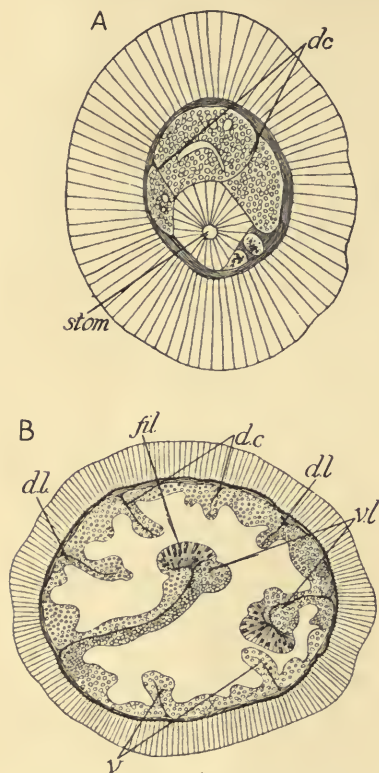


FIG. 60.—Two transverse sections through a larva of *Urticina crassicornis* to show the formation of mesenteries. (After Appellöf.)

A, section through post-oral region of larva. B, section through middle of larva. *dc*, dorsal couple of mesenteries; *dl*, dorso-lateral mesenteries; *fil*, mesenterial filament; *vl*, ventro-lateral mesenteries; *v*, ventral mesenteries.

ment is only temporary, it is some considerable time afterwards that a permanent attachment is effected and the **pedal disc** of the adult formed. Before this occurs the rudiments of the first eight tentacles make their appearance. Each arises as a simple outpouching of one of the eight chambers into which the coelenteron is divided (Fig. 59, B), and all appear to arise about the same time; those belonging to the dorsal and ventral chambers and to the lateral chambers are larger than those belonging to the other four chambers.

The thickened edges of the mesenteries, where they end freely in the coelenteron below the stomodaeum, are known as the **mesenterial filaments**. In the adult *Urticina* each filament is composed of a median strip of cells containing gland cells and **cnidoblasts**, flanked by two strips of cells carrying long cilia. The mesenterial filaments appear on the ventro-lateral mesenteries long before they appear on the others. They first appear in the neighbourhood of the stomodaeum and grow downwards as simple streaks of columnar epithelium; then the central portion shows the glandular modification of its cells, and much later the lateral portions develop cilia. The other filaments make their appearance in the same manner much later, when tentacles have already been developed. According to Appellöf, and here he has the support of other authors such as Gardiner (1902), the filaments are composed of ectoderm which has grown down from the stomodaeum.

In Alcyonaria where, as in the young *Urticina*, there are eight mesenteries, two only of these, the so-called dorsal mesenteries, bear filaments which carry cilia,—the other filaments being purely glandular in character whilst the ciliated filaments are devoid of gland cells. Following Wilson (1883), who is the best authority on Alcyonarian development, the two dorsal filaments are usually said to be of ectodermal origin whilst the others are stated to be endodermal, but the evidence which he adduces in favour of this view is, however, neither thorough nor convincing.

As the filaments are stated to close round the body of ingested prey and to form a sort of temporary alimentary tube within the coelenteron, and as their cells are stated to be the cells which secrete the digestive ferment, one would at first sight naturally expect them

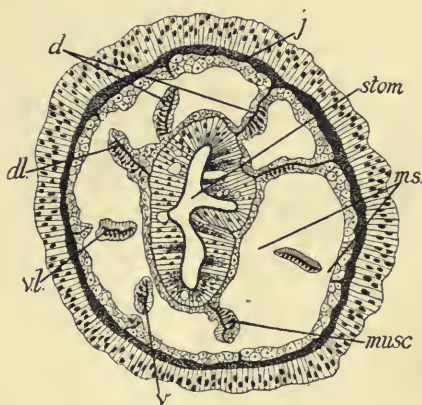


FIG. 61.—Transverse section through a larva of *Urticina crassicornis* in which the tentacles have just been developed. (After Appellöf.)

Letters as in preceding figures. In addition, *j*, jelly or supporting lamella; *ms*, mesenterial stomata; *musc*, muscular thickening on mesentery.

to be of endodermal origin. It is distinctly stated that in Alcyonaria the two dorsal ciliated filaments do not take part in the process of digestion, and if they are of ectodermal origin this is also what one would expect. But if we accept Appellöf's account of the development of the filaments in Zoantharia, we must suppose that the ectoderm in these animals has acquired digestive functions. Since in all groups of the animal kingdom which have been carefully examined, the

distinction between protective ectoderm and digestive endoderm is the first physiological differentiation to be established, and the most deeply rooted, one would imagine it is unlikely that Zoantharia should in this respect form a solitary exception.

But some observations by Miss Pratt on the digestion of Alcyonaria (1905), appear to us to place the whole matter in a new light. She finds that gland cells similar to those found in the six ventral digestive filaments are found also in the stomodaeum, and that the tissues in these filaments are so similar to the stomodeal tissue that she believes that in Alcyonaria as in Zoantharia all the filaments originate from the

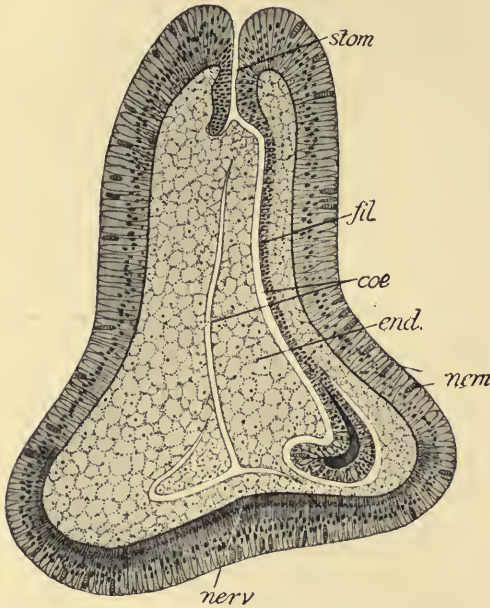


FIG. 62.—Longitudinal section through the larva of *Agaricia agaricites* to show the ectodermal origin of the mesenterial filament. (After Duerden.)

coe, coelenteron; *end.*, endoderm; *fil*, mesenterial filament; *nerv*, nervous tissue at the aboral end of larva; *nem*, nematocyst.

ectoderm. The effect of the digestive juice is not to dissolve the bodies of the prey, but to break them up into granules, which are then ingested whole by the **endoderm** cells covering the mesentery beneath the filament. The cells forming the filament do not ingest anything. It thus appears that this so-called ectodermal digestion is merely a preparatory process similar to that exercised by salivary glands in Mammalia, which, like the filaments, are of ectodermal origin, and that in all cases the final digestion and the assimilation are functions performed by the endoderm alone.

The muscular thickenings which run along the faces of the mesenteries appear about the same time as the tentacles. The supporting lamella becomes beset with branches on one side which

are secreted by the overlying endoderm cells, these increase in number and develop basal longitudinal muscular tails. The muscles first appear on the ventro-lateral mesenteries, and afterwards on the others. Those on the ventral mesenteries are turned away from one another, and those on all the other mesenteries are developed on that side of each mesentery which faces towards the ventral mesentery of its own side. It follows that the muscle thickenings on the dorsal mesenteries are also turned away from one another.

The dorsal and ventral couples which are attached to the ends of the stomodaeum are known as **directive mesenteries**. In many Actinozoa the ends of the stomodaeum are developed into strongly ciliated grooves—the so-called **siphonoglyphes** or **gonidial** grooves. In practically all, including all Alcyonaria, one end of the stomodaeum is thus modified; this is called the ventral end, and to this end the ventral directive mesenteries are attached.

The arrangement of muscle thickenings just described is the same as that which persists for life in the family Edwardsiae, in which family also, as in the young *Urticina*, there are only eight fully formed mesenteries and eight tentacles. *Urticina* therefore passes through an “Edwardsia” stage in development, and this has been proved to be true of every Hexactinian whose development has been worked out.

In the very oldest specimens of *Urticina* which Appellöf was able to rear he found that extra mesenteries were being developed. These extra mesenteries consist of two on each side, four in all, and each of the new mesenteries was in such a position as to make a pair with a ventro-lateral or lateral mesentery, and each bore a muscle thickening facing the muscle of its fellow in the pair (see Fig. 67). Such a **pair**, consisting of two mesenteries facing one another, is to be carefully discriminated from a **couple**, the two mesenteries forming which are situated at symmetrical points on opposite sides of the stomodaeum.

Since the dorsal and the ventral couples of mesenteries may also be regarded as forming two pairs, we reach in this way a total of six pairs of principal mesenteries, and this is what is known as the typical Hexactinian arrangement, the most widely distributed arrangement amongst Zoantharia. The powerful sphincter muscle which in the adult closes the mouth was represented in the oldest of the artificially-reared specimens merely by a thin sheet of circular fibres.

Appellöf has also examined the development of a species of the commonest genus of sea-anemones, *Actinia*. In this species, however (*Actinia equina*), the earlier part of the development is passed through in the coelenteron of the mother, and Appellöf was unable to obtain a complete series of stages of this form; however, one or two points of interest were made out.

The endoderm originates by proliferation from the ectoderm cells; a proliferation probably confined to one pole. A hollow two-layered planula larva is formed which is devoid of a mouth; but a mouth is

formed later by the fusion of the two layers of the body wall at the oral pole and their perforation at this point.

The larva possesses an anterior wisp of long cilia, the cells carrying which are excessively attenuated and have all the appearance of sense cells; and at their bases are a few rounded cells with tails, obviously ganglion cells. In the larvae of *Agaricia* according to

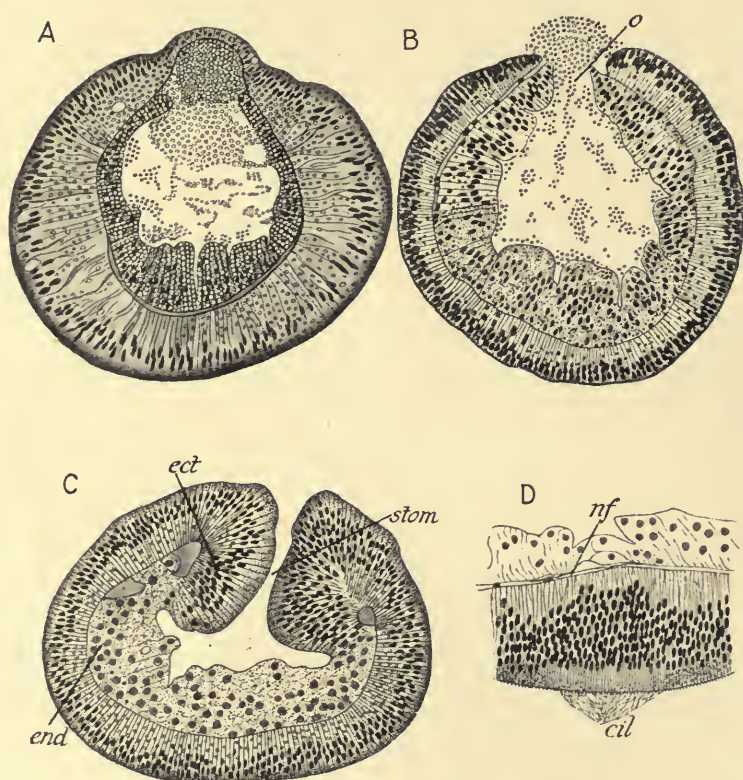


FIG. 63—Stages in the development of the larva of *Actinia equina*. (After Appellöf.)

A, stage just before the formation of the mouth, the endoderm is already absorbed over the spot where the mouth will be formed. B, stage when the mouth is formed. C, stage after formation of stomodaeum. D, aboral pole of free-swimming larva much enlarged. *cil*, long aboral cilia; *nf*, nerve fibres. Other letters as before.

Duerden (1902), although there is no bunch of long cilia at the aboral pole, there is at this spot a comparatively thick layer of nerve fibres (Fig 62).

In the species *Actinia bermudensis*, the development of which has been worked out by Cary (1910), although the egg passes through the earlier stages of development within the coelenteron of the mother, yet the endoderm appears to be formed by invagination

just as in *Utricina crassicornis*. On the other hand, in the species *Metridium marginatum* which has been examined by McMurrich (1891), and *Sagartia parasitica* and *Adamsia palliata*, which have been examined by Faurot (1903), although the eggs are expelled from the mother previous to fertilization yet the endoderm appears to be formed by proliferation from the outer cells of the embryo, that is, from cells which become the ectoderm; and in the two latter species examined by Faurot this occurs at a very early period of development. On the whole this method of forming the endoderm appears to be much commoner than the method of invagination among Zoantharia, and it is the only method recorded for Alecyonaria. In many cases the endoderm cells are so swollen that, when the mesenteries appear, the whole coelenteron is choked up by these cells and only slit-like remnants of the cavity of the coelenteron remain.

The two families of Cereanthidae and Zoanthidae are formally classed along with the Hexactiniae as Zoantharia, but they exhibit a very different arrangement of mesenteries and in each case the egg develops into a most characteristic larva. A good summary of what is known about the larvae of both families is given by Carlgren (1906).

The larva of the Cereanthidae is termed **Arachnactis**, and it is characterized by the excessive prolongation of the free-swimming stage. Two sets of tentacles, an inner and an outer, and numerous mesenteries are developed whilst the larva still continues to swim. Of these mesenteries, there is a ventral pair of "directives" attached to one end of the stomodaeum, and two "couples" attached to its sides. The space which should be occupied by the dorsal directives is at first empty, but young mesenteries appear in it later, varying in number with the age of the larva. They are formed alternately to the right and to the left of the median line, and at first they are short, only later reaching the stomodaeal wall.

The larva of the Zoanthidae appears under two varieties, in one of which (**Zoanthella**) there is a transverse girdle of strong cilia, whilst in the other (**Zoanthina**) there is a longitudinal band of cilia as locomotor organ. It develops no tentacles until twelve mesenteries

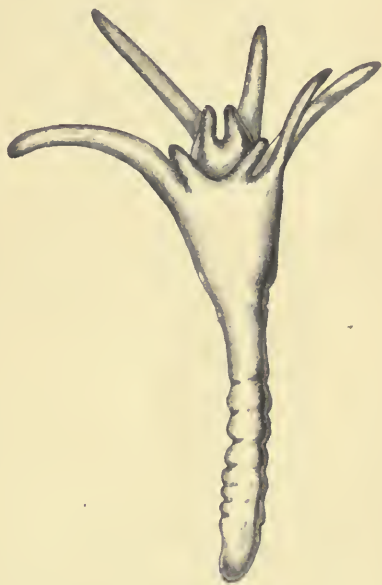


FIG. 64. —The Arachnactis larva of *Cereanthus membranaceus*. (After Carlgren.)

have been formed, and then the twelve are developed in a single cycle. The twelve mesenteries are arranged in six pairs which correspond to the six pairs of Hexactiniae, but the dorsal "directives" are short and do not reach the stomodaeum, and one mesentery of each of the lateral and ventro-lateral pairs remains short, whilst its fellow is long and joins the stomodaeum. In the space which intervenes between the ventral "directives" and the ventro-lateral pair on each side, there is a growing zone where new pairs of mesenteries are added, one fellow of each new pair being long and one short.



FIG. 65.—The *Zoanthina* larva of a Zoanthid. (After Carlgren.)

It appears from this brief review that the larvae of Cereanthidae, unlike the Hexactiniae, do not pass through an "Edwardsia" stage in their development, but that nevertheless they may be regarded as springing from a stock, common to the Hexactiniae, Edwardsiae, and themselves,

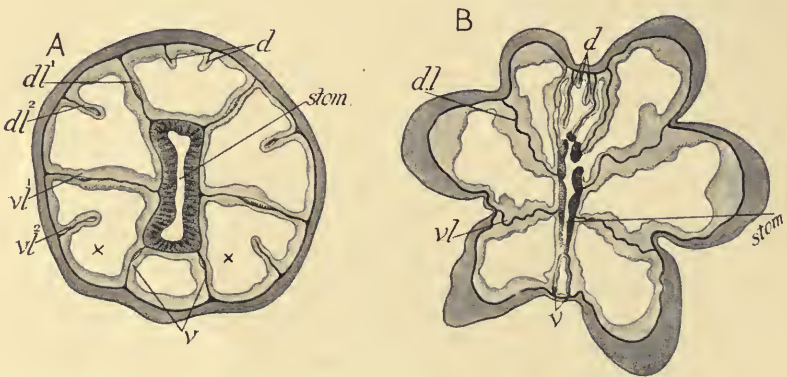


FIG. 66.—Transverse sections of Actinozoan larvae. (After van Beneden.)

A, section of *Zoanthina* larva. B, section of *Arachnactis* larva. *d*, (in A) dorsal directive mesenteries, (in B) indefinite number of mesenteries occupying the place of the dorsal directives; *dl*, dorso-lateral mesenteries; *dl'*, long dorso-lateral mesenteries; *dl''*, short dorso-lateral mesenteries; *v*, ventral directive mesenteries; *v'*, ventro-lateral mesenteries; *v''*, long ventro-lateral mesenteries; *v'''*, short ventro-lateral mesenteries; *xx* (in A) mark the places where additional pairs of mesenteries are added.

in which only six mesenteries were developed. The Zoanthidae on the contrary may almost be said to pass through a Hexactinian stage in their development.

We have much less information on the development of Alcyonaria than on that of Zoantharia. The best account is that of Wilson, to which the more recent accounts by Koch of the development of *Gorgonia* (1887), and by Hickson of the development of *Alcyonium*

(1901), have added nothing of any importance. Wilson worked on the species *Renilla reniformis* and *Leptogorgia virgulata* (1883). The eggs are expelled from the parent colonies and fertilized in the sea. The endoderm appears to be formed by proliferation, and all the eight mesenteries appear at once. The arrangement of the muscular thickenings on these mesenteries differs only from that in the *Edwardsia* stage of *Hexactiniae*, in the fact that the thickenings of the ventral directives face each other instead of being turned away from each other. Wilson's observations on the origin of the filaments have already been dealt with.

The *Alcyonaria* differ less in this respect from the *Edwardsiae* than these differ from the *Cereanthidae*, and the real ground of their separation from the *Zoantharia* lies in the method of forming the skeleton, as will now be made clear.

The popular name Sea-Anemone is usually given to those *Zoantharia* which do not develop a calcareous skeleton, whilst those which do form skeletons are termed Coral-forming Polyps—or briefly, Corals. The development of the skeleton in these was first worked out by Lacaze-Duthiers (1864), but the subject was again taken up and thoroughly examined by von Koch (1897), whose latest investigations deal with the Mediterranean species *Caryophyllia cyathus*.

The first part of the skeleton to appear is the **basal plate** which is secreted by the pedal disc of the polyp. This basal plate appears as six separate areas of calcareous deposit, one area being situated beneath the space intervening between each pair of mesenteries. They eventually coalesce to form, first a six-rayed star and then a circular disc. In the centre of each of the original areas the process of secretion of calcareous matter continues more actively than elsewhere, and the consequence of this is the formation of six radiating **septa** of calcareous matter, each septum being covered by an inwardly projecting fold of the pedal disc. The edge of the basal plate becomes raised into a rim, owing to the upward extension of the skeleton-forming area on the side of the polyp, and in this way the beginning is made of a **theca** or cup in which the polyp sits.

Both septa and thecal wall grow in height: soon a set of six secondary septa alternating with the primary ones make their appearance, whilst in the centre of the basal plate there appear two or

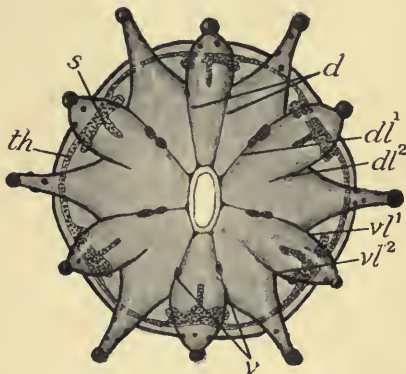


FIG. 67. — Young living *Caryophyllia cyathus* seen from above. The calcareous skeleton shows through the transparent tissue. (After von Koch.)

Letters as in preceding figures. In addition, *s*, one of the primary septa; *th*, wall of theca.

three small knobs which will later coalesce so as to form the **columella**. The columella is the median pillar which projects upwards from the base of the theca, indenting the base of the polyp. The primary septa become extremely thick where they join the thecal wall. Still later, cycles of tertiary septa make their appearance, and from the edges of these structures isolated pillars become separated which form the **pali**.

The skeleton of Zoantharian corals is therefore purely derived from an external exudation, and in this respect it contrasts most markedly with the skeleton of Alcyonaria. In his paper on *Renilla* (1883), Wilson has described the origin of a typical Alcyonarian

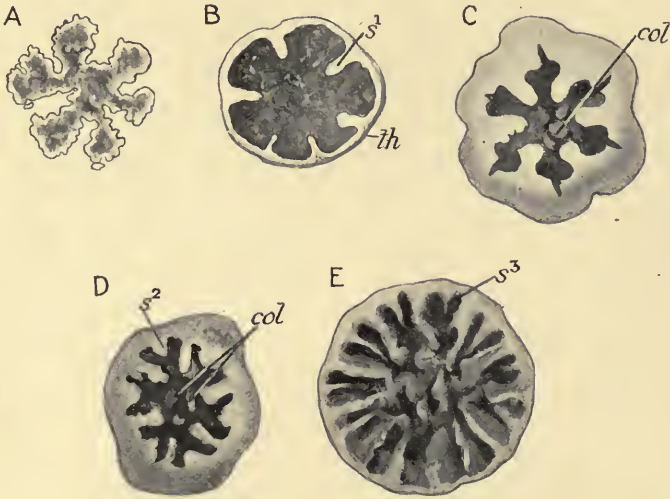


FIG. 68.—Five stages in the development of the skeleton of *Caryophyllia cyathus*. (After von Koch.)

A, the six primary areas of deposit coalescing to form a star-shaped figure. B, the thecal wall just formed. C, the thecal wall thickened opposite the bases of the septa. D, the appearance of the secondary septa and of the columella. E, tertiary septa formed. *col*, columella; *s*¹, primary septum; *s*², secondary septum; *s*³, tertiary septum; *th*, wall of theca.

skeleton. The lower cells of the ectoderm, corresponding roughly in position to the interstitial cells of *Hydra*, acquire calcareous concretions in their interior and migrate into the jelly. These concretions form the characteristic Alcyonarian spicules. But in *Renilla*, oval, wine-red, calcareous bodies are also formed in endodermal cells, and both kinds of spicules are found in the adult. In their characteristic skeleton therefore, as has already been said, lies the real distinguishing mark of Alcyonaria.

IV. CTENOPHORA

The fourth group of Coelenterata differ profoundly from all the rest, not only in their completely pelagic life, with no trace of a fixed

stage anywhere in their ontogeny, but also in the possession of a well-developed nervous and sensory centre at the aboral pole, a part of the body which in other free-swimming Coelenterata is the least sensitive portion of the whole surface. The whole development is also of a widely different type from that of other Coelenterata, so that at first sight it is difficult to find any points of resemblance.

The most primitive type of Ctenophore known is that included in the order Cydippidea. Unfortunately such forms cannot be regularly obtained; occasionally they turn up in great swarms, and then for years it will be difficult if not impossible to procure them. On the other hand *Berœ* is a form which is abnormal in many respects, but which can be obtained regularly in the Mediterranean, at least at one season of the year, and it has been made the subject of much experimental work. Two species of *Berœ* occur in the Mediterranean, *B. forskalii* and *B. ovata*. The development of these two seems to be identical for all practical purposes and our illustrations will be drawn from each.

BERŒ

Berœ differs from primitive Ctenophora in possessing an enormously expanded stomodæum, recalling the cavity of the bell of a medusa, and also in not having any vestige of tentacles.

We owe our first account of the development of *Berœ* to Chun (1880), and his account has been supplemented by those of Driesch (1895), Ziegler (1898), and Fischel (1897 and 1898), all of whom approached the subject from the standpoint of Experimental Embryology.

If *Berœ* be kept in an aquarium it will deposit its ripe eggs. These are translucent spheres about 1 mm. in diameter, covered by a tough membrane. They contain a large amount of food-yolk. The nucleus is situated near one pole (the upper), and at this pole the most of the protoplasm of the egg is massed, the rest of the egg consisting of food-yolk.

Development goes on within the membrane up to the formation of a complete larva, and owing to the transparency of the eggs the greater part of the development can be studied in the living object; but larvae can be preserved in osmium

acid and embedded in celloidin and then examined by cutting them into series of sections. The egg divides into two, and then four equal segments, by means of furrows which begin at the upper



FIG. 69.—Side view of the segmenting egg of a Ctenophore (*Callianira bialata*). (After Metschnikoff.)

Only one half of the egg is seen; it is in the 16-cell stage. *mac*, macromere; *mic*, micromere.

pole and slowly make their way through the yolky portion of the egg. The four segments then divide into eight, not as one finds in

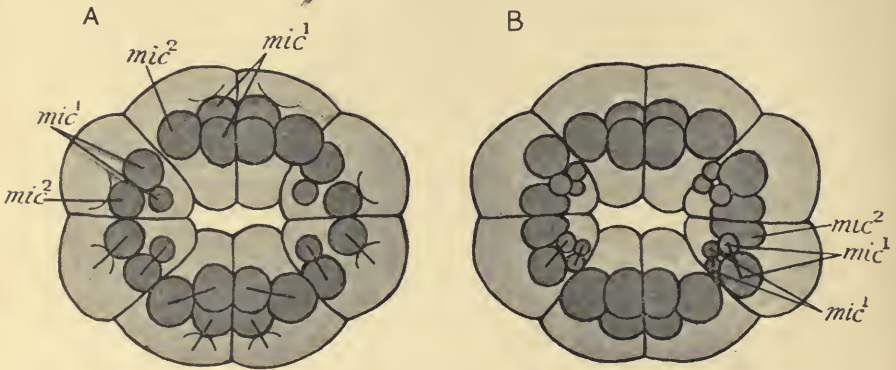


FIG. 70.—Two views of the developing egg of *Berœ ovata* seen from above. (After Ziegler.)

A, the first-formed micromeres have just divided and a second micromere has been budded off from each macromere. B, the daughters of the first micromeres have divided again. *mic¹*, daughters of first-formed micromeres; *mic²*, micromeres budded off subsequently.

other eggs by a circular furrow, but by oblique almost vertical furrows, which separate off four inner larger cells from four outer smaller cells.

The eight cells are arranged in two linear rows of four each. These rows stand opposite to one another and form an ellipse-like

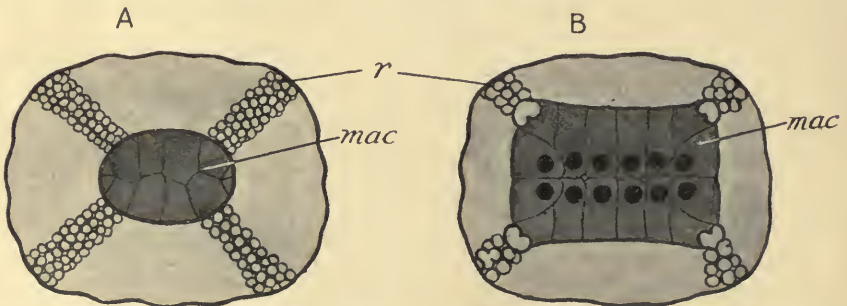


FIG. 71.—Oral and aboral views of the embryo of *Berœ ovata* in a later stage. (After Ziegler.)

A, from aboral pole. B, from oral pole. *mac*, macromeres; *r*, small ectoderm cells which later will develop into the ribs of the adult.

figure, the long axis of which is at right angles to the stomach plane of the adult, and is identical with the funnel plane of the adult Ctenophore. These eight cells are termed the **macromeres**. Then each macromere, by unequal division, buds off a much smaller cell termed a **micromere** at the upper pole, and thus a 16-cell stage is reached.

Now Ziegler (1898) has shown that the process of division of a

blastomere takes nearly an hour to accomplish. During the process of the division of the eight blastomeres into two tiers of cells, the cytoplasm flows from the daughter cell, which is originally the larger, upwards into the smaller cell; so, by the time the division is accomplished the original proportions of the two cells have become reversed, so that what was originally macromere is now micromere and *vice versa*.

At the next cleavage eight more micromeres are budded off; this is the division of the macromeres of the 16-cell stage; and the first-formed micromeres divide, and thus the cleavage is complete, every cell in the egg having divided, and a total of thirty-two cells has been reached. Each macromere with the micromeres to which it gives rise, may be termed an **octant** of the egg. In Fig. 69 the egg of another Ctenophore is shown in this stage of development, seen from the side. All Ctenophora, the development of which has been examined, seem to agree in the way in which the cleavage of the egg is carried out, and this figure may therefore be taken as representing what goes on in *Berœ*.

In the outer octants the division of the first-formed micromeres is unequal, the smaller daughter cell being the smallest of all three sets of micromeres, and the larger daughter the largest of them; the new micromeres which have just been budded from the macromeres being intermediate in size. In the middle octants the first-formed micromeres divide equally.

In the next period of cleavage the micromeres alone divide, the macromeres remaining quiescent. The smallest micromere divides into two equal parts. Its sister cell separates off towards the upper pole as a smallest tertiary micromere, and, as all the daughters of the first-formed micromeres in the middle

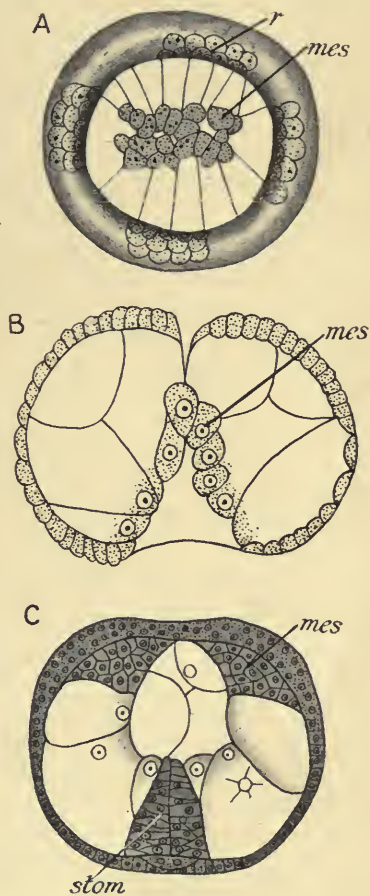


FIG. 72.—Illustrating the origin and fate of the so-called mesoderm in a Ctenophore embryo (*Collianira bicalata*). (After Metschnikoff.)

A, view from oral pole at the time when the "mesoderm" is being budded off. B, optical longitudinal section of a slightly later stage, showing rotation of the macromeres and the consequent invagination of the "mesoderm." C, optical section of a still later stage, showing accumulation of mesoderm at upper pole and formation of stomodaeum. Letters as before. *mes*, mesoderm.

octants likewise throw off a smallest micromere, there arises in this way a crown of smallest micromeres surrounding one pole of the embryo.

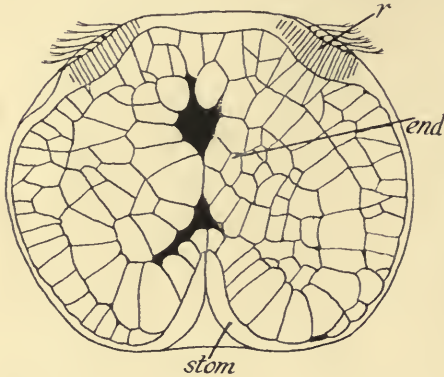


FIG. 73.—Optical section of embryo of *Beröe forskalii* showing the beginning of the endodermal cavities. (After Chun.)

end, parenchyma-like endoderm; *r*, rib; *stom*, stomodaeum which forms the so-called "stomach."

In the middle octants also the four smallest micromeres divide first, whilst the eight larger micromeres flatten out and commence to spread over the macromeres, after which they also divide. From this time on, division of the micromeres occurs rapidly, and the sheet of cells to which they give rise spreads more and more over the surface of the macromeres. The macromeres are originally exposed both above and below but the upper opening is narrowed as the edge of the ring of smallest micromeres extends inwards, whilst the larger micromeres rapidly extend downwards over the surface of the macromeres. This over-spreading of the macromeres by smaller cells is termed **epibole**. It is a process often met with in the development of animals and is to be regarded as a variety of **gastrulation**.

There can now be seen, radiating from the upper pole, four streaks of specially small and rapidly dividing cells; these are the forerunners of the "**ribs**" of the adult which carry the comb-like plates of cilia. Each streak corresponds to a pair of ribs.

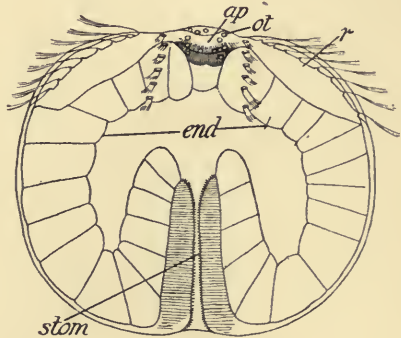


FIG. 74.—Optical section of embryo of *Beröe forskalii* in a later stage of development, with a hollow endodermal sac. (After Chun.)

Letters as before. In addition, *ap*, apical nervous plate; *ot*, otolithic concretions.

Just before the lower pole of the macromeres is completely covered by the advancing ectoderm, each macromere buds off downwards, a small cell. We thus get a circle of sixteen small cells at the

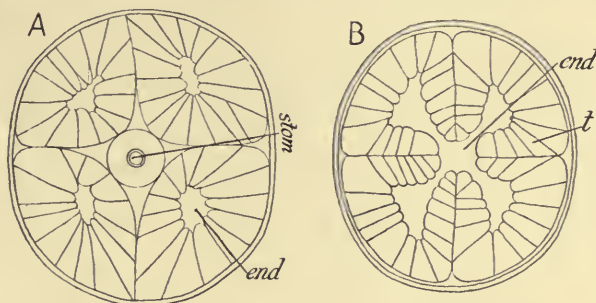


FIG. 75.—Two optical sections through the embryo of *Berœ forskalii*. (After Chun.)

A, through the stomodaeum. B, above the stomodaeum near the aboral pole.
end, cavity of the gastric sac. t, taeniola.

vegetative pole; these are the rudiment of the so-called **mesoderm**. The macromeres now rotate in such a way that the “mesodermal” cells are rotated upwards and inwards, and eventually come to lie at the upper pole of the macromeres. Here they undergo rapid division and form a cross, the two longer arms of which extend in the direction of the long axis of the embryo, while the two shorter ones are transverse to that axis (Fig. 72).

The ectodermal skin is now completed, and the macromeres now undergo rapid division, forming a parenchyma-like tissue. Between ectoderm and endoderm jelly appears as a secretion; and into this jelly wandering cells are budded from the cross of “mesoderm” cells. These cells become connected with one another, with the ectoderm and with the endoderm by their processes, so as to produce a cell-network which simulates connective tissue; it is, however, certain that many,

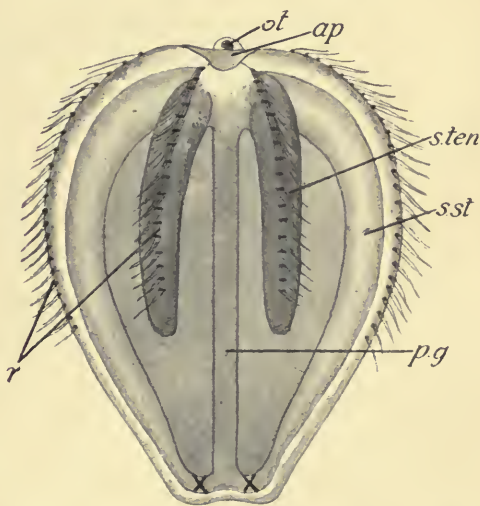


FIG. 76.—Larva of *Berœ forskalii* four days old, viewed from “stomach-plane.” (After Chun.)

The paragastric canals have forked and united at x with the sub-ventral or sub-“stomachic” canals. The sub-tentacular canals are still short. Letters as before. x, forks of paragastric canal; pg, paragastric canal; sst, sub-stomachic canal; sten, sub-tentacular canal.

if not most, of the cell-processes are contractile, and therefore these wandering cells are to be regarded as muscular.

In the endoderm there appear slit-like spaces between the cells here and there, and these now coalesce so as to form a single roomy, gastric cavity. At the lower pole the **stomodaeum** now makes its appearance as an invagination of the ectoderm. This, as it grows upwards, indents the endodermic sac and constricts it into right and left halves. An indentation occurs in this sac at each side of a line which is at right angles to the plane of the stomodaeum, and in this way a four-lobed sac is formed. We might with perfect justice describe the process as a formation of four ridges or **taeniolae**, which grow into and indent the cavity of the endoderm sac.

Meanwhile, the "**combs**" of cilia have appeared in the regions, where, at an earlier stage, the streaks of rapidly-dividing ectoderm

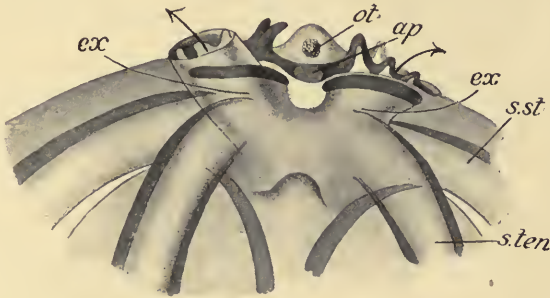


FIG. 77.—Part of apical region of larva of *Beröe forskalii* viewed from stomach-plane. (After Chun.)

Letters as before. *ex*, excretory vessel rising from the funnel.

cells were noticeable. Thus the ribs of the adult are established. At the upper pole, groups of stiff cilia supporting otolithic masses are formed, and in this way the **apical sense-organ** is completed.

We have now an oval embryo containing a four-lobed gastric sac, whose walls are formed of vacuolated cells with stiff membranes, and having on one side a mouth leading into a flattened stomodaeum which projects inwards into its interior. Running like the meridians on a globe are eight ribs of thickened ectoderm, each bearing a series of combs of cilia, and converging to a polar plate at the pole opposite the mouth: this plate carries groups of stiff converging cilia which support an otolith where they meet.

At this stage the embryo escapes from the egg-membrane and begins life as a free-swimming larva. The later history has been followed only by Chun and has been deduced from the examination of specimens caught by the Plankton net. From these he concludes that the **meridional canals** appear on the periphery of the endodermic pouches as everted grooves. First the **sub-tentacular** and then the **sub-stomachic** canals appear, then the two **paragastric** canals arise as

independent evaginations. All grow down towards the edge of the mouth and here each one forks, and adjacent forks unite with one another, and so a circular canal is formed. This is a peculiarity of *Berœ* as opposed to other Ctenophora. From the gastric sac two canals extend upwards towards the aboral pole of the larva and fuse with the ectoderm at the sides of the apical plate. Here openings are made to the exterior. These canals are called **excretory canals**, and out of them a current of water flows (Fig. 77). It is probable that this current forms the exhalent portion of a respiratory current, and that water enters by the mouth to replace it. Finally, the meridional canals give off short outgrowths which, in one species, anastomose with one another so as to form a network.

CALLIANIRA

The main difference between the development of *Berœ* and that of other Ctenophora lies in the presence of tentacles more or less modified in the other groups.

The best account of the development is that given by Metschnikoff of *Callianira* (1885). From this account we learn that the two main arms of the "mesodermal cross," after having given off a certain number of wandering cells, give rise to the tissue which forms the axis of the tentacles. The **tentacles** themselves appear as invaginations—the **tentacle pockets**—from the base of which the real tentacle sprouts. These tentacle pockets indent the endodermic sac in a plane at right angles to that in which it is indented by the stomodaeum.

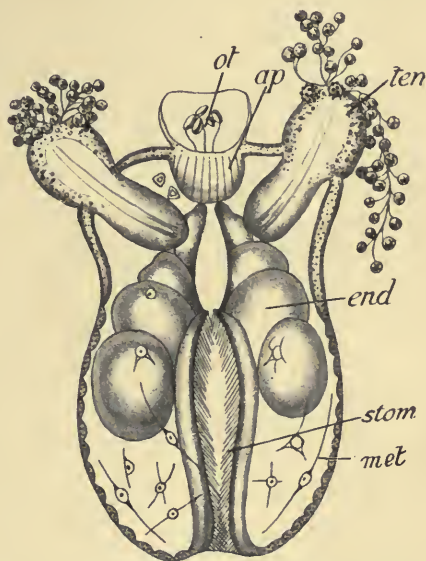


FIG. 78.—The free-swimming larva of *Callianira bialata* viewed from the stomach-plane. (After Metschnikoff.)

ten, freely projecting tentacle; *met*, wandering cells with contractile processes.

AFFINITIES OF CTENOPHORA WITH OTHER COELENTERATA

Now, when we review the account which has just been given of the development of *Berœ*, there is really only one point where any marked similarity with the developmental stages of other Coelenterata shows itself, and this is when the ectoderm has completely invested the macromeres, and these latter have broken up into a mass of cells like plant "parenchyma," with only slits between them. *This stage*

recalls the solid planula stage of other Coelenterates, the slit-like spaces being comparable to the incipient absorption spaces which are the first stage in the formation of the gastric cavity in other Coelenterates.

Perhaps we might go farther and find in the stage which succeeds to this a similarity to Actinozoon development. In the development of Actinozoa an ectodermal stomodaeum is also formed, and the primary lobing of the enterocoelic sac by four folds in *Berœ* might be compared to the outgrowth of taeniolae or septa in Actinozoa. There would, however, remain an irreconcilable difference, viz., that the first tentacles in Actinozoa sprout from the pouches, whereas in Ctenophora they occur between them—for in Ctenophora, as we have seen, the tentacle pockets cause the formation of taeniolae and therefore alternate with the pockets of the gut.

Reverting, however, to the planula stage common to all Coelenterates, a comparison of the later history of this stage in the various groups reveals the real relationship of the Ctenophora to the rest. In Hydrozoa, Scyphozoa, and Actinozoa, the planula, after a brief period of swimming, fixes itself by its aboral pole, which becomes the root of the future colony; but in Ctenophora the planula never fixes itself but remains free-swimming and develops a complicated sense-organ at the aboral pole.

Hence, if all Coelenterata have sprung from a planula-like ancestor, the Ctenophora must represent a branch which never deserted the free-swimming life, and which in consequence must represent the main stem of Coelenterates, while the other groups, though far more abundant at the present day, must represent degenerate offshoots of this stock. Of these we may suppose that the Actinozoa represent a group which assumed a bottom life later than the rest, and in which, consequently, evolution had gone farther, and a stomodaeum had been formed. In accordance with this conclusion we find that Ctenophora present resemblances to the larvae of the higher forms in far greater degree than do other Coelenterata, for it is to be expected that higher forms would arise from a dominant free-swimming group rather than from a degenerate sessile one.

EXPERIMENTAL EMBRYOLOGY OF COELENTERATA

But though in their later larval life the Ctenophora retain many primitive features, in their earlier embryonic life they have undergone great specialization. This will be made clear by contrasting the results obtained by Zoja (1895–1896), who experimented with the eggs of Hydromedusae, and those obtained by Driesch (1895) and Fischel (1897–1898), who experimented with the eggs of *Berœ*.

Zoja worked with the genera *Liriope*, *Geryonia*, *Mitrocoma*, *Clytia*, and *Laodice*, and he separated the first blastomeres of the segmenting egg with a needle. In the case of *Clytia* and *Laodice* he found that a single blastomere of the 16-cell stage was capable of developing

into a normal planula, and that in all cases one of the first four blastomeres could do so. From such a blastomere in *Clytia* a hydroid was reared, and in *Liriope* a fully-developed medusa with four tentacles was reared.

Now Driesch and Morgan (1895) made a number of experiments on the eggs of *Berœ* of which the most interesting are these. By means of a fine scalpel they cut pieces from the unsegmented egg. Such mutilated eggs mostly died, but about sixteen out of five hundred survived, and eight of these developed into larvae with a diminished number both of ribs and endodermal pouches.

From this experiment Driesch and Morgan draw the conclusion that the material required to form definite regions of the embryo is localized in definite parts of the egg. This conclusion is amply confirmed by the result attained from separation of the first blastomeres of the egg by means of a scalpel. Each of the first two blastomeres produces an embryo with four ribs. Each one of the first four blastomeres forms a larva with two ribs only; and further, when one blastomere is separated from the first four the remaining three blastomeres form an embryo with six ribs.

Fischel (1897-1898) improved on Driesch and Morgan's methods: he separated the blastomeres from one another by subjecting the egg to pressure, and by pinching the egg-membrane with forceps. By this means he found he could make one embryo produce three smaller embryos with a lessened number of ribs, and he found that the united number of their ribs amounted to the total of a normal embryo. By pressure he also separated the smallest micromeres, *i.e.* those which give rise to the apical plate, into two portions, and from these resulted an embryo with two apical plates. When pressure was applied in later stages the result was, not to produce several larvae with a lessened number of ribs, but to break up the ribs already formed into several pieces. In larvae with four ribs, produced from one of the first two blastomeres, three endodermal pouches are formed, not two as one would expect (Fig. 79). But Fischel points out that whereas the first two are produced by the ingrowth of taeniolae in the tentacle plane, the small third one owes its origin to the fact that the stomodaeum

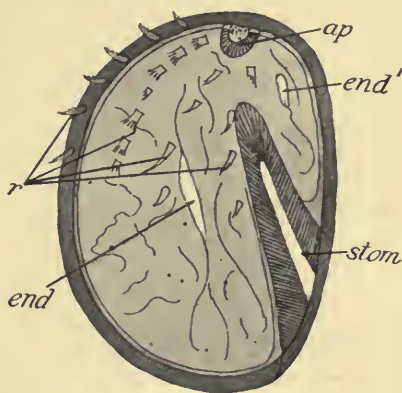


FIG. 79.—An embryo of *Berœ ovata* with four ribs and two endodermal pouches, and a small extra third pouch; obtained by isolating one of the first two blastomeres of *Berœ ovata*. (After Fischel.)

end, one of the two normal endodermal pouches; *end'*, the small extra endodermal pouch; *r*, the four ribs. The other letters as before.

originates close to one side of the larva, not at the absolute edge as it should do were the embryo a perfect half; in consequence of this fact the growing stomodaeum indents the endodermic sac unevenly, cutting off a little third pouch.

From the fact also that in this half larva, on the side next where the missing half should be, the endoderm is not naked but covered with ectoderm; and from the fact that by separating the lower ends of the macromeres he succeeded in producing a form with two stomodaea, Fischel concludes that although the material destined to form the specialized ribs and the apical plate is originally rigidly localized in the germ, this is not the case with the rest of the ectoderm. This unspecialized ectoderm spreads till it covers all the exposed macromeres, whilst the stomodaeum is formed owing to the action on this general ectoderm of a stimulus proceeding from the lower ends of the macromeres.

From a review of the work of all these experimenters we draw the conclusion that in the eggs of Hydromedusae, up to the 16-cell stage, the part resembles the whole in its constitution; and the question whether one portion shall form only part of an embryo or whether it shall form a whole embryo, depends on whether or not it remains in connection with its fellows. In Ctenophora, however, we must conclude that the part is quite different from the whole, and that the parts destined to form the ribs and apical plate are mapped out even in the unsegmented germ; these parts must, therefore, be represented by portions of the cytoplasm of the egg, not by nuclei.

The egg is incapable of regenerating a lost part, but in this respect a remarkable observation of Chun's (1880) must be borne in mind. He experimented with the eggs of *Bolina* and obtained half larvae just as did Driesch and Fischel with *Berœe*. But Chun kept his half larvae living for weeks, till they developed generative organs on their meridional canals, and he states that the missing half was post-generated. This observation has been recently confirmed by Mortensen.

That an animal in its young stages should possess no powers of regeneration, but should acquire them when it is older, is a curious fact but not unprecedented, for the same thing occurs in Ascidians. We have seen that the specialization of the egg for the formation of organs is a specialization of plasma, but it will be shown later in this volume that this specialization must be regarded as due to an influence emanating from the nucleus of the ovum during the period of its growth and ripening. We must, I think, attribute the secondarily acquired power of regeneration to a reorganization of the cytoplasm, due to renewed influences emanating from the nucleus.

ANCESTRAL MEANING OF THE PLANULA

We have now to consider the meaning of the development of the planula. We have already put forward the hypothesis that the planula represents a free-swimming ancestor common to all

Coelenterata. Now the planula appears under two forms: in Scyphozoa and in some Actinozoa as a hollow two-layered vesicle with a terminal opening, and in Hydrozoa and many Actinozoa as a solid mass of endoderm surrounded by a skin of ectoderm.

Which of these two is the more primitive and which the derived form? In answer to this question we say at once, *the first of these is the more primitive*, because it alone exhibits a structure which is a physiological possibility for a self-supporting animal. A solid internal mass of cells would be quite functionless in an animal that had to get its own living.

The stage of the planula in development is preceded by the stage of the hollow blastula, in all cases which have been thoroughly examined. The hollow blastula is changed into the planula either (*a*) by intucking or invagination of one end, (*b*) by active proliferation of cells proceeding from one end and filling up the interior, or (*c*) by proliferation of cells from the whole internal surface. We have already pointed out that, whereas (*c*) is described only in cases of eggs developing rapidly inside the bell of a vestigial medusa, or with a shortened development in which the hydroid stage is almost eliminated and the egg develops directly into a medusa, and that the assertion of its occurrence even in these cases may be based on a mistake in the observations; on the other hand (*a*) and (*b*) occur in eggs with a long larval development.

We may take it therefore that these latter methods of endoderm formation represent the least modified form of development, and that the ancestral blastula was developed into the ancestral planula by a proliferation of cells at one pole only, or by an invagination of the cells forming the wall of the blastula at this pole.

If this be admitted, however, we have no difficulty in deciding that invagination must be more primitive than polar proliferation. Our reason for that decision is that polar proliferation would be meaningless in an adult animal, whereas invagination means, primarily an increase in surface area of a portion of the animal, and secondarily an inbending and the consequent continuous preservation of a cavity between the invaginated cells, which cavity is destined to contain food.

In fact, as Korschelt and Heider point out, a ciliated animal, progressing forward in one direction, tends to create suction behind it, so that particles struck backwards by the cilia tend to accumulate there; just as may be observed at the tail of an express train as it dashes past a station. Here then would be sufficient inducement for the tendency to increase and exaggerate the function of ingestion—a function which all the cells of the planula originally must have possessed,—and so we may suppose that an endoderm and an ectoderm would become specialized from an indifferent layer of cells.

As the endoderm cells increased in number it became necessary that they should find room, and this they did by bending inwards, and so the planular stage is reached. When this stage is repeated

in ontogeny, and when the food necessary for the embryo is stored up within its cells in the form of yolk-grains, and has not to be sought for outside, then the inbending can be replaced by solid proliferation because the larval gut is no longer a functional organ.

We are thus led to form the following conception of the past history of the lower Metazoa. A widespread and dominant race of blastula-like animals once swarmed in the primeval seas. Some of these took a creeping life and eventually gave rise to the group of sponges; others kept to the free-swimming life and developed into planulae, and so gave rise to the Coelenterata. Some of these planulae, by the specialization of the cilia into comb-like locomotor organs, became Ctenophora; whilst the remainder adopted a fixed life and attached themselves by their aboral poles. This change occurred in different divisions of the stock at different stages of the evolution of the internal organs of the planula ancestor, and in this way the groups of Hydrozoa, Scyphozoa, and Actinozoa arose.

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