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A TREATISE

ON

COMPARATIVE EMBRYOLOGY

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CHAPTER VI.

CŒLENTERATA[1].

Hydroidea. The most typical mode of development of the Hydroidea is that in which the segmentation leads directly to the formation of a free ciliated two-layered larva, known since Dalyell's observations as a planula. The planula is characteristic of almost all the Hydromedusæ with fixed hydrosomes including the Hydrocoralla (Stylasteridæ and Millepora), the most important exceptions being the genus Tubularia and one or two other genera, and the fresh-water Hydra.

In a typical Sertularian the segmentation is approximately regular[2] and ends according to the usual accounts in the formation of a solid spherical mass of cells. A process of delamination now takes place, which leads to the formation of a superficial layer of cubical or pyramidal cells, enclosing a central solid mass of more or less irregularly arranged cells.

The embryo, in the cases in which it is still contained within the sporosack, now begins to exhibit slight changes of form, and

[1] I. HYDROZOA.

1. **Hydromedusæ.** { *Hydroidea.* / *Trachymedusæ.* }
2. **Siphonophora.** { *Calycophoridæ.* / *Physophoridæ.* }
3. **Acraspeda.**

II. ACTINOZOA.

1. **Alcyonaria.** (Octocoralla.)
2. **Zoantharia.** (Hexacoralla.)

III. CTENOPHORA.

[2] For a detailed description of the development of a single species the reader referred to Allman's description of Laomedia flexuosa, No. 149, p. 85 *et seq.*

one extremity of it begins to elongate. It soon becomes free, and rapidly assumes an elongated cylindrical form, while a coating of cilia, by means of which it moves sluggishly about, appears on its outer surface. A central cavity appears in the interior, and the inner cells form themselves into a definite hypoblast. The larva has now become a planula, and consists of a closed sack with double walls. It continues for some few days to move about, but eventually drops its cilia, and becomes dilated at one extremity, by which it then becomes attached. The base of attachment becomes gradually enlarged so as to form a disc, which spreads out and is frequently divided by fissures into radiating lobes. The free extremity becomes enlarged to form the eventual calyx.

Over the whole exterior a delicate pellicle—the future perisarc—now becomes secreted. Round the edge of the anterior enlargement a row of tentacles makes its appearance. These, in the embryos of the Tubularian genera, lie some little way behind the apex of the body. After a certain time the perisarc, which has hitherto been continuous, becomes ruptured in the region of

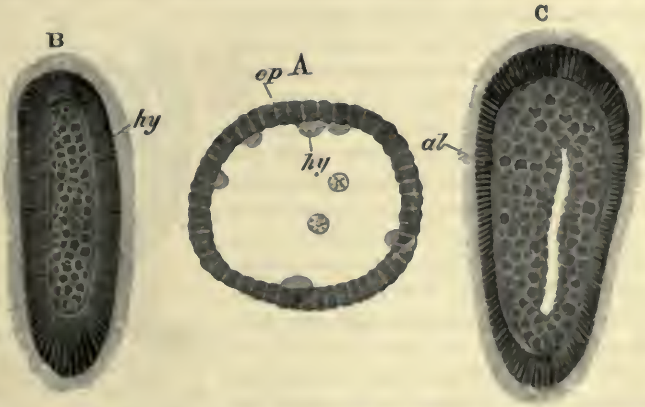

FIG. 68. THREE LARVA STAGES OF EUCOPE POLYSTYLA. (After Kowalevsky.)

A. Blastosphere stage with hypoblast spheres becoming budded off into the central cavity.

B. Planula stage with solid hypoblast.

C. Planula stage with a gastric cavity.

ep. epiblast; *hy.* hypoblast; *al.* gastric cavity.

the calyx, and the tentacles become quite free. At about the same period a mouth is formed at the oral apex.

The development of Eucope polystyla (fig. 68), one of the Campanularidæ, deviates according to Kowalevsky (No. 147) in somewhat important points from the usual type. The whole development takes place after the deposition of the ovum. The segmentation results in the formation of a single-walled blastosphere with a large central cavity (fig. 68 A). This cavity, somewhat as in Ascetta, becomes filled up with a not clearly (?) cellular material derived from the walls of the blastosphere, which must be regarded as the hypoblast (fig. 68 B). The larva elongates and becomes ciliated, and the epiblast at its two extremities becomes thickened, and is stated by Kowalevsky also to become divided into two layers. The alimentary cavity appears as a slit in the middle of the hypoblast (fig. 68 C). The cilia after a time disappear, and the larva then becomes fixed by one extremity. It flattens itself out into a disc-like form, becomes divided into four lobes, and covered by a cuticle (perisarc). From the disc the stalk grows out which dilates at its free extremity into the calyx.

In both the groups (Tubularia and Hydra) which are exceptional in not having a ciliated planula stage, its absence may be put down to an abbreviation of the development, and in fact a two-layered quiescent stage, through which the embryo passes, may be regarded as representing the planula stage.

The development of Tubularia, which has been described in detail by Ciamician, takes place in the gonophore[1]. The segmentation is irregular and leads to the formation of an epibolic gastrula, four large central cells constituting the hypoblast[2]. The larva now elongates, and grows out laterally into two processes which constitute the first pair of tentacles. At this stage it closely resembles the larvæ of some Medusæ. Additional tentacles are soon formed; and a central cavity appears in the hypoblast, the cells of which have in the meantime become more numerous (fig. 69). The tentacles are directed towards

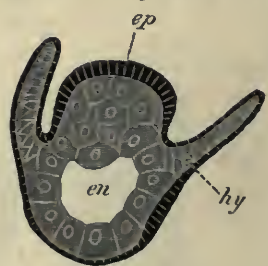

FIG. 69. LONGITUDINAL SECTION THROUGH A LARVA OF TUBULARIA MESEMBRYANTHEMUM WHILE STILL IN THE GONOPHORE. The lower end is the oral one.

ep. epiblast; *hy.* hypoblast of tentacle; *en.* enteric cavity.

[1] *Vide* Ciamician, *Zeit. f. wiss. Zool.*, Bd. XXXII. 1879.

[2] In examining the segmentation by means of sections I have failed to detect an epibolic gastrula or such irregularity as is described by Ciamician. Prof. Kleinenberg informs me that he has been equally unsuccessful.

the aboral side, which is considerably more prominent than the oral one. They contain a hypoblastic axis. The aboral end continues to grow and the tentacles gradually assume a horizontal position. A constriction now appears, dividing the larva into an aboral portion which will eventually form the stalk, and an oral portion. At the apex of the latter a row of short tentacles—the future oral tentacles—now appears. The larva has at this stage the form known as Actinula. In this condition it becomes hatched, and shortly afterwards it becomes fixed by the aboral end and grows into a colony.

The development of Myriothela (Allman, No. 150) takes place on the Tubularian type. The ovum invested by a delicate capsule becomes freed by the rupture of the gonophore, and is then taken up by the remarkable claspers characteristic of the genus. In the claspers it becomes fecundated and undergoes its further development. After segmentation a gastric cavity is formed, and provisional tentacles arise as a series of conical involutions which subsequently become evoluted. Permanent tentacles are formed as conical papillæ on a truncated oral process. After hatching it has a few days' free existence, and then becomes attached, and loses its provisional tentacles.

Although Hydra itself constitutes the simplest type of Hydrozoon, its development, which has been fully investigated by Kleinenberg (No. 161), is in some respects a little exceptional. The segmentation is regular, but a segmentation cavity is not formed. The peripheral layer of cells gradually becomes converted into a chitinous membrane, which is perhaps homologous with the perisarc of marine forms. Between the membrane and the germ a second pellicle makes its appearance. The above changes require about four days for their completion, but there next sets in a period of relative quiescence which lasts for some 6—8 weeks. During this period the remaining development is completed. The cells of the germ first fuse together. In the interior of the protoplasm a clear excentric space arises, which gradually extends itself and forms the rudiment of the gastric cavity. The outer shell in the meantime becomes less firm, and is finally burst and thrown off, owing to the expansion of the embryo within.

The outermost layer of the protoplasm becomes, relatively to the inner layer, clear and transparent, and there thus arises an indication of a division of the walls of the archenteric cavity into two zones, or layers. These layers, which form the epiblast and hypoblast, are definitely established on the appearance of cells with contractile tails[1] in the clear outer zone, between which the interstitial epiblast cells subsequently arise.

The embryo, still forming a closed double-walled sack, elongates itself, and at one pole its wall becomes very thin. And at this point a rupture takes place which gives rise to the mouth. Simultaneously with the mouth the tentacles become formed as hollow processes, according to Mereschkowsky two being formed first and subsequently the others in pairs. Very shortly

[1] These cells are the so-called nerve-muscle cells. Their nature is discussed in the second part of this work.

afterwards the hitherto uniform hypoblast becomes divided up into distinct cells. The thin inner pellicle which persists after the rupture of the outer membrane becomes in the meantime absorbed. With these changes the embryo practically acquires the characters of the adult.

Trachymedusæ. Amongst the Trachymedusæ, which as has now been satisfactorily established develop directly without alternations of generations, the embryology of species both of the Geryonidæ and the Æginidæ has been studied.

In all the types so far investigated the hypoblast is formed by delamination, and there is a more or less well-marked planula stage.

The development of Geryonia (Carmarina) hastata has been studied by Fol (No. 155) and Metschnikoff (No. 163)[1]. The ovum, when laid, is invested by a delicate vitelline membrane and mucous covering. Its protoplasm is formed of an outer granular and dense layer, and a central mass of a more spongy character. The segmentation is complete and regular, and up to the time when thirty-two segments have appeared each segment is composed of both constituents of the protoplasm of the ovum. A segmentation cavity appears when sixteen segments are formed, and becomes somewhat larger at the stage with thirty-two. At this stage the process of delamination commences. Each of the thirty-two segments, as shewn in the accompanying diagram (fig. 70), becomes divided into two unequal parts. The smaller of these is formed almost entirely of granular material; the larger contains portions of both kinds of protoplasm. In the next segmentation the thirty-two large cells only are concerned, and in each of these the line of division passes between the granular and the transparent protoplasm. The sixty-four lenticular masses of granular protoplasm thus formed constitute an outer closed epiblastic vesicle, within which the

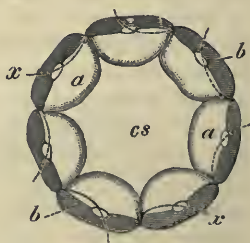

FIG. 70. DIAGRAMMATIC FIGURE SHEWING THE DELAMINATION OF THE OVUM OF GERYONIA. (Copied from Fol.)

cs. segmentation cavity; *a.* endoplasm; *b.* ectoplasm. The dotted lines shew the course of the next planes of division.

[1] In the succeeding account I have followed Fol, who differs in some minor points from Metschnikoff.

thirty-two masses of transparent protoplasm form an hypoblastic vesicle. The embryo at this stage is shewn in optical section in fig. 71.

The epiblastic vesicle now grows rapidly, while the hypoblastic vesicle remains nearly passive and becomes somewhat lens-shaped. At one point its wall comes in close contact with the epiblast. Elsewhere a wide cavity is developed between the two vesicles which becomes filled with gelatinous tissue. At this period cilia appear on the surface, and the larva becomes a planula.

The succeeding changes lead rapidly to the formation of a typical Medusa. Where the epiblast and hypoblast are in contact the former layer becomes thickened and forms a disc-shaped structure. The centre of this becomes somewhat protuberant, fuses with the hypoblast and then becomes perforated to form the mouth (fig. 72 *o*). The edge of the disc forms a thickened ridge, the rudiment of the velum (*v*), which is entirely formed of epiblast. At its edge six tentacles (*t*) arise, into which are continued solid prolongations of the wall of the now somewhat hexagonal gastric chamber. The hypoblastic axes of the tentacles soon lose their connection with the gastric wall.

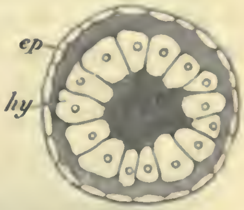

FIG. 71. EMBRYO OF GERYONIA AFTER DELAMINATION. (After Fol.)

ep. epiblast; *hy*. hypoblast.

Up to this time the larva has retained a more or less spherical form, and the cavity on the under side of the umbrella has not yet become developed. The latter now becomes established by the whole disc assuming a vaulted form with the concavity directed downwards. The lining of the cavity so formed is derived from the epiblast of the disc already spoken of.

FIG. 72. OPTICAL SECTION THROUGH THE ORAL POLE OF GERYONIA AFTER THE APPEARANCE OF THE GELATINOUS TISSUE OF THE DISC. (After Fol.)

o. mouth; *v*. velum; *t*. tentacle.

The shaded part represents the gelatinous tissue.

The exact mode of formation of the gastrovascular canals has not been worked out. It has however been established by the researches of the

Hertwigs (No. 146) and Claus (No. 153) that the radial and circular vessels of this system are connected together in adult Medusæ by an hypoblastic lamella; so that these canals would seem to be the remnants of an once-continuous gastric cavity. This mode of formation is established in the case of the medusiform buds; and it would therefore seem, as pointed out by the Hertwigs, a fair deduction that it occurs in the larva—a conclusion which is confirmed by the primitive extension of the gastric cavity to the edge of the disc at the time when its walls give rise to the solid axes of the tentacles. In the course of the subsequent retirement of the gastric cavity from the edge of the disc the gastrovascular canals probably take their origin, though Fol was unable to follow the changes which result in their formation.

On the completion of the above changes the larva has become a fully formed Medusa, but it undergoes a not inconsiderable metamorphosis before the attainment of the adult state.

Two species of Æginidæ have been studied by Metschnikoff (163), viz. *Polyxenia leucostyla* (*Ægineta flavescens*), and *Æginopsis mediterranea.* In both of these forms the segmentation

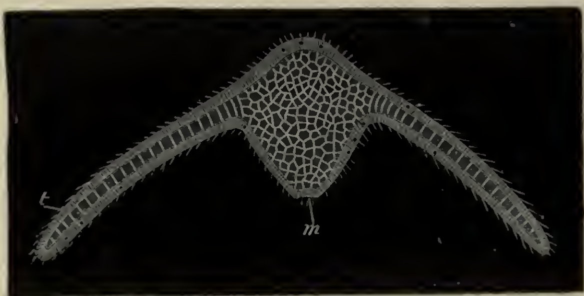

FIG. 73. A THREE-DAYS' LARVA OF ÆGINOPSIS WITH TWO TENTACLES. (After Metschnikoff.)
m. mouth; *t.* tentacle.

results in the formation of an elongated two-layered ciliated planula, without a central cavity. The two ends of this grow out into two long processes—the rudiments of a pair of at first aborally directed arms—which contain a solid hypoblastic axis (fig. 73). At this stage the larva closely resembles the larva of Tubularia. An alimentary cavity is hollowed out in the centre of the hypoblast which soon opens by a wide oral aperture (*m*). A second pair of arms becomes formed, which are at first much shorter than the original pair; with their formation a radial symmetry is acquired. Sense-organs become at the same time developed, and the whole embryo assumes a medusiform character. Fresh tentacles arise, the velum and cavity of the umbrella become established, but these changes do not involve any points of very special interest.

Siphonophora. The development of the Siphonophora has been the subject of careful investigation by Haeckel (158) and Metschnikoff (163). The ova are large and usually (except Hippopodius) without a membrane.

They are formed of a peripheral denser layer of protoplasm and a central spongy mass. They usually undergo their entire development in the water. In some instances they have been successfully reared by artificial impregnation.

As an example of the Calycophoridæ I shall take Epibulia aurantiaca, a form allied to Diphyes, the development of which has been studied by Metschnikoff[1].

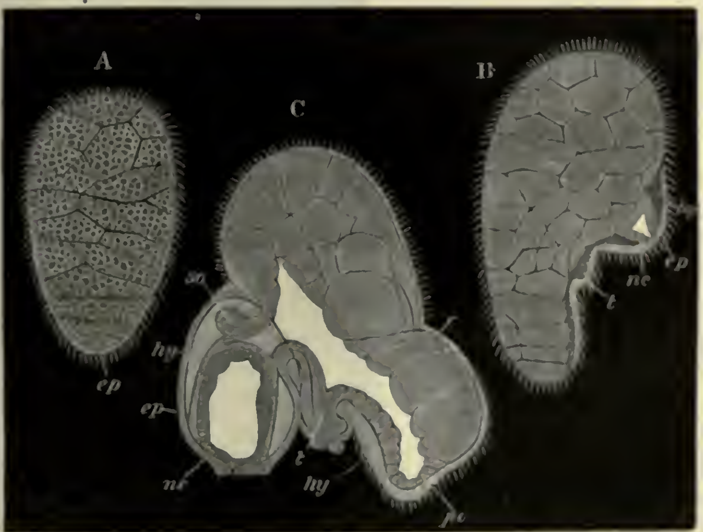

FIG. 74. THREE LARVAL STAGES OF EPIBULIA AURANTIACA. (After Metschnikoff.)

A. Planula stage.

B. Six-days' larva with nectocalyx (*nc*) and tentacle (*t*).

C. Somewhat older larva with gastric cavity.

ep. epiblast; *hy.* hypoblast; *so.* somatocyst; *nc.* nectocalyx; *t.* tentacle; *c.* large yolk cells; *po.* polypite.

[1] In my description of the development of the Siphonophora I employ Huxley's terminology.

There is a regular segmentation, unaccompanied by the formation of a segmentation cavity. At its close the ovum becomes a spherical ciliated embryo. This embryo soon becomes elongated, and its cells differentiate themselves into a central and a peripheral layer—the epiblast and the hypoblast (fig. 74 A). At this stage the larva has the typical planula form. The epiblast is especially thickened at a pole, which may be called the oral pole, and towards the side of this, which will be spoken of as the ventral side. Adjoining this thickened layer of epiblast a special thin layer of hypoblast becomes differentiated, which in opposition to the main mass of large nutritive cells forms the true hypoblastic epithelium (fig. 74 B, *hy*). On this thickening two prominences make their appearance (fig. 74 B). The oral of these is the rudiment of a tentacle (*t*), and the aboral of a nectocalyx (*nc*).

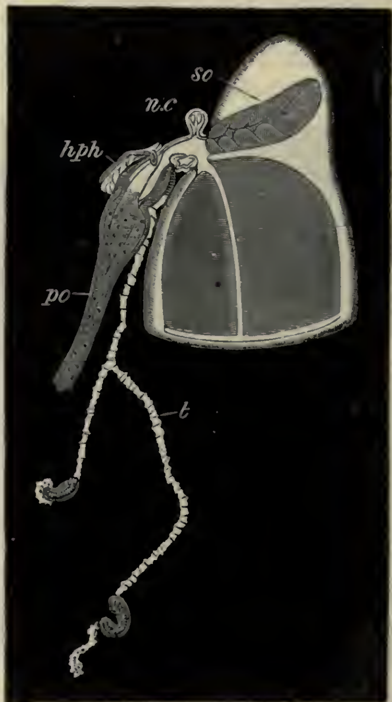

FIG. 75. AN ADVANCED LARVA OF EPIBULIA AURANTIACA WITH ONE LARGE NECTOCALYX. (After Metschnikoff.)

so. somatocyst; *nc.* second imperfectly developed nectocalyx; *hph.* hydrophyllium; *po.* polypite; *t.* tentacle.

The former of these elongates itself in succeeding stages into a process of both epiblast and hypoblast. The central part of the nectocalyx on the other hand appears to originate from a thickening of the epiblast in which the cavity of the bell becomes subsequently hollowed out. Between this part and the external epiblast which gives origin to the outermost layer of the nectocalyx a layer of hypoblast is interposed. When the nectocalyx has become to a certain extent established a cavity—the commencement of the primitive gastrovascular cavity of the adult—appears in the general hypoblast between the epithelial and nutritive layers in the immediate neighbourhood of its attachment. This cavity becomes prolonged into the nectocalyx to form the four gastrovascular canals; while the hypoblast at the upper end of the nectocalyx forms the somatocyst (fig. 74 C, *so*). The primitive enteric cavity once formed rapidly extends, especially in an oral direction (fig. 74 C), and forms a widish cavity in the oral part of the embryo. At the pole of this part (fig. 74, *po*) is eventually formed the opening of the mouth, and the contained cavity becomes in a special sense the gastric cavity. This region of the embryo may be spoken of as the polypite. The nectocalyx grows with great rapidity and soon forms by far the most prominent part of the larva (fig. 75). The true gastric region or polypite (fig. 75, *po*) continues also to grow, and a mouth becomes formed at its extremity. The aboral end of the original body of the embryo gradually atrophies.

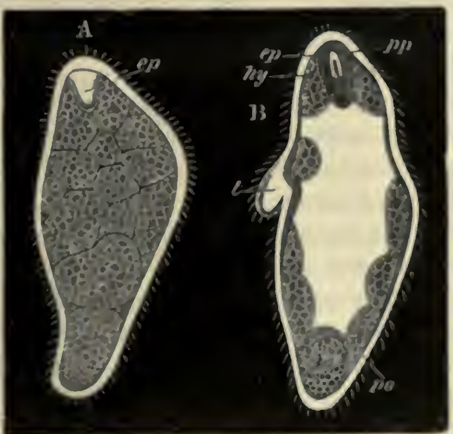

FIG. 76. TWO STAGES IN THE DEVELOPMENT OF STEPHANOMIA PICTUM. (After Metschnikoff.)

A. Stage after the delamination. *ep*. epiblastic invagination to form pneumatocyst.

B. Later stage after the formation of the gastric cavity in the solid hypoblast, *po*. polypite; *t*. tentacle; *pp*. pneumatophore; *ep*. epiblastic invagination to form pneumatocyst; *hy*. hypoblast surrounding pneumatocyst.

At the junction of the nectocalyx and polypite the cœnosarc becomes formed, and rudiments of a second nectocalyx (*nc*) and second polypite early become visible; while a hydrophyllium is formed as a bud which covers over the first polypite and tentacle (*hph*). With the development of the hydrophyllium the first segment, if the term may so be used, is complete. The second segment of which a rudiment is already present as a second polypite is intercalated between the first segment and the necto-calyces.

Amongst the Physophoridæ there is a considerable range of variation in development; though the variations concern for the most part not very important points. The simplest type hitherto observed is that of *Stephanomia* (Halistemma) *pictum*. The segmentation and formation of a two-layered planula (fig. 76) take place in the usual way. Between the solid central mass of nutritive hypoblast cells and the epiblast an epithelial hypoblastic layer becomes interposed which undergoes a special thickening at the aboral pole. At this pole a solid involution of epiblast next becomes formed, to which a layer of hypoblast becomes applied. The structure so formed is the rudiment of the pneumatocyst (*ep*). In the next stage the air-cavity of the pneumatocyst becomes established within the epiblast.

The gastrovascular cavity is formed in the midst of the nutritive hypoblast cells, which then become rapidly absorbed leaving the gastrovascular cavity entirely enclosed by the epithelial layer of hypoblast (fig. 76 B).

By the above changes the more important organs of the larva have become established. The one end forms the pneumatophore, and the other, the oral part, the polypite. Between the two there is already present the rudiment of a tentacle, and a second tentacle soon becomes formed. The mouth arises as a perforation at the oral end of the larva.

The pneumatophore contains a prolongation of the gastrovascular cavity, the fluid in which bathes the outer hypoblastic wall of the pneumatocyst. It has however no communication with the enclosed cavity of the pneumatocyst. In the later developmental stages the size of the pneumatophore becomes immensely reduced in comparison with the remainder of the larva.

The development of Physophora agrees closely with that of Stephanomia except in one somewhat important point, viz. in the development of a provisional hydrophyllium. This arises as a prominence at the aboral pole, containing a prolongation of the gastrovascular cavity. Between the epiblast and hypoblast of the prominence gelatinous tissue becomes deposited, and the hydrophyllium is thus converted into a large umbrella-like organ enclosing the polypite. The two together have a close resemblance to an ordinary Medusa, the polypite forming the manubrium, and the hydrophyllium the umbrella. The hydrophyllium is eventually thrown off.

An important type of Physophorid development is exemplified in Crystalloides, a genus closely allied to Agalma. In this type the greater part of the original ovum, instead of directly giving rise to the polypite, becomes a kind of yolk-sack, from which the polypite is secondarily budded (fig. 77, *yk*). *Agalma sarsii* is in this respect intermediate between Crystalloides and Physophora. Both these types are remarkable for developing a series of provisional hydrophyllia (fig. 77, *h.ph.*). In both genera the first of these develops as in Physophora, and for a long time is the only one functional.

The conclusions to be drawn from the above description may be summed up as follows. In all the Siphonophora, so far observed, the starting-point for further development is a typical ciliated two-layered planula. The inner layer or hypoblast is mainly formed of large nutritive cells. From these cells an epithelial hypoblastic layer becomes secondarily differentiated, the exact relations of which differ somewhat in the various types. The nutritive cells themselves do not appear to become directly converted into the permanent hypoblastic tissues. The development of the adult from the planula commences by the thickening of the epiblastic layer, usually at one pole (the future proximal or aboral pole), and the formation at this pole of a series of bud-like structures (in the growth of which both embryonic layers have a share), which become converted into the hydrophyllia, nectocalyces etc. The main oral part of the planula becomes generally converted into the polypite, though in some instances (Crystalloides) it remains as a yolk-sack, and only secondarily gives rise to a polypite.

Two very different views have been taken as to the nature of the various component parts of the Siphonophora, and the embryological evidence has been appealed to by both sides in confirmation of their views. By Huxley and Metschnikoff the various parts—nectocalyces, hydrophyllia, hydrocysts, polypites, generative gonophores etc. are regarded as simple organs, while by Leuckart, Haeckel, Claus etc. they are regarded as so many different individuals forming a compound stock. The difference between these two views is not merely as to the definition of an individual[1]. The question really is, are these parts originally derived by the modification of complete zooids like the gonophores and trophosomes of the fixed Hydrozoa stocks, or are they structures derived from the modification of the tentacles or some other parts of a single zooid?

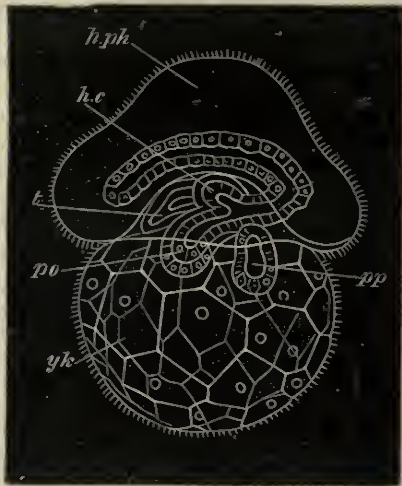

FIG. 77. LARVA OF CRYSTALLOIDES. (After Haeckel.)

h.ph. hydrophyllium; *h.* hydrocyst; *t.* tentacle; *pp.* pneumatophore; *po.* polypite; *yk.* yolk-sack.

The difficulty of deciding this point on embryological evidence depends on the fact that ontologically a tentacle and a true bud arise in the same way, viz. as papilliform outgrowths containing prolongations of both the primitive germinal layers. The balance of evidence is nevertheless in my opinion in favour of regarding the Siphonophora as compound stocks, and the views of Claus on this subject (*Zoologie*, p. 271) appear to me the most satisfactory.

The most primitive condition is probably that like Physophora in an early stage with an hydrophyllium enclosing a polypite (cf. Haeckel and Metschnikoff). In this condition the whole larva may be compared to a single Medusa in which the primitive hydrophyllium represents the umbrella of the Medusa, and the polypite the manubrium. The tentacle which appears so early is probably not to be regarded as a modified zooid, but as a true tentacle. The absence of a ring of tentacles is correlated with the bilateral symmetry of the Siphonophora.

The primitive zooid of a Siphonophora stock is thus a Medusa. Like Sarsia and Wilsia this Medusa must be supposed to have been capable of budding. The ordinary nectocalyces by their resemblance to the umbrellas of typical Medusæ are clearly such buds of the medusiform type. The same may be said of the pneumatophore, which, as pointed out by Metschnikoff, is identical in its development with a nectocalyx. Both are formed by a

[1] From the expressions used by Huxley, *Anatomy of Invertebrated Animals*, p. 149, it appears to me possible that his opposition to Leuckart's view is mainly as to the nature of the individual.

solid process of epiblast in which a cavity—the cavity of the nectocalyx or pneumatocyst—is eventually hollowed out. Around this there appears a double layer of hypoblast containing a prolongation of the gastrovascular cavity; and this is in its turn enclosed by a layer of epiblast which forms the covering of the convex surface of the nectocalyx and the external epiblast of the pneumatophore.

The generative gonophores are clearly also zooids, and the hydrophyllia are probably a rudimentary form of umbrella. In many cases (Epibulia, Stephanomia, Halistemma etc.) the hydrophyllium of the primitive polypite (manubrium) is absent. In such instances it is necessary to suppose that the umbrella of the primitive zooid of the whole colony has become aborted. Leuckart originally took a somewhat different view from the above in that he regarded the starting-point of the Siphonophora to be a compound fixed Hydrozoon stock, which became detached and free-swimming.

Acraspeda[1]. The embryonic development of several of the forms of the Acraspeda has been investigated by Kowalevsky (No. 147) and Claus (No. 153). Their observations seem to point to an invaginate gastrula being characteristic of this group.

Amongst the forms with alternations of generations and a fixed larval form Chrysaora and Cassiopea have been most fully investigated. The ovum of the former undergoes the first embryonic phases while still in the ovary. In the latter it is enclosed amongst the oral processes. A complete and more or less regular segmentation leads to the formation of a single-walled blastosphere with a small segmentation cavity. The wall of the blastosphere next becomes invaginated, giving rise to an archenteron (fig. 78 A). The blastopore soon closes up, and the archenteron is converted into a closed sack completely isolated from the epiblast (fig. 78 B). The surface of the larva becomes in the meantime covered with cilia. The free larval stage thus reached is similar to the ordinary Hydrozoon planula. After the closure of the blastopore the larva becomes elongated, and one end becomes narrowed. By this narrowed extremity the larva soon attaches itself, and at the opposite and broader end a fresh involution of the epiblast appears (fig. 78 C); this gives rise to the stomodæum, which is placed in communication with the archenteron on the absorption of the septum dividing them. The relation of the stomodæum to the original blastopore has not been determined.

[1] I use this term for the group, often known as the Discophora, which includes the Pelagidæ, Rhizostomidæ, and Lucernaridæ.

At the point of attachment there is developed a peculiar pedal disc, and around the mouth there appears a fold of epiblast which gives rise to an oral disc (fig. 78 D). Two tentacles first make their appearance, but one of these is primarily much the largest, though eventually the second overtakes it in its growth.

FIG. 78. FOUR STAGES IN THE DEVELOPMENT OF CHRYSAORA. (After Claus.)

A. Gastrula stage.
B. Stage after closure of blastopore.
C. Fixed larva with commencing stomodæum.
D. Fixed larva with mouth, short tentacles, etc.
ep. epiblast; *hy.* hypoblast; *st.* stomodæum; *m.* mouth; *bl.* blastopore.

A second pair of tentacles next becomes formed, giving to the larva a 4-radial symmetry. Between these four new tentacles subsequently sprout out, and in the intermediate planes four ridge-like thickenings of the hypoblast, projecting into the cavity of the stomach, make their appearance. They imperfectly divide the stomach into four chambers, to each of which one of the primary tentacles corresponds; they may be regarded as homologous with the mesenteries of the Actinozoa. The number of tentacles goes on increasing somewhat irregularly up to sixteen. All the tentacles contain a solid hypoblastic axis. Muscular elements are developed from the epiblast.

With the above changes the so-called Hydra tuba or Scyphistoma form is reached (vide fig. 85). The peculiar strobilization of this form is dealt with in the section devoted to the metamorphosis.

Aurelia is stated by Kowalevsky to develop in the same way as Cassiopea; and the one stage of Rhizostoma observed is that in which it has a (probably invaginate) gastrula form.

In Pelagia the ovum directly gives rise to a form like the parent. The segmentation and the invagination take place nearly as in Cassiopea, but the archenteric cavity is relatively much smaller, and the large space between it and the epiblast becomes filled with the gelatinous tissue which forms the umbrella. The blastopore does not appear to close but to become directly converted into the mouth. As in Cassiopea the larva takes a somewhat four-sided pyramidal form. The mouth is placed at the base. The pyramid becomes subsequently flatter, and at the four corners four tentacles grow out which increase to eight by division. The flattening continues till the larva reaches a form hardly to be distinguished from the Ephyra resulting from the strobilization of the fixed Scyphistoma form of other Acraspeda.

Alcyonidæ. In the Alcyonidæ the segmentation appears always to lead to the formation of a solid morula, which becomes a planula by delamination. The true enteric cavity is formed by an absorption of the central cells, but the axial portion of the gastric cavity and mouth are formed by an epiblastic invagination.

The development of these types has been mainly studied by Kowalevsky (147), and my knowledge of his results is derived from German abstracts of the original Russian memoirs.

In *Alcyonium palmatum* the impregnation is external. The segmentation is very exceptional in character. It commences with the formation of a series of irregular prominences on the surface of the ovum, which become segmented off to form a superficial layer of epiblast cells. The inner mass of protoplasm then divides up into polygonal cells to form the hypoblast, which would thus seem to be formed by a kind of delamination. In *Clavularia crassa* (No. 168) there is a complete segmentation followed by a delamination. The larva of *Al. palmatum* elongates and becomes ciliated, and so assumes the characters of a typical planula. The central hypoblast is formed of an outer granular stratum with imperfectly differentiated cells —the true hypoblast—and an inner homogeneous mass with vacuoles.

Some of the larvæ become fixed, while others coalesce together and form a large mass, the fate of which has not been further studied. An invagination of epiblast takes place at the free end of the fixed larva, which gives rise to the so-called gastric cavity, *i.e.* the axial portion of the general enteric cavity, which would appear to be in reality a kind of stomodæum. Around the gastric cavity the hypoblast forms eight mesenteries, the chambers between which are filled with the homogeneous material which occupied the centre of the ovum in the previous stage. It is to be presumed, though not stated, that by an absorption of the blind end of the stomodæal invagination the gastric chamber is placed in free communication with the spaces between the mesenteries[1]. During the next stage the young Alcyonium also acquires eight tentacles, which arise as hollow papillæ opening into the eight mesenteric chambers. By this stage also the matter filling up the mesenteric chambers is nearly absorbed.

Between the epiblast and hypoblast there is formed an homogeneous membrane, which penetrates in between the two layers of hypoblast which form the mesenteries. On the outer side of this membrane, and therefore presumably derived from the epiblast, is a layer of connective-tissue cells, which eventually gives rise to the abundant gelatinous tissue (cœnenchyma) in which the skeletal elements are deposited. In *Sympodium coralloides* Kowalevsky (No. 168) has shewn still more completely the derivation of the stellate mesoblast cells from the epiblast. He finds that the calcareous spicula develop in these cells as in the mesoblast cells of sponges. The branched gastrovascular canals in this tissue are outgrowths of the primitive enteric cavity. A layer of circular muscles is formed at a late period from the epiblast, but the longitudinal muscles of the mesenteries on the inner side of the homogeneous membrane are regarded by Kowalevsky as hypoblastic.

A ciliated planula with delaminated hypoblast is also found in Gorgonia and *Corallium rubrum*. In the former genus at the time when the larva becomes fixed, the hypoblast is formed of two strata, an outer one of columnar cells, and an inner one of round ciliated cells lining a central enteric cavity. The inner layer is believed by Kowalevsky to become eventually absorbed and to be homologous with the inner granular mass of Alcyonium.

Zoantharia. Amongst the Zoantharia several forms have been investigated by Kowalevsky (147) and Lacaze Duthiers (170), of which some are stated by the former author to pass through an invaginate gastrula stage, while in other instances the hypoblast is probably formed by delamination.

To the first group belongs an edible form of Sea Anemone found near Messina, Cerianthus, and perhaps also Caryophyllium. In the first of these segmentation results in the formation of a blastosphere. A normal invagination obliterating the segmentation cavity then ensues, and the blastopore narrows to form the mouth. The borders of the mouth bend inwards and so give rise to the gastric cavity (stomodæum) which as in the Alcyonidæ is lined by epiblast. Simultaneously with the formation of the mouth there appear the two first mesenteries.

In Cerianthus the segmentation is unequal, the early stages are the same as in the Actinia just described, but the hypoblast cells give rise

[1] The German abstract is very obscure as to the formation of the mouth.

to a mass of fatty material filling up the enteric cavity, which becomes eventually absorbed.

In the majority of the Zoantharia so far investigated, including species of Actinia, Sagartia, Bunodes, Astroides, Astræa, the segmentation, which is often unequal[1] and not accompanied by the formation of a segmentation cavity, results in a solid two-layered ciliated planula. In these forms the impregnation takes place in the ovary, and the early stages of development are passed through in the maternal tissues.

One end of the planula becomes somewhat oval and develops a special bunch of cilia. At the other end a shallow depression appears, which becomes deeper and forms an involution lined by epiblast. This involution is the stomodæum, and becomes the so-called gastric cavity. The true enteric cavity lined by hypoblast is for some time filled with yolk material. The larva always swims with the aboral end directed forwards.

Between the two embryonic layers a homogeneous membrane is formed, similar to that already described in the Alcyonidæ.

The further development of the larvæ especially concerns the formation of mesenteries, tentacles and calcareous skeleton. With reference to this subject the observations of Lacaze Duthiers are especially valuable and striking.

In the adult it is usually possible to recognise in the tentacles a symmetry of six. There are six primary tentacles, six secondary, twelve tertiary, twenty-four quaternary, etc. In the hard septa of the skeleton the same law is followed up to the third cycle, but beyond that, in the cases where the point can be verified, there appear to be only twelve septa in each additional cycle. The observations of Lacaze Duthiers have shewn that this symmetry is only secondarily acquired and does not in the least correspond with the succession of the parts in development.

His observations were conducted on three species of Zoantharia without a skeleton, viz. Actinia mesembryanthemum, Sagartia, and Bunodes gemmacea; while Astroides calycularis served as the type for his investigations on the corallum. It will be convenient to commence with his results on Actinia mesembryanthemum which served as his type.

The free cylindrical embryo, with the aboral end directed forwards in swimming, first becomes somewhat flattened and the mouth elongated. A bilateral symmetry is thus brought about. Two mesenteries now make their appearance transversely to the long axis of the mouth, which divide the enteric cavity into two *unequal chambers*. The mesenteries consist of a fold of hypoblast with a prolongation of the epiblast between the two

[1] I have this on the authority of Kleinenberg. The existence of an unequal segmentation probably indicates an epibolic gastrula.

limbs of the fold. The larger chamber next becomes divided by two fresh mesenteries into three, and a similar division then takes place in the smaller chamber. The stage with six chambers is almost immediately succeeded by one with eight, owing to the appearance of two fresh mesenteries in the second-formed set of chambers. At the stage with eight chambers there is a marked period of repose. The number of chambers is increased to ten by the division of the third-formed set of chambers, and to twelve by the division of the fourth-formed set. It will be observed that the number of the chambers increases in arithmetical progression by the continual addition of two, alternately cut off from the primitive large and small chambers. The freshly formed chambers are always formed immediately on one side of the primitive mesenteries. The stages with six and ten are of very short duration. The two primitive chambers are necessarily at the ends of the long axis of the mouth. After the division of the enteric cavity into twelve chambers, these chambers become about equal in size, and the formation of the tentacles commences. The law regulating the appearance of the tentacles is nearly the same as that for the mesenteries, but is not quite so precise. One tentacle makes its appearance for each chamber. The most remarkable feature in the appearance of the tentacles is due to the fact that the tentacle surmounting the primitive largest chamber arises before any of the others, and long retains its supremacy (fig. 80 A). This fact, coupled with the inequality of the two primitive chambers, supplies some grounds for speculating on a possible descent of the Cœlenterata from bilaterally symmetrical forms with distinctly differentiated dorsal and ventral surfaces. The supremacy of the first-formed tentacle is not confined to the Actinozoa, but as has already been indicated, is also found in the Scyphistoma (p. 166) of the Acraspeda.

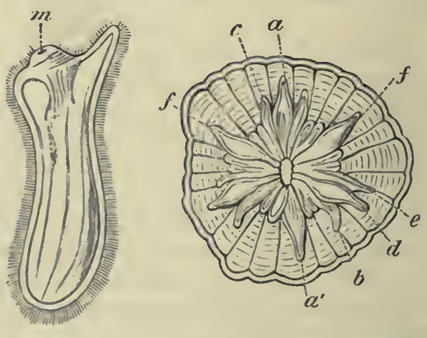

FIG. 80. TWO STAGES IN THE DEVELOPMENT OF ACTINIA MESEMBRYANTHEMUM. (After Lacaze Duthiers.)

In the younger ciliated embryo A, viewed from the side, only one tentacle is developed. *m*. mouth.

The older larva B is viewed from the face when 24 tentacles have just become established. The letters shew the true order of succession of the tentacles; but *e* and *f* are transposed.

After the twelve tentacles have become established they become secondarily divided into two cycles of six respectively larger and smaller tentacles, which alternate with each other. The two tentacles pertaining to the two original chambers belong to the cycle of larger tentacles. The mesenteric filaments appear first of all on the primary pair of septa. The increase in the number of tentacles and chambers from 12 to 24 has been found to take place in a very remarkable and unexpected way. The law is expressed by Lacaze Duthiers as follows. "The appearance of the new chambers is not, as has been believed, a consequence of the production of a single chamber between each of the twelve already existing chambers, but of the birth of two new chambers in each of the six elements (chambers) of the smaller cycle." The result of this law is that a pair of tentacles of the third cycle is placed in every alternate space, between a large and a small tentacle, of the two already existing cycles, which may conveniently be called the first and second cycles (fig. 80 B).

The twenty-four tentacles formed in the above manner are obviously at first very irregularly arranged (fig. 80 B), but they soon acquire a regular arrangement in three graduated cycles of 6, 6 and 12. The first cycle of the six largest tentacles is the large cycle of the previous stage, but the two other cycles are heterogeneous in their origin, each of them being composed partly of the twelve tentacles last formed, and partly of the six tentacles of the second cycle of the previous stage.

The further law of multiplication has been thus expressed by Lacaze Duthiers: "The number of chambers and still later that of the corresponding tentacles is carried from 24—48 and from 48—96 by the birth of a pair of elements in each of the 12 or 24 chambers, above which are placed the smallest tentacles which together constitute the fourth or fifth cycle. Since, after the formation of each fresh cycle, the arrangement of the tentacles again becomes symmetrical, it is obvious that all the equal sized cycles except the first are formed of tentacles entirely heterogeneous as to age."

The fixation of the free swimming larva takes place during the period when the tentacles are increasing from 12 to 24.

The general formation of the chambers in Bunodes and Sagartia is nearly the same as in Actinia.

In the two types of Actinozoa with an embolic gastrula stage the laws as to the formation of the tentacles do not appear to be the same as those regulating the forms observed by Lacaze Duthiers.

In Cerianthus four tentacles are formed simultaneously at the period when only four chambers are present. In Arachnitis (Edwarsia) the succession of the tentacles is stated (A. Agassiz, 166) to resemble that in Cerianthus. There are originally four tentacles, and at one extremity of the long axis of the mouth are the oldest tentacles, while at the other tentacles are constantly added in pairs. An odd tentacle is always found at the extremity of the mouth opposite the oldest tentacles.

In the other species with an embolic gastrula eight tentacles would seem to appear simultaneously at the period when eight chambers are present; though on this point Kowalevsky's description is not very clear. The presence of such a stage would seem to indicate a close affinity to the Alcyonidæ.

Amongst the sclerodermatous Actinozoa, except Caryophyllium, the embryo closely resembles that of the delaminate Malacodermata. The first stages occur in the ovary, and the larva is dehisced into the body cavity as a two-layered ciliated planula.

The laws affecting the formation of the first twelve tentacles and septa appear to be nearly the same as for the Malacodermata. The hard parts begin as a rule to be formed when twelve tentacles have appeared, at which period also the fixation of the larva takes place. On fixation the larva becomes very much flattened.

The first parts of the corallum to appear are twelve of the septa, which arise simultaneously in folds of the enteric wall in the chambers *between the mesenteries*, and correspond therefore with the tentacles and not, as might be supposed, with the mesenteries. Each septum is formed by the coalescence of three calcareous plates which originate in separate centres of calcification. The concrescence of the three produces a Y-shaped plate with the single limb directed inwards and the two limbs outwards (fig. 81). The theca does not arise till after the septa have become formed, and is at first a somewhat membranous cup quite distinct from the septa. The columella is formed still later by the coalescence of a series of nodules which are formed in a central axis enclosed by the inner ends of the septa.

After the formation of the theca the septa become divided into two cycles by the predominant growth of six of them. On the coalescence of the septa with the theca the space between the two limbs of the Y becomes filled up with calcareous tissue. The law of the formation of the third cycle of septa (12—24) has not been worked out, so that it is not possible to state whether it follows the peculiar principles regulating the growth of the tentacles.

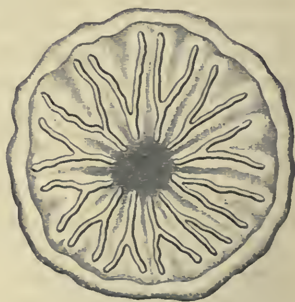

FIG. 81. LARVA OF ASTROIDES CALYCULARIS SHORTLY AFTER IT HAS BECOME ATTACHED. (After Lacaze Duthiers.)

The figure shews the development of the Y-shaped septa in the intervals between the mesenteries. The position of the latter is indicated by the faint shading. The theca has become developed externally.

The whole of the skeletal parts occupy a position between the epiblast and hypoblast, and are exactly homologous in this respect with the skeleton of the Alcyonidæ. By Lacaze Duthiers they are however believed to originate in the hypoblast, but from the observations of Kowalevsky there can be little doubt that they arise in the connective tissue between the two embryonic layers which is probably epiblastic in origin.

A peculiar larva, probably belonging to the Actinozoa, has been described by Semper[1]. It has an elongated form and is provided with a longitudinal ridge of cilia. There is a mouth at one end of the body and an anus at the opposite extremity. The mouth leads into an œsophagus, which opens

[1] "Ueb. einige tropische Larven-formen." *Zeit. f. wiss. Zool.*, vol. XVII. 1867.

freely into a stomach with six mesenteries. In the skin are numerous thread-cells. A mesotrochal worm-like larva, also provided with thread-cells, and found at the same time, was conjectured by Semper to be a younger form of this larva.

Ctenophora. The ovum of the Ctenophora is formed of an outer granular protoplasmic layer and an inner spongy mass with fatty spherules. It is enveloped in a delicate vesicle, the diameter of which is very much greater than that of the contained ovum. This vesicle appears to be filled with sea-water, in which the ovum floats.

Fertilized ova may usually be easily obtained by keeping the captured adults in water from 12—24 hours. The two main authorities on the development of these forms (Kowalevsky, No. 147 and 178 and Agassiz, No. 172) are unfortunately at variance on one or two of the most fundamental points. It seems however that the embryonic layers are formed by a kind of epibolic gastrula; while the true gastric cavity, as distinct from the gastrovascular, is formed by an invagination, and deserves therefore to be regarded as a form of stomodæum.

The early stages are very closely similar in all the types so far observed. Segmentation commences by the outer layer of the ovum, which throughout behaves as the active layer, forming a protuberance at one pole, which may be called the formative pole. Close below this protuberance is placed the nucleus. In the median line of the protuberance a furrow appears (fig. 82 A),

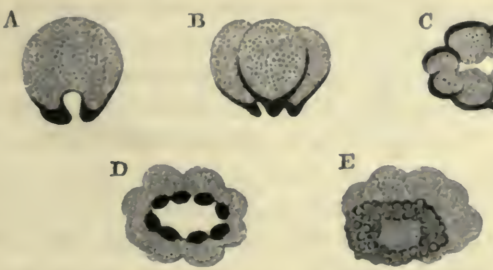

FIG. 82. FIVE STAGES IN THE DEVELOPMENT OF IDYIA ROSEOLA. (After Agassiz.)
The protoplasmic layer of the ovum is represented in black.

which gradually deepens till it divides the ovum into two. The granular layer follows the furrow so that each of the fresh segments, like the original ovum is completely invested by a layer of granular protoplasm. Each segment contains a nucleus. A second similar division at right angles to the first gives rise to four segments (fig. 82 B), and the segments so formed become again divided into eight (fig. 82 C). In the division into eight, which takes place in a vertical plane, the segments formed are of unequal size, four of them being much smaller than the others. The eight segments are arranged in the form of a slightly curved disc round a vertical axis—the future long axis of the body;—and there is a cavity in this axis which, like the segmentation cavity of *Sycandra raphanus*, is open at both extremities. The disc with its concavity on the side of the formative pole has the shape sometimes of an ellipse (fig. 82 C) and sometimes of a rectangle, in which the four small spheres occupy the poles of the longer axis. A bilateral symmetry is thus even at this stage clearly indicated.

In the next phase of segmentation the granular layer surrounding each segment again forms a protuberance at the formative pole, but, instead of each segment becoming divided into two equal parts, the protoplasmic protuberance alone is divided off from the main segment. In this way sixteen spheres become formed, of which eight are large and are formed mainly of the yolk material of the inner part of the ovum, and eight are small and entirely composed of the granular protoplasm. The eight small spheres form a ring on the formative surface of the large spheres (fig. 82 D).

The small spheres now increase very rapidly (fig. 82 E), partly by division *and partly by the formation of fresh cells from the large spheres;* and spread over the large spheres, forming in this way an epibolic gastrula. They constitute a layer of epiblast. (Fig. 83 A.) The large cells in the meantime remain relatively passive, though during the process they divide, in some cases more or less irregularly, while in Eucharis they divide into sixteen. The axial segmentation cavity would seem during the process to become obliterated.

There is an important discrepancy between the statements of Kowalevsky and Agassiz as to the course of the growth of the small cells. According to Agassiz the small cells grow most rapidly at the formative pole and cover this before they meet at the opposite pole. The reverse statement is made by Kowalevsky. It would seem that the above discrepancy is due to an interchange on the part of the one or the other of these authors of the two poles of the embryo, in that according to Agassiz the formation of the mouth takes place *at the formative pole*, and according to Kowalevsky *at the pole opposite to this.*

Without attempting to decide between the above views, we shall speak of the pole at which the mouth is formed as the oral pole.

The formation of the alimentary cavity commences shortly after the complete investiture of the embryo by the epiblast cells. At the oral pole an invagination of epiblast cells takes place (fig. 83 B), which makes its way towards the opposite pole. More especially from the figures given by Agassiz, and from the explanation of his plates, it would seem that a large chamber is formed in the hypoblast at the end of the invaginated tube, into which this tube soon opens (fig. 83 C). The invaginated tube would seem to give rise to the so-called stomach, while the chamber at its aboral extremity is no doubt the infundibulum, which as may be gathered from Kowalevsky's statements, is lined by a flattened epithelium. At a later period the gastrovascular canals grow out from the infundibulum as four pouches, which are surrounded by, and grow at the expense of, the large central cells, which have in the meantime arranged themselves in four masses, and appear to serve as a kind of yolk. The nuclei of these large cells according to Kowalevsky disappear, and the cells themselves break up into continually smaller masses.

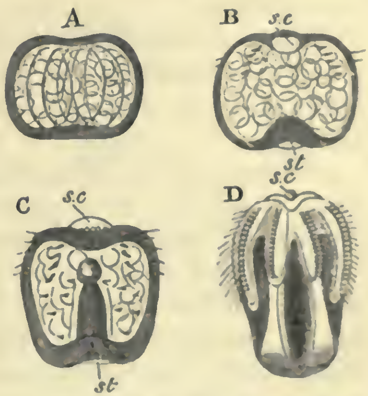

FIG. 83. FOUR STAGES IN THE DEVELOPMENT OF IDYIA ROSEOLA. (After Agassiz.)

s.c. sense capsule; *st.* stomodæum.

The main difficulty in the above description of Agassiz is the origin of the infundibulum. In the absence of definite statements on this head it seems reasonable to conclude that it arises as a space hollowed out in the central cells, and that its walls are formed of elements derived from the yolk cells[1]. On this interpretation the alimentary canal of the Ctenophora would

[1] Chun (No. 174) gives a short statement of his observations, which accords with the interpretation in the text.

consist, as in the Acraspedote Medusæ and Actinozoa, of two sections: (1) A true hypoblastic section consisting of the infundibulum and the gastro-vascular canals derived from it; and (2) an epiblastic section—the stomodæum—forming the stomach.

The observations of Kowalevsky on the alimentary system do not wholly tally with those of Agassiz. He finds that the oral side of the embryo becomes hollowed out, and that the hollow, lined by flattened cells, becomes constricted off as the infundibulum, from which the radial canals subsequently grow out. To the infundibulum there leads a narrow canal lined by a columnar epithelium which becomes the gastric cavity.

While the alimentary canal is becoming formed a series of important changes takes place in other parts of the embryo. The rows of locomotive paddles first appear as four longitudinal equidistant linear thickenings of the epiblast near the aboral pole (fig. 83 D). On the projecting surface of these ridges stiff cilia appear which coalesce together to form the paddles. While the embryo is still within the egg the rows of paddles are quite short and also double. There are in Pleurobrachia about eight or nine pairs of paddles in each row. Each double row eventually separates into two.

In all the forms except the Eurostomata (Beroe) two tentacles grow out as thickenings of the epiblast (fig. 84 B, *t*.). They are placed at the opposite poles of the long transverse axis of the embryo.

A process of the contractile gelatinous tissue of the body, the origin of which is described below, makes its way, according to Kowalevsky, into the tentacles.

The central apparatus of the nervous system and the otoliths are formed at the aboral pole from a thickening of the epiblast, but the full details of their formation have not been elucidated. It may be well to preface my account of their development with a short statement of their adult structure.

They consist in the adult of a vesicle with a ciliated lining situated at the bifurcation of the two anal tubes, and of certain structures connected with this vesicle. From the floor of the vesicle is suspended a mass of otoliths by four leaf-like bodies known as suspenders. The roof is very delicate and has the form of a four-sided pyramid. Six openings lead into the vesicle. Through four of these, placed at the four corners, there pass out four ciliated grooves continuous with the suspenders. These grooves, after leaving the otolithic vesicle, bifurcate and pass to the eight rows of paddles. At the two sides the walls of the vesicle are continuous with two thickened ciliated plates with swollen edges, opposite the centres of which are two lateral openings into the vesicle, completing the six openings. Through the lateral openings the sea water is driven by the action of the cilia of the plates.

The development of these parts is as follows—In the aboral thickening of epiblast a cavity makes its appearance, the walls of which constitute the rudiment of the otolithic vesicle (fig. 83 B and C, *s.c.*). The roof of the cavity is extremely delicate. On each side of it a thickening of cells becomes established, regarded by Kowalevsky as the rudiment of the nervous ganglia. These thickenings appear to give origin to the lateral ciliated plates. The otoliths arise from cells at four separate points at the corners of the ciliated plates opposite the rows of paddles (fig. 84 A, *ot.*).

In Pleurobrachia there is at first only one otolith at each corner. The otoliths are gradually transported towards the centre of the vesicle (fig. 84 B, *ot.*) and are there attached, though the four leaf-like suspenders do not arise till very late. The otoliths go on increasing in number throughout life.

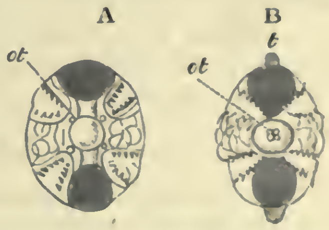

FIG. 84. TWO STAGES IN THE DEVELOPMENT OF PLEUROBRACHIA RHODODACTYLA. (After Agassiz.)
ot. otolith; *t.* tentacle.

The gelatinous tissue of the Ctenophora appears as a homogeneous layer between the epiblast and the yolk-cells, and is probably homologous with the layer formed in the same situation in all other cœlenterate forms. Into the layer a number of anastomosing cells, mainly derived from the epiblast, though according to Chun (No. 174) also in part from the hypoblast, make their way. These cells would appear to be mainly, if not entirely (Chun), of a contractile nature. It is probable that the great mass of the gelatinous tissue of the adult is an intercellular substance derived from these cells.

The whole of the above changes are completed while the embryo is still enclosed in the egg capsule. During their accomplishment the oro-anal axis, which was originally very short, increases greatly in length (fig. 83), so that the embryo acquires an oval form similar to that of the adult.

The exact period of leaving the egg does not appear to be very constant, but the hatching never takes place till the embryo has practically acquired all the organs of the adult.

In the majority of types the differences between the just hatched larva and the adult are inconsiderable, and in all cases the larva has a somewhat oval form. In the case of the Tæniatæ (Cestum, etc.), the larva has the characteristic oval form, and the subsequent changes amount almost to a metamorphosis.

The larva of the Lobatæ, such as Eucharis, Bolina, etc., can hardly be distinguished from Pleurobrachia, and undergoes therefore considerable changes after hatching.

Eucharis multicornis while still in the larval condition is stated by Chun to become sexually mature.

The new genus Ctenaria recently described by Haeckel, which is intermediate between the Ctenophora and the Medusæ clearly proves that the Ctenophora are more closely related to the Medusæ than to the Actinozoa; but their development, especially the presence of a stomodæum, shews that they have affinities (in spite of the rudimentary velum of Ctenaria) with the Acraspedote as well as with the Craspedote Medusæ; and it may be noted that the Acraspeda have undoubted affinities with the Actinozoa.

Summary and general considerations.

Even in the adult condition the lower forms of Cœlenterata do not rise in complexity much beyond a typical gastrula. Ontogeny nevertheless brings clearly to light the existence of a larval form—the planula—which recurs with fair constancy amongst all the groups except the Ctenophora.

We are probably justified in assuming that the planula is a repetition of a free ancestral form of the Cœlenterata. The planula, as it most frequently occurs, is a two-layered ciliated nearly cylindrical organism, with at most a rudimentary digestive cavity hollowed out in the inner layer, and as a rule no mouth. In the outer layer are numerous thread-cells.

How many of these characters did the ancestral planula possess? I think it is not unreasonable to assume that the only two characters about which there can be much doubt are the rudimentary condition of the digestive cavity and the absence of a mouth. Paradoxical as it may seem, it appears to me not impossible that the Cœlenterata may have had an ancestor in which a digestive tract was physiologically replaced by a solid mass of amœboid cells.

This ancestor was perhaps common to the Turbellarians also. The constant presence of thread-cells in the inner layer of their epiblast fits in with their derivation from a form similar to the planula. While the solid parenchymatous digestive canal of Convoluta and Schizoprora and other forms amongst the Turbellarians, though very probably secondary, may perhaps be explained by such a view of their origin.

The planula in its primitive condition is not bilaterally symmetrical, but frequently, as amongst the Actinozoa, it becomes flattened on two sides before undergoing its conversion into the adult form. Perhaps the bilateral form of planula is the starting point both for the Cœlenterata and the Turbellaria. In this connection the peculiar unilateral development of a tentacle in Scyphistoma and Actinia should be noted.

The planula occurs in the majority of sessile forms of Hydrozoa except the Tubularidæ and Hydra. It is also characteristic of the Trachymedusæ and Siphonophora. Amongst the Acraspeda it is also present, but has an exceptional mode of ontogeny which is discussed in connection with the germinal layers.

It is characteristic both of the Octocoralla and Hexacoralla, but is not found in the Ctenophora.

In the Tubularidæ and in Hydra an abbreviated development leads no doubt to the absence of a *free* planula stage, and the absence of a larval form amongst the Ctenophora may, as has already been stated, be probably explained in the same way.

The Cœlenterata of all the Metazoa are characterized by the greatest simplicity in the arrangement of their germinal layers; and for this reason very considerable interest attaches to the mode of formation of the layers amongst them. Two germinal layers are constantly found, which correspond *in a general way* to the epiblast and hypoblast. It might have been anticipated that a certain amount of uniformity would have existed in the mode of formation of the layers. This however is not the case. In perhaps the majority of forms they become differentiated by a process of delamination, but in a not inconsiderable minority the two layers owe their origin to an invagination.

Delamination is constant (with the doubtful exception of some Tubularidæ) amongst the Hydromedusæ and Siphonophora. It is perhaps in the main characteristic of the Actinozoa.

Invagination by embole takes place, so far as is known, constantly amongst the Acraspeda and frequently amongst the

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Actinozoa; and an epibolic invagination is characteristic of the Ctenophora.

If confidence is to be placed in the recorded observations on which this summary is founded, and there is no reason why in a general way it should not be so placed, the conclusion is inevitable that of the above modes of development the one must be primitive and the other a derivative from it, for, if this conclusion be not accepted, the absolutely inadmissible hypothesis of a double origin for the Cœlenterata would have to be adopted.

Two questions arise from these considerations:—

(1) Which is the primitive, delamination or invagination?

(2) How is the one of these to be derived from the other?

There is a great deal to be said in favour of both delamination and invagination; but it will be convenient to defer all discussion of the question to the general chapter on the formation of the layers throughout the animal kingdom.

The hypoblast cells are often filled with yolk material, and secondary modifications are thus produced in the development. The most important examples of such modifications are found in the Siphonophora and Ctenophora.

In the simplest forms amongst the Hydrozoa there is no trace of a third layer or mesoblast. The epiblast is typically formed, as was first shewn by Kleinenberg, of an epithelial layer and a subepithelial interstitial layer of cells. The cells of the former are frequently produced into muscular or nervous tails, and those of the latter give rise to the thread-cells and generative organs and in some cases to muscles[1]. In many cases, amongst all the Cœlenterate groups, and constantly amongst the Ctenophora the epiblast is simplified and reduced to a single layer. The hypoblast undergoes in most cases no such differentiation but simply forms a glandular layer lining the gastric chamber and its prolongations into the tentacles; but in the Actinozoa it appears to give rise to muscles, and strong evidence has been brought forward to shew that in some groups it gives rise to the generative organs.

Between the epiblast and hypoblast a structureless lamella appears always to be interposed.

[1] The questions relating to the generative organs of the Cœlenterata are dealt with in the second part of this work.

In many Cœlenterata further differentiations of the epiblast are present. In many forms the layer gives rise to a hard external skeleton. This is most widely spread amongst the Hydrozoa, where in the majority of cases it takes the form of the horny perisarc, and in the Hydrocoralla (Millepora and Stylasteridæ) of a hard calcareous skeleton. The skeleton in these forms, though closely resembling the mesoblastic skeleton of the Actinozoa, has been shewn by Moseley (164) to be epiblastic.

In the Actinozoa an epiblastic skeleton is exceptional, and according to most authorities absent. Quite recently however Koch (167) has found that the axial branched skeleton of most of the Gorgonidæ, viz. the Gorgoninæ and Isidinæ, is separated from the cœnosarc by an epithelium, which he believes to be epiblastic, and to which no doubt the axial skeleton owes its origin. A similar epithelium surrounds the axis of the Pennatulidæ.

In the Medusæ the epiblast also gives rise to a central nervous system, which however continues to form a constituent part of the layer, and to the organs of special sense[1].

A special differentiation of the hypoblast is found in the solid axis of the tentacles. This axis replaces the gastric prolongation found in many forms, and the cells composing it differentiate themselves into a chorda-like tissue, which has a skeletal function, and is no longer connected with nutrition. This axis is placed by many morphologists amongst the mesoblastic structures.

In all the higher Cœlenterata certain tissues become interposed between the epiblast and hypoblast, which may be classified together as the mesoblast.

The most important of these are

(1) The various distinct muscular layers.

(2) The gelatinous tissue of the Medusæ and Ctenophora.

(3) The skeletogenous tissue of the Actinozoa.

In most cases the muscular fibres are connected with epithelial cells, but in certain forms amongst the Medusæ and in the majority if not all the Actinozoa they constitute a distinct layer, sometimes separated from the epiblast by a structureless mem-

[1] The differentiation of the nervous and muscular systems in the Hydrozoa is treated of in the second part of this work.

brane, *Æquorea Mitrocoma.* Such layers when on the outer side of the membrane separating epiblast and hypoblast are undoubtedly epiblastic in origin, but in some cases amongst the Actinozoa they adjoin the hypoblast, and are very probably derived from this layer.

The origin of the gelatinous tissue is still involved in much obscurity.

It originates as a homogeneous layer between epiblast and hypoblast, which in the Hydromedusæ never becomes cellular though traversed by elastic fibres.

In the Acraspeda it contains anastomosing cells in the main apparently (Claus) derived from the hypoblast, and in the Ctenophora it is richly supplied with muscular stellate cells for the most part of epiblastic origin, though some are stated by Chun to come from the hypoblast. On the whole it seems probable, that the gelatinous tissue may be regarded as a product *of both layers;* and there are some grounds for thinking that it is an immense development of the membrane always interposed between the two primary layers. It must however be borne in mind that a membrane, regarded by the Hertwigs as the equivalent of the ordinary membrane between the epiblast and hypoblast, can be usually demonstrated on both surfaces of the gelatinous tissues in Medusæ. The skeletogenous layer of the Actinozoa is probably the morphological homologue of the gelatinous tissue; but the evidence we have is on the whole in favour of the connective-tissue cells it contains being epiblastic in origin. It gives rise to the skeleton of the Hexacoralla, to the spicular skeleton of Alcyonium, the axial skeleton of Corallium, and the skeleton of the Helioporidæ and Tubiporidæ.

Alternations of generations.

Alternation of generations is of common occurrence amongst the Hydrozoa, and something analogous to it has been found to take place in Fungia amongst the Actinozoa. It is not known to occur in the Ctenophora.

The chief interest of its occurrence amongst the Hydromedusæ and Siphonophora is the fact that its origin can be traced to a division of labour in the colonial systems of zooids so characteristic of these types.

In the Hydromedusæ an interesting series of relations between alternation of generations and the division of the zooids into gonophores and trophosomes can be made out. In Hydra the generative and nutritive functions are united in the same individual. The generative swellings in these forms cannot, as has been ably argued by Kleinenberg, be regarded as rudimentary gonophores, but are to be compared to the generative bands developed in the Medusæ around parts of the gastro-vascular system. A condition like that of Hydra, in which the ovum directly gives rise to a form like its parent, is no doubt the primitive one, though it is not so certain that Hydra itself is a primitive form. The relation of Hydra to the Tubularidæ and Campanularidæ may best be conceived by supposing that in Hydra most ordinary buds did not become detached, so that a compound Hydra became formed; but that at certain periods particular buds retained their primitive capacity of becoming detached and subsequently developed generative organs, while the ordinary buds lost their generative function.

It would obviously be advantageous for the species that the detached buds with generative organs should be locomotive, so as to distribute the species as widely as possible, and such buds in connection with their free existence would naturally acquire a higher organization than the attached trophosomes. It is easy to see how, by a series of steps such as I have sketched out, a division of labour might take place, and it is obvious that the embryos produced by the highly organized gonophores would give rise to a fixed form from which the fixed colony would be budded. Thus an alternation of generations would be established as a necessary sequel to such a division of labour. To test the above explanation it is necessary to review the main facts with reference to alternations of generations amongst the Hydromedusæ.

Hydromedusæ[1]. In many instances amongst the Tubularidæ, Sertularidæ and Campanularidæ medusiform buds are produced which become detached and develop sexual organs.

[1] For a full account of this subject the reader is referred to the beautiful memoir of Allman (No. 149).

Such Medusæ are divided into two great groups, the Ocellata and Vesiculata, according to the characters of the marginal sense organs. In the Ocellata the sense organs have the form of eyes, and in the Vesiculata of auditory vesicles. The latter seem to be usually budded off from the Campanularia stocks, and the generative organs extend in folded bands over the radial canals. These bands have been regarded by Allman as composed of rudimentary gonophores, and he called the Medusæ which give rise to them blastochemes. He regards them as representing a more complicated type of alternation of generations with three instead of two generations in the series. The Hertwigs have brought what appear to me conclusive grounds for rejecting this view, and have demonstrated that the generative organs of these types resemble those of ordinary Medusæ.

In many forms the medusiform buds though fully developed do not become detached; whether detached or not they are known as phanerocodonic gonophores. In other forms again buds which begin as if they were going to form Medusæ never reach that condition but remain permanently in an undeveloped state. They have been called by Allman adelocodonic gonophores.

In all the above cases two generations at the least interpose between the successive sexual periods, viz.:—

(1) A trophosome produced directly from the ovum.

(2) A gonophore budded from this.

In a very large number of types the gonophores do not develop directly on the hydroid stem, but arise on specially modified zooids resembling rudimentary trophosomes which have been named blastostyles by Allman. On the sides of each blastostyle a series of gonophores usually becomes developed. The blastostyles either remain exposed as in all the Gymnoblastic or Tubularian Hydroids, or as in all the Calyptoblastic Hydroids (Sertularidæ and Campanularidæ) they become invested by a special case—known as the gonangium—which is formed of perisarc lined by epiblast. In the forms with blastostyles three generations interpose between the successive stages of sexual reproduction, (1) the trophosome developed directly from the ovum, (2) the blastostyle budded from this, (3) the gonophore budded from the blastostyle.

Such being the main facts, in order to prove that the existing condition of polymorphism amongst the Hydromedusæ is to be explained as hypothetically suggested above, it is still necessary to shew that (1) the free medusiform gonophores are really only modified trophosomes, or rather that the trophosomes and gonophores are both modifications of some common type, and (2) that the fixed so-called adelocodonic gonophores are retrograde derivatives of the free medusiform gonophores. Unless these points can be established it might be maintained that the Medusæ were special zooids, developed *de novo* and not by a modification of trophosome zooids. To demonstrate these propositions at length would carry me too far into the region of simple Comparative Anatomy, and I content myself with referring the reader to a discussion of the Hertwigs (No. 146, p. 62) where the first point appears to me fully established. With reference to the second point I will only say that the structure and development of the adelocodonic gonophores can only be explained on the assumption that they are retrograde forms of the phanerocodonic gonophores, and that the opposite view, that the phanerocodonic gonophores are derived from the adelocodonic, leads to a series of untenable positions.

The Trachymedusæ, as has been shewn above, develop directly. They are probably derived from gonophores in which the trophosome has disappeared from the developmental cycle.

To sum up, three types of development are found amongst the Hydromedusæ.

(1) No alternations of generations. Permanent form, a sexual trophosome. *Ex.* Hydra.

(2) Alternations of generations. Trophosome fixed, gonophore free or attached. *Ex.* Gymnoblastic and Calyptoblastic Hydroids, and Hydrocoralla.

(3) No alternations of generations. Permanent form, a sexual Medusa. *Ex.* Trachymedusæ.

Siphonophora. In the Siphonophora alternations of generations take place in the same way as in the Hydromedusæ, but the starting point appears to be a Medusa. The gonophores may remain fixed or become detached.

Acraspeda. With the exception of Pelagia and Lucernaria, in which the development involves a simple metamorphosis, all the Acraspeda undergo a form of alternations of generations. The ovum, as already described, develops into a fixed form—the Scyphistoma—which increases asexually by normal budding, and can even form a permanent colony.

The formation of the sexual Medusa form takes place by a kind of strobilization of the body of the fixed Scyphistoma. A series of transverse constrictions becomes formed round the body below the mouth, dividing it up into corresponding rings, each of which eventually gives rise to a Medusa known as an Ephyra (fig. 85). In each of these rings is a dilation of the stomach, and a section of each of the four rudimentary mesenteries described in connection with the development of the Scyphistoma. As the constrictions become deeper the segments of the body between them become disc-like, and their edges are produced into eight lobes containing prolongations of the gastric cavity (fig. 85 C). The lower surface of each disc, which forms the future aboral surface of the Medusa, becomes convex, in part owing to the development of gelatinous tissue. On the opposite surface a muscular layer becomes developed. During the above process the body of the Scyphistoma gradually grows in length and continues to be segmented, so that a series of Ephyræ are uninterruptedly formed, of which those near the base are the youngest. The original terminal ring of tentacles of the Scyphistoma gradually atrophies.

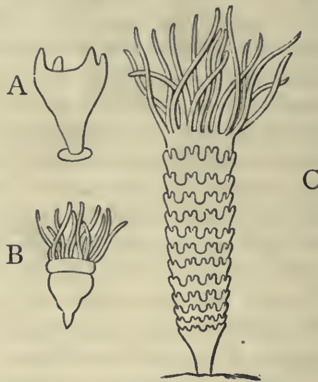

FIG. 85. THREE STAGES IN THE ALTERNATIONS OF GENERATIONS OF AURELIA AURITA. (From Gegenbaur.)

A. Polype stage.
B. Commencing strobilization.
C. Completed strobilization.

In the further development of the Ephyræ each of their eight lobes becomes bifid at its extremity.

As the Ephyræ successively reach this condition they become detached, and by a series of remarkable changes, amounting almost to a metamorphosis, and accompanied by an enormous growth in size, reach the adult condition.

The alternation of generations in the Acraspeda cannot be quite so simply explained as in the Hydromedusæ, though the principle is probably the same in the two cases.

Actinozoa. Amongst the Actinozoa there occurs in Fungia a peculiar process which is, as shewn by Semper (171), in many ways analogous to alternations of generations[1]. From the larva a nurse-stock is developed, at the end of which a cup-like coral

[1] Vide also Moseley. *Notes by a Naturalist of the Challenger*, pp. 524 and 525.

resembling the adult is formed as a bud. The bud becomes detached and then gives rise to a permanent sexual Fungia. From the nurse-stock there is formed however a fresh bud at the centre of the scar left on the detachment of the old one. The fresh bud eventually becomes separated from the nurse-stock leaving a small portion of its stem behind; each succeeding bud similarly leaves a small portion of its stem, so that the nurse-stock eventually acquires a jointed appearance. In the above process we clearly have, as in the Hydromedusæ, a non-sexual form—the nurse-stock—produced directly from the larva, giving rise by budding to a sexual form; all the conditions of an alternation of generations are therefore fulfilled. It seems however possible that the nurse-stock itself may eventually become sexual.

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