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TEXT-BOOK
OF THE
EMBRYOLOGY OF INVERTEBRATES

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OF THE

EMBRYOLOGY OF INVERTEBRATES

BY

DR. E. KORSCHELT,
PROFESSOR OF ZOOLOGY AND COMPARATIVE
ANATOMY IN THE UNIVERSITY
OF MARBURG.

DR. K. HEIDER,
PROFESSOR OF ZOOLOGY IN THE UNIVERSITY
OF BERLIN.

TRANSLATED FROM THE GERMAN
BY
MATILDA BERNARD.

REVISED AND EDITED WITH ADDITIONAL NOTES
BY
MARTIN F. WOODWARD,
DEMONSTRATOR OF ZOOLOGY, ROYAL COLLEGE OF SCIENCE, LONDON.

VOL. IV.

AMPHINEURA, LAMELLIBRANCHIA, SOLENOCONCHA,
GASTROPODA, CEPHALOPODA, TUNICATA, CEPHALOCHORDA.

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PREFACE.

THE present volume constitutes the final instalment of the translation of the *Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere*, and contains the Mollusca, the Tunicata and the Cephalochorda.

The immense strides which have been made during the last eight years in the study of invertebrate embryology have necessarily rendered much of this work out of date, and in no part is this more apparent than in the chapter on the Tunicata, and especially in the sections dealing with *Salpa*. Up to the time of the appearance of this work in 1893, our knowledge of the embryology of this genus was mainly based upon the results of Salensky's investigations. His conclusions were so startling that our authors expressed considerable doubt concerning their accuracy, but, owing to the absence of any other observations, were obliged to incorporate them in this work. Since that time, the important investigations made by Brooks, Heider and Korotneff have appeared, and these necessitate an entire revision of the section dealing with the embryology of *Salpa*. I, however, did not feel that it lay within my province to rewrite this section, so I have contented myself with appending numerous footnotes pointing out wherein the recent investigators differ in their observations and conclusions from those cited in these pages. It is, however, impossible to do full justice to this subject by means of footnotes, and the student who desires to study the subject thoroughly is referred to the original monographs.

The Tunicates, more than any other group, seem of recent years to have occupied the attention of embryologists, and the large amount of work which has been done on this group, especially in France, with regard to both the sexual and the asexual methods of reproduction, will be gathered from the additional literature appended to Chapter xxxv., only a small proportion of which could be referred to in the footnotes.

In the Mollusca also a great deal of work has been done, especially in connection with cell-lineage, and the formation of the mesoderm and of the larval kidney, in spite of which the last two points still remain obscure. Since I am more familiar with the Mollusca than with any other group of Invertebrata, I have revised the chapters dealing with this phylum somewhat more thoroughly than the rest of the volume: I have appended numerous notes, inserted some fresh paragraphs, and made certain alterations in the text which appeared justified by recent investigations.

I must again express regret that so long a time has intervened between the publication of the German edition of this work and the appearance of the last volume of the English translation. Volumes ii., iii. and iv. came into the hands of the translator only in 1897, and the task of bringing them out being necessarily somewhat lengthy, it has been impossible sooner to offer the completed work to the English-speaking student, to whom it should be of great service.

MARTIN F. WOODWARD.

ROYAL COLLEGE OF SCIENCE, LONDON.
June, 1900.

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I. The Development of Chiton.

The external characters of the larva of *Chiton* and the development of the same were described many years ago by LOVÉN (No. 10), while the formation of the germ-layers and the various internal changes have since been investigated with the assistance of modern methods by KOWALEVSKY (Nos. 6-8).*

Oviposition and Nature of the Eggs. The eggs pass from the genital duct into the mantle-groove of the female in an immature condition, and are there fertilised by the sperm which the male has discharged into the water; after this they are deposited either singly or in groups. They are found floating freely in the water; but, in some cases, as in *C. Polii*, the eggs are retained, until the embryo is mature, within the mantle-cavity of the female. Each egg is enclosed within a spiny shell, the surface of which is marked out into polygonal areas. The form of these spines varies in the different species and genera. The egg itself does not appear to be very rich in yolk.

1. The Cleavage and the Formation of the Germ-Layers.

The cleavage is total and practically equal, the egg being divided by two meridional grooves first into two and then into four blastomeres of almost equal size. At the eight-blastomere stage, however, a slight differentiation of the cleavage-spheres lying at the animal pole takes place, four larger (vegetative) and four smaller (animal) blastomeres being distinguishable. The animal pole is marked by the polar bodies which lie almost exactly over the point of intersection of the cleavage-planes. During the further course of cleavage, the blastomeres of the vegetative half are at first to be distinguished by their larger size, the smaller size of those of the animal pole being due to their more rapid division. In the later stages, as in the earliest, there is also a certain resemblance to the conditions found in the Gastropoda which are characterised by a stage consisting of four macromeres and four micromeres (Fig. 40 *C*, p. 109). We find here the

---

gastres are Mollusca at all. According to SEDGWICK, the most important difference between the Solenogastres and all other Mollusca is that in the former the gonad opens directly into the pericardium. This distinction does not appear to us to be so vital when we remember that in some Molluscs the gonad communicates directly with the kidney, the latter in turn opening into the pericardium, and further that the cavities of all three organs are parts of the primitive coelom.—ED.]

* [METCALF (No. I.) has since reinvestigated the embryology of *Chiton*, paying special attention to the cleavage and cell-lineage, his observations entirely confirming those made by KOWALEVSKY.—ED.]

expression of a kind of radial symmetry, which is still more marked in the Gastropoda at a somewhat later stage (Fig. 40 *D* and *E*), and, according to KOWALEVSKY's figures, is sometimes also met with in *Chiton*. At first the cells increase in number in a more regular manner than in the later stages.

Cleavage results in the production of a somewhat flattened, and therefore hemispherical blastula, the vegetative pole of which consists of comparatively few but very large cells (Fig. 1 *A*.) As the cells continue to divide, an *invagination of the vegetative half* (*B*) takes place. In this way the cleavage-cavity, which was never large, is further compressed.* The *invagination-gastrula* (*B*) which at first is somewhat depressed, now elongates in the direction of the invagination (*C*). The archenteron also grows larger. In its wall, near the blastopore, there appear two cells which, as compared with the rest,

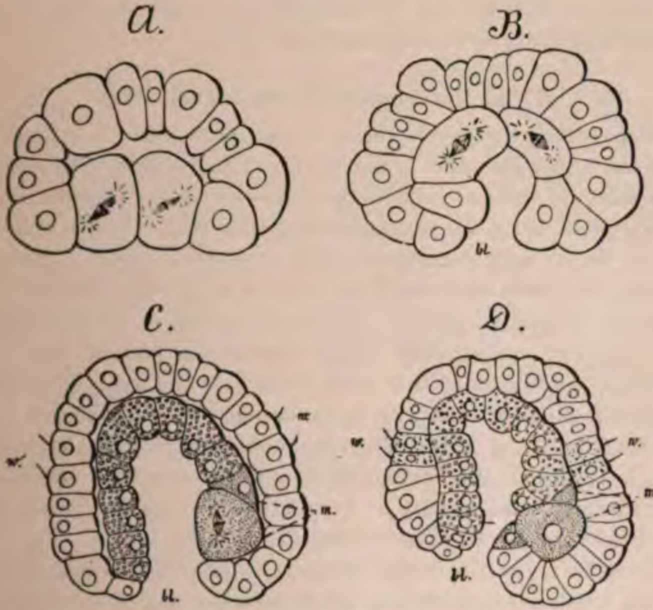


FIG. 1.—*A-D*, sections through embryos of *Chiton Polii* at the blastula and gastrula stages (after KOWALEVSKY). *bl*, blastopore ; *m*, rudiment of the mesoderm ; *w*, rudiment of the ciliated ring [velum].

---

* [METCALF (No. I.) finds a large blastocoele which is not wholly obliterated during the later development.—ED.]

are specially large (*C*, *m*). These cells which, as well as others situated near them, at first lie in continuity with the entoderm, represent the rudiment of the mesoderm. They soon shift out of the series of entoderm-cells into the cleavage-cavity (*D*, *m*). The mesoderm-rudiment which thus arises seems at first to have a regular bilateral arrangement in keeping with its origin, *i.e.*, two groups of large cells lying near the blastopore can be seen, but this regularity is soon lost, the cells, which subdivide further, becoming scattered. In this respect, and perhaps also in the manner of its origin, the mesoderm of *Chiton* may be compared with that of other Molluscs (Lamellibranchia, p. 29, Gastropoda, p. 117).

2. The Development of the Larval Form.

Even before the development of the germ-layers has progressed thus far, alterations take place in the external shape of the embryo. Two adjacent rows of cells in the ectoderm of the gastrula become distinguished from the rest as bearing cilia (Fig. 1 *C*, *w*), and these divide the larva into an anterior and a posterior section. Similarly, a group of cells lying at the pole furthest away from the blastopore becomes covered with cilia. These two groups of ciliated cells are the rudiments respectively of the ciliated ring [velum] and of the frontal or apical ciliated tuft (Figs 2 and 3, *w* and *ws*). Very similar embryonic stages are met with in the ontogeny of other Mollusca, *e.g.*, *Patella* (Fig. 50, p. 124). The pre-oral ciliated ring in the Lamellibranch larvae is also formed of two rows of cells. Indeed, the ciliated ring seems usually to be biserial; though, in *Patella*, there are three rows of cells (Figs. 52 and 53, pp. 126, 127).

As the body extends in the direction of its principal axis, the blastopore, which has hitherto lain at the posterior pole, assumes another position and form. It shifts to that side of the larva which later becomes the ventral surface, and, owing to the growth of the dorsal surface, gradually approaches the ciliated ring (Fig. 1 *B-D*). The blastopore, as it shifts its position, loses its circular form, and, as far as we can make out from the figures, assumes the form of a transverse slit (Fig. 3 *B*). Meantime, the continuous growth of the dorsal surface causes the aperture to shift more and more towards the ciliated ring, and it is finally found immediately behind it (Fig. 2 *A*). This slit-like aperture, however, no longer corresponds fully to the blastopore, since the ectoderm surrounding the latter has sunk below the surface, and the actual primitive mouth thus comes to lie at the inner end of a laterally compressed ectodermal tube which for some time longer continues to deepen (Fig. 2 *A*, *oe*). This ectodermal invagination, the stomodaeum, represents the rudiment of the fore-gut (buccal mass and oesophagus). In connection with it there appears later, as a ventral outgrowth, the radular sac (Fig. 2 *B*, *r*).

The "shifting" of the blastopore just described agrees closely with the processes to be met with in the Gastropoda (p. 141), and we are inclined in both cases to assume that we are really dealing with the closing from behind forward of an originally slit-like blastopore.

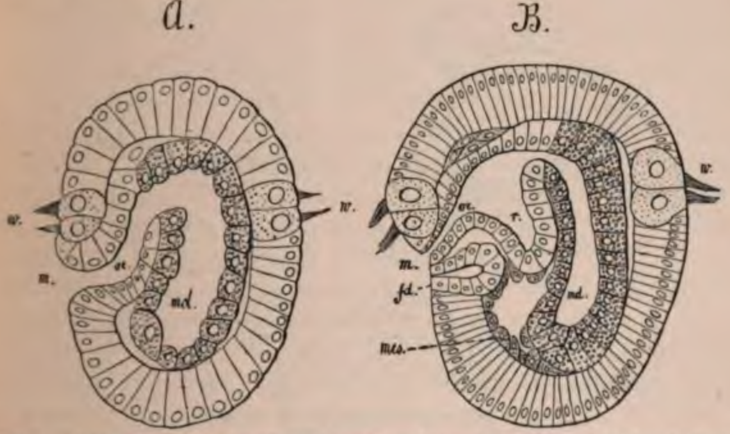


FIG. 2.—*A* and *B*, median longitudinal sections through embryos of *Chiton Polii* at different ages (after KOWALEVSKY). *fd*, pedal gland; *m*, mouth; *md*, enteron; *mes*, mesoderm; *oe*, stomodaeum; *r*, radular sac; *w*, ciliated ring (velum).

The more active growth of the part lying behind the ciliated ring is accompanied by reduction of the anterior section which formerly preponderated (Figs. 1 and 2). The embryo, which is now almost pear-shaped, may become free at this stage (*e.g.*, *Chiton marginatus*, LOVÉN). The larvae of this latter form carry a large ciliated tuft at the frontal pole (Fig. 3 *A*). The embryos of other Chitones remain longer in the egg, and before attaining free life approach more nearly the form of the adult (Fig. 3 *C*).

The larvae of the Chitones resemble those of the Annelida, and since a *Trochophore* exceedingly like that of the Annelida is found in other Molluscs (Figs. 18, 51, 53), we are justified in instituting such a comparison here also, even although the resemblance is not so close. We have here a pre-oral ciliated ring, and the origin and position of the different sections of the intestinal canal is the same as in the *Trochophore*. The larva, at first, has no anus, as the terminal segment of the alimentary canal only appears later at the posterior end of the body in the form of an ectodermal invagination, the proctodaeum (Fig. 9). An organ which is of great importance in interpreting the larva, the apical plate, is not present in the early stages of *Chiton*, but the cerebral ganglia arise later in the position which this organ occupies in the Annelida; in the free-swimming larva of *Chiton Polii* these ganglia are found beneath the ciliated tuft on the frontal pole (Fig. 5.), and may therefore be regarded as representing the apical plate. Thus, to make the comparison complete, only the primitive kidneys are wanting. So far these have not been found, although they occur in other Molluscs (pp. 39 and 136).

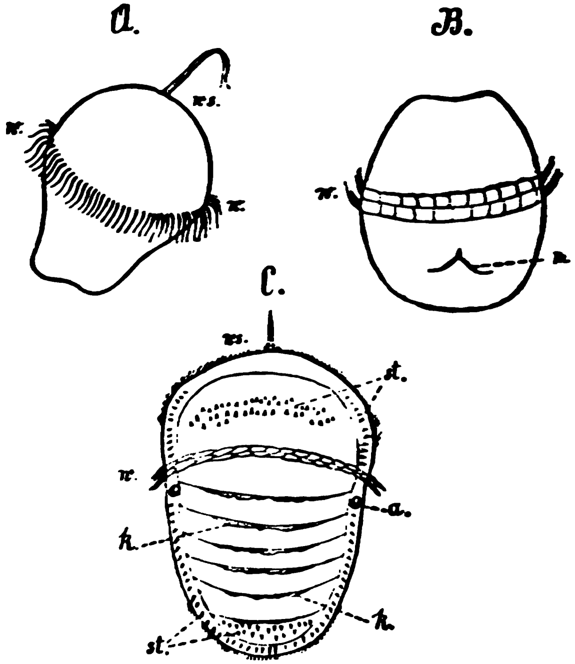


FIG. 3.—*A*, larva of *Chiton marginatus* (after LOVÉN); *B*, embryo; and *C*, larva of *C. Polii* (after KOWALEVSKY); *a*, eye; *k*, rudiments of shell-plates; *m*, mouth; *st*, spines; *w*, ciliated ring (velum); *ws*, apical ciliated tuft.

3. The Further Development of the Larva and Metamorphosis.

The changes that now take place in the larva are introduced by considerable growth of the posterior region of the body (Figs. 2 and 5), a process which recalls the development of this same section in the Annelidan *Trochophore* into the trunk region of the worm (Vol. i., Fig. 120, p. 269; *cf.* also Chapter xxxiii.). In the case of *Chiton*, it is especially the dorsal surface which increases in size (Fig. 5). In some cases, these changes take place even in the embryo, and as these forms have received more attention than the others, they will serve for description, as these processes have a very similar course in all Chitones.

To the organs which we have already found in the larva, a new one is added at a somewhat early stage: this is a sac-like gland, opening behind the oral aperture (Fig. 2 *B*, *fd.*). According to KOWALEVSKY this organ, which he regards as the pedal gland, is unpaired and originates as a thickening and depression of the ectoderm, but this origin has not been fully established. Structures corresponding to the "pedal gland" will again be met with in the Gastropoda. The nature of this organ in *Chiton* is not yet quite clear, and, as it appears to degenerate later, its efferent duct closing first, KOWALEVSKY regards it as a larval organ.

As the post-oral portion of the body elongates, the intestine also increases in length (Fig. 5); but its posterior end does not as yet communicate with the exterior. It has already been shown that, in the Annelidan *Trochophore*, the anus is wanting, or else the intestine is in a very backward stage of development.

The mesoderm which, as has already been described, first arose as two groups of cells continuous with the entoderm, and shifted later into the cleavage-cavity near the blastopore, has become richer in cells, and with the progressive growth of the larva has extended between the ectoderm and the entoderm. Now, as when it first appeared, it shows a bilateral arrangement, *i.e.*, in young embryos (aged twelve hours or slightly older, Fig. 3 *B*), the mesoderm takes the form of two compact cell-bands situated on the ventral side of the embryo and lying internal to the ectoderm. We may claim these as mesoderm-bands, since they later undergo division into a splanchnic layer applied to the embryonic intestine and a somatic layer lining the ectoderm (Fig. 4 *A* and *B*). The cavity lying between them (*coe*) which is paired, is consequently to be regarded as a true coelom. It develops earlier in the anterior than in the posterior part of the body. Thus, when two distinct cavities almost lined with epithelium are to be found in front, there is still a solid mass of cells in the posterior region. The reader will here doubtless recall conditions prevailing among the Annelida. It should also be mentioned here that the regular arrangement of the mesoderm just described is soon lost, as the mesoderm-cells grow into the primary body-cavity in a manner similar to that observed in other Molluscs (Figs. 5, 9). A large complex of mesoderm-cells, which at first remains lying at the posterior end of the body (Fig. 5) yields later the chief material for the formation of various organs (circulatory, excretory and genital organs).

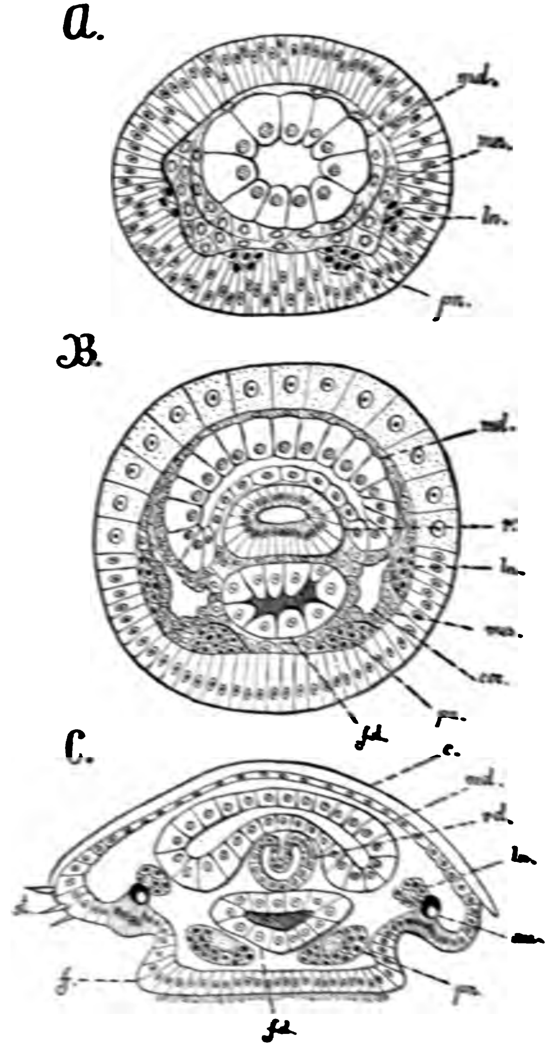


Fig. 4.—A—C, Transverse sections through embryos or larvae of [illegible] Chiton Polii (after Kowalevsky). A, through the posterior part of the body of a young embryo, B and C, through the anterior part of the body of more advanced embryos; au, eye; c, shell; f, [illegible] of foot; fd, pedal gland; ln, lateral nerve-cord; md, enteron; ms, mesoderm; pn, pedal nerve-cords; s, cuticular sac of spines; ed, ectoderm.

According to the figures before us, the mesoderm in *Chiton* shows a specially primitive condition, the coelomic sacs being very large, and by far the greater part of the mesoderm formed up to this time being related to them (Fig. 4, *A* and *B*). In other Molluscs they are much smaller and do not assume the characteristic shape found in the Annelida. As a rule, the mesoderm-bands disintegrate very early. In the remains of these bands, if not also in the scattered portions of mesoderm, a division into layers takes place which gives rise to the pericardial cavity (which is thus coelomic in origin). It would be of great value to ascertain the relation of the pericardium to the first (bilateral and bilaminar) mesoderm-rudiment in the Amphineura, especially as in some of them we find very primitive conditions prevailing in that the genital glands are immediately connected with the pericardium and the genital products thus pass direct into the latter, as, in the Annelida, they pass into the body-cavity, and are conducted thence to the exterior by the nephridia (Solenogastres).

The central nervous system in *Chiton* consists of the oesophageal ring and four large nerve-trunks, two pedal and two visceral, running from it. The anterior portion of the nervous system is constituted by the cerebral ganglia which arise from the ectoderm as two thickenings lying side by side at the anterior part of the body. According to KOWALEVSKY, these ganglia lie at the frontal pole beneath the ciliated tuft (Fig. 5, *cg*), constituting the apical plate (see p. 6, and below). The pedal and visceral commissures similarly arise from the ectoderm by the differentiation and separation of cell-strands, stages of which may be seen in Fig. 4, *A*-*C*, *pn*, *ln*.

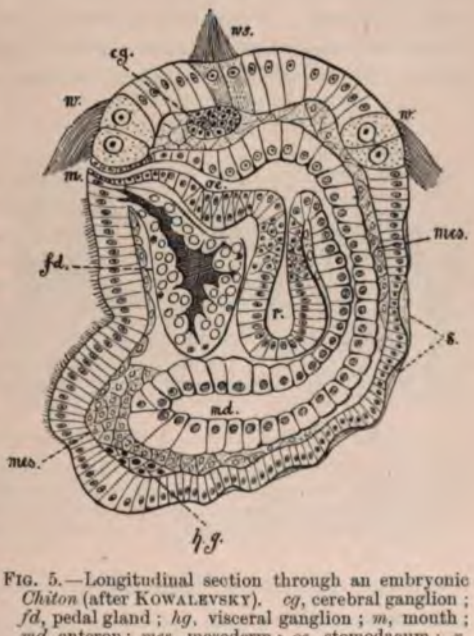
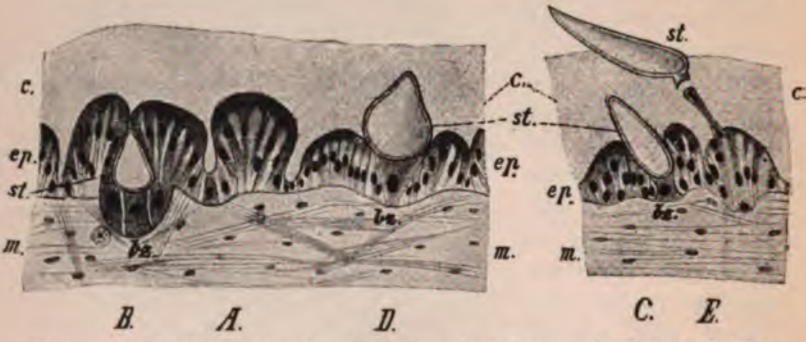


FIG. 5.—Longitudinal section through an embryonic *Chiton* (after KOWALEVSKY). *cg*, cerebral ganglion; *fd*, pedal gland; *hg*, visceral ganglion; *m*, mouth; *md*, enteron; *mes*, mesoderm; *oe*, stomodaeum; *r*, radular sac; *s*, shell-rudiment; *w*, ciliated ring [velum]; *ws*, ciliated tuft.

We have already mentioned that we thought ourselves justified in comparing the rudiments of the cerebral ganglia with the apical plate of the Annelidan *Trochophore* (p. 6). The connection of this rudiment with the lateral trunks of the nervous system in the larva cannot as yet be clearly established. KOWALEVSKY speaks of the two organs as discontinuous. The cell-mass at the posterior end of the body described as the visceral ganglion (Fig. 5, *hg*) is (as regards its ganglionic nature) of the same significance and origin.

Actual ganglia, indeed, are not developed in the nervous system of *Chiton*, where we find the ganglionic cells distributed along the entire length of the longitudinal commissures, nevertheless it appears from KOWALEVSKY's ontogenetic researches that these trunks are greatly swollen both anteriorly and posteriorly. The transverse commissures no doubt form in the same way as the longitudinal trunks.

When the embryo (*Chiton Polii* and *C. olivaceus*) has attained a stage somewhat like the one described above, it leaves the egg and becomes a free-swimming larva. At this stage, a fresh differentiation makes its appearance in the form of a segmentation affecting the dorsal surface. Here, seven consecutive segments may be distinguished, separated from one another by shallow grooves (Figs. 5 and 9). These structures are indications of the future shell; this eventually consists of eight plates, but the eighth segment only appears at a later stage.



FIGS. 6 and 7.—Two sections through the mantle-epithelium of *Chiton Polii* (after BLUMRICH). *A*, epithelial papilla without spine; *B-D*, papillae in various stages of spine-formation; *E*, later stage of the same; *bz*, formative cells of the spines; *c*, cuticular covering of the body; *ep*, mantle-epithelium; *m*, mantle-tissue; *st*, spines.

The ectodermal skeleton in *Chiton* falls under two categories: (1) the eight calcareous dorsal plates and (2) isolated spines and plates situated anteriorly, posteriorly and laterally to the former (Fig. 8, *st*). These spines are of special interest, being a characteristic feature not only of *Chiton* but also of all other Amphineura.

According to KOWALEVSKY, the spines of the larval *Chiton* originate within the cells—the cells, at those points where the spines arise later, being richly vacuolated; within these cells, the spicula are said to appear as rudiments and only later break through the surface of the body. The description of the embryonic development of the spines given by KOWALEVSKY is not easily reconcilable with the observations made by other zoologists on their formation in the adult *Chiton* (*e.g.*, those of REINCKE, No. 14, and recently those of BLUMRICH, No. 1), and other Amphineura (*Proneomenia*, THIELE, No. 1). According to these observers, the spines arise as cuticular secretions in depressions of the mantle-epithelium, the whole being covered by a thick cuticle (Figs. 6-8, *c*).

In the mantle-epithelium there are papilla-like swellings (Fig. 6 *A*) in which at a later period the formation of spines takes place. These papillae become differentiated in the following way: broad cells appear at their bases, and to these smaller cells become applied laterally (Fig. 6 *B*), the whole structure thus assuming the character of an ectodermal depression. A special basal cell (*bz*) is said to be pre-eminently the formative cell of the spine, which is first to be recognised as a small rounded structure within the papilla. It then increases in size (Fig. 6 *B*), presses apart the cells of the papilla and passes out of the latter (*C* and *D*). As the epithelial cells round the papilla continually secrete cuticular substance, the spine is pressed upwards. The basal (formative) cell from which it formerly rose is during this process drawn out like a thread (Fig. 7 *E*), the spine for a long time remaining in connection with it. The base of the spine, in contradistinction to the main calcareous shaft, consists of a chitinous substance and surrounds the latter like a cup, the whole being now far removed from the smaller papilla-cells. The latter, probably, give the spine its characteristic markings. The formation of the spine is completed by the secretion of a peg-like terminal knob by the formative cell, from which the spine then detaches itself. The neighbouring cells may also secrete another chitinous ring composed of several pieces round the base of the actual spine.

It is a remarkable fact that these spines somewhat resemble in their origin the setae found in the Annelida in ectodermal depressions; this has already repeatedly been pointed out (REINCKE, SEMPER, v. JHERING) and HATSCHEK and THIELE have again recently laid great stress on this point. We shall refer to it again later (Chapter xxxiv.).

While the spines show a formation *sui generis*, the dorsal plates are comparable with the shell-structures of other Molluscs. Their position on the back of the larva corresponds to that of the shell-gland in the larvae of the Lamellibranchia and Gastropoda (*cf.* Figs. 4 and 5; Figs. 56, p. 135, and 57, p. 137). As in these latter forms, a cuticle first appears above the epithelium (Fig. 9, *c*) and, beneath this cuticle, the calcareous substance is then secreted (Fig. 9, *k*).

Each plate begins to form independently; the calcareous secretion takes place first at the anterior border of each segment, and proceeds backwards from this point.

The segmentation of the shell is a peculiarity of the Chitones and does not occur in other Molluscs. Although the impression of segmentation is given (Figs. 3 *C*, and 9), this term is not, strictly speaking, applicable here, since there is no corresponding segmentation of the body. The shape of the shell is perhaps rather due to its mode of origin. We have already seen that the spines are cuticular structures, and this is of special interest since, in Molluscs as primitive as the Solenogastres, they are the only hard structures of the integument besides the cuticle. It has already been mentioned that the spines may assume a plate-like shape, and if we bear in mind the development of the spines in such forms as very young *Dondersia* (*cf.* Fig. 10 *C*, p. 17), it appears probable that the dorsal plates of the Chitones may have developed out of such modified spines,* either through the broadening of individual spines or through the fusion of several to form a single plate. In this respect *Dondersia* is of special interest, for this form, in which actual dorsal plates do not occur,

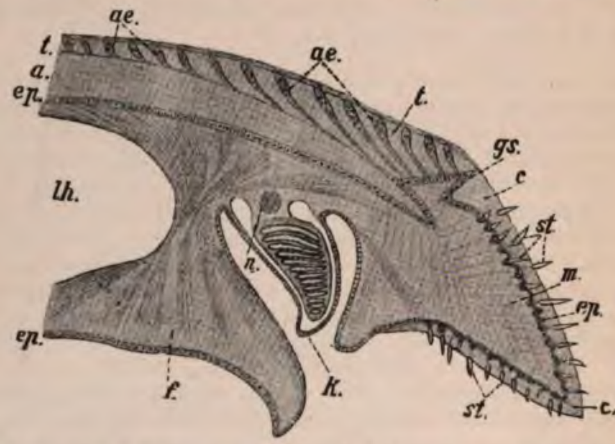


FIG. 8.—Portion of a transverse section through a *Chiton* (diagrammatic, chiefly after BLUMRICH): *a*, articulamentum; *ae*, aesthetes; *c*, mantle-cuticle; *ep*, ectoderm covering body and mantle, forming papillae in the mantle-region: *f*, foot; *gs*, cornice-like projection of the mantle; *k*, gill, with the branchial artery cut through on its left and the branchial vein on its right, between the two lies the lateral (visceral) nerve-strand (*n*); *lh*, body-cavity; *m*, mantle; *st*, spines; *t*, tegmentum, with another thinner and specially differentiated cuticular layer above it.

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* The derivation of the dorsal plates of *Chiton* from its spines was attempted by GEGENBAUR (in his Grundriss der vergl. Anatomie) as early as 1878; his views have recently been adopted by BLUMRICH, but THIELE assumes different origins for the dorsal plates and the spines, and attempts to explain a part of the former (the articulamentum) as an inner integumental skeleton.

shows, in its youth, a remarkable resemblance to *Chiton* in the arrangement of its broad, leaf-like dorsal spicula. The first appearance of the shell in the Molluscs will be discussed further in Chapter xxxiv.

The dorsal plates of *Chiton* consist of two layers, an upper layer which is continued into the thick cuticle of the mantle, the so-called *tegmentum*, and a subjacent calcareous layer, the *articulamentum* (Fig. 8, *t* and *a*). In tracing the origin of the shell from spines, we should have to imagine the articulamentum as arising from the latter, which, as can easily be explained by their origin, remained lying beneath the cuticle where they became expanded. The cuticle above the calcareous plates which have thus arisen becomes the tegmentum of the shell. The retention of single modified spines or complexes of spines, which is determined by the segmentation of the shell into separate plates, would then be explicable by the manner of life of the animal, the body of which, at first perhaps of considerable length, was able to roll up.

The shell of *Chiton* is characterised not only by its segmentation, but by the presence within it of cellular strands. These are the *aesthetes* (Fig. 8, *ae*) which may be simple or branched, and are accordingly composed of a smaller or a larger number of long cells. These sometimes occur in the tegmentum and extend from its outer surface, where each is covered by a cuticular cap, to a cornice-like fold of the mantle at the lateral margin of the shell (Fig. 8, *gs*). These cell-strands have developed from the epithelial cells of the mantle, which underwent great elongation during the secretion of the cuticle through pressure of the surrounding cells. While that part of the mantle to which they belong, and which secretes the tegmentum, undergoes marked lateral displacement during the growth of the shell, they, in consequence of their length, are able to retain their primitive connection with the surface of the shell, and yet to remain attached by their bases to the epithelium of the lateral cornice of the mantle (Fig. 8). This latter epithelium is also partly concerned in the secretion of calcareous shell-substance and, in this way, the aesthetes appear to perforate the articulamentum which has in reality been secreted round their bases. These structures have been held to be sensory organs. They can hardly be tactile organs, but they may perhaps serve other sensory purposes which are unknown to us. The eyes discovered by MOSELEY (No. 11) on the shell of a few exotic Chitones must doubtless be regarded as further modification of the aesthetes.

Figs. 5-9 show clearly that the shell of *Chiton* is, just like that of other Molluscs, a cuticular structure. While the articulamentum, in consequence of lying immediately above the epithelium, can readily increase in thickness, the tegmentum, from its position, must grow chiefly at its margin.

The development of the shell commences even during larval life. But, since some Chitons leave the egg-membrane only at a very late stage, the free-swimming stage is in their case of comparatively short duration. The commencement of metamorphosis is indicated by the compression and final degeneration of the cells of the ciliated ring which from the first were distinguished from the surrounding ectoderm by their size and structure (Figs. 5 and 9 *wr*). It must be further mentioned that in the older larvae, two eyes are said to be present, which curiously enough lie, not in the actual pre-oral section, *i.e.*, in front of the ciliated ring, but behind it (Fig. 3 *C*). These eyes are still to be found in the young *Chiton*, but, whereas they were at first superficial in position, they are now found beneath the epidermis (Fig. 4 *C*) and are consequently still nearer than before to the lateral nerve-trunk.*

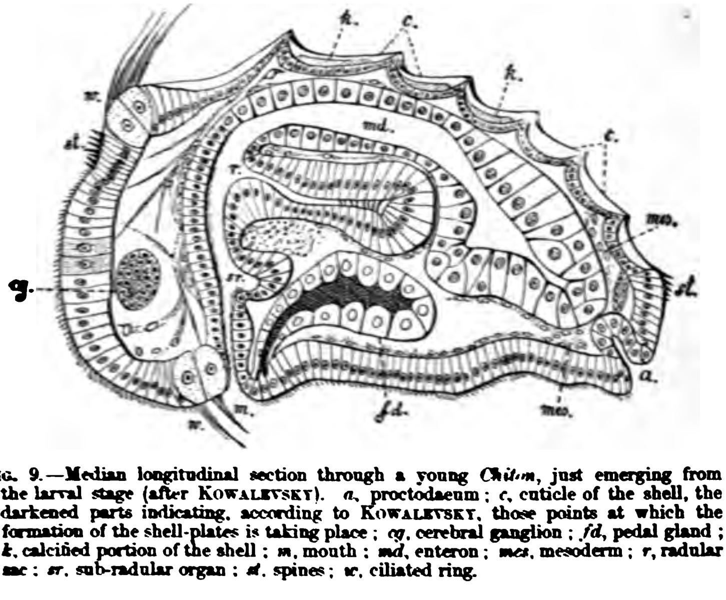

FIG. 9.—Median longitudinal section through a young *Chiton*, just emerging from the larval stage (after KOWALEVSKY). *a*, proctodaeum ; *c*, cuticle of the shell, the darkened parts indicating, according to KOWALEVSKY, those points at which the formation of the shell-plates is taking place ; *cg*, cerebral ganglion ; *fd*, pedal gland ; *k*, calcified portion of the shell ; *m*, mouth ; *md*, enteron ; *mes*, mesoderm ; *r*, radular sac ; *sr*, sub-radular organ ; *st*, spines ; *wr*, ciliated ring.

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* [PELSENEER (App. Lit. on Lamellibranchia, No. IV.) regards these eyes of the larval *Chiton* as homologous with the cephalic eyes which have recently been discovered in the adult *Mytilidae* under the branchial filaments. In the larva, they are situated outside the velar area as is the case also in *Chiton*, whereas the eyes of the typical Gastropods arise within the velar area.—ED.]

When the larva changes into the adult, the external form is modified not only by the continuous lengthening of the posterior region of the body but also by the rotation of the pre-oral region towards the ventral surface. A comparison of Figs. 5 and 9 shows clearly the beginning of this process.

A further approximation towards the shape of the adult is brought about by the development of a fold growing out on either side of the body at its dorso-lateral angle, thus giving origin to the mantle. At the same time, the ventral surface becomes specialised by the growth of its cells, which multiply and give rise to the flattened foot. The area between the mantle and the margin of the foot becomes the slightly invaginated mantle-cavity (Fig. 4 *C*).

Nothing, to our knowledge, is known of the origin of the gills, but, considering the simplicity of their form, it is very probable that they arise as papilla-like prominences on the body-surface. In the adult they form on each side a row of consecutive bipectinate ctenidia.

Among the internal changes we note the formation of an ectodermal invagination (Kowalevsky) at the posterior end of the body; this is the proctodaeum which gives rise to the anus and the base of the intestine (Fig. 9, *a*). In the stomodaeum, the radular sac has increased considerably in size, and the radula itself has already appeared within it. In front of the latter another ventral outgrowth of the wall of the stomodaeum has formed; this widens later, and at its base a thickened cell-mass can be recognised. We here appear to have the so-called sub-radular organ of the adult, which has been accurately described by Haller (No. 2). A further differentiation of the alimentary canal is caused by a ventral swelling of the enteron, which is perhaps the first indication of the liver (Fig. 9).

The further development of the larvae of *Chiton* has not as yet become known, but it is evident that they already resemble the adult in various ways, apart from the incompleteness of their internal organisation.

II. The Development of Dondersia.

The development of *Dondersia banyulensis** has been investigated by Pruvot. This form is allied to *Proneomenia* (Fig. 147, Chap. XXXIII., Hubrecht, No. 5), possessing like the latter, a vermiform body (40 mm. long and 1 mm. broad) capable of coiling up spirally.

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* [Simroth (Zeitschr. f. wiss. Zool., Bd. lvi., 1893) has created the genus *Myzomenia* for this species.—Ed.]

The dorsal and lateral parts of the body bear spicules; on the back, these are inclined towards one another and form a projecting ridge in the dorsal-median line, elsewhere (especially at the sides) the spines become flattened and imbricated.* A groove is found on the ventral surface as in many other Solenogastres (Fig. 147 *B*, Chap. XXXIII.).

Dondersia lays its eggs singly. They are opaque and surrounded by a delicate envelope which is only developed after the egg has passed from the pericardium into the nephridia which serve as genital ducts. According to PRUVOT, the envelope is formed by the latter, which no longer possess the function of excretory organs.

The cleavage is, from the first, slightly unequal: the egg breaks up into two unequal blastomeres which, through division, yield three small cleavage-spheres and one large one (*cf.* Lamellibranchia, Fig. 11 C). The next stage, one of eight cells, is reached by the bipartition of the micromeres and the unequal division of the macromere. No further micromeres are cut off from the macromere, which now breaks up into two and then into four macromeres, while the seven primary micromeres divide in fourteen and then into twenty-eight. In this stage, the *invagination* begins, and the entoderm-cells disappear within the cap formed by the more rapidly dividing ectoderm-cells. The embryo now has a conical cap-like shape, the aperture of the invagination occupying the whole of its lower side. At this time, the cilia appear, a ciliated area arising at the frontal pole, *i.e.*, at the pole opposite to the blastopore (PRUVOT), as well as round the latter; a ciliated ring also forms which encircles the whole body about half-way up, the cilia here being specially strong. This stage may be compared with the one described above in Chiton in which the ciliated ring rises at the gastrula stage.

The embryo of *Dondersia* soon changes its shape, the body becoming divided by circular grooves into three sections: (1) an anterior section consisting of two rows of ciliated cells with a few specially strong and long cilia at the apex, (2) a middle section carrying the ciliated ring, and (3) a very large posterior section also formed of two rows of cells, at the end of which lies the aperture of invagination. PRUVOT regards this latter as the blastopore, and points out

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* These statements, which are necessary to enable us to understand the development of this animal, are taken from a short treatise by PRUVOT (No. 13) on some Solenogastres of the Mediterranean. The author intends to publish a more complete work on the structure and development of these forms. HEUSCHER (No. 5) has published a treatise on the organisation of another species of [illegible]

that at first it is somewhat elongate and reaches (on the dorsal side ?) almost to the ciliated ring, but later becomes circular (Fig. 10 *A*). The further development of the larva, as described by PRUVOT (*A* and *B*) makes his interpretation of this depression (at least in the later stages) appear somewhat doubtful.

About this stage the embryo appears to become free, for the stage depicted in Fig. 10 *A* is called by PRUVOT a larval stage. The aperture of invagination has already narrowed, and is terminal in position.

The further transformation of the larva is said to take place in the following way. From within the invagination a button-like structure gradually grows out, which corresponds to the posterior end of the animal (Fig. 10, *B* and *C*), and carries at its end the remains of the blastopore. This latter must be regarded as having been previously displaced inwards. With the button-like terminal region a conical part is also gradually evaginated (*B*), and this is destined to yield the greater part of the definitive body. On this the leaf-like spicules are already appearing (*B*, *sp*). These are said to arise, as asserted for *Chiton* (p. 11), as intracellular secretions, only breaking out of these cells as they increase in size. The conical part now grows considerably, and new spicules continue to be formed; the anterior part of the larva, on the contrary, degenerates rapidly, and finally appears only as a small collar at its anterior end. The larva is at last no longer able to swim about in the water, for the cilia degenerate together with the cells that carry them. The two posterior rows of cells also (those of the third section, Fig. 10, *A* and *B*) are thrown off.

FIG. 10.—*A*-*C*, stages in the metamorphosis of *Dondersia banyulensis*; *A* and *B*, larvae 36 and 100 hours old respectively; *C*, young animal, seven days old, immediately after metamorphosis (after PRUVOT). *e*, aperture of invagination; *wk*, ciliated ring; *sp*, calcareous spicules; *dp*, dorsal calcareous plates (dorsal spicules).

This section of the body is called by PRUVOT the mantle-section in the older larvae (*B*), and this name seems to be justified by its relation to the adult body which is in process of formation. Between the process of invagination just described and the formation of the adult body, various other formative processes take place, but these apparently occur within the larval body, and have so far not yet been investigated. Essential differences are to be found between the development of *Dondersia* and that of *Chiton*; although, in the latter also, it is chiefly the part of the larval body lying behind the ciliated ring that, by its elongation, becomes changed into the body of the adult. The pre-oral part of the larva (*i.e.*, the part lying in front of the ciliated ring) is here retained, as in *Chiton*, and yields the corresponding part of the adult body. It appears that, in *Dondersia banyulensis*, there are two lobe-like projections at the anterior end of the body, and that these are already distinct in the young animal (Fig. 10 *C*). The mouth is said to be wanting until metamorphosis commences; the entoderm is present in the form of a solid mass, at the sides of which two mesoderm-bands lie. This latter condition would agree with that described for *Chiton* (p. 7), and is interesting inasmuch as the mesoderm-bands in other Molluscs are not usually so distinct. Unfortunately, no further details are known either of the internal or of the external development of *Dondersia*. It should, however, be stated that seven calcareous plates are found on the back of the young animal which has only just undergone metamorphosis (Fig. 10 *C*), these being formed of rectangular spicules arranged one behind another. The resemblance of this stage to a young recently metamorphosed *Chiton* is striking, the latter also possessing seven such plates. In what way this condition can be reconciled with that of the adult *Dondersia* we do not know: this can only be made clear by the investigation of transition-stages. The young animal has lateral spicules which are plate-like and imbricated, and which, in the adult, seem to be less developed, as far at least as can be judged from the statements as yet made on the subject.

The form of the larva of *Dondersia*, like that of the *Chiton*, may be traced back to that of the *Trochophore*. We have already pointed out various specially striking points of resemblance between the development of *Dondersia* and that of *Chiton*. The elongation of the posterior section of the body recalls here almost more than in *Chiton* the growing of the post-oral section of the Annelidan *Trochophore* into the trunk of the worm (Vol. i., Fig. 120, p. 269). This is specially striking if we examine the *Mitraria* larva (Vol. i., Fig. 124,

p. 276), in which the posterior end of the body is at first also surrounded by the cap-like anterior part of the larva and hidden within it. Since the Amphineura are very primitive representatives of the Molluscan type, such comparisons are not unjustifiable, although the unusual length of the body in this form alone determines a greater change in the more compact larva. We shall return to this point again in discussing the relationships of the Mollusca (Chap. xxxiv.)

[PRUVOT (No. II.) has since published a preliminary account of the development of *Proneomenia*. Unfortunately there are no illustrations and, as the ontogenetic processes are very peculiar, it becomes somewhat difficult to trace the origin of the definitive structures. We gather that the developmental processes closely resemble those seen in *Dondersia banyulensis* (*Myzomenia*), the earlier stages up to the formation of an invagination-gastrula being practically identical in the two forms. Similarly, *Proneomenia* develops a ciliated larva, divided into three segments and provided with a long apical flagellum. The layer forming the primary invagination (? archenteron) does not correspond to the definitive entoderm, but gives rise to *all* the tissues of the trunk. By the tangential division of its cells, it gives rise to a superior entodermic mass resting upon a single layer of cells; the latter increases by the radial division of its cells and becomes infolded, forming three invaginations; of these the middle one, which remains open, becomes the future proctodaeum, while the two lateral ones close and are transformed into the masses of mesoderm, the lateral mesoderm-bands. The lower layer, which now has the form of a vault, represents the ectoderm of the trunk. The lips of the proctodaeum now grow out to form the caudal button which first projects into the cavity of the ectodermal vault, but later, together with the entire vault, becomes evaginated through the depression at the posterior end of the larva. This conical protuberance with the caudal button and the proctodaeum at its extremity represents the trunk of the young *Proneomenia*. The entoderm still remains as a solid mass with the mesoderm-bands on either side and in contact with the proctodaeum behind. The next important change is the appearance of three ventral invaginations of the larval ectoderm, just behind the circle of large cilia on the middle segment; the median of these invaginations, the larval stomodaeum, is merely transitory, while the two lateral ones are concerned in the formation of the ectoderm and mesoderm of the head. These two unite, forming a transverse band capping the anterior end of the entodermic mass and prolonged posteriorly at two points to meet the mesoderm-bands of the trunk; this portion appears to form the muscles, while the more dorsal elements of the invagination form the cerebral ganglia. The cells of the apical plate seem to take no part in the formation of the nervous system. The ectoderm of the head appears to form entirely from these anterior invaginations, while that of the trunk develops from the primary posterior invagination. The latter is now completely evaginated, and has developed the provisional imbricated spicules. In this way the young *Proneomenia* is developed under cover of a provisional ectoderm which serves as a locomotory organ and is thrown off at the moment of metamorphosis. The adult does not exhibit a distinct head but, during development, this structure is perfectly distinct and arises quite independently of the trunk.

A very striking resemblance, possibly of great significance, is to be noted between the developing Solenogastres and certain Lamellibranchia (DREW, App. Lit. Lamellibranchia, No. II.). In *Yoldia*, we find the young Mollusc developing under cover of a segmented, ciliated larval test provided with an apical tuft. Here also the trunk and head-regions originate separately, the former possibly from the posterior blastoporic end, and the latter including the cerebral ganglia from a pair of invaginations at the antero-ventral end of the larva. As in the Solenogastres, the larval locomotory ectoderm is thrown off during metamorphosis. The resemblance in the early cleavage has been already pointed out. These very striking resemblances, suggesting as they do a connection between the Solenogastres and the Lamellibranchia, require further and more complete investigation.—ED.]

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CHAPTER XXX.

LAMELLIBRANCHIA.*

Systematic :—

I. **Protobranchia**, gills bipectinate, branchial processes plate-like and not reflected, foot with creeping sole.

Nucula, Yoldia, Solenomya.

II. **Filibranchia**, gill-filaments distinct and reflected; solid interlamellar junctions, cilia forming interfilamentar junctions.

Arca, Mytilus, Modiolaria, etc.

III. **Pseudolamellibranchia**, the gill-filaments reflected and loosely connected by ciliated discs or vascular junctions, interlamellar junctions vascular; gills folded and filaments at base of grooves modified.

Pecten, Ostrea, etc.

IV. **Eulamellibranchia**, gill-filaments of plate-like gill connected by vascular interfilamentar and interlamellar junctions, reflected.

Cardium, Teredo, Cyclas, Unio, Venus and most Lamellibranchs.

1. Oviposition and Care of the Brood.

The eggs of the Lamellibranchia may be discharged into the water and there fertilised (*Modiolaria* and *Mytilus edulis*, Lovén, Barrois, Wilson ; *Ostrea virginiana*, Brooks, No. 16 ; and pro-

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* We have, chiefly for practical reasons, placed the Lamellibranchia before the Gastropoda, because their larval forms appear to be more primitive, and their further development is usually more simple. The relation of the Lamellibranchia to the other divisions of the Mollusca will be discussed later (Chap. xxx.). In the classification of the Lamellibranchs, we have followed Pelseneer's recent works, but it should be mentioned that Grobben has quite recently adopted a new stand-point in classifying the Lamellibranchia, and has expressed himself as opposed to the use of the gills as the determining feature in their classification (Beiträge zur Kenntniss des Baues von *Cuspidaria* (*Neaera*) *cuspidata*, etc. Arb. Zool. Inst. Wien. Bd. x. 1892).

bably also *Pecten*, FULLARTON, No. 14). This form of oviposition is common among marine forms, but among fresh-water and a few marine forms the female takes considerable care of the brood. In these latter cases, fertilisation occurs either in efferent genital ducts or in the branchial cavity, into which the spermatozoa have passed from outside. In *Unio* and *Anodonta*, for instance, the eggs which are discharged into the inner division of the supra-branchial cavity are driven by the stream of respiratory water filled with sperm into the cloaca, and thence into the external division of the supra-branchial cavity, and so into the interfoliar cavity of the outer gill-lamella where they pass through their embryonic development. In *Pisidium*, the eggs lie in special brood-pouches at the base of the gills, and, in *Cyclas* also, brood-capsules are formed in the gills by growths of the epithelium between the septa, and in each of these an egg or embryo lies. Embryos have even been observed in such pouches nourishing themselves by swallowing the branchial epithelial cells (STEPANOFF, No. 54, ZIEGLER, No. 60). *Dreissensia* is peculiar among fresh-water Lamellibranchs in this respect, and it discharges its eggs direct into the water like the marine forms mentioned above (KORSCHELT, No. 27). On the other hand, in some marine Lamellibranchs, care is taken of the brood. The eggs of *Teredo*, for example, are retained in the branchial chamber (HATSCHEK), and in *Ostrea edulis* they are found, up to the time when the free-swimming larva develops, within the mantle-cavity (MÖBIUS No. 37, HORST, No. 19). *Entovalva mirabilis* forms a bell-shaped brood-cavity at the posterior end of the body through the fusion of the two halves of the mantle, in which the embryos remain till the *Trochophore* stage is reached (VOELTZKOW, No. 57).

The spherical eggs are loosely surrounded by a thin, structureless membrane (vitelline membrane), which may be lost even during embryonic life (*e.g.*, in *Teredo*). Sometimes the egg-integument is exceedingly delicate, and disappears even during the earliest stages of development, and then the eggs pass out direct into the water (*Dreissensia*, *Mytilus*, *Ostrea*). On the other hand, the envelope may be thicker and multilaminar as in *Cardium exiguum*, the eggs of which with their vitelline membranes have a lenticular form and are attached to firm objects by the mother (LOVÉN, No. 33). In some genera (*Anodonta*, *Unio*, *Cyclas*), a chimney-like appendage, the micropyle, is found on the egg-integument (Fig. 22, *m*, p. 50).

2. Cleavage and Formation of the Germ-layers.

In those forms in which the cleavage of the egg has been carefully investigated (*Unio, Anodonta, Cardium, Cyclas, Teredo*), its course is so uniform that we may conclude that it is the same in those eggs of which only a few but similar stages have been observed (*Ostrea edulis, Pecten, Mytilus edulis*, Möbius, Horst, Fullarton, Barrois and Wilson). Cleavage is always unequal; the first cleavage-plane divides the egg into two cells, a very large macromere and a much smaller micromere (Fig. 11 *A*). In *Teredo*, a corresponding differentiation is indicated even before cleavage by the different constitution of the protoplasm at the vegetative and at the animal poles of the egg. The plane dividing the two blastomeres passes through the point where the polar bodies lie. The micromere next divides into two (Fig. 11 *B*), and almost at the same time, or else a little later, the macromere gives origin to a new micromere (*C*). The new cell then divides, and the process of the abstriction of a micromere from the large cleavage-sphere is repeated (*D*) again and again, the large cell yielding micromeres which then divide (*E*). Finally, the micromeres, seen from the surface, resemble a cap placed upon the remains of the macromere, which at last also divides into two similar cells (macromeres) (Fig. 11 *F*).*

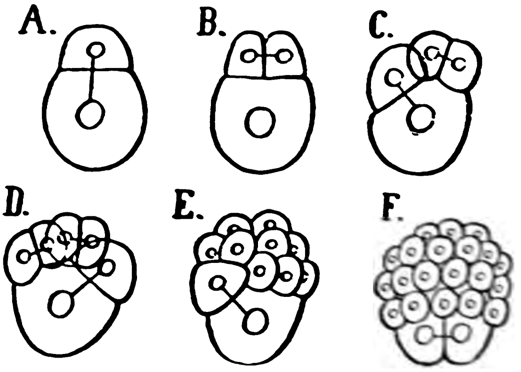

Fig. 11.—*A-F*, diagrams illustrating the cleavage of the egg in the Lamellibranchia. The lines connecting the nuclei of two cells indicate that the pair has arisen from the division of one cell.

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* [It is commonly held that the entoderm arises solely from the macromeres after the latter have ceased giving origin to micromeres, and that, at the four-celled stage (Fig. 11 *C*), the rudiment of the entoderm lies entirely within the single macromere. This appears to be the case in *Cyclas* according to Stauffacher (No. VI.), but in *Unio*, on the contrary, Lillie (No. III.) asserts that at this stage, each blastomere contains the rudiments of both ectoderm and entoderm. The cleavage in *Unio* appears, on superficial

The cells do not necessarily always divide in exactly the way described. For example, a new micromere may be constricted off before the one last formed has divided; but this does not indicate any essential deviation from the course above described. This is also the case in the apparently divergent method of cleavage seen in *Modiolaria* and *Ostrea virginiana*, as was recognised long ago by LOVÉN, and was again pointed out by ZIEGLER. In the two Lamellibranchs just named, during the first stages of cleavage, a very remarkable process takes place, a part of the large sphere rising up from it like a distinct blastomere, but not, like the true blastomeres, entirely separating from it; at a later stage, this protuberance is withdrawn into the macromere. On account of this process, which is probably determined by the relative distribution of the protoplasm and the yolk in the egg, the first stages of *Modiolaria* and *Ostrea virginiana* differ in appearance from the diagrams given above; they may, however, be referred to these, as is evident after the degeneration of the false blastomere.

RAY LANKESTER long ago described the cleavage of the egg in *Pisidium pusillum*, a form nearly related to *Cyclas*, into four spheres of equal size, from each of which a smaller cell became constricted (No. 29). If this is really the case, this method of cleavage would not correspond to that known to occur in other Lamellibranchs, but would rather closely resemble the cleavage of the Gastropod egg (p. 108). This condition of the egg of *Pisidium* is however so peculiar when compared with that of other Lamellibranch eggs that it requires to be further investigated.

In describing the stages of cleavage, we have so far dealt only with their outward form. Although the manner in which this arises in the various eggs is very similar, nevertheless certain differences of internal constitution are very soon evident. In one case, a cavity, the cleavage-cavity, soon appears between the micromeres and the macromeres. [In *Cyclas*, at the 13-celled stage, STAUFFACHER.] This increases considerably in size, as the division of the cells continues, and leads to the formation of a blastula, such as is found in *Cyclas*, *Pisidium* and the *Unionidae*, the wall of which is not uniform in thickness. In other cases, the cleavage-cavity is not so large, especially at first (*Mytilus*),* while in *Teredo*, as well as in

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examination, to be precisely similar to that described above, but neither the first nor the second cleavage separates the animal from the vegetative cells, as RABL asserted, this separation, according to LILLIE, only occurring at a later period, and thus the entoderm arises both from the micromeres and the macromeres. LILLIE suggests that the unequal cleavage in *Unio* is due to the fact that the rudiment of the immense shell-gland is to be found in the large cell, and he further accounts for the minute size of the entomeres on the ground that the intestine remains undeveloped until a late stage.—ED.]

* The observations of BARROIS, made on *Mytilus* (No. 1) are only known to us from the abstract in the *Jahrsberichte*, but, taken together with the statements of WILSON (No. 59) are probably to be understood in the way indicated above.

Ostrea virginiana, it is altogether wanting (Figs. 12 and 14 *A*). The micromeres then lie immediately upon the macromeres, the consequence being that, as they multiply, they surround the latter. An epibolic gastrula is thus produced (Figs. 12 and 14 *A*), such as, according to LOVÉN, is found in *Modiolaria* and *Cardium*. In the last stages of cleavage, the two primary germ-layers are already differentiated, the micromeres corresponding to the ectoderm and the macromeres to the entoderm.

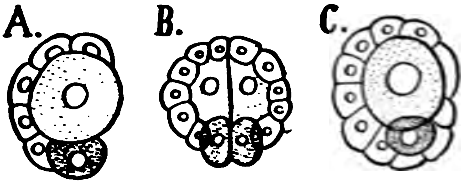

FIG. 12.—*A-C*, embryos of *Teredo* during the formation of the germ-layers (after HATSCHEK). The entoderm-cells are lightly dotted, while the mesoderm-cells are more darkly marked; the unshaded part is ectoderm.

This also applies to those cases in which a cleavage-cavity forms and the gastrula arises through *invagination* (fresh-water Lamellibranchs, RAY LANKESTER, ZIEGLER, LILLIE). In *Cyclas*, for instance, a shallow depression forms in the blastula (Fig. 13 *A*), the vegetative pole of which is no longer to be distinguished by the larger size of its cells, and, by a further invagination of the cells at this point, a small archenteron is formed (Fig. 13 *B*). This is also the case in *Pisidium*. The blastopore takes the form of a slit lying in the median line, and in this way the embryo early assumes a bilateral symmetry. The blastopore soon closes, so that the archenteron loses its connection with the exterior and lies as a closed sac in contact

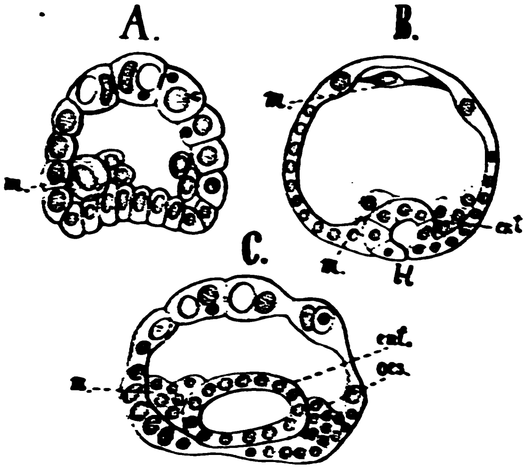

FIG. 13.—*A-C*, sections through embryos of *Cyclas cornea*. *A*, blastula-stage. *B*, gastrula-stage. *C*, stage succeeding the closure of the blastopore (after ZIEGLER). *bl*, blastopore; *ent*, entoderm; *m*, mesoderm; *es*, rudiment of the stomodæum.

with the ectoderm (Fig. 13 *C*). It is not known whether the blastopore closes from behind forward, so that its relations to the mouth and anus are still uncertain. [In *Unio* (LILLIE) the blastopore is said to close by the forward growth of its posterior lip, the ventral plate.]

In the *Unionidae* also there is an invagination-gastrula, but the archenteron is here still smaller than in *Cyclas* (GOETTE, Fig. 23 *A-C*, *e*, p. 51).

The presence of an invagination-gastrula in the *Unionidae* was first observed by RABL in 1876 (No. 43), and SCHIERHOLZ in 1878 (Nos. 47-49), and the gastrula was said to have a specially large archenteron (Fig. 22, p. 50), but it is impossible to reconcile either the position or the large size of this archenteric invagination with the later development of the embryo, especially as the alimentary canal is at first very inconspicuous. According to GOETTE'S recent description (No. 15), this deep depression represents the shell-gland which is here specially strongly developed, the archenteron, on the contrary, being reduced (Fig. 23 *A-C*, *sd* and *e*). The subject will be discussed more in detail in connection with the further development of the *Unionidae* (p. 49). [LILLIE (No. III.) has shown definitely that the large invagination observed by RABL and SCHIERHOLZ was the temporarily inturned shell-gland, the true archenteron being very small.]

Between the extreme cases of epibolic and embolic gastrulation, such as are offered by *Cyclas* on the one hand and *Teredo* on the other, *Ostrea* forms to a certain extent a transition. In the European as well as in the American Oyster, the micromeres have been observed to grow round the macromeres, of which there are only one or two present at this stage (Fig. 14 *A*). HORST and BROOKS agree in denying the presence up to this stage of a cleavage-cavity, but such a cavity arises as soon as the macromeres increase in number.

As the micromeres even during epibole projected slightly beyond the macromeres at the vegetative pole, a depression arises in this region. When the macromeres now divide, a stage arises, with an almost triangular blastopore, which cannot be distinguished from an invagination-gastrula (Fig. 14 *B*). During these processes, important alterations have taken place in the form of the embryo; an invagination closely resembling the archenteron in form, the so-called shell-gland, has appeared (Fig. 14 *B* and *C*, *sd*). To this and the further transformation of the embryo (*C-E*) we shall return later.

Conditions similar to those in the Oyster are found also in the Lamellibranchs examined by LOVÉN (*Modiolaria* and *Cardium*), in which the abundance of yolk determines the early circumcrescence of the entoderm-elements, which latter only then commence to divide. A cavity then appears to arise between the ectoderm and the entoderm, and stages occur exactly resembling Fig. 14 *B*. In *Teredo*, the separation of the two primary germ-layers and the increase of the entoderm-cells takes place at later stages (Figs. 12 and 15, pp. 26 and 31).

During the act of gastrulation (*Teredo*, *Unionidae*) or even before it commences (*Cyclas*), the *rudiment of the mesoderm* appears in the embryo. In the epibolic gastrula of *Teredo*, there are two large cells which, according to **Hatschek**, are to be traced back to the macromeres, lying symmetrically to the median plane at the posterior edge of the blastopore (Fig. 12 *A* and *B*). They are soon grown round by ectoderm and are thus drawn into the interior of the embryo (Fig. 12 *C*). In *Ostrea edulis*, corresponding cells are found in a similar position (Fig 14 *C*), and conditions similar on the whole are also found in *Cyclas*.* These two cells have been assumed to be *primitive mesoderm-cells* [mesodermal teloblasts] homologous to

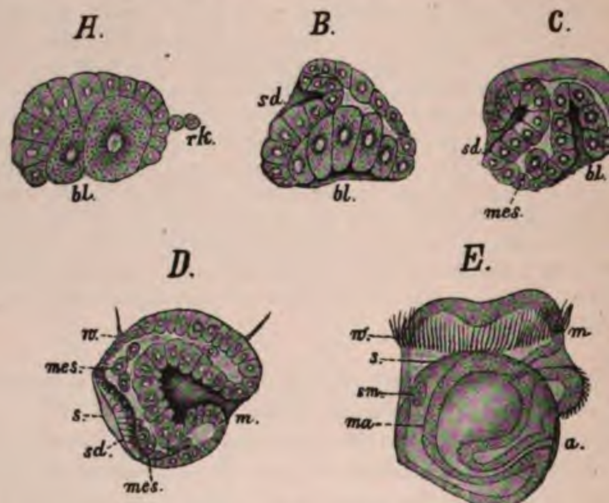

FIG. 14.—*A*-*E*, various stages of development of the Oyster (*A* of *Ostrea virginiana* after BROOKS, *B*-*E*, of *Ostrea edulis* after HORST). *a*, anus; *bl*, blastopore; *m*, mouth; *ma*, stomach; *mes*, mesoderm-cells; *rk*, polar bodies; *s*, shell (in *D*, unpaired embryonic shell-rudiment); *sd*, shell-gland; *sm*, the anterior adductor muscle; *w*, pre-oral ciliated ring.

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*[In *Cyclas*, after the macromere has given origin to the last micromere (about the 30-celled stage), it divides into two cells of equal size, from each of which a large cell segments off into the cleavage-cavity. These are the two primary mesoderm-cells. The two small remnants of the macromeres form the entoderm (STAUFFACHER, No. VI).—ED.]

those in the Annelida, from which by repeated division the mesoderm-bands are formed. In this way, the bilateral symmetry of the body would find an early expression in the rudiment of the mesoderm.

Two mesoderm-bands, which, however, are not nearly so regular in their arrangement as in the Annelida, have also been discovered by RABL and HATSCHEK. HORST has described similar conditions in *Ostrea*, and ZIEGLER'S account of *Cyclas* also, on the whole, agrees with the above. The latter author, however, does not exclude the idea of a further participation of the ectoderm in yielding the mesoderm-elements, and RAY LANKESTER also was formerly in favour of the partial derivation of the mesoderm from the ectoderm (*Pisidium*). There was therefore a general inclination not to derive the whole of the mesoderm in the Lamellibranchia from the primitive mesoderm-cells.

Unio, a form in which the mesoderm and the germ-layers in general were first demonstrated by RABL, although indeed not very accurately (*cf.* pp. 27 and 50), shows most markedly the method of formation of the primitive mesoderm-cells [mesodermal teloblasts] and the mesoderm-bands. But since the entodermal nature of the large invagination in the *Unionidae* must be considered as refuted, these conditions also cannot be regarded as sufficiently established. RABL found, in *Unio*, two cells which even in the blastula-stage are distinguished by their size from the rest. At the commencement of gastrulation, these pass into the cleavage-cavity, and then lie symmetrically to the median line. The active multiplication of these two cells is said to give origin to the mesoderm-bands.

It must here be mentioned that the presence of the large cells that were found by RABL within the young embryo is confirmed by the later descriptions of SCHIERHOLZ (No. 49) and GOETTE (No. 15) (Fig. 23 *A*, p. 51). According to GOETTE'S figures, these might also lie near the blastopore, since the latter is apparently not far removed from the shell-invagination which RABL mistook for the archenteron (Fig. 23 *A*). The mesoderm-bands in the Lamellibranchia cannot, as a rule, be said to be very distinct.

[The primitive mesoderm-cells in *Unio* lie in the cleavage-cavity immediately posterior to the blastopore, and give rise to two mesoderm-bands by teloblastic growth. There are in addition certain mesoblastic cells (the larval mesoblast of LILLIE) situated anteriorly to the archenteron, which have the character of a mesenchyme, and possibly form the larval adductor muscle and the myocytes.]

Summary. The differentiation of the germ-layers in the Lamellibranchia takes place very early. Even during cleavage the two primary layers can be clearly distinguished, and the rudiment of the middle germ-layer can also be recognised very early (Figs. 12-14). After the gastrula-stage is reached, the mesoderm is found in the form of more or less massive accumulations of cells (mesoderm-bands), apparently proceeding from the posterior pole, between the ectoderm and the entoderm. The bilateral symmetry of the germ early finds expression in the rudiment of the mesoderm and in the position of the blastopore.

3. Development and Structure of the Trochophore Larva.

There is, in the development of the Lamellibranchia, a stage which more or less closely resembles the *Trochophore* larva of the Annelida, and which has therefore received the same name (Ray Lankester, Hatschek). This stage is most marked, as we should naturally expect, when it is represented by a free-swimming larva, such as is found among the marine Lamellibranchs (*Teredo*, *Cardium*, *Mytilus*, *Ostrea*, etc.), but can be clearly recognised also in other forms (*Cyclas*, *Pisidium*). In the *Unionidae*, the *Trochophore* stage has undergone much greater modification. Thus among the marine Lamellibranchs we find, as a rule, that the primitive larval form has been retained in a less specialised condition than among the fresh-water forms, and this affords a further confirmation of a phenomenon which is very wide-spread in the animal kingdom. One fresh-water Lamellibranch, however, *Dreissensia polymorpha* (evidently in consequence of its late transference to fresh water) exhibits a larva agreeing exactly with those of the marine Lamellibranchia (Korschelt, No. 27, Blochmann, No. 3, Weltner, No. 58).

The structure and development of the *Trochophore* larva have been best investigated by Hatschek in *Teredo*; in addition, Brooks and Horst have published observations upon the larva of the Oyster, and Lovén upon those of various other Lamellibranchs (*Modiolaria*, *Cardium*, *Montacuta*). The *Trochophore* stage of the fresh-water Lamellibranchs has been carefully investigated in *Cyclas* by Ziegler. We shall here for the most part follow Hatschek's account of the larva of *Teredo*, since this form, of all those as yet known, most clearly exhibits the Trochophoran condition. The larva of *Ostrea edulis* which, with regard to the formation of the alimentary canal, shows (according to Horst) a still simpler condition, agrees very closely with *Teredo*.

A. The Trochophore stage as a free-swimming larva.

We have already (p. 23) described a few stages in the development of *Teredo*, in which an epibolic gastrula is formed (Fig. 12 *A*-*C*). Further changes begin by the overgrowth of the mesoderm-cells lying at the edge of the blastopore by the ectoderm; the former thus become enclosed within the embryo, the blastopore closing in consequence of the further growth of the ectoderm (Fig. 12 *C*). The relation of the blastopore to the mouth which now forms could not be established in *Teredo*, but the closure of the blastopore on the ventral side seems to take place in the neighbourhood of the future mouth. This latter arises at a somewhat later stage in the form of an ectodermal invagination (Fig. 15 *A*). A comparison of this stage with those that lead to the *Trochophore* shows us that the longitudinal axis of the latter is not identical with that of the gastrula, but apparently cuts it at almost a right angle. A similar condition is found in *Ostrea* (Fig. 14 *A*-*E*). In the Oyster, the blastopore does not close, but becomes carried into the interior of the embryo by an invagination of the ectoderm, the stomodaeum. The blastopore thus persists as the opening between the stomodaeum and the enteron. The transformation of the archenteron into the enteron of the larva can take place more simply in *Ostrea*, inasmuch as the embryonic entoderm here consists, even at an early stage, of a large number of cells (Fig. 14 *A*-*D*). In *Teredo*, on the contrary, the two large entoderm-cells are retained for a very long time, only a few smaller entoderm-cells becoming abstricted from them (Fig. 15 *B*). The development of the enteric cavity and its close connection with the stomodaeal invagination thus occur later (Fig. 15 *C*).* Consequently, the intestine of *Teredo* can only become capable of functioning at a much

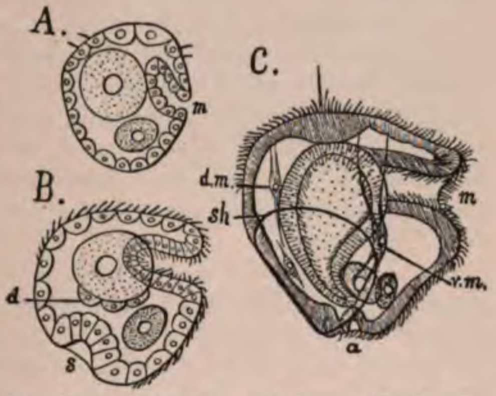

FIG. 15.—*A*-*C*, embryos and larva of *Teredo* (after HATSCHEK). The entoderm-cells are lightly and the mesoderm-cells more darkly dotted; *a*, anus; *d*, rudiment of the enteron; *dm*, dorsal, *vm*, ventral retractor muscles; *m*, mouth; *s*, shell-gland; *sh*, shell.

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* The statement of BROOKS that, in the American Oyster, the blastopore closes and the mouth and anus appear as new structures in no way connected with it, cannot be reconciled with the account given by HORST. We should then have a condition such as is found in the fresh-water Lamellibranchia (p. 40). Such a condition would have to be regarded as a specialised one, and we should therefore the less expect to find it in the free-swimming larvae of the marine Lamellibranchia.

later stage than that of *Ostrea*. The proctodaeum also seems to develop earlier in the latter. In *Teredo*, according to HATSCHEK, the terminal portion of the intestine arises as an *ectodermal invagination at the posterior end of the body* (proctodaeum), which afterwards becomes connected with the enteron (Fig. 15 *C*, *a*).

Even before the processes just described are completed, other important changes, especially affecting the external shape of the embryo, have taken place. At the time of the formation of the stomodaeum, the ectoderm began to separate from the entoderm, thus giving rise to the primary body-cavity and at the same time causing a striking alteration in the shape of the embryo (Figs. 14 and 15). The latter, which hitherto was almost egg-shaped, now broadens anteriorly, the pre-oral part assuming the shape of a somewhat flattened cupola, while post-orally the body tapers slightly: in fact, the larva assumes the shape with which we became familiar in the Annelidan *Trochophore* (Vol. i., p. 265, etc.).

During this alteration in the shape of the embryo, the ciliation characteristic of the *Trochophore* also appears, two rows of cells lying in front of the mouth and encircling the cephalic area becoming covered with cilia (Fig. 15 *A*). The pre-oral ciliated ring consisting of a double row of cells thus arises, but, in the following ontogenetic stages of *Teredo*, this is the less distinct, as the whole body becomes covered with cilia, most of which are lost again later. Then, only the biserial pre-oral ciliated ring persists, while behind the mouth are seen the first indications of a post-oral ciliated ring. These are gradually continued towards the dorsal side until the closed post-oral uniserial ciliated ring is produced (Fig. 18 *w*). Between the two rings, a zone of more delicate cilia is retained; this is called by HATSCHEK the adoral ciliated zone. Behind the anus, also, a small ciliated area is found. A tuft of strong cilia or a single thick cilium, found in many Lamellibranch larvae in the centre of the cephalic area, makes the likeness to the Annelidan *Trochophore*, already produced by the form of body and distribution of the cilia, still more striking (Fig. 18).

While the post-oral ciliated ring and the adoral zone no doubt assist in the capture of food, the pre-oral ring is specially adapted for locomotion. In accordance with this function it is always found specially well developed in the free-swimming larvae, in which the post-oral ring and the other ciliation may degenerate. This important locomotory organ attains in many larvae so great a development that the anterior part of the body carrying it projects beyond the rest of the body. This becomes very pronounced at a stage when a slight constriction of the body behind the pre-oral ring is found, as in the Oyster depicted in Fig. 16. It is this specially noticeable part of the larval body that has been called the *velum*. It can, in later stages, be retracted within the shell by special muscles (ventral and dorsal retractor muscles, Fig. 16, *vm* and *dm*, and Fig. 18), so that the larva appears highly contractile. In the anterior (pre-oral) part, *i.e.*, in the region of the velum, the larva is often more or less strongly pigmented (*Dreissensia*), and has thus a peculiar and striking appearance (Fig. 17 *A*).

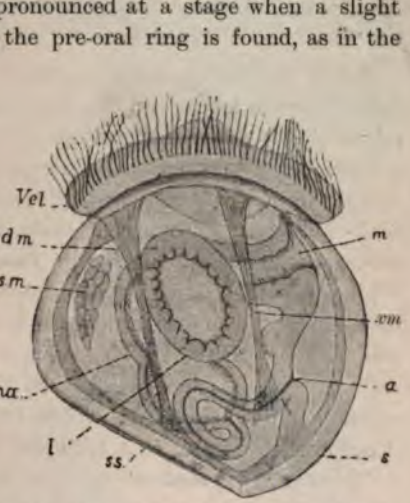

FIG. 16.—Larva of *Ostrea edulis* (from RYDER, No. 46, after HUXLEY); *a*, anus; *dm*, dorsal retractor muscle; *l*, liver; *m*, mouth; *ma*, stomach; *s*, shell; *sm*, anterior adductor muscle; *ss*, shell-hinge; *Vel*, velum; *vm*, ventral retractor muscle.

The velum is such a powerful locomotory organ that the larva is able to swim with great rapidity in definite directions, and thus does not merely float about in the water like many ciliated larvae. Such a swimming larva, in the position in which it is usually seen at the surface of the water, *i.e.*, with the velum directed upward, presents a very characteristic appearance (Fig. 17 *A*). The strong covering of cilia carries on an almost continual rowing motion. When the larva is in this position, the whole of the upper part of the body is covered by the velum. The large size of this organ in comparison with the rest of the body can be distinctly seen in older stages of, for example, the *Dreissensia* larva (Fig. 17 *C*) in which the massive velum is extended far beyond the valves of the shell. In this form, the retraction of the velum is assisted by the development of a median groove which divides the velum into two and enables these two cushion-like halves to be folded together. The velum in this way has a peculiar double appearance which is most marked when it is being extended, but is also evident even when it is fully expanded (Fig. 17 *B*, and Fig. 20). The double velum of the Gastropoda is thus recalled, and the resemblance is much more striking here than in the reduced velum of *Cyclas*, in which ZIEGLER pointed it out (p. 45).

Most Lamellibranch larvae seem to leave the egg-envelope at a very early stage, and either remain sheltered within the body of the mother for a long period, like *Teredo* and the European Oyster, or else at once enter on free life. This latter is the case with the American Oyster and *Modiolaria* as well as with *Mytilus* and *Dreissensia*. The minute and somewhat pear-shaped larvae of the last-named form are met with swimming freely on the surface of the water before attaining the *Trochophore* stage as well as at that stage.

Before indicating further points of resemblance between the Lamellibranch larvae and the Annelidan *Trochophore* connected specially with the internal organisation, we must first draw attention to a character, not hitherto considered, which distinguishes these larvae at once from all other (non-Molluscan) larvae. This is the so-called *shell-gland*. At a somewhat early period in *Ostrea*, as early as the gastrula-stage (Fig. 14 *B*), in *Teredo* rather later, a part of the ectoderm, which is somewhat thickened by the lengthening of its cells, forms a trough-like depression on the dorsal surface near the posterior pole (Fig. 15 *B*). This depression, which represents the rudiment of the shell-gland, soon deepens considerably, so that it appears like a blind tube (Figs. 14 *C*, and 22, p. 50). It has a glandular character, inasmuch as its cells show the longitudinal striation characteristic of many glandular cells: it soon also begins to secrete a substance which can be seen as a thin integument over the external aperture and the margin of the shell-gland (Figs. 14 *C*, and 15 *B*). This is the first indication of the shell, and it is thus seen that the latter in its earliest rudiment is unpaired.

In the further course of development the invagination of the shell-gland flattens out again, first becoming reduced to a shallow depression covered by the rudiment of the shell (Figs. 14 *D*, and 23), and later disappearing altogether. The shell at the same time increases in size, and now, like a saddle, covers a part of the dorsal and lateral surfaces (Figs. 15 *C*, 14 *E*, and 23 *C*). By the extension of the shell over the sides of the larvae, the way is prepared for the duplication of the former, and very soon a median dorsal dividing line can be seen separating the shell into two laterally situated valves. This line corresponds to the hinge-margin of the adult shell: it is indicated in Figs. 15 *C* and 14 *E* by the straight line on the back of the larva (cf. also the method of formation of the definitive shell in *Cyclas*, p. 43). The large size subsequently attained by the shell in the free-swimming larva is to be seen in Figs. 16 and 17 *B* and *C*. The shell is seen to project beyond the body, a condition only rendered possible by the formation of the right and left mantle-folds which has already taken place. These folds are formed as lateral outgrowths of the ectoderm, the outer layer of ectodermal cells being in close contact with the shell, while the inner surface of the outgrowth is separated from the keel-shaped ventral region of the larva by a deep fissure—the mantle-cavity (HATSCHEK). The reader should compare this with the formation of the mantle in *Cyclas* at a later stage (p. 43).

The shell, in the condition just described, is already a real protection to the larva, for, on account of the contractility of the velum, the whole body can be withdrawn between the two valves. The shell increases in size as the larva grows; in *Dreissensia* concentric bands of growth can soon be recognised, their number increasing more and more with age. The growth of the larva of *Dreissensia*, and also that of the larvae of marine Lamellibranchs before metamorphosis, is very considerable.

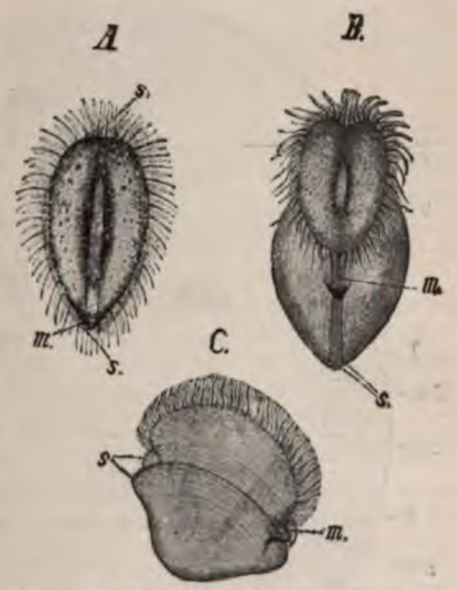

FIG. 17.—*A*-*C*, larvae of *Dreissensia polymorpha* in various positions: *A*, surface view of the velum; *B*, antero-ventral aspect; *C* (older larva), seen from the side (original); *m*, oral region; *s*, shell. The velum, especially in *A*, appears strongly pigmented. In *C*, retractors are faintly seen running back from the velum.

It need hardly be specially pointed out that the *Trochophore* of the Lamellibranchia and of the Mollusca in general is, by the possession of a shell, distinguished in a very noteworthy manner from the *Trochophore* larva of other groups. Thus we see that, in spite of all the important points of agreement, differentiation in a special, and, for the Mollusca, characteristic direction, takes place at this early stage. Other Molluscan characters affecting the body of the *Trochophore* externally, are the foot which arises as an outgrowth of the body-wall between the mouth and the anus, and the gill-rudiments, which are first indicated by papilla- or ridge-like outgrowths of the ectoderm: but these changes will be dealt with later when considering the transformation of the larva into the adult. Before entering upon this subject, we have to describe an important character of the *Trochophore* larva itself, which marks still more strongly its resemblance to the Annelidan *Trochophore*.

Restricting ourselves for the present to the ectodermal structures, we find, in the centre of the cephalic area, beneath the strong flagella, where such are present, an ectodermal thickening which, in form and position, corresponds essentially to the neural plate of the Annelid larvae (Fig. 18, *sp*; *cf.* also Vol. i., Fig. 118, p. 265, and Fig. 120, p. 269, &c.). From this thickening, which must be regarded as the neural or apical plate, and which later yields the cerebral ganglia, a system of peripheral nerves is said to extend. [In *Ostrea* there is a distinct but shallow depression formed in this thickened area during the development of the cerebral ganglia.]

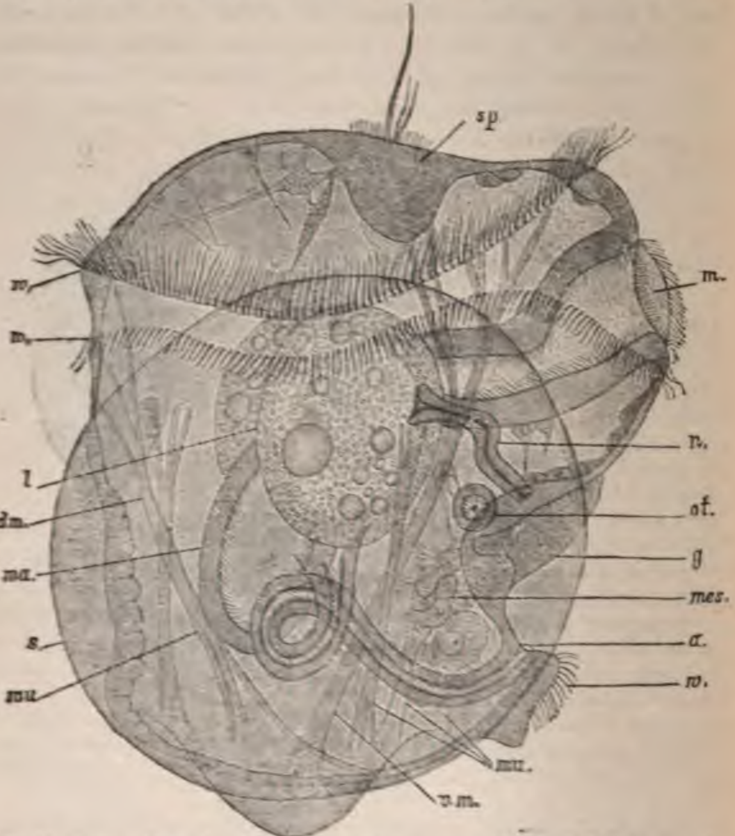

FIG. 18.—Larva of *Teredo* (after HATSCHEK). *a*, anus; *dm*, dorsal retractor muscle; *g*, ventral (pedal) ganglion; *l*, liver; *m*, mouth; *ma*, stomach; *mes*, mesoderm; *mu*, retractor muscles; *n*, head-kidney; *ot*, otocysts; *s*, shell; *sp*, neural plate; *vm*, ventral retractor muscle; *w*, post-anal ciliated tuft; w_{i}, pre-oral, w_{ii}, post-oral ciliated ring.

In the Annelidan *Trochophore*, a nerve-ring is found beneath the pre-oral ciliated ring (Vol. I., p. 266). Such a nerve-ring is, as far as we know, not yet demonstrated in the Lamellibranch larva, but, considering the great agreement in other respects between the two larval forms, it is very probable that it is present.

Besides the neural plate, there is, according to **HATSCHEK**, in the larva of *Teredo*, another constituent part of the nervous system, *viz.*, the rudiment of the ventral, sub-oesophageal ganglion, lying as a large ectodermal thickening between the mouth and the anus (Fig. 18, *g*); this becomes the *pedal ganglion* of the Mollusca. Commissures between the two central organs of the nervous system which would make the comparison with the supra-oesophageal ganglion and the chain of ventral ganglia of the Annelida still more striking, have not been found at this stage (**HATSCHEK**).

On either side of the ventral ganglionic mass, the otocysts arise as small ectodermal invaginations in the same position as in the Annelidan *Trochophore* (Fig. 118 *B*, p. 265). Fine hairs are attached to their walls, and in the centre of each is a strongly refractive round otolith (Fig. 18, *ot*).*

The eye-spots with lenses embedded in them, which **LOVÉN** observed in a few pelagic Lamellibranch larvae (*e.g.*, *Mytilus*), apparently arise at a later stage of development, *i.e.*, after the larva has passed out of the actual *Trochophore* stage. They then lie near the oesophagus, and thus behind the pre-oral ciliated ring, and cannot therefore be compared with the eyes of the Annelidan larva which lie on the cephalic area, *i.e.*, in front of the pre-oral ciliated ring.

[**PELSENEER** (No. IV.) has recently discovered that these eyes are retained in the adult *Mytilidae* and in *Arvicula*, where they are situated at the base and under cover of the anterior filament of the internal branchial lamella; they are innervated from the brain. They are not homologous with the larval eyes of the Gastropoda, which occur on the velum, and are therefore true cephalic eyes, but are possibly homologous with the larval eyes of *Chiton* (p. 14).]

The oesophagus and the base of the intestine of *Teredo* arose, as has already been mentioned, as ectodermal invaginations (Fig. 15 *A* and *C*). Before they both become finally connected with the enteron, the latter assumes a sac-like shape, through the active

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* [Although arising near the pedal ganglia, the otocysts are innervated from the cerebral ganglia, as in the Gastropoda. This primitive condition is still to be seen in *Nucula* and its allies, where also the otocysts retain, even in the adult, their connection with the exterior by a long canal opening on the surface of the foot. In other forms the nerve of the otocyst is bound up with the cerebro-pedal commissure so as to be indistinguishable in the adult.—ED.]

growth and division of the large entoderm cells, which until now have remained only slightly differentiated. These cells are, in *Teredo*, retained in this primitive condition for a very long time (Fig. 15 *B*): it is evident that they contain, stored up in them, a rich supply of nutritive material, which is gradually used up in the formation of the larval body; the presence of this food renders an early development of the intestine, such as takes place in *Ostrea*, unnecessary (Fig. 14). At first the intestine makes but a simple bend, and seems to resemble in shape that of the Annelidan *Trochophore*, but soon, as a consequence of its elongation, it forms several coils (Fig. 18).

We have, so far, left out of consideration the primitive mesoderm-rudiment and its derivatives, which are, nevertheless, of great importance. According to **Rabl** and **Hatschek**, the symmetrically arranged mesoderm-bands run forward from the two primitive mesoderm-cells [mesodermal teloblasts] which at first lie near the blastopore and afterwards (ventrally) at the sides of the anus. The constituents of these mesoderm-bands are, as in the Annelida, yielded by the division of the primitive mesoderm-cells, which long retain unchanged the character of the blastomeres (Fig. 15). The mesoderm-bands of the Lamellibranchia do not appear so distinct or so highly developed as those of the Annelida, since, from an early period, cells bud off from the main mass of the mesoderm which become distributed in the primary body-cavity.* These give rise to the muscles of the larva; the originally round cells lengthen, send out processes, and, finally, by assuming a fibrous structure, produce the fibres of the retractor muscles (Figs. 15 *C*, and 18). The retractors of the velum which run from the posterior part of the shell to the cephalic area form first. Then several shorter muscles are added, also running from the inner surface of the shell in the region of the hinge, and finding points of insertion in the post-oral region of the body (Fig. 18). These muscles seem to serve chiefly for closing the shell (**Hatschek**), but this function is carried out principally by the muscles which, soon forming from long mesoderm-cells, traverse the body-cavity dorsally to the intestine, running from one shell-valve to the other. This shell-adductor appears very early in the larvae of many Lamellibranchs (Fig. 16, *sm*).

* [According to **Lillie** (No. III.), this larval mesoderm has in *Unio* an origin quite distinct from the mesodermal teloblasts which form the mesoderm-bands. The larval mesoderm has more the character of a mesenchyme, and is situated in front of the blastopore, whereas the mesodermal teloblasts are situated behind the blastopore; the former gives origin to the larval muscles. The position of the larval and adult mesoderm is well seen in Figs. 22 and 23 *A*.—**Ed.**]

Quite near the mesoderm-bands, at their anterior end, an organ is developed which makes the comparison of the Lamellibranch *Trochophore* with the Annelidan larva almost complete, *viz.*, the *larval* or *head-kidney*. According to the observations of HATSCHEK, who first discovered this organ, it is a long tubular structure with a narrow cavity (Fig. 18 *n*). In later stages it lengthens further; its external end becomes applied to the ectoderm and opens on to the exterior through a fine aperture. Its cavity is lined with fine cilia directed outwards, and its inner end seems to widen out like a funnel towards the body-cavity. This organ, which was also observed by ZIEGLER in *Cyclas*, thus possesses all the peculiar characteristics of the head-kidney found in the Annelidan larva. The same primitive excretory organ is also found in the *Trochophore* of the Gastropoda (p. 136).

HATSCHEK thinks it probable that, in *Teredo*, the canal of the larval kidney communicates with the body-cavity, but ZIEGLER was not able to convince himself that this is the case in *Cyclas*. In the latter, the inner end of the canal is lost in a mass of mesoderm-cells. ZIEGLER assumes that the canal is formed of large perforated cells such as occur in this organ in the Gastropoda.*

B. The Trochophore stage of Fresh-water Lamellibranchia.

Among the fresh-water Lamellibranchs, as has already been pointed out (p. 30), only *Dreissensia* has a free-swimming larva, which, indeed, exhibits exactly the same characteristics as are found in the *Trochophore* and later stages of the marine Lamellibranchia. For this reason, the larva of *Dreissensia* has already been considered in the previous section (Fig. 17, p. 35). A special resemblance exists between the larvae of *Dreissensia* and those of *Mytilus* as described by WILSON (No. 59).

The conditions found in *Dreissensia* form an interesting contrast to those met with in other fresh-water Molluscs and to those of fresh-water Annelida, Turbellaria and Hydrozoa, since all these forms have lost the free-swimming larva. This is explained on the belief that *Dreissensia*, which is a near relation of *Mytilus*, has migrated from the sea into fresh-water only at a recent date, and has consequently retained the free-swimming larva together with other characteristics of a marine form, v. MARTENS (No. 34).

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*[The recent observations of MEISSENHEIMER (App. Lit. Gastropoda, No. XVIII.) on the head-kidney of *Limax* tend to show that there is no communication between the lumen of this organ and the body-cavity. On the other hand, STAUFFACHER (No. VII.) maintains that, in *Cyclas*, this organ does communicate with the primary schizocoele.—ED.]

The other fresh-water Lamellibranchs show the *Trochophore* form merely as one of the stages of their embryonic development, and in them, as compared with the marine Lamellibranchia, it has greatly degenerated. The fact that this degeneration has taken place is made clear by the complicated form of the alimentary canal. In *Cyclas* and *Pisidium*, as well as in the *Unionidae*, the blastopore closes; the ectoderm then becomes separated from the archenteron, so that there is now an entirely closed entoderm-sac. This latter only becomes connected again with the ectoderm at a later stage. This takes place first through the stomodaeal invagination, whose relation to the blastopore, in consequence of the entire obliteration of the latter, has not been ascertained, and then through the formation of the proctodaeum.[*] When the entoderm-sac thus becomes connected with the ectoderm at two points, the rudiment of the alimentary canal is formed. This latter is probably composed of the same constituent parts as that of the *Trochophore*, although its formation has been less direct.

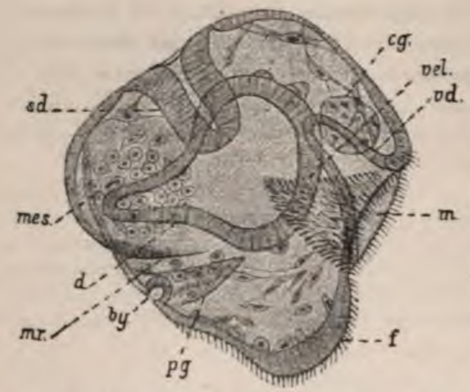

Fig. 19.—Embryo of *Cyclas cornea* at the *Trochophore* stage (combined from E. Ziegler's figures); *by*, byssus; *cg*, cerebral ganglion; *d*, enteron; *f*, foot; *m*, mouth; *mes*, mesoderm; *mr*, rudiment of the mantle; *pg*, pedal ganglion; *sd*, shell-gland; *vd*, stomodaeum; *vel*, velar area.

The velum, that specially important organ of the Lamellibranch larva, is very much reduced in those forms which do not swim about freely at the *Trochophore* stage. In *Cyclas*, all that remains of the ciliated apparatus of the *Trochophore* is a small ciliated area extending above and below the mouth and at its sides. Ziegler has homologised this ciliated area with the adoral ciliated zone of the *Trochophore*, and believes that the part of the velum connected with feeding is partly retained while the part chiefly connected with locomotion and which was no longer used has completely disappeared. The reduction of the velum has led to a corresponding reduction of the larval muscles.

It has already been mentioned that the larval kidney is found in *Cyclas*. Of the other Trochophoral organs, Ziegler was only able

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[*] The statements that the blastopore becomes directly transformed into the anus (as in *Pisidium*, Ray Lankester) require confirmation, since the more primitive Lamellibranchia show an entirely different relationship (p. 31). Ziegler's account of the processes in *Cyclas*, indeed, seems to show that the anus arises at the posterior end of the slit-like blastopore which has already closed. A proctodaeal invagination seems in any case to be absent in this form.

to demonstrate the presence of the mesoderm-bands, the shell-gland and the neural plate.

The organisation of the embryos of fresh-water Lamellibranchs just described renders it indisputable that they represent the *Trochophore* stage. As in *Cyclas*, so in *Pisidium* this point can be proved; in the *Unionidæ*, indeed, the modification has been greater, and it is therefore very difficult to recognise in them the organisation of the *Trochophore*. Even here, however, there is a remains of the ciliated apparatus (Figs. 22-24, p. 53) which causes the well-known rotation of the embryo within the egg-integument, but this ciliated area, according to the definite accounts of SCHIERHOLZ, SCHMIDT and GOETTE, does not lie anteriorly, but in the posterior part of the body, so that it cannot here be considered as a vestige of the velum, as some have attempted to maintain, but rather as corresponding to the ciliated anal tuft.

4. The Transformation into the Adult.

It will be seen from the foregoing account that the presence of a free-swimming larva is to be regarded as an indication of a primitive condition in the Lamellibranchia. We should consequently expect to find in those forms that possess this ontogenetic stage that the changes which bring about the transformation of this free larva into the adult would also be of a primitive character. But, unfortunately, the whole of the further development is not known in the case of any marine Lamellibranch, so that we are obliged to confine ourselves chiefly to the fresh-water Lamellibranchia in discussing this subject, although, as we have seen, we must, for the most part, regard them as modified forms. In *Cyclas*, however, among the latter, the *Trochophore* stage is distinctly developed, and we are therefore perhaps justified in assuming that the process of metamorphosis has, in this case, not undergone any very great modification. For purposes of comparison, we shall avail ourselves of the few data which have been obtained relating to the development of the marine Lamellibranchs.

The mantle develops as early as the *Trochophore* stage in the marine Lamellibranchia, and, with the shell, surrounds a large part of the body. On each side, the mantle-folds are separated by a narrow but deep fissure-like cavity from the keel-shaped body (*Teredo*). The foot is not to be seen at this stage (Fig. 18); it arises at a later stage as a hollow outgrowth of the ectoderm into which a great mass of mesoderm-cells find their way. The gills arise in its neighbourhood either as two ectodermal ridges one on either side of the body at the point where the inner lamella of the mantle-fold is continuous with the body-epithelium (*Teredo* and *Cyclas*), or else at the same spot as a single row of papillae (*Mytilus*, *Dreissensia* and the *Unionidae*, and, according to JACKSON, in *Ostrea*).

Fig. 20.—Older larva of *Dreissensia polymorpha* (original). *f*, foot; *m*, mouth; *s*, shell; *v*, velum.

In those stages of *Cyclas* and *Pisidium* which must be regarded as the equivalents of the *Trochophore*, the foot has already attained a considerable size. It occupies the whole of the ventral surface between the mouth and anus in the form of a massive projection of the ectoderm (Fig. 19 *f*). At a later stage it extends in length and, in form and position, shows the same relation to the rest of the body as it does in the adult (Fig. 21).

In the free-swimming larva, the foot is already of considerable size. Although at first merely a truncated structure projecting only slightly below the shell, it soon grows in length, and can be protruded far beyond the shell when it appears to make vermiform movements and to function as a tactile organ (Fig. 20).

At this stage, therefore, the larva, besides its provisional locomotory organ, the velum, also possesses the locomotory organ of the adult Lamellibranch. Further, the foot usually, as far as we can judge from *Dreissensia*, is retracted while the larva (which is still very active) swims about; in this respect Fig. 20, which depicts the foot as extended in a larva with an expanded velum, is not quite true to nature. Such a condition does, however, occasionally occur when a larva has just extended the velum and is beginning to retract the foot which was protruded beyond the shell as a sensory organ.

The surface of the foot, at the *Trochophore* stage as well as later, is covered with fine cilia. At the posterior upper boundary of this ciliated area, in *Cyclas*, a pit-like depression of the ectoderm is found on each side of the middle line, lying exactly above the mass of cells from which the pedal ganglion develops (Figs. 19 and 21). This is the paired rudiment of the byssal gland.

These two depressions together with the whole of the ectoderm lying between them soon sink in deeper, having then only one common aperture; their epithelium becomes modified into glandular cells which secrete the well-known byssal threads that serve for the attachment of the embryo or young Lamellibranch (Fig. 21, *by*). As the body grows further, the paired rudiment of the byssal gland is drawn further and further inward, and finally opens out through a long duct with a narrow aperture. This gland degenerates later (in *Cyclas*), and in the adult is a mere sac-like vestige. In other Lamellibranchs, on the contrary, as is well known, it functions throughout life and is very highly developed (*cf.* p. 59).

In *Entovalva*, discovered by VOELTZKOW (No. 57) living in the intestinal canal of *Synapta*, at the posterior margin of the keel-shaped foot, a similar structure was found, which is brought into use as the Lamellibranch moves forward and attaches itself. From its position, it might well correspond to the modified byssal gland but this requires further investigation. In *Gastrochaena*, a Lamellibranch that inhabits a calcareous tube, there is an attaching apparatus in the foot consisting of ectodermal depressions surrounded by glandular cells; the secretion of the latter serves for attaching the broad sole of the foot to the inner surface of the tube, but is said not to correspond to the byssus which, according to SLUITER (No. 53), completely degenerates in this animal. In *Entovalva*, the foot attains a very high degree of development and the mantle grows over the shell (as also in *Gastrochaena*, *cf.* p. 62); in other ways the development of this parasitic Lamellibranch is not peculiar. It shows typical *Trochophore* larvae, which develop in a brood-cavity formed by the mantle; they pass thence into the intestine of the Holothurian host, reach the exterior with its excrement, and there develop further (no doubt in the usual way). Not until fairly well developed do these young Lamellibranchs enter the mouth of a Holothurian and pass into the oesophagus.

At the time when the external form of the foot is already well developed, the ad-oral ciliated area, which has been referred to the ciliation of the *Trochophore*, is still retained (Fig. 21 *A* and *B*); the shell, on the other hand, undergoes a decided transformation which brings it nearer its adult form. According to ZIEGLER, whose account we here follow so far as concerns *Cyclas*, an accumulation of small calcareous concretions can be seen on each side of the dorsal middle line beneath the unpaired cuticular integument (Fig. 21 *A*, *s*). These masses increase and soon take the form of the definitive shell (Fig. 21 *B*, *s*). There is now a shell-plate on each side; the two, however, are not in contact, but are somewhat far removed from the middle line. A band-like thickening of the cuticular shell-integument then develops in this interspace, connecting the dorsal margins of the two shell-valves just below the umbones; this represents the ligament.

Before the formation of the shell has advanced thus far, the mantle has already begun to form. At the two sides of and above the anus an outgrowth of the ectoderm arises (Fig. 19 *mr*), forming a fold which extends anteriorly and posteriorly over the body (Fig. 21 *A*, *mr*).

As in *Teredo* (p. 34), the mantle extends with the shell from the dorsal to the ventral side. The outer lamella of the mantle is closely applied to the shell, while its inner lamella bounds the mantle-cavity which has arisen with the growth of the mantle. As the shell grows the mantle also increases more and more in size, and the two now enclose a large part of the body (Figs. 21 *B*, and 31, p. 75).

The siphons, where found, appear to develop at a very late stage. They are formed from the edges of the mantle, which become closely applied and fuse, the parts destined to form siphons then growing out into long, tubular structures.

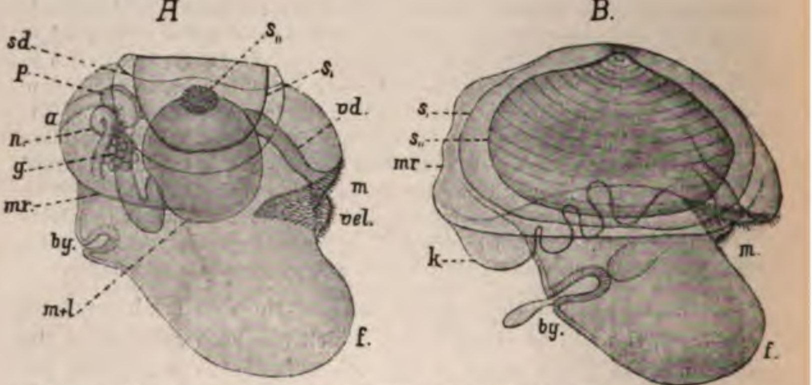

FIG. 21.—*A* and *B*, embryos of *Cyclas cornea* (after ZIEGLER). *a*, anus; *by*, byssus; *f*, foot; *g*, genital rudiment; *k*, gill; *m*, mouth; *m+l*, stomach and liver; *mr*, edge of the mantle; *n*, kidney; *p*, pericardium; $s_{,}$, unpaired shell-plate; $s_{,,}$, rudiment of the right calcareous shell-valve; *sd*, shell-gland; *vd*, stomodaeum; *vel*, velar area.

Within the mantle-cavity another ectodermal fold appears on either side of the body, developing from behind forward like the mantle itself. This paired fold is the first rudiment of the gills (Fig. 21 *B*, *k*), which arise in the same way in *Teredo*. The branchial fold is covered by fine cilia. Thus, in *Cyclas* and *Teredo*, the earliest gill-rudiment exhibits the form of a plate, and at first shows no indication of the slits and bars so characteristic of the adult. The further differentiation of the gills, resulting in the formation of the gill-slits and filaments, takes place from the anterior end of the fold. Starting from the lower free edge, a series of vertically placed parallel grooves make their appearance on the outer surface of the gill-plate, and a corresponding series also appears on the inner side of the fold.

These grooves deepen until individual members of the outer series meet and fuse with the corresponding grooves of the inner series. Perforation takes place along this line of fusion, and in this way gill-slits arise which lie vertically to the longitudinal axis of the branchial lamella. As the grooves start from the extreme ventral edge, the slit is open below, and the branchial plate becomes broken up into filaments (Fig. 21 *B*).

We have here described the way in which the gills arise in the two Lamellibranchs whose ontogeny happens to be best understood, but this description does not apply to all Lamellibranchs ; indeed, it is even probable that the condition described above is a specialised one. Thus, in various Lamellibranchs which possess a typical *Trochophore* larva, *e.g.*, *Mytilus*, *Dreissensia* and *Ostrea*, the gills arise as a row of papillae consecutively arranged, which become subsequently connected together to form the gill-lamellae. The formative processes which take place in these cases will be detailed below (p. 68).

[A third method which occurs in *Scioberetia* (BERNARD, No. I.) and *Pholas* (SINGERFOOS, No. V.) somewhat resembles that seen in *Cyclas* and *Teredo*. As in the latter, a gill-plate first appears, but the gill-slits do not at first extend to the ventral edge of the fold, consequently, perfectly distinct gill-filaments are not formed, but only gill-bars alternating with slits, the gill-plate retaining its original continuity below the slits.]

In connection with the external form of the Lamellibranchia we have still to mention the *labial palps* (*oral lobes*). These, in the adult, are divided into an upper (anterior) and a lower (posterior) pair. In *Cyclas*, according to ZIEGLER, they arise in the following manner. The ciliated area surrounding the mouth becomes divided into an upper and a lower portion by a groove which runs out on either side from the angle of the mouth. The first of these must be reckoned as the upper and the second as the lower lip. These two areas by further growth give rise to the labial palps. At the time when the mantle grows down over the upper lip, a median depression appears in the latter, and a similar depression is to be found in the lower lip, each of the lips being thus divided into two lateral portions. These now begin to grow out as folds, and develop into the labial palps.

[In most Lamellibranchs the two halves of the upper and lower lips are connected by bridges above and below the mouth, the division into right and left palps being more apparent than real. This condition appears to be brought about by the stronger growth of the lateral parts of these structures.]

This origin of the labial palps partly confirms the assumption made by LOVÉN that the velum of the larva may pass over directly into the adult palps. In the double nature of this organ LOVÉN finds agreement with the double velum of the Gastropoda, a resemblance which is strengthened by ZIEGLER'S observation of the median division of the ciliated area of *Cyclas*. The small section of the ciliated area lying above the mouth might then be regarded as the last vestige of the former ciliated ring of the *Trochophore*. The ciliated area of *Cyclas*, however, as we have just shown, seems rather to correspond to the ad-oral ciliation of the larva (p. 40). And since this serves for feeding more than for locomotion we see that a part of the larval body passes over into a similarly functioning organ of the adult animal. The significance of the labial palps lies principally in their relation to the capture of food, in which they assist through their position and their ciliation (THIELE, No. 55). An exact knowledge of the fate of the entire velum, *i.e.*, of the pre-oral ciliated portion of the body in a marine Lamellibranch, would be of great value.

The metamorphosis of the Lamellibranch larva into the adult is characterised chiefly by the complete degeneration of the pre-oral part of the body which was so large in the former. In the larva, the highly developed velum spreads out between the mouth and the shell (Figs. 15-18, pp. 31-36 and Fig. 19, p. 40), but, as development proceeds, this area becomes contracted (Fig. 21 *A*), and finally almost entirely disappears, in keeping with the condition of the adult, in which the cephalic region is almost completely lost.

While the external changes of form just described have been taking place in the embryo, a marked advance has also taken place in the inner organisation, but this will be entered into later on. The young of *Cyclas* and *Pisidium* leave the mother only when they possess, on the whole, the same organisation as the adult.

Divergencies in the Metamorphosis accompanying the Monomyarian Condition.

Among those forms classed by the older malacologists as the Monomyaria, the transition from the larva to the adult has only been well investigated in *Ostrea*, and their development, judging from this form, seems up to a certain point to agree closely with that of other marine Lamellibranchia. We have already seen how close the agreement is in the early stages of development (p. 28 Fig. 14 and Fig. 16, p. 33). The *Trochophore* larva already possesses an adductor muscle (Fig. 16, *sm*), formed from elongate mesoderm-cells which become arranged side by side and attached to the two valves of the shell. This adductor in *Ostrea* lies dorsally to the alimentary canal, and thus corresponds in position to the anterior adductor of the Dimyarian forms, which also lies dorsally to the oesophagus (Fig. 31, *vsm*, p. 75). The adductor in the adult Monomyarian, however, lies ventrally to the intestine (Fig. 31, *hsm*); it thus occupies the same position as the posterior muscle in the Dimyaria, and is undoubtedly to be homologised with this latter. The adductor of the larval oyster therefore cannot be the same as that of the adult. This difference, which has been emphasised by several investigators (HUXLEY, HORST, etc.), is explained by the study of the later development (JACKSON, Nos. 22 and 23.)

A larval stage in which only one adductor muscle (the anterior) is present, or in which the anterior adductor is better developed than the posterior adductor, which is only in the act of appearing, is met with in a large number of Lamellibranchs, *e.g.*, *Cardium*, *Montacuta*, *Modiolaria*, *Mytilus*, *Dreissensia*, *Pisidium*. In the *Unionidae* also the anterior adductor seems to appear first, as, indeed, is the case in nearly all the Lamellibranchs as yet investigated in this respect.

In *Cyclas*, on the contrary, according to ZIEGLER, the posterior adductor develops before the anterior, but it has already been pointed out that in the related form, *Pisidium*, the anterior appears first. LACAZE-DUTHIERS (No. 28) maintained that the posterior adductor develops first in *Mytilus*, but this is due to the fact that the larval stages examined by this author as well as by LOVÉN (No. 33) were too old. According to WILSON (No. 59), in the young *Mytilus* larva the anterior adductor develops earlier than the posterior, and this is also the case in the nearly related form *Dreissensia* (KORSCHELT, No. 27).

After the anterior adductor has appeared in *Ostrea*, a posterior adductor lying ventrally to the intestine arises in the same manner as in the Lamellibranchs mentioned above (JACKSON). *Ostrea*, and no doubt the other Monomyaria as well, possess for a time two adductors (an anterior and a posterior) of almost equal strength, and thus resemble the Dimyaria. Only as the anterior of these two muscles degenerates does *Ostrea* assume a Monomyarian condition.

Even if the Lamellibranch larvae do for a time possess only one adductor, we have no right to speak, as has often been done, of a Monomyarian stage, and to consider the permanent condition of the Monomyaria as having arisen through an arrest of development in this direction, *i.e.*, through the defective development of a second muscle. The Dimyaria hence do not pass through a Monomyarian stage in the proper sense of the term, but the

Monomyaria probably invariably possess in youth the two typical adductors of the Dimyarian.

[The fact that the anterior adductor almost invariably appears before the posterior, not only in the Dimyaria, but also in the Monomyaria, in which latter group it is only a larval structure, might seem to suggest that this muscle was a phylogenetically older structure than the posterior adductor, and that the Lamellibranchia were originally Monomyarians, not, like the existing Monomyaria, with a single muscle represented by the posterior adductor, but with the anterior adductor alone developed (JACKSON). Palaeontology does not, however, bear out this view; the oldest known Lamellibranchs found in the Cambrian belong to the *Nuculidae* and *Arcidae*, which are typically Dimyarian.]

The young of *Ostrea* agrees, not only in the possession of two adductors, but also in other points of its organisation, with the larvae of other Lamellibranchs, but at a later stage it changes from a free to an attached manner of life.

The larva, which has hitherto swum about freely, possessing two quite symmetrical shell-valves and two adductor muscles, attaches itself by means of a secretion produced by the left lobe of its mantle; the latter stretches beyond its valve, and, applying itself to the stone or shell to which the valve is to adhere, secretes shelly matter which serves to cement the valve to its support (HUXLEY, RYDER). In the further development, we now from this time find an inclination to that radial symmetry which can be recognised in the adult Oyster, and which is often found in animals that assume an attached manner of life. The anterior adductor now degenerates and the only remaining adductor muscle (the posterior adductor) enlarges and shifts almost to the centre of the animal. The anterior part of the body gradually rotates (round its vertical axis)* through an angle of about 90°, so that the mouth, which at first lay very near the free edge of the shell, comes to lie near the umbo. This rotation also explains the great and almost circular extension of the gills and the mantle found in the adult. The condition of the foot in the Lamellibranchia depends largely upon its use or disuse. In *Ostrea*, the shell becomes permanently attached at the close of the free-swimming *Trochophore* stage; the foot is therefore unnecessary before fixation

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* [Vertical in relation to the substratum, the true transverse axis of the animal. This rotation is possibly due in large measure to the degeneration of the anterior adductor muscle and of the velum.—ED.]

and useless afterwards, and has almost entirely disappeared from even the embryonic stages of growth (JACKSON). In *Pecten*,* another Myomyarian, on the contrary, the foot is very well developed in the nepionic period, and serves as a locomotory organ; during metamorphosis it becomes considerably reduced though, with its byssal gland, it is still present in the adult, but no longer serves as a locomotory organ, since the animal now swims by clapping its shell-valves together. In other Lamellibranchs also, *viz.*, those forms which spend the greater part of their life attached to some foreign body, *e.g.*, *Dreissensia polymorpha*, the foot which, at first, is very large (Fig. 20, p. 42), becomes very much reduced in size as the animal develops. After the velum has degenerated and before attachment, *Dreissensia* passes through a stage in which it creeps about very actively with the help of its foot (No. 27). This form at a later stage also occasionally moves about, but, in consequence of the great reduction of the foot, its movements are very slow (No. 58).

[In those Lamellibranchs which, in the adult stage, lead a fixed life, attached by means of a *byssus* to the substratum, the portion of the foot carrying the byssal gland is retained, although the locomotory function of the foot may be completely lost, *e.g.*, *Anomia*. In *Ostrea*, where the attachment is brought about by a secretion of the left mantle-lobe, all trace of the foot is lost in the adult.]

5. The Development of the Unionidae.

The development of the *Unionidae* differs so essentially from that of the other Lamellibranchia that, except with regard to the cleavage of the egg, it must be treated separately. It has evidently undergone radical modification through change of the external conditions of life, and the whole of its later development is no doubt influenced by the assumption of a temporary parasitism by the young or larvae, which become attached to the gills or to the integument of fishes. We thus find, in the *Unionidae*, superadded to the normal course of development, as observed in the marine Lamellibranchs, an additional and unique larval form which cannot be compared with the larva of the latter, and which possesses characters not present in the adult.

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* The development of *Pecten* has been investigated by FULLARTON, from whose treatise, which is illustrated by four plates (No. 14), we gather that this form develops exactly like other marine Lamellibranchs up to the later larval stages. The transformation of the larva into the adult was not observed.

The ontogeny of the *Unionidae* has been studied by a number of zoologists. **Flemming**, **Rabl**, **Goette** and **Schierholz** have investigated their embryonic development, while the later stages of their development, which were examined by **Forel** (No. 13), **Leydig** (No. 32), **Braun** (Nos. 4 and 5), **Balfour**, **F. Schmidt** (No. 50) and others, have recently been reinvestigated by **Schierholz** and **Goette**.

[Still more recently, **Lillie** (No. III.) has reinvestigated the entire course of development in *Unio complanata*, paying special attention, however, to the cell-lineage.]

A. Development of the Early Stage.

It has already been mentioned that the *Unionidae* show an invagination-gastrula (p. 27, etc.) and that, before the latter develops, large mesoderm-cells bud off from the wall of the blastula and enter the cleavage-cavity. Before the formation of the very insignificant archenteron which, like that of other Lamellibranchs, is derived from the macromeres resulting from the unequal cleavage, a depression appears on the blastula and deepens more and more (Fig. 22, *sd*). This depression is formed by large cells which are granular and therefore appear dark, and its whole form is such that we can easily understand why it was long mistaken for the archenteron (p. 27). This depression, however, does not occur on the ventral side of the embryo, but upon its dorsal surface; it gradually flattens out again and above it the shell-integument appears (Figs. 23 *A*-*C*, 24 *A*). This structure is therefore, as **Goette** proved, the shell-gland.*

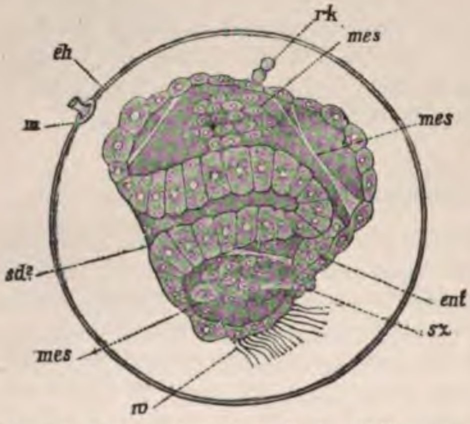

Fig. 22.—Embryo of *Anodonta* in the vitelline membrane (after **Schierholz**); *ent*, entoderm-rudiment (archenteron); *eh*, vitelline membrane; *m*, micropyle; *mes*, mesoderm-cells, some of which have turned into muscle-cells; *rk*, polar bodies; *sd*, shell-gland; *sz*, lateral cells; *w*, posterior ciliated area [ventral plate].

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* [According to **Lillie** (No. III.) the entomeres which eventually become invaginated to form the archenteron are derived from all the four cleavage-

The shell forms in exactly the same way as in the marine Lamellibranchs (Figs. 14, p. 28, and 15, p. 31) and in *Cyclas* (Fig. 19, p. 40), except that the shell-gland is specially large and appears very early. This early development of the shell, as suggested by GOETTE, is probably due to the great importance of the shell to the larva in its free life which we shall discuss later, and, in the same way, we may explain the degeneration of the intestine by the parasitic life of the larva, in consequence of which the intestine is not required to fulfil its ordinary functions until a late stage.

In spite of the highly modified character of the larvae of the *Unionidae*, we are able to make a comparison between their organs and those of the typical *Trochophore* larva. Apart from the entodermal and mesodermal parts which have already been mentioned (pp. 27 and 28), the most striking feature is the ciliated area (Figs. 22-24, *w*), which is evidently the last vestige of the ciliation of the free-swimming larva. This ciliated area, termed the ventral plate, does not, as was at first supposed, correspond to a remains of the velum, but represents the whole ventral surface plus the posterior end of the body, and is therefore rather to be compared with the ventral ciliation or with the anal ciliated area of the *Trochophore*

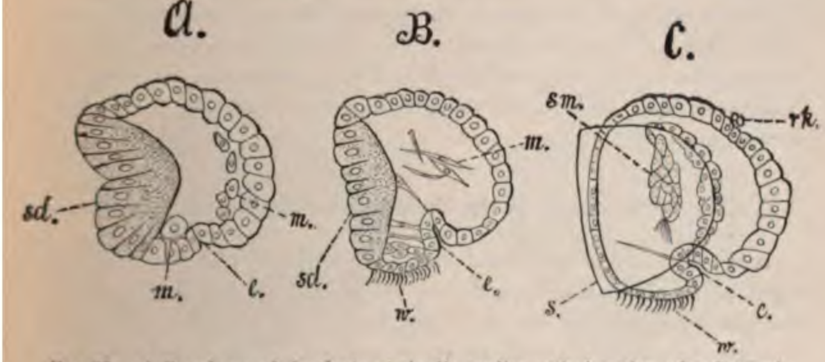

FIG. 23.—*A*-*C*, embryos of *Anodonta piscinalis*, median optical section (after GOETTE); *e*, entoderm-rudiment (archenteron); *m*, mesoderm; *rk*, polar bodies; *s*, shell; *sd*, shell-gland; *sm*, adductor muscle; *w*, posterior ciliated area [ventral plate].

spheres resulting from the first two divisions, that is to say, neither the first nor the second cleavage-plane divides the egg into an animal cell and a vegetative cell as stated by RABL. LILLIE further finds that the small archenteron is formed before the invagination of the shell-gland, which latter, however, soon eclipses the former. Of the two groups of mesoderm-cells represented in Figs. 22 and 23 *A*, those above the shell-gland would correspond with LILLIE's larval mesenchyme, while those below this structure and behind the blastopore, *e.g.*, the large cell in Fig. 23 *A*, represent the adult mesoderm which forms teloblastically from the pair of mesoderm-cells. For more detailed figures see LILLIE's paper.—ED.]

larva (Figs. 15 and 18). The broad part of the body in the embryo of *Anodonta* which lies in front of the shell and of the entodermal vesicle would correspond to the velum, *i.e.*, to the pre-oral part of the *Trochophore*. In the younger embryo depicted in Fig. 22, this part appears to be formed solely by a somewhat thin layer of cells, while, in the embryo represented in Fig. 24 *A*, it has a thick wall, consisting of cells containing vacuoles such as ZIEGLER has described in the reduced velum of *Cyclas*. The shape of this part of the embryo recalls the swollen pre-oral portion or *cephalic vesicle* of the Gastropodan embryos, a condition still more marked in them than in *Cyclas*, as ZIEGLER pointed out. [LILLIE also regards this area as the head-vesicle].

In this region of the embryo, the polar bodies are occasionally met with (Figs. 22 and 23 *C*) and these afford an indication for the correct orientation of the embryo which is not otherwise very easy to determine, and which was usually misinterpreted by the earlier investigators.

B. The Development of the Embryo into the Parasitic Larva.

It is evident from the above that the peculiarities in the development of the *Unionidae* appear very early and affect both the inner and the outer organisation of the embryo. In the stage up to which we have followed its development, it resembles a rounded vesicle of somewhat irregular form consisting of a single layer of ectoderm on the inner side of which there appear here and there single muscle-like cells; these belong to the mesoderm, the cells of which have increased in number, some becoming lengthened (Figs. 23 and 24). In this young embryo, the shell at first lies like a saddle upon the dorsal side (Fig. 23 *C*, and 24, *s*).

The rudiments of the shell-valves appear later beneath the unpaired cuticular shell. The shell probably arises here in the same way as in *Cyclas*; each shell-valve in the *Unionidae* appears to be three-sided and has its ventral point bent like a hook, a modification connected with the manner of life of these forms. The shell carries on its outer surface a number of small hooklets which, together with the two terminal hooks just mentioned, serve for attaching the Lamellibranch to the body of its host during its parasitic life (Figs. 25 and 26, *sh*). Before the shell has developed thus far, a radical transformation of the whole body takes place. The ventral part of the body, which was not previously covered by the shell but projected beyond it (Fig. 24 *B*), now becomes withdrawn or rather invaginated towards the hinge of the shell, *i.e.*, towards the dorsal side (Fig. 25 *A*), and the whole body is thus divided into two halves, each belonging to one of the valves of the shell (Fig. 25 *A* and *B*). The mantle arises in this way and at this stage is remarkably large, greatly preponderating over the rest of the body, which only later redevelops by the outgrowth of the central portion of the body (Fig. 25).

Before the withdrawal of the central portion of the body, four groups of bristles were developed from the ectoderm on either side of the embyro (Fig. 24 *B*, *so*); during the invagination-processes just described these organs lengthen and, in consequence of these changes, are then found on the inner surface of the mantle. Each of these organs consists of a long columnar cell which gives origin to a number of long and fine sensory bristles (at first four to ten in number, later as many as thirty) that perforate the thin ectodermal cuticle (**Flemming**). These sensory organs are apparently of importance to the larva in the process of attaching itself to the fish-host and are acquired at a late embryonic stage.

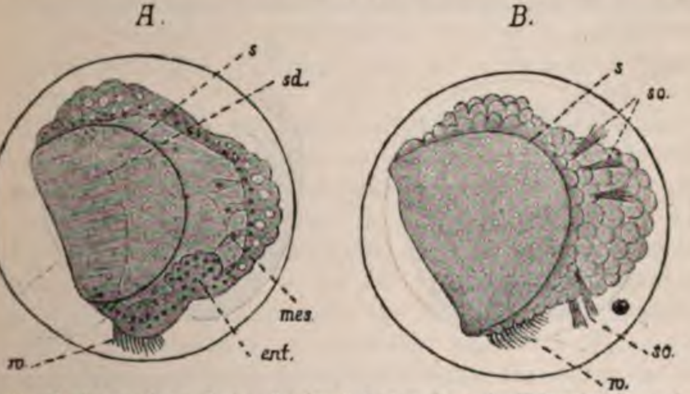

Fig. 24.—Embryos of *Anodonta*. (*A* founded on a figure by **Flemming**, somewhat diagrammatic, *B* after **Schierholz**). *A*, optic section with the outline of the shell superimposed; *B*, superficial view; *ent*, entoderm (archenteric rudiment); *mes*, mesoderm; *s*, unpaired shell; *sd*, shell-gland; *so*, sensory bristles; *w*, ciliated area [ventral plate].

We may accordingly regard these sensory organs as differentiations of the mantle, and can hardly consider them to be related to the velum, as **Schierholz** was led to believe on account of the position of one of them. This particular organ occupies an isolated position and has shifted in front of the oral aperture (Fig. 26 *A*).

These peculiar organs are believed to communicate to the larva the stimulus produced by coming into contact with a fish, and thus to give rise to the muscular movements which cause the shell-valves to close and the larva to become hooked on to the host.

There are a few more important organs to be mentioned in connection with the further development of the larva of the *Unionidae*, the first of these being the powerful adductor muscle of the shell. This arises very early through the increase in number of the mesoderm-cells, which are still only slightly differentiated [larval mesenchyme, LILLIE] (Fig. 23 *C*, *sm*), these cells lengthening and becoming attached to the shell-valves. The short but broad muscle thus passes through the body-cavity from one valve to the other (Fig. 25 *B*, *sm*). Besides this large muscle, there are a number of other weaker muscles in the form of long mesoderm-cells attached in various directions to the ectoderm, like the muscles which, in the *Trochophore*, bring about the contractions of the larval body. SCHIERHOLZ [and LILLIE] ascribe to the continuous contraction of these muscles the withdrawal of the central part of the embryo above mentioned. There are also, according to SCHMIDT, special muscles in the form of modified mantle-cells connected with the shell-hooks.

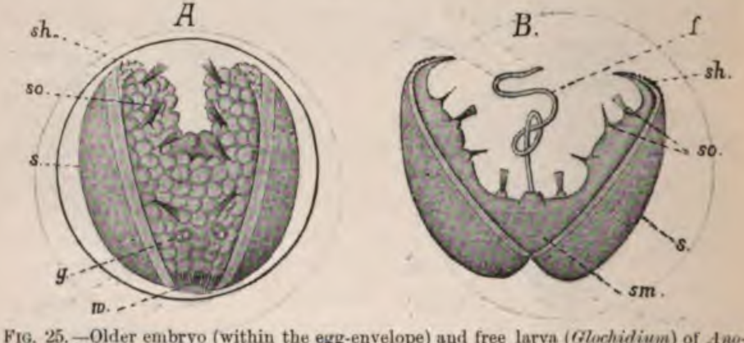

FIG. 25.—Older embryo (within the egg-envelope) and free larva (*Glochidium*) of *Anodonta* (after SCHIERHOLZ and FOREL). *f*, larval filaments; *g*, lateral pits; *s*, shell; *sh*, shell-hooks; *sm*, adductor muscle; *so*, tufts of setae representing the sensory organs; *w*, ciliated area.

A peculiar and characteristic larval organ arises in the median line between the two halves of the mantle as an invagination of the ectoderm (RABL). It grows inwardly as a long glandular tube which coils several times round the adductor of the shell and secretes a filament of tough substance which projects from the aperture of the gland (Figs. 25 *B* and 26 *A*, *f*). This organ has been regarded as a byssal gland corresponding to the homonymous organ of other Lamellibranchs, but this view, in spite of the similar function of the two organs, is not justified, since the two organs do not agree in position, and since two ectodermal invaginations appear later on the foot of the larva which must be considered as the homologues of the byssal gland (CARRIÈRE, F. SCHMIDT, SCHIERHOLZ). The glutinous filament must therefore be regarded as a distinct larval organ.

The position of this filament is very remarkable in so far as it is said to be pre-oral (Fig. 26 *A*). The mouth has been pressed unusually far back and, like the intestinal canal (*d*), now belongs to the small posterior part of the larva. This displacement has been traced to the great development of the adductor muscle (*sm*), but the morphological conditions of this larval stage as compared with the former *Trochophore*-like stage seem to us to require further elucidation.

[LILLIE (No. III.) describes the *thread-gland* as arising from one of the cells of the head-vesicle; this cell elongates and grows backward beneath the hinge-line until it reaches the posterior end of the body. The cell now becomes tubular, the thread occupying the lumen of the gland. LILLIE believes that the thread is formed as an actual metamorphosis of the substance of the cell; he regards this gland as primarily excretory, and thinks that the utilisation of its secretion as an attaching filament was secondarily acquired. During the transformation of the larva into the *Glochidium*, the aperture of the thread-gland undergoes a remarkable change in position, shifting from its former antero-dorsal situation to the middle of the ventral surface.]

Between the brush-like sensory organs and the ciliated area and near the posterior angle of the valves, two ectodermal depressions are to be seen on the embryo; these are the so-called lateral pits, as to the significance of which authors are not very clear. If we rightly understand the somewhat obscure description given by SCHIERHOLZ, he implies that large cells at the base of these pits (no doubt corresponding to the lateral cells of the young embryos) give rise to the pedal ganglia. But since the pedal ganglia, as in *Cyclas*, lie below the depressions which yield the byssal gland, these early-formed pits may be related to the latter (?). In *Cyclas* also the paired rudiment of the byssal gland appears very early (Figs. 19 and 21). Taking these facts into consideration, together with the position of the pits with relation to the foot, it is possible that this interpretation of the lateral pits as the first rudiments of the byssal glands is correct. The formation of the actual byssal gland in *Anodonta*, however, seems to take place at a later stage.

When the embryo has attained the stage of organisation just described, it is ready for ejection from the mother; on coming into free contact with the water, the egg-envelope bursts and the embryo emerges from it. The larva thus set free is known as the *Glochidium*. The embryos found by the older investigators (RATHKE, JACOBSON) in the gills of Lamellibranchs and considered to be parasites were called *Glochidium parasiticum*.

The remarkable fact that the *Glochidia* remain for a time parasitic on fishes was discovered by LEYDIG (No. 32) and then further investigated by BRAUN. F. SCHMIDT and SCHIERHOLZ have recently given a detailed description of what takes place, and we shall here follow chiefly their account. The larvae, when freed from the mother, become connected together in large masses by means of their glutinous filaments, and in this form rest at the bottom of the water, occasionally rotating upwards.* Chance brings them no doubt into contact with fish, and a few of them succeed in attaching themselves to these by the help of their shell-hooks. *Unio* only attaches itself to the gills of fish, but the *Glochidia* of *Anodonta*, which are more richly provided with hooks, may also become attached to the fins and the skin.

The hook-apparatus, according to SCHIERHOLZ, is less developed in *Unio*, and it is an interesting fact that it may be altogether wanting in certain North American *Unionidae* (LEA). The same is the case, according to v. JHERING'S recent observations (No. 25), in the larvae of South American *Unionidae*, which are devoid of the tufts of setae, and perhaps also of the larval filament. In these American *Unionidae*, therefore, the biological conditions seem to differ somewhat from those of the European forms, and it would be interesting to ascertain the conditions of parasitism in the larvae of these Lamellibranchs.† The larval filament and the shell-hooks are wanting in the *Glochidium* of *Anodonta complanata*, although in other respects the organisation of these larvae is the same as that of other *Glochidia*, and they lead a parasitic life (SCHIERHOLZ).

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* [It is often stated that the *Glochidia* are only discharged when fish are in the neighbourhood, but LATTER (Proc. Zool. Soc., 1891) found that he could produce a discharge of *Glochidia* by gently stirring the water in which the Anodons were lying. He also observed cord-like ejection of *Glochidia* from an undisturbed Anodon in its native water. The *Glochidia* cannot swim, but when discharged sink to the bottom, where they lie on their dorsal surfaces, the thread streaming up into the water. In this position the *Glochidium* lies powerless to move in any direction, and here, too, it dies unless a suitable "host" is brought into contact with its thread.—ED.]

† We do not know of any other statements upon this subject, although it is not impossible that such may exist among the mass of malacological literature which is difficult to review; v. JHERING mentions that he found Unionid larvae on fish in South America.

A cyst soon forms from the tissues of the fish and encloses the parasitic *Glochidium*. A peculiar mushroom-like growth formed by large cylindrical cells of the embryonic mantle serves for absorbing the tissues of the host, and especially the fin-rays in which the shell-hooks are embedded. The larva is no doubt nourished in this way until its intestinal canal becomes functional.

The time during which the *Glochidium* remains parasitic on the fish appears to be determined by the favourable or unfavourable conditions of temperature, and varies from a few weeks to several months. SCHIERHOLZ and BRAUN found that the larvae remained seventy-two to seventy-three days on the fish, during which time they develop the definitive form.

The South American relations of our *Anodonta* have larvae differing greatly in shape, so that v. JHERING, who found these larvae within the mantle-cavity of the parent, would have taken them for parasites had not all doubt as to their being Lamellibranchs been removed by the agreement of the egg-envelope and its micropyle with the envelope of the ovarian eggs (No. 25). In these forms the embryos are found in the inner gills, not, as in our native *Unionidae*, in the outer gills. The body in the South American forms is composed of three sections: (1) a conical anterior portion covered with cilia; (2) a large middle portion containing internally the entoderm-elements and two kidney-like structures (byssal glands?); the dorsal side of this region is only partly covered by a delicate shell-integument; (3) the short caudal end, which forks, and consequently terminates in two rounded prominences, beset with bent hook-like setae.

A very peculiar organ possessed by these larvae is a very thin but broad and flat band considered by v. JHERING to be the byssus. This band is almost at the middle of the body and is attached to the ventral surface, from which it runs forward. It is somewhat broader than the body, and six to ten times as long. It is said also to be connected with the anterior part of the body.

According to the somewhat vague account given by v. JHERING of the larva named by him "*Lasidium*," and in the absence of any statements as to the development of this larval form, it is at present impossible to compare it with the entirely different Unionid larvae (*Glochidia*) or with the larvae of other Lamellibranchs.

C. The Transition to the Adult.

Very soon after attachment, as early as the second day, the larval organs which enabled the *Glochidium* to establish itself on its host, *viz.*, the glutinous filament and the brush-like sensory organs, degenerate. A wide pit-like depression of the ventral surface arises behind these organs as they degenerate; this depression involves the two lateral pits already present in the embryo (Fig 26 *A* and *B*, *g*). At this place, the foot now appears as a blunt cone and soon grows rapidly. The wall-like outer margins of the two lateral pits also increase in height. These prominences become the rudiments of the gills which first appear in the form of two knobbed papillae (F. Schimdt).

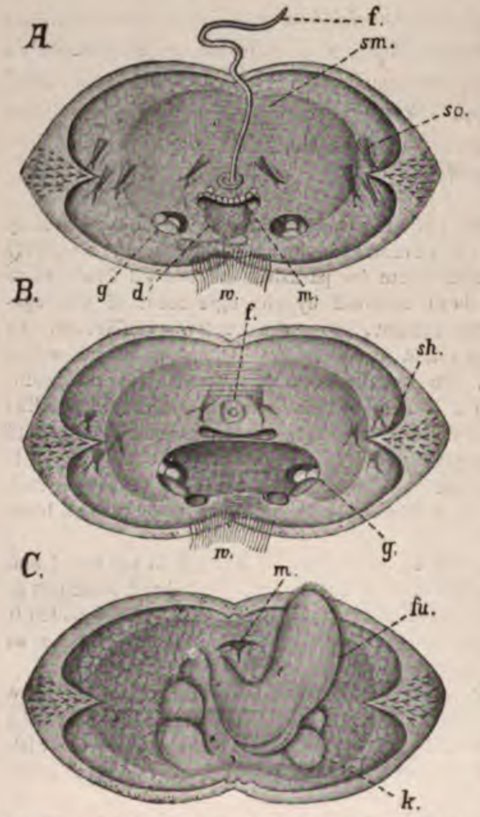

Fig. 26.—*A-C*, larvae of *Anodonta* (after Schierholz). *d*, rudiment of the intestine; *f*, larval filament; *fu*, foot; *g*, lateral pits; *k*, gills; *m*, mouth; *sh*, shell-hooks; *sm*, adductor muscle; *so*, sensory organs; *w*, ventral plate (ciliated area).

Fig. 26 *C* shows the rudiments of the gills at a somewhat later stage. The foot is here found well developed, and both it and the gills are ciliated. The posterior ciliated area of the embryo (*w*), which was still visible when the foot had attained a considerable size, now disappears. Of the larval organs, the shell-hooks and the large adductor muscle are still to be seen. The first are for the present retained, the shell in other respects also retaining its embryonic form until the young Lamellibranch leaves the fish; indeed the embryonic shell can still be made out in the shell of the adult. The longer of the two free sides of the three-sided embryonic shell must be considered to correspond to the anterior end of the animal, and in this position it can actually be found as a small prominence on the umbo of the adult shell (Braun).

The powerful adductor muscle of the larva agrees in position with the anterior adductor of the marine *Trochophore* larva. It is, according to Braun and F. Schimdt, merely a larval organ, and degenerates completely later, so that the two adductors of the adult must be regarded as new formations. In opposition to this view we have the statement of SCHIERHOLZ that the larval muscle only partly degenerates, some of it passing over into the anterior adductor of the adult. This latter condition would agree with the fact that the anterior adductor appears first in most Lamellibranchs, and for a long time is the only adductor present (p. 48); BRAUN, however, has maintained his original view against that of SCHIERHOLZ.

The formation of the intestine is also apparently greatly influenced by the specialised conditions of the larva. The archenteron had already lost its connection with the ectoderm before the commencement of parisitism, and lay in contact with the ectoderm as an entodermal vesicle closed on all sides. In this condition it remains for a very long time; the larva either does not require nourishment or obtains it as described above through the mushroom-shaped growth of the mantle. The small entoderm-vesicle is now found in the posterior part of the larva lying rather closely applied to the ectoderm. The swelling carrying an invagination known by authors as the oral shield (Fig. 26 *A*, *m*) has also shifted posteriorly. The sac of the oral or middle shield of authors is the rudiment of the stomodaeum, and appears as a transverse slit (Fig. 26, *m*). By the development of the foot this organ is pressed forward. The entoderm-vesicle also lengthens from behind forward and fuses with the ectodermal rudiment of the stomodaeum. At the posterior end where the entoderm vesicle is in contact with the ectoderm, the anus now breaks through, without the formation of an ectodermal invagination (F. SCHMIDT, SCHIERHOLZ). The formation of the other organs, in so far as they present peculiar features, will be described later.

When the young Lamellibranch leaves the fish, it moves about with great activity by means of its foot, which has in the meantime become perfected, having lengthened very much and become geniculate. On its lower surface it carries a groove which represents the rudiment of the byssal gland. The latter arises, as in *Cyclas*, in the form of two pits situated posteriorly on the pedal swelling. In consequence of an invagination which forms later, these pits come to lie at the base of a funnel-shaped pit which is afterwards continued into the longitudinal groove just mentioned. The persistent byssal gland of other Lamellibranchs exhibits similar morphological conditions to those already described in connection with the *Unionidae* and *Cyclas*.

6. The Formation of the Organs.*

A. The Shell.

The shell, as in the Gastropoda, is unpaired in its origin, and is formed by a secretion of the epithelium of the shell-gland (Figs. 14, p. 28, and 15, p. 31). This embryonic cuticular shell is retained and passes over into the periostracum (epidermis) of the adult shell. The latter arises through a secretion of granular calcareous substance; this at first accumulates in two complexes lying symmetrically at the two sides of the body beneath the cuticular shell (Fig. 21 *A*, p. 44), which, by further increase, yield the shell-valves. These grow out dorsally until they meet. The dorsal part of the cuticular shell that lies between the two calcified shell-valves which are growing towards one another yields the ligament of the shell (ZIEGLER, p. 43). The larval shell which thus arises and which has a very simple structure, is retained in *Ostrea*, the *Unionidae* and, as has recently been proved, in a number of other Lamellibranchs (RYDER, JACKSON, BRAUN, SCHIERHOLZ). It is found as a minute prominence on the umbo of the large shell when the latter has not, as is often the case with the *Unionidae*, been destroyed through mechanical causes.

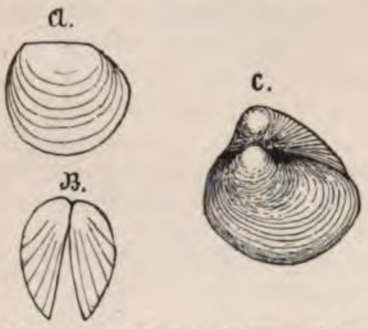

FIG. 27.—*A* and *B*, early stages of the larval shell of *Ostrea edulis*, seen from the side and from behind; *C*, somewhat later stage ("prodissoconch") of the larval shell of *Ostrea virginiana*, oblique side view. This particular larva had just attached itself, the left shell being already lightly fastened to the substratum (after JACKSON).

The larval shell usually differs in shape from the shell of the adult, and is even sometimes very unlike the latter. As a rule, the shell changes very much during development. The youngest stage of the bivalve shell is characterised by a straight hinge-line and the slight development of the umbones. This can be seen in Fig. 27 *A*, and still better in Figs. 14-16, pp. 28-33). This stage (Fig. 15 *C*, p. 31), follows directly upon that of the unpaired cuticular shell, and must be supposed to have arisen out of the latter by the gradual swelling and upward growth of the shell on either side of the dorsal middle line, causing a slight infolding along this line which gives origin to the straight hinge. This straight hinge changes, as the shell soon begins to

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* We here treat of the formation of the organs only in so far as this has not already been considered.

curve and appears more arched (Figs. 27 *B* and 18, p. 36), and finally the umbones appear. The form of the shell seems to be developed in this way in many Lamellibranchs, as may be seen from the figures given by LOVÉN and JACKSON and other authors. JACKSON (No. 22) gives a special description of its development in *Ostrea* (Fig. 27 *A-C*), and we were ourselves able to observe its rise in a very similar manner in *Dreissensia* (No. 27).

It is hardly necessary for us to point out the great difference that exists in the two forms just named between the larval and the adult shell, and this is still more the case in such Lamellibranchs as *Pecten* and the *Aviculidae*, the larval shell of which resembles that depicted in Fig. 27 *C*. This latter form of shell (the prodissoconch of JACKSON) * represents a stage passed through by many Lamellibranchs. JACKSON is therefore inclined to consider this form of shell as specially primitive. In keeping with this view, we find that *Nucula*, which, in consequence of other features may be regarded as a primitive form, and which is found in the lower Silurian [*Ctenodonta*, one of the *Nuculidae*, occurs in the Cambrian], has a shell of somewhat the same shape as the above.

The young shell grows by the secretion from the mantle-cells of new calcareous material; this is deposited both on its inner surface and at its margin. These deposits give rise to the lamellate and zoned character of the adult shell. In older stages, these growth-processes take place chiefly at the peripheral parts of the mantle. There appears to be no essential difference between the manner of formation of the inner (nacreous) and the outer (prismatic) layers of the shell; the one may pass into the other. The prismatic structure of the outer layer is apparently due to the fact that the originally rounded calcareous granules became polygonal through mutual pressure. For details as to the formation of the Lamellibranch shell we are indebted especially to the researches of TULLBERG (No. 56), EHRENBAUM and F. MÜLLER (Nos. 11 and 38).

The growth of the periostracum also takes place at the edge where this latter passes over into a fine cuticle which covers the (ectodermal) epithelium of the pallial margin. At the periphery, where the calcareous shell ends, we thus have the same condition as is shown in early embryonic times by the whole shell; the shell-integument, as a cuticle, covers the mantle-epithelium. Indeed, the whole of the Lamellibranch shell is to be regarded as a cuticular structure covering the mantle-epithelium.

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* In contradistinction to the adult shell (the "dissoconch") JACKSON has named the young arched form with well-developed umbones (Fig. 27 *C*) the "prodissoconch," because it usually precedes the adult form of shell, as has been shown above.

In the case of Lamellibranchs inhabiting a tube, *e.g.*, the *Gastrochaenidae*, this latter is secreted in the same way as the shell; the free edges of the mantle bend over the wide open shell-valves and are thus able to form the tube (SLUITER, No. 53). The structure of the calcareous tube of *Gastrochaena* seems closely to resemble that of the shell.

We still have to mention the relation of the muscles to the shell. The adductor muscles, as is well known, are inserted into the shell and the relation of the epithelium to these muscles is interesting. At the points of insertion, the epithelium must either be modified or must altogether degenerate. EHRENBAUM assumes that it degenerates, and ascribes to the muscles themselves the capacity for secreting the shell-substance (!). As the animal and its shell grow, the adductor muscles, especially the posterior adductor, continually change the position of their attachments on the shell. At their points of insertion, a shell-substance is produced, the so-called transparent substance, and the presence of this substance on the inner side of the shell indicates the course taken by the wandering muscle. But that this substance is secreted by the muscle itself is very improbable, and we therefore prefer to follow the older account of TULLBERG, according to which there is, between the muscle and the shell, an epithelium which produces the shell-material.

B. The Nervous System.

All the ganglia originate as thickenings of the ectoderm, which subsequently become separated from the latter. The ganglia arise separately and become connected later by commissures.

It has already been mentioned that the cerebral [cerebro-pleural] ganglion arises in the *Trochophore* larva as a neural plate (Figs. 15, p. 31, 18, p., 36). This consists at first of large closely crowded cells which, by active division, give rise to a multilaminar cell-plate. The upper layer of this plate which remains continuous with the body epithelium becomes raised up, the lower cell-mass becoming detached from it in the form of two groups of cells. These are the two halves of the cerebral ganglion, the connecting commissures of which no doubt arise in the same way, becoming severed from the ectoderm (this, according to ZIEGLER, is probably the case in *Cyclas*). F. SCHMIDT, indeed, has claimed for the cerebral ganglia of the *Unionidae* distinct origins and secondary connection by means of a commissure, a condition which will be described in connection with the Gastropoda (Chap. XXXII.). In *Anodonta*, the two halves of the ganglion arise near the mouth and are separated by the stomodaeum, above which the commissure extends as a loop.

The pedal ganglia, in *Cyclas* and the *Unionidae*, according to the somewhat similar accounts of ZIEGLER and F. SCHMIDT, with which also that of SCHIERHOLZ can be harmonised, in their formation are associated with the byssal gland. Shortly before the paired byssal gland becomes invaginated (Fig. 19, p. 40), at the point where it is to form, a number of cells become detached from the ectoderm. These at first lie beneath the floor of the invagination, but then separate from the latter and shift further forward, at the same time coming closer together, forming the rudiments of the pedal ganglia (Fig. 21 *B*, p. 44, and Fig. 31, p. 75).

In *Teredo*, the pedal ganglion, according to HATSCHEK, arises as an ectodermal thickening even before the foot begins to form (Fig. 18, *g*, p. 36). It occupies at first a large part of the ventral surface, but appears to decrease in size after its detachment from the ectoderm. During its severance, the mesoderm grows round it. The division into two parts is not so distinct here, but is indicated by a median line. The two halves of the ganglion are thus in this case connected from the first. When the foot rises up and grows out on the ventral side of the larva, the ganglion remains lying at its base.

In their manner of formation the *visceral ganglia* agree closely with the cerebral and the pedal ganglia. They arise in the groove between the gills and the body, almost at the posterior end of the foot.

The *cerebro-visceral* [*pleuro-visceral*] *commissure* has its origin, according to ZIEGLER, in a cell-strand which becomes detached from the ectoderm in the groove between the gill and the body, and runs forward from the visceral ganglion, and later becomes a commissure.

[In *Nucula* and the Protobranchia generally, distinct pleural ganglia are present. These are situated immediately behind the cerebral ganglia at the commencement of the visceral commissures; here, also, the pleuro-pedal commissures are for some distance independent of the cerebro-pedals. In other Lamellibranchs, the pleural ganglia are fused with the cerebral. DREW was, however, unable to trace a distinct origin for the pleural ganglia in *Yoldia*.]

C. The Sensory Organs.

The Eyes. It may be stated with some certainty that the simply constituted eyes of the border of the mantle, *i.e.*, the so-called *invaginations*, or optic pits, and the *compound eyes* arise through a comparatively slight differentiation of the mantle-epithelium.

The *invaginations*, the optic nature of which is, indeed, doubtful, are pit-like depressions of the epithelium, in the cells of which pigment is deposited, while the pit itself becomes filled with a mass of what appears like a secretion (conjectured to be a lens).

The *compound eyes* arise as convex thickenings of the mantle-epithelium at certain points. In these, conical sensory cells are distinguished from the pigment-bearing and supporting cells lying between them by the development of crystal cones and a cornea. The visual cells are connected with the fibres of a nerve which is a branch of the mantle-nerve (CARRIÈRE, PATTEN, RAWITZ).

The eye which thus arises shows some similarity to the compound eye of the Annelida as recently described by ANDREWS.* These eyes of the Lamellibranchia cannot well be compared with the compound eyes of the Arthropoda, since the latter are far more complicated in structure. It is evident that in neither case can there be any real homology.

The Eyes of Pecten. The mantle-eyes of *Pecten*, the morphology and physiology of which are still somewhat obscure, were investigated from the ontogenetic point of view by PATTEN (No. 39), but his study of them was not altogether satisfactory, so that we must content ourselves with a short reference to them.

The eyes of *Pecten*, unlike the two modifications of the edge of the mantle just described in other Lamellibranchs, are highly developed organs (Fig. 28). The principal constituents of the eye of *Pecten* are as follows: there is a cornea behind which lies a large lens; behind the lens comes a retina composed of a ganglionic layer, followed by a layer of rod-bearing cells, the most remarkable feature of the retina being that the rods are directed away from the light and towards the posterior wall of the eye. This latter is covered behind by an integument of pigment-cells, in front of which lies the tapetum, which has a metallic lustre. The innervation of the eye is double, and takes place by means of a nerve (Fig. 28, *7*), which sends out one branch to the base of the eye, and thence direct to the optic cells, while the second branch enters the eye laterally, becoming connected first with the ganglionic layer, and through it coming into contact with the optic cells. For the further complications found in this eye we must refer our readers to the special works of CARRIÈRE, BÜTSCHLI, PATTEN and RAWITZ.

PATTEN was able to establish ontogenetically that the eyes at the edge of the mantle in *Pecten* arise as knob-like thickenings of the ectoderm. As these thickenings rise up and become more and more distinct from the surrounding ectoderm, an ectodermal cone grows down from the surface towards the interior. While active increase in number of the cells brings about the growth of the whole structure, the ectodermal mass directed inwards becomes marked off from the outer epithelium, a process which is assisted by the growth of

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* Compound eyes of Annelids, *Journal of Morphology*, Vol. v., 1891.

connective tissue-cells between the inner ectoderm-mass, this tissue forming a continuous layer between the two. From this, *i.e.*, from mesodermal elements, the lens, according to PATTEN, is formed, while the inner ectodermal mass yields the principal constituent of the eye.

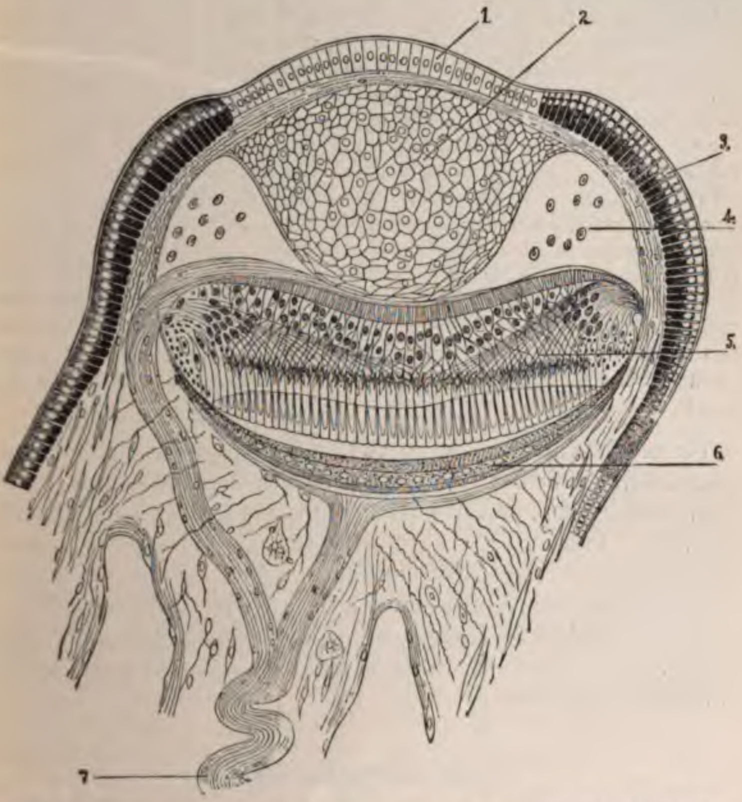

FIG. 28.—A section through an eye of *Pecten* (after PATTEN from HATSCHEK'S *Text-book of Zoology*). *1*, cornea; *2*, lens; *3*, pigmented ectoderm; *4*, blood-sinus round the lens; *5*, retina, with superficial ganglionic layer and backwardly directed rods; *6*, pigment-layer, with the tapetum lying in front of it; *7*, optic nerve.

The way in which the various layers, the ganglionic cell-layer, the retina, the argentea, and the tapetum, etc., arise out of this mass is described, but these difficult points are not made sufficiently clear.

Further details concerning the ontogeny of these very peculiar eyes and especially as to the origin of the rods are much to be desired. The solution of these problems seems all the more desirable as the eye of *Pecten*,* in its structure stands almost alone among Molluscan eyes. With regard to their morphological interpretation, we are inclined to agree with BÜTSCHLI (No. 7) who showed how the pigment cell-layer of the posterior wall of the eye passes over into the retina, a closed vesicle being thus formed in the eye, its anterior wall consisting of the retina and its posterior wall of the pigmented integument. This vesicle must be supposed to have arisen by invagination and abstriction from the ectoderm, a view with which PATTEN's observation of a solid ingrowth can be reconciled. The description given by PATTEN also of the rise of the lens outside of the optic vesicle supports such a condition if we do not assume a mesodermal origin for the lens but rather imagine a second process of invagination such as occurs in the Cephalopodan eye. The rise of the lens outside of the optic vesicle makes it possible for the more superficial wall of the latter to be changed into the retina, a change which is impossible where the lens has itself arisen from this outer wall, as is the case in the Gastropoda and in some of the Cephalopoda also. The position of the rods is hereby explained (BÜTSCHLI). Since these always arise at the free ends of the cells, they are directed forward when the deeper wall of the optic vesicle is transformed into the retina (Gastropoda, Cephalopoda); but are, on the contrary, directed backward when the retina is derived from the outer or superficial wall of the vesicle. The latter must originally have been the case in *Pecten*.

The **otocysts** arise, in *Teredo* and *Anodonta*, near the pedal ganglion as invaginations of the ectoderm which then become abstricted from the latter and provided with otoliths and sensory hairs (Fig. 18, *ot*, p. 36). In *Cyclas*, the otocysts lie at the two sides of the embryo, behind the lateral end of the ciliated area. [In the Protobranchia the otocysts retain their connection with the exterior throughout life.]

Spengel's olfactory organs and the **abdominal sensory organs** (THIELE) show, by their structure, that they are mere modifications of the body-epithelium.

D. The Alimentary Canal.

The structure of the alimentary canal, being greatly influenced by adaptation to different conditions of life, varies in certain points in the different forms. In *Ostrea*, for example, the archenteron is said to pass over direct into the definitive intestine the blastopore remaining open, while in *Teredo*, as well as in *Cyclas* and the *Unionidae*, the blastopore closes and a true stomodaeum forms. This condition, and

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* *Spondylus* has eyes similar in structure to those of *Pecten*. The eyes found on the dorsal papillae of *Onchidium* also resemble those of *Pecten* in so far as the rods in them are turned away from the light. We thus find similar complicated structures, which must have arisen in altogether different ways.

its relation to the other ontogenetic processes, have already been described in a former section (p. 30). The ectodermal invagination yields the oesophagus; the stomach, liver and intestine are entodermal. The anus, in the majority of cases observed, seems to have been formed by direct fusion of the entoderm with the ectoderm, so that the posterior part of the intestine would be entodermal; in *Teredo*, however, there is, according to HATSCHEK, a proctodaeal invagination, and a similar invagination is described by VOELTZKOW as occurring in *Entovalva* (No. 57).

The further development of the intestine consists in its increase in length, as a result of which it becomes coiled. A circular constriction marks off the stomach from the intestine. As early as the *Trochophore* stage, a pair of sac-like outgrowths appear in connection with the stomach; this is the rudiment of the liver (Fig. 16, p. 33) with which the yolk-laden remains of the macromeres become incorporated (Fig. 18, p. 36). A peculiar phenomenon in connection with these two liver-sacs, which at first are spherical, is the occurrence of rhythmical movements; these are no doubt to be traced back to the action of mesoderm-cells which have become apposed to the entoderm wall (LOVÉN, ZIEGLER). The passages from the liver into the stomach which at first are wide, become narrow later and form the efferent ducts; the bulgings found on the liver-sacs mark its separate lobes and lobules (Fig. 31, *l*, p. 75).

In the stomodaeum of *Cardium*, LOVÉN observed a small bulging of the ventral wall which involuntarily recalls the radula-sac of other Molluscs, an organ which is known to be wanting in the Lamellibranchia. It cannot be connected with the crystalline style-sac, as this is invariably an entodermal derivative. The sac which contains the crystalline style is formed as an outgrowth of the wall of the stomach. This structure which, as has long been known, occurs also in the Gastropoda, appears, according to the most recent view, to yield a secretion (the crystalline style) which serves for enveloping solid particles of food, and thus protects the wall of the intestine (BARROIS). No statements as to the ontogenetic formation of the crystalline style-sac are known to us.

The layer of muscle and connective tissue which forms the outer wall of the intestine is yielded by the mesoderm-cells distributed in the primary body-cavity, which become applied either to the entoderm or to the ectoderm.

E. The Gills.

In those Lamellibranchs in which the formation of the gills has been studied, they are found to arise in one of two [three, *cf.* p. 45] different ways which are somewhat difficult to harmonise in their early stages. According to one method, which has already been described for *Cyclas* and *Teredo* (pp. 42 and 44), a fold resembling the mantle-fold rises between the latter and the foot, and develops from behind forward. The outer and inner surfaces of these folds show groove-like depressions lying at right angles to the longitudinal axis of the folds ; these grooves deepen and, meeting those of the opposite surface, fuse together. As the gill-fold becomes perforated along these lines, fissures result which extend in from the free margin of the folds towards their bases (Fig. 31, p. 75). The gill now consists of a series of consecutive lobes which decrease in size from before backward.

According to the other method of gill-formation, which has been observed in *Mytilus*, *Dreissensia*, *Ostrea* (a somewhat similar method being found also in the *Unionidae*),* a papilla arises on each side of the body between the mantle and the median visceral mass, and behind these new papillae arise (Fig. 26 *C*). A longitudinally placed row of papillae thus arises by the continued development of fresh papillae behind those already formed. These, by the development of interfilamentar junctions, form the inner branchial leaf, while the outer leaf is produced by a similar row of papillae which arise somewhat later.

The further development of the papillae was studied by Lacaze-Duthiers in a form belonging to the last category, *viz.*, in *Mytilus edulis* (No. 28). Jackson also has recently investigated the formation of the gills in *Ostrea*, and has arrived on the whole at the same results as Lacaze-Duthiers (No. 22).

During the development of the inner branchial leaf, the papillae increase in number, new ones continually budding out posteriorly.

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* This seems also to be indicated by the observations made by Lovén on *Montacuta*. The filiform permanent gill, of *Pecten* at any rate, arises as papillae, and Ray Lankester states that the gills of *Pisidium* appear first in the form of papillae, although these, from the figures, at first look like the mere swellings of a fold. These statements recall the condition in the nearly related genus *Cyclas*, in which also papilla-like structures produced by the splitting of a leaf are found as the rudiments of the gills. It is, however, possible that *Pisidium*, in the formation of its gills, may be somewhat nearer the primitive condition.

The papillae are thickened at their free ends (Fig. 29 *A*). The continued extension, anteriorly and posteriorly, of these free ends leads to fusion of the papillae, so that the series may now be regarded as a membrane perforated by parallel vertical slits, this membrane representing the rudiment of the inner branchial leaf. In most Lamellibranchs, however, each leaf consists of two lamellae. The second or ascending lamella of the inner leaf arises by the bending inward of the free edge of the primary fold formed by the fusion of the papillae (Fig. 29 *B*); this new lamella then grows upward parallel to the (now outer or descending) lamella towards the base of the latter. The inner lamella thus formed is at first an unbroken membrane, the slits only appearing in it when it has increased in size.

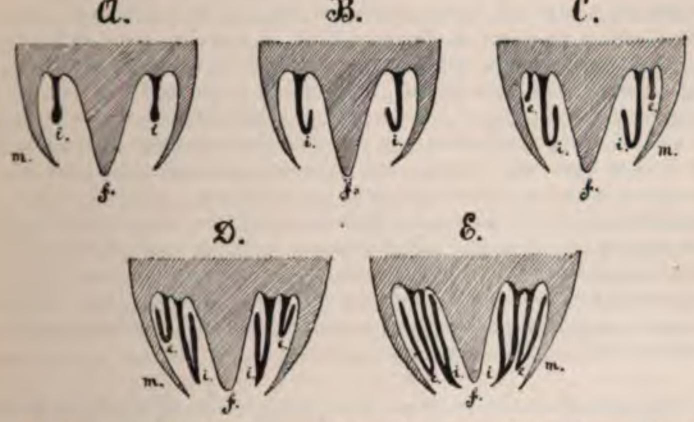

FIG. 29.—Diagram of the development of the gills in a Lamellibranch possessing two branchial leaves on each side. *i*, inner, *e*, outer branchial leaf; *f*, foot; *m*, mantle.

The outer branchial leaf now appears and becomes applied to the posterior half of the base of the inner leaf when the latter consists of about twenty papillae and when its inner or ascending lamella is partly formed (Fig. 29 *C*). The outer leaf forms on the whole in the same way as the inner, but, in it, papillae are said to form anteriorly as well as posteriorly, and the leaf, in order to yield a second lamella, bends outwards and not inwards (Fig. 29 *D*). The fusions of the free edge of the inner lamella of the inner leaf and the outer lamella of the outer leaf with the integument of the body take place later, and vary in extent greatly in different Lamellibranchs, being altogether wanting in some.

In *Mytilus*, as in some other Lamellibranchs (*e.g.*, *Pecten*, *Arca*) the gills, even in the adult, consist of individual filaments which, however, are arranged in just the same way as the branchial leaves of other forms. The inner row becomes bent inward to form the ascending lamella of the inner leaf, while, in the case of the outer leaf, the filaments are bent outward (Fig. 29 *E*). A section of these gills has the form of a *W*, and thus resembles a section of the gill-leaves in the Eulamellibranchs (Fig. 30 *E*). The free ends of the filaments seem to be connected by a continuous strand of tissue running parallel to the length of the gill-leaf. This latter must be regarded as the modified representative of that transverse connection found uniting the free ventral ends of the papillae when the gill first arose, shifted dorsally. The papillae themselves correspond to the filaments of the adult gill. Since, in *Mytilus* also, the reflected or ascending portion of the gill is at first represented by a solid plate (see the above description of the development of the gill) in which the slits arise secondarily, the *Mytilus* gill, in its later stages, passes through a condition resembling that seen in the earliest gill-rudiment in such Lamellibranchs as *Cyclas* and *Teredo* [or better still, in *Pholas*, SINGERFOOS], the gills of which originate as leaves. There is therefore some difficulty in regarding, with many authors, the later filiform condition of the gill as an original condition. This difficulty is increased by the fact that the gills of *Mytilus*, *Pecten*, etc., which consist of single filaments, have, when regarded as a whole, the general characters of a branchial leaf with descending and reflected or ascending lamellae, the descending and ascending limbs of the same filament being united together by fusions of tissue at certain points, the so-called interlamellar junctions; further, the adjacent filaments of the same row, both in the ascending and descending limbs, are held together by the interlocking of some specially long cilia. Wherever, therefore, we have gills consisting of independent but reflected filaments, the assumption that these filaments might have arisen by a secondary separation of the gill-bars in a primary branchial plate is suggested (p. 72).

It appears that the papillae correspond to the gill-bars or, as they are generally termed, filaments of the adult and the slits to the interstices between these bars. The differentiation of the bars would then have to take place from the posterior end of the gills. The gill of the adult Lamellibranch is usually a much more complicated structure than the larval gill up to the stage we have described. Between the filaments of each lamella, as well as between the ascending and descending lamellae of each leaf, there are connections which may consist of solid cell-strands, of hollow vascular junctions, or simply of interlocking cilia, so that the leaves are connected by longitudinal interfilamentar and by transverse lamellar junctions. The mesoderm of the papillae yield the connective tissue, the blood-vessels and the skeletal rods which support the gill-bars, and from thence extend in certain forms into the complicated junctions found in most Lamellibranchs (Eulamellibranchs and Pseudolamellibranchs).

In cases in which, as in *Cyclas*, the rudiment of the gill is leaf-like and only breaks up later into consecutive lobes through the slits which arise in it, we may assume that these lobes unite later, like the papillae, to form the branchial leaf.

If we compare the origin of the gills in *Teredo* and *Cyclas* on the one hand and *Mytilus*, etc., on the other, we might at first feel inclined to regard the method seen in the former as the more primitive, since the formation of the leaf precedes that of the papillae. The gill originates as a leaf, and is only later broken up by incisions into separate lobes which are arranged in the same way as the papillae in other cases. This view, which is founded on the ontogeny of a few forms such as *Teredo* and *Cyclas*, which in other respects are undoubtedly specialised, cannot, however, in any way be reconciled with the morphological conditions of the definitive gill in the different Lamellibranchs. A comparative study of these latter suggests rather that the origin of the gills in the form of papillae, as in *Mytilus*, was the primitive condition.

Unfortunately very little is as yet known as to the mode of formation of the gills, but if we examine the apparently carefully investigated development of these organs in *Mytilus* and *Ostrea*, we find that certain ontogenetic stages can be most exactly matched in the shape of the gills of certain adult Lamellibranchs. Thus, in *Dimya*, according to DALL, the gill on each side consists of one row of branchial filaments (Fig. 30 *B*) and in *Amusium Dalli* (and as it appears also in *Arca ectocomata*) there are two such rows on each side (Fig. 30 *C*).* The branchial filaments are not connected, and thus represent the ontogenetic stage at which there are one or two rows of papillae. The further development of the gills may be imagined to have taken place by the free ends of the branchial filaments becoming connected, in the manner illustrated in the ontogeny of *Mytilus* (p. 68). In this way the row of branchial filaments gave rise to the branchial leaf. This leaf doubled back on itself, when an increase of surface was needed and growth in a straight direction was not possible on account of the want of room in the shell (Fig. 29 *B-E*). The ascending (reflected) lamella of the branchial leaf thus arose; the free edge of which may finally fuse with the mantle, as is the case, for example, with the ascending lamella of the outer branchial leaf in the *Unionidae* (Fig. 30 *E*).

That form of gill which consists of single filaments, bent back upon themselves, thus indicating the two lamellae of the later branchial leaf (Fig. 30 *D*) has repeatedly been held to be very primitive and has been thought to represent the stage succeeding that in which the gills consisted of two straight rows of filaments (Fig. 30 *C*). Such gills are found in *Trigonia* (PELSENEER) and *Arca noae* which may be considered as very old forms. The gill-leaf consisting of two lamellae was thought to have arisen from the union of these reflected filaments. To us, the reflection of the single filaments and their regular, almost leaf-like arrangement, such as is seen in the gills of *Pecten* and *Mytilus*

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* We follow here the accounts given by PELSENEER, DALL and MITSUKURI of the morphological conditions of the Lamellibranch gills. It is impossible to decide how far these may represent primitive conditions or may to some degree be degeneration-phenomena, for it is evident that these latter do occur and cause a reduction of the gill-leaves.

and even in *Arca*, is very difficult to explain. When isolated filaments for the sake of increase of surface grow in length, they are not likely to retain such a regular arrangement, even if we bear in mind their position in one row, the limited space within the Lamellibranch shell, and the circulation of the water between them. We therefore think ourselves justified in assuming, in the case of those Lamellibranch gills which, while filiform in structure, show such a regular leaf-like shape, a secondary breaking up of a gill which originally consisted of two plates to which allusion has already been made (p. 70). A satisfactory explanation of these obscure points can, however, only be obtained by comprehensive investigation not only of the gills themselves but also of the whole structure of those Lamellibranchs which may be regarded as transitionary forms.

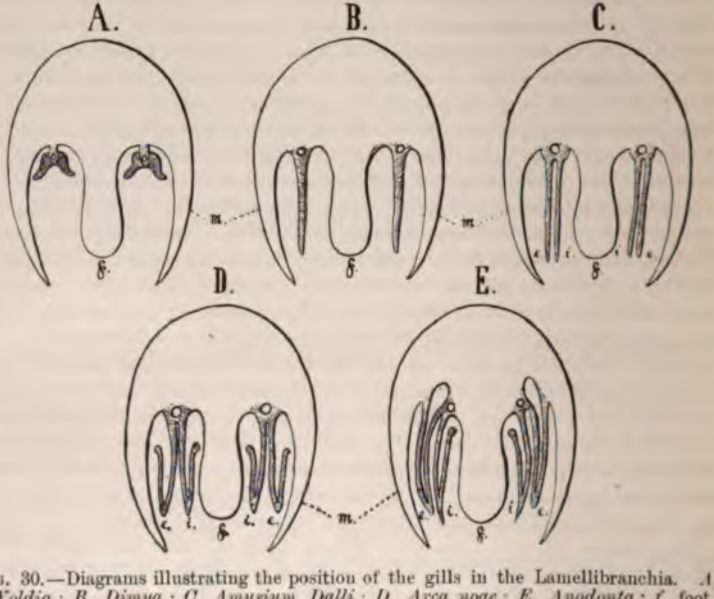

FIG. 30.—Diagrams illustrating the position of the gills in the Lamellibranchia. *A*, *Yoldia*; *B*, *Dimya*; *C*, *Amusium Dalli*; *D*, *Arca noae*; *E*, *Anodonta*; *f*, foot; *m*, mantle; *i*, inner, *e*, outer branchial leaf.

We may regard as the most primitive form of the Lamellibranch gill a ridge [the ctenidial axis] with two rows of branchial filaments. In place of the filaments, triangular leaflets must originally have been present, with vertically expanded surfaces, placed transversely to the long axis of the ridge, a condition permanently retained in the gills of *Nucula* and *Yoldia* (Fig. 30 *A*, MITSUKURI). Taking into account the similar form of the gills in the Aspidobranchiate Gastropoda, this latter condition might be regarded as the original condition. It is, indeed, not essentially different from that with the double row of papillae, since the leaflets correspond in every respect to the still unreflected papillae.

The leaflets by lengthening and narrowing gave rise to the filaments. The gill of *Nucula* is further primitive in its free pointed posterior termination, and may without further question be directly homologised with the bipectinate gill of the lowest Gastropods. This last view of the Lamellibranch gill, which was advanced years ago by LEUCKHART (No. 30), has recently, owing to the researches of PELSENEER (Nos. 40 and 41), MENEGAUX (No. 35), and others, received great support and has become almost universally adopted. The ontogenetical fact that one of the rows (the inner row) appears first and the other (outer) row only much later does not, indeed, appear to be in harmony with it. In tracing the gill back to that primitive form, we should expect that the two rows of papillae would arise almost simultaneously.

The rise of the gills in the form of leaves, as in *Teredo* and *Cyclas*, may, according to the present state of our knowledge, best be compared to the production of the branchial filaments or papillae from the ridge. We should, indeed, require to understand more exactly the way in which the second branchial leaf found in these animals arises. We must be careful not to ascribe too great significance to the method of formation of the gills in *Teredo* and *Cyclas*, because these are, as has already been shown, highly specialised Lamellibranchs, and because, in the nearly related *Pisidium*, the leaf-like rudiment of the gills is far less distinct (according, at least, to RAY LANKESTER). These varied conditions are somewhat difficult to reconcile, and their explanation is very desirable. So far, there are many indications that, in the development of the Lamellibranch gills, great modifications have been introduced which render it very difficult to form conclusions as to their original constitution.

F. The Body-cavity, the Blood-vascular System and the Kidney.

The development of the closely related structures, the body-cavity, the blood-vascular system and the kidney, have been investigated in the *Unionidae* and in *Cyclas*, but are best known in the latter. Our information on these points is due to the investigations of LEYDIG, STEPANOFF, GANIN and v. JHERING, which have recently been extended and supplemented by ZIEGLER. The history of the mesodermal structures, in *Cyclas* and the remaining Lamellibranchs has, indeed, not yet been exhausted, as will be evident from the following account.

The first rudiment of these mesodermal structures appears at a time when the embryo, through the development of the foot and the formation of the mantle-folds passes out of the *Trochophore* stage, *i.e.*, at a stage occurring between the two depicted in Figs. 19, p. 40, and 21 *A*, p. 44.

In the *Trochophore* there is on each side of the intestine a compact mass of mesoderm-cells (Fig. 19, *mes*) which ZIEGLER claims as the mesoderm-bands. In the anterior end of each of these masses, a cavity arises which soon, by the regular arrangements of its cells into an epithelium, assumes the form of a vesicle. This is the paired rudiment of the pericardium.

The **rise of the paired pericardial vesicles** out of the bilateral mesoderm-rudiment so nearly resembles the formation of the primitive segments in the Annelida and the Arthropoda that we must regard the pericardial vesicles as coelomic sacs and their cavities as the secondary body-cavity. The coelom in the Lamellibranchs, however, only attains a very small size, and the *definitive body-cavity* which contains the organs arises independently of the former as a *pseudocoele*. The view that the pericardial sacs must be regarded as the coelom rests chiefly on the fact that the kidney shows the same relation to this cavity (Fig. 32) as do the nephridia in the Annelida to the cavities of the primitive segments (secondary body-cavity). This relationship is very early developed in the embryo of *Cyclas*.

The kidney (organ of Bojanus). Behind the pericardial vesicle, the mesoderm-cells soon become grouped in the form of a tube, the lumen of which communicates with the cavity of this vesicle. This tube, which at first runs upwards, and then again bends downwards, is the *rudiment of the organ of Bojanus* (Fig. 21 *A*, *n*, p. 44). Its upper end, which opens into the pericardial vesicle (Figs. 21, 32) is lined with cilia. The resemblance thus brought about between the organ of Bojanus and a nephridium is heightened later when the lower end of the canal fuses with the ectoderm and communication with the exterior is thus established (Fig. 31, $n_{,,}$).

From ZIEGLER's description, it is not clear whether the formation of the efferent duct takes place through the direct fusion of the lower end of the rudiment of the kidney with the ectoderm, or whether an invagination of the ectoderm takes part in it. ZIEGLER's statements on the whole support the first hypothesis, which also agrees with the manner of formation of the nephridia in the Annelida as described by BERGH.* But since, as we shall see, in the Gastropoda and also in the Annelida (Vol. i., p. 297), an ectodermal invagination takes part in the formation of the nephridia, this question cannot here be decided.

The statements which have been made as to the rise of the kidneys as mere depressions of the ectoderm (RAY LANKESTER, GANIN) must be considered as refuted, especially as the morphological agreement of the organs with the nephridia of the Annelida points to a similar method of formation. We are indeed led to look for a still closer relation of the nephridia, when forming, with the coelomic sacs, and such a relation will be found in the Gastropoda.

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* R. S. BERGH. Neue Beiträge zur Embryologie der Anneliden. I. Zur Entwicklung und Differenzirung des Keimstreifens von Lumbricus. *Zeitsch. f. wiss. Zool.* Bd. l. 1890.

32 *A*, *n*). The right and left pericardial vesicles now grow towards each other and unite above the intestine at the two sides of which they formerly lay; in exactly the same way they unite below the intestine, *i.e.*, ventrally to it (Fig. 32 *A*-*D*), the intestine having been previously invested by certain of the mesoderm-cells which were distributed in the primary body-cavity.

The circumcrescence of the intestine by the pericardial vesicles and the fusion of these latter, as described by ZIEGLER, strikingly recalls the fusion of two primitive segments in the Annelida to form a segmental cavity (Vol. i., p. 290). We have already drawn attention to the relation of the kidneys (nephridia) to the pericardial cavity. The walls of the pericardial vesicles which come into contact and which, in following the comparison, would be the equivalent of the intestinal mesenteries, seem completely to degenerate, so that the cavities of the two pericardial vesicles unite together to form a common cavity. The formation of the heart, which will be described immediately, takes place outside of this space, *i.e.*, outside of the secondary body-cavity and within the primary body-cavity. This also would agree with the condition in the Annelida, where the dorsal vessel arises between the splanchnic layer of the mesoderm and the entoderm, and therefore in the primary body-cavity (Vol. i., p. 291).

The formation of the heart is introduced by the circumcrescence of the intestine by the pericardial vesicles. The wall of the vesicles which is turned to the intestine yields the wall of the ventricle. This statement made by ZIEGLER must be taken to mean that, from that wall of the vesicle, elements are produced by delamination which yield the heart, while the wall of the pericardial vesicle itself represents the investing peritoneal epithelium (Fig. 32 *B* and *C*). The same process would be repeated in the formation of the auricles. These latter had already arisen as the invaginations of the pericardial vesicles described above (Fig. 32 *A*). These invaginations unite with the opposite wall of the pericardial vesicle and the auricles, which form by the widening of the originally narrow invaginations, fuse with the rudiment of the ventricle (Fig. 32 *B*-*D*). At the points of junction, the apertures and valves between the ventricles and the auricles arise.

The efferent and afferent *vessels of the heart* (aortae and branchial veins) arise separately from the rudiment of the heart and are no doubt formed by the grouping together of those mesoderm-cells which are derived from the wall of the pericardium, or were already present in the body-cavity, *i.e.*, they originate as cavities between cavity arises which soon, by the regular arrangements of its cells into an epithelium, assumes the form of a vesicle. This is the paired rudiment of the pericardium.

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* R. S. Bergh. Neue Beiträge zur Embryologie der Anneliden. I. Zur Entwicklung und Differenzirung des Keimstreifens von Lumbricus. *Zeitsch. f. wiss. Zool.* Bd. l. 1890.

As the kidney develops further, its tube becomes coiled (Figs. 21 *A* p. 44, and 31). Three sections can then be made out in it; a short ciliated section, a long glandular section and an efferent section. The latter, which is not ciliated in the embryo, shows ciliation at a later stage when the efferent duct of the genital organs opens into it near its end, and it thus serves to transmit the genital cells.

The three sections of the embryonic kidney are the same as those that can be distinguished in the adult organ, but the latter is further modified in so far as the middle section is more coiled. This gives rise to the renal sac and to the more complicated portion, the renal coil of the *Unionidae*; the middle segment is that portion of the kidney where secretion takes place. In the *Unionidae*, and in other Lamellibranchs, the middle section is not so much coiled as in *Cyclas*, but the area of the secretory epithelium is increased by the formation of internal folds. In the primitive forms (*Nucula*, *Solenomya*), the kidney retains the form of a slightly coiled tube, the inner wall of which shows no great increase of surface.

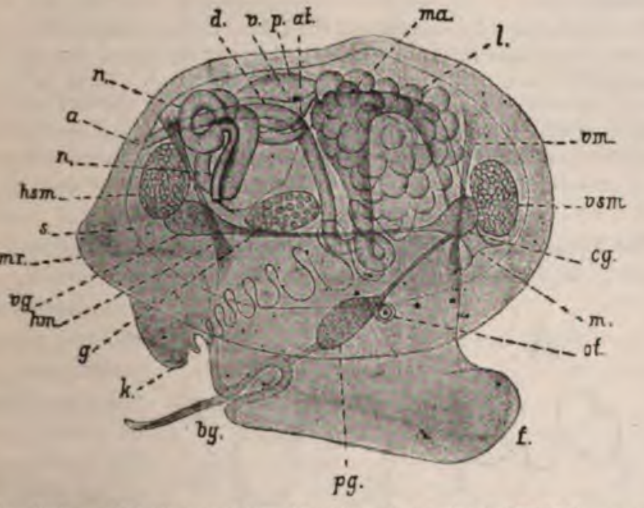

FIG. 31.—Embryo of *Cyclas cornea* (combined from figures by E. ZIEGLER). *a*, anus; *at*, auricle; *by*, byssal thread and gland; *cg*, cerebral ganglion; *d*, intestine; *f*, foot; *g*, genital rudiment; *hm*, posterior retractor of the foot; *hsm*, posterior adductor; *k*, gill; *l*, liver; *m*, mouth; *ma*, stomach; *mr*, edge of the mantle; *n*, and *n*,,, kidney; *ot*, otocyst; *p*, pericardium; *pg*, pedal ganglion; *s*, shell; *v*, ventricle; *vg*, visceral ganglion; *vm*, anterior retractor of the foot; *vsm*, anterior adductor.

When the body grows longer, as in the *Unionidae*, the gills also lengthen and the organ of Bojanus takes up a somewhat different position. Its original position between the pericardium and the posterior adductor which is illusthe mesodermal tissues of the latter. The passage of these out of the pericardium that surrounds them is, owing to the nature of their origin, easily understood (Fig. 32 *C* and *D*).

This method of formation of the heart from the mesial walls of the pericardial vesicles explains how, in the adult, the intestine traverses the heart. Phylogenetically, this condition is supposed to have arisen through a blood-sinus surrounding the intestine developing thicker walls and thus becoming the heart (GROBBEN). Since the vessels arise distinct from the heart, such an origin of the latter is not in any way improbable. On the other hand the fact that, in the Lamellibranchia, a paired heart lying dorsally to the intestine, and with each half enclosed in a separate pericardium may occur (*Arca*) has led to the conclusion that the unpaired heart which, in the higher forms, surrounds the intestine, might have arisen by the fusion of these two hearts (THIELE, Chap. xxx.). This view seemed to be supported by the fact that the double heart is found in just those forms that are very primitive, and, further, that a double heart is also present in various Annelids.

The paired origin of the heart (Figs. 32 and 33 *C*), might perhaps be regarded as a primitive feature and as indicating that the heart was originally a paired vessel, but this view is not justified, since it is supported merely by the paired development of the coelom and the part taken by the latter in the formation of the heart. A comparison with the manner in which the heart arises in the Annelida and its formation in the Lamellibranchia should help to elucidate these points (*cf.* Vol. i., p. 291).

In the Annelida, the paired origin of the heart is still more marked than in the Lamellibranchia. Even during the growth of the primitive segments towards the dorsal middle line the rudiment of the dorsal vessel appears on that side of the splanchnic layer which is turned towards the entoderm (Fig. 33 *A*, I. and II.). The dorsal vessel is therefore paired and, as the primitive segments grow further, shifts towards the dorsal line (*A* II. and III.) On this line, the two rudiments of the heart finally meet (*A* IV.) and fuse to form the unpaired dorsal vessel, except in those forms in which they remain distinct in the adult. With this latter condition in which the dorsal vessels remain distinct, the heart of *Arca* shows the greatest agreement. We must suppose that, in *Arca*, each of the two pericardial sacs, by the invagination of its inner wall, developed a ventricle (Fig. 33 *B*, I.-IV., *h*). The fusion of the pericardial sacs above and below the intestine did not take place, and in this way the union of the two rudiments of the heart was prevented. In most Lamellibranchs, on the contrary, the circumcrescence of the intestine takes place: the whole median wall of the pericardial vesicles takes part in the formation of the ventricle, and the latter thus surrounds the intestine. (Fig. 33 *C*, I.-IV.). The rise of this single ventricle from distinct rudiments is suggested here also, and the double character is still more recognisable in the rise of the auricles, which originate as invaginations of the outer walls of the pericardial vesicles (Fig. 32). But this double character may, as already mentioned, be derived from the connection of the formation of the heart with the paired coelomic sacs. Further, the paired character of the heart, as represented in the adult condition, seems to us easily explained by these ontogenetic processes.* The fact that, in the paired heart of *Arca*,

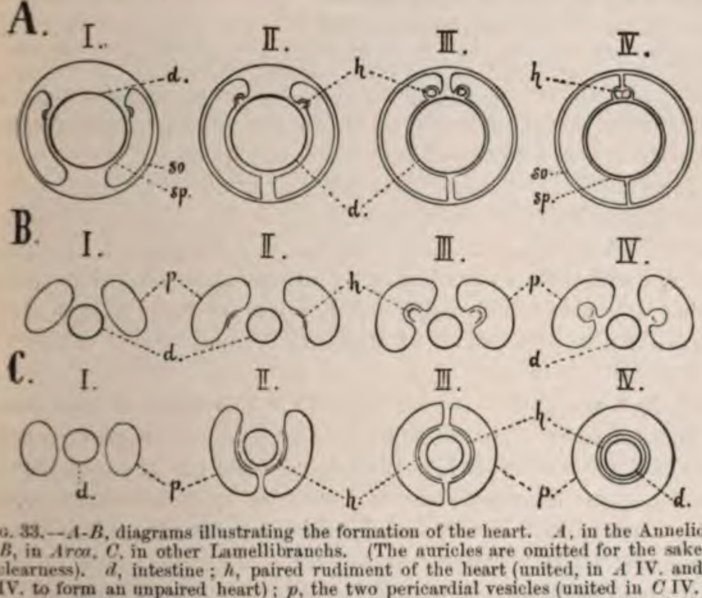

FIG. 33.—*A*-*B*, diagrams illustrating the formation of the heart. *A*, in the Annelida, *B*, in *Arca*, *C*, in other Lamellibranchs. (The auricles are omitted for the sake of clearness). *d*, intestine; *h*, paired rudiment of the heart (united, in *A* IV. and *C* IV. to form an unpaired heart); *p*, the two pericardial vesicles (united in *C* IV. to form the pericardium); *so*, somatic, *sp*, splanchnic layer of the coelomic sac (primitive segments).

there is a common anterior and posterior aorta, seems to point rather to the breaking up of an originally single heart than to the union of two distinct hearts. The paired dorsal vessel of the Annelida often shows connection between the two parts,† and this also might be a

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* GROBBEN, who advocates such a view of the Lamellibranch heart, speaks of the "retention of an ontogenetic stage through an arrest of development." It appears to us also that the method of formation described would facilitate the development of a double heart in cases in which such a heart would be of advantage to the animal.

† *Megascolex*, *Microchaeta* and *Acanthodrilus* show the recurrence of connections between the two hearts. In another *Acanthodrilus* almost the whole of the dorsal vessel is paired and is without transverse connections, but in its anterior part there is still a connection. BEDDARD, Note on the Paired Dorsal Vessel of Certain Earthworms. *Proc. Roy. Phys. Soc. Edinburgh.* Vol. viii., 1885.

consequence of its having developed from an originally single rudiment.

An attempt has been made to explain the rise of a paired heart (as the original condition) through the relation of the two parts to the gills lying at the two sides of the body (THIELE, Chap. xxx.). If the paired heart really represents the primitive condition, this explanation would be very plausible, but the Annelida, Arthropoda and Amphineura all agree in showing us the heart as an unpaired organ lying dorsally to the intestine.

We have still to mention that the heart in a few more modified forms (*Teredo*, *Ostrea*, *Mülleria*) lies ventrally to the intestine. In these cases, the union of the pericardial vesicles to form the unpaired heart has no doubt taken place beneath the intestine. [In *Nucula*, *Arca* and *Anomia*, the heart is dorsal to the intestine.]

The condition of the secondary body-cavity and the kidneys in the Lamellibranchia recalls very strikingly those found in the Crustacea and *Peripatus* (*cf.* Vol. ii., p. 180, and Vol. iii., p. 204). In these latter, a part of the coelom is directly incorporated in the kidney, with which it is also functionally united. We are perhaps justified in regarding the pericardium of the Lamellibranchia, into which the renal funnel opens as it does in the Arthropoda into the cavities of the primitive segments (or coelom), as the homologue of the end-sac of the excretory organs in these forms. The fact that the coelom-sacs of the two sides are here united, can make no difference, for this does not cause the heart to lie, as may at first appear, in the secondary body-cavity, but it is still found outside that cavity, as it is also in the forms mentioned above.

If the pericardium possesses the morphological significance ascribed to it, we might perhaps expect that its physiological function should be modified in the same way as in those forms in which the secondary body-cavity has entered into such close relation to the kidney. This assumption seems actually to be confirmed, when we consider the so-called pericardial gland. This gland, the so-called red-brown organ or Keber's organ, arises as outgrowths of the epithelium of the pericardial wall and lies either on the auricles or on the anterior part of the pericardium (GROBBEN). This organ is most probably excretory and, since it owes its origin to the pericardial epithelium, it seems not unsuitable to ascribe to the latter a similar significance. The close relation in point of position existing between both the pericardium and the pericardial gland and the blood-vascular system, makes such a view appear possible.

According to our present anatomical and ontogenetical knowledge, the communication between the pericardial cavity and the blood-vascular system which was formerly assumed, does not exist. The idea of an admixture of water with the blood which was also held must be regarded as exploded, quite apart from the fact that the transmission of water from outside through the organ of Bojanus into the pericardium seems from recent researches to be highly improbable (RANKIN). The structure of the organ itself as well as the direction of the cilia within it are unfavourable to such a process. Indeed the whole idea of the reception of water into the body of the Lamellibranch from without, which has often been adopted as an explanation of the swelling of the foot, must be regarded as refuted. The pores which were supposed to conduct water from without into the foot could not be demonstrated ontogenetically (ZIEGLER). The swelling of the foot, as is evident from the statements of a number of authors (CARRIÈRE, FLEISCHMANN, SCHIEMENZ, RANKIN, etc.), is rather due to the fact that the greater part of the blood is driven into this organ. This is brought about through the blood being retained in the foot, the valve at the entrance to the sinus venosus being closed and the blood which was emerging from the foot being thus retained within it. Besides this, the quantity of blood already in the foot is increased through the flow of fresh blood from the anterior aorta. When the foot is extended, the sphincter at the point where the posterior aorta emerges from the heart contracts, so that the greater part of the blood is obliged to flow through the anterior aorta into the foot. During this process, a certain amount of blood still circulates in the heart, so as to prevent an arrest of the whole circulation. When the valve in the sinus venosus opens, the blood flows out of the foot, and as the latter ceases to extend, the sphincter of the posterior aorta opens again, until, when the animal moves on again the same process is repeated.

G. Musculature and Connective Tissue.

The only organs as yet referred to as differentiations of the mesoderm have been the coelom, the kidney and the blood-vascular system, but there are other structures mesodermal in origin, which, indeed, up to the present have received little attention from zoologists; these are the musculature and the connective tissue, and, further, the genital organs, which will be dealt with immediately. The muscle-cells are formed by the detachment of single cells from the mesoderm-mass, the distribution of these in the pseudocoele, and the further growth of the isolated cells into contractile fibres. When considering the larval forms, we pointed out that these fibres become applied to one another to form larger complexes which are the muscles of the larva and the adult (Fig. 15, p. 31; Fig. 18, p. 36). The musculature of the foot arises from the great increase in number of the cells detached from the mesodermal mass, and the massive connective tissue both of the foot and of the rest of the body has the same origin.

H. The Genital Organs.

The ontogeny of the **genital organs** has not as yet been sufficiently studied. In *Cyclas*, the **genital glands** originate from the two mesoderm-bands and lie, as a rather large mass of cells, beneath the pericardial vesicle and close under its wall (ZIEGLER). A somewhat later stage in the development of these glands is depicted in Fig. 21 *A*, *g*, p. 44. At a still later stage, they form two club-shaped masses, the broad surfaces of which meet in the middle plane, lying above the cerebro-visceral commissure (Fig. 31, *g*).

From what is as yet known of these glands in the Lamellibranchs, they do not bear any direct relation to the pericardial sacs, *i.e.*, to the epithelium of the secondary body-cavity, as was found to be the case in the Annelids and as we shall presently see that they do in other Mollusca. Our knowledge of the subject is far too slight to justify further conclusions, but we may suggest that the close relation of the coelom to the kidney has led to an alteration in the conditions and thus to a gradual shifting of the genital rudiment out of the coelom. The efferent ducts must at the same time have undergone alteration, but with respect to these points, ontogeny fails us and we can only draw our deductions from the anatomical conditions.

The relation of the efferent genital ducts varies in the Lamellibranchia. Most usually, they open on the surface of the body independently of the nephridia. In by far the greater number of the Eulamellibranchia they open into the supra-branchial cavity near the external aperture of the kidneys. In other Lamellibranchs, they and the efferent ducts of the kidneys open into a common cloaca (*Arca*, *Pinna*, *Ostrea*, *Cyclas*); in others again, they emerge further back in the organ of Bojanus (*Anomia*, *Spondylus*, *Pecten*, *Lima*), and only in a few primitive forms (*Nucula*, *Solenomya*) do the genital products pass into the kidney, not far from the reno-pericardial aperture (PELSENEER, No. 41).

Distinct efferent ducts for the kidneys and the genital organs are found in such forms as, from their structure, may be considered as phylogenetically younger than the others, while the two organs are connected in those Lamellibranchs which, by their organisation and their early geological occurrence, are proved to be of greater age (v. JHERING). These facts indicate that the origin of the efferent genital ducts is to be traced to the nephridia and that they only gradually became separated from these latter organs. Among the Lamellibranchs, processes may have taken place similar to those in certain Annelida (*Capitellidae*), in which new ducts are developed out of the nephridia for the genital products. Such a modification of the nephridia which originally served for conducting the genital products would be explicable as a consequence of the modified function of the coelom and the shifting of the genital glands thus brought about.*

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* A summary of these points which have been established chiefly by Lacaze-Duthiers and v. Jhering will be found in No. 24, by the last-named author, as well as in Bronn's Klassen und Ordnungen der Thierreichs, Bd. iii., Abth. i. Pelseneer has also recently given an account of these conditions.

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CHAPTER XXXI.

SOLENOCONCHA (SCAPHOPODA).

(DENTALIUM.)

THE ontogeny of *Dentalium* was investigated many years ago (1857) by LACAZE-DUTHIERS, and more recently (1883) by KOWALEVSKY with the aid of sections; the researches of KOWALEVSKY, however, do not extend so far into the life of the animal as do those of LACAZE-DUTHIERS, the former having been able to observe the larva only up to the sixth or seventh day, while the latter was able to keep the larvae alive until they were thirty-five days old. We therefore still have to refer, for many points, to the older accounts of LACAZE-DUTHIERS.

The genital products are discharged into the water through the right renal aperture, fertilisation taking place outside of the body. The eggs, which are not very rich in yolk, are surrounded by a thin envelope.

1. Cleavage and Formation of the Germ-Layers.

The cleavage is total, the egg dividing into two cleavage-spheres, one of which is somewhat larger than the other. The larger sphere then, by division, gives rise to a new sphere, and the smaller sphere also divides into two, so that we have now one macromere and three micromeres. It is possible that additional micromeres are segmented off from the larger sphere. The former divide repeatedly, so that there is soon a great number of the micromeres lying upon a single macromere which still remains rather large. This latter also finally divides into two and then into four macromeres. This method of cleavage shows considerable resemblance to that most common among the Lamellibranchia. Further division and the formation of a central cavity give rise finally to a blastula, one half of which consists of small and the other of large cells (Fig. 34 *A*). The animal pole of this blastula is therefore easily distinguished from the vegetative pole; the latter soon becomes somewhat flattened, its cells becoming invaginated to form the archenteron (*B*). *Dentalium* has thus a typical invagination-gastrula (*C*) whose transverse axis is somewhat broader than its invagination-axis. A few large blastomeres soon become detached from the outer surface and pass into the cleavage-cavity (Fig. 34 *C*). Here they become arranged with bilateral symmetry and are found, especially at later stages, near the blastopore. They represent the rudiment of the mesoderm (*mes*). This latter, which at first consists of only a few large cells, soon takes the form of two groups of cells which, after increasing still further in number, form the two mesoderm-bands which lie near the archenteron.

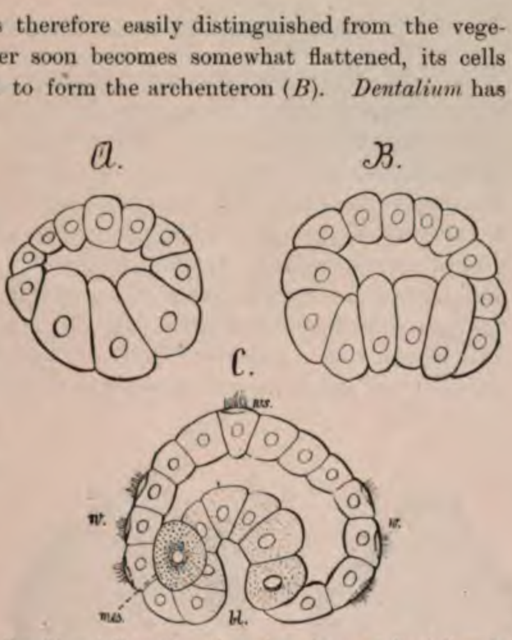

FIG. 34.—*A*-*C*, sections through embryos of *Dentalium* in the blastula and gastrula-stages (after KOWALEVSKY). *bl*, blastopore; *mes*, rudiment of the mesoderm; *w*, cells of the ciliated ring; *ws*, ciliated tuft.

The mesoderm-rudiment, as has been mentioned, shows a bilateral symmetry, but this is not so regular as, for instance, in *Chiton* (p. 4). In some, indeed, of KOWALEVSKY's figures the bilateral symmetry is distinct, but in others it appears to be less regular. This also applies to the mesoderm in its later development. A cavity does, indeed, appear in the mesoderm which KOWALEVSKY is inclined to regard as the coelom, but the stage in which it appears is a comparatively late stage, the body being already somewhat developed. These points are, in fact, not sufficiently well understood to justify us in drawing any definite conclusions.

In connection with the formation of the mesoderm, it should be mentioned further that, at the blastula-stage, *i.e.*, when invagination is commencing, isolated cells of various sizes are to be met with in the cleavage-cavity; these may possibly be mesoderm-cells, although KOWALEVSKY himself seems to be inclined to think that the mesoderm arose in the way above described, and to consider the occurrence of these cells in the cleavage-cavity as abnormal.

2. The Development of the Form of the Larva.

As early as the gastrula-stage, the embryo becomes free and is capable of active locomotion, some of the ectoderm-cells being already covered with cilia (Fig. 34 *C*). Besides those ciliated cells which lie at the cephalic pole and later form the ciliated tuft, the young larva has three rows of such cells lying one behind the other at the middle of the body of which they form a large part (Figs. 34 *C* and 35 *A*). Since these ciliated cells represent the pre-oral ciliated ring, the post-oral part of the larva is very little developed. At this early stage, the larva consists of comparatively few cells, which are still very large, as is evident from a glance at Fig. 35 *A*. In later stages, as the larva grows in size and as its cells increase in number, the rows of ciliated cells are less conspicuous as compared with the rest of the body (Fig. 36 *A*), and finally appear as a single though somewhat broad ciliated ring (Fig. 35 *A*-*C*). Meantime, the ciliated tuft at the cephalic pole has become more conspicuous, and a large part of the anterior section of the body has also become covered with delicate cilia (Fig. 35 *B*).

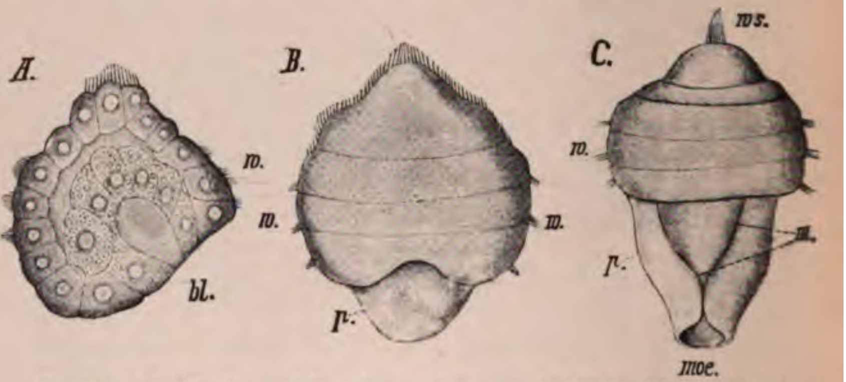

FIG. 35.—*A*-*C*, three larvae of *Dentalium* aged respectively 12, 24 and 37 hours (after KOWALEVSKY). *bl*, blastopore; *m*, mantle-fold; *moe*, permanent posterior aperture of the mantle; *p*, posterior part of the body; *w*, ciliated ring; *ws*, apical ciliated tuft.

In the youngest larvae, *viz.*, at the gastrula-stage, the blastopore was terminal, *i.e.*, opposite to the cephalic pole (Fig. 34 *C*), but it soon changes its position, shifting forward towards the ciliated ring along the future ventral surface (Fig. 35 *A*). The larva thus assumes a somewhat irregular shape, the flattened ventral surface being somewhat backwardly inclined. At the same time, the pre-oral part of the larva, that lying in front of the ciliated ring, has become more conical, and the posterior (post-oral) part somewhat lengthened (Fig. 36 *A*). The blastopore, which has now become narrow and slit-like, is displaced inwards by the development of an ectodermal depression, the stomodaeum, which gives rise to the buccal mass and the external aperture of which persists as the adult mouth (Fig. 36 *A*). The early larval stages of *Dentalium* closely resemble those of *Patella*, as may be seen by comparing Figs. 35 and 36 with Fig. 50, p. 124.

If we were justified in comparing the larvae of the Amphineura and of the Lamellibranchia with the Annelidan *Trochophore* (pp. 5, 32 and 128), we may also attempt a similar comparison for the larva of *Dentalium*. In spite of the fact that the neural plate and the kidney, two important organs of the *Trochophore*, have not as yet been demonstrated in the larva of *Dentalium*, we can still see a very striking resemblance to the *Trochophore*. Thus, in the conical pre-oral region with its apical tuft of cilia, in the pre-oral ciliated ring, in the relation of the blastopore to the future mouth, and in the development of the body by an elongation of the post-oral region, we see distinct Trochophoran characters. The anus only appears at a later stage together with the paired rudiment of the cerebral ganglion (which is perhaps connected with the cephalic plate). The larva of *Dentalium*, however, may be distinguished by the presence

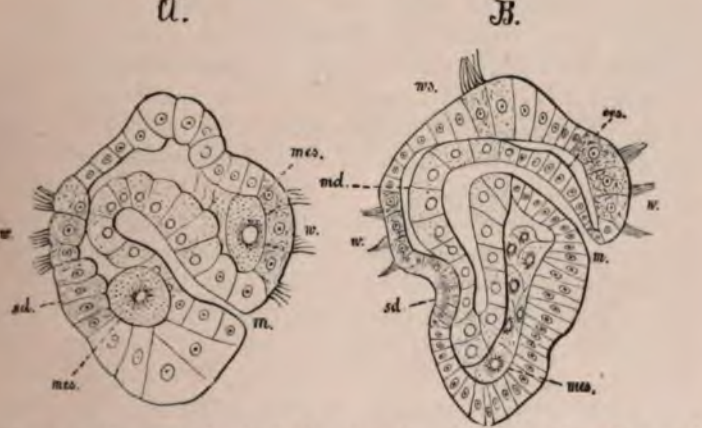

FIG. 36.—*A* and *B*, median longitudinal sections through larvae of *Dentalium* aged respectively about 14 and 34 hours (after KOWALEVSKY). *m*, mouth; *md*, enteron; *mes*, mesoderm; *oes*, stomodaeum; *sd*, shell-gland; *w*, ciliated ring; *ws*, ciliated tuft at the cephalic pole.

of a certain character typical of the Molluscan larva. Thus, a dorsal invagination of the ectoderm (Fig. 36, *sl*) becomes differentiated at a very early stage (*A*), then deepens and flattens out again later; this organ, from its development and subsequent modification, as well as in its position, is seen to be the shell-gland, a structure peculiar to the Mollusca. A comparison of the figures of the *Dentalium* larva with those of the Lamellibranch and Gastropodan larvae (Figs. 14, p. 28, 15, p. 31, and Fig. 50, p. 124) will enable the reader without further assistance to recognise the great resemblance in the position of the organs in these different larval forms. As the shell of *Dentalium* is secreted on the dorsal surface of the posterior section of the body, just where the shell-gland appears, it shows the same manner of origin and shape as the young shells of other Molluscs. It shows special resemblance with that of the Lamellibranchs, since it extends like a saddle from the back on to the two sides of the body, but, whereas the young Lamellibranch shell soon becomes bivalve, the shell of *Dentalium* remains single, *i.e.*, it remains to a certain extent at a stage which, in the Lamellibranchs, was found to precede the bivalve shell (p. 60).

Before the shell develops, further important changes take place in the free-swimming larva of *Dentalium*, the post-oral region being the first affected by them. During the early stages, this section is very inconspicuous (Fig. 34 *C*), but it soon increases in size. This region by its growth gives rise to the greater part of the adult body, the pre-oral section degenerating almost completely. We find in this respect a similarity between *Dentalium* and the Amphineura (pp. 5 and 6), and when treating of these processes in the latter, they were compared with the corresponding processes of metamorphosis in the Annelida.

At an early stage, the pre-oral portion of the body becomes somewhat swollen and distinctly marked off from the post-oral part (Figs. 35 and 36 *B*). The definitive mouth is derived from an invagination lying immediately behind the ciliated ring (Fig. 36, *m*). The depression on the dorsal side which is to be regarded as the shell-gland (*sl*) has already been mentioned. When the post-oral section has increased still further in size, two folds laterally placed arise on it; these grow out towards the ventral middle line and at a somewhat later stage meet, at first near the posterior end (Fig. 35 *C*, *m*). These folds, the free edges of which fuse later, represent the rudiment of the mantle which thus rises here very much in the same way as in the Lamellibranchia. The folds enclose a ventral swelling, the foot (Fig. 38 *B*, *f*), at the base of which the otocysts are to be recognised early. These lie rather near the ciliated ring and arise as depressions of the ectoderm which become detached from the latter as closed vesicles. The pedal ganglia also develop as paired thickenings of the ectoderm near the otocysts; at a later stage, they also become detached through delamination. In the middle line of the foot, there seems to be an invagination which perhaps corresponds to the pedal gland described for *Chiton*.

While these changes are taking place in the post-oral part of the larva, the pre-oral section which, in consequence of the preponderance of the former region, appears comparatively reduced, also undergoes modification. Thus, two ectodermal depressions appear close to the ciliated tuft; these at first are shallow, but deepen more and more (Fig. 37 *A* and *B, cg*) and eventually give rise to two closed vesicles which are the paired rudiment of the cerebral ganglion. The cells lining these depressions are, at first, directly continuous with the ectoderm of the cephalic pole, the two depressions being connected together by the cells surrounding the apical ciliated tuft, and thus they represent a common brain-rudiment. The invaginations, which have become tubular, grow in further and further until they reach the walls of the stomodaeum (Fig. 37 *B*). At the same time, by the active proliferation of their cells, they become considerably thickened. They also finally become detached from the ectoderm (*C*) and undergo differentiation into fibrous masses and ganglionic cells, so that there is no room for doubt as to their ganglionic character. Only at a later stage does a commissure form between the two halves of the ganglion which now lose their vesicular character.

The pedal ganglia, as above shown, arise by delamination from the ectoderm, while the cerebral ganglia originate as invaginations. This is somewhat remarkable, since the cerebral ganglia arise, as a rule, through delamination, in other Mollusca. Considering the greater contractility of the larva, the presence of such invaginations suggests a more or less temporary infolding of the surface. KOWALEVSKY assumes that these ganglia first arose as a surface thickening, and explains the invagination of the ganglionic rudiment as due to the absence of room for surface-expansion owing to the limitation of the pre-oral area by the forward concentration of the ciliated ring. The development of the cerebral ganglion in *Dentalium* recalls the condition which we shall find in various Gastropods, where it undoubtedly arises by invagination (p. 191). Since, in these latter cases, we have to do with more specialised forms, it would be desirable, in instituting a comparison with *Dentalium*, to ascertain in what way the cerebral ganglion arises in the more primitive Gastropoda, especially in the Diotocardia.

While the nervous system is forming through the processes just described, both the ciliated tuft and the ciliated ring undergo reduction (Fig. 37). This is especially the case with the latter which, in accordance with the nomenclature used for other Molluscs,* is here also called the velum. The velum is the chief swimming organ and, when it degenerates, the larva has to adopt another method of locomotion. At the stage depicted in Fig. 38, the velum appears still greatly developed, but, as the conical apical pole has degenerated, the anterior section of the larva now seems flattened and plate-like. When the velum is more reduced and the other parts of the body (the shell, the foot, etc.) better developed, the larva sinks to the bottom, where it still swims to some extent by means of the velum, but also creeps with the assistance of its foot, just as do other Molluscan larvae when passing over to the adult form (*cf.* p. 42 and Figs. 53, 54, 67, etc.). The free-swimming life of the larva lasts quite four days, during which time it does not, like the larvae of the Lamellibranchia and the Gastropoda, move at the surface of the water, but appears to maintain itself at various depths (LACAZE-DUTHIERS).

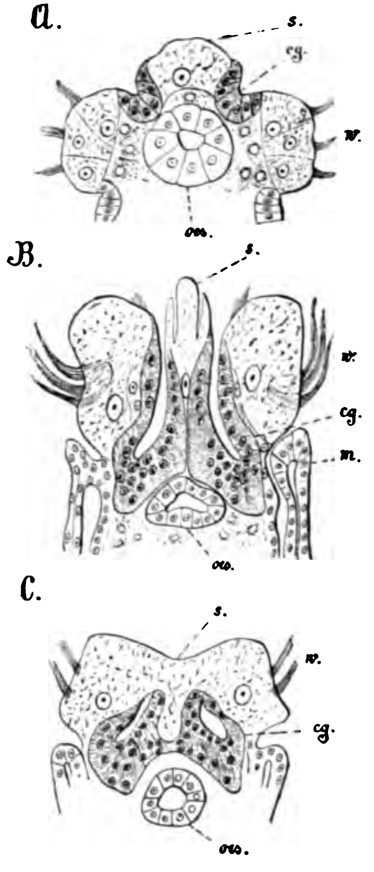

FIG. 37.—*A-C*, frontal sections through older larval stages of *Dentalium*, showing the formation of the brain (after KOWALEVSKY). *cg*, rudiment of the cerebral ganglion; *m*, mantle; *oes*, stomodaeum; *s*, cephalic pole; *w*, pre-oral ciliated ring.

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* *Cf.* on this point pp. 33 and 125.

3. The Transformation of the Larva into the Adult.

Even at the time when the larva sinks to the ground, though still at first moving with the help of the velum, the principal organs of the adult are already present as rudiments. This last period of its development is therefore marked by the growth and the further development of rudiments already present in it.

If we examine the larva externally (Fig. 38 *B*), we find that the shell has grown much larger. At first it was a disc-like structure lying on the back, but then it became saddle-shaped, growing down the sides of the larva till its free edges united in the ventral middle line (Fig. 38 *A*). In the ventral parts of the shell, a parallel striation can be recognised (Fig. 38 *B*), representing lines of growth, so that the growth takes place here in the same way as in the shells of the Lamellibranchia (Fig. 27, p. 60). As the shell increases in size, the fusion of the ventral margins becomes closer. At first the anterior aperture of the shell is still considerably wider than the posterior, a condition connected with the shape of the larva (Fig. 38 *B*), but when the velum degenerates and the shell lengthens, the anterior aperture becomes relatively smaller. The shell now appears almost cylindrical, its anterior aperture being somewhat wider than its posterior aperture. Its increase in size is caused by the secretion of new shell-material from the anterior tubular margin of the fused mantle-folds, the newly formed parts being marked off from the older parts by circular boundary lines; these latter give the shell the appearance, especially in older animals, of being segmented (Fig. 39). At a later stage the shell assumes a dorsal curvature and gradually acquires the tubular conical shape found in the adult. The anterior and posterior apertures, which originated through the lateral growth

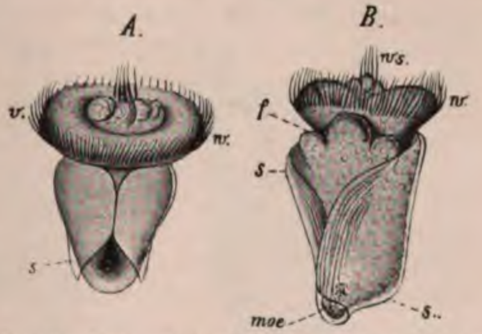

FIG. 38.—Larvae of *Dentalium*, *A* at the end of the second day and *B* on the third or fourth day. *A*, seen from the ventral side, *B*, seen somewhat obliquely from the same side (after LACAZE-DUTHIERS). *f*, foot; *moe*, posterior aperture of the mantle; *s*, shell; *w*, ciliated ring (*v*, velum); *ws*, ciliated tuft.

and ventral fusion of the shell-plate (Fig. 39 *A* and *B*), are retained throughout life.

The shape of the shell, which is at first cylindrical and then tusk-like, is due to the mantle first assuming this form. The latter has already been mentioned as growing out, like the shell, from the back in the form of two folds, which fuse ventrally. Like the shell also it remains open anteriorly and posteriorly. Anteriorly it grows together with the shell in the form of a tube for some distance over the body which lies entirely hidden within it. The foot which, as we saw, originated as a large ventral swelling behind the oral aperture, can be extended for some distance beyond the anterior aperture of the mantle. It soon assumes the triangular form characteristic of *Dentalium* (Fig. 39 *A* and *B*, *f*). In spite of the early development of this exceedingly characteristic shape, it is not to be considered a primitive feature, but must be regarded rather as a later acquisition, as it is wanting in a few genera PLATE (No. 3). In *Siphonodentalium* and *Cadulus* the two lateral lobes are wanting, these genera apparently exhibiting a more primitive form of foot.

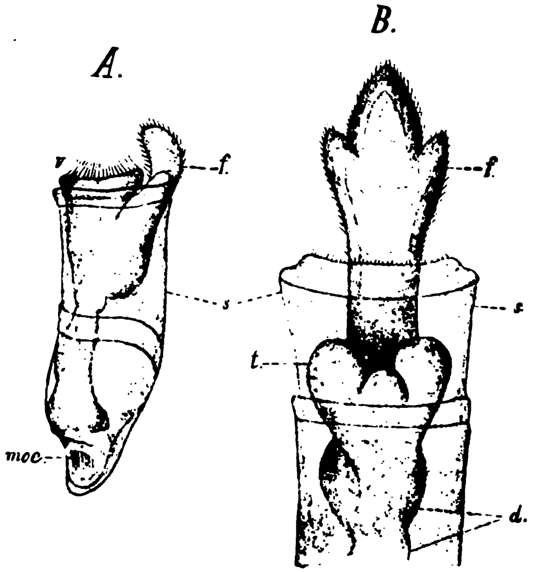

FIG. 39.—*A*, a larva of *Dentalium* undergoing metamorphosis; *B*, anterior portion of a young *Dentalium* (after LACAZE-DUTHIERS). *d*, intestinal canal; *f*, foot; *moc*, posterior aperture of the mantle; *s*, shell; *t*, tentacle-rudiment; *v*, velum.

At a somewhat later stage, at which the velum is still retained, the foot is found protruded from the shell (Fig. 39 *A*). This stage, as well as the younger one depicted in Fig. 38 *B*, recalls that stage in the Lamellibranch larva in which the larval and the adult organs of locomotion are present and functional at the same time (Fig. 20, p. 42). At the posterior end of the larva, an early specialisation of the mantle-folds produced a well-marked channel, lined with powerfully ciliated cells (Fig. 38 and 39, *mœ*). This ciliation is connected with the circulation of the water, which is further promoted by the ciliation of the mantle-cavity.

The foot, as already mentioned, lies in front of the oral aperture. It is here that the prominences arise which give origin to the tentacles (Fig. 39 *B*, *t*). According to Lacaze-Duthiers, there are at first three of these, two lateral and one smaller median prominence (Fig. 39 *B*). These structures, by lengthening, give rise to the tentacular filaments which are so numerous in the adult. The description given does not explain the relation of the filaments to the prominences and to the oral aperture, but the condition of the tentacles in the adult enables us to form some conclusions on this subject. In the adult, the mouth lies surrounded by leaf-like labial appendages at the apex of an egg-shaped projection which, together with the tentacular filaments that are innervated from the cerebral ganglion, must be regarded as the cephalic region. The tentacular filaments arise from two lobes lying at the base of the cephalic projection, so that here also, there are three prominences which might be traced back to those found in the larva. We should then, as in the Gastropoda, consider the middle prominence as the rudiment of the oral cone, and the lateral prominences as the two original tentacles, from which later the tentacular filaments arise.

A similar view of the tentacle-filaments of the adult is taken by Thiele (Literature to Chapter xxxiii.), who compares the two lobes or tentacular shields with the large tactile lobes of *Haliotis* which are beset with tufts. These latter, if lengthened, would result in structures resembling the tentacular filaments. Quite recently Plate (No. 3) also has accepted this view, ascribing to the three prominences on the head of the young animal the above significance.

The radular sac arises during the later stages of larval life as an outgrowth of the stomodaeum. The anus also appears in the larva as a slight depression of the ectoderm behind the base of the foot. The enteron, according to Kowalevsky, becomes connected with it direct, without the formation of an ectodermal rectum.

Further ontogenetic processes especially connected with the development of the inner organs, are described by LACAZE-DUTHIERS, but these processes, which are evidently very difficult to make out, could, at the time when he wrote, only be studied in the complete animal, and could not thus be clearly understood. The above account, in which the most essential ontogenetic phenomena are described, must here suffice, and for further information we must refer the reader to the original treatise on the subject (No. 2).

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CHAPTER XXXII.

GASTROPODA.

Systematic Order:—

I. **Prosobranchia** (Streptoneura).

The gill or gills lie in front of the heart. The pleurovisceral connectives are crossed. The sexes are distinct (save in *Valvata*, *Marsenina* and a few parasitic forms).

Sub-order 1.—Diotocardia. The heart has usually two auricles. The ctenidia are bipectinate and free distally. The pedal centres form long ganglionic cords connected by transverse commissures and closely associated with the pleural centres. Gonad opens into right nephridium (save in *Neritidae*). The nephridium is generally paired.

(*a*) Zygobranchia. Ctenidium paired, ventricle traversed by rectum, two nephridia; shell with apical or marginal slit or row of perforations.

Haliotis, *Fissurella*, *Pleurotomaria*.

(*b*) Azygobranchia. One ctenidium (left of Zygobranchs); two auricles (right ending blindly); heart traversed by rectum (except in *Helicinidae*); nephridium generally paired, operculate.

Turbo, *Trochus*, *Neritina* (one kidney, distinct genital aperture). *Helicina* (pulmonate, no ctenidium, one auricle).

(*c*) Docoglossa. Gill single or absent; heart with single auricle, ventricle not traversed by rectum; two osphradia: two kidneys.

Patella (ctenidia absent), *Acmaea*.

Sub-order 2.—Monotocardia. Heart with one auricle; kidney and gill unpaired, the latter monopectinate and attached for its whole length (save in *Valvata*). The nerve-ganglia distinct and concentrated round oesophagus; pedal commissures rare. Genital aperture distinct, dioecious with rare exceptions.

To this order belong by far the greater number of Prosobranchia, all, indeed, of those the development of which is dealt with here except the forms named above. *Janthina, Murex, Buccinum, Purpura, Nassa, Fulgur, Fusus, Fasciolaria, Strombus, Rostellaria, Crepidula, Calyptraea, Vermetus, Bythinia, Paludina, Thyca, Stilifer, Entoconcha*, etc.

Sub-order 3.—Heteropoda (Nucleobranchia). The character of the nervous system, the position of the gill, ventricle and auricle the same as in the Monotocardia. Foot developed into a fin.

Oxygyrus, Atlanta, Pterotrachea, Carinaria, Firoloida.

II. Opisthobranchia.

The gill and auricle generally behind the ventricle (except in *Actaeon*). Pleurovisceral commissures rarely crossed (*Actaeonidae*). Hermaphrodite, marine.

Sub-order 1.—Tectibranchia. Shell generally present, often much reduced and internal, wanting in *Runcina* and *Pleurobranchea*; with mantle-cavity containing a ctenidium.

Actaeon, Bulla, Acera, Gasteropteron, Philine, Aplysia, Pleurobranchus, Pleurobranchea, Umbrella.

Sub-order 2.—Nudibranchia. Without shell in adult stage; mantle, ctenidium and osphradium wanting.

Tritonia, Doris, Chromodoris, Polycera, Tergipes, Elysia, Aeolis, Doto, Fiona.

III. Pteropoda.

Pelagic Gastropods in which the head is much reduced, and the foot is developed like a fin; now generally classed with the Opisthobranchia.

Sub-order 1.—Thecosomata. With calcareous or cartilaginous shell, with mantle and mantle-cavity.

Spirialis, Limacina, Tiedemannia, Cymbulia, Cavolinia, Hyalocylix, Styliola, Cleodora, Creseis.

Sub-order 2.—Gymnosomata. Without shell and mantle.
Clione, *Pneumodermon*.

IV. PULMONATA.

Principally fresh-water or terrestrial. Ctenidium wanting; mantle-cavity modified as a lung. The pleurovisceral commissures are not crossed. Hermaphrodite.

Sub-order 1.—Onchidiacea. Marine or littoral, without shell; anal and pulmonary orifice posterior.

Onchidium, *Vaginulus*.

Sub-order 2.—Basommatophora. Fresh-water and terrestrial (usually maritime) Pulmonates. Eyes at the bases of the tentacles.

Limnaea, *Planorbis*, *Ancylus*, *Auricula*.

Sub-order 3.—Stylommatophora. Terrestrial Pulmonates. Eyes at the tips of the tentacles.
Succinea, *Vitrina*, *Clausilia*, *Bulimus*, *Helix*, *Testacella*, *Daudebardia*, *Limax*, *Arion*.

1. Oviposition and Character of the Egg-capsules and Egg.

The Gastropoda * are mostly oviparous, but oviposition takes place in such a variety of ways that we can only give a few examples.

An exceedingly simple method of oviposition is found in *Patella*, the eggs of which are laid singly and are apparently fertilised in the water, as copulatory organs are wanting in this genus. It was therefore possible to fertilise these eggs artificially (PATTEN, No. 82). Each egg is surrounded by a somewhat thick radially striated envelope which has a funnel-like projection with a wide aperture (the micropyle).

In most Gastropoda, however, fertilisation takes place within the body of the mother, and the eggs are not laid singly but unite to form larger or smaller masses of spawn. The spawn may have the form of disc-shaped or long hyaline gelatinous masses (fresh-water Pulmonates). Each egg within the gelatinous mass is further

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* A more detailed description of the spawn of land and fresh-water Gastropods is given by PFEIFFER (No. 88). A detailed account of oviposition in Gastropods and notices of the literature on the subject are given by KEFERSTEIN (No. 52) and can also be obtained from the treatises referred to in the Literature. [A good general account of the egg-capsules will be found in FISCHER'S *Manuel de Conchyliologie*, 1887.—ED.]

surrounded by a transparent membrane. In certain marine Gastropoda, *e.g.*, in various Opisthobranchia, this gelatinous spawn attains a great size, forming long, ribbon-like coils (*Aeolis*) or round cords repeatedly bent back on themselves (*Aplysia*). In these cords, the eggs either lie irregularly or else are arranged in one or more rows. The mass of spawn often takes the form of a ribbon which is spirally coiled (*Doris*, *Doto*, *Pleurobranchus*, etc.). These gelatinous masses frequently contain a very large number of eggs, the spawn of a single *Doris* having been estimated to contain 600,000 eggs. The spawn sometimes has the form of a gelatinous sac attached to the substratum by a stalk and containing thirty to forty eggs (*Tergipes*, according to SALENKA, No. 114).

The eggs of the Heteropoda are also laid in gelatinous masses which take the form of long ropes (*Carinaria*, *Pterotrachea*, *Firoloida*) according to FOL (No. 31); only the *Atlantidae* (*Atlanta*, *Oxygyrus*) seem to lay their eggs singly, each surrounded by a gelatinous envelope. The eggs of the Pteropoda also are found in gelatinous masses which are usually tubular in shape. These tubes contain a great number of eggs placed either one behind the other or else close together. The spawn less frequently appears in the form of a thin membranous plate (*Creseis aciculata*), or as round balls containing a large number of eggs (*Clione*).*

In *Fissurella* also the spawn forms a gelatinous mass containing a large number of eggs and deposited on stones. The Prosobranchia for the most part differ greatly from the above in their method of oviposition. A variable number of eggs are usually enclosed in an egg-capsule, the shape of which varies in different forms. Besides the eggs, this capsule contains a fluid or viscid substance which serves as nourishment to the embryo. We are hereby reminded of the Oligochaeta and Hirudinea (*Gnathobdellidae*) in the cocoons of which several embryos are found floating in a nutritive fluid (Vol. i., pp. 281 and 391). The comparison becomes all the more striking when we find that in a few Prosobranchs, as in the Oligochaeta (p. 281), not all the eggs in a capsule develop, but a few, or it may be a large number disintegrate, and serve as food for those that survive. In many Prosobranchia, however, all the eggs in a capsule develop, in *Fulgur*, from 12 to 14, in *Nassa*, from 5 to 15, etc. In *Purpura floridana*, the capsules contain many eggs, all of which undergo

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* Detailed statements as to the oviposition in the Pteropoda and also in the Heteropoda are found in the works of FOL (Nos. 31 and 32).

cleavage, some of the embryos, however, develop no further, but perish, their remains being devoured by the other embryos. This is also the case, according to McMurrich, in a few species of *Crepidula*, and in *Urosalpinx* (Brooks). *Fasciolaria* lays about 200 eggs in each capsule, but only 4 to 6 of these develop, and this is also the case with *Buccinum undatum*. Each capsule of *Purpura lapillus* contains 400 to 600 eggs, only 10 to 16 of which develop into mature embryos (Selenka). The egg-capsule of *Neritina fluviatilis* also shelters a large number of eggs (according to Blochmann 70 to 90) although only a single embryo in it attains complete development (Claparède). In this case, the unfertilised eggs divide soon after the polar bodies have formed, and break up into irregular heaps of protoplasmic spheres, being in this way distinguished from the eggs undergoing cleavage.

In shape and structure, these egg-capsules vary greatly. As a rule they are formed of tough leathery or parchment-like integument and are in some cases approximately spherical, but appear flattened on the side by which they are attached to foreign objects. This is the case in *Neritina*, the older cocoons of which easily divide into two hemispherical halves. To allow the brood to escape, the capsule occasionally has an aperture closed by a delicate membrane, situated opposite to the point of attachment. Several capsules are usually found together, as in *Buccinum undatum*, *Fusus antiquus* and others, the capsules of which are piled one upon another, thus forming an enormous mass of spawn. They occasionally appear laterally compressed and, in one species of *Fusus* observed by Bobretzky, are round plano-convex discs, attached by the flattened side. The capsules of *Busycon* (*Fulgur*) also are leaf-like or rather disc-shaped; these are arranged in a row like a roll of coins, and are attached to a common filament. These capsules have an aperture opposite to the points of attachment for the escape of the brood.

In *Nassa mutabilis*, the capsules are cup-shaped and attached by the obliquely truncated end, the opposite pointed end carrying an aperture at first closed by a membrane. The surface of these capsules shows polygonal markings which form rib-like or membranous ridges. They are found united into large clumps on sea-weeds and worm-tubes.

The cup-like capsules of many Prosobranchia are arranged in groups attached by their narrow ends drawn out into stalks (*Murex*). Here also, the aperture of the cup is closed by a membranous cover, which opens when the brood is ready to hatch. In *Purpura lapillus* 10 to 15 such capsules, which, however, are more flask-shaped and of leathery consistency, are fastened to a similarly constituted, structureless membrane which, in its turn, is attached to a stone. The same is the case with the capsules of *Fasciolaria tulipa*, in which the edges of the cup are continued into a wavy membrane. The form of this latter capsule seems to come nearest that of the well-known *Janthina*, the cup-like capsules of which are attached to a kind of raft by means of which the animal floats in the sea. This float is a large spindle-shaped body formed of the same substance as the capsules and containing air-spaces. It is connected by its pointed end with the foot of the animal and from its lower side the capsules hang. The float is also found in the male, and without its aid the animal cannot move about freely in the water, so that it must not be regarded merely as an organ connected with oviposition, although it may perhaps be considered to have been primarily developed for this purpose.

The conditions of oviposition in the terrestrial Gastropoda differ somewhat from those of the aquatic forms. The eggs of the former may also be surrounded by a gelatinous albuminous substance and may be connected together into spawn-masses which resemble rows of beads (*Limax*) or else may be massed in larger numbers to form gelatinous balls (*Onchidium*). In the latter case, the structure of the spawn is rather more complicated, each egg being surrounded by a mass of albumen which is enclosed in a transparent but resistant envelope. The latter lengthens in a line with the two opposite poles of the oval albuminous mass, forming at each end a thread which is continued into the envelope of another egg, so that the eggs constituting the spawn are connected into wreath-like chains which are again surrounded by the common gelatinous mass. The albuminous mass surrounding the egg usually, in the terrestrial Gastropoda, becomes still further protected by a firm membrane impregnated by lime-salts. A more or less thick calcareous shell is thus formed around the egg; this, even in *Helix pomatia*, is of somewhat firm consistency. The eggs are usually deposited in great numbers (60 to 80 in *Helix pomatia*) in small holes in the ground prepared by the parent animal and are then covered over with earth. Species of *Bulimus* which live on trees roll up leaves into the form of cornucopiæ and lay in these their soft-shelled eggs.

The eggs of the terrestrial Pulmonata attain a considerable size. Even the eggs of *Helix pomatia* measure 6 mm. in diameter. Those of the Ceylon form, *Helix (Acavus) Waltoni* are as large as a sparrow's egg (P. and F. SARASIN, No. 102), and those of an American species of *Bulimus* which are oval, measure 5 cm. in length and are therefore larger than the eggs of pigeons. These eggs, in consequence of their firm, smooth shell, closely resemble the eggs of birds, but are distinguished from the latter by the fact that the actual egg (the yolk) is always very small and floats in a great mass of viscid transparent matter enclosed within the egg-shell. But although the yolk or the egg-cell, as compared with the size of the egg is almost nil, the mature embryo almost completely fills the shell, having increased in size to this extent at the expense of the surrounding mass of nutrient material.

Some Gastropods take care of their eggs. Those species of *Crepidula* which are immovably fixed to one spot (*C. fornicata*, *plana*, and *convexa*, McMurrich, No. 70, Conklin, No. IV) retain the egg-capsules, which are attached to the substratum, under cover of the shell. The wall of the capsules thus protected are naturally of delicate nature. *Vermetus* attaches a few capsules to the inner surface of its shell, near the aperture of the latter (Lacaze-Duthiers). In comparatively few Gastropods, the whole development is passed through within the body of the mother. These forms are therefore viviparous. The best known example is *Paludina* (*Viviparus*) *vivipara*, the eggs of which develop in the oviduct, which functions as a uterus, until the form of the adult is reached. Its course of development, however, exactly resembles that of other Prosobranchia. The egg is surrounded by a conspicuous layer of albumen, which again is enclosed in a membrane that runs out into a twisted stalk, so that a kind of cocoon is formed. As a rule, only one egg lies within this envelope, but two are sometimes found in it (Leydig, No. 68), the resemblance to the egg-capsules of other Prosobranchia being thus heightened. Similarly, in a few species of *Melania* [in *Typhobia* and *Nassopsis*], the embryos develop in the uterus, and are only born when they have attained the adult form.

[In some species of *Melania* and in *Spekia*, the embryos develop in a special brood-pouch formed by an ectodermal invagination near the right cephalic tentacle. The viviparous habit appears to be largely confined to fresh-water forms.]

A few Pulmonata are, like the Prosobranchia above-mentioned, viviparous, the development of the embryo here also taking place in the oviduct which is transformed into a uterus. This is the case in a few species of *Clausilia*, *Pupa*, *Helix* and *Vitrina*. Nearly related species are often found to differ greatly in their methods of reproduction, some being oviparous, and others viviparous (No. 102).

The actual egg of the Gastropods, if not specially large, is fairly rich in yolk which is often yellow, but occasionally of some other colour (blue-green in *Patella*); this frequently renders the egg quite opaque. A clear protoplasmic region can frequently be distinguished from a more opaque region laden with yolk, the difference between the animal and the vegetative pole being thus indicated (Fig. 40 *A* and *B*).

In some Gastropod eggs there is less yolk than in others. *Paludina* may be cited as an extreme case on the one hand, and *Nassa* and *Fusus* on the other. The egg itself is usually surrounded by a clear viscid mass which, in its turn, is again enclosed in a transparent envelope. It has already been mentioned that other envelopes may be added, and that several eggs may be enclosed in a common capsule.

2. Cleavage and Formation of the Germ-Layers.

In spite of the great number of forms among the Gastropoda and the different development of the several divisions, we can, in every case which has been investigated, recognise a common plan in the cleavage of the egg, although at times this is more or less obscured by modifications introduced by the variations in the amount of the yolk present.

In this respect we have resemblance to the Lamellibranchs, but the course of cleavage itself is different in the Gastropoda. The phenomena of cleavage have been studied in a large number of Gastropods and may therefore be considered as pretty accurately understood. As early as 1850, the cleavage of the Gastropod egg was described by WARNECK (No. 130), very completely, considering the time at which he wrote. And since then it has been investigated by a number of zoologists, among whom we may mention FOL, BOBRETZKY, RABL, MARK, BLOCHMANN and others (see the literature appended to this chapter).

In all Gastropods, as far as is known, cleavage is total; at first it may be equal, but it very soon becomes unequal. The egg, in many cases, is divided up into two large blastomeres of almost equal size by a median groove which cuts it below the polar bodies (Fig. 40 *A*). A second furrow, which is also meridional, divides the egg into four almost equal blastomeres (*B*, *I-IV*). These four cells, owing to the nature of the second cleavage, often lie in such a way that two are in contact with one another in the centre of the egg and thus separate the other two (Fig. 48 *A*, p. 120) [see Conklin, No. IV, pp. 44-53 on this point]. At the line of junction between the first two blastomeres, the transverse axis of the future embryo can already be seen, while the plane at right angles to this represents the sagittal plane of the embryo. The position of the axes is thus determined very early as was seen to be the case in other animals.*

An equatorial furrow cuts off from these four cleavage-cells four smaller cells so that the embryo now consists of four macromeres and four micromeres (Fig. 40 *C*, *I-IV* and *I'-IV''*), the latter lying at the animal pole. The relative size of these blastomeres varies considerably in different Gastropods. In *Patella* (Patten, No. 83), and in *Paludina*, for instance, the micromeres are not much smaller than the macromeres, whereas in *Fulgur*, the micromeres in comparison with the macromeres, which are very rich in yolk, are hardly visible (McMurrich, No. 70). These differences are no doubt determined by the amount of yolk present in the eggs.

As cleavage proceeds, four more micromeres arise (*D*, *I''-IV''*), as before, from the macromeres. As a rule, this process is repeated once more, and in this way three generations of micromeres arise from the macromeres; this, however, is not the case in all forms. The nuclear spindles in the macromeres depicted in Fig. 40 *E*, show that these cells are preparing to divide to form the third generation of micromeres. In the meantime, the already formed micromeres have, by division, increased still further in number; sometimes, however, they do not multiply until later. In *Neritina*, according to Blochmann, the first and second generation of micromeres (*I-IV* and 1-4) divide first, but in *Planorbis* the twelve cleavage-spheres which now compose the embryo undergo almost simultaneous division (Rabl). In the example depicted in Fig. 40 *E*, the twenty-four-celled stage is reached by a division of the first generation of micromeres quickly followed by the division of the second generation and the abstriction of the third row of micromeres from the macromeres as indicated by the nuclear spindles in *I''-IV''* and *I-IV*, *E*. The macromeres, through this last division, are either considerably

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* [This seems to hold good for all those forms in which the position of the first two cleavages has been investigated in relation to the axis of the adult body. Conklin, for instance (No. 25), concludes that, in *Crepidula*, the first furrow corresponds to the transverse axis and divides the egg into an anterior and a posterior half, while the second furrow lies in the longitudinal axis and denotes the division of the egg into a right and a left half. Heymons (No. XII.) finds a similar condition in *Umbrella*. *Cf.* also the position of the axis at a somewhat later stage, as given on p. 143.—Ed.]

reduced in size (Fig. 40 *H*), or, as is most frequently the case, are retained for some time longer as specially large cells (*F* and *G*), the micromeres which have arisen from them shifting towards the animal pole. The multiplication of the latter continues and leads to the development of a cap of smaller cells which lies upon the macromeres (*F* and *G*, etc.).*

The great agreement of the various stages of cleavage in the Gastropoda with those of the Turbellaria is very striking, as may be seen from a comparison of Fig. 40 with Fig. 75, Vol. i., p. 162. This is most marked in stages *C*-*E* of Fig. 40, but the later stages *F* and *G* also show great resemblance to the corresponding stages in the Turbellaria (Vol. i., Fig. 75 *F* and *E*). The radial structure does not, indeed, in the Gastropoda, extend as far as in the Turbellaria, and cannot be directly compared with that of the Polyclad embryo, because the radial cells of the latter are to be regarded as the rudiment of the mesoderm (Vol. i., Fig. 75 *C* and *E*), while, in the Gastropods, they are ectodermal. The radial structure in the two cases is, however, only apparent, since the axes of the body can early be demonstrated both in the Turbellaria and the Gastropoda. In a similar way we might speak of a radial symmetry in connection with the stages of cleavage of many other animals. Further, this radial symmetry is very soon lost in the Gastropod embryo by the appearance of the paired rudiment of the mesoderm which gives the embryo a marked bilateral character. It has, however, been asserted (MANFREDI, No. 72), that in *Aplysia*, when the embryo consists of eight blastomeres only, the mesoderm arises as four cells through division of the four micromeres; this, if true, considerably strengthens the resemblance

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* [Since this work was published, a large number of observations relating to the early stages in the cleavage of the Gastropodan egg have been recorded, all of which lend additional support to the belief expressed above (p. 106) that a common type or plan could be recognised in the segmentation of the eggs of all the various divisions of the Gastropoda.

Thus, it is possible to trace the origin of the ectoderm in every case to three quartettes of micromeres which are cut off successively from the macromeres, complication being introduced, in some cases, by the secondary division of the first and second quartettes before the separation of the third and last quartette from the macromeres, and in other cases, by the lesser development of the yolk and consequent slighter differentiation of the blastomeres, thus making it difficult to identify the macromeres.

A very striking feature, common to the development of most Gastropodan eggs and well shown in Fig. 40 *C*, *D* and *E*, has been termed the spiral cleavage. Thus, as early as the third cleavage, *i.e.*, the formation of the first quartette of micromeres, a curious obliquity becomes evident. This obliquity is visible in the nuclear spindle even before the completion of the division, but becomes more apparent at its close, when the cells of the upper quartette (micromeres) lie in the furrows between the cells of the lower quartette (macromeres). This "spiral" character is generally more apparent than is represented in Fig. 40 *C*, but is well shown in *D* in the case of the second quartette of micromeres. Spiral cleavage is of particular interest in view of the fact that, in sinistral Gastropoda, the obliquity takes the reverse inclination to that which is found in dextral forms (CRAMPTON, No. V and HOLMES, No. XIIIA). For a general discussion of the significances of the forms of cleavage in the Gastropodan egg see CONKLIN (No IV, pp. 185-192).—ED.]

to the Turbellaria, but the mode of formation of the mesoderm described by this author so little agrees with what is found in other Gastropods, that it must be regarded as quite improbable, especially when we remember that **Blochmann**, who investigated the ontogeny of *Aplysia* at the same time as **Manfredi**, saw nothing of this process, and **Mazzarelli** who, quite recently, has made similar investigations, describes the formation of the mesoderm in an entirely different way.

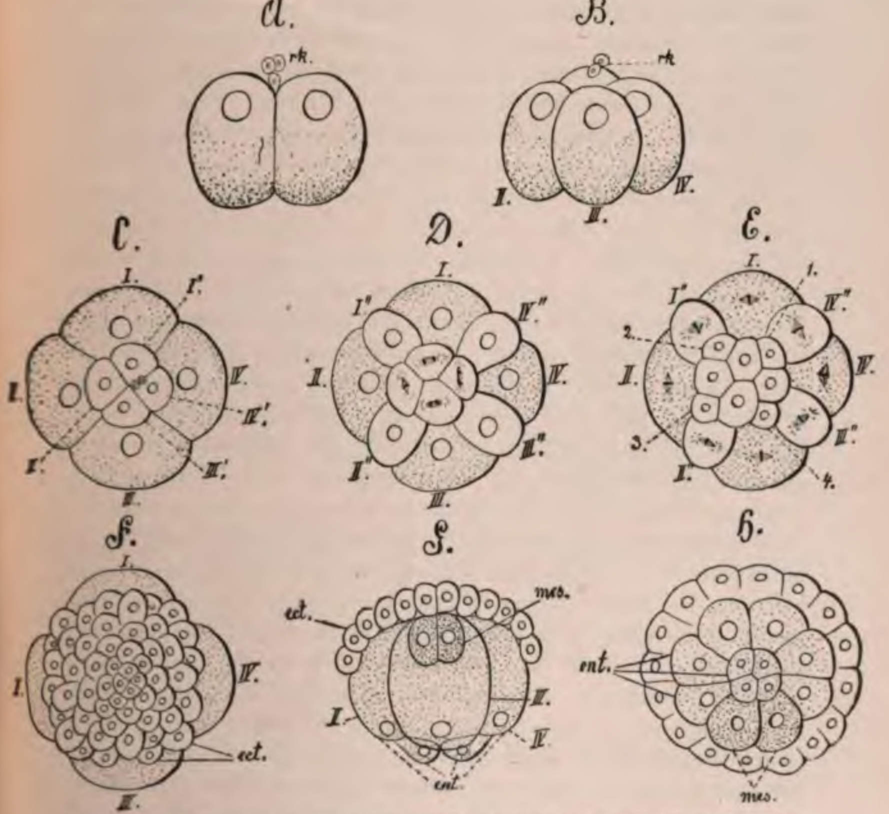

Fig. 40.—*A-H*, diagrams in illustration of the cleavage and formation of the germ-layers in the Gastropoda (principally after **Rabl** and **Blochmann**). *A* and *B*, seen from the side; *C-F*, seen from the animal, and *H* from the vegetative pole; *G* represents an optical section. *I-IV* denote the large cleavage-spheres, from which the micromeres (*I'-IV'*, *I''-IV''*) are abstricted by successive divisions, 1-4, micromeres, arising from *I'-IV'*. *ect*, ectoderm; *ent*, entoderm; *mes*, mesoderm; *rk*, polar bodies.

The rudiments of the germ-layers develop, as in the Amphineura and Lamellibranchia, very early. In *Planorbis*, according to **Rabl**, the posterior of those two macromeres which are in contact with one another mesially, divides into two cells, the smaller of which shifts towards the centre of the egg. The other three macromeres also give off such a small cell towards the centre, so that there are now four small entoderm-cells (Fig. 40 *H*). The posterior macromere then divides into two large cells of about equal size (*H*, *mes*) and the other macromeres also divide (*H*, *ent*). In *Neritina*, a similar process takes place, but the size and position of the cells is somewhat different (Fig. 40 *G*, *mes* and *ent*). In *Crepidula* and *Umbrella* also (Fig. 48 *B*, p. 120), one of the posterior macromeres gives rise to an entomere and to a cell which divides into a right and a left half. These two last cells are the primitive mesomeres and, according to their origin, either already lie in the primary body-cavity (*G*) or else are pressed into that cavity later. This latter is the case when, as in *Planorbis* (Fig. 40 *H*), these cells (*mes*) at first form a continuous circle with the large cells (*ent*). A cleavage-cavity is sometimes first developed at this stage, by the partial separation of the layer of micromeres from the macromeres, or else it forms still earlier, so that even before the stage represented in Fig. 40 *H*, the embryo may exhibit the form of a blastula with a wall much thickened at the vegetative pole, in which case an invagination-gastrula results (*Planorbis*).* In the first case, however, in spite of the fact that the formation of an epibolic gastrula has already commenced (*G*) or has been actually attained through the failure of the micromeres to rise up from the macromeres, an invagination may also take place later owing to the appearance of a rather large cleavage-cavity. In this latter case, however, the germ-layers may also already have appeared as rudiments. The macromeres next give off at the vegetative pole a few small cells (*G* and *H*, *ent*) which, together with the former, represent the rudiment of the entoderm. The rudiments of the three germ-layers are now visible; the ectoderm has arisen from the micromeres, the entoderm is represented by the macromeres and their last derivatives, and, finally, the mesoderm is found in the form of two cells (derived from one of the [posterior] macromeres).†

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* [The cleavage-cavity seems to be very variable in the Gastropoda, and even in those forms in which it is most conspicuous, it is found to vary at different stages of cleavage. This variation is most noticeable in *Limax*, and KOFOID (No. XIV) thinks that this cavity is connected with the excretory processes of the blastomeres. The cavity is most developed in those Gastropods in which the gastrula is embolic and, during invagination, it becomes temporarily obliterated, but re-appears later (*Planorbis*, RABL, No. 90).—ED.]

† [It will be seen that if the interpretations given on p. 107 of the relation between the first and second cleavage-planes and the axis of the adult body

The formation of the germ-layers does not take place in all Gastropods in the manner just described, indeed, the layers form in very different ways in diverse Gastropods, as might be expected from the variations found in the manner of cleavage. It has already been mentioned that such variations occur in spite of strong general resemblance. The method of cleavage described above applies, with slight modifications, to many Gastropods. We append a list of a few genera chosen as representatives from the different divisions in which this is the case: among the Prosobranchia, *Fissurella* (No. 12), *Neritina* (No. 7), *Crepidula* (Nos. 24 and 25), *Bythinia* (Nos. 91, 101 and 28), *Vermetus* (No. 99), *Fusus* (No. 11), *Entoconcha* (No. 76); among the Heteropoda, *Firoloida* and *Pterotrachea* (No. 31); among the Pulmonata, *Planorbis* (No. 91), *Limnaea* (Nos. 130 and 131), *Limax* (Nos. 130 and 73), *Onchidium* (No. 51); among the Opisthobranchia, *Doto*, (No. 91), *Ercolania* (No. 124), *Tethys* (No. XXVI), *Umbrella* (No. XII); among the Pteropoda, *Cavolinia*, *Cymbulia* (No. 32), *Clione* (No. 55).

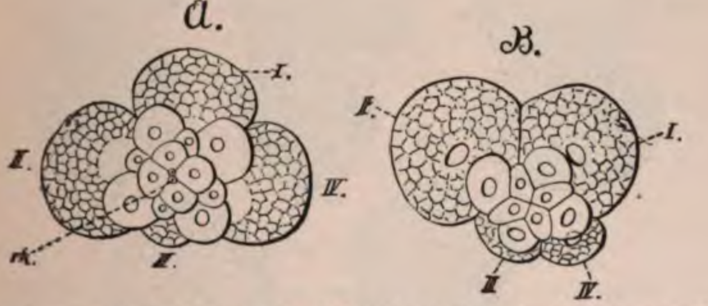

FIG. 41.—Stages in the cleavage of *Cavolinia tridentata* (*A*) and *Aplysia limacina* (*B*) (after FOL and BLOCHMANN). *I.-IV.*, the four macromeres, above them lie the micromeres and the polar bodies (*rk*).

Certain modifications in the cleavage are no doubt principally determined by the amount of yolk in the egg. These are connected specially with the size of the macromeres. In *Cavolinia* and *Cymbulia*,

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are correct, then there must be two anterior and two posterior macromeres, and it is from one of the latter that the primitive mesomere is now said to arise. It seems further probable that the first mesomere arises from the left posterior macromere in dextral and from the right in sinistral Gastropoda. In spite, however, of the large amount of evidence which is accumulating in favour of this view we must, when we consider the great difficulty in tracing the relations of the early cleavage-planes, wait for further observations, especially on Prosobranchs, before we finally conclude that this origin of the mesoderm is typical of all Gastropoda. See footnote, p. 119.—ED.]

for instance, one of the four macromeres is markedly smaller than the others, although the cleavage, in other respects, follows the usual course (Fig. 41 *A*). At the four-celled stage in *Aplysia*, two blastomeres are distinguished by their smaller size, a difference which can be recognised in the later stages also (Fig. 41 *B*). Although the two smaller macromeres are still visible at this stage (*B*, *III.* and *IV.*), yet in later ontogenetic stages, only the two larger ones are still distinct, and these are apparent until grown over by the micromeres (epibolic gastrulation, RAY LANKESTER, Chap. xxvi., Lit. No. 29; MANFREDI, No. 72, BLOCHMANN, No. 8). Another Opisthobranch, *Acera*, resembles *Aplysia* in this respect (RABL, No. 91).

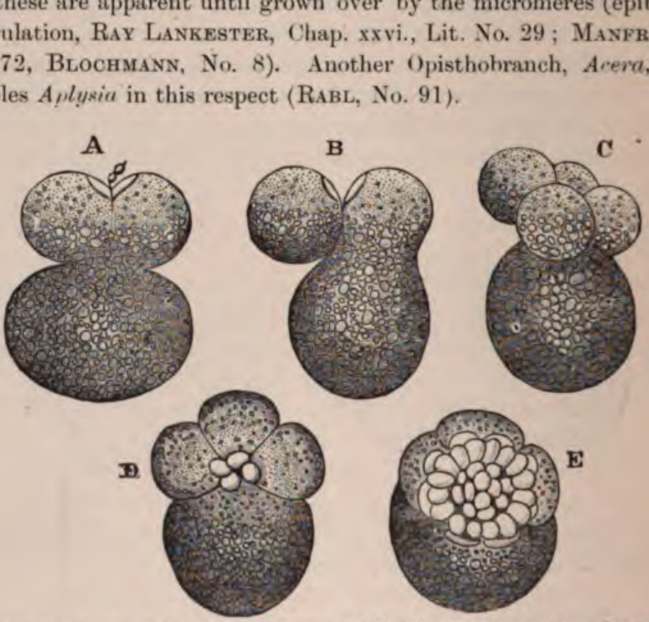

FIG. 42.—*A*-*E* stages of cleavage in *Nassa mutabilis* (after BOBRETZKY from BALFOUR'S Text-book). *A*-*C*, formation of the macromeres, on which, in *D*, four, and in *E* a large number of micromeres lie.

The first stages of cleavage, in *Nassa mutabilis*, are very striking and peculiar (BOBRETZKY, No. 11). The egg contains a large amount of food-yolk, and the formative protoplasm is aggregated at the animal pole, over which the polar bodies are situated. An equatorial and a vertical furrow, the former near the animal pole, appear simultaneously, and divide the ovum into three segments, two smaller blastomeres which are produced by the vertical furrow and one large brown sphere, minus a nucleus and consisting entirely of yolk-material (Fig. 42 *A*). The two blastomeres thus rest upon this sphere somewhat like a germ-disc, except that the yolk has in this case not attained to any great size. This condition soon disappears, the yolk-sphere fusing with one of the blastomeres (Fig. 42 *B*); at the four-celled stage, produced by a triple segmentation of the large sphere and division into two of the small blastomeres, it reappears (*C*). The yolk-sphere, which at this stage is distinct from the blastomeres, again fuses with one of the cleavage-spheres, and it thus happens that the eight-celled stage (*D*) does not essentially differ from the usual condition (Fig. 40 *C*) except for the fact that one of the macromeres is specially large, the greatest mass of the yolk having accumulated in it. The further cleavage seems to take place in a regular manner and in a way similar to that above described. Finally, here also, a large number of very small micromeres lie like a disc or cap upon the four macromeres (Fig. 42 *E*). At a later stage, in *Nassa*, there is one large cell which is specially distinguished from the rest. While the other cells divide further it remains, on account of its large amount of yolk, almost unchanged. It represents a kind of food-yolk which, in a much more specialised form, will be found again in the Cephalopoda.

The preponderance of one macromere over the three others is found to a striking degree in *Purpura* (SELENKA, No. 115) and in *Urosalpinx* (BROOKS, No. 17; CONKLIN, No. 24), forms which in their ontogeny seem to resemble *Nassa*.

3. The Formation of the Germ-layers.

The first appearance of the germ-layers in a few forms has already been alluded to in connection with the phenomena of cleavage, but in other forms these layers arise in a somewhat different way, their origin in some cases being so differently described by authors that this point calls for special attention.

Gastrulation is attained in different ways in accordance with the variations in cleavage. In the simplest cases, *e.g.*, *Planorbis* and *Patella*, a blastula with a comparatively large cleavage-cavity arises (Fig. 43). The vegetative pole of the blastula is formed by the

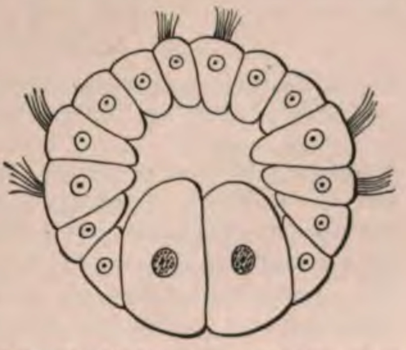

FIG. 43.—Blastula-stage of *Patella* (after PATTEN). The ciliated tuft (at the cephalic pole) and the ciliated ring are already indicated.

macromeres and consequently appears much thickened. After the mesoderm has become differentiated, the entomeres begin to increase in number (Fig. 40 *H, ent*), and the whole entoderm becomes invaginated into the cleavage-cavity, and thus a typical invagination-gastrula forms (*Planorbis*, RABL). In *Patella*, on the contrary, an extremely large solid ingrowth of macromeres takes place from the vegetative pole of the blastula (Figs. 49 and 50, p. 124). From this ingrowth, the mesoderm and entoderm become differentiated and, at a later period, an archenteric cavity forms within the till now solid entoderm (PATTEN, No. 83).

In a few Gastropods, such as *Bythinia* and *Limnaea*, a cleavage-cavity is present at an early stage, but this soon disappears; the blastula now becomes flattened, the macromeres prepare to invaginate, and the micromeres, advancing towards the vegetative pole, grow over the mesoderm which, has already formed, and a part of the entoderm (RAY LANKESTER, No. 63; WOLFSON, No. 131; ERLANGER, No. 28). Gastrulation follows the same course in *Paludina*, with the distinction that, in this form, the cleavage-cavity is from the first very small, and the mesoderm only later becomes recognisable (*cf.* p. 134, BÜTSCHLI, No. 18). In the Heteropoda also (*Firoloida* and *Carinaria*) a more or less flattened blastula with a slit-like blastocoele, the animal end of which is composed of small and the vegetative of large cells (Fig. 44 *A*), gives rise by a similar process

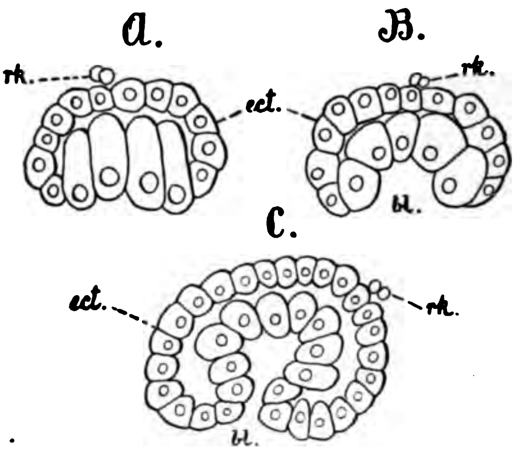

FIG. 44 —*A-C*, embryos of *Firoloida Desmaresti* in the stage of gastrula-formation (after FOL). *bl*. blastopore; *ect*, ectoderm; *rk*, polar bodies.

to the gastrula (Fig. 44 *B*). When gastrulation commences, and during its course, the cleavage-cavity is but slightly developed, or even entirely degenerates, but enlarges considerably at a later period through the greater development of the ectoderm. The archenteric cavity also is large (Fig. 44 *C*), and the archenteron thus represents a wide sac (FOL, No. 31). These stages resemble those of *Paludina.*

The partial circumcrescence of the macromeres by the ectoderm, as it occurs in the last-named form, is a first indication of the transition to the epibolic gastrula which is formed at an early stage in the Pteropoda (*Cymbulia*, *Clione*). The cleavage-cavity here is either entirely reduced or but slightly indicated. The thin layer of ectoderm-cells then lies in close contiguity to the entoderm (Fig. 45 *A*). But even here an invagination takes place. The middle entoderm-cells shift upwards, the ectoderm at the same time growing out still further towards the vegetative pole and thus narrowing the blastopore, and the epibolic gastrula thus has the appearance of an invagination-gastrula (Fig. 45 *B*). A similar process was described in connection with the Lamellibranchia (*Ostrea*, p. 27).

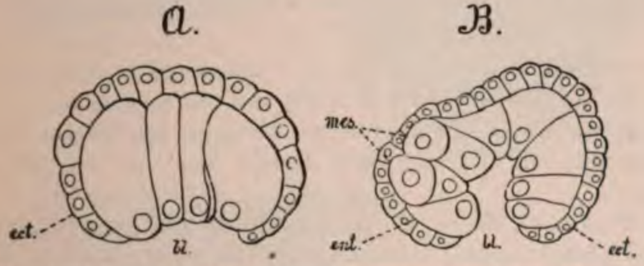

FIG. 45.—*A* and *B*, embryos of *Clione limacina* showing the formation of the germ-layers (after KNIPOWITSCH). *bl*, blastopore; *ect*, ectoderm; *ent*, entoderm; *mes*, mesoderm.

The gastrula arises by epibole in *Fusus* (BOBRETZKY, No. 11), *Aplysia* (BLOCHMANN, No. 8), *Crepidula* (CONKLIN, No. 24) and *Vermetus* (SALENSKY, No. 99). In these forms, the ectoderm, as a thin layer, surrounds the four yolk-laden macromeres, from which, at a later stage, small cells become detached, chiefly at the vegetative pole, that is, in the neighbourhood of the blastopore; by the development of these small cells an archenteron is formed, bounded dorsally by the four macromeres and ventrally by these small cells. In *Neritina*, these cells form early, before the circumcrescence of the macromeres has proceeded so far (Fig. 40 *G*, *ent*). According to Blochmann (No. 7), the smaller entoderm-cells shift beneath the layer of ectoderm towards the animal pole and here form, above the macromeres, a kind of cap (Fig. 46). In this way an archenteron arises, which is bounded partly by smaller entoderm-cells and partly by the macromeres. *Neritina* in this point more nearly resembles the forms considered above, in which there was a transition from an epibolic to an invagination-gastrula. A cap of micromeres at first lies on the large macromeres, somewhat as in Fig. 40 *F* and *G*, but a cleavage-cavity soon appears between the micromeres and the macromeres. As the circumcrescence of the macromeres advances, the archenteron develops, although in a way which deviates from that commonly met with.

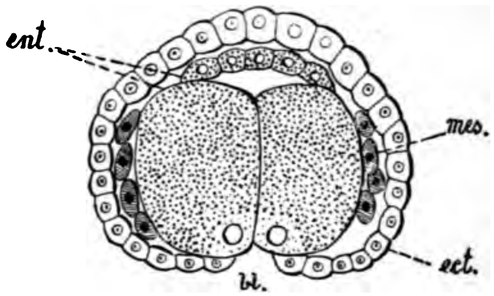

Fig. 46.—Embryo of *Neritina fluviatilis* in optical section (after Blochmann). *bl*, blastopore; *ect*, ectoderm; *ent*, entoderm; *mes*, mesoderm.

In *Urosalpinx*, *Fulgur*, *Purpura* and *Nassa* also, gastrulation takes place through epibole (Brooks, No. 17; McMurrich, No. 70; Bobretzky, No. 11), and in these forms, on account of the great abundance of yolk, other variations in the formation of the germ-layers are caused. It has already been shown that in *Nassa mutabilis* the one of these forms which has received most attention, as well as in *Urosalpinx* and *Purpura*, one of the macromeres which is specially rich in yolk is far larger than the others (Fig. 42 *D*). The micromere-layer lies on the macromeres in the form of a disc or cap (Fig. 42 *E*). When the micromeres grow out towards the vegetative pole, the three smaller macromeres also take part in the process of shifting and in so doing increase in number (Fig. 47 *B*, *hy*). Finally, these cell-complexes, which represent the rudiment of the entoderm, become more and more shifted towards the vegetative pole (Fig. 47 *C* and *D*). They line a cavity which corresponds to the future lumen of the enteron. It is the protoplasmic parts of the macromeres that are at first used for the formation of the epithelium of the enteron; the rest forms a kind of food-yolk upon which the cells of the germ-layers lie like a germ-disc (Fig. 47 *B*). As far as can be seen from

Brooks' description, the entoderm forms in an exactly similar way in *Urosalpinx*. A mass of food-yolk is also formed in *Fusus*, *Vermetus*, *Aplysia*, etc., by those macromeres which attain to so considerable a size.

The Mesoderm. In connection with the account given of the processes of cleavage, it was stated that the middle germ-layer arises very early. In *Planorbis*, one of the posterior of the four macromeres* divides, giving rise to an entomere and to the primitive mesomere, which latter eventually yields the two primitive mesoderm-cells, as already shown (p. 110). These are soon pressed into the cleavage-cavity, and, by their increase in number, give rise to the two mesoderm-bands. This seems also to be the case in the Ptero-

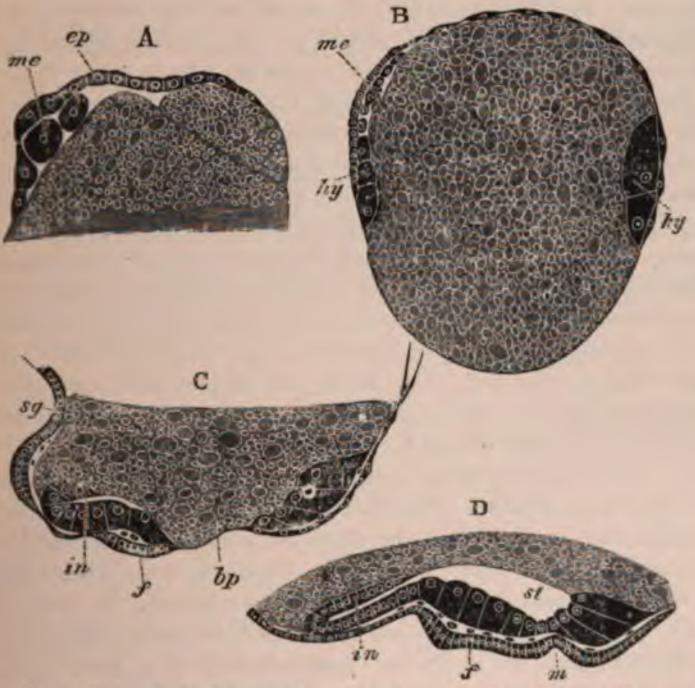

Fig. 47.—*A-D*, longitudinal sections through embryos of different ages of *Nassa mutabilis* (after Bobretzky, from Balfour's Text-book). *bl*, blastopore; *ep*, ectoderm; *f*, rudiment of the foot; *hy*, entoderm; *in*, intestine; *m*, mouth; *me*, mesoderm; *sg*, shell-gland; *st*, enteron.

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* [This cell is believed to be homologous in all Gastropods and is now designated D by students of cell-lineage.—Ed.]

poda (*Clione*, Knipowitsch, No. 55). In this case also, the division of one of the four macromeres is said to give rise to two cells which are soon driven inwards, these two symmetrically placed cells denoting the posterior end. Knipowitsch conjectures that in those Pteropoda in which, according to Fol, one of the macromeres is distinctly smaller than the others, this smaller macromere yields the primitive mesoderm-cells (Fig. 41 *A*, *III*). In *Clione*, each of the two cells which arise by the division of the macromere again divides into two large cells (mesoblasts, Fig. 45 *B*, *mes*), which now take up a symmetrical and bilateral position at the posterior end and, by continuous multiplication, give rise to smaller cells.

The radial character of the cleavage, which is so marked during the early stages (Fig. 40 *C-E*), is much modified by the differentiation of the mesoderm, and, when the two mesoderm-cells appear, the germ attains a true bilateral symmetry (Fig. 40 *H*). This is the case in *Planorbis* and a similar condition is shown in *Bythinia* also. As in *Planorbis*, the primitive mesoderm-cells in *Bythinia* arise from one of the posterior blastomeres, which is to be regarded as a mesentomere, *i.e.*, it divides into two cells, one of which remains as an entomere in the position occupied by the posterior macromere, while the other shifts slightly forward. This latter cell divides into two cells in such a way that the two lie side by side ; these are the mesodermal teloblasts which give rise to the mesoderm-bands (v. Erlanger, No. 28). The mesoderm rises in a similar manner in *Crepidula* (Conklin, No. 24) * and *Neritina* (Blochmann, No. 7), although a few slight modifications are here brought about by gastrulation taking place through epibole in consequence of the large size of the macromeres, or by a near approach to this form of gastrulation. In *Neritina*, a cell becomes detached from one of the posterior macromeres which, by division, gives rise to the two mesoderm-cells (Fig. 40 *G*). This process can be made out very distinctly in the eggs of an Opisthobranch (*Umbrella*) examined by Heymons (Fig. 48). Here also a smaller entoderm-cell and a larger mesoderm-cell (*B*, *ent* and *m*) arise through the division of one of the posterior macromeres (*A* and *B*). This primitive mesomere divides into two laterally placed mesoderm-cells (*C*, *um*) which soon give rise to the two mesoderm-bands, formed of a few large cells containing yolk and other smaller cells (*D* and *E*). The rise of the mesoderm from one of the posterior

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* [Conklin (No. IV.) now finds that, in *Crepidula*, the mesoderm does not arise until after two further divisions, but regards this as an exceptional condition.—Ed.]

macromeres described in the last-named form seems to represent the method of formation of the mesoderm most commonly found in the Gastropoda.[*]

Far greater modification seems to prevail in the formation of the mesoderm in those forms which, like *Nassa*, are exceedingly rich in yolk, and yet it appears to us that it would be possible to trace back

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[*] [The early developmental history of the mesoderm has now been investigated in so many different Gastropods, all of which show such close agreement on this point, that we must carefully bear in mind the possibility of this method of mesoderm-formation being typical of the entire group. The mesoderm almost invariably first appears as a single cell which is constricted from one of the posterior macromeres; this unpaired mesomere then divides into two cells, bilaterally arranged, which, as mesodermal teloblasts, give origin to the paired mesoderm-bands. The macromere from which the first mesomere originates is possibly the left posterior in all dextral Gastropods, and the right posterior in sinistral forms (CRAMPTON). In the great majority of the Gastropoda, soon after the last quartette of micromeres has arisen, this macromere divides, thus giving origin to two cells, one of which is an entomere, while the other is usually the primary mesomere, more rarely, *Patella* (PATTEN), and *Crepidula* (CONKLIN now withdraws the account given above), the two cells represent an entomere and a mesentomere, the complete separation of the mesoderm from the entoderm only taking place after further divisions. The origin of the mesoderm in *Crepidula* is expressed by CONKLIN as follows:—

- D (left posterior macromere).
  - ME
    - ME^1 (right)
      - Me^1
        - m^1 small mesomere.
        - M^1e^1
          - M^1 mesodermal teloblast.
          - e^1 secondary entomere.
      - E^1 primary entomere.
    - ME^2 (left)
      - E^2 primary entomere.
      - Me^2
        - M^2e^2
          - e^2 secondary entomere.
          - M^2 mesodermal teloblast.
        - m^2 small mesomere.
  - D entomere.

In the majority of Gastropoda in which this point has been investigated, as, for instance, *Planorbis*, *Limax*, *Physa*, *Siphonaria*, *Tethys*, *Umbrella*, etc., the condition is, as stated above, much simpler and may be expressed thus:—

- D
  - MM
    - M^1 right mesodermal teloblast.
    - M^2 left mesodermal teloblast.
  - D entomere.

While the greater part of the mesoderm arises from the paired mesoderm-bands, a smaller and more scattered portion appears to arise on either side of the body from the ectoderm. This was suggested by HEYMONS in *Umbrella* (No. XII.) and has since been confirmed by CONKLIN for *Crepidula* (No. IV.) and WIERZEJSKI for *Physa* (No. XXVII.); the scattered mesoderm has been compared with the larval mesoderm of *Unio* (LILLIE).—ED.]

the mode of formation of this layer in *Nassa* as given by **Bobretzky** (No. 11) to the method described above. In sections made through such a stage in the egg of *Nassa* (Fig. 42 *E*), under a cover of smaller cells, a few larger cells can be seen projecting into the cleavage-cavity. The projecting cells detach themselves and yield a few somewhat large cells which from this time lie in the cleavage-cavity. These are the first mesoderm-cells and, since the cells from which they were abstricted evidently correspond to one of the smaller macromeres (Fig. 42 *E*), the mesoderm has an origin similar to that in the cases previously considered. The smaller mesoderm-cells at first present soon again divide (Fig. 47 *A*), and here also seem to yield structures akin to mesoderm-bands (Fig. 47 *B*).

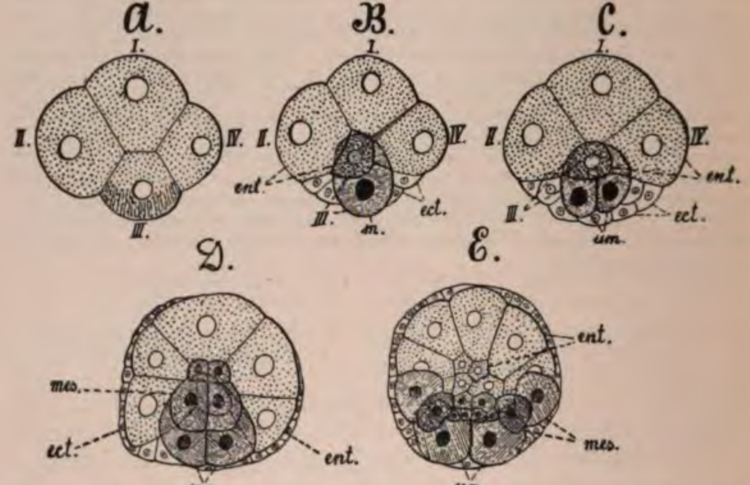

FIG. 48.—*A-E*, a few stages of the cleavage and formation of the germ-layers of *Umbrella* (after **Heymons**). *A* shows the four macromeres; *B*, the division of the mesentomere; *C*, the formation of the primitive mesoderm-cells; *D* and *E*, the formation of the mesoderm-bands. *I-IV*, the four macromeres, or their derivatives. *ect*, ectoderm; *ent*, entoderm; *m*, the primitive mesomere; *mes*, mesoderm; *um*, the paired mesoderm-cells (mesodermal teloblasts) resulting from the division of *m*.

The mesoderm is also found to arise from the macromeres in various other forms, *e.g.*, in *Limnaea* (**Wolfson**, No. 131) and *Fulgur* (**McMurrich**, No. 70), and *Janthina*, in which form, according to **Haddon** (No. 40) it becomes separated from the macromeres at the top of the blastopore. At a stage in which the ectoderm-cap has not completely grown round the macromeres, the peripheral macromeres yield the mesoderm-cells. **Haddon**'s account is too slight and his figures too vague to allow any conclusions to be arrived at regarding the origin of the mesoderm in *Janthina*. There are also various other descriptions of the origin of the mesoderm in the Gastropoda which, as they are still less well founded, cannot here be considered.

The mesoderm arises in *Patella*, as above, in connection with the entoderm, but at a stage when further differentiation has taken place in the embryo (PATTEN, No. 83). In *Patella*, there is a blastula, from which the entoderm arises, as already shown, by the ingrowth of large cells at the vegetative pole (Figs. 49 and 50). There are at first four large cells, occupying the same relative positions as do the four macromeres in other forms. Now, however, according to PATTEN, a cell arises on each side of these four blastomeres which, by division, gives off into the cleavage-cavity another rather large cell. These two cells are regarded by PATTEN as mesentoderm-cells (Fig. 50 *A*, *em*), and from them the two primitive mesoderm-cells (mesodermal teloblasts) are derived. These lie near the blastopore, at the posterior end of the larva and increase in number later from behind forward (teloblastically). In this way the mesoderm-bands arise, these being, according to PATTEN, developed with special regularity in *Patella* (Figs. 51 and 52, p. 126).

The mesoderm, in the Gastropods, has generally been considered to arise in connection with the primitive entomeres before the formation of the archenteron, but it has recently been asserted that it arises in the form of coelomic sacs, an assertion which was specially startling because it was supposed that the Molluscs showed no sign of the formation of enterocoeles, such conditions having so far never been observed. In the differentiation of the mesoderm, especially in the development of the pericardium, the Mollusca, it is true, show great agreement with certain "Enterocoelia," and there is no doubt that, like these, they possess a secondary body-cavity, but, in this respect, they approximate most nearly towards the Annelida, the formation of the mesoderm from mesodermal teloblasts being like that in the latter group. Considering all that is as yet known of the formation of the mesoderm, we cannot agree with the results obtained by ERLANGER for *Paludina*, and must continue to be sceptical about them until they are better supported or are actually confirmed by new investigations (if possible made on other forms as well).

v. ERLANGER'S account is as follows: From the rather wide archenteron of *Paludina* a bilobed outgrowth appears which gives the impression of a double coelomic sac such as occurs for instance in various Echinoderms (Vol. i., pp. 407-409). This sac, which rises from the archenteron near the blastopore, becomes detached later from the entoderm and now represents a vesicle closed on all sides and symmetrical in form. The outer and inner walls approach the ectoderm and the entoderm respectively so that at this stage we might speak of a somatic and a splanchnic layer. It is evident that, up to this point, the condition of the mesoderm closely resembles that of the coelomic sacs in other animals. This, however, soon changes, for the coelomic sacs, by giving off single cells, break up altogether, leaving only two insignificant vesicular vestiges surrounded by irregularly distributed mesoderm-cells on the ventral side of the archenteron. These will be referred to again later.*

Other descriptions in which the middle germ-layer is derived direct from the ectoderm are difficult to reconcile with the accounts we have given of the formation of the mesoderm. Such an ectodermal origin is attributed to the mesoderm in *Fusus* (BOBRETZKY, No. 11) in *Vermetus* (SALENSKY, No. 99) and in various other Gastropods (FOL). The eggs of *Vermetus* are very rich in yolk. The ectoderm lies as a thin layer upon the macromeres, almost entirely enclosing them. Near the blastopore, the increase in number of the cells of the ectoderm is said to give rise to a thickening which is the rudiment of the mesoderm. In *Fusus*, BOBRETZKY regards the latter as arising by a proliferation of cells from the lips of the blastopore. According to SALENSKY, this mesoderm-rudiment is bilaterally symmetrical like the mesoderm-bands, but another independent formation of mesoderm is said to take place in the neighbourhood of the shell-gland. SALENSKY is inclined to regard this part of the mesoderm as having arisen through delamination from the ectoderm near which it lies, *i.e.*, from the dorsal part of the body. There is some similarity between this last view and the account given previously by P. SARASIN (No. 101) of the origin of the mesoderm. According to SARASIN, growths of the ectoderm occur at certain points of the body from which mesodermal elements become detached. This takes place partly at an early stage of embryonic development and partly later. Since this material becomes abstricted at various times and at different parts for the formation of those organs which are usually regarded as mesodermal, SARASIN is unable to assume the existence of one uniform mesoderm-layer and therefore takes somewhat the same stand-point as that adopted later by KLEINENBERG in so decided a manner for the Annelida (Vol. i., pp. 292 and 293). Primitive mesoderm-cells and mesoderm-bands in *Bythinia* have been more recently described by ERLANGER (No. 28) and, according to the very definite account of SARASIN, we should have to show whether, besides this distinct mesoderm-rudiment, a further formation of mesodermal elements takes place from the ectoderm, as

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* [In spite of the more recent investigations on this point, the true origin of the mesoderm in *Paludina* must still be regarded as undecided. In his most recent publication, ERLANGER (No. X.) gives figures which are difficult to interpret in any other way than he has done. Consequently, he still regards *Paludina* as enterocoelic, but he finds, besides the coelomic sac, paired primitive mesoderm-cells near the blastopore which may be the forerunners of the cells which form the enterocoeles. He suggests that the sparsity of yolk has made *Paludina* more primitive in this respect than other Gastropoda. TÖNNIGES (No. XXV.), who has specially investigated this point in *Paludina*, concludes, but without reference to ERLANGER'S latest work, that the mesoderm arises shortly after the formation of the gastrula by a wandering in of ectoderm-cells from that portion of the ventral surface which is formed by the closing of the blastopore; the mesoderm then spreads out to form a ventral sheet which extends by growth on either side of the archenteron. Soon, however, its cells become scattered in the cleavage-cavity without forming a secondary coelom. SCHMIDT (Nos. XX. and XXI.), who has confined his attention to Pulmonates, finds no support for ERLANGER'S views in the origin of the mesoderm of these forms. An investigation on this point in some of the primitive Prosobranchia is very desirable.—ED.]

has been assumed or conjectured in connection with other forms (Annelida, Echinodermata) and specially for the Mollusca (*cf. Cyclas*, p. 29). It must be regarded as a striking fact that even those zoologists who, like ERLANGER, are very decided as to the derivation of the whole mesoderm from the mesoderm-bands, allow that some of the elements of the connective tissue arise from the ectoderm. For example, the so-called "nuchal" cells on the posterior edge of the velum on the "neck," *i.e.*, an accumulation of specially large ectodermal cells, pass inward so as to become distributed in the connective tissue. Although of different appearance from the other elements of the connective tissue, they appear to belong to the latter.*

4. The Rise of the Larva and its Relation to the Adult Form.

The variations which we have found in the development of the germ-layers among the Gastropoda naturally lead us to expect variations in the external form of the embryo. In the development of the latter, an important part is played by the smaller or larger amount of yolk contained in the egg. Besides this, however, adaptation to the manner of life of the various forms has to be considered, for the greater number of Gastropod larvae swim about freely for a long time before assuming the adult form. Now although the larvae, in essential points, can be traced back to a fundamental form, the differentiations found in the various divisions are somewhat far-reaching, so that we are obliged to consider the different larval forms apart. We shall first, however, describe the development of a few specially characteristic forms so as to give the reader a general idea of the subject and to make possible a comparison with other divisions of the Mollusca.

The development of the larval form of *Patella* has been described in detail by PATTEN (No. 83), and since this Prosobranch, which belongs to one of the most lowly groups, apparently most nearly attains the typical larval form, its ontogeny will occupy us first. Unfortunately the development of this form has only been followed by PATTEN up to a stage at which the larva is still far removed from the shape of the adult.

The ontogeny of Patella shows primitive conditions in so far as the egg-envelope is thrown off very early, even while cleavage is still

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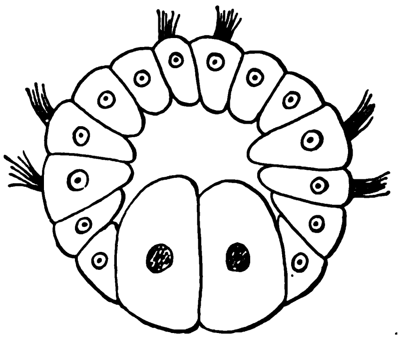
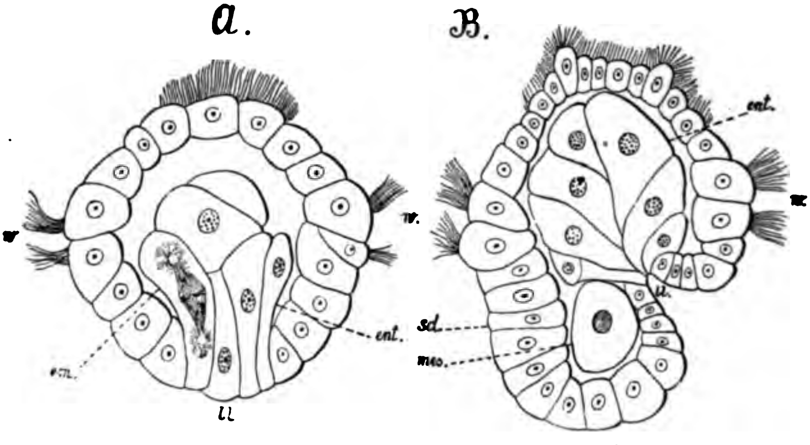
* [The above somewhat conflicting accounts of the rise of the mesoderm, taken in connection with the more recent observations of CONKLIN (No. IV.), HEYMONS (No. XII.), and WIERZEJSKI (No. XXVII.), seem to render it highly probable that the middle germ-layer has, in all Gastropoda, as has been suggested for the Lamellibranchia, a double origin: (1) from primitive mesoderm-cells giving origin to the lateral mesoderm-bands; and (2) from the ectoderm at a later stage as paired differentiations nearer the anterior end of the body.—ED.]

going on. Since cilia appear as early as the blastula-stage (Fig. 49), the embryo is very soon able to move about freely and thus becomes a larva. In this way, *Patella* resembles a Lamellibranch, but such early locomotion is not common among the Gastropods, most of the larvae hatching at a much later stage. The ingrowth of entoderm and the differentiation of the mesoderm take place, as already described (pp. 114 and 121), from the thickened vegetative pole of the blastula (Figs. 49 and 50). The blastopore lies at the vegetative pole which at the same time corresponds to the posterior end of the larva. The principal axis of the larva, at this stage, passes through





Figs. 49 and 50.—Embryos of *Patella* at the blastula-stage and at the commencement and completion of gastrulation (after Patten). *bl*, blastopore; *em*, mesentomere; *ent*, entoderm; *mes*, mesoderm; *sd*, shell-gland; *wr*, ciliated ring.

the middle of the blastopore and the opposite pole at which later the apical plate develops. Through the appearance of the mesoderm, the larva becomes bilaterally symmetrical. The blastopore soon changes its position, shifting forward on the ventral surface, as a consequence of the active growth of the dorsal surface. The rudiment of the velum which was indicated at the blastula-stage has now become more distinct (Figs. 49 and 50). In later stages, the displacement of the blastopore becomes much more striking, and recalls the condition already described in connection with *Dentalium* (Figs. 34 and 36, p. 91). The blastopore, during this process, changes from its round form and becomes slit-like (Fig. 51 *B*). At its posterior end, two cells are distinguished by their special size. They soon become covered with cilia (Figs. 51 and 52), and may well be compared to the anal cells of other Gastropods which will be described later (p. 142). The slit narrows and closes in from behind forward. The anterior part of the blastopore remains in the form of a round pit in the position of the future mouth; later, the blastopore is carried inwards by a depression of the ectoderm, the stomodaeum, which occurs at this point. This depression represents the rudiment of the oesophagus (Fig. 50 *B*), the blastopore persisting as the opening between the stomach and oesophagus. Out of this solid mass of cells, which still represents the entoderm, the enteron forms later

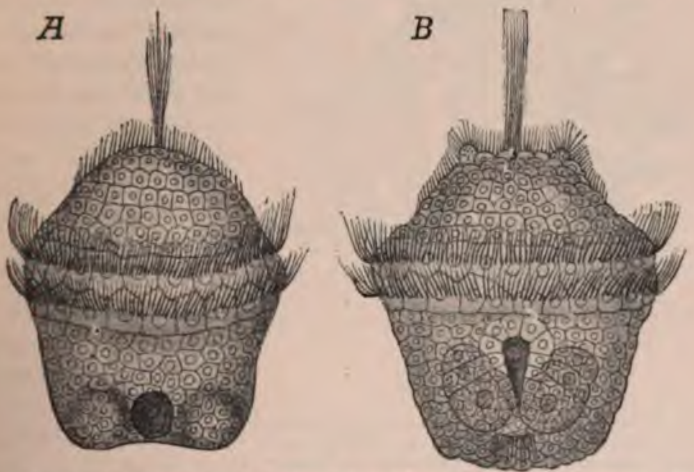


FIG. 51.—*Trochophore* larvae of *Patella* at two different stages (after PATTEN). In *A*, the two lateral pedal swellings can be seen near the circular blastopore. In *B*, the blastopore appears lengthened. Near it can be recognised the rudiments of the two mesoderm-bands, and behind it the anal ciliated tuft.

through a rearrangement of the cells which also increase greatly in number (Fig. 52). From the posterior end, where the mesoderm-cells lie, two very regular mesoderm-bands grow out (Fig. 52). The shell-gland appears dorsally before this stage as a depression formed of columnar ectoderm-cells; over this gland, the shell-integument is secreted later.

Patten asserts that the foot arises at a very early stage in a remarkable manner. It is said to be produced from two prominences which lie ventrally at the posterior end of the body (Fig. 51 *A*). These flank the blastopore on either side at a time when the latter still is a round aperture. As soon as it is displaced anteriorly, they shift together and unite to form the foot, the double origin of which can be recognised even in later stages through the presence of a median groove.

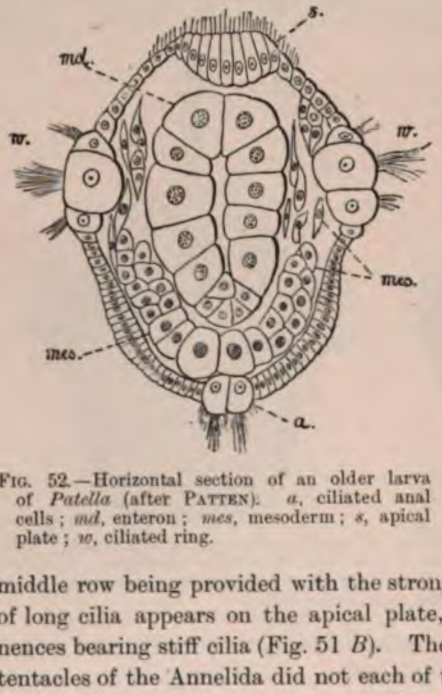


Fig. 52.—Horizontal section of an older larva of *Patella* (after Patten). *a*, ciliated anal cells; *md*, enteron; *mes*, mesoderm; *s*, apical plate; *w*, ciliated ring.

Up to this stage, the pre-oral region was specially large and bell-shaped (Fig. 51). It is separated from the posterior section by the pre-oral ciliated ring, which is composed of three rows of cells, the middle row being provided with the strongest cilia (Fig. 52). A tuft of long cilia appears on the apical plate, and near it lie two prominences bearing stiff cilia (Fig. 51 *B*). These would recall the cephalic tentacles of the Annelida did not each of them consist of a single cell. As development advances, the pre-oral part flattens out considerably, and the apical plate, which has already appeared as a median thickening (Fig. 52, *s*), now takes up a considerable part of the pre-oral section (Fig. 53, *sp*). At the posterior end of the larva also, a tuft of long cilia can be seen; these belong to the anal cells above-mentioned. The shell-gland which was previously invaginated has now flattened out, and the dorsal surface even appears convex. The epithelium, which was formerly very thick in this region, now consists merely of flattened cells (Fig. 53). The shell itself has become cup-shaped. The somewhat swollen edge which is seen bordering the shell represents the margin of the mantle, the mantle itself being covered by the thin horny shell. The enteron has considerably widened and is now sac-like and, connected with it posteriorly, a pointed appendage can be seen; this unites later with the ectoderm to form the anus. In the stomodaeum, which has now enlarged, an outgrowth (r) is visible; this is the rudiment of the radular sac which was found to appear in an exactly similar way in the Amphineura and the Scaphopoda.

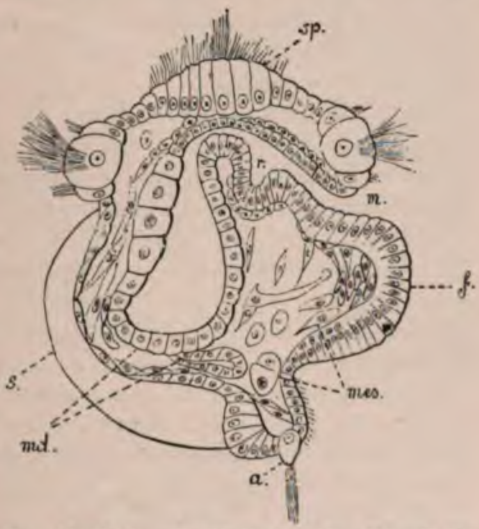


FIG. 53.—Median longitudinal section through the larva of *Patella* in the later *Trochophore* stage (after PATTEN). *a*, the ciliated (anal) cells at the posterior end ; *f*, foot ; *m*, mouth ; *md*, enteron ; *mes*, mesoderm ; *r*, radular sac ; *s*, shell ; *sp*, apical plate.

On each side of the mouth, right and left, a depression appears even at an earlier stage; this deepens to form a vesicle, which finally becomes separated from the ectoderm. The two vesicles thus formed are the otocysts. They lie at the base of the foot, which is commencing to develop into a large prominence and in which there is a rich accumulation of mesoderm-cells. The mesoderm has lost its regular arrangement, single cells becoming detached from the mesoderm-bands, and being distributed in the primary body-cavity; these no doubt represent the rudiment of the covering of the ectodermal and entodermal organs already formed. Certain of these cells elongate and give rise to muscle-fibres, a number of which become attached to a point on the dorsal surface, where they finally become firmly connected with the shell, and yield the retractor muscle by means of which the larval body can be withdrawn into the shell, as soon as the latter has attained the proper size.

In the stages depicted in Figs. 51 and 52, and even in the later condition, a median section of which is given in Fig. 53, the *Patella* larva closely resembles the *Trochophore* stage met with in the

Lamellibranchs (*cf.* Figs. 15 and 18, pp. 31 and 36). This resemblance is not only an external one, but extends to the inner structure also. There is thus a *Trochophore* stage in the Gastropods also (Ray Lankester, No. 63); it is not, indeed, usually developed in so typical a way as in *Patella*, but shows certain modifications. These modifications are either definite characteristics of the Gastropod larva or are transformations undergone by the primitive larval form as a consequence of altered conditions of life, especially by the presence of a greater abundance of yolk causing an abbreviation or the suppression of the larval stage and many modifications of the processes of development.

Besides the outward resemblance to other Molluscan larvae (Lamellibranchia, Scaphopoda, Amphineura) which is at once evident, we have the inner organisation correspondingly developed. We have already mentioned the apical plate and the pre-oral ciliated ring (Figs. 52 and 53), but we have to add to these the post-oral ciliated ring which has been demonstrated in the Gastropod larvae, *e.g.*, in *Crepidula*, *Fulgur*, *Fasciolaria* and other Prosobranchia, as well as in Heteropoda, Opisthobranchia and Pteropoda (Gegenbaur, Krohn, Fol, Brooks, McMurrich, etc.). It consists of a row of cilia which lie immediately behind the mouth and run parallel with the pre-oral ciliated ring (Fig. 54, $p_{,,}$, p. 130). Between this and the pre-oral ring there are also delicate cilia which correspond to the so-called ad-oral ciliated zone of the Lamellibranch larva. The whole apparatus, in any case, serves, as in the Lamellibranchs, for forwarding particles of food to the mouth, while the pre-oral ring, as the velum proper, is chiefly of locomotory significance. The ciliated tuft at the cephalic pole completes the resemblance to the *Trochophore* of other Molluscs (Fig. 3, p. 6, and Fig. 36, p. 91) and the Annelida (Vol. i., Fig. 118, p. 265). In the pre-oral section, in the region of the apical plate, eye-spots may occur. The post-oral otocysts lying at the sides of the mouth have already been mentioned.

The alimentary canal, like the other organs, shows the same structure as in other *Trochophore* larvae. It is composed of the entodermal mid-gut, the enteron, and of an ectodermal fore-gut, the stomodaeum, and perhaps also of an ectodermal hind-gut, the proctodaeum (?): at a later stage, the radular sac, that special character of the Gastropods which distinguishes them from the Lamellibranchs, appears in the stomodaeum (Fig. 53, *r*).

Among the organs found in the Gastropod larva, one is of special significance when comparison is made with the Annelidan *Trocho-*

phore, *viz.*, the paired primitive (larval or head-) kidney. This organ, as already noted, is conspicuous in the larval Lamellibranchs and in the Annelida (*cf.* p. 39 and Vol. i., p. 267). It has not, indeed, been discovered in *Patella*, but we may reasonably expect that it will be found in this form which in most other points is so primitive, especially as it is found in other Gastropods of a less simple type of development, such as the fresh-water Prosobranchia (*Bythinia*, *Paludina*, p. 136) and the Pulmonata (p. 178). A tubular primitive kidney has recently been described as occurring in the larva of an unidentified marine Gastropod (v. ERLANGER, No. 28). The primitive kidneys in their original form appear as tubular structures, the relation of which to the primary body-cavity is probably the same as in the Lamellibranchs, and these organs open outwards on the ventral side of the body behind the velum. These primitive excretory tubes are either quite short (*Paludina*, Fig. 59 *B*, *un*, p. 139) or else longer, as in *Planorbis*, in which case each kidney consists of a V-shaped tube (Fig. 78, *un*, p. 177).

Besides the primitive tubular kidney, various groups of ectoderm-cells have been claimed as primitive excretory organs. BOBRETZKY thus interpreted two rounded cell-growths which appear near the rudiment of the foot. Similar organs have been found by McMURRICH in *Fulgur* (No. 70). SARASIN describes, in *Bythinia*, ectoderm-cells of excretory nature which are connected with the velum. [In *Crepidula*, CONKLIN (No. IV.) finds paired groups of ectodermal cells, situated just behind the velum, which are eventually cast off; he regards them as excretory.] These ectodermal cells frequently contain concretions which are said to be extruded, a fact which has led authors to attribute an excretory function to them. They are very soon to be recognised owing to their granular contents; in *Neritina*, such granular cells, which later give rise to velar cells, may be clearly distinguished even during cleavage among the micromeres (BLOCHMANN, No. 7). Two rows of granular cells which lie along the edge of the velum have been described in *Onchidium* by JOYEUX-LAFFUIE (No. 51).*

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*[HEYMONS describes, in *Umbrella*, the presence of paired groups of ectodermal excretory cells, situated near the anus; of these, the right group alone attains functional development and sinks under the surface of the ectoderm. He regards these as homologous with the similar cells situated near the velum in the Prosobranchia. CONKLIN (No. IV.), however, thinks that they are only analogous, since they arise from totally distinct blastomeres; the anterior ectodermal excretory cells are found in three of the great Gastropodan orders. MAZZARELLI (No. XV.), who has studied the ectodermal or anal kidney of *Aplysia*, considers that it is not to be regarded as a larval organ; he maintains that it does not disappear, but represents the rudiment of the definitive kidney. The true internal primitive kidney is so far known to occur only in the Pulmonata and in two fresh-water Prosobranchia and possibly in one marine Gastropod, concerning which ERLANGER is unable to inform us whether it was an Opisthobranch or a Prosobranch. Thus it will be seen that this supposed primitive organ is found to be most highly developed in those most specialised forms, the Pulmonata, and that it is only elsewhere known to occur in two Prosobranchs. A further search for this organ in some of the more primitive marine Prosobranchia is much needed.—Ed.]

It is only in comparatively few Gastropods that the *Trochophore* is developed in such a pronounced manner as in *Patella*, this being no doubt due to the fact that, in most Gastropods, a great part of the development of the embryo takes place under the protection of the egg-shell or in the egg-capsule. The *Trochophore* stage is nevertheless to be found in all Gastropods, although it is more distinct in some than in others. In these latter, as a rule, the larva attains free life at a stage in which its shape has already undergone several modifications. The later ontogenetic stages of *Patella* are not known, but the larva, at the stage in which it is provided with a foot and a fairly developed shell, still resembles the *Trochophore*, so that we may assume that it does not undergo any further changes except those which are determined by its transformation into the adult. This also seems to be the case in *Fissurella* as far as its development is known (BOUTAN, No. 12). In this Gastropod, the velum broadens somewhat and assumes a bilateral form. This was also already described in the Lamellibranch larva, and *Fissurella* does actually show a certain resemblance to the later stages of these forms (Fig. 17, p. 35), if we leave out of consideration the shell which in the one case is single and in the other bivalve.

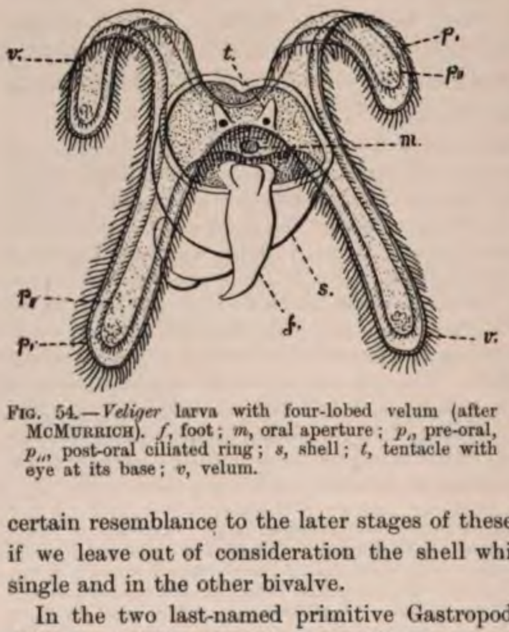

FIG. 54.—*Veliger* larva with four-lobed velum (after MCMURRICH). *f*, foot; *m*, oral aperture; $p_{,}$, pre-oral, $p_{,,}$, post-oral ciliated ring; *s*, shell; *t*, tentacle with eye at its base; *v*, velum.

In the two last-named primitive Gastropods, the velum does not differ essentially from the Lamellibranch velum, but in most other forms its shape becomes modified in a manner specially characteristic of the Gastropoda. The bilateral development of the velum which is already indicated in *Fissurella* is, in those Prosobranchs the eggs of which are rich in yolk (*Neritina*, *Vermetus*, *Fulgur*), evident when the velum first appears as a rudiment. This organ appears in the embryo at first in the form of two specially marked rows of cells (*Neritina*) or two curved ridges which unite only later to form the velum, the dorsal union of the two ridges often taking place very late. In its later development, in the Prosobranchia and especially in the Opisthobranchia, Heteropoda, and Pteropoda, the velum by its great lateral growth, assumes a bilobed form (Fig. 55 *A-C*). It becomes at the same time very large and is a most efficient locomotory organ. It is beset with large, strong cilia, which may be replaced by much smaller cilia at the junction of the two wing-like lobes, the bilateral character thus becoming still more apparent (Fig. 72, p. 162). The larval stage which is provided with this very characteristic locomotory apparatus has been called the *Veliger* stage (Ray Lankester). The great size which may be attained by the velum can be seen from Fig. 54, which represents the *Veliger* larva of a Prosobranch (species

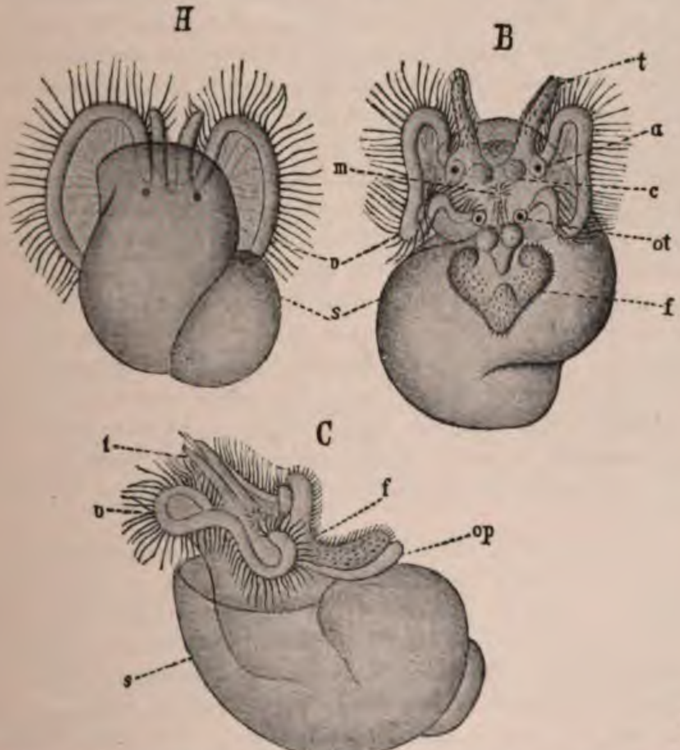

Fig. 55.—*A*, embryo, *B* and *C*, *Veliger* larvae of *Vermetus* at different stages (after Lacaze-Duthiers). *A*, dorsal aspect; *B*, ventral aspect; *C*, lateral aspect. *a*, eyes; *c*, rudiments of the cerebral ganglia; *f*, foot; *m*, mouth; *ot*, otocyst; *op*, operculum; *s*, shell, *t*, tentacle; *v*, velum.

unknown). Each of the velar lobes is drawn out longitudinally so that the whole velum appears to consist of four lobes. In *Atlanta*, the velum is very large and here each of the lateral parts splits up into three, the velum thus consisting of six lobes (Fig. 67, p. 155).

In other respects the development of the body has advanced considerably at the *Veliger* stage. The shell, which at first is cup- or cap-shaped, increases in size through the addition of new layers, this fact being indicated, as in *Dentalium* and the Lamellibranchs, by the appearance of lines of growth. But as the addition of new material takes place in an irregular manner, *i.e.*, as the new layers of shell are not all of equal width and, further, follow the curvature of the visceral sac, the shell soon loses its symmetrical shape and begins to coil (Fig. 55). The visceral sac is separated by the projecting lip-like edge of the mantle from the rest of the body, especially from the head and trunk. A slit-like depression usually appears on the right side in front of the edge of the mantle; this depression extends posteriorly so that the mantle now covers a cavity, the mantle- (or pallial) cavity, in which the gills arise later as outgrowths of the body-wall. The intestine opens into this cavity, the anus having arisen as an ectodermal depression primarily situated somewhat ventrally at the posterior end of the body. At first this lies in the median plane, but is usually displaced to the right side later, shifting at the same time forward, and somewhat dorsally. This displacement is a result of the fixed and rigid nature of the shell covering a large part of the body (*cf.* p. 146).

The rudiment of the foot appears early and may attain large proportions in the *Veliger* larva. In *Vermetus*, it is paired at least anteriorly (Fig. 55 *B* and *C*). In this larva the foot, however, is more complicated than Fig. 55 would lead us to believe. The double character of its rudiment is noteworthy as a peculiarity which recurs in other Gastropods (*Patella*, Fig. 51 *A* ; *Limnaea*, RAY LANKESTER, No. 63; *Succinea*, F. SCHMIDT, No. 109) in very early stages. In *Succinea*, the foot arises in the form of two distinct prominences separated by a broad furrow; these outgrowths afterwards approach each other and fuse to form the median foot, a process similar to that described for *Patella* (p. 126).

On the postero-dorsal surface of the foot, a plate composed of the same substance as the shell is secreted (Fig. 55 *C*, *op*). This is the operculum. The otocysts lie in close contact with the foot (*B*, *ot*).

In the young stages of the *Veliger* larva two prominences appear on the velar area; these soon extend and lengthen and can be recognised as the tentacles (Fig. 55, *t*). At their bases, the eyes (*a*) arise. Both the tentacles and the eyes are, by their origin, indisputably proved to belong to the primary cephalic section, and it is of special interest that the tentacles occupy the same position as the cephalic tentacles of the Annelida and the Annelidan larvae (Vol. i., Figs. 120 *B*, p. 269, and 121, p. 270).

The velum may still persist after the foot has attained a considerable size and when the development of the other organs also is far advanced, but it gradually diminishes in size and finally degenerates, the larva thereby passing over to the adult condition which, indeed, had already been nearly approached. Two small rounded ciliated lobes may persist near the mouth as the remains of the velum, as was observed by **Ray Lankester** in *Limnaea* (No. 63), and **Joyeux-Laffuie** in *Onchidium* (No. 51). These are said to give rise to the sub-tentacular lobes or lip-tentacles; these two structures would thus have an origin similar to that which we felt inclined to assume for the oral lobes of the Lamellibranchs (p. 45).

The perfectly developed *Veliger* larva is found almost exclusively among the marine Gastropoda, the young of which swim about freely for a long time. Among fresh-water Gastropods, *Neritina* passes through a stage with a well-developed bilobed velum resembling that depicted in Fig. 55 (*Vermetus*), but the *Veliger* larva does not lead a free life, but passes through this stage within the egg-capsule. When the embryo leaves the capsule it shows the adult form (**Claparède**, No. 23). *Neritina* is one of those fresh-water forms which can also live in salt water. This fact, and the presence of the well-developed *Veliger* stage, suggest that it has only recently adopted a fresh-water existence. In other fresh-water Prosobranchs, as well as in aquatic and terrestrial Pulmonates, the *Veliger* stage is much reduced. *Onchidium*, however, among the Pulmonates, in this respect resembles *Neritina*.

Onchidium, a Pulmonate living between tide-marks, not only passes through a *Trochophore* stage but, while still within the egg-shell, becomes a *Veliger* larva with coiled shell and a large bilobed velum. In the course of further development, the velum degenerates, only two rounded lobes which lie laterally to and somewhat in front of the mouth being retained as the lip-tentacles. The embryo, on leaving the egg-shell has, on the whole, the same shape as the parent (**Joyeux-Laffuie**, No. 15). The condition we have just described would be very remarkable in a Pulmonate, did not the organisation and the manner of life of this form give some cause for the assumption that it may have been derived from a marine ancestor (possibly an Opisthobranch). *Onchidium* lives in the littoral zone, within the reach of the tides, hidden in rocky fissures, where it lays its gelatinous egg-masses. These are washed by the sea water, and JOYEUX-LAFFUIE was able to develop them by keeping them damp and immersing them from time to time in sea water. The eggs therefore develop under conditions not very different from those of marine Gastropods.

Although, as a rule, the *Veliger* stage is much reduced in fresh-water and terrestrial Gastropods, the *Trochophore* form is still more or less distinctly developed in them. In the Pulmonates, the *Trochophore* stage is present but is not very conspicuous (p. 177); in *Paludina*, however, it is unmistakable, although this Gastropod is viviparous (Fig. 56). *Paludina*, in many other respects besides the retention of the *Trochophore* stage, is an archaic form and, as its ontogeny has been so carefully studied, we shall give a special account of its development. The principal sources of our knowledge concerning the ontogeny of *Paludina* are the works of LEYDIG (No. 68), RAY LANKESTER (No. 64), BÜTSCHLI (No. 18) and v. ERLANGER (No. 27), and we have also observations made by RABL (No. 92) and BLOCHMANN (No. 8). ERLANGER'S account is the most recent and the most complete in every respect.

The Development of Paludina. The fertilised egg of *Paludina vivipara* develops into an almost spherical blastula which becomes somewhat flattened later and contains a distinct cleavage-cavity. The flattening takes place in connection with gastrulation, the cleavage-cavity during this latter process being almost completely obliterated by the development of the archenteron, so that a stage is here brought about similar to that which occurs in other Gastropods, especially in *Firoloida* (Fig. 44 *B*, p. 114). The gastrula, which at first is almost kidney-shaped, with a wide blastopore, expands by growth and becomes bell-shaped in *Firoloida* (Fig. 44 *C*). The blastopore narrows to a slit.

The formation of the mesoderm has already been described. On this point, we follow the older statements of BÜTSCHLI, according to which the mesoderm is present in the form of two mesoderm-bands which, during the gastrula-stage, consist of few cells but increase later (Fig. 56 *A*), *i.e.*, show the same condition as in other Gastropods (*cf.* p. 121). The greater part of these bands soon undergoes disintegration, breaking up into separate cells which become irregularly distributed in the cleavage-cavity.

Meanwhile, by the development of two rows of large ciliated ectoderm-cells, placed transversely to the gastrula-axis, the *Trochophore* stage is reached. The pre-oral ciliated ring thus borders the cephalic area, which has become larger by the increase in number of the cells (Fig. 56 *A*). The blastopore marks the posterior end of the embryo, but in consequence of somewhat stronger growth and the consequent bulging of the ventral surface it is shifted slightly dorsally. The blastopore is said to be retained in *Paludina* and to pass over into the anus (BÜTSCHLI, V. ERLANGER). It has, however, been asserted that the blastopore closes (RABL) and that the mouth and the anus are only indirectly related to the primitive mouth, as we shall describe later (*cf.* p. 141).* A large, somewhat sunken area, which lies dorsally in front of the blastopore and consists of columnar ectoderm-cells (Fig. 56 *B*, *cd*), represents the shell-gland, above which the chitinous shell soon appears. An ectodermal depression (*m*) which appears on the ventral side behind the ciliated ring, and which becomes connected later with the archenteron, yields the stomodaeum. At this stage, the anterior part of the embryo has lost its former bell-shape and has become more flattened (Fig. 56 *B*). The mesoderm has lost its regular arrangement and has become for

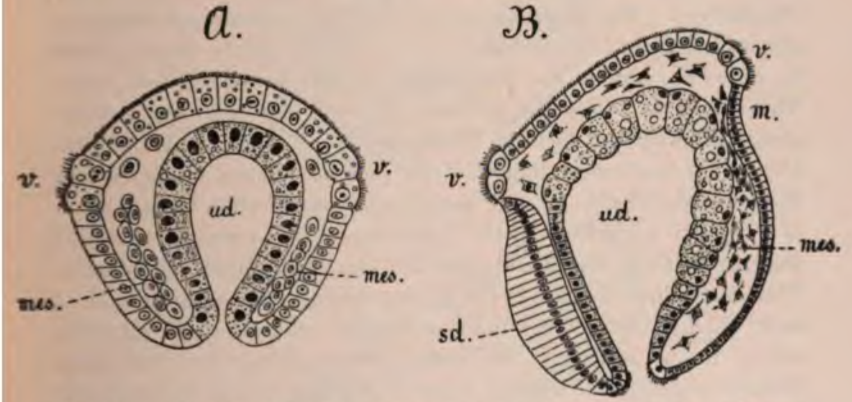

FIG. 56.—*A* frontal and *B* sagittal section of two embryos of *Paludina* of different ages (after TÖNNIGES). *m*, region where the mouth develops at a later stage; *mes*, mesoderm-bands (in *A*) and scattered mesoderm-cells (in *B*); *sd*, shell-gland; *ud*, archenteron; *v*, velum.

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* [TÖNNIGES (No. XXV.), the most recent investigator of the development of *Paludina*, finds that the oval blastopore closes from before backward, and that it does not give rise to the anus, which, as a secondary formation, appears at the point where the blastopore closes.—ED.]

the greater part distributed in the form of isolated spindle-shaped cells in the primary body-cavity. Its further development will be described later, but we must here refer to one of the organs formed from the mesoderm, the primitive kidney, since this is essentially a larval organ.

Each of the **primitive kidneys** arises from a compact mass of mesoderm-cells, two such masses lying at the sides of the embryo behind the velum. A lumen now appears in the mass, which, by lengthening somewhat, becomes a short tube and, coming into contact with the ectoderm, fuses with the latter and thus opens externally not far behind the velum. The ectoderm sinks in somewhat at this point later; in *Bythinia*, this ectodermal invagination is even very deep and forms the longer, distal part of the primitive kidney (v. ERLANGER). The inner surface of the tube becomes covered with cilia especially at the blind end. The primitive kidney remains short in *Paludina*, but, in the Pulmonata, appears as a long bent tube. This is said to possess an internal aperture, that is to say, it communicates with the (primary) body-cavity (p. 179). v. ERLANGER was unable to convince himself of the presence of such an aperture in *Paludina* and *Bythinia** and, taking into consideration the condition of the primitive kidneys in the Annelida, we may conclude that it is wanting in these forms and that the two renal tubes end blindly. This is certainly the case in the earlier stages. At the inner end of each kidney, there is a bundle of spindle cells which in all cases extend to the ectoderm, and serve for suspending the renal tube. This latter attains its highest degree of development at the somewhat advanced stage shown in Fig. 99, and degenerates later (BÜTSCHLI, v. ERLANGER).

The Trochophore form of the embryo is now specially modified by the development of the foot on the ventral surface as a massive prominence (Figs. 56 *B* and 57, *f*). The appearance and rapid increase in size of this organ leads to a considerable displacement of the other parts of the body (Figs. 56 *B* and 58). The pre-oral part of the body becomes still more flattened out. The mouth shifts to the anterior end and the velum finally appears displaced to a dorsal position (Fig. 58). The oral aperture and the anus lie at the two opposite ends of

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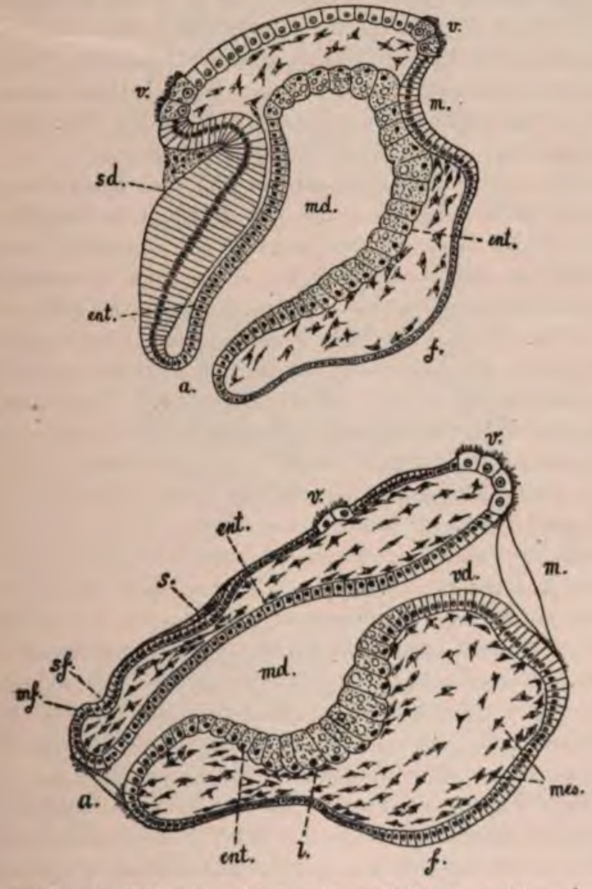
*[v. ERLANGER (No. 71), however, describes an internal aperture in Pulmonates. MEISSENHEIMER (Nos. XVII. and XVIII.) has made a most careful investigation of this point in *Limax* and is firm in his belief that there is no internal opening in that Pulmonate. He derives the entire organ from the ectoderm.—ED.]

the body. The shell-gland now becomes modified by the invagination of its greatly thickened epithelium and by the appearance within the invagination of the brown "chiton-plug" described by BÜTSCHLI (Fig. 57). During the further growth of the embryo, the gland becomes flattened out and its cells lose their long columnar character



FIGS. 57 and 58.—Sagittal section of two embryos of *Paludina vivipara* (after TÖNNIGES). *a*, anus; *ent*, entoderm; *f*, rudiment of foot; *l*, rudiment of liver; *m*, mouth; *md*. enteron; *mes*, mesoderm-cells; *mf*, first indications of the mantle-fold; *s*, shell-gland; *sf*, shell-groove; *v*, velum.

and the epithelium finally becomes very thin (Fig. 58). At this stage, lying above the shell-gland which is now slightly depressed, there can be seen not only the remains of the chitinous plug but the shell-integument itself (*s*). The shell now extends rapidly over the dorsal surface by the growth of its free edge which is still in close contact with a thickened layer of ectoderm, the cells of this thickening being concerned in the secretion of the shell. Beyond this thickening, the mantle-fold (Fig. 58, *mf*), as a slight upgrowth of the ectoderm, is situated dorsally to the anus. When the latter is displaced forward by the more rapid growth of the posterior dorsal part of the body (Fig. 59 *A*), the mantle either grows out further or else the surface of the body behind the mantle and in front of the anus sinks in somewhat; the depression which is thus formed is the rudiment of the mantle-(pallial) or branchial cavity (Fig. 59 *A*, *mh*). The anal aperture now comes to lie in this depression.

Turning to the internal organs, we find that the fusion of the stomodaeum with the enteron has now taken place (Fig. 58). The rudiment of the liver appears ventrally as a sac-like outgrowth of the enteron, and the radular sac arises from the stomodaeum. As the mesodermal structures (the pericardium, the heart and the kidneys, Fig. 59) become differentiated, those on the right side attain a greater size than those on the left, so that a marked asymmetry is already evident in these internal organs. The rectum, which formerly ran directly backward, now comes to lie at right angles to the longitudinal axis in consequence of the displacement of the anus described above and, later, runs obliquely to the right side.

The inner asymmetry precedes the outer, and has therefore been used as an explanation of the asymmetrical structure of the body (*Bythinia*, P. SARASIN, No. 101). When we spoke above of a displacement of the anus the expression used was not strictly accurate, since the distance between the mouth and the anus remains almost the same. Marked growth, on the contrary, takes place first in the dorsal surface and later especially in the left posterior part of the body. Although the area lying between the mouth and the anus does not grow appreciably, considerable increase in size occurs in the posterior region (Fig. 59 *A*-*C*), and it results that the parts that have not grown now seem to belong more to the anterior portion of the body which as a whole is now much larger. BÜTSCHLI has paid special attention to these processes in *Paludina* (No. 19). The left posterior part of the body, in consequence of the processes of growth just described, is much swollen and this leads to the formation of the visceral sac directed backward to the left and to the (apparent) shifting forward to the right of the anus and the parts surrounding it. The swelling of the posterior dorsal parts of the body to form the visceral sac is determined by the advancing growth of the inner organs. The subject of the asymmetrical shape of the body will be alluded to further on (p. 143).

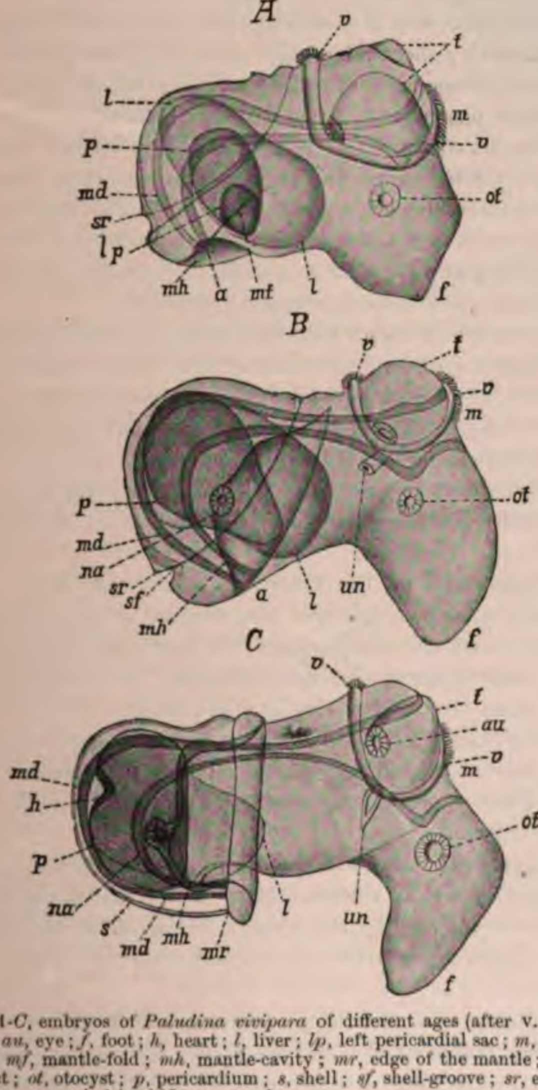


Fig. 59.—*A*-*C*, embryos of *Paludina vivipara* of different ages (after v. Erlanger). *a*, anus; *au*, eye; *f*, foot; *h*, heart; *l*, liver; *lp*, left pericardial sac; *m*, mouth; *md*, enteron; *mf*, mantle-fold; *mh*, mantle-cavity; *mr*, edge of the mantle; *na*, efferent renal duct; *ot*, otocyst; *p*, pericardium; *s*, shell; *sf*, shell-groove; *sr*, edge of shell; *t*, tentacle; *un*, primitive kidney; *v*, velum.

It has already been mentioned that the anal aperture lies in the mantle-cavity. This latter has deepened during the processes just described through the rising up and growth of the margin of the mantle, but it also becomes affected by the asymmetrical development of the embryo. It is soon evident that the part of the cavity lying on the right side is much deeper than that lying on the left, and the cavity shortly becomes confined almost entirely to the right side in consequence of the twisting of the embryo. On this side there opens into it not only the rectum, but the efferent ducts of the now developed definitive kidney and of the genital organs. At a later stage, the mantle-cavity extends dorsally and thence over to the left side. Above the mantle lies the shell which passes from its earlier flat shape to a more arched form, till it becomes a somewhat deep cup (Fig. 59 *A* and *B*), and, finally, in consequence of its one-sided growth, becomes coiled (*cf.* p. 147).

While the above processes have been going on, the anterior part of the body also has undergone essential alteration. The velum has degenerated more and more, while the foot has greatly increased in size (Fig. 59 *A*-*C*). At its base, the otocysts (*ot*) have appeared as ectodermal depressions which soon became cut off as closed vesicles. In the posterior dorsal part of the foot, the operculum is secreted in a manner similar to the secretion of the shell (Fig. 99, *op*, and Fig. 92, *op*).

The tentacles arise on the velar area as two very large swellings which soon increase in height and thus become conical (Fig. 59 *A*-*C*, *t*). At their bases the eyes appear. At the stage depicted in Fig. 59, both these organs can be recognised as belonging to the velar area, since the ciliated ring is still present as a narrow band. In these later stages, when, in keeping with the shape of the body, the velum has become almost bilobed, it may be compared with the sail of the *Veliger* larva of the marine Gastropods which, however, is much more distinctly bilobed.

The further development of the embryo is chiefly determined by the continued growth of the visceral sac as a result of the perfecting of the inner organs, and by the increase in size of the foot and of the tentacles. This may best be seen by comparing Fig 59 with Figs. 99 and 100.

Before closing this section we must deal with one or two other morphological points which could not earlier receive the consideration they deserve. The first of these concerns the shape and transformation of the blastopore. In its simplest form, the blastopore has been described as a rounded aperture appearing at the vegetative pole; this aperture, without undergoing essential change of form, may pass, by gradually narrowing, into the mouth. An ectodermal depression does, indeed, regularly accompany this process, pushing the actual blastopore some distance inward. Such a direct passage of the blastopore into the mouth has been claimed by BOBRETZKY for *Fusus* and by FOL for the Pteropoda and Heteropoda. The narrowing of the blastopore may, further, lead to its direct closure, but even in such cases, the stomodaeum forms at the same spot, as, for instance, in *Nassa* and *Neritina* (BOBRETZKY and BLOCHMANN). The point at which the blastopore closes and where the adult mouth eventually forms, no longer corresponds to the vegetative pole, *i.e.*, to the end of the embryo which is turned away from the animal pole, but, in consequence of the growth of the postero-dorsal region, has shifted somewhat towards the animal pole and is found behind the velum. This last condition of the blastopore is that which is by far the most frequent among the Gastropoda. Here also the blastopore is at first round and may have a considerable diameter, but it soon becomes narrow and slit-like (*Planorbis*, *Patella*, *Paludina* and many other Gastropods). The slit-like blastopore closes from behind forward, and its anterior end either passes direct into the mouth, as in *Planorbis*, *Limnaea*, and *Patella* (according to RABL, RAY LANKESTER, WOLFSON, PATTEN) or closes completely, in which case, at the last point to close, an ectodermal depression forms which yields the stomodaeum. This latter is the case in *Aplysia*, *Bythinia*, and *Crepidula* (BLOCHMANN, SARASIN, v. ERLANGER, CONKLIN). The formation of the definitive mouth is always connected with an invagination of the ectoderm.

The slit-like blastopore, if regarded as open from its posterior to its anterior end, seems to occupy the whole length of the later ventral surface. Its posterior end no doubt still corresponds approximately to the former vegetative pole, its anterior end lying immediately behind the velum. Now while, in the majority of cases as yet known, the blastopore closes from behind forward, in *Paludina*, as already described, the posterior part of it is said to persist and to yield the anus in the same way as the anterior part in the above cited cases yielded the mouth. If this is actually the case, it can only be explained by means of the view adopted by BÜTSCHLI, according to which both the mouth and anus arise by the differentiation of the blastopore. BÜTSCHLI found an indication of this in RAY LANKESTER'S observations on *Limnaea*, in which form, the slit-like blastopore, the anterior end of which becomes the mouth, extends as far as to the anal region. Since that observation was made, other cases have become known of certain relations existing between the anus and the blastopore. v. ERLANGER, for instance, described the blastopore of *Bythinia* as a slit, the posterior end of which lies at the spot where the anus forms later (Fig. 96 *B*, p. 210), and even in *Paludina* itself it appears indisputable that the slit-like blastopore extends almost to the velum, *i.e.*, to the spot which corresponds to the mouth that forms at a later stage. Further support for this view is found in the condition of some Opisthobranchs (*Doris*, *Aplysia*, according to LANGERHANS and BLOCHMANN), in which the anal cells are found exactly at the posterior end of the blastopore which here also is slit-like. It should be mentioned further of those two anal cells that, in various Gastropods, they mark at an early stage and in a striking manner the position of the anus (pp. 154 and 160). They coincide in position with the two cells which, in *Patella*, appear behind the blastopore (p. 125). The anterior end of the blastopore in the forms just named, also, becomes the mouth, so that the relations of the blastopore to the mouth and to the anus in these forms are specially distinct and the apparently divergent condition of *Paludina* is thus explained.

Greater attention has been paid to the form and the transformations of the blastopore in the Gastropoda than in other animals, and the subject therefore has received special consideration from us. It was not our intention to give an exhaustive account of the observations made in connection with it chiefly because these are to some extent unreliable. We have therefore selected only such statements as seem to some degree well-founded, though even these need more careful examination. It seems, however, to be proved by these observations that, in the Gastropoda, there are relations between the blastopore on the one hand and the mouth and anus on the other. We consequently find, in the Mollusca, conditions similar to those previously met with by us in the Arthropoda, in which class also, the mouth and anus are either directly or indirectly related to the blastopore (*cf.* Vol. iii., p. 412). The condition of *Paludina* may recall the Echinoderms, in which the blastopore passes direct into the anus (Vol. i., p. 359). The condition of the Gastropods is, however, in any case, to be| traced back to corresponding processes met with in the formation of the Annelidan *Trochophore* (Vol. i., p. 265). In the latter, the blastopore at first lies at the vegetative pole of the embryo. It then extends and occupies the whole length of the ventral surface which, however, is not very great. When it closes from behind forward, its anterior end passes over into the mouth, this latter lying behind the pre-oral ciliated ring, as in the Gastropoda. The anus, however, arises at the posterior end of the larva which previously corresponded to the vegetative pole and thus to the position of the blastopore. The conditions here are thus evidently very like those in the Molluscs.

These last considerations lead us to the **changes of shape undergone by the embryos in early stages.** Even before the Gastropod egg is affected by cleavage, and while it is undergoing this process, the animal and vegetative poles may be distinguished. The blastopore at first corresponds to the vegetative pole, but, as it lengthens, it encroaches upon the future ventral surface, while the animal pole appears to lie on the dorsal surface. The part of the ectoderm that forms at the animal pole seems to shift later to the anterior end of the embryo around which the velum is developed. The axis which passes through the animal and vegetative poles of the early stages does not, therefore, in the Gastropoda, correspond, as might be supposed, to that passing through the apical plate and the anus of the larva, but lies more or less at an angle to the latter. It has already been shown that the definitive axes are laid down at an early stage in the embryo (p. 107). The identification of these axes is by no means easy, especially as the shape of the larva undergoes a certain amount of modification according to the quantity of yolk deposited in the egg. On this account, FOL'S statement that the shell-gland appears at the animal pole requires further investigation. It is a striking fact, however, that in the Cephalopoda it actually has such a position, a fact which will be discussed later.* The shell-gland, as is well known, lies dorsally on the embryo, whereas the pedal prominence arises on the ventral side between the mouth and the anus. In their most primitive condition the embryos, or larvae of the Gastropoda, are quite symmetrical ; only later does the body become asymmetrical through displacement of the internal and external organs.

Considerations relating to the asymmetry of the Gastropoda.

The development of the body during its ontogeny follows the course which we are inclined to believe was taken by the Gastropoda phylogenetically in attaining their present asymmetrical condition. There can be no doubt that the Gastropoda are derived from symmetrical forms, for we find the other members of the Molluscan phylum, which had the same ancestors as the Gastropoda, symmetrically developed. This is confirmed by ontogeny, for the symmetrical form is long retained in the embryo although it is eventually lost in consequence of the unequal growth of the various regions of the body. It is especially

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* [For a review of the facts relating to the shifting of the larval axes see CONKLIN (No. IV.) and LILLIE (App. to Literature on Lamellibranchia, No. III).—ED.]

the left side that grows more actively, and this is the reason why the posterior parts (especially the anus and the organs surrounding it)

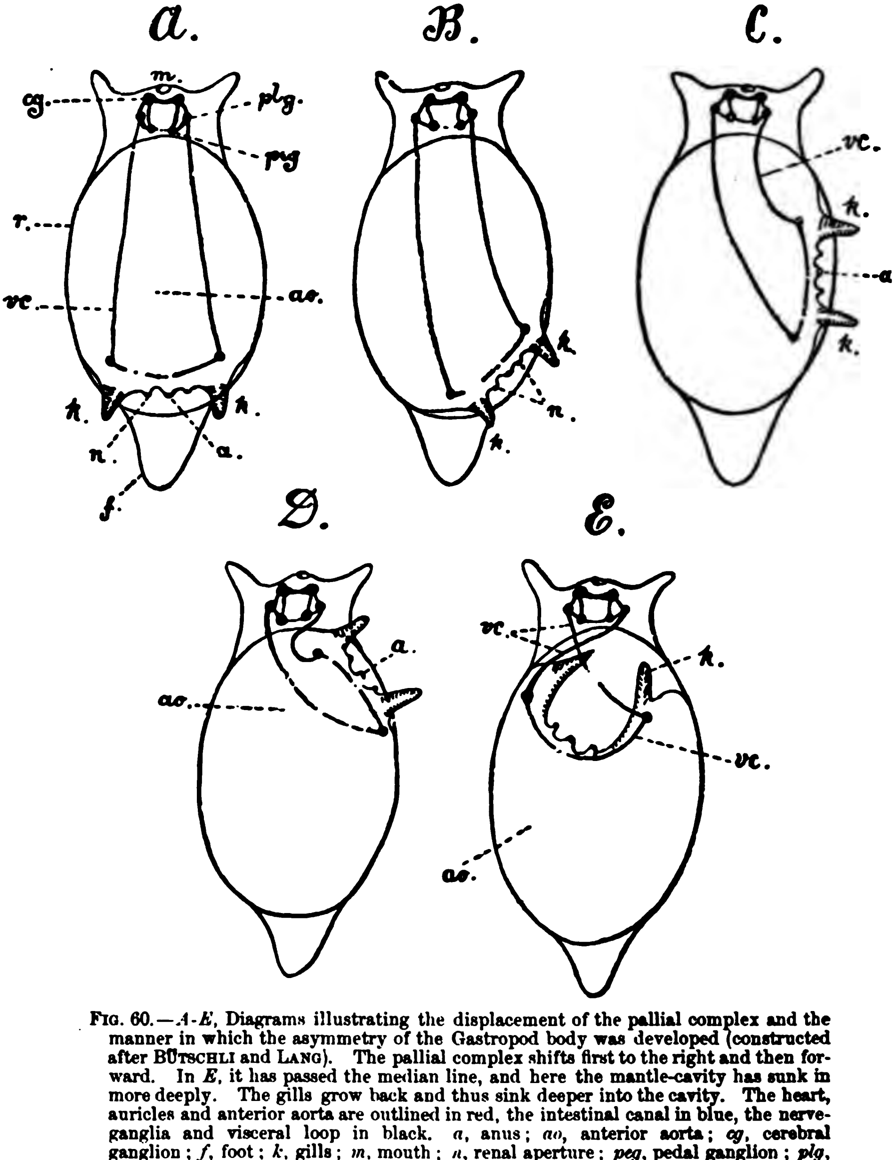

Fig. 60.—*A*-*E*, Diagrams illustrating the displacement of the pallial complex and the manner in which the asymmetry of the Gastropod body was developed (constructed after Bütschli and Lang). The pallial complex shifts first to the right and then forward. In *E*, it has passed the median line, and here the mantle-cavity has sunk in more deeply. The gills grow back and thus sink deeper into the cavity. The heart, auricles and anterior aorta are outlined in red, the intestinal canal in blue, the nerve-ganglia and visceral loop in black. *a*, anus; *ao*, anterior aorta; *cg*, cerebral ganglion; *f*, foot; *k*, gills; *m*, mouth; *n*, renal aperture; *peg*, pedal ganglion; *plg*, pleural ganglion; *r*, edge of the mantle and shell; *vc*, visceral commissure.

are displaced anteriorly to the right, but at the same time they retain their original position with relation to the anterior end, because the region lying between them and the anterior end on the right side does not grow. These phenomena have been described by various zoologists who have treated of the ontogeny of the Gastropoda (P. SARASIN, FOL, BOBRETZKY, etc.).* SPENGEL (No. 122), also, has made them the subject of detailed consideration in adult animals, and more recently BÜTSCHLI especially has given a careful description of them (No. 19). LANG has recently made a further attempt to explain them from a phylogenetic point of view (No. 61).

Ontogenetically as well as phylogenetically, the asymmetry rests in any case upon the greater growth of one side, usually the left, and the consequent shifting of the left posterior part of the body to the right and of the whole posterior region anteriorly. In this process we start with a very simple, *Chiton*-like Mollusc, whose dorsal surface with its investing shell is only slightly arched. The foot projects only a little way beyond the visceral sac. The anus lies at the posterior end, the paired apertures of the nephridia and the gills lying near and symmetrically to it (Fig. 60 *A*). The mantle-cavity also, to which these organs belong, is found at the posterior end. The way in which the shifting forward to the right of this posterior complex of organs (pallial complex) may be imagined to have taken place may best be seen from the diagrams given in Fig. 60 (BÜTSCHLI and LANG). The asymmetry which is brought about by the shifting of the pallial complex to a position near the anterior end of the body (*D*) is found in the Opisthobranchia and Pulmonata; when the pallial complex, in shifting forward, crosses the median line (*E*), as in the Prosobranchia (including the Heteropoda), the pleuro-visceral commissures become crossed (chiastoneury, streptoneury, Fig. 60 *E*), a condition not found in the two divisions mentioned above, and indicating a specially high degree of asymmetry.†

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* [It is manifestly impossible in a work of this nature to review all the numerous theories relating to the asymmetry of the Gastropoda. The views adopted by our authors are those of BÜTSCHLI and LANG, but the reader should consult SIMROTH'S account of the Mollusca in BRONN'S *Klass. u. Ordnung. d. Thierreichs*, Bd. iii. Lief. 22 u. 23, 1896, where an excellent summary of both the earlier and the more recent views, including those of PELSENEER and PLATE, will be found.—ED.]

† [In *Actaeon*, a form which, in spite of its peculiarities, must be regarded as most nearly allied to the Opisthobranchs, we find that pleuro-visceral connectives exhibit a streptoneurous condition, and in certain other forms also (*Philine*, *Aplysia*, etc., a streptoneurous condition is also found in the Pulmonate genus, *Chilina*) an indication of this condition is to be seen. The condition met with in these forms is thought to be a highly specialised one,

The cause of this asymmetry is to be sought in the manner of life of the Gastropoda, i.e., in the development of the foot as a massive creeping organ and in the simultaneous development of the shelly covering of the body. At first the visceral mass was fairly equally distributed over the body, which was covered only by a flattish shell. These original forms no doubt most nearly resembled the Chitones, apart from the segmentation of the shell found in the latter. So as to give greater freedom to the head which carried the sensory organs and the mouth, to allow the foot to grow larger and also to make it independent of the rest of the body, this organ became restricted to a smaller part of the body. This led to the formation of the high visceral sac, to which, as the part specially needing protection, the shell also became restricted, although the head and foot might still be drawn in under the latter, which consequently had to be of larger size than would be necessary in a merely protective covering. The animal was thus obliged to carry not only the high visceral dome, but a calcareous shell capable of accommodating the whole body. If this heavy mass became too high, it would be in a state of unstable equilibrium and would naturally become inclined, the best inclination being backward, as hindering the animal least in creeping. But since the mantle-cavity with its important organs (the gills, the apertures of the intestinal canal, the kidneys and the genital organs) lay at the posterior end of the body, such a backward inclination of the visceral mass would be so unfavourable as to be at first impossible and the only inclination which seems possible would be to the side. This lateral projection of the sac, however, too greatly impeded locomotion, and in spite of the disadvantages mentioned above, the visceral dome tended to incline backward. If we assume that the visceral dome inclined to the left side, the great pressure from the left would tend to squeeze the pallial complex towards the right. Herein, therefore, lay the cause of that displacement to the right and then forward which has been described above (Fig. 60). Ontogenetically, this process takes the form of more active growth of the posterior part of the body on the left side, which leads to the bulging of the visceral sac, and the forward displacement of the anus then follows (*cf.* p. 138).

It would not be surprising if the pressure of the inclined visceral

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for, from the study of other points in their anatomy it has long been concluded that the Opisthobranchs and Pulmonates (*i.e.*, the Euthyneura) are to be derived from the Prosobranchia after the latter attained the streptoneurous condition. If this is the case, we must regard the condition met with in the Euthyneura as a retrogressive one and not as an arrested stage in the rotation of the pallial complex.—Ed.]

mass led, not only to the shiftings we have mentioned, but also to the degeneration of single organs. LANG, in this way, traces back the absence of the organs originally forming the left part of the pallial complex (the left gill and the left renal aperture, etc.) which is to be noticed in various Gastropods (*e.g.*, the Monotocardia among the Prosobranchia and the Opisthobranchia) to the fact that the left side was exposed to specially strong pressure, through which these organs were prevented from functioning and degenerated. In other cases (*Haliotis*) the right (originally the left) gill is said to be smaller than the left (originally the right), and there is also an inequality in the kidneys of those Gastropods (*Haliotis*, *Patella*) in which the excretory organ is paired.*

The inclination of the visceral sac naturally led to its becoming coiled. LANG rightly traces this to the fact that, in order to avoid distortion, the upper side has to grow more than the lower. This unequal growth gives rise finally to the spiral coiling of the sac, which is followed in its shape by the shell. In those shells that are inclined to the left, further room for extension is given on this side, especially when the shell and visceral sac are directed backward. This unequal growth determines the formation of the so-called dextrally twisted shell. An original inclination to the right must be assumed for the shell that shows the sinistral twist. In other respects the process is the same in the two cases. The causes that lead to the inclination to one side or the other are difficult to determine, indeed, at the present time, they are hardly known.†

Some of the sinistrally twisted Gastropods have their inner organs arranged in the same way as the ordinary dextrally twisted forms. In such cases we have a false coiling which, it has been assumed, arose through the flattening of a dextrally twisted shell to such an extent that it became coiled in one plane. In this case the spiral might again assert itself on the side opposite to that on which the umbilicus originally lay, and in this way a false spiral might form on the umbilical side and a false umbilicus on the spiral side (SIMROTH, v. JHERING, LANG, No. 61). An indication of such a process

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* [This unequal development of the gills is very marked in *Pleurotomaria*, the right (originally left) gill being much the shorter of the two; this is the gill which is suppressed in the Monotocardia. Curiously enough the kidneys in some Diotocardia (*e.g.*, *Haliotis*, *Patella*) show exactly the reverse condition to that seen in the gills, *i.e.*, the right (primary left) kidney is much larger than the left (primary right); nevertheless, it is apparently the latter nephridium which persists in the Monotocardia.—ED.]

† [See footnote, p. 108, on the cleavage of the egg of sinistral Gastropods.—ED.]

is found in the Pteropoda that have a sinistrally twisted shell, but in other respects show the structure of dextrally twisted forms; these have the operculum also sinistrally twisted, whereas spiral opercula elsewhere always have a twist opposite to that of the shell (PELSENEER, No. 86).

[Forms with a dextral organisation in a sinistral shell, and which are supposed to have arisen as above, have been termed ultra-dextral. The commencement of an ultra-sinistral coiling is seen in *Planorbis corneus*, which possesses a true sinistral organisation with a shell which otherwise would be regarded as a flattened dextral coil. The embryo of this Gastropod, however, possesses a well-marked sinistral shell.]

The asymmetry characteristic of the Gastropoda may, however, become more or less marked by the acquisition of a secondary bilateral symmetry. This is the case in forms which, like the Pteropoda, have become adapted to a free-swimming manner of life. In such cases the principal cause of the asymmetry, which we found to be the creeping manner of life in connection with the development of a high visceral mass, falls into the background. The fact, however, that there are Gastropods which again become almost symmetrical while still leading a creeping life, but in which the shell has altogether or partly degenerated, as is the case in *Onchidium* and the *Limacidae*, shows what an important part is played in these processes by the covering of the body.

5. The Development of the External Form of the Body in the Different Divisions of the Gastropoda.

A. Prosobranchia.

We have already repeatedly alluded to the development of the larval form of the Prosobranchia and to its transformation into the adult,* the principal features in these processes, the development of the *Trochophore* and *Veliger* larvae and their transformation into the adult are thus known to the reader. Certain divergences, however, occur among the Prosobranchia, especially in the earlier ontogenetic stages, causing a modification of the external form of the body, and thus requiring special consideration.

It has already been stated (pp. 112, 116) that the eggs of many Gastropods are very rich in yolk, and this influences not only the

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* *Cf.* pp. 123, 131 and 134 on the development of *Patella*, *Vermetus* and *Paludina*, also Figs. 49-59.

formation of the germ-layers but also the development of the external shape of the body. This is the case, for instance, in *Nassa*, *Fusus*, *Fulgur*, *Natica* and others. Even in *Vermetus*, the *Veliger* stage of which we became acquainted with (Fig. 55), the *Trochophore* form is no longer distinctly developed. The velum appears at first in the form of two wavy cell-bands at the anterior end of the ventral surface and near it appear the rudiments of the tentacles ; immediately behind them are the mouth and the pedal swelling. The latter appears as a rudiment when the velum is only slightly developed and is far from complete dorsally. The rudiments of the organs, with the exception of the dorsally placed shell-gland, are thus here crowded together into a very limited area of the very large embryo. This is the case to a far greater extent when the egg is still richer in yolk, as, for instance, in *Fulgur* (McMurrich, No. 70). The first rudiments of the organs are here so crowded together that we might almost speak of a germ-disc in contrast to the large yolk-mass of the egg. We should then see the commencement of processes which, in a far higher degree, will be met with in the Cephalopoda. Thus in eggs very rich in yolk we may speak of a "blastoderm" which grows round the yolk, *i.e.*, the macromeres, and, indeed, the layer of micromeres is here greatly reduced as compared with the yolk-mass of the macromeres, as may be seen by a glance at Fig. 42 *D* and *E*, p. 112, and Fig. 47 *A* and *B*, p. 117. If we compare these figures with those of the blastula and invagination-gastrula of *Patella* (Figs. 49 and 50), *Planorbis* or *Paludina*, it is evident that these altered conditions must bring with them modifications in the external shape of the body.

In *Nassa mutabilis*, which we select for description as the best investigated if not the most extreme form in this respect, there is a point at the vegetative pole which remains for some time uncovered by cells (Figs. 61 *A*, *bl*, and 47 *C*, *bp*). This is the blastopore which closes later, the stomodaeum arising in this region (Fig. 47 *D*, *m*). In *Fusus*, the eggs of which exhibit a similar condition, the blastopore is said to persist and to pass over into the mouth (Bobretzky). The foot appears very early as a broad swelling behind the blastopore, even before the rudiment of the velum has arisen (Fig. 61 *A*, *f*). Near it lie the groups of ectoderm-cells (*ex*) which have been claimed as an excretory apparatus (external kidney). The velum (*v*) appears in front of the blastopore, advancing from the ventral to the dorsal side. Dorsally, the shell-gland appears, and over it the shell-integument. At a later stage, the anterior part together with the foot becomes marked off from the principal part of the embryo which contains the yolk (Fig. 61 *D*), the anterior part becoming swollen up like a vesicle (Fig. 63, *ce*, *v*). This phenomenon can be observed, still better than in *Nassa*, in a species of *Fusus* examined by BOBRETZKY.

In this form, the foot and especially the anterior part of the body appear to be swollen into a large vesicle (Fig. 62 *A* and *B*, *kb*), and this part is therefore here also sharply marked off from the posterior part of the embryo. This swollen part, which corresponds to the pre-oral section of the *Trochophore* larva, and which is found in other Prosobranchs, as well as in various other Gastropods (Pulmonates), has been called the cephalic vesicle. The embryo in consequence presents a very characteristic appearance (Figs. 62, *kl*, and 81, *kbl*).

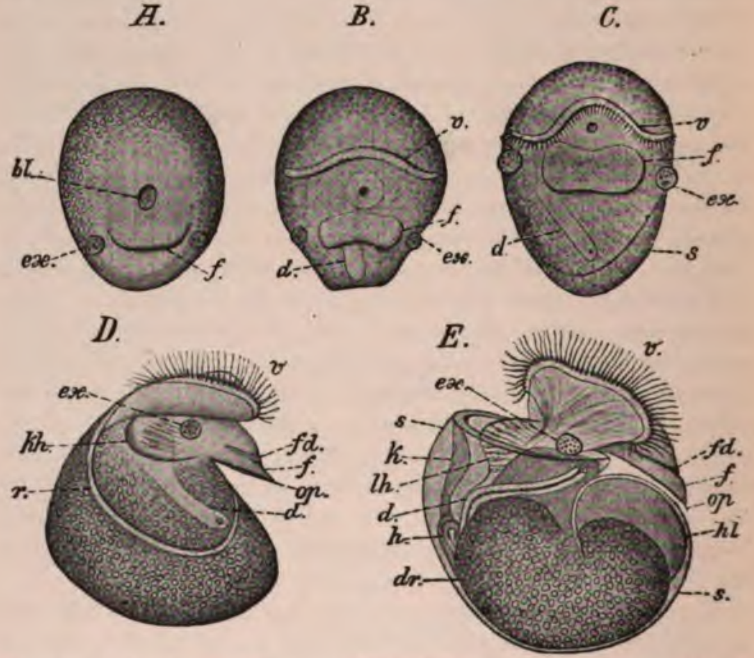

FIG. 61.—*A*-*E*, embryos of *Nassa mutabilis* of different ages (after BOBRETZKY). *bl*, blastopore ; *d*, posterior tubular portion of the enteron ; *dr*, yolk ; *ex*, group of ectodermal excretory cells ; *f*, foot ; *fd*, pedal gland ; *h*, rudiment of the heart ; *hl*, posterior hepatic lobe, near which can be seen, to the left, the anterior hepatic lobe, and above the latter the intestine (*d*) and the anus ; *k*, rudiment of gill ; *kh*, pallial cavity ; *lh*, larval heart ; *op*, operculum ; *r*, margin of the shell (*s*) ; *v*, velum.

The condition of the entoderm or yolk is of special significance for the embryos now under consideration. The sac-like rudiment of the enteron is seen to be open towards the yolk (Figs. 47 *C* and *D*, 62 *B*, and 63), which occupies the posterior and dorsal portion of the embryo. The enteron consists of an anterior wider section and a posterior tubular section (Figs. 47 *D*, and 62, *md*). The latter is at first parallel to the longitudinal axis, but soon lies obliquely to it, becomes connected with the ectoderm, and opens out through the anus which still lies in the ventral middle line (Fig. 61 *C*). At a later stage, the posterior part of the intestine assumes a still more oblique position and the anus comes to lie on the right side (Fig. 61 *D* and *E*). Here also the pallial cavity arises as a sickle-shaped depression of the ectoderm, this cavity in *Nassa* being altogether restricted to the right side of the embryo. The asymmetry seems still more marked here than in *Paludina* (p. 138). The shell also shares in this asymmetry; by its rapid growth it has become cup-shaped and covers the greater part of the visceral dome (Fig. 61 *D*). The operculum appears as a delicate plate in the posterior dorsal part of the foot (*C* and *D*, *op*). In the foot can be seen a ventral tubular ectodermal depression, which is no doubt the rudiment of the pedal gland (Figs. 61 *E* and *D*, and 63). The velum, which is not yet closed dorsally, has lost its former almost circular shape through the shifting forward of the mouth and the appearance at this point of a notch (Fig. 61 *C*). It at the same time increases in size and thus assumes the bilobed form which we have already described in connection with

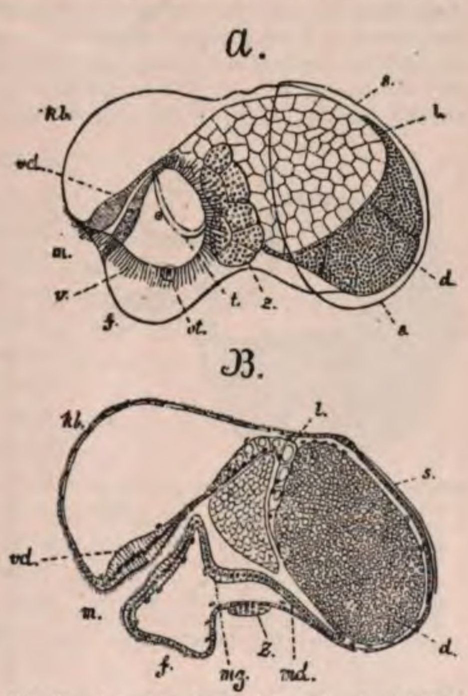

FIG. 62.—*A*, surface view, and *B*, median longitudinal section through an embryo of *Fusus* (after BOBRETZKY). *d*, yolk; *f*, foot; *kb*, cephalic vesicle; *l*, liver; *m*, mouth; *md*, enteron; *mg*, stomach; *ot*, otocyst; *s*, shell; *t*, tentacle; *v*, velum; *vd*, stomodaeum; *z*, sub-velar cells.

other Gastropod larvae. *Nassa* now shows a strong general resemblance to such larvae, as is evident from Fig. 61 *E*. This is also the case with *Fusus*, the embryos of which also at first deviate in several points from the usual shape and resemble those of *Nassa*.

Bobretzky has described in connection with *Nassa* and *Fusus* an organ of which no account has as yet been given; this is the so-called "*larval heart*," which has also been found in other Gastropoda (*e.g.*, by **Salensky** in *Calyptraea*, No. 98). This larval heart (Fig. 61 *E*, *lh*) is said to be a part of the ectoderm lying dorsally behind the velum, which is connected with mesodermal elements and carries on contractile movements. Other parts of the embryo, such as parts of the cephalic vesicle and the foot, are said to be capable, like this region, of contractile movements.

Fig. 63.—Longitudinal section through an embryo of *Nassa mutabilis* at a slightly older stage than in Fig. 61 *D* (after Bobretzky from Balfour's Text-book). The cephalic section and the foot of the embryo have separated to a great extent from the yolk which forms the posterior part of the embryo. *ce.v*, cephalic vesicle; *f*, foot; *m*, mouth; *st*, stomach.

Remarkable transformations in the shape of the body take place in some Prosobranchs which become adapted to a parasitic life on or in various Echinoderms (Asteroids, Echinoids and Holothuroids). An excellent example of this is afforded by *Entoconcha mirabilis* described by **Joh. Müller** (No. 76,) as occurring in the body-cavity of *Synapta digitata* attached to the wall of the intestine. The body of this animal has the form of a long vermiform coiled tube which in no way recalls that of a Gastropod, but its brood-cavity contains embryos very like those of other Prosobranchs. These have a velum (not, it is true, very highly developed), a spirally coiled shell, a foot with an operculum, otocysts, etc. Their further development is not known, but it is probable that they live freely for a time, like the young *Entovalva* (p. 43), and only later wander into a Holothurian.

In explaining the remarkable transformation undergone by *Entoconcha* in consequence of its parasitic life, two Prosobranchs described by P. and F. **Sarasin** (*Thyca entoconcha* and *Stilifer Linckiae*) are of great value (No. 103). These forms live parasitically on Asteroids, either piercing the integument by means of a proboscis-like structure (*Thyca*) or else sinking bodily into it (*Stilifer*). Even these ectoparasitic Gastropods show decided changes in their structure, and this would be still more the case if they were to penetrate through the integument of the host and reach the body-cavity. The possibility of such a breaking in of the parasite from without is shown by the *Stilifer*, which has already buried itself deep in the skin. The external shape as well as the inner organisation finally undergo, as in many other parasites, such a far-reaching alteration, that there is hardly any resemblance left to the former Gastropod, the parasite having degenerated into a mere tube, like *Entocolax* or *Entoconcha*, on which are devolved the functions of feeding and reproduction alone (W. VOIGT, No. 129; BRAUN, No. 15; SCHIEMENZ, No. 108).

B. Heteropoda.*

The ontogeny of the Heteropoda closely resembles that of the Prosobranchia to which in other respects also they are nearly related, but the special form of the adult Heteropod determines certain variations especially affecting the later stages of development. The ontogeny of the Heteropoda has been made the subject of special study by LEUCKART (No. 67), GEGENBAUR (No. 37), KROHN (No. 58A) and FOL (No. 31).

We have already become acquainted with a few of the younger stages of the embryo of *Firoloida* (Fig. 44 *A-C*, p. 114). The oldest of these stages was an invagination-gastrula. The inner end of the archenteron soon assumes a remarkable bilobed form, which recalls the enterocoelic formation of the mesoderm as described by ERLANGER in connection with *Paludina* (p. 121), but which is no doubt explained by the fact that the shell-gland which arises dorsally grows as a conical invagination towards the archenteron, causing a depression in the latter. When the shell-gland begins to flatten out again (Fig. 64), the archenteron also assumes a more regular form, becoming wider and sac-like. The blastopore passes over into the permanent mouth (Fig. 64, *o*). The shell-gland at first appears filled by a plug of brownish substance (s'); in *Paludina*, where a similar feature was

FIG. 64.—Embryo of *Firoloida Desmaresti* (after FOL). *c*, the primary body-cavity; *g*, archenteric cavity; *o*, mouth; *p*, foot; *s*, shell-gland; s^1, shell-plug; *v*, velum.

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* [The Heteropoda, or Nucleobranchia, are very generally regarded as a minor branch of the Prosobranchia, being classed under the Monotocardia as a subdivision of the Taenioglossa.—ED.]

observed by Bütschli, the plug was said to be expelled before the actual shell formed, whereas Fol believes here that this mass which fills the shell-gland passes directly into the shell when that depression flattens out again.

In the stage depicted in Fig. 64, the pre-oral ciliated ring has made its appearance and in this way the velar area (*vv*) becomes bounded. Behind the mouth, the rudiment of the foot (*p*) appears as a prominence which widens and thus assumes the form of a plate (Fig. 65 *B*). On either side at its base, the otocysts (*ot*) appear, while, anteriorly, the bilobed pedal gland forms as an ectodermal invagination. The posterior part of the foot at this early stage secretes a thin plate (*op*) which, in position and function, corresponds to the operculum of the Prosobranchia. Fine calcareous concretions become deposited beneath the shell-integument, and lead to the development of the calcareous shell. Unequal growth here also causes the shell soon to assume a coiled form, at least in the later stages. In *Firoloida* and *Pterotrachea*, the shell has only two whorls; in *Carinaria* and *Atlanta* it coils several times.

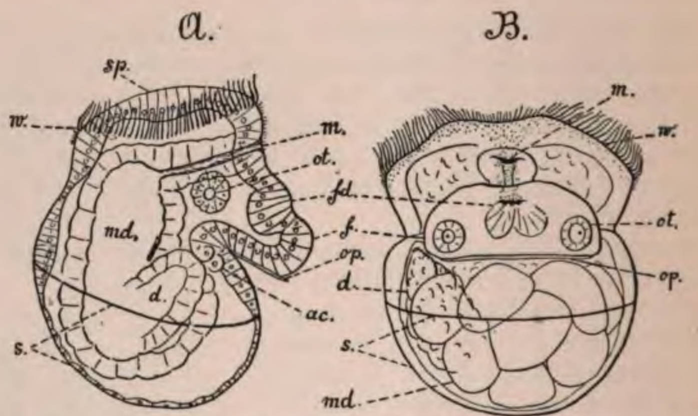

Fig. 65.—Embryos of *Firoloida Desmaresti*. *A*, seen from the right side, *B*, from the ventral side (after Fol). *ac*, anal cells; *d*, posterior part of the enteron; *f*, foot; *fd*, pedal gland; *m*, mouth; *md*, enteron; *op*, operculum; *ot*, otocyst; *s*, shell; *sp*, apical plate; *w*, ciliated ring.

Up to this point, the alimentary canal is without an anus. According to Fol, two large cells which appear behind the foot indicate, even in the stage depicted in Fig. 64, the position of this organ, and at this point the enteron, which is bent anteriorly, becomes connected with the somewhat depressed ectoderm (Fig. 65, *ac*).

These specially marked cells lay originally in the ventral middle line; they however shift towards the right side in consequence of the unequal growth which takes place also among the Heteropoda, and the anus is thus found on the right side, as we have already seen to be the case in various other Gastropods (p. 142). At this stage, the embryo is almost in the condition of the *Trochophore*. It then soon passes over to the *Veliger* stage, the velum being bilobed (Fig. 66). This bilobed character is at first made evident by the mouth shifting into a notch of the pre-oral ciliated ring.

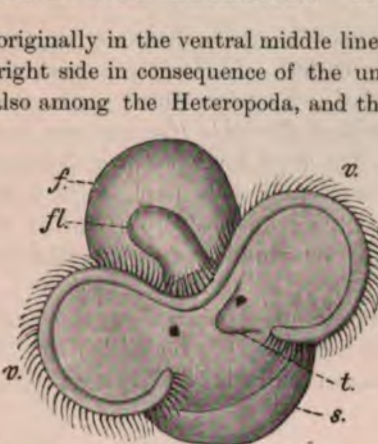

FIG. 66.—Larva of *Firoloida* with velum extended (after KROHN). *f*, foot; *fl*, rudiment of fin; *s*, shell; *t*, right tentacle, at the base of which the right eye is visible; the left tentacle is still wanting, but the eye is present; *v*, velum.

So far, the course of development in the various Heteropoda seems to be very similar (FOL). The round embryo, which is now provided with a bilobed velum, a foot and a cup-shaped shell, moves about by means of its cilia within the gelatinous egg-rope, which has become hollow; it, however, soon leaves this to swim about as a free larva (Fig. 66), circling slowly in the water (GEGENBAUR). The movements become more rapid and the larva more active when the lobes of the velum increase in size and are able to act independently of one another. According to KROHN, in *Firoloida* and *Pterotrachea*, the velum becomes drawn out on each side into two long and very narrow streamers, the larva then presenting an appearance similar to that of the *Veliger* larva depicted in Fig. 54, p. 130. In *Atlanta*, the velum is drawn out into three streamers

FIG. 67.—Larva of *Atlanta* with extended velum (after GEGENBAUR). *f*, foot; *fl*, rudiment of the fin; *op*, operculum; *ot*, otocyst; *s*, shell; *v*, velum.

(Fig. 67), which, however, are considerably shorter than those just mentioned. In *Carinaria*, again, the streamers are longer, and the lobes, cut up into three parts, cause this larva greatly to resemble that of *Firoloida* (GEGENBAUR and KROHN).

The great development of the locomotory organs in the Heteropoda causes their metamorphosis to be very marked. At its commencement, a cylindrical process with a rounded free end appears on the anterior side of the foot immediately in front of its base (Figs. 66 and 67, *fl*); this soon lengthens and carries on continuous swinging movements. This is the rudiment of the fin which, in its origin, must be regarded as belonging to the foot. In the course of metamorphosis, the cylindrical process becomes flattened laterally, and thus approaches the form of the keel-like fin of the adult (Fig. 68, *fl*). This flattening extends from behind forward; for a time, in the already keel-shaped fin, a portion of the former cylindrical process is found; this, in *Firoloida*, is attached somewhat nearer the anterior margin, but in *Pterotrachea* somewhat further back. By degrees this also is drawn into the flattened fin (KROHN). In some species of *Atlanta*, the fin appears from the first as a laterally flattened projection on the anterior side of the foot and thus here more nearly resembles its definitive shape. In this form, also, the sucker can already be seen, lying close to the posterior margin of the keel-like foot, this position

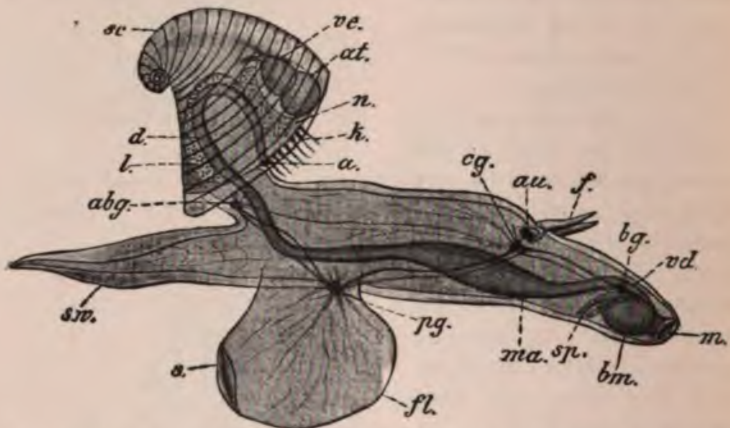

FIG. 68.—Lateral aspect of a *Carinaria* (after SOULEYET and GEGENBAUR). *a*, anus; *abg*, abdominal ganglion; *at*, auricle; *au*, eye; *bg*, buccal ganglion; *bm*, buccal mass; *cg*, cerebral ganglion; *d*, intestine; *f*, tentacles; *fl*, fin; *k*, gill; *l*, liver; *m*, mouth; *ma*, stomach; *n*, kidney; *pg*, pedal ganglion; *s*, sucker; *sc*, shell; *sp*, salivary gland; *sw*, tail; *vd*, oesophagus; *ve*, ventricle.

showing it to be the principal part of the Gastropod foot. This is evident from the fact that the fin originates at the anterior end of the foot, the posterior side of the latter being covered by the operculum (Figs. 66, 67); the intermediate part, *i.e.*, the actual rudiment of the foot, must therefore in any case be concerned in the formation of the sucker (Fig. 69 *A*), unless we are to regard the latter as a secondary formation. The sucker usually appears much later; in *Firoloida*, it is only found in the male, and has therefore here become merely a sexual character. Here and in *Carinaria* (Fig. 68), the sucker lies somewhat far down at the margin of the fin, and thus becomes absorbed in the latter, its pedal character being in this way still more marked. That the sucker is not merely a supplementary differentiation of the fin is proved by forms such as *Oxygyrus* in which it is independent of the fin and lies behind the latter (Fig. 69 *A*). We have here great agreement with the condition of some Prosobranchs (*Rostellaria*, *Strombus*, Fig. 69 *B*), in which the posterior part of the foot, as the carrier of the operculum, is sharply marked off from the anterior part. This view corresponds on the whole with that adopted by GEGENBAUR and recently especially by GROBBEN (No. 38), as to the significance of the foot in the Heteropoda.

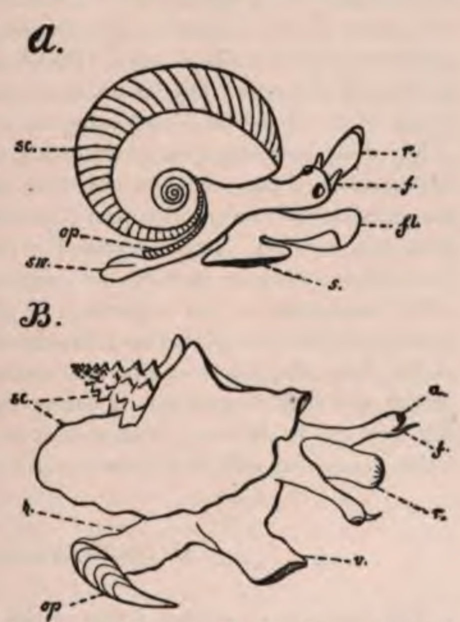

FIG. 69.—*A*, *Oxygyrus*, *B*, *Strombus*, each viewed from the side (after SOULEYET and KIENER). *a*, eyes; *f*, tentacle; *h*, posterior part of the foot; *op*, operculum; *r*, proboscis; *s*, sucker; *sc*, shell; *sw*, tail (most posterior section of the foot); *v*, anterior part of the foot.

The tail found in the Heteropoda (Fig. 68, *sw*), also arises from the foot, in *Atlanta* as a projection lying close behind the sucker (KROHN). As it increases in size, this process, which also is cylindrical, presses that part of the foot which bears the operculum more to the dorsal side, a position which is constant in forms like *Atlanta*, in which the operculum is retained throughout life. The operculum, however, as well as the shell, is frequently thrown off during the metamorphosis (*Firoloida*, *Pterotrachea*).

While these changes have been taking place in the foot, the velum has gradually attained its highest development and then commences to degenerate. The rudiments of the tentacles have already appeared on the velar area; these arise, curiously enough, quite asymmetrically. One tentacle only is present at first (Fig. 66, *t*). At the bases of the tentacles, the eyes appear. In some forms, the tentacles may be reduced again (*Pterotrachea*). Before the shell is thrown off, the velum has for the most part degenerated, only a few traces of it being still found near the eyes.

The body increases greatly in length, not only on account of the development of the caudal section just described, but also through the extension of the anterior part (the development of the so-called proboscis, Fig. 68). In consequence of the great lengthening of the foot and the anterior part of the body, the visceral sac lies, as in other Gastropods, on the upper side of the body (Fig. 68). At the junction of the visceral sac and the dorsal wall of the anterior part of the body, the mantle-cavity has arisen and the gill has formed. Where the shell is retained, it covers the visceral sac (*Carinaria*, Fig. 68), and in *Atlanta*, which also as an adult possesses a shell, the whole animal can still be withdrawn into it.

C. Opisthobranchia.

The ontogeny of various forms of the Opisthobranchia has been studied by many zoologists. The embryonic development and the younger stages of the free-swimming larvae were those usually investigated, the animals being difficult or even impossible to keep in confinement during the later stages. SARS (Nos. 104 and 105) and LOVÉN (No. 69) established the chief features of their ontogeny, while at a later period ADLER and HANCOCK (No. 1), NORDMANN (No. 80), VOGT (No. 127), SCHULTZE (No. 113), and KEFERSTEIN (Nos. 52 and 53), occupied themselves principally with the development of the larval forms and of the shape of the body. RAY LANKESTER (Lamell. Lit., No. 29), TRINCHESE (No. 125), BLOCHMANN (No. 8), RHO (No. 93), turned their attention also to the internal processes, especially to the earliest ontogenetic stages. References to the other authorities on this subject will be found in the literature appended to this section and in the course of our account.*

In consequence of the rich supply of yolk in the egg, gastrulation seems usually to take place by epibole.† The blastopore, at one period, is a slit of variable length (*e.g.*, in *Fiona* and *Elysia*, HADDON, No. 40; *Ercolania*, TRINCHESE; *Aplysia*, BLOCHMANN). This slit closes from behind forward and, in some cases, altogether disappears, the mouth then arising as an ectodermal invagination at the point at which it closes. This is the case, according to BLOCHMANN, in *Aplysia* and a similar condition may, according to VOGT's account, be found in *Elysia*. In *Fiona*, according to HADDON, the slit-like blastopore closes from behind forward and either passes directly into the mouth or the latter is invaginated at the spot where the former finally closes. Such a condition can be gathered from the descriptions given by TRINCHESE (No. 125) and LANGERHANS (No. 62) of the *Aeolidae* and *Doris*, but these accounts are not very clear. From all these statements, however, it appears tolerably certain that the mouth corresponds in position to the anterior end of the slit-like blastopore.

The changes that take place in the large entoderm-cells are significant in connection with the further shaping of the embryo. These have been specially observed in *Aplysia* by BLOCHMANN. Cleavage is unequal from the first and, at the four-celled stage, two of the cells are very much larger than the remaining two, and this is still apparent after the abstriction of the micromeres, when we find two very large and two smaller macromeres (Fig. 41 *B*). In consequence of the smaller amount of the yolk contained in the latter, they soon divide and give rise to a mass of small entoderm-cells, while the two large macromeres (Fig. 41 *I* and *II*) are retained in their full size. The ectoderm-cells grow over the entomeres and the smaller entoderm-cells separate from the two large macromeres which

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* [Recent workers on this group have devoted themselves mainly to the question of cell-lineage, see HEYMONS (No. XII.) and VIGUIER (No. XXVI.). MAZZARELLI (No. XVI.) has, however, made some additional observations on the larval *Aplysia*.—ED.]

† [HEYMONS (No. XII.), who has investigated the early stage in the ontogeny of *Umbrella*, finds that the gastrula is here intermediate between the epibolic and the embolic type, as is the case in so many other Gastropods. His work, which is an important one, deals largely with the cell-lineage and the early ontogenetic stages. *Umbrella*, in its cleavage, appears to conform to the normal Gastropod type, the process of entoderm-formation is quite unlike that described by BLOCHMANN in *Aplysia*, the yolk being equally distributed between the four macromeres and the entodermic epithelium arising in a more normal manner.—ED.]

are still undivided. An archenteron forms between them, lined partly by the small entomeres and partly by the two persistent macromeres (Fig. 70). Here also there is a suggestion of a condition intermediate between an epibolic and an invagination-gastrula, as is said to be the case in other Gastropods (*cf.* p. 115). The closure of the blastopore and the sinking in of the stomodaeum already described (Fig. 71, *m*), take place immediately after this stage. Where the macromeres are not in direct contact with the ectoderm, the smaller entoderm-cells spread out (Fig. 71). The gut, still partly bordered by the macromeres which have shifted apart, now resembles a closed sac.* Up to this point there has been no sign of the mesoderm-rudiment which, according to BLOCHMANN, appears late in the form of two small masses of cells lying to the right and left of the stomodaeum, the origin of which could not be established. TRINCHESE, on the other hand, described, in the *Aeolidae*, two large and distinct primitive mesoderm-cells which may be traced back, like those of the mesoderm-rudiment found by RHO in *Chromodoris*, to the macromeres. [See the more exact work of HEYMONS (No. XII.) on *Umbrella* in this connection, and footnote, p. 119].

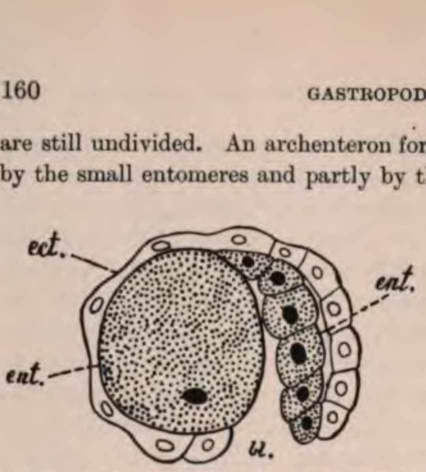

FIG. 70.—Embryo of *Aplysia limacina* in optical section (after BLOCHMANN). *bl*, blastopore; *ect*, ectoderm; *ent*, entoderm.

At the side of the embryo opposite to the mouth, the shell-gland arises as a depression which at first is shallow, but deepens later (Fig. 71 *A*, *sd*); above this, the shell-integument is soon secreted. Two cells (*az*), which lie on the ventral side in front of the shell-gland and which, in consequence of their large size, rise above the surface (Fig. 71), mark the position of the anus, which appears late. These anal cells could be seen in *Aplysia* in earlier stages, lying at the posterior edge of the blastopore. They had been already described by LANGERHANS in several Opisthobranchs (*Acera*, *Aeolis*, *Doris*) and had been connected with the formation of the anus; the same

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* [MAZZARELLI (No. XVI.) does not appear to have traced the ultimate fate of the two smaller macromeres, but one would imagine, from his description, that they form part of the ectoderm. He regards the small entomeres seen in Fig. 71 as derivatives of the two large macromeres and, judging from his Fig. 12, Pl. x., small cells are constricted off from the macromeres. His observations are not clear, but they seem to differ from those of BLOCHMANN.—ED.]

significance is ascribed to them by **Trinchese** in the *Aeolidae* and by **Fol** in the Heteropoda and Pteropoda.

The ciliated cells of the pre-oral ring have already become differentiated, the velar area being thus marked off (Fig. 71, *v*). Ventrally behind the mouth, the foot appears as a swelling (*f*); behind it can be recognised the anal cells (*az*). The shell-integument has already developed further. The *Trochophore* stage is here less marked than in many other Gastropods, as the embryo undergoes certain modifications in consequence of the richer supply of yolk. Such a stage, however, has been distinctly recognised by **Ray Lankester** and **Trinchese** and other observers in Opisthobranchs which have been investigated by them. An embryo of *Aplysia* figured by **Ray Lankester** * shows the greatest resemblance to the embryos of *Firoloida* depicted in Fig. 65 *A*.

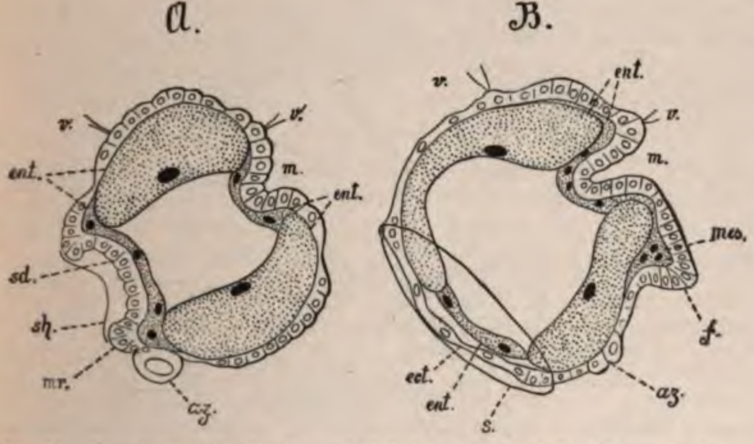

Fig. 71.—Two stages in the development of *Aplysia limacina* (after **Blochmann**). *az*, anal cells; *ect*, ectoderm; *ent*, entoderm; *f*, foot; *m*, mouth; *mes*, mesoderm; *mr*, margin of the mantle; *s*, shell; *sd*, shell-gland; *sh*, shell-integument; *v*, velum.

The *Trochophore* stage, by the transverse extension of the velum, passes into the *Veliger* stage, in which, owing to processes of growth similar to those already described, the symmetrical shape undergoes certain modifications. In most respects, indeed, the ontogenetic processes which now follow closely resemble those described for the Prosobranchia, so that we need here only touch upon the principal features.

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* (See Lit. to Lamellibranchia, No. 29, Pl. 8, Fig. 17.)

The two lobes of the velum are very large and give the larva a characteristic appearance (Fig. 72, *v*). They remain undivided, are very broad and are beset with long thick cilia; the fissure between them, however, usually carries short and delicate cilia, the bilobed character of the velum being in this way emphasised. The shell has lost its flat and (later) cup-like shape and, in the free-swimming larva, has already become coiled. The foot (*f*) develops an operculum on its dorsal surface. We thus find, in the Opisthobranchia, the same general condition already met with in the Prosobranchia and the Heteropoda. Although most Opisthobranchs, as adults, are entirely devoid of a shell, or else, as in the majority of the shell-bearing forms, have a highly specialised, often greatly reduced, or even internal shell, the larva possesses a coiled, often nautiloid shell into which the body can be withdrawn and which can be closed by an operculum (M. SARS). The shell is usually thrown off and the operculum almost invariably has the same fate. When, however, the adult possesses a shell, we may fairly safely assume that this has been derived from the larval shell. In only a few Opisthobranchs is the shell of the adult so large that the whole body of the animal can be

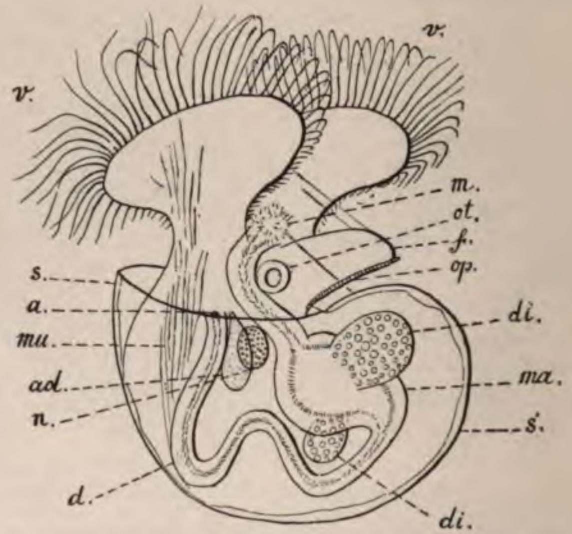

FIG. 72.—*Veliger* larva of an Opisthobranch. *a*, anus; *ad*, anal gland (? probably an excretory organ, like *n*); *d*, alimentary canal; *di*, diverticulum of the stomach; *f*, foot; *m*, mouth; *mu*, muscle (retractor of the velum); *op*, operculum; *ot*, otocyst; *s*, shell; *v*, velum.

withdrawn into it; the retention of the operculum as in *Actaeon* (*Tornatella*) is quite exceptional. According to TRINCHESE, the larval shell in some forms (Saccoglossa) shows a delicate reticulate structure on its surface; in most other larvae it is smooth.

Passing now to the internal organisation of the *Veliger* larva, we notice first that, from the oral aperture which lies at the ventral incision of the velum, the stomodaeum (which only at a later stage is provided with a radula) runs backward and becomes connected with the large enteron. From this latter, there are two lateral outgrowths which differ in size (Fig. 72, *di*); these are formed of specially yolk-laden cells and thus no doubt owe their origin to the macromeres. The intestine also arises as a diverticulum of the entoderm-sac; it then lengthens considerably, bends forward and, after uniting with the ectoderm at the right side of the body, opens outward rather far forward, near the edge of the shell (Fig. 72).

Little is as yet known as to the differentiation of the mesoderm in the Opisthobranchia. A strong muscle, sometimes composed of two branches, runs back from the velum, becoming attached to the shell posteriorly (Fig. 72, *mu*). Another shorter retractor of the velum extends between the base of this organ and that of the foot. This arose from single spindle- or star-shaped mesoderm-cells which came to lie on the right side of the larva in this region.

This latter muscle carries on regular rhythmical movements and, on this account, has, according to TRINCHESE, falsely been regarded by several observers as a heart. The so-called larval heart which has been described in connection with the Prosobranchia (*Nassa*, Fig. 61 *E*, *lh*, p. 150) differs somewhat in position from this retractor, but is, like it, composed of long mesoderm-cells.

According to the accounts of the Opisthobranchs now under consideration, no primitive kidneys resembling in shape those occurring in the Prosobranchia (*Paludina*) and Pulmonata (p. 136) have been found in them, but vesicular structures which lie in the dorsal region behind the velum to the right and left of the oesophagus have been described as primitive kidneys. These have been regarded as excretory organs chiefly because they are filled with strongly refractive concretions. They seem never to possess efferent ducts.*

The views taken of the excretory organs of the Opisthobranchia seem to us to be somewhat confused. TRINCHESE, for instance, has described a paired or unpaired sac-like gland with a longer or shorter efferent duct which

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* [These appear to be ectodermal in origin (HEYMONS) and analogous to the ectodermal anal kidney of the Prosobranchia (p. 129 and No. XV.).—Ed.]

opens out near the anus as an anal gland. In *Ercolania*, this gland is unpaired and strongly pigmented. A glandular structure described by Rho in *Chromodoris* is said also to open near the anus. This involuntarily recalls the rudiment of the kidney of the adult, a view which has recently been adopted by Mazzarelli (No. 74 and No. XV.). This author derived similar structures from the mesoderm. One organ especially which, curiously enough, was assumed to be an "anal eye," excited attention. This lies in various Opisthobranch larvae (in *Aplysia*, *Philine*, *Pleurobranchus*, *Doris*, *Aeolis*, Lacaze-Duthiers and Pruvot, No. 60) on the ventral side, near the anus; it is strongly pigmented and is no doubt identical with the glandular structures above mentioned. According to Mazzarelli, as already mentioned, it is derived from the mesoderm, but Lacaze-Duthiers and Pruvot, who investigated the origin of this hypothetical larval eye more closely, traced it back to the ectoderm. This was also the result of the ontogenetic researches of Heymons as to the origin of this structure, and it cannot therefore be regarded as a nephridium, but must rather be compared with those excretory organs which, like the sub-velar cells described in the Prosobranchia, are yielded by the ectoderm (p. 129). The excretory character of the organ seems indisputable, but no decision as to its homology can be arrived at until its development and future fate in the different forms of Opisthobranchs are better known.

Among the sensory organs of the larva, the large otocysts at the base of the foot deserve special mention. As in other pelagic larvae, strong cilia appear at the centre of the velar area in various forms (*Fiona*, *Polycera*, *Elysia*, *Philine*, Haddon, No. 40). In the *Aeolidae*, the end of the foot carries a few long stiff cilia. Eyes are found on the velar area in those cases at any rate in which tentacles also appear there as rudiments, but are altogether wanting in many larval forms.

The greatly modified forms found among the Opisthobranchia, such as the genera *Limapontia* and *Phyllirhoe*, like the more primitive forms, have larvae with bilobed velum and shell provided with an operculum (Adler and Hancock, No. 2; Schneider, No. 112).

Our knowledge of the transformation of the larva into the adult rests principally upon the statements of Max Schultze and Nordmann made with regard to *Tergipes Edwardsii* and *T. lacinulatus* (Nos. 80 and 113).

The larva of *Tergipes Edwardsii*, when still provided with a shell, already seems to have lengthened somewhat. The two velar lobes are unusually large and oval. On the velar area are situated a pair of tentacles and, at the base of these, the eyes. The larvae probably swim about for some time at this stage. The mantle then withdraws from the shell and comes into closer contact with the body. The way is thus prepared for the casting of the shell which takes place while the velum is still fully developed. We thus have a

Veliger larva without shell or operculum, which presents a very peculiar appearance (Fig. 73 *A*). This larva, in the length of its body already shows a distinct approach towards the adult condition. In the *Tergipes* observed by M. SCHULTZE, the passage from the larva to the adult is somewhat different, the velum degenerating in this form before the shell is thrown off. In this last case, the larva must have adopted earlier the creeping manner of life. The shell-less larvae of *Tergipes Edwardsii*, with their large vela at first swim about with even greater rapidity than the shelled forms, but then gradually begin to creep, as the body increases in size (Fig. 73 *B*). The lobes of the velum commence to degenerate until they are reduced to a pair of rounded processes lying in front of the mouth (Fig. 73 *C*), which, it has been assumed, change into the labial palps.

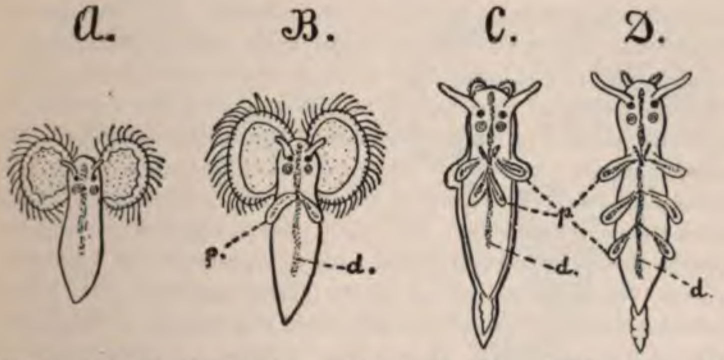

FIG. 73.—*A*-*D*. Veliger larvae and young of the *Tergipes Edwardsii* (after NORDMANN). *d*, alimentary canal; *p*, dorsal papillae.

This view of the transformation of the remains of the velum into the sensory organs near the mouth, has been adopted especially by LOVÉN, who already held a similar view as to the origin of the oral lobes in the Lamellibranchs (p. 46). RAY LANKESTER holds that, in *Limnaea*, the remains of the velum pass over into these subtentacular lobes; but this point has been disputed in connection with this form. It has already been stated (p. 133) that the observations made by RAY LANKESTER for *Onchidium* were confirmed by JOYEUX-LAFFUIE.

While the larva is still provided with the large velar lobes, one pair of the dorsal appendages (cerata) arise which are so characteristic of the Nudibranchs and into which the diverticula of the enteron soon extend (Fig. 71 *C*). Another pair of these intestinal diverticula has already formed and these belong to the next pair of cerata. As other processes develop, the young animal approaches more and more nearly to the adult form, but has first to pass through a moult (NORDMANN), during which it remains entirely quiescent, surrounded by the cast skin as by a transparent sheath. This membrane is no doubt to be regarded as the cast off cuticle.

D. Pteropoda.

The early development of the Pteropoda closely resembles that of other Gastropods. We have already seen that the embryo at first has the form of an epibolic gastrula and passes from this to an invagination-gastrula (Fig. 45 *A* and *B*, p. 115). The entoderm, at a later stage, by the great increase in number of its cells, is transformed direct into the epithelium of the archenteron; but, in some forms, the macromeres seem to be retained for a long time, the transition to the definitive entoderm being then less simple. The blastopore is slit-like and situated at the vegetative pole. After its closure, the mouth arises at the same spot through an ectodermal depression. From the published accounts, we may assume that the mouth then shifts its position or, in consequence of the further growth of the embryo, changes its shape. At one end of the embryo a circle of strongly ciliated cells marks off the velar area, immediately behind which the mouth now lies. At a point almost opposite the cephalic area, on the dorsal surface of the embryo, an ectodermal depression appears which varies in size in the different genera; this is the shell-gland. The whole of the interior of the embryo is filled with yolk-laden macromeres. The velum becomes more distinct, and, behind the mouth, the foot appears as a large outgrowth. When the otocysts arise near the foot and the two anal cells (which also occur in the Pteropoda) behind it, the embryo passes into the *Trochophore* stage which greatly resembles that met with in the Opisthobranchs, or the corresponding stage in *Firoloida* (Fig. 65).

At the stage just described, or even earlier, the embryo may become free and may swim about actively, since it is already provided with a velum. Up to this point the different Pteropods develop in much the same way, but differentiations soon appear in the development of the larval form, especially with regard to the shape of the velum and the shell. The Gymnosomata also diverge from the other forms in so far as the *Veliger* stage gives rise to a peculiar larval form encircled with several ciliated rings.

A certain differentiation in the development of the early larval stages is also caused by the fact (stated by FOL) that the order in which the organs (velum, mouth, shell-gland, foot, etc.) appear, varies greatly in different forms. The comparison of corresponding stages is in this way rendered somewhat more difficult, but the final result is, as already stated, very similar.

The embryonic development of a large number of Pteropoda (*Cavolinia* (*Hyalea*), *Hyalocylix*, *Creseis*, *Styliola*, *Cleodora*, *Cymbulia*, *Clione*) has been closely studied by FOL, who has also described the further development and the metamorphosis of these animals (No. 32). The phenomena connected with metamorphosis had previously been investigated especially by JOH. MÜLLER, GEGENBAUR, and KROHN in the above genera as well as in *Tiedemannia* and *Pneumodermon* (Nos. 77-79, 37 and 58*a*).

Thecosomata. The *Trochophore* stage soon passes into the *Veliger* stage, a dorsal and a ventral incision appearing in the velum, which thus becomes bilobed. This organ is bordered anteriorly by a circle of strong cilia serving for locomotion, and posteriorly by weaker cilia which conduct food to the mouth (GEGENBAUR, FOL). In *Cleodora* a band of cilia appears on the velar area at a time when the larva is still at the *Trochophore* stage. Other Pteropods, *e.g.*, *Cavolinia*, carry on the velar area a central ciliated tuft, such as has been met with in other Molluscan larvae.

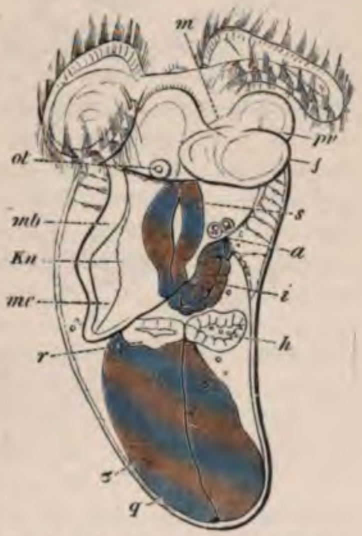

FIG. 74.—Larva of *Cavolinia tridentata*, seen from the right and ventral side (after FOL, from BALFOUR'S Text-book). *a*, anal region, with the two anal cells; *f*, mesopodium; *h*, heart; *i*, intestine; *kn*, contractile dorsal sinus; *m*, oral region; *mb*, mantle; *mc*, mantle-cavity; *ot*, otocyst; *pn*, rudiment of fin; *q*, shell; *r*, renal sac; *s*, stomach; *σ*, food-yolk.

The size of the velum varies greatly. In *Cavolinia*, where it is retained for only a short time, it is less extensive. In Fig. 74, we see the velum in a slightly older larva of such a form. In *Cleodora*, *Cymbulia*, *Tiedemannia* (Fig. 75 *A* and *B*) the velum is much larger, and each of the two lobes is again subdivided, so that the whole appears to consist of four lobes. This condition is specially distinct in a larva belonging to the genus *Creseis* and described by GEGENBAUR (Fig. 75 *C*), in which the velum is still of considerable size when the shell has grown to a great length. A strong retractor starts from the anterior part of the body and is inserted at the posterior end of the shell (Fig. 76 *A*, *r*).

The shell originates from the shell-gland which has shifted towards the end of the body. According to Fol, a plug of strongly refractive substance is very often to be found in the shell-gland; in some cases, this plug is perhaps formed abnormally, but in *Cymbulia* it no doubt represents the normal condition. The substance is then said to spread out under the shell which is secreted as a cuticular integument, after the shell-gland has gradually flattened out. It is at first shaped like a watch-glass, then deepens and becomes cup-shaped (*Cavolinia*, *Cleodora*, etc.), or else it becomes rounded and almost oviform like the embryonic chamber of the Cephalopoda. This is the case in *Creseis*, *Cymbulia*, and the Gymnosomata. The shell, which now becomes calcified, grows by the addition of new layers to the margin of the embryonic shell, their boundaries being recognisable as zones of growth. In this way, the large larval shell which, in the *Cavoliniidae* and Gymnosomata is long and in the *Cymbuliidae* coiled is formed (Figs. 74, *q*, 75 *A-C*, 76 *A*, *s*).

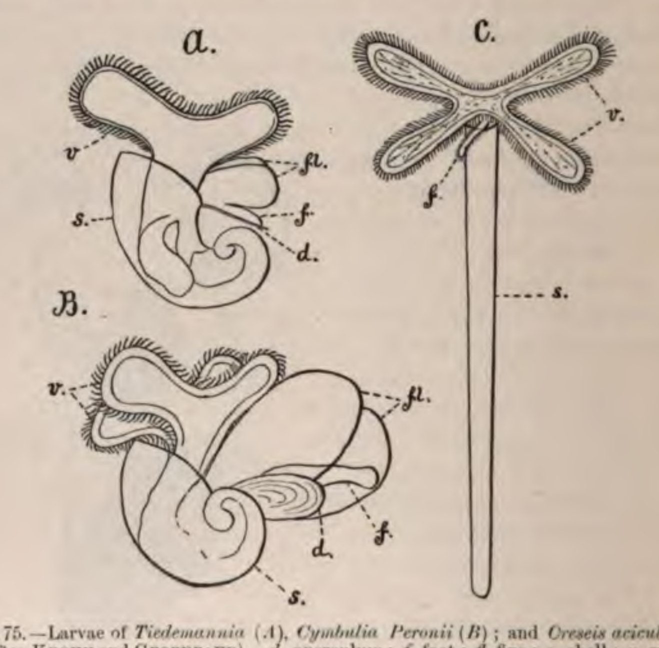

Fig. 75.—Larvae of *Tiedemannia* (*A*), *Cymbulia Peronii* (*B*); and *Creseis acicula* (*C*) (after Krohn and Gegenbaur). *d*, operculum; *f*, foot; *fl*, fins; *s*, shell; *v*, velum.

In the *Cavoliniidae*, the shell of the adult forms very simply from the larval shell, by the addition of further layers to its anterior margin, but the latter is marked off by a constriction from the part which represents the adult shell; here also, in *Cavolinia*, a transverse wall is secreted, after the body of the animal has withdrawn from the posterior part of the shell. This larval shell is afterwards lost. In other *Cavoliniidae*, the larval shell is retained even in the adult (*Styliola*), the posterior part of the body not being withdrawn from it (*Creseis*). The coiled larval shell of the *Limacinidae* passes directly over into the adult shell, new coils merely being added to those already present (*Limacina*, *Spirialis*). In the *Cymbuliidae*, the larval shell can hardly be distinguished from that of the young animal undergoing metamorphosis. This calcareous shell is thrown off, the cartilaginous shell of the adult surrounded by the mantle then appearing; this shell arises by the thickening of the connective tissue and can therefore not be in any way compared to a true Molluscan shell (PELSENEER).

The transformation of the shell just described is one of the most conspicuous features among the external alterations undergone by the larva. In the *Cavoliniidae*, the shell lengthens, and, in the *Cymbuliidae* and *Limacinidae*, becomes rolled up (Fig. 75 *A* and *B*). Even in the straight shells of the *Cavoliniidae* we find a slight flexure of the posterior end which gives the shell the shape of a hunting horn. It is a curious fact that the concavity of this slightly bent shell does not correspond to the ventral side, but lies dorsally. This must be connected with a twisting undergone by the posterior part of the body in these forms (BOAS, Nos. 9 and 10). The coiled shell in any case represents the more primitive condition and persists throughout life in the *Limacinidae*, which are also provided with an operculum.

The development of the foot exercises a great influence on the changes that take place in the external form of the body. The foot originally was a large projection lying behind the mouth. While the middle part of the foot does not increase greatly in size, and at first is conical or linguiform, two projections arise at its sides and grow out rapidly (Fig. 74, *pn*, and 75 *A*, *fl*) in the form of two large lobes, the so-called fins (Fig. 75 *B*, *fl*). The great size which may be attained by the fins in the further course of metamorphosis is already sufficiently known. The median lobe of the foot also increases in size. In the *Cymbuliidae*, a filiform appendage develops on it posteriorly. Ontogeny proves indisputably that the fins owe their origin to the foot, as was observed long ago by JOH. MÜLLER and KROHN.

The *Veliger* larva of the Pteropoda shows great agreement with that of the Opisthobranchia, a fact which is specially evident in the forms that have a coiled shell (Figs 75 *A*, and 72, p. 162). The posterior part of the foot here also usually carries an operculum which, in the *Limacinidae*, is retained throughout life, and in the *Cymbuliidae*, is thrown off after the shell has been lost; but in those Pteropods that have straight shells an operculum is not found. A well-developed primitive kidney is not known to occur in the Pteropoda; they may, in this respect, resemble the Opisthobranchia, a comparison which would be supported by their internal organisation. We have here, for instance, as in the Opisthobranchs, the two sacs filled with food-yolk as appendages of the enteron. In the formation of the alimentary canal, the entoderm becomes differentiated in such a way that the median (ventral and dorsal) parts become the epithelium of the archenteron, while the lateral parts which appear composed of large cells rich in yolk, by growing out into caeca, become the nutritive diverticula. These caeca have been supposed to yield the liver, but this organ, according to Fol's statements, forms independently of them as an outgrowth of the archenteron. A posterior tubular diverticulum of the archenteron runs out towards the ventral surface and fuses with the ectoderm at the spot where the anal cells lie to form the anus. This lies either in the middle line behind the foot, shifting secondarily to the left side (*Cavoliniidae*) or else it lies from the first on the right side of the body (*Cymbuliidae*, Gymnosomata). There are also other indications of asymmetry, such, for instance, as the lateral position of the mantle-cavity. This indicates that the Pteropoda which, as adults, are somewhat symmetrical in structure, are derived from asymmetrical forms.

As the fins increase in size, the velum gradually degenerates. The mouth takes up its final position between the fins. The disappearance of the velar area leads to the *great reduction of the large section of the larval body which lies in front of the foot*. At a later stage, the two tentacles bud out in this region, carrying the eyes. This reduction of the anterior part of the body as compared with the massive foot, which has shifted far forward, is specially characteristic of the Thecosomata. In *Tiedemannia*, however, the oral region becomes raised up to form the proboscis which bends backward. After the growing shell has reached the base of the foot, a slit-like invagination appears in the *Cavoliniidae* (according to Fol) on the right side between the base of the foot and that of the velum, extending then dorsally and ventrally. The mantle-cavity thus formed finally encircles the body (visceral dome) on three sides, so that the latter is connected with the mantle or shell (in the *Cavoliniidae*) only on the left dorsal side.

The ventral position of the mantle-cavity in the *Cavoliniidae* is very striking, as this cavity, in other Gastropods, is dorsal in position. According to BOAS, the visceral dome and the shell connected with it have undergone torsion. This view is supported by the fact that, in younger larvae, the bent apex of the shell is directed not, as in the adult, dorsally, but to the left. It is at once evident that this process may be classed with those already described in connection with the acquisition of asymmetry by the Gastropoda (p. 143), but in this case other changes have been added in adaptation to a different manner of life.

We shall not here give any special account of those ontogenetic processes such as the formation of the otocysts, the radular sac, etc., which take place in the same way as in other Gastropods.

Gymnosomata. The *Trochophore* is followed by a larva provided with a large bilobed velum and a pointed foot (Fig. 76 *A*, *f*). The shell, which at first is cup-shaped but later oviform, as it grows in length, becomes a tube widening out anteriorly (Fig. 76 *A*), on which, as a rule, the zones of growth are recognisable as intervals varying in width. The larva does not long remain at this stage, in which it closely resembles the straight-shelled Thecosomata. The shell is thrown off and the velum degenerates. When it disappears, or even sooner, three ciliated rings appear on the body (Figs. 76 *B* and 77 *A*). In those larvae that develop ciliated rings even before the disappearance of the velum and the casting of the shell, these are distributed in such a way that the most anterior ring lies between the

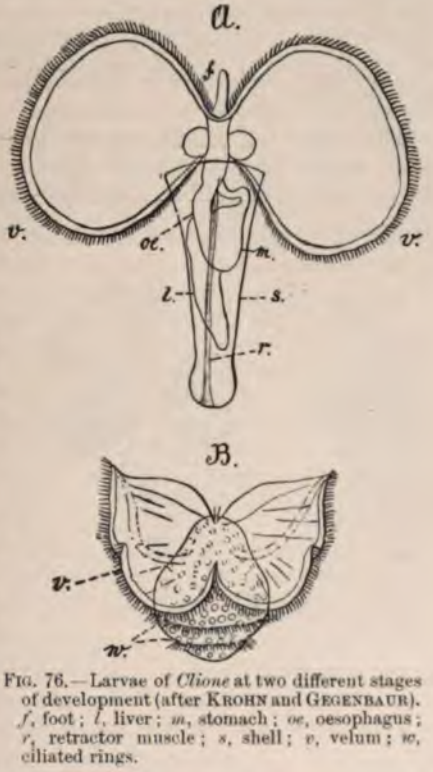

FIG. 76.—Larvae of *Clione* at two different stages of development (after KROHN and GEGENBAUR). *f*, foot; *l*, liver; *m*, stomach; *oe*, oesophagus; *r*, retractor muscle; *s*, shell; *v*, velum; *w*, ciliated rings.

velum and the foot, and the posterior ring immediately in front of the aperture of the shell. In this case, the posterior part of the body is still of some length; in other larvae, the posterior ciliated ring is found almost at the end of the body (Fig. 76 *B*). The velum seems to bear no relation to the ciliated rings. After it degenerates, the larva presents an appearance which, for a Mollusc, is very peculiar, recalling rather the Annelid larvae which are encircled with several ciliated rings. These also are at a stage following the *Trochophore* larva, as already mentioned (Vol. i., p. 277), and as we were able to see in various polytrochan larvae. This comparison to an Annelid larva has already been instituted by **Gegenbaur**, and the fact has been emphasised that the resemblance is accidental and of no great significance.

Our knowledge of the ontogeny of the Gymnosomata relates entirely to *Clione* and *Pneumodermon*, two forms which seem to agree pretty closely in the general features of their development, as shown by **Joh. Müller**, **Gegenbaur**, **Krohn** and **Fol**. As most of these larval Gymnosomata have not been traced to the adult stage, it is by no means certain that the larvae examined belonged to these genera.

The mouth lies on the anterior, proboscis-like projection, and the anus, which is displaced to the right, ventrally between the first and second ciliated rings. Two pointed outgrowths lying near the mouth represent the rudiment of the so-called cephalic cone (Fig. 77 *B*). Somewhat further back, but in any case in front of the anterior ciliated ring, the rudiments of the acetabuliferous appendages appear (**Joh. Müller**). [These, according to **Pelseneer**, are derivatives of the proboscis.] When the proboscis is evaginated at a later stage, these seem shifted further back, being now situated on its posterior part (Fig. 77 *B*). The foot was previously referred to as a pointed ventral appendage, lying behind the first ciliated ring. Before this stage, an anterior, horseshoe-shaped lobe forms in the posterior concavity of the pointed part of the foot. Immediately behind the anterior lobe of the foot, on either side of the posterior lobe, the first rudiment of the fins can

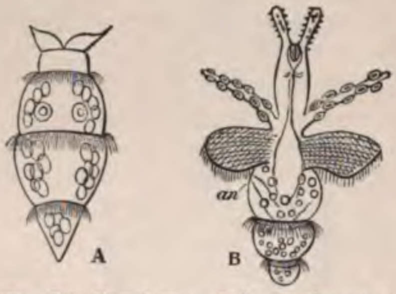

Fig. 77.—Two larvae of *Pneumodermon* at different ages (after **Gegenbaur**, from **Balfour**'s Text-book). *an*, anus.

be seen as very small, rounded lobes projecting from depressions in the body (Krohn).

The further metamorphosis consists in the growth of these parts and the degeneration of the ciliated rings. The most anterior of these is the first to disappear and then the middle ring; the posterior ring is still to be found when the young animal attains its full size, but no doubt degenerates later.

We must here add a few words of explanation as to the position assigned by us to the Pteropoda. Until recent times, the Pteropoda were often regarded as a special class equivalent to the Gastropoda, Cephalopoda, etc., although some zoologists objected to such a classification. For anatomical and ontogenetic reasons the Pteropoda are now classed with the Gastropoda,[*] being placed specially near the Opisthobranchia, as is indicated by the form of the central nervous system and their circulatory apparatus, as well as by the structure of their genital ducts and by their hermaphroditism. Another important factor in classing the Pteropoda is found in the organ which gives the body its characteristic shape, *viz.*, the swimming apparatus. The manner in which the fins arise proves that they are derived from the transformed lateral parts of the foot. It is an interesting fact that in some Pteropoda (the Gymnosomata) the propodium has still retained its function as a creeping sole, serving, like the sucker of the Heteropoda, for attachment (Souleyet, No. 121; Grobben, No. 39). The fins have been regarded by some as epipodia, but Pelseneer, on the contrary, considers them to be widenings of the whole margin of the foot. Such fin-like widenings (swimming lobes) are found in certain Opisthobranchs, and the derivation of the Pteropoda from such forms seems to be suggested. Grobben, as well as Boas and Pelseneer (No. 84), the two more recent investigators of this subject, have recently given active adherence to this view. Lateral widenings of the sole of the foot are found in *Acera*, *Gasteropteron*. These Opisthobranchs which, like the Pteropoda, can swim freely by flapping these fin-like foot-lobes have therefore been regarded as the starting-point for the latter group. From such Opisthrobranchs the Thecosomata would first have to be derived, as has been done by Pelseneer, who traced back the Thecosomata to forms like *Acera* among the Bulloidea, whereas he derives the Gymnosomata from forms like *Aplysia*, in which latter the swimming lobes are, as in the Gymnosomata, somewhat more dorsal in position. Pelseneer, in his classification of the Opisthobranchia, places the Thecosomata directly after the Bulloidea, and the Gymnosomata near the Aplysoidea. Boas also regards the Pteropoda as very nearly related to the

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[*] Among the maintainers of this view we may mention Fol, Spengel, Grobben, Boas, and Pelseneer. In R. Hertwig's text-book, the Pteropoda are classed as a subdivision of the Gastropoda, and Claus also recently gives them a similar position, placing them after the Opisthobranchia. [Practically all zoologists now class the Pteropoda with the Gastropoda and most accept Pelseneer's views according to which they find their nearest allies in the Tectibranchiate Opisthobranchs. Pelseneer further separates the Gymnosomata from the Thecosomata, placing the latter with the Bulloidea and the former with the Aplysoidea (see Challenger Reports, Vol. xxiii.)—Ed.]

Opisthobranchia and points out the great similarity existing between the internal organisation of the Bulloidea and that of the Thecosomata. Between the Gymnosomata and the Thecosomata he finds a great distinction, since he cannot regard the fins in the two divisions as homologous. Since, however, according to him, the Gymnosomata, like the Thecosomata, are to be traced back to Tectibranchia, they have in any case a common root. It appears to us that their development is in favour of a connection between them. Their larval forms agree closely, the resemblance between the long, straight shell of the Gymnosomatous larva and that of the Thecosomata being specially striking. This is a feature which points to a long period of pelagic life of the adult, for the larvae of the Opisthobranchs also live in the sea. We might therefore assume that the Gymnosomata are to be traced back to forms resembling the ancestors of the Thecosomata, which only later underwent the changes now found in their structure and development. We can hardly regard as of much importance the apparent retention of a primitive feature in presence of a small creeping foot in the Gymnosomata, since single primitive characters may be retained in forms which in other respects are highly specialised. It is also by no means certain that this character has not been secondarily acquired.

We have felt justified in treating the Pteropoda separately from the Opisthobranchia on account of the great deviations found in the structure of the body. In so doing, we do not wish in any way to deny their relation to forms like the Bulloidea and especially *Gasteropteron*. It is possible that there may be even closer ontogenetic relationship to these forms than is at present known. This would be the case if the ontogeny of a Cephalophoran described by C. Vogt were really found to refer to *Gasteropteron*, as was conjectured by Gegenbaur (No. 128). This *Veliger* larva develops two fin-like structures, and yet, in consequence of various other characteristics, is not comparable to a Pteropod-larva. The conical shell with its transverse lines of growth, further, resembles the shell of the Gymnosomata and would be little suitable to an Opisthobranch. It is thrown off even within the egg-shell. The view that the larva now under consideration belongs to *Gasteropteron* has been directly denied by Krohn (No. 58b) who regards another larva as being that of *Gasteropteron*. We are not acquainted with any more recent accounts of this very interesting larva which may be of great importance in determining the view which should be taken of the Pteropoda.

E. Pulmonata.

The transition from the ontogeny of the Opisthobranchia to that of the Pulmonata is afforded by *Onchidium*, a form which has already been alluded to p. 133. This amphibious form, which lives on the sea-shore, develops embryos with a large bilobed velum. The two lobes are beset with long cilia, while small and delicate cilia are found at the incisions between the lobes. This embryo thus greatly resembles the *Veliger* larva of the Opisthobranchia. Although the adult is shell-less, the embryo has a coiled shell like that of a marine Gastropod.

The operculum, on the contrary, is wanting according to JOYEUX-LAFFUIE (No. 51) and the foot which, even in the *Veliger* stage, is very large is also covered at its anterior and dorsal side with delicate cilia. The shell is thrown off during embryonic life, and the velum also degenerates within the egg-shell.

With regard to the absence of the operculum which, according to JOYEUX-LAFFUIE can hardly be doubted, it should be pointed out that this organ is as a rule not found in the Pulmonates.

The marine *Amphibola*, however, has an operculum showing the usual structure and position (*i.e.*, lying posteriorly on the back of the foot, No. 66). Unfortunately, this Australian form is little known; a more accurate knowledge of its anatomy and ontogeny is very desirable. According to SEMPER (No. 118, ii., p. 100), the embryos of *Auricula* and *Scarabus* have opercula.

In *Onchidium*, after the shell has been thrown off, the mantle, with the reduced pulmonary cavity, shifts dorsally and, with the kidney, opens by a median aperture at the posterior end of the body. The hitherto asymmetrical anus (lying on the right side) also assumes a median position at the posterior end of the body. In some species, the pulmonary, renal and anal orifices open through a common aperture on to the surface of the body. The loss of the shell thus leads to the acquisition of a secondary symmetrical position of the organs, a phenomenon that may also occur in other slug-like forms (as also in various Opisthobranchs).

With regard to the further development of *Onchidium*, it need here only be noted that the form of the adult is attained within the egg.

The *Vaginulidae*, forms usually placed near to *Onchidium*, no longer possess, according to SEMPER and v. JHERING, either the fully developed bilobed velum or the larval shell (No. 116), although the spawn appears to have the same constitution as that characteristic of *Onchidium* (p. 104). These forms would therefore appear more adapted to a terrestrial existence, if the short statements as to their development should be corroborated.

Onchidium and *Vaginulus* are both opisthopneumonic, and this fact, taken together with the other features of their organisation as well as their ontogeny, suggests that they represent forms which, from a condition like that of the marine Opisthobranchs, have become adapted to a terrestrial existence. The classification of *Onchidium* and *Vaginulus* among the Pulmonata which might, on account of the peculiarities above mentioned, appear doubtful (JOYEUX-LAFFUIE), has been strengthened by the more recent observations on this subject (v. Jhering, No. 46; Simroth, No. 120).[*] Since the *Veliger* stage may still be found even among the undoubted Pulmonates, although usually in a somewhat reduced condition, no objection can be made to this classification from the ontogenetic stand-point. Their development, however, shows in an unmistakable manner that we have to do with transitionary forms, a fact which is further confirmed by their manner of life, especially by that of *Onchidium* (p. 133).

The velum, it should be mentioned, is, according to Semper, well developed in some tropical forms (*Auricula, Scarabus*, No. 118), in the same way as in *Onchidium* (R. Bergh, No. 5, p. 175). Semper assumes that the larvae of these forms swim about freely in the sea. Since they, as already stated, also possess an operculum, they bear a great resemblance to the Opisthobranch larvae. As a rule, the velum is much reduced in the Pulmonates. These pass through the invagination-gastrula stage, the manner in which this gastrula arises being modified in many ways according to the varying amount of the yolk. Thus the archenteron, in consequence of being composed of the large, yolk-laden cells, appears at first as a massive structure with a narrow lumen, but at a later stage widens out and becomes a spacious sac. The originally narrow cleavage-cavity also gradually widens out. The embryo is now spherical. Its animal pole is often marked by the presence of the polar bodies; at the opposite vegetative pole is found the blastopore, which at first is wide, but narrows later and usually becomes slit-like. It closes from behind forward, but, apparently, a small anterior aperture may remain. At this point, in the midst of an ectodermal depression, the mouth forms, and, when the blastopore is retained, it becomes displaced somewhat far inward by the stomodaeum to the point at which the stomach commences (Fol, No. 33; Rabl, No. 91; Wolfson, No. 131).

The spherical or often somewhat ventrally flattened form of the embryo undergoes some alteration in consequence of the appearance of the shell-gland, the foot and the velum. The shell-gland arises as an ectodermal invagination on the dorsal surface opposite the mouth (Fig. 78). It may sink in so deep that it has repeatedly been mistaken for the rudiment of the proctodaeum. It flattens out again

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[*] [Plate (*Zool. Jahrb. Anat.*, Bd. vii., 1894) who has recently made a thorough study of the anatomy of *Onchidium*, concludes that while these forms are true Pulmonates, they nevertheless show affinities with the Tectibranchiate Opisthobranchs. He places the *Onchidiidae* and *Vaginulidae* as direct derivatives of the primitive pulmonate on a branch quite independent of the Stylommatophora or Basommatophora.—Ed.]

later, secreting the shell in the usual way; in *Limax*, however, the shell of which is at first internal, the shell-gland is pouch-like and becomes abstricted from the ectoderm (FOL). A swelling of the body behind the mouth indicates the position of the foot (Fig. 78). The velum appears in the form of two transverse swellings (formed of large, richly vacuolated cells) in front of the mouth, which run as bands round a large part of the anterior body, but for a time do not meet, or else, as in *Planorbis*, in consequence of the very much reduced condition of the velum, never completely unite (Fig. 78, *v*). At this stage, we may, with RAY LANKESTER, consider the embryo as equivalent to the *Trochophore;* occasionally, as in *Limnaea*, even the external form of the *Trochophore* is preserved, a large pre-oral portion of the body being marked off from the posterior portion by the velum (RAY LANKESTER, FOL). A thickening at the pre-oral pole denotes the apical plate. That the bilobed character of the velum so characteristic of the *Veliger* larva is found here also is due to its mode of origin. As a rule, not only the *Veliger* stage but the *Trochophore* stage as well is much reduced, the principal features of the latter, however, are still to be found.

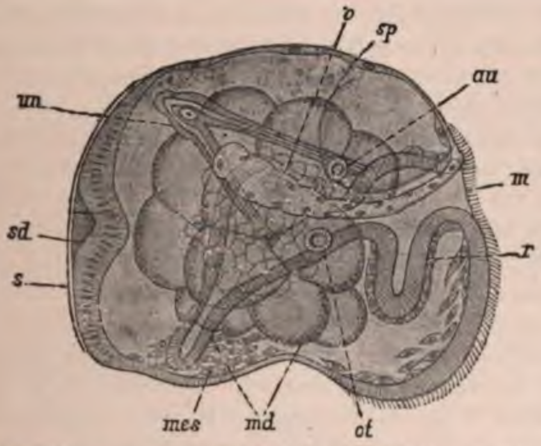

FIG. 78.—*Planorbis* embryo, seen from the side (after RABL). *au*, eye; *m*, mouth; *md*, enteron and digestive gland (large cells); *mes*, mesoderm; *ot*, otocyst; *r*, radular sac; *s*, shell; *sd*, shell-gland; *sp*, apical plate; *un*, primitive kidney; *v*, velum.

At the stage which more or less corresponds to the *Trochophore*, the alimentary canal consists of a stomodaeum from which a radular sac soon grows out ventrally (Fig 78, *r*) and the still undivided and exceedingly large archenteron (*md*). Some of the cells of the latter, in consequence of the albuminous matter which has been brought from without through the mouth into the lumen of the intestine, have a swollen appearance (Figs. 70-80); others, however, which lie posteriorly and ventrally are smaller, indeed, through more active division, they may even be specially small. They form a diverticulum of the entoderm which is directed backward (Fig. 78) and represent the rudiment of by far the greater part of the enteron. The cells containing albumen, which continue to increase in size, pass over into the formation of the liver later. At first the intestinal cavity appears bounded partly by a large-celled and partly by a small-celled epithelium. The posterior diverticulum of the enteron comes into contact with the ectoderm in the ventral middle line, behind the foot. This part at first bulges somewhat outward, forming the anal prominence. Later on, the entoderm-diverticulum here fuses with the ectoderm to form the anus.

The resemblance of the stage just described to the *Trochophore* stage is heightened by the presence of a paired primitive kidney, which, in the fresh-water Pulmonates, has a very characteristic origin and shape (Figs. 78-80, *un*). Even at an early stage, a remarkably large cell can be seen on each side below the dorsal part of the velum; these two cells yield the principal constituents of the primitive kidney, and have been claimed as velar cells which have entered the body-cavity (WOLFSON), this view being no doubt suggested by the vacuolated character of the velar cells as well as by the condition of those Prosobranchs in which complexes of ectodermal cells which are certainly excretory are apparently closely related to the velum. This view can, however, hardly be correct, and, taking into consideration the usual method of formation of the primitive kidneys, we prefer the view of RABL that these large cells are to be derived from the mesoderm.* They lie at the posterior part of the mesoderm-bands which are already disintegrating. In each of these cells, a cavity which at first resembles a vacuole appears, lengthening as soon as the cell itself lengthens. The cell then becomes bent and forms the principal part of the primitive kidney, the canal of which is thus intra-cellular in its origin (GANIN, No. 35; RABL, No. 91; WOLFSON, No. 131). The large cell yielding the primitive kidney is joined by a few of the adjacent mesoderm-cells and the canal, by becoming connected with the ectoderm, opens

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* [See footnote, p. 179.—ED.]

externally. The apertures of the two kidneys lie at the two sides of and behind the velum. The inner end of the primitive kidney is usually regarded by authors as communicating with the primary body-cavity by a ciliated aperture.* In the terrestrial Pulmonates this has been maintained with certainty for *Helix* (*Acavus*) by P. and F. SARASIN (No. 102) and JOURDAIN, as well as MEURON (Nos. 50 and 75), arrived at the same result.

The primitive kidneys of the terrestrial Pulmonates, which were early recognised by O. SCHMIDT and GEGENBAUR, are somewhat differently constituted from those of the aquatic forms. They also have the form of bent tubes opening externally through wide apertures in front of the border of the mantle, but they are composed of a large number of cells arranged like an epithelium, none of which are distinguished by their special size (JOURDAIN, MEURON, SARASIN).

DE MEURON considers that, in *Helix*, the primitive kidney arises chiefly from the ectoderm, but holds also that the innermost part may be derived from the large mesoderm-cells. But since these latter, in the aquatic Pulmonates, yield the principal part of the primitive kidneys, the derivation of these organs from the mesoderm appears more probable. We need not, however, exclude the supposition that, as in the primitive kidneys of the Prosobranchs, an ectodermal invagination takes part in the formation of the peripheral part and that this latter, in terrestrial Pulmonates, is specially extensive.

At the time when the primitive kidneys attain their full development, the external form of the embryo also undergoes further alteration. The shell-gland begins to lose its pouch-like form and gradually flattens out. The ectodermal epithelium belonging to the shell-area still appears formed of columnar cells. Over this area lies the shell

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* [v. ERLANGER (No. VII.) has since described the detailed structure of the larval kidney in *Planorbis* and *Limnaea*; he finds a specialised ciliated cell (the funnel-cell) which puts the tube into communication with the body-cavity, and then a long tubular segment containing a flagellum and a terminal portion which opens on to the exterior, this latter portion ERLANGER thinks may be ectodermal in the Euthyneura, while the remainder is mesodermal. In the Pulmonata he finds a swollen ampulla at the junction of the two segments. The development of this organ has been more recently investigated by MEISSENHEIMER (No. XVII.), and this observer maintains that, in *Limax*, the primitive kidney is wholly ectodermal, and here he is at variance with most other observers. As he also maintains that the heart and definitive kidney similarly arise from a common ectodermal rudiment, we think that his views require further confirmation before we can accept them. MEISSENHEIMER (No. XVIII.) has also given a most elaborate account of the structure of this organ in which he differs from ERLANGER in one important respect, *viz.*, he is unable to find any opening into the body-cavity and thinks that ERLANGER mistook a large vacuole which is invariably present in the end-cell for an opening.—ED.]

which has now become cap-like. The margin of the shell seems buried in a groove, a swelling of the ectoderm, the margin of the mantle, having formed here. The whole embryo has somewhat lengthened, and the foot stands out more distinctly (Fig. 79).

The foot in *Limnaea*, which at first appears as an unpaired swelling, is said to assume a bilobed form (Ray-Lankester). Such a bilobed foot seems often to occur among the Gastropoda. We have already met with it in *Succinea*, *Patella* and *Vermetus* (p. 132). Fol also observed this later development of the bilobed form in the foot of *Limnaea*, as well as in *Planorbis* and *Ancylus*, though in these last two animals it was less striking. Ray Lankester compares this to the transformation of the foot into the paired fin in the Pteropoda.

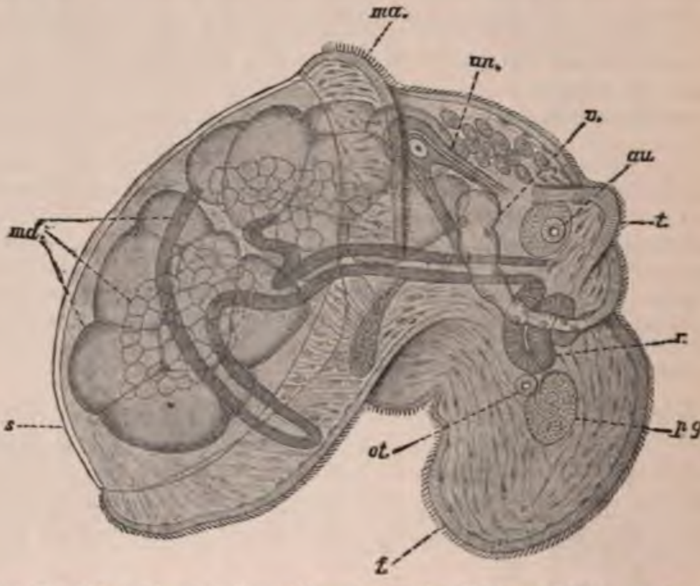

Fig. 79.—Older embryo of *Planorbis*, seen from the side (after Rabl). *au*, eye; *f*, foot; *ma*, margin of the mantle; *md*, enteron and digestive gland (large cells); *ot*, otocyst; *pg*, pedal ganglion; *r*, radular sac; *s*, shell; *t*, tentacle; *un*, primitive kidney; *v*, velum.

The outgrowth of the body-epithelium to form the foot causes a considerable enlargement of the ventral portion of the inner cavity of the larva, and a similar cavity is produced pre-orally by the dilatation of the part which is encircled by the velum. A similar process has already been met with in the Prosobranchia (p. 150). The anterior swollen part of the embryo is known as the cephalic vesicle and the wide space as the cephalic cavity. Special attention has been directed to this part in consequence chiefly of the pulsating movements which may occur here, a peculiarity also found in the nuchal and the pedal regions of the embryo.

It has repeatedly been stated that certain regions of the body-covering, those to which a large number of mesoderm-cells became attached, carry on contractions which sometimes follow one another with considerable regularity, this last fact having led to their being called "larval hearts." The circulation of the body-fluid is, in any case, promoted by these contractions, but it seems doubtful whether they should be described as actual pulsations. Sometimes the movements that thus occur are somewhat irregular, and RABL found that, occasionally, contraction of one part of the body is followed by extension of another part, but we cannot consider this to be regular rhythmical movement. The embryo moves in consequence of these contractions. It is well known, however, that Gastropod embryos are able in addition, in consequence of their rich ciliation, to rotate within the egg-envelope.

Since the embryo, by taking in the albuminous fluid contained within the egg-shell, feeds independently and also has a circulation of its own and special excretory organs, the velum may serve as a respiratory apparatus, this function being also exercised by it in addition to its locomotory function in the free-swimming larvae. In the embryos of terrestrial Pulmonates, a special respiratory organ develops, the caudal vesicle (podocyst), which will be further described below.

The very large apical plate of the embryo has considerably thickened and has become bilobed. According to RABL, the cerebral ganglion is derived from it, though in other Pulmonates the formation of this ganglion has been thought to arise differently (p. 191). At the posterior end of the "apical plate" the eyes arise as ectodermal pits. Two large superficial prominences, which soon become conical, arise laterally to the optic vesicles and represent the rudiments of the tentacles. Both eyes and tentacles belong to the pre-oral section, whereas the otocysts arise behind the velum (Figs. 79, 80 *au*, *t*, *ot*).

Up to this point, the embryo is fairly symmetrical in shape, but this symmetry is disturbed chiefly by the further development of the shell which grows towards the right more strongly than towards the left (Fig. 80). The edge of the mantle, which now bulges out more than before, is of course also affected by this unequal growth. The anus is pressed out of its median position to the right. It is evident from this that processes occur in the later development of the Pulmonates similar to those already met with in the metamorphosis of other Gastropods.

As the mantle extends further, its growth takes place more rapidly on the right than on the left side. In front of the anus an indentation forms which at first is shallow but soon becomes deeper; this is the rudiment of the respiratory cavity which continues to widen and thus comes to include the anus and the apertures of the adult kidney. This cavity itself opens externally only through a narrow aperture, the respiratory aperture, which lies rather far forward on the right side of the body.

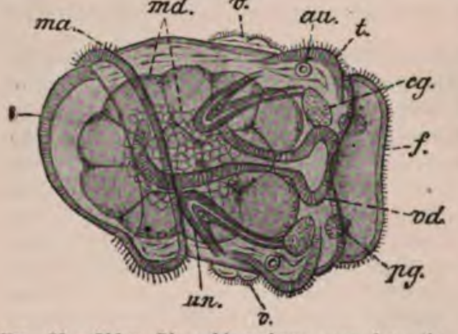

FIG. 80.—Older *Planorbis* embryo, seen from the back (after RABL). *au*, eye; *cg*, cerebral ganglion; *f*, foot; *ma*, edge of the mantle; *md*, enteron and digestive gland; *pg*, pedal ganglion; *s*, shell; *t*, tentacle; *un*, primitive kidney; *v*, velum; *vd*, stomodaeum.

The formation of the respiratory cavity has also been viewed in another way; *viz.*, as a fusion taking place between the margin of the mantle and the body, only a small aperture being left, which, as respiratory aperture, leads into the greatly deepening cavity. In this way, the respiratory cavity is shown to be the transformed pallial or branchial cavity. In the Basommatophora this is indisputable, as a gill is in some forms found in the cavity (*Amphibola*). The respiratory cavity in the Stylommatophora has, on the contrary, been regarded as not homologous with the branchial cavity, but rather as the ureter transformed into a respiratory organ. On this account v. JHERING termed the terrestrial Pulmonates the Nephropneusta, thus distinguishing them from the aquatic Pulmonates, which he named the Branchiopneusta (Nos. 45 and 46.) We ourselves do not find anything in the manner of formation of the respiratory cavity in land Pulmonates to justify so different an interpretation of it. The mantle-cavity in the Prosobranchia may also at first, as here, arise apparently in the form of an ectodermal depression. The homology between the respiratory cavity of the land Pulmonates and that of the water Pulmonates, which in itself is so probable, is further supported by the fact that in some of the former (*Testacellidae*, PLATE, No. 89) a sensory organ is present in it which corresponds to SPENGEL's olfactory organ found lying near the gills in the mantle-cavity of other Gastropods.

Towards the end of that period of embryonic life during which the embryo may be compared with the larva of other Gastropods, the sinuses in the head and the foot which gave rise to the embryonic circulation above described undergo gradual degeneration. In the same way the primitive kidney disappears and the permanent kidney functions in its stead.

The final form of the animal is reached by the growth of the parts now present. The respiratory cavity and the edge of the mantle extend more to the left, the shell taking the same course. The head becomes more distinct, rising up from the foot, which, in its turn has increased considerably in size and has approached nearer its definitive form. The velum has disappeared, a portion of it, according to Ray Lankester, giving origin to the labial palps (p. 133). This latter view seems quite in keeping with the position of the velum, but is set aside as improbable by Fol and is directly refuted by Wolfson.

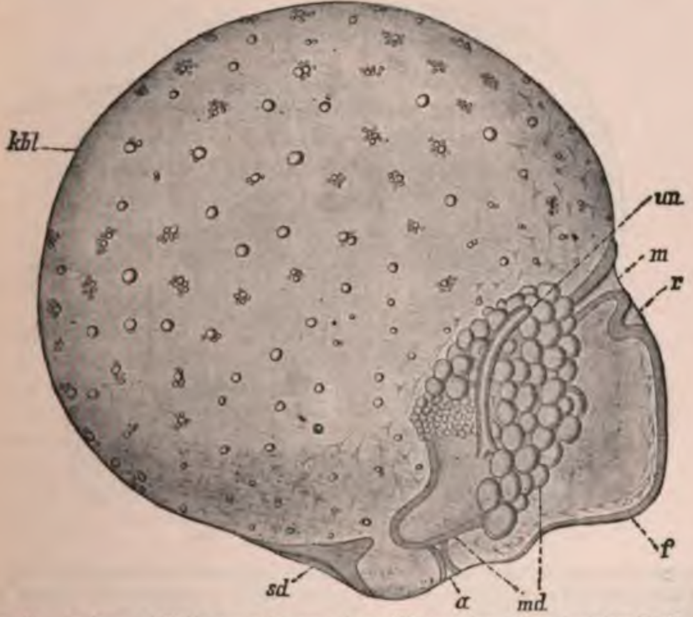

Fig. 81.—Embryo of *Helix pomatia* seven days old, seen from the side (after Fol). *a*, anus; *f*, foot; *kbl*, cephalic vesicle; *m*, mouth; *md*, enteron and digestive gland; *r*, radular sac; *sd*, shell-gland; *un*, primitive kidney.

The shell is still cup-shaped, but is already asymmetrical. Further unequal growth on one side leads to coiling both of the shell and the visceral dome.

Our account has, so far, referred chiefly to the development of the fresh-water Pulmonates, especially to that of a few forms which have been particularly carefully investigated, such as *Limnaea* and *Planorbis*. These latter have been described in detail by Ray Lankester (No. 63), Rabl (No. 91), Fol (No. 33), and Wolfson (No. 131) to whose descriptions we must refer the reader for further details. Fol has also included various other fresh-water Pulmonates as well as terrestrial Pulmonates in his comprehensive researches. These latter forms, which had already been studied by GEGENBAUR, differ from the aquatic Pulmonates in some points of their development and therefore require separate treatment.*

The ontogeny of the stylomatophorous terrestrial Pulmonates is characterised by the development of exceedingly large provisional organs, *viz.*, the *cephalic* and *pedal vesicles.* These larval organs appear early. At a stage which corresponds somewhat to the *Trochophore* stage, the embryos (of *Limax*, *Arion*, *Helix*, *Clausilia*) are distinguished by the great swelling of the pre-oral section of the body. At the stage of which we speak, this cephalic vesicle is so large as almost to eclipse the rest of the embryo. At a rather later stage also (Fig. 81), the cephalic vesicle (*kbl*) is still very large, but

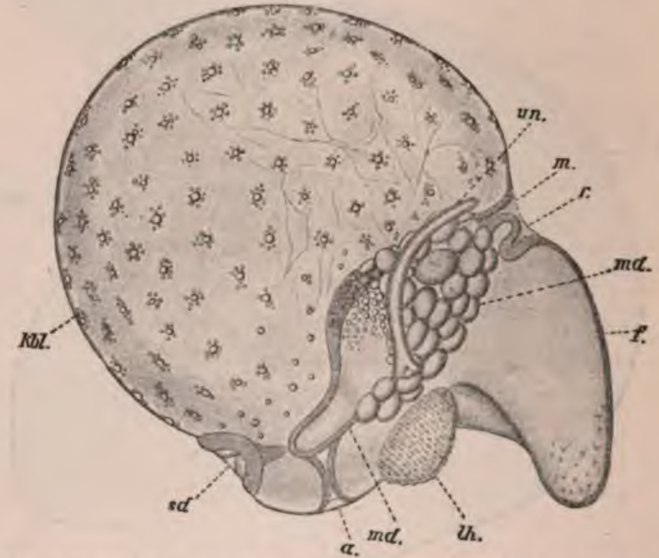

FIG. 82.—Embryo of *Helix pomatia*, ten days old, seen from the side (after FOL). *a*, anus; *f*, foot; *kbl*, cephalic vesicle; *lh*, larval heart; *m*, mouth; *md*, enteron and digestive gland; *r*, radular sac; *sd*, shell-gland; *un*, primitive kidney.

* [See also the more recent works of HOLMES (No. XIII.), KOFOID (No. XIV.). MEISSENHEIMER (No. XVII.), SCHMIDT (No. XX.) and WIERZEJSKI (No. XXVII.), These deal for the most part with the cleavage and cell-lineage. MEISSENHEIMER's researches on *Limax*, however, are carried further and should be consulted in connection with the development of the Stylommatophora.—ED.]

the foot now bulges out and also commences to swell up into a vesicle. Little now remains of the Trochophore shape. At a stage somewhat younger than that depicted in Fig. 81, a slight vestige of the velum is still to be found in two transverse ciliated ridges which lie on either side of the mouth and run towards the shell-gland. These, however, do not extend up to the mouth, and soon disappear. In *Arion* and *Limax*, no traces of the velum are to be found (Fol). These embryos, like those of the aquatic Pulmonates, are able to rotate within the egg, being covered with cilia.

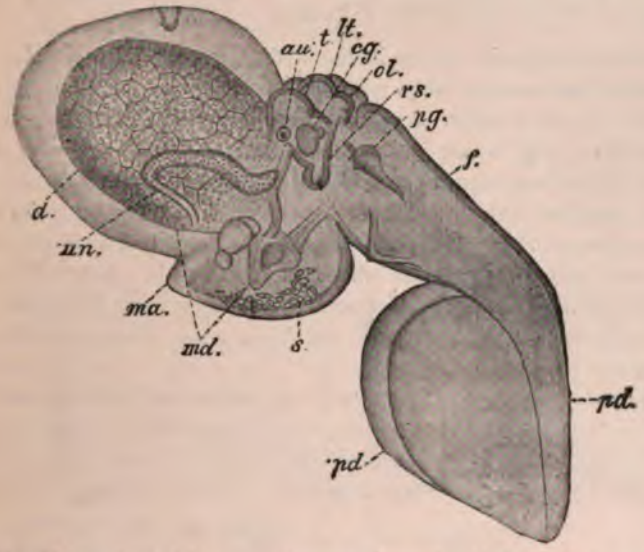

Fig. 83.—Older embryo of *Limax maximus*, seen from the side (after Fol). *au*, eye; *cg*, cerebral ganglion; *d*, yolk-material; *f*, foot; *lt*, labial palp; *ma*, mantle-fold; *md*, enteron and digestive gland; *ol*, upper lip; *pd*, podocyst; *pg*, pedal ganglion; *rs*, radular sac; *s*, shell; *t*, tentacle; *un*, primitive kidney.

The position of the different organs of the embryo can be understood most easily by reference to Fig. 81. The oesophagus is followed by the enteron from which the digestive gland composed of large albumeniferous cells is already becoming differentiated, posteriorly the enteron is lined by smaller entoderm-cells. The anus lies behind the pedal swelling, and behind it again, marking the dorsal side, is found the shell-gland. A pit lying near the mouth represents the rudiment of the radular sac which, according to Fol, arises in the stomodaeum, which has not yet fully sunk in, and is thus near the oral aperture, but is soon drawn into the buccal cavity. Near the enteron can be seen the tube of the primitive kidney which is as yet unbent and which, according to **Fol**, opens outward at the posterior base of the foot. Almost in this region, but somewhat behind the foot, lies an organ described by **Fol** as the larval heart.

The so-called larval heart (Fig. 82, *lh*) consists of a bulging of the ectoderm with which numerous mesoderm-cells become connected. This specially differentiated part of the covering of the body which, when the mantle-cavity forms later, is drawn into it and thus comes to lie more to the right, carries on regular pulsations and is regarded by **Fol** as an organ for promoting the embryonic circulation. It thus belongs to the category of larval hearts which have already been alluded to (p. 152).

While the cephalic vesicle in the later stages decreases in size, the foot lengthens considerably. At first it is cylindrical, but it soon spreads out more and more and now becomes a massive club-shaped organ (Fig. 83), which is known as the *caudal vesicle*, and more recently has been named the *podocyst* (**Jourdain**, **Sarasin**). As it is richly supplied with mesoderm-cells which become applied to its wall, it is capable of contraction and carries on rhythmical movements which alternate with those of the cephalic vesicle. It is evident that this large vesicular swelling is a circulatory or respiratory apparatus and it may be that it also serves for nutrition, since diosmotic processes take place in it.

The podocyst is specially large in the embryos of various species of *Helix* (**Gegenbaur**, **v. Jhering**, **Fol**, **Sarasin**). It here spreads out laterally, and thus assumes the form of a broad plate which, towards the end of the "larval period," lines the whole of the inner cavity of the egg-shell. P. and F. **Sarasin**, in describing a *Helix* (*Acavus Waltoni*, Fig. 84) found in Ceylon, show that the podocyst covers like a cap the shell of the very large embryo in which several coils have already developed. In this form also, in which the pedal vesicle is specially highly developed, pulsating movements were perceived in that organ. When it has reached its highest development, two wide canals within the foot start from the vesicle, one passing to the brain along the ventral side and the other running

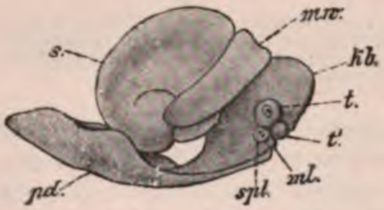

FIG. 84.—Embryo of *Helix* (*Acavus*) *Waltoni*, seen from the side (after P. and F. **Sarasin**). *kb*, cephalic vesicle; *ml*, oral lobes; *mw*, mantle-swelling (collar); *pd*, podocyst; *s*, shell; *spl*, sensory plate; *t*, upper, *t'*, lower tentacle.

dorsally towards the viscera which are surrounded by a blood-sinus. A provisional circulation thus exists side by side with the definitive circulation.

Towards the end of embryonic life, the pedal vesicle decreases in size. It remains at first as an appendage to the foot, but this vestige also disappears, being absorbed. The foot thus assumes its final shape. A median invagination, which only appears at a late stage on the foot near the mouth and lengthens out posteriorly into a tube, represents the rudiment of the pedal gland (FOL).

Apart from the development of these embryonic organs which are here specially large, the further development of the embryo resembles that of other Gastropods and especially of the aquatic Pulmonata. This also applies to the shell where this is not vestigial and internal as in many terrestrial Gastropods. Where there is an internal shell, as in *Limax* and *Arion*, the shell-gland becomes disconnected from the ectoderm, as already explained. The shell remains internal, being hidden beneath the mantle, and is a vestigial structure. In *Arion* it consists merely of a number of disconnected calcareous granules.

It is a striking fact that, in *Clausilia*, according to GEGENBAUR, the shell also at first lies internally enclosed in the epithelium of the shell-gland. Only when this latter, as well as the mantle-tissue above it, disappears, does this internal shell become external, develop and become coiled. As far as we know, this somewhat inexplicable observation of GEGENBAUR has not been corroborated.* We feel inclined to explain the phenomenon described on the belief that there is retained a small aperture over the shell as it lies within the shell-gland, this gland flattening out at an unusually late stage.

6. The Formation of the Organs.

A. The Shell.

We have already, in treating of the external shape of the body, repeatedly alluded to that of the shell, so that only a few further remarks need be added. The shell arises from the shell-gland, and, when the latter has flattened out, appears cap-like. At first, therefore, there is great resemblance in this point to the Lamellibranchs. Here also a shell-integument forms first, beneath which the calcareous substance is deposited later. The further processes are altogether like those in the Lamellibranchs as given more in detail on p. 60. The

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* [SCHMIDT (No. XXI.) has since confirmed GEGENBAUR's observations that the shell-gland closes completely and later opens out again both in *Clausilia* and *Succinea*.—ED.]

unequal growth which leads to the coiling of the shell, has already been described (p. 147) and so have the special shapes assumed by the shell (*e.g.*, Pteropoda) and the partial or total loss of the shell in the Heteropoda, Opisthobranchia, Pteropoda and Pulmonata.

It is a striking fact that a few specially low forms of Gastropoda such as *Haliotis* and still more *Patella* and *Fissurella*, are distinguished by a reduction of the coils and the adoption of a flat cup-shaped shell. In youth, the shell was, as in other Gastropods, distinctly coiled. This can be seen particularly well in *Fissurella* (Fig. 85 *A*-*C*). The margin of the shell is at first unbroken, but a slit appears in it later lying above the slit which occurs in the mantle of these forms (Fig. 85 *A*). The shell-slit is of special interest because it is present in two of the oldest fossil Gastropods, *e.g.*, *Pleurotomaria* and *Bellerophon*, both of which are found in the Cambrian.* The ontogeny of *Fissurella* would suggest that these forms with slit shells have been derived from forms in which the margin is not slit. In many forms the slit is retained as such (*Scissurella*, *Emarginula*, and fossil as well as recent Pleurotomariae), in others, as the shell grows further; the most posterior portion of the slit becomes cut off by shelly matter from the rest of the slit and, as this continues to take place throughout life, we find in such forms as *Haliotis* a series of consecutive apertures in the shell; in other cases, the slit becomes to a great extent closed by a shell-substance of peculiar structure which is seen extending along the length of the whorls as the slit-band. In *Fissurella*, the margin, as it grows further, is unbroken (Fig. 85 *B*). The reduction of the coiled part of the shell and the fairly equal growth of the whole margin leads finally to the slit taking up a central position near the apex of the adult shell (Fig. 85 *C*). The shell of *Fissurella* has now passed from a coiled form to that of a flattened cone; this change is due, as in other Gastropods with similarly simple shells, to the manner of life and, as ontogeny shows, must be regarded as a phenomenon of degeneration. The symmetry of the shell is thus of a secondary character.

B. The Nervous System.

The nervous system usually arises by delamination (Fig. 88, *cg*, *pl*, *p*, p. 194), but it cannot be doubted that, according to recent

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* A description of the development of the Gastropoda at the different geological epochs has been given by KOKEN (No. 56). See also ZITTEL'S *Palaeontologie*.

researches, the cerebral ganglion or part of it, is, in certain cases, formed by an invagination of the ectoderm. So far as is as yet known, the cerebral ganglion alone has such an origin; all the other ganglia arise as ectodermal thickenings which later split off from this germ-layer.

An accurate knowledge of the structure of the nervous system of the adult is very desirable as a help to understanding the processes of development, especially as some confusion prevails as to the naming of the different parts of that system, one and the same ganglion sometimes bearing several different names, while, on the other hand, different ganglia receive similar names. We shall therefore describe side by side some of the principal types of nervous system found in the Gastropoda (Fig. 86 *A-C*).

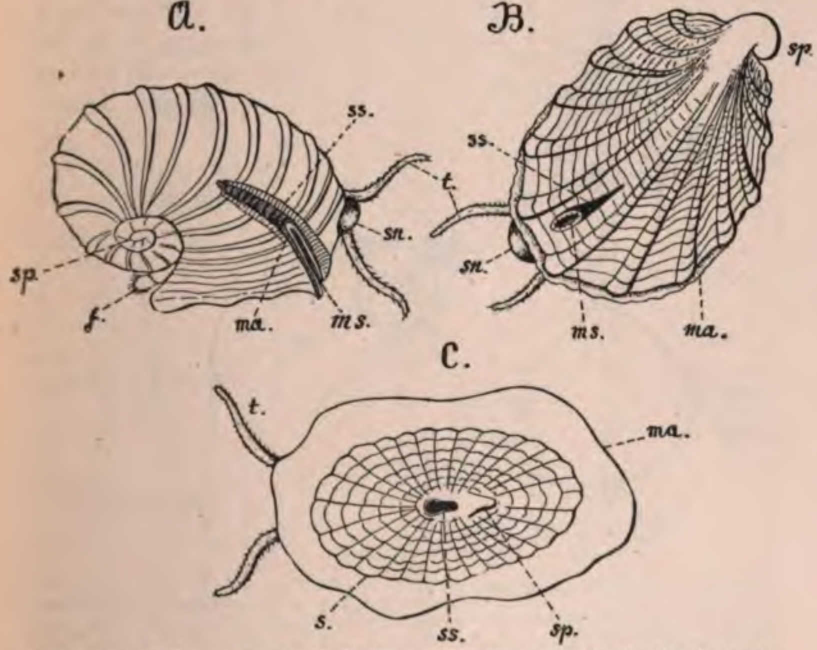

FIG. 85.—*A-C*, three stages in the development of *Fissurella* showing the changes in the shell (after BOUTAN). The animal, as depicted in *C*, has very nearly attained the adult form. *f*, part of the foot; *ma*, mantle; *ms*, mantle-slit; *s*, shell; *sn*, snout; *sp*, apex of the shell; *ss*, shell-cleft; *t*, tentacles.

The nervous system of the Gastropoda consists of the two cerebral ganglia, which are connected by the supra-oesophageal cerebral commissure (*A-C*, *cg*). Below the oesophagus, and connected with the cerebral ganglia by connectives, lie the pedal ganglia (*peg*), which innervate the foot and are joined together by a commissure. In this way a ring corresponding to the oesophageal ring of the Annelida and Arthropoda is formed. The resemblance ceases when we come to the other constituent parts of the nervous system. A large nerve runs back from the cerebral ganglia on each side, swelling to form two lateral ganglia, the pleural ganglia (*A-C*, *plg*). These are connected with the pedal ganglia by the pleuro-pedal connectives. From the pleural ganglia, again, two lateral strands run back and end in the one or two connected abdominal ganglia (Fig. 85 *B*, *abg*). Another lateral ganglion is formed in each of these lateral strands which are known as the pleuro-visceral commissures. These two last ganglia may be called the visceral ganglia (*B* and *C*, *vg*). In the Prosobranchia, the pleuro-visceral commissures undergo displacement in consequence of the twisting of the body already described (*cf.* p. 145 and Fig. 60), the right commissure coming to lie above and the left commissure below the intestine (Fig. 86 *A*). The original right visceral ganglion is thus displaced to the left side and becomes the supra-intestinal ganglion (*spg*), while the original left visceral ganglion now lies on the right side and is known as the sub-intestinal ganglion (*sbg*). The abdominal ganglia (*abg*), in consequence of the twisting, come to lie dorsally to the intestine. In this way arises the crossing of the pleuro-visceral commissures (chiastoneury) characteristic of the Prosobranchia.

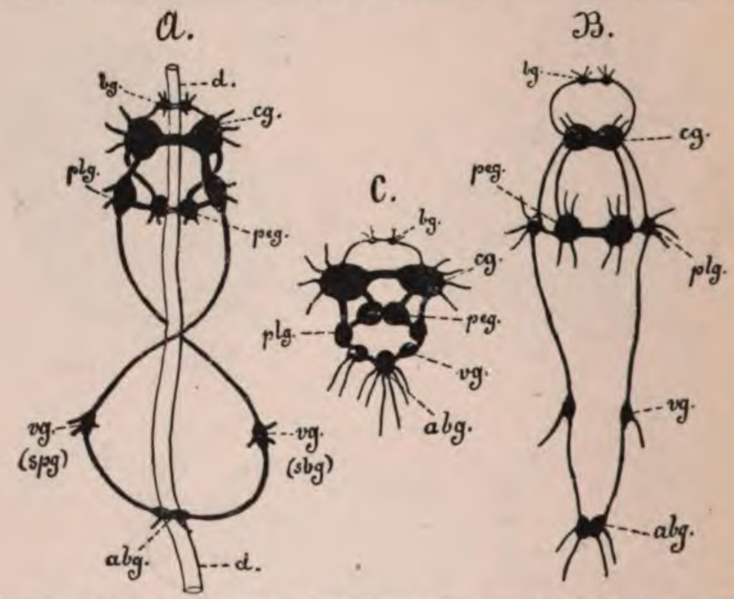

FIG. 86.—*A-C*, Diagrams of the nervous system of a Prosobranch (*A*), an Opisthobranch (*B*), and a Pulmonate (*C*). *abg*, abdominal ganglia; *bg*, buccal ganglia; *cg*, cerebral ganglia; *d*, alimentary canal diagrammatically represented as a straight tube; *peg*, pedal ganglia; *plg*, pleural ganglia; *sbg*, sub-, and *spg*, supra-intestinal ganglion; *vg*, visceral ganglia.

In the Pulmonata, the commissures are, as a rule, decidedly shorter than in the other divisions, and the whole of the nervous system appears concentrated round the oesophagus (Fig. 86 *C*).

The **cerebral ganglia** might at once be referred back to the apical plate of the *Trochophore*, were it not for the fact, about which authors seem to be fairly unanimous, that the ganglia here appear in the form of two distinct thickenings of the ectoderm (Fig. 68, *cg*) which only unite later by the formation of the cerebral commissure. P. SARASIN, indeed (No. 101), has stated for *Bythinia*, that the two ectodermal thickenings at first are connected by a median ectodermal growth, and thus (in their origin at any rate) suggest a common rudiment, but this method of formation, which in itself is very probable, has been directly denied, not only for *Bythinia* but for the related form *Paludina* (v. ERLANGER, Nos. 27 and 28). The two thickenings belong to the velar area, lying laterally in it in front of the mouth. Even if the cerebral ganglion forms with the help of an invagination, its rudiment is paired. In the Pulmonata, in which this method of formation of the brain is best known, there are at first the two ectodermal thickenings which here also yield the principal mass of the cerebral ganglia in the usual way. Then, when these are already partly detached from the ectoderm, a depression of the ectoderm occurs at the lower edge of the posterior tentacles; this becomes continually deeper, and thus forms a tube (SARASIN'S cerebral tubes). According to P. and F. SARASIN, in *Helix* (*Acavus*) *Waltoni*, there are two such cerebral tubes on each side (Fig. 87 *A*, *ct*) while, in *Limax*, only one is found on each side (HENCHMAN, No. 42; F. SCHMIDT, No. 110). The blind ends of the cerebral tubes become applied to the rudiments of the cerebral ganglia which have become further differentiated (Fig. 87 *A*, *ct*, *cg*), and fuse with these to form that part of the brain which is known as the accessory lobe (Fig. 87 *B*, *ct*). They then become abstricted from the superficial epithelium. Their lumina can still be recognised as fissures (Fig. 87 *B*), but these soon entirely disappear, the formation of the brain being thus practically completed. A differentiation of the principal part of the brain into ganglionic cells and fibrous tissue had already taken place.

SARASIN'S observations with regard to the cerebral tubes, which were on the whole confirmed by the researches of F. SCHMIDT and HENCHMAN, afford an explanation of the apparent contradiction involved in the two views of the origin of the cerebral ganglia, which were derived by one author by invagination, and by another in the same or related forms by delamination. Both these views are founded on fact, each being observed at a different stage of development. In this respect, those forms in which the brain arises as two depressions of the velar area, as is the case, according to FOL, in the Pteropoda, require more careful investigation. The two invaginations are no doubt present, as we gather from FOL's description, but the question arises whether they yield only a part or the whole of the cerebral ganglion. From what we as yet know, the latter view is the more probable, and is further rendered possible by the fact that in a Prosobranch (*Vermetus*) also, the whole of the cerebral ganglion originates from two invaginations (SALENSKY). These first appear on the velar area as two thickened plates which then sink inwards.

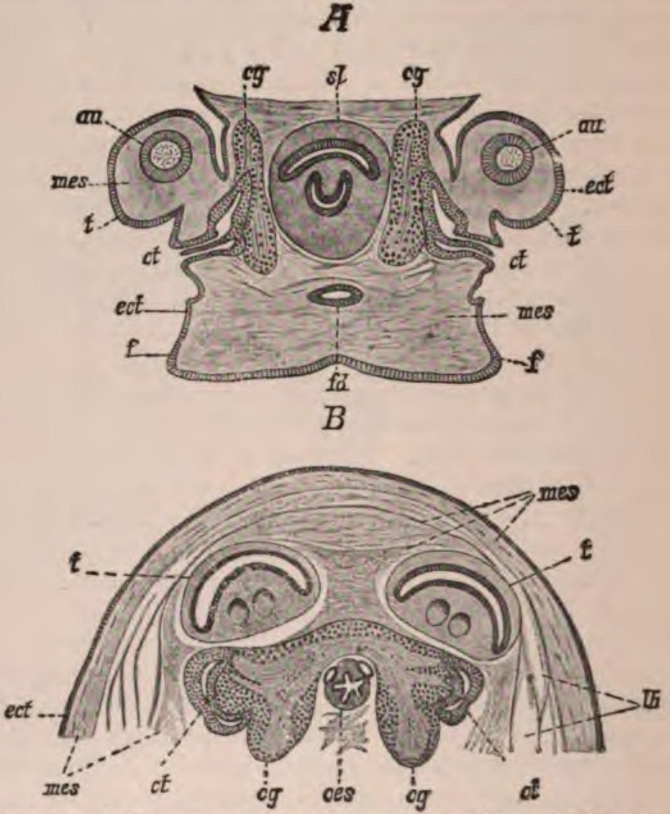

FIG. 87.—*A* and *B*, transverse sections through two embryos of *Helix* (*Acavus*) *Waltoni*, at different stages (diagrammatic after P. and F. SARASIN). In *A*, the dorsal, in *B*, the ventral part of the section is shown. *au*, eye; *cg*, cerebral ganglia; *ct*, cerebral tubes (in *B*, as the accessory lobes); *ect*, ectoderm; *f*, foot; *fd*, pedal gland; *lh*, body-cavity; *mes*, mesoderm-tissue; *oes*, oesophagus (in *B*, with the salivary ducts); *sl*, buccal mass (in *A*, with oesophagus and radular sac); *t*, tentacles.

The two tubes that arise in this way unite to form the brain and become detached from the superficial ectoderm. The cerebral ganglia were seen to form in exactly the same way in *Dentalium* (p. 93). It would in any case be interesting to learn in what way this condition may be reconciled with that described for the Pulmonata. The rise of the brain through delamination, which was observed in various Prosobranchs (SARASIN, WOLFSON, HADDON, McMURRICH, v. ERLANGER, etc.), in Heteropoda (FOL) and perhaps also in Opisthobranchs (RAY LANKESTER) appears in any case to be the more usual.

The pedal ganglia arise laterally or rather on the under surface of the foot, near the otocysts, the position of which has already been described more than once (Fig. 88 *B*, *p*). These ganglia at first are not connected with each other nor with any other ganglia. The **commissures** and **connectives** * are secondary structures, *i.e.*, they arise only after the detachment of the ganglia from the ectoderm as outgrowths of the ganglia, a point on which the statements of all observers agree. Where, as in the Pulmonates, the ganglia lie close together, the distinct ganglia, in the course of growth become connected at an early period.

Besides the original commissure connecting the pedal ganglia in the Pulmonates, a second smaller commissure appears lying more posteriorly. Since this second commissure is also present in adults, it was thought that it might belong to a second pair of ganglia, but this view is not supported by ontogeny, as each of the two ganglia first appear as distinct structures, the apparent division in them arising only secondarily (F. SCHMIDT). [This second commissure appears to be specially developed in the Opisthobranchs, where it is known as the parapedal commissure.]

The commissures and connectives, so far as their origin has been traced, arise by the growing out of peripheral parts of the ganglia, and the same origin has been assumed for the peripheral nerves (SALENSKY, HENCHMAN, v. ERLANGER, F. SCHMIDT, etc.). P. SARASIN, indeed, as above stated, maintained that the two halves of the cerebral ganglion separated as one connected organ from the ectoderm, and RABL assumed, as we saw (p. 181), that they arose from a common rudiment, the apical plate. It is therefore in any case probable that the cerebral commissure may have arisen from the middle part of the common ectodermal thickening. Such an origin for the commissures and the connectives is on the whole very probable, but is not supported by the observations so far made, indeed, in *Bythinia*, investigated by SARASIN, the common origin of the two cerebral thickenings has been denied (v. ERLANGER, No. 28).

The **buccal ganglia**, as was first shown by SARASIN and as has been confirmed by subsequent investigators, arise as cell-growths of the stomodaeum. The wall of the stomodaeum becomes thickened, and while the cells lying on the inner side retain the cylindrical shape, a number of smaller cells appear on the outer side (Fig. 88 *B*, *bg*). These become differentiated into two swellings which lie near the

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* Following LACAZE-DUTHIERS and SPENGEL (No. 122), we distinguish the strands which connect the ganglia of one and the same side as connectives from the transverse strands which connect the right and left halves of a pair of ganglia, these latter being commissures.

stomodaeum and the radular sac and form the rudiments of the buccal ganglia.

The formation of these ganglia recalls to some extent that of the frontal ganglion in the Insecta, which also arises from the stomodaeum (vol. iii., p. 328).

The **pleural ganglia** form, in *Paludina* and *Bythinia,* as two lateral ectodermal thickenings lying somewhat ventrally behind the velum (Fig. 88 *A*, *pl*), and the two **visceral ganglia** also arise ventrally and laterally, though farther back than the pleural ganglia (v. Erlanger). They lie near the edge of the mantle, and near the

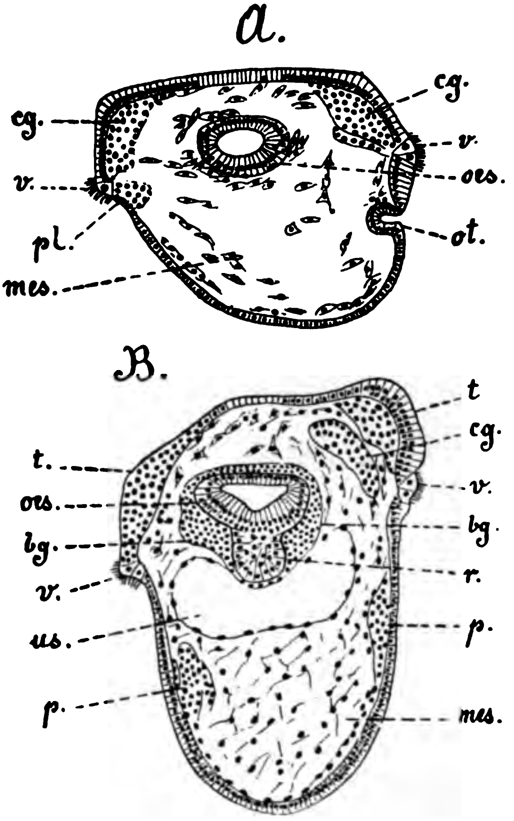

Fig. 88.—Transverse sections through the anterior region of two embryos of *Paludina* at the stage represented in Fig. 59, *A* and *B*, p. 139 (after v. Erlanger). *bg*, buccal ganglia; *cg*, cerebral ganglia; *mes*, mesodermal tissue; *oes*, oesophagus; *ot*, otocyst; *p*, pedal ganglia; *pl*, pleural ganglion; *r*, radular sac; *t*, rudiment of tentacle; *us*, primitive sinus; *v*, velum.

constriction which divides the visceral mass from the cephalic and pedal parts of the body, laterally and somewhat ventrally to the alimentary canal. It is important to note that these two pairs of ganglia, on their first appearance, are quite symmetrical, and that the asymmetry which is so characteristic of the Prosobranchia appears in them only later as a consequence of unequal growth of the different regions of the body. This leads to the right visceral ganglion shifting first dorsally and then over the oesophagus, while the left lies below this tube. In this way, these ganglia become the supra- and sub-intestinal ganglia.

This process has already been theoretically examined, and illustrated by Fig. 60 *A-E*, p. 144. Ontogenetically, the process is similar, but is less distinct on account of the connecting strands of the visceral loop, which are either wanting or difficult to make out. Indeed, the study of the development of the nervous system is often rendered difficult by the fact that the ectodermal rudiments are so indistinctly marked off from the mesoderm, as may be gathered both from the text and the figures of older and more recent authors. This difficulty no doubt gave rise to the view that the nervous system in the Gastropoda was of mesodermal origin, which was supported by BOBRETZKY's observations (No. 11).

The **abdominal ganglion** arises, in *Paludina* and *Bythinia*, as an unpaired ectodermal thickening on the floor of the mantle-cavity at its posterior end, being found dorsally to the heart.

As already mentioned, all the ganglia are said to arise independently and to become secondarily connected by commissures. Where, as in *Bythinia*, the ganglia lie very near each other, they are, according to ERLANGER, more distinct in the embryo and only later shift nearer to one another. P. SARASIN, in these very forms, derived the pedal and intestinal ganglia as well as the abdominal ganglion from a common ventral ectodermal thickening, and therefore was able to compare them to the ventral chain of ganglia of the Annelida, whereas the prevailing opinion now is that only the pedal ganglia or rather the pedal strands (which in some Prosobranchia are provided with transverse connecting strands) can be considered as the true homologues of the ventral cords.

Even in the Pulmonata, in spite of the great concentration of the nervous system peculiar to this division, the ganglia appear as distinct rudiments, and only become connected later. We have repeatedly alluded to the conditions in the Pulmonates, which have recently been very thoroughly examined by A. HENCHMAN and F. SCHMIDT, although we have dealt principally with the Prosobranchia, in which the processes can be more easily understood on account of the intervals between the ganglia being greater. The formative processes in the Pulmonata agree on the whole with those in the Prosobranchia.

C. The Sensory Organs.

The appearance of **the tentacles** as prominences on the velar area has already been several times alluded to in connection with the external form of the body (Figs. 54, 55, 59, 78, 79, etc.). They lie immediately above the rudiment of the brain and, when this becomes detached from the ectoderm, remain as large thickenings of the latter (Fig. 88 *B*, *t*). In position, they correspond to the cephalic tentacles of the Annelida, a correspondence which would be all the more striking if we could definitely homologise the rudiment of the cerebral ganglion with the apical plate. The anterior and lower tentacles in the terrestrial Pulmonates arise somewhat later in the closest proximity to the bases of the posterior tentacles (ophthalmophores). In the terrestrial Pulmonates, the cephalic region in which these organs originate, and where also the cephalic invagination occurs, has been called the sensory plate. P. and F. SARASIN found here in *Helix* (*Acavus*) a number of small bulb-like specialisations of the ectoderm (Fig. 39 *A*, *s*, and *B*) which, by the similarity of their structure to the lateral line organs of the Vertebrata, were shown to be sensory organs. On each side of the section of the embryo given in Fig. 89 *A*, two of these organs can be seen in a depression, and it is possible that the cerebral tubes which arise at these points originate from them. These lateral organs are found in other parts of the body as well, and have also been met with in a somewhat similar form in adult Gastropods. It is, however, probable that the organs now under consideration do not persist and we must therefore regard them as temporary larval organs.

A similar significance is ascribed by P. and F. SARASIN to the cerebral tubes described above (p. 191) as taking part in the formation of the brain, these being also considered as vanishing sensory organs. They may have actually functioned in the ancestors of the Gastropoda, as is assumed to be the case with the conjectural olfactory organ of the Annelida. They now give rise to part of the brain, just as in the Annelida, where the origin of the brain is traced to the pre-oral sensory organs (KLEINENBERG, Vol. i., p. 288).

The **eyes** develop in a very simple way. They first appear almost simultaneously with the rudiments of the tentacles, at the ventral edge of which a depression takes place. This deepens to form a vesicle which finally becomes detached from the ectoderm and is then found below the integument. Each optic vesicle frequently, as in *Paludina*, lies on a prominence at the base of the tentacle. Where the eyes are found on the tentacles themselves, as in the posterior tentacles of terrestrial Pulmonates, they are raised up as the tentacle grows. The eyes are already visible when the tentacles are first indicated (FOL).

The next step in the development of the eyes is the deposition of pigment in the proximal part of the optic vesicle. The cells of this region increase and yield the retina, while the distal part forms the cornea. Two structures arise within the optic vesicle as secretions of the cells; these are the lens and the vitreous body which are at first homogeneous and strongly refractive. In the latter, delicate fibres appear which run from the retina to the lens (v. ERLANGER, No. 27).

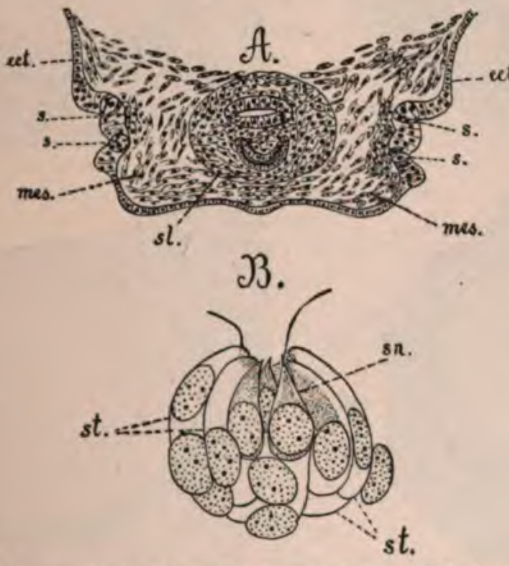

FIG. 89.—*A*, Transverse section through a young embryo of *Helix* (*Acavus*) *Waltoni*, *B*, one of the lateral organs (*A*, *s*) highly magnified (after P. and F. SARASIN). *ect*, ectoderm; *mes*, mesoderm; *s*, lateral organs of the sensory plate; *sl*, posterior part of the buccal mass, including transverse section of the oesophagus and the radular sac; *sn*, sensory cells; *st*, supporting cells.

According to SALENSKY, the formation of the eyes, in *Vermetus*, is connected with the invagination of the cerebral ganglion. They appear as rounded thickenings at the edge of the plate which later sinks in to form the brain; these soon become hollow and form vesicles similar to those described above as rudiments of the eyes, and then shift inwards in connection with the invagination. Only somewhat late, when the lens has already been secreted, do they lose their connection with the cerebral invagination. The further development of the eyes apparently takes the course described above. This method of formation of the eyes recalls the condition in those Gastropods in which they lie upon the brain (many Opisthobranchs). The eyes of *Vermetus*, however, so far as we know, lie externally at the bases of the tentacles.

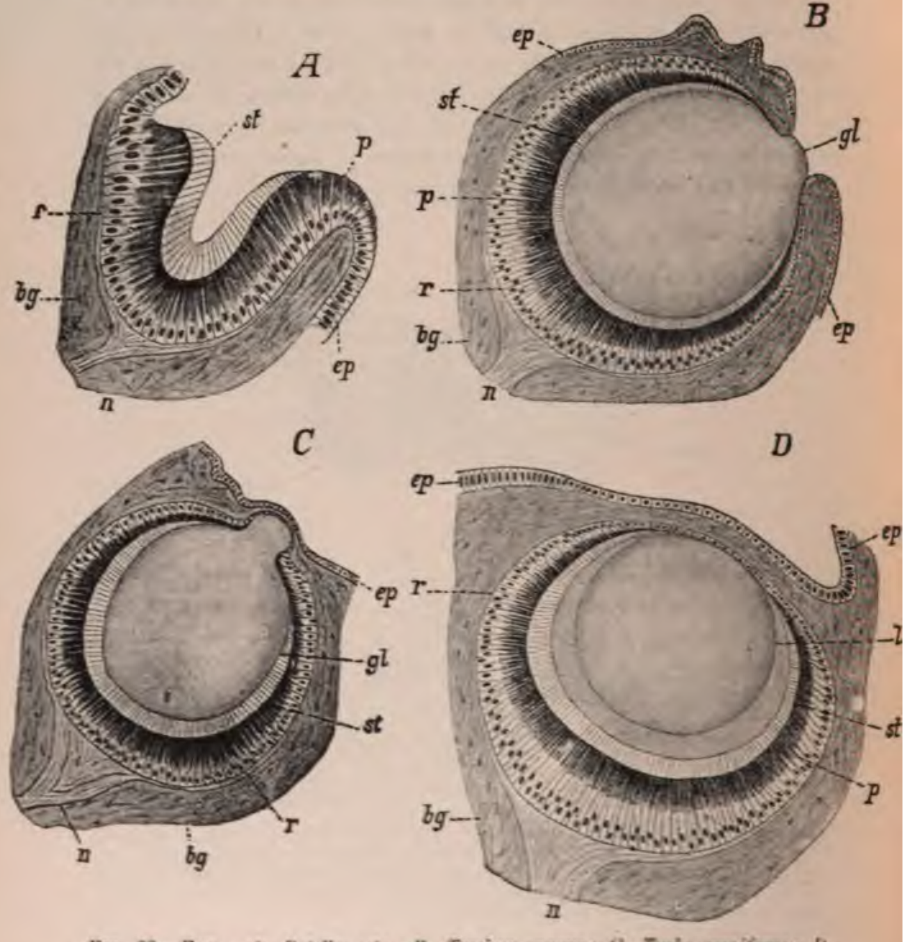

FIG. 90.—Eyes.—*A*, *Patella rota*; *B*, *Trochus magus*; *C*, *Turbo creniferus*; *D*, *Murex brandaris* (after HILGER). *bg*, connective tissue; *ep*, ectoderm; *gl*, vitreous body; *l*, lens; *n*, optic nerve; *p*, pigment; *r*, retina; *st*, rods.

The ontogeny of the Gastropod eye is of great interest in so far as it may, at some of its stages, be compared with the adult condition of the eye in various forms. *Patella*, for instance, has eyes which are placed in the usual position, but which are mere pit-like depressions of the surface (Fig. 90 *A*). In *Haliotis*, *Trochus*, etc., the pit is deeper and becomes a vesicle which, however, remains open (Fig. 90 *B*). Its lumen is filled with a strongly refractive gelatinous mass (*gl*) known as the vitreous body. In other forms the vesicle has closed (*C*) and, finally, the higher form of Gastropod eye (*D*) provided with a so-called lens and vitreous body is developed (FRAISSE, No. 34; HILGER, No. 43; PELSENEER, No. 85). [In most Diotocardia the optic vesicle is open, but in the specialised *Helicinidae* and *Neritidae* (the Gymnopoda of FISCHER) and in the *Turbinidae* it is closed as in all the Monotocardia.]

The first-named Prosobranchs are held on other grounds to be primitive forms, and the simple structure of the eye seems therefore probably a primitive condition. If this supposition is correct, we should here see with special clearness the gradual development of the optic organ up to its present level.

According to CARRIÈRE (No. 22), in cases where the eyes are regenerated, their formation takes place in the same way as when they arise ontogenetically. The ectodermal epithelium is thus at a later time also capable of giving rise to the sensory organs.

The **otocysts,** which are specially distinct in the larva, and the origin of which has already been alluded to several times (Figs. 55, 59, 65, 72, 79), appear as depressions of the ectoderm on either side of the pedal rudiment, near the pedal ganglion, with which, however, they do not come into any closer relation as they are innervated from the brain (LACAZE-DUTHIERS). When cut off from the ectoderm, these walls are still formed of long cylindrical cells which flatten later; but, for a time, the anterior and ventral part of the vesicles still remain thick. From this part of the wall, the otolith or otoliths (otoconia) are secreted; these structures become detached from the wall and rest upon the sensory hairs which have arisen on the cells.

Spengel's (olfactory) organ (osphradium) only develops at a later stage (*Paludina*). It arises as an ectodermal thickening composed of several layers of cells. Where, as in *Paludina*, pits are found in the organ, these are caused by depressions in the thickened ectoderm (v. ERLANGER).

The pectinate condition of this organ, which is found in many Gastropods, arises in a similar way. The organ was originally paired and lay near the gill, as may still be the case in Zygobranchiate Diotocardia. Where it is single, as in the Monotocardia and the Euthyneura, this is in all cases connected with the asymmetry caused by the torsion of the visceral mass.

D. The Pedal Glands.

In the larvae of various Gastropods, *e.g.*, *Nassa* (Figs. 61 *D* and *E*, 63), *Vermetus*, *Murex*, *Firoloida* (Fig. 65), etc., a deep tubular or sac-like ectodermal depression has been described in the foot; this shows great agreement in position with the pedal gland found by KOWALEVSKY in the embryos of *Chiton*. Such a rudiment is perhaps also present in *Dentalium*. In *Nassa*, this gland forms a rather long tube, and in *Murex* it has a similar form (BOBRETZKY, No. 11); in *Firoloida*, it is said to be much shorter and bilobed (FOL, No. 31, Fig. 65, *fd.*). SALENSKY describes, in *Vermetus*, the formation of two ectodermal invaginations in the foot, the one lying at the anterior and the other at the posterior end. The canals lengthen inwards and fork, so as to yield the glandular portion. Various glands are known in adult Gastropods also lying one behind the other in the sole of the foot (CARRIÈRE, No. 21). The connection of the rudiments we have just described with these glands does not as yet appear to be clearly demonstrated. It is well known that various glands also occur at the anterior end and in the sole of the foot in Lamellibranchs which have been homologised with the anterior and posterior pedal glands of the Prosobranchia (BARROIS, No. 3), but whether such a homology is correct still seems doubtful.*

E. The Alimentary Canal.

The **Stomodaeum** first appears as an ectodermal depression in which can soon be recognised a ventral outgrowth, the *radular sac* (Figs. 53, p. 127, 78, p. 177 and other figures). This sac sometimes appears even before the stomodaeum is completely invaginated and consequently lies near the aperture of invagination, as in *Helix* (Figs. 81 and 82, p. 184). When the radular sac lengthens, it undergoes dorso-ventral flattening. Its lateral margins then bend upward so that it assumes the form of a channel, the dorsally directed cavity of which is filled with a mass of connective tissue. The wall of the channel is formed of the upper and the lower epithelium, the latter taking the principal part in the **formation of the radula.** The first indication of this organ is found early in the form of a thin cuticle in the radular sac. The formation of the radula, an organ which has been studied in the adult by RÖSSLER (No. 95), and RÜCKER (No. 96), and others, takes place in the following way: The teeth themselves are secreted by the cells which lie ventrally at the blind end, while the basal membrane upon which the teeth are borne is

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* [The pedal glands may attain enormous development in the Pulmonata: this is especially noticeable in *Nanina*, where the gland takes the form of a very large tube bent on itself and extending along the greater part of the foot. The gland either opens between the head and foot, as in *Helix*, or on the postero-dorsal surface of the latter, as in *Helicarion*.—ED.]

yielded by the lower epithelium (Fig. 91 *A*). The large groups of tooth-forming cells (odontoblasts) form a kind of cushion or bed upon which the teeth are modelled (Fig. 91 *A* and *B*). In the shape of this cushion, the future form of the tooth is already shown. In the Opisthobranchia and the Pulmonata, a special differentiation occurs, only a few (four to five as seen in longitudinal section) * very large cells undertaking the formation of one tooth (Fig. 91 *B*, *od*); the most anterior of these large cells is said to yield the part of the basal membrane that underlies the tooth now in course of formation.

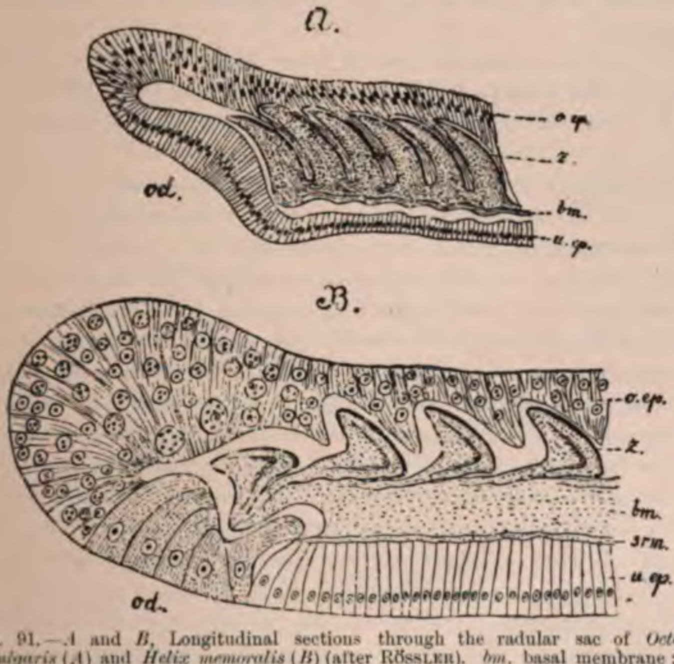

FIG. 91.—*A* and *B*, Longitudinal sections through the radular sac of *Octopus vulgaris* (*A*) and *Helix memoralis* (*B*) (after RÖSSLER). *bm*, basal membrane; *od*, odontoblasts; *o*, *ep*, upper epithelium; *srm*, sub-radular membrane; *u*, *ep* lower epithelium; *z*, teeth.

The tooth thus produced fuses with the basal membrane and with the prolongation of the basal part of the last tooth (Fig. 91 *B*). When a tooth is thus completed, this cell-group undertakes the

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* [There are in reality eight to ten of these large cells concerned in the secretion of each tooth, the cells being arranged in two parallel series, so that, in a longitudinal section, like that shown in Fig. 91, only one row is seen at a time. It is probable that the three most posterior pairs of these odontoblasts secrete the main body and hook of the tooth, the next transverse pair secreting the base, while the most anterior pair secretes the sub-radular membrane.—ED.]

formation of the next tooth of the same longitudinal row. The number of teeth in a transverse row corresponds to the number of groups of odontoblasts. The formation of the radula is, however, not altogether completed by the processes just described, for the upper epithelium yields a viscid fluid secretion which forms an enamel-covering to the teeth. The gradual shifting forward of the newly-formed teeth to replace those which are continually being worn away in front, is brought about to a great extent by the growth of the surrounding tissues, and is no doubt also caused by the action of the muscles at the anterior part of the odontophore (RÖSSLER).

The radula appears to form in other Molluscs that are provided with it (Cephalopoda, Fig. 91 *A*, and Amphineura) in just the same way as in Gastropods; it will not, therefore, be necessary to describe it in detail again.

The **salivary glands** arise somewhat late as diverticula of that part of the stomodaeum which lies in front of the radular sac.

The **enteron,** in various Gastropods, arises to a certain extent in a different way, as the accumulation of yolk or of a secondary nutritive mass at various points of the gut frequently retards its development and may even, where the mass is very voluminous, strongly influence the manner of formation of the intestinal canal. In many cases, however, the formation of the enteron takes a very simple course, the invaginated entoderm-vesicle increasing in size by the continuous division of its cells, fusing anteriorly with the stomodaeum and growing out posteriorly into a conical terminal section which becomes connected with the ectoderm to form the anus. It has already been explained that the posterior section of the enteron may at first run straight back, but may later bend forward to the right, and that this is connected with the acquisition of asymmetry. The coils made by this section of the gut as it lengthens are not of essential importance and need not therefore be specially described. There are, however, other important alterations brought about by the deposition of nutritive masses in the enteron. This process of deposition takes place in a very simple manner in *Paludina* (BÜTSCHLI). The ventral part of the entoderm here becomes even at early stages especially large through the increase in size of the cells and the deposit in them of drops of secondary yolk (Figs. 57, 58 and 59, p. 137, etc.). This thickening of the wall of the enteron is evidently due to the absorption of the surrounding albumen; this albumen being received especially into the ventral entoderm and deposited there. At a later stage, the whole of the sac-like anterior part of the enteron is affected by these deposits, which, however, are always greatest on the ventral side. The dorsal and anterior part, with which the oesophagus becomes connected, is marked off into a sac-like *stomach*, while the part that lies ventrally and more posteriorly, and which contains by far the largest amount of deutolecithal constituents, yields the liver. The latter, originally spherical, soon becomes lobate. LEYDIG describes the gradual development which commences with a few large lobes; then, by subdivision of these, an increasing number of small ones arise, until, when the embryo is ready for birth, continued division has led to the formation of numerous long follicles.

It has been observed in most cases that those parts of the entoderm that are laden with nutritive substance pass over into the liver or else are connected with its formation; it appears doubtful to us whether this is invariably the rule, since these parts vary greatly in the position they occupy in the enteron, as will be shown later.

The accumulation of nutritive material in the ventral entoderm is still more striking in the Heteropoda than it is in *Paludina*. FOL, in connection with the Heteropoda, speaks of a ventral nutritive sac formed of immense, greatly swollen cells which is abstricted from the stomach so as to become the rudiment of the liver, its glandular character being soon proved by the development of several lobes. A ventral nutritive sac is also found in the later stages of *Limnaea*; but it is expressly stated that this does not take part in the formation of the liver, but that the latter arises quite independently of it as two small caeca which grow out at the end of the stomach (WOLFSON, No. 131).

It is impossible to ascertain the correctness of the various statements made as to the manner of formation of the liver. These statements differ so greatly, and in the present state of our knowledge are so difficult to compare with one another, that we are justified in assuming that more careful research will greatly modify them. This is all the more probable as it is evident that the processes under consideration are difficult to interpret.

In the Pteropoda also, the liver is said to arise as a finger-shaped outgrowth of the ventral wall at the posterior end of the stomach, near which a second outgrowth soon appears (FOL). In the Pteropod larva, the nutritive material is stored up in the cells forming the walls of two sac-like outgrowths of the stomach, which are at times separated from the latter by stalks. These nutritive sacs, one of which is usually larger than the other, differ slightly in position in the different forms, but generally appear to open into the stomach at its postero-ventral end, so that a relation between the nutritive sacs and the liver seems probable. As the liver continues to develop, the sacs decrease in size.

The two entodermal stomach-diverticula of different sizes are, as already mentioned, also found in the larvae of the Opisthobranchia (Fig. 72, *di*, p. 162). They are here said to belong rather to the dorsal and anterior part of the stomach (RHO, No. 93; FISCHER, No. 30). According to FISCHER, they become transformed direct into the liver, forming the outgrowths which enter the dorsal papillae (cerata). The left diverticulum yields the principal lobe of the liver, while the right, in the Nudibranchia, is of small size.

In the Pulmonata, the position of the nutritive masses is somewhat different. It has been asserted that, in them, the principal mass of large cells filled with albumen lies at the dorsal side. The large dimensions attained by this part of the entoderm is evident from Figs. 78-83, pp. 177-185, depicting the embryos of *Planorbis*, *Helix* and *Limax*. The entoderm-cells in other parts, however, remain small, especially ventrally and posteriorly, and these parts give rise to the posterior portion of the intestine which takes the course already described. The small-celled portion of the entoderm spreads out further at a later

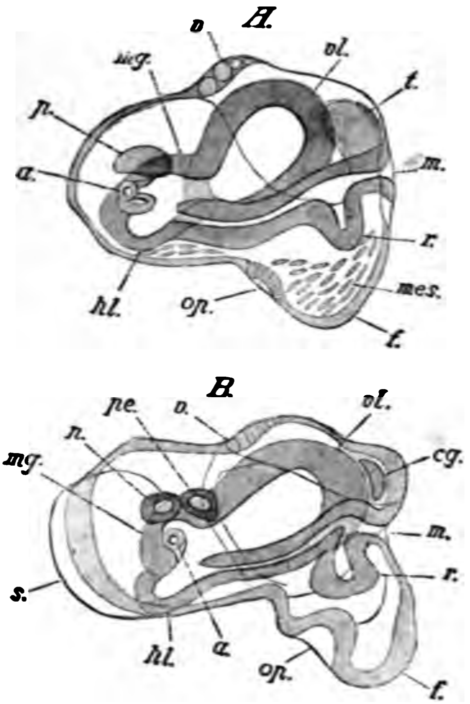

FIG. 92.—*A* and *B*, embryos of *Bythinia tentaculata* at different stages (after V. ERLANGER). *a*, anus; *cg*, cerebral ganglion; *f*, foot; *hl*, posterior lobe of the liver; *m*, mouth; *mes*, mesoderm; *mg*, stomach; *n*, rudiment of the kidney; *op*, operculum; *p*, pericardial sac; *pe*, pericardium; *r*, radular sac; *s*, shell; *t*, tentacle; *v*, velum; *vl*, anterior hepatic sac.

stage, and the albuminiferous cells seem to be pressed more to the left (Fig. 78).

The complexes of nutritive cells are said to be dorsal in position in the land Pulmonates also, and the direct rise of the liver from them has been described (JOURDAIN, No. 49). It appears, however, from the figures of Pulmonates, especially of the land-form before us, that the large-celled mass extends well to the ventral side of the stomach, so that there is here perhaps after all a near approach to the conditions described above. The fact that the intestine, the stomach and the liver are not clearly marked, makes it difficult to ascertain the exact relation of these parts which is further complicated by a frequent displacement of these organs. In *Bythinia*, the intestine arises from the posterior part of the conical enteron, while the larger part gives rise to the liver and stomach (P. SARASIN, v. ERLANGER). The liver appears in the form of a very wide anterior and a smaller

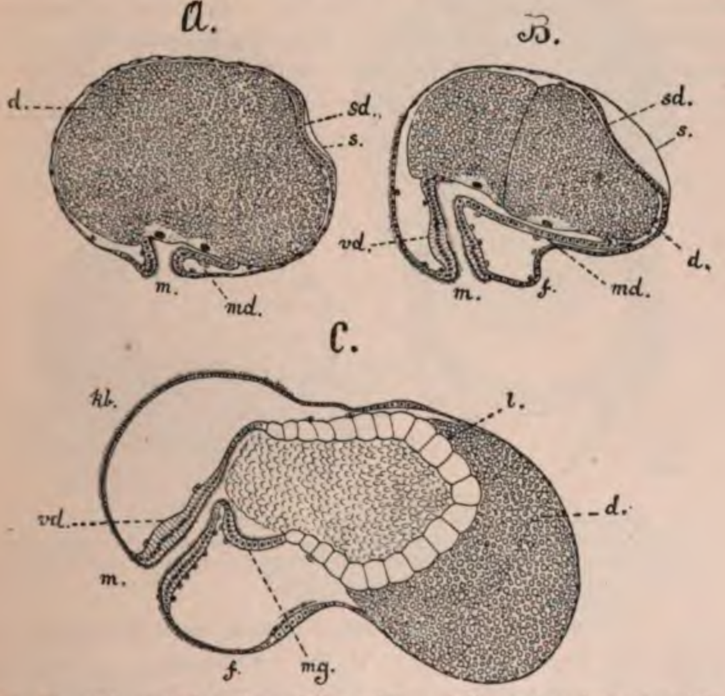

FIG. 93.—*A-C*, sagittal sections of the embryos of *Fusus* at various stages (after BOBRETZKY). *d*, yolk; *f*, foot; *kb*, cephalic vesicle; *l*, liver; *m*, mouth; *md*, enteron; *mg*, stomach; *s*, shell; *sd*, shell-gland; *vd*, stomodaeum.

posterior outgrowth (Fig. 92, *vl*, *hl*), while the stomach (*mg*) arises from a small dorsal part of the enteron lying between these two. Into the stomach open the oesophagus, the intestine and the two hepatic sacs.

In the cases so far considered, the enteron has at first a sac-like form; this, however, soon becomes differentiated by the concentration of the nutritive yolk or by the absorption of albumen by the cells in one part of the enteron. In other cases, however, the accumulation of food-yolk in the entoderm is so great that the sac-like rudiment of the enteron is not able to develop at once. In *Fusus*, for instance, according to BOBRETZKY, at a time when the oesophagus, the shell-gland and the mesoderm are already well developed, the entoderm consists of only a few large cells which are to a great extent filled with yolk, having a small protoplasmic portion directed towards the mouth (Fig. 93 *A*). At this point, the division of the macromeres gives rise to new entoderm-cells which are much smaller and soon rise up from the macromeres, thus forming the rudiment of the midgut, especially that of the stomach, which then, through the formation of a posterior conical process, gives rise to the intestine (Fig. 93 *A* and *B*, *md*). The increase in number of the entoderm-cells is continued at the expense of the food-yolk, which is now pressed further back. While, ventrally, the stomach becomes more distinctly marked off (Fig. 62, p. 151 and 93, *mg*), the recently developed dorsal parts of the entoderm become filled with deutolecithal spherules and thus have a glassy appearance like the

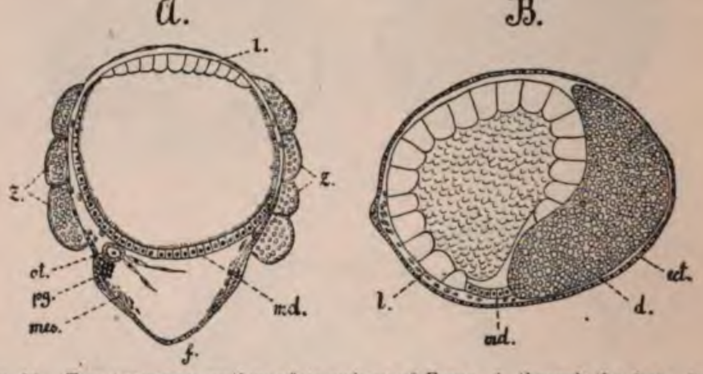

FIG. 94.—Two transverse sections of an embryo of *Fusus*, *A*, through the foot; *B*, a more posterior section (after BOBRETZKY). *d*, yolk; *ect*, ectoderm; *f*, foot; *l*, liver; *md*, entoderm lining the stomach; *mes*, mesoderm; *ot*, otocyst; *pg*, pedal ganglion; *z*, sub-velar cells.

albuminous cells of other Gastropods described above. The yolk-mass, which is still very large, limits directly the lumen of the entoderm-vesicle (Figs. 92 and 93). This latter is already found to be partly filled with disintegrated yolk-substance (Fig. 62 *B*), this being taken up by the large entoderm-cells, which, according to BOBRETZKY, represent the rudiment of the liver (Figs. 62, 93 and 94, *l*). The large-celled "hepatic vesicle" may be said to form the

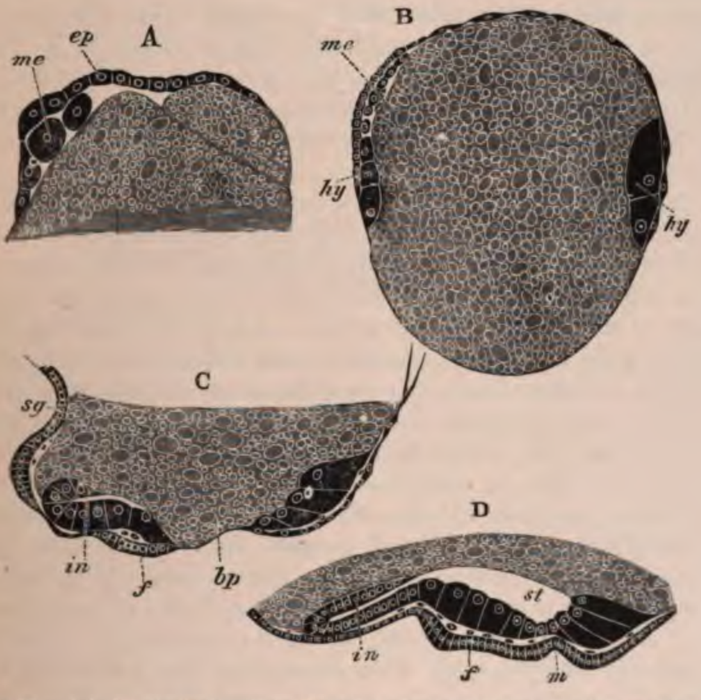

FIG. 95.—*A-D*, longitudinal sections through embryos of *Nassa mutabilis* at different ages (after BOBRETZKY, from BALFOUR'S Text-book). *bp*, blastopore; *ep*, ectoderm; *f*, rudiment of foot; *hy*, entoderm; *in*, epithelium of the enteron; *m*, mesoderm; *sg*, shell-gland; *st*, lumen of the enteron.

dorsal and posterior part of the entoderm-sac, if the rudiment of the intestine is left out of consideration (Figs. 93 and 94, *md*). It occupies the left side of the body while the food-yolk is pressed more to the right. From the sections given in Figs. 93 and 94 a good idea of the relative positions of these parts and of the stomach may be gained. The food-yolk still directly limits the lumen of the intestine, but is gradually absorbed as development advances.

A still further specialisation of the enteron along the lines seen in *Fusus* is found in the egg of *Nassa* which is still more richly supplied with yolk. The formation of the germ-layers in this egg has already been described (p. 116). The entoderm is found here as a slightly developed single layer of cells on the ventral side of the embryo. The stomach and rudiment of the intestine appear when the massive food-yolk which, at first, presses closely upon the entoderm, separates from it (Fig. 95 *C* and *D*). Owing to this origin of the enteron, its lumen is here also directly bounded on one side by the yolk, which, even at a later time, is very extensive (Fig. 61 *D* and *E*, p. 150), and fills the whole of the posterior part of the body. The intestine still appears open towards the yolk-mass (Fig. 63, p. 152) and, in its further development, no doubt follows the same course as that of *Fusus*.

The nutritive substance is, as we have seen, stored up in various parts of the entoderm, and seems frequently to influence the development of the liver. It is inherently probable that the liver originates from definite parts of the entoderm, always appearing in the same region of the enteron, but this process may be modified through the various ways in which the nutritive mass is deposited. From the different conditions found, we seem to be able to conclude with some certainty that the whole of the anterior part of the enteron was originally specially utilised for the storing of the nutritive material.

The *anus* forms in most cases through the direct fusion of the entodermal intestine with the surface of the body, though some authors (Wolfson, No. 131; P. Sarasin, No. 101; Jourdain, No. 49, etc.) speak of the development of a proctodaeum. As the latter is said to occur in other Molluscs, *e.g.*, *Chiton*, *Teredo*, *Entovalva*, and as it is found in the Annelid larvae, the structure of which is remarkably similar to that of the forms we are now considering, its presence cannot be regarded as *a priori* improbable. In by far the greater number of Molluscan embryos, however, a proctodaeum is not developed.

F. The Gills.

The gills have been found to develop in some Prosobranchia as consecutive prominences on the ectoderm. These prominences correspond to single branchial leaflets. Mesoderm-cells enter into them and form a septum in each leaflet. The gill commonly seems to appear only after the mantle-cavity has formed, arising within the latter (Figs. 61, *k*, p. 150, and 99 and 100, p. 214), but occasionally it may be found at an earlier period on the surface of the body, as in *Fasciolaria* (OSBORN, No. 81).

Bipectinate plumose gills, a pair of which is found in *Fissurella* and *Haliotis*, are considered as the most primitive, and we may assume that the single monopectinate gill of the Monotocardia is to be derived from these, one of the gills (originally the left) disappearing through the shifting of the pallial complex while the other (originally the right), by fusion with the inner wall of the mantle-cavity, loses one of the rows of its leaflets.* So little attention has as yet been bestowed on the development of the gills in the Gastropoda that it is impossible to confirm by their ontogeny this view which in any case is very probable. The derivation of the single gill from the double gill is also plausible because the former is found not only in the most primitive Gastropods, but also in the Amphineura, the lowest Lamellibranchs and the Cephalopoda, *i.e.*, in all the principal divisions of the Mollusca.

G. The Differentiation of the Mesoderm-rudiment, the Development of the Body-cavity, the Nephridial and Circulatory Systems.

Apart from the primitive kidneys (pp. 136, 178) little has yet been recorded of the formation of the mesodermal organs. We have already shown that the mesoderm appears as a bilateral rudiment which is soon found in the form of two cell-masses, comparable to the mesoderm-bands of the Annelida, at the posterior end of the body near the blastopore (Figs. 96, 48, 51, 52, 56). The distinctness of these two cell-masses varies in the different forms; they may also be considerably reduced in size at an early stage, single cells being detached from them and becoming distributed in the primary body-cavity. By the development of a cavity in each of these cell-masses, right and left coelomic sacs are formed (Fig. 56 *A* and *C*), in which a somatic and a splanchnic layer can be distinguished. As a rule, however, this process is not so simple as that described for *Bythinia* by v. ERLANGER. The detachment of the cells from the two masses usually occurs very quickly, the two coelomic sacs being then much more difficult to recognise. They represent, in the main, the rudi-

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*[In *Trochus*, the septum, which separates the two sets of leaves of the single gill, is attached (except at the free end) to the mantle-wall along both its margins; in this way one set of gill-leaves becomes enclosed in a small cavity which only communicates with the general pallial cavity in front. These gill-leaves are much reduced in size as compared with the set which project into the main mantle-cavity, and it is easy to see that a further stage in this process might result in a complete fusion of the septum with the mantle-wall and thus cause a suppression of the one set of gill-leaves. There is every reason to believe that the monopectinate gill arose in this way.—ED.]

ment of the pericardium; the process is therefore very similar to that described (p. 74) in connection with the Lamellibranchs. The lumen of the sacs is to be regarded, here also, as further development shows, as the secondary body-cavity, while the definitive body-cavity proceeds from the cleavage-cavity which contains numerous scattered mesoderm-cells.

The whole mesoderm-rudiment is not, as already mentioned, used up in the formation of the coelomic sacs; occasionally even compact masses of mesoderm remain which have been distinguished as cephalic or trunk-mesoderm and from which, by delamination, somatic and splanchnic layers have been derived. According to this view, the definitive body-cavity would arise at least to some extent in the form of a coelom. This subject will be referred to again later (p. 217). It is generally assumed that the definitive body-cavity arises out of the primary body-cavity in which the cells detached from the mesoderm-bands become distributed, yielding connective tissue and musculature. With regard to the latter, the origin of the columellar muscle has been somewhat more carefully examined;

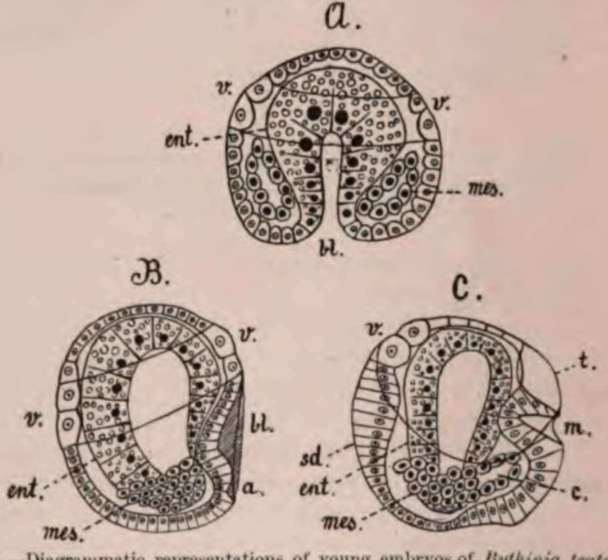

FIG. 96.—Diagrammatic representations of young embryos of *Bythinia tentaculata*; *A*, frontal section; *B* and *C*, from the right side (after v. ERLANGER). *a*, anal region; *bl*, blastopore; *c*, coelom; *ent*, entoderm; *m*, mouth; *mes*, mesoderm-rudiment; *sd*, shell-gland; *t*, ectodermal thickening, from which the tentacles and the cerebral ganglion are produced; *v*, velum.

it is found to arise by the concentration of mesoderm-cells at the base of the foot.

The development of the mesoderm and of the parts connected with it has recently been specially studied by v. ERLANGER in *Paludina* and *Bythinia*. As v. ERLANGER found that these organs developed here in the same way as in the Lamellibranchs, and, since the investigations of other zoologists which were less comprehensive led to less satisfactory results, we shall here follow principally the statements of this author.

The two mesoderm-sacs, above mentioned, approach each other and come to lie ventrally between the archenteron and the ectoderm, where they fuse. Occasionally, in later stages, a septum is retained as an indication of the former partition-wall (Fig. 98 *A*, *sp*). In the further course of development, the right half of the sac grows much more vigorously than the left, and the whole sac extends dorsally to the right side (Figs. 59 *A*, and 97). Differentiation now sets in, the walls of the two later ventral angles of the sac becoming thickened and subsequently forming distinct outgrowths (Fig. 97, *n* and *n'*). These outgrowths, according to ERLANGER, are the rudiments of the definitive kidneys which are consequently, like the pericardial sacs, paired on their first appearance. The left rudiment soon disappears,

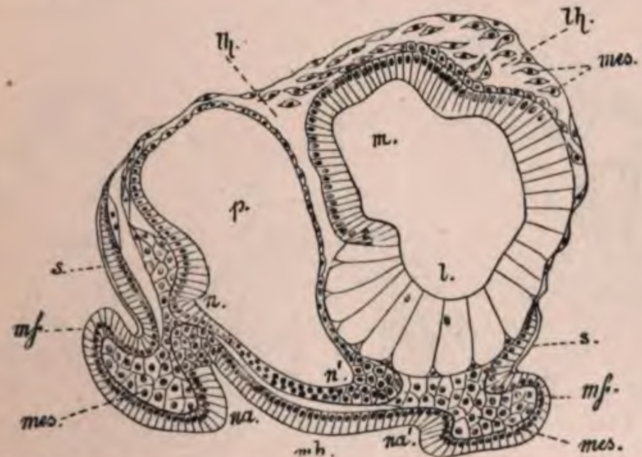

FIG. 97.—Transverse section through the pericardial region of an embryo of *Paludina vivipara* at the stage depicted in Fig. 59 *B*, *p* (after v. ERLANGER). *l*, liver; *lh*, body-cavity; *m*, stomach; *mes*, mesodermal tissue; *mf*, mantle-fold; *mh*, mantle-cavity; *n*, rudiment of definitive, *n'*, of abortive kidney; *na*, *na'*, rudiments of efferent ducts of the same; *p*, pericardium; *s*, shell.

while the right forms a sac (Fig. 101, *n*) and unites with the ectoderm to form the efferent duct. In *Bythinia*, the kidney can at this stage be recognised as a derivative of the posterior part of the pericardial sac (Fig. 92 *B*, *n*). At a later stage, a process grows out from its postero-ventral part and becomes connected with the ectoderm of the mantle-cavity, so that the lumen of the kidney now communicates with the latter. In *Paludina*, the formation of the efferent renal duct (ureter) takes place from the mantle-cavity, which at an earlier stage sank in on the right ventral side. The pallial depression is prolonged in the direction of each of the kidney-rudiments (Fig. 97, *na* and *na'*). The branch running towards the right kidney is specially distinct, being longer than that running towards the left rudiment; the latter, indeed, has no permanent significance on account of the degeneration of this left rudiment. The right branch of the mantle-cavity, however, then fuses with the right kidney, and thus becomes its ureter (Figs. 59 *B*, and 98, *na*).

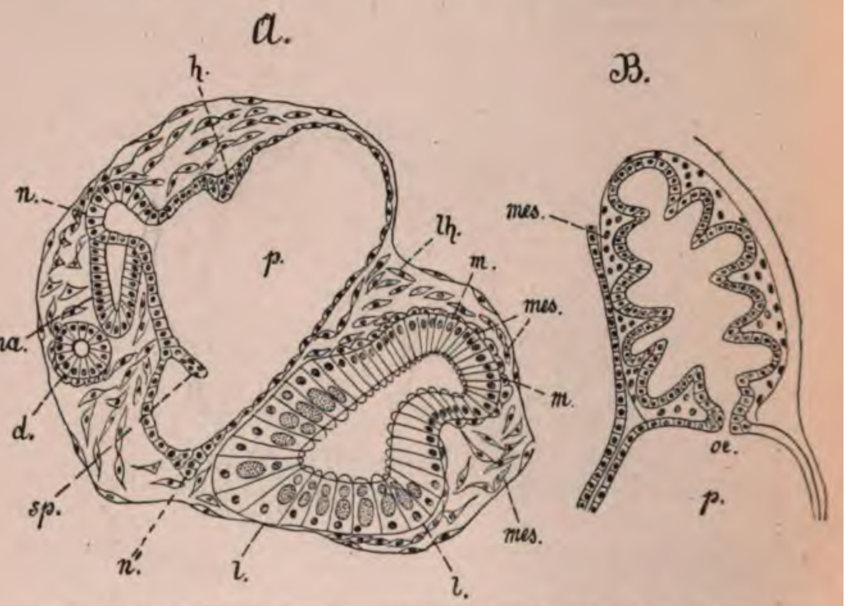

FIG. 98.—*A*, transverse section through the pericardial region of an embryo of *Paludina vivipara* at the stage depicted in Fig. 59 *C*. *B*, the kidney of an almost mature *Paludina* embryo (after V. ERLANGER). *d*, intestine; *h*, rudiment of heart; *l*, liver; *lh*, body-cavity; *m*, stomach; *mes*, mesodermal tissue; *n*, definitive, *n'*, abortive kidney; *na*, efferent duct of the former; *oe*, aperture of the kidney into the pericardium; *p*, pericardium; *sp*, pericardial septum (remnant of partition-wall).

The ectodermal origin of the ureter can be recognised even at a later stage in its histological structure. The duct formed as above has been distinguished, as primary ureter, from the secondary ureter met with in the terrestrial Pulmonates. In some of these latter, the primary ureter opens into the pulmonary cavity in the way above described. In others, it is continued as a channel in the wall of this cavity, and in others, again, this channel partly or altogether closes and, becoming finally altogether detached from the wall of the respiratory cavity, yields the secondary ureter which, in the most extreme cases, such as *Helix pomatia*, runs alongside of the rectum and, with it, ends near the respiratory aperture (v. JHERING, No. 46; BRAUN, No. 14).

The origin of the ureter as a part of the pulmonary cavity which at first is channel-like but closes to form a tube later, gathered with some certainty from the study of comparative anatomy, is entirely confirmed by ontogeny (BRAUN, BEHME, No. 4). The kidney, in the embryos of *Helix pomatia*, opens near the primitive kidney in a depression of the body which represents the rudiment of the respiratory cavity. As this cavity deepens, the glandular part of the kidney and the primary ureter become differentiated. At the posterior part of the pulmonary cavity, the latter passes into a channel which runs through the whole cavity and ends only at the respiratory aperture. The channel is very broad and is distinguished by its high cylindrical epithelium from the rest of the respiratory cavity which is lined with flattened epithelium. The channel closes later, its edges bending together and fusing from behind forward, and the secondary ureter thus formed now represents a closed tube which opens in the neighbourhood of the anus.

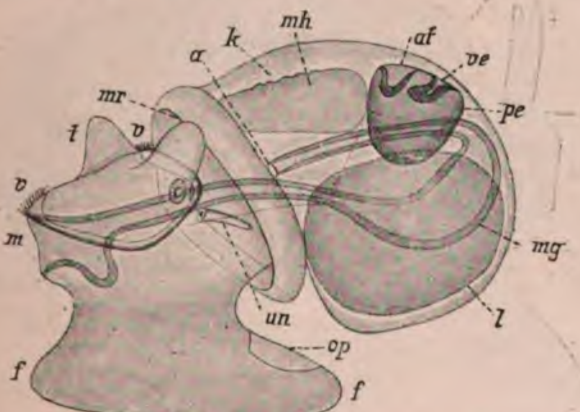

FIG. 99.—Older embryo of *Paludina vivipara* (after v. ERLANGER). *l*, liver; *un*, primitive kidney; *v*, velum; the rest of the lettering as in Fig. 100.

The secondary ureter is a new acquisition within the division of the Stylommatophora, as v. JHERING has shown. It occurs only in the so-called Nephropneusta. Among these, however, in one and the same genera, forms are met with possessing the secondary ureter and others exhibiting the much more primitive conditions found in the aquatic Pulmonates, as **Braun** has shown. From this we may gather that the division of the Pulmonates into Branchiopneusta and Nephropneusta is not justifiable. It has already been shown (p. 182) that we cannot regard the pulmonary cavity as a transformed ureter, but must consider it as the pallial cavity, corresponding to that in other Gastropods.

The kidney now enlarges considerably and its walls become folded (Fig. 98 *B*). At first only a few such folds are formed, and the renal cavity is still spacious, but at a later stage the lamellae almost completely fill it. v. **Erlanger** points out that the complicated kidney of *Paludina* thus passes through a stage which is retained throughout life by the very simple kidney of *Haliotis*. The opening of the kidney into the efferent duct gradually approximates to the reno-pericardial pore (Fig. 100). The latter is (with some exceptions) known to be retained in the Gastropoda, so that the details given under the Lamellibranchia (p. 74, etc.) as to the connection between the coelom and the nephridia are applicable here.

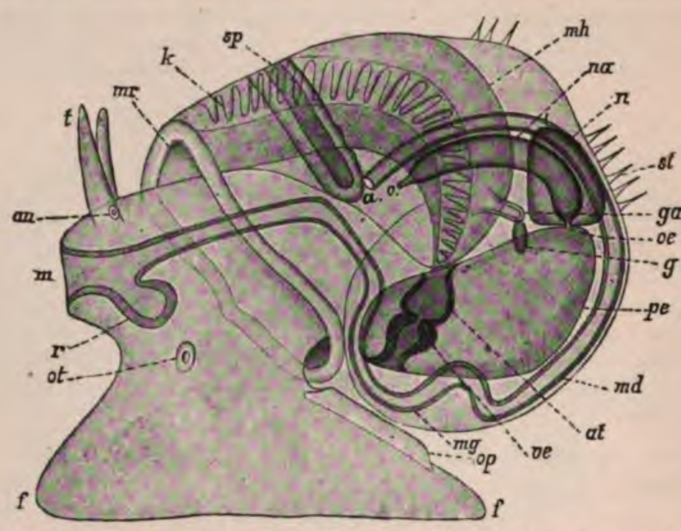

Fig. 100.—An almost mature embryo of *Paludina vivipara* (after v. **Erlanger**). *a*, anus; *at*, auricle; *au*, eye; *f*, foot; *g*, genital gland; *ga*, efferent genital duct; *k*, gill; *m*, mouth; *md*, intestine; *mg*, stomach; *mh*, mantle-cavity; *mr*, edge of the mantle; *n*, kidney; *na*, ureter; *o*, aperture of the ureter into the mantle-cavity; *oe*, reno-pericardial pore; *op*, operculum; *ot*, otocyst; *pe*, pericardium; *r*, radular sac; *sp*, Spengel's organ; *st*, spines on the shell; *t*, tentacle; *ve*, ventricle.

Most of the Gastropoda possess only one kidney, but those Prosobranchs that are provided with two auricles (Diotocardia, such as *Haliotis*, *Patella*, *Fissurella*, *Trochus*) have a second kidney. It is an interesting fact that this original paired character still finds expression in the development of the kidney in *Paludina*. In the adult, this kidney lies, as in most Gastropods, to the left of the rectum and must therefore, as was shown above, have been the right kidney before the twisting of the posterior part of the body took place (Fig. 100 *A-E*, p. 214). This view is admirably supported by v. ERLANGER'S researches, since, according to his account, it is the rudiment of the right kidney which develops further, while the left degenerates. P. SARASIN'S researches also show that, in *Bythinia*, the rudiment of the kidney lies on the right side and is displaced to the left later.

The one kidney which persists in most Prosobranchs (Monotocardia) thus corresponds to the (definitive) left kidney which, before the twisting took place, was the right kidney of those forms which still possess two renal organs. In these latter, however (*Haliotis*, *Fissurella*, *Turbo*, *Trochus*) the right kidney is usually well developed, the left, on the contrary, being reduced. It thus appeared possible that the permanent kidney of the Monotocardia might correspond to the right kidney of the Diotocardia, a view which has been put forward several times (PERRIER, No. 87). Ontogeny, however, as well as the fact that, in the Diotocardia, the right nephridium serves for conducting to the exterior the genital products (see below, p. 220) indicate that it is the left (which before torsion is the right) kidney that persists and is alone retained in the Monotocardia (RAY LANKESTER, No. 65; V. ERLANGER, No. 29).

The pericardial sac has several times been mentioned. The term pericardial is here hardly correct, since the kidney also originates from this sac, to which, further, the *heart* owes its origin. This organ has now become very large and has thin walls (Fig. 99). Dorsally, and to the left of the renal outgrowth of the pericardium, a channel-like invagination representing the rudiment of the heart (Fig. 98, *h*) appears and occupies the whole length of the sac. The channel becomes more and more marked off from the pericardium *i.e.*, it becomes a tube which at first still remains open toward the primary body-cavity. This tube, by finally closing and remaining connected with the wall of the pericardium only at its two ends, gives rise to the heart which now, as a tube, lies within the pericardium, its two ends opening into the primary body-cavity. At a somewhat earlier stage, a constriction appears near the middle of this tube, by means of which the auricle and ventricle are divided from one another (Figs. 99 and 100).

The **vessels** arise as inter-cellular spaces in the mesodermal tissue of the primary body-cavity, and are thus at first quite independent of the heart. We have already repeatedly spoken of embryonic or larval blood-sinuses, some of which, being capable of carrying on rhythmical movement, have been assumed to be larval hearts. The rudiments of the vessels first appear as such blood-sinuses of different sizes; in *Paludina*, for instance, a large sinus is found beneath the intestine (Fig. 88 *B*, *us*, p. 194). The gradual narrowing of these spaces, which are surrounded by a layer of flat cells, and their connection with the open ends of the heart gives rise at the end of the ventricle to the aorta and at that of the auricle to the efferent branchial vein. The other vessels arise in a corresponding manner.

The heart, in the Gastropoda, forms in a less primitive way than in the Lamellibranchia (p. 76). This is not surprising, since the circulatory and respiratory organs of the Gastropoda have undergone far-reaching alterations in consequence of the asymmetrical shape of the body. The presence of two auricles, however, and the perforation of the heart by the alimentary canal in a few Prosobranchs (Diotocardia) point to conditions resembling those found in the Lamellibranchs. We might even believe that the heart in both divisions arose ontogenetically in a similar way, and might then consider the region at which the heart formed in the pericardium as the boundary between the two coelomic sacs.

It is an interesting fact that we have, persisting throughout life, in *Dentalium*, a condition similar to that seen in the developing heart in the Gastropoda, which, as we have seen, arises as an infolding of the pericardium. According to PLATE (Solenoconch. Lit., No. 3), the heart of *Dentalium* represents a sac-like invagination of the pericardium, and the blood-vessels also are found in a condition similar to that in Gastropod embryos, being mere spaces in the mesoderm between the other organs. The structures regarded by PLATE as pericardium and heart, however, are but slightly developed, and the nephridia are not connected with the pericardium. It is well known that *Dentalium* is a form already highly differentiated, but it may be possible that in this respect a primitive character is retained. It appears also that, among the Amphineura, the Solenogastres show a similar primitive condition, while, in the *Chitonidae*, the circulatory system is much more highly organised, the heart being entirely surrounded by the pericardium and provided with efferent and afferent vessels.

The different positions assumed by the heart in the various divisions of the Gastropoda, which are considered of great systematic significance, are connected with the shifting of the different regions of the body to which allusion has already repeatedly been made (p. 144). One of the auricles, as was seen, is almost always lost in the process. If the pallial complex is only displaced to the side, the gill lies behind the heart, the auricle behind the ventricle (this is notably the case in the Opisthobranchia); but, if the pallial complex shifts quite to the front, the gill will be found in front of the heart and the auricle in front of the ventricle (Prosobranchia).

Other descriptions of the rise of the pericardium, the kidney and the heart.* In the formation of the pericardium as described above, this organ was treated as if it corresponded to the whole of the coelom, but v. ERLANGER's observations on *Paludina* and *Bythinia* may also be interpreted as showing that only a part of the original coelom persists as the pericardium while the rest disintegrates, as we saw to be the case in the formation of the definitive body-cavity in the Arthropoda. SALENSKY also, at a somewhat later stage of the embryos of *Vermetus*, speaks of a somatic and a splanchnic layer which are apposed to the ectoderm and the entoderm respectively and which enclose a large space as a (temporary) secondary body-cavity. The two layers of the mesoderm are, however, so indistinct in the Mollusca that we are unable to speak of them with any certainty and, until more detailed statements are made, must regard them as only definitely differentiated in the pericardium. SALENSKY, who regarded this large space as the coelom, considers that the heart arose from it in a way similar to that above described. With this may be reconciled the earlier accounts of GANIN (No. 35), BÜTSCHLI (No. 18) and especially of P. SARASIN (No. 101) and SCHALFEEW (No. 106) which refer partly to the Prosobranchia and partly to the Pulmonata.

It is easier to reconcile the older and more recent researches with regard to the rise of the heart than with respect to the origin of the kidney. This organ was indeed early derived from the mesoderm by constriction from the pericardium (SCHALFEEW) or at least in the neighbourhood of the latter (SALENSKY), the efferent ducts being derived from an (ectodermal) invagination of the mantle-cavity, but the majority of authors trace back the whole kidney to an ectodermal invagination. After what has been said above (p. 74) as to the formation of the nephridia in the Lamellibranchia and the Annelida, it cannot be doubted that the first method is the more probable.†

H. The Genital Organs.

The development of the genital organs has been best observed in *Paludina*, a form belonging to the Prosobranchia in which the sexes are distinct (v. ERLANGER). In these animals, the condition of the

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* The literature connected with the formation of the mesodermal organs is, like that connected with the ontogeny of the Gastropoda in general, rich in contradictory statements. Where recent researches may be considered to have disproved older statements, we have ignored the latter. Lack of space has prevented us from taking into consideration all the published data of a confirmatory nature. A summary of these is to be found in v. ERLANGER's works (Nos. 27 and 28).

† [The recent investigations made by MEISSENHEIMER (No. XVII.) on the development of these organs in *Limax* do not at present help to clear up the confusion relating to their origin, as they are too startling to be accepted unsupported. MEISSENHEIMER maintains that the heart and kidney arise from a common ectodermal rudiment, a condition which, so far as we are aware, appears to be quite unique.—ED.]

genital organs is far simpler than in the hermaphrodite Pulmonates which have repeatedly been studied but are far from being fully understood, and we shall therefore consider *Paludina* first. The first rudiment of the genital organs here appears at a time when the velum is still present, and the primitive kidney at its highest development, *i.e.*, somewhat at the stage of Fig. 99. The male and female genital rudiments are similar.

The **germ-gland** arises as a rounded outgrowth of the pericardial sac near the rudiment of the (original) left kidney (Fig. 101, *g*), which, as has been stated, degenerates. This outgrowth becomes separated from the pericardial sac as a spherical vesicle which approaches the **efferent genital duct** (*ag*) that has now also appeared as a rudiment. The latter arises as an ectodermal invagination from the mantle-cavity, and, according to v. ERLANGER, it is very probable that the duct of the (original) left kidney changes direct into the genital duct. It grows out further (Fig. 102, *ag*) and becomes united with the vesicular rudiment of the germ-gland (Fig. 100, *g* and *ga*). The genital gland and its efferent duct now increase considerably in length

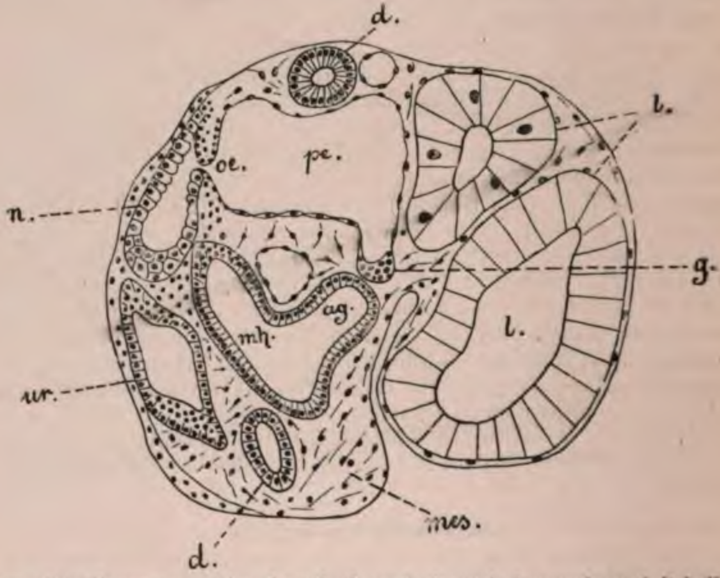

FIG. 101.—Transverse section through the posterior end of an embryo of *Paludina vivipara* in the stage depicted in Fig. 99 (after v. ERLANGER). *ag*, efferent genital duct; *d*, intestine; *g*, rudiment of the genital gland; *l*, liver; *mes*, mesodermal tissue; *mh*, mantle-cavity; *n*, kidney; *oe*, reno-pericardial pore; *pe*, pericardium; *ur*, ureter.

and begin to coil, but there is as yet no sexual differentiation save that this increase in growth takes place at an earlier stage in the male than in the female.

The **male genital apparatus** of *Paludina* is composed of the germ-gland just described, which becomes the testis, of the efferent duct, which has also been to some extent described, and of a much longer section, the vas deferens; the latter, which leads to the penis, develops in a somewhat different way. This part of the vas deferens arises in the form of a groove in the base of the mantle-cavity into which the previously formed (primary) efferent duct opens. The groove closes and, in the form of a tube, extends as far as the right tentacle where the penis develops.

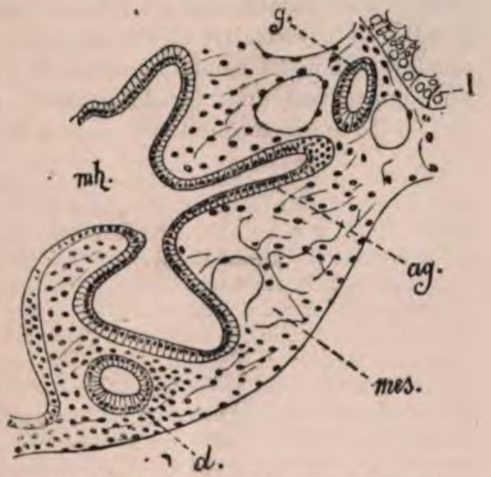

FIG. 102.—Portion of a sagittal section of an embryo of *Paludina vivipara* in a younger stage than that depicted in Fig. 100 (after V. ERLANGER). *ag*, efferent duct; *d*, intestine; *g*, rudiment of the genital gland; *l*, liver; *mes*, mesodermal tissue; *mh*, mantle-cavity.

In some Prosobranchs, this **seminal groove** is retained throughout life and is continued from the male genital aperture in the mantle-cavity to the tip of the penis. We thus find here, as in the formation of the secondary ureter of the Pulmonates, conditions which are permanent in other forms appearing as consecutive ontogenetic stages.

The **female genital apparatus** of *Paludina* does not develop as early as that of the male. Whereas the chief features of the latter can be recognised at the end of embryonic development, those of the female cannot be distinctly made out until several weeks after birth. At this stage, the rudiments of the albumen-gland appear in the form of eight to twelve tubular outgrowths near the point where the ectodermal efferent duct unites with the germ-gland. The ovary is still represented by a tube lined by undifferentiated epithelium. The short tube which extends from the ovary to the albumen-gland is said to be derived from the mesodermal rudiment, like the short piece which, in the male apparatus, runs from the testis to the commencement of the so-called primary (ectodermal) efferent duct. The whole of the remaining efferent apparatus in the female corresponds to the primary efferent duct in the male, and the former, like the latter, opens into the mantle-cavity. There is, in the female, no part corresponding to the secondary efferent apparatus of the male. Apart from this last portion the genital apparatus in the male and in the female thus agree closely in their development, the principal constituent parts being apparently quite homologous (v. ERLANGER).

The relation of the germ-glands to the pericardium, which was only conjectured to exist in the Lamellibranchia (p. 82), is definitely proved by v. ERLANGER to exist in the Gastropoda. The genital glands arise as growths of the pericardial wall, and thus bear to this latter the same relation as do the genital products in the Annelida to the peritoneal epithelium (Vol. i., p. 297). In this way we obtain a further support for the coelomic nature of the pericardial sac. Since, in the lower forms, the nephridia function in conducting the genital products to the exterior, it appears as if, in the Gastropoda, the nephridium, which no longer functions as a kidney, might become directly modified as the efferent genital duct. As we have seen in the Solenogastres (p. 9), the nephridia transmit the genital products, and even in some Prosobranchs (*i.e.*, the majority of the Diotocardia) the right nephridium serves in addition as a genital duct; such a modification of the efferent renal ducts is therefore not surprising.

The **hermaphrodite genital organs** of the Pulmonates have repeatedly been made the subject of careful ontogenetic research (EISIG, No. 26; ROUZAUD, No. 94; BROCK, No. 16; SIMROTH, No. 119; KLOTZ, No. 54), but so far no satisfactory conclusion as to their origin has been arrived at. The conditions are here very complicated and obscure. The point of greatest importance is to ascertain the relations between the various ducts of the hermaphrodite forms and the simple efferent apparatus of the dioecious forms and finally to trace the former to the latter. We cannot state definitely that the separation of the sexes is the primitive condition, although this seems highly probable, since the older Gastropods (the Diotocardia) are dioecious and the most specialised forms (Opisthobranchia, Pulmonata) are hermaphrodite. As the accounts so far published do not enable us to obtain a clear conception of the development of the hermaphrodite genital organs, it is only possible to consider them by the light of the better understood development of the dioecious Prosobranchia.

At the very outset of this investigation, however, a difficulty is occasioned by the question as to whether the genital apparatus is derived from one common rudiment or from two or three distinct rudiments. The whole apparatus, the germ-gland included, has been derived from a single ectodermal thickening which extends and becomes differentiated later (**Rouzaud**). There can, however, be but little hesitation in at once excluding this view, inasmuch as the hermaphrodite gland is, in any case, yielded by the mesoderm. [The gonad is probably derived from the apparently undifferentiated blastomeres.] With regard to the ectodermal part, *i.e.*, the efferent ducts and accessory structures, there may certainly be two distinct types of development according as the copulatory organ lies separately from the female genital aperture or is united with it in a common atrium. In the first case, the genital apparatus would, as in the Prosobranchs (*Paludina*), consist of three parts, *viz.*, of the germ-gland, of the primary (nephridial), and of the secondary (ectodermal) efferent ducts together with the penis. This is evidently the case in *Limnaea*, as we may conclude from the observations of **Eisig** and **Klotz**.

The genital apparatus of *Limnaea* appears as a rudiment even before the hatching of the young animal. The penis appears first as an ectodermal invagination at the base of the right tentacle. The hermaphrodite duct arises independently of it as a strand-like structure. The mesodermal character which has repeatedly been assumed for it appears doubtful. We are inclined rather to consider it as ectodermal, a view which is supported in the literature on the subject. This strand is of special importance, as it splits later into two parts, one of which represents the rudiment of the uterus and the other that part of the vas deferens which is known as the prostate (Fig. 103, *ut*, *vd*). The hermaphrodite gland arises independently of this strand from the mesoderm [? primitive blastomeres]. A short process of the mesodermal rudiment yields the proximal portion of the efferent duct, while the distal part arises from the cellular strand mentioned above (Fig. 103, *zg*, **Brock**, **Klotz**). The spermetheca becomes

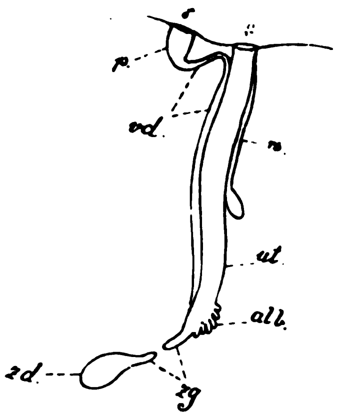

Fig. 103.—Diagram representing a later stage in the development of the genital organs of a Pulmonate. *alb*, albumen-gland; *p*, penis; *rs*, spermetheca; *ut*, uterus; *vd*, vas deferens; *zd*, hermaphrodite gland; *zg*, hermaphrodite duct; ♂ and ♀, genital apertures.

abstricted from the uterine portion of the common duct in a way similar to that in which the prostatic part of the vas deferens arose from it earlier. These abstrictions take place by means of longitudinal folds which grow into the common canal that arose when the strand became hollow. The albuminiparous gland arises in the form of a number of tubular outgrowths near the proximal end of the uterus (Fig. 103, *alb*).

The origin of the male and female ducts through the division of a common rudiment may be demonstrated with some certainty in the various hermaphrodite forms that have been investigated. When we take into consideration, in this connection, that, in the Opisthobranchia, the transmission of the two kinds of genital products takes place through a common duct (Fig. 104 *B*) and that, in the Pulmonates also, their transmission takes place for a longer or shorter distance through the same duct, the division into male and female ducts occurring later (Fig. 104 *C*), we may with safety assume that these two ducts have arisen phylogenetically also through the splitting of *one* duct and that thus the Opisthobranchs exhibit the more primitive condition. If we then take one step further back, we may trace back the common efferent duct of the hermaphrodite Gastropoda to the efferent apparatus of the dioecious forms. We here naturally presuppose that we regard the separation of the sexes as the primitive condition and hermaphroditism as the derived condition. Since also in dioecious animals, ova are often met with in the testis and *vice versâ*, and, further, in other divisions of the animal kingdom in which separation of the sexes is the rule, hermaphroditism occurs in a few highly differentiated forms, such an assumption is not inadmissible.

The question now arises how the connection is established between the penis and the genital aperture in those forms in which these two arise separately. In the Opisthobranchia, a groove runs from the aperture of the common duct to the introvertible penis which here also is found near the right tentacle (Fig. 104 *B*). Where the common duct becomes divided up into a female and a male portion the channel starts from the aperture of the latter, and, by the closure of the groove and its detachment from the ectoderm, the part of the vas deferens arises which lies nearer the penis, the process being similar to the formation of the secondary vas deferens in the Prosobranchia (Fig. 104 *C*). It is in any case probable that, ontogenetically, the formation takes place in this way, although this has not yet been proved.

In Fig. 104 *A*-*E* we have attempted to give some idea of the way in which these processes may have taken place. The modifications brought about by the earlier closing of the channel, by the later separation of the male duct, and by the invagination, in the course of ontogeny, of the rudiment of the penis (*D*) are self-evident.

In cases in which, finally, the penis becomes shifted towards the female genital aperture, and the two join to form a common atrium, as in the Stylommatophora (Fig. 104 *E*), the rudiment of the ectodermal parts form from a common rudiment. In these cases, we have only to distinguish between the mesodermal rudiment of the hermaphrodite gland (or the hermaphrodite organ) and the ectodermal rudiment of the primary and secondary ducts and copulatory apparatus.

The significance of these processes is still little understood, and it is doubtful if ontogeny will throw much light upon the subject. Summaries and critical descriptions of these ontogenetic processes are given by ROUZAUD, BROCK, SEMPER (No. 117), SCHIEMENZ (No. 107), and KLOTZ (No. 54).

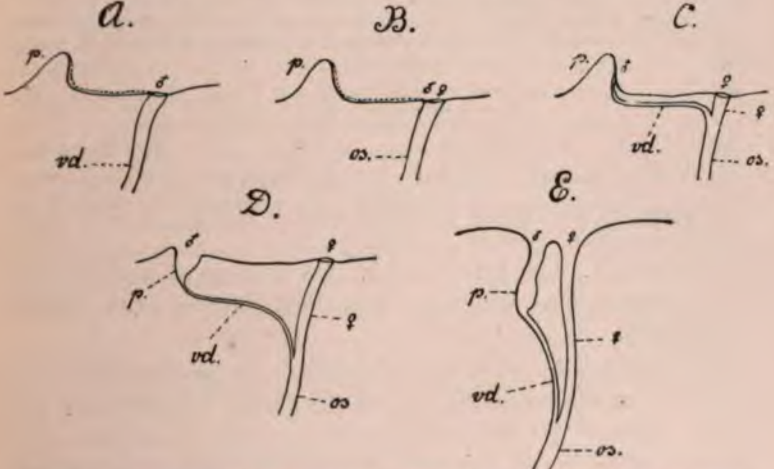

FIG. 104.—*A*-*E*, diagrams illustrating the manner in which the genital apparatus opens out at different ontogenetic stages. *A*, in a dioecious Gastropod; *B*-*E*, in hermaphrodite Gastropods. *os*, ovoseminal duct; *p*, penis; *vd*, vas deferens; ♂ and ♀ genital apertures or the terminal portions of the corresponding efferent ducts.

[The interpretation of the complicated conditions met with in the hermaphrodite genitalia of the Opisthobranchia and Pulmonata is one of those difficult problems upon which ontogeny throws little light. We think there can be little doubt that it will be found more profitable to leave the ontogenetic side alone and accept the obvious and comparatively simple interpretation offered by the study of the comparative anatomy of these organs.

In existing Gastropoda, we seem to have every stage in the development of the secondary genital ducts preserved to us, so that, starting from the simple condition of the Diotocardia, where the gonads discharge by the still functional right kidney, we pass to the Monotocardia, where the right kidney has lost its excretory function and serves solely to transmit the genital products, and where also we find a secondary duct appearing in the male in the form of a groove leading forward to a non-introvertible penis. A condition similar to this is found in many of the hermaphroditic Tectibranchia, which, however, generally show an albumen-gland and a spermetheca, while the open groove-like vas deferens leads down to an introvertible cephalic penis. The next change which occurs is the closure of the groove-like vas deferens and its separation from the ectoderm as a tube. This brings us to the condition seen in *Actaeon* and then to the Basommatophorous Pulmonata, where the male aperture is distinct from the female. The only break in the series is that between the Basommatophorous and Stylommatophorous Pulmonata, due to the development in the latter of a secondary oviduct which extends from the primitive genital aperture (now closed) down to the cephalic penis, and opens with that structure through an atrium. With regard to the origin of this secondary oviduct, two possible interpretations present themselves, one being that the secondary oviduct has arisen as a groove, like the vas deferens, and, like that structure, has secondarily closed together with the primary genital aperture, so that both products are discharged by a single anterior aperture, or it may be that the primitive genital orifice has shifted by growth down the side of the body towards the penis and, finally, an atrial involution has caught up both these apertures, so that they now communicate with the exterior by a common aperture. The fact that these stages are not recapitulated in the ontogeny is not, we think, of much importance, for we know that ontogeny by no means always recapitulates phylogeny, and that this is especially the case in forms which, like these Mollusca, have a considerable amount of yolk.—ED.]

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CHAPTER XXXIII.

CEPHALOPODA.

Systematic :—

I. TETRABRANCHIA, with two pairs of gills, two pairs of auricles, two pairs of kidneys, external chambered shell and a large number of tentacles round the mouth. Funnel consisting of two lobes ; without ink-sac.

1. Nautiloidea.
2. Ammonoidea.

II. DIBRANCHIA, with one pair of gills, one pair of auricles, one pair of nephridia, with internal shell, the chambers of which are seldom distinct (*Spirula*, *Belemnites*) often reduced or absent. Round the mouth eight to ten arms. The two halves of the siphon united to form a tube ; an ink-sac generally present.

1. Decapoda, with ten arms.
    - (A) Phragmophora.
        - *Spirulidae.*
        - *Belemnitidae.*
        - *Belemnoteuthidae.*
        - *Acanthoteuthidae.*
    - (B) Oigopsida.
        - *Ommastrephidae.*
        - *Onychoteuthidae.*
        - *Cranchiidae.*
        - *Chiroteuthidae.*
    - (C) Myopsida.
        - *Loliginidae.*
        - *Sepiolidae.*
        - *Sepiidae.*
2. Octopoda, with eight arms.
    - *Cirrhoteuthidae*, with fins.
    - *Philonexidae*, *Tremoctopus*, *Philonexis.*
    - *Argonautidae.*
    - *Octopodidae*, *Octopus*, *Eledone.*

1. Oviposition and the Constitution of the Egg.

The egg of a Cephalopod, before it is mature and at the time of oviposition, is surrounded by a protective envelope which, in the different forms, may assume very various shapes. A large number of eggs are usually laid at one spot, forming a large mass of spawn.

In *Sepia*, the eggs constituting the mass are distinct from one another. Each of them is surrounded by a compact, spindle-shaped, black capsule of leathery consistency which, at one end, runs out into a process, by means of which the eggs are attached close to one another to some firm object. The egg-capsules attain about the size of a hazel nut. In *Rossia* and *Sepiola* * also, the eggs are laid separately and are attached to some object or else to each other, but the envelope is less thick and is even transparent (*Sepiola*). The eggs of *Loligo*, on the contrary, are laid in gelatinous tubes, each tube containing a large number (in *Loligo vulgaris*, as many as eighty or more). The tubes are attached by one end to some firm substratum. As they stand out from their point of attachment radially, they form a kind of tassel. Such large tassels are found attached to plants, pieces of wood, stones, etc.

The eggs composing a mass of spawn, resembling Cephalopodan spawn—dredged by GRENACHER off the Cape de Verde Islands and attributed by STEENSTRUP to one of the *Teuthidae* (*i.e.*, to a form something like *Ommastrephes*, No. 14), are also surrounded by a gelatinous mass, but are not contained in distinct tubes. This spawn forms a gelatinous mass 75 cm. long and 15 cm. thick which resembles a sausage. Within the gelatinous cover, the violet-coloured spherical eggs are arranged in fairly regular spiral coils, their number amounting to thousands. Each egg, as in *Loligo*, is surrounded by a firm envelope. A similar envelope which must be regarded as the chorion (p. 246) also surrounds the eggs of the Octopoda.

In *Octopus* and *Argonauta*, the chorion of the oval egg is drawn out into a stalk. The stalks of a number of eggs become connected

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* According to STEENSTRUP (No. 42), the ontogeny of *Sepiola* as given by various authors (P. van BENEDEN, METSCHNIKOFF, USSOW) refers rather to a species of *Loligo*; further obscurity being due to the fact that the masses of spawn found and investigated have been attributed to Cephalopods to which they did not belong. Egg-masses produced by *Loligo vulgaris*, a Myopsid, are said to have been ascribed to *Ommastrephes sagittatus*, a form belonging to the group of the Oigopsida. This led to the inaccurate conclusion that forms remote from one another in systematic position showed great similarity in their development. According to STEENSTRUP, this resemblance in development is due rather to the fact that they all belong to the genus *Loligo*, and theoretical conclusions founded on this similarity would thus be of no value.

together, large egg-bundles being thus produced, the bundles again uniting to form aciniform masses (*Argonauta*). In *Eledone* also, the threads from the chorion of the long eggs unite to form a stronger strand, which then becomes attached to the substratum (JOUBIN, No. 21). We have ourselves found that the eggs of *Eledone* (apparently *E. moschata*) are attached by their stalks to the substratum in pairs or in groups of two or four. A number of such groups are found in close juxtaposition, giving rise to a spawn-mass consisting of sixty to seventy eggs. The long ovate eggs of this *Eledone* are very large, measuring (including the envelope) 15 mm. in length, while those described by JOUBIN are only about half this length.

In Sepia, the stalks of the individual eggs become twisted together, the result being a rather large strand of eggs closely arranged round a central axis. These strands are attached to rocks, the female covering them with her body and, by the promotion of a continuous flow of water, assisting in their development (SCHMIDTLEIN).* The eggs of *Argonauta* are still further protected by the mother, as the spawn is attached to the inner side of her shell and carried about by her. [*Nautilus* (WILLEY, No. IV.) lays solitary eggs of great size, each egg-capsule measuring 45 mm. by 16 mm. and containing one egg 17 mm. long and very rich in yolk.—ED.]

The capsules or the gelatinous masses which surround the eggs and the cementing substance by means of which they are attached are secreted by special glandular portions of the oviducal wall and by the nidimental glands. Where there is no such special development of glands in the genital apparatus, as in the Octopoda, the eggs are surrounded by the chorion alone. This latter, however, is also found round eggs surrounded by firm capsules or gelatinous masses. At the animal pole of the egg, the chorion is perforated by the micropyle (Fig. 105, *m*).

The conditions under which copulation and the fertilisation of the egg take place in the Cephalopoda are so peculiar that we must devote some attention to them. In the Octopoda, fertilisation probably takes place in the oviduct. The spermatophores are introduced by the help of the hectocotylised arm into the mantle-cavity or the oviduct. In *Argonauta*, *Tremoctopus* and *Philonexis*, it is well-known that the detached hectocotylised arm of the male is found in the mantle-cavity of the female. The female in the two last-mentioned forms possesses a receptaculum seminis in the form of an outgrowth of the oviduct which serves for the reception of the sperm (BROCK).

In the Oigopsida, as in the Octopoda, fertilisation takes place within the mantle-cavity, the spermatophores being introduced into that cavity and attached to various parts of its inner wall. Among the Myopsida, in the

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* Beobachtung über die Trächtigkeit und Eiablage verschiedener Seethiere. *Mittheil. Zool. Stat. Neapel.* Bd. i. 1879.

female of *Rossia* (according to the verbal statements of F. C. v. Maerenthal) there is a well-marked area near the mouth of the oviduct within which the spermatophores are attached. In the nearly related *Sepiola* (also according to researches by v. Maerenthal not yet published), there is a pouch-like depression of the integument lying laterally to the mouth of the oviduct for the reception of the spermatophores; this has been hitherto erroneously regarded as a terminal portion of the oviduct itself.

In the other Decapoda, copulation takes place in an exceedingly peculiar way, the spermatophores not being brought into the mantle-cavity, but attached near the mouth on the outer integument of the lip (buccal membrane) of the female. Glandular invaginations of the integument, in which the spermatozoa that escape from the spermatophores are stored, are found in this position in *Sepia* and *Loligo* (Vialleton), in *Sepioteuthis* and no doubt also in the other genera (v. Maerenthal).

In this last case, it is evident that fertilisation takes place only when the eggs are expelled through the funnel and are retained for a time near the mouth by the arms. The future leathery egg-capsule (of *Sepia*) is either still soft at this time and penetrable by the spermatozoa (?) or only forms after these have penetrated the egg (through the micropyle of the chorion), the still fluid glandular secretion being subsequently poured over the eggs by the funnel. This would then also no doubt apply to the gelatinous mass (in *Loligo*). It is an interesting fact that artificial fertilisation of mature eggs taken from a female *Loligo Pealii* was brought about by means of seminal fluid found in the spermatophores of the buccal membrane (Watase, No. 50). The same conditions are found in *Rossia*.

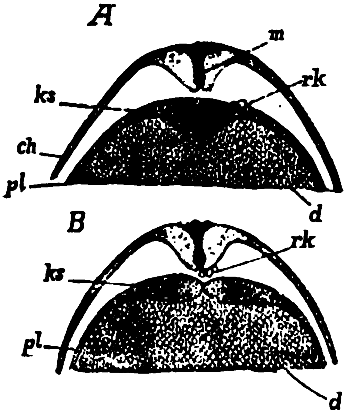

Fig. 105.—The upper pole of the egg of *Argonauta argo* in optical section. *A*, before fertilisation; *B*, shortly after fertilisation (after Ussow). *ch*, chorion; *d*, yolk; *ks*, germ-disc; *m*, micropyle; *pl*, peripheral protoplasm; *rk*, polar bodies.

The eggs of the Cephalopoda are unusually rich in yolk, and consequently attain a considerable size, a point in which they are essentially distinguished from those of other Molluscs. The eggs of *Sepia*, for instance, are fully as large as a pea (*Sepia officinalis*). The eggs of *Eledone* may be still larger and are exceedingly rich in yolk (p. 237). The eggs of other Cephalopods, such as *Loligo* and *Octopus*, are less rich in yolk and therefore distinctly smaller; those of *Argonauta* are even rather small, measuring, however, 1·3 mm. in longitudinal diameter. The food-yolk, which consists of rather fine granules, always constitutes by far the greatest mass of the egg. The egg, in shape, is usually oval (*Loligo, Eledone, Octopus, Argonauta*) or spherical, as in *Sepia* and the Cephalopods investigated by GRENACHER (p. 267). The massive food-yolk is completely invested by a comparatively thin layer of the formative protoplasm, which thickens to form a disc-shaped accumulation at the upper or future animal pole of the egg beneath the micropyle. This is the future germ-disc (Fig. 105, *ks*) and is sharply marked off from the food-yolk. In consequence of this peculiarity, and others to be described later, the eggs of the Cephalopoda afford the *most perfect examples of meroblastic cleavage.*

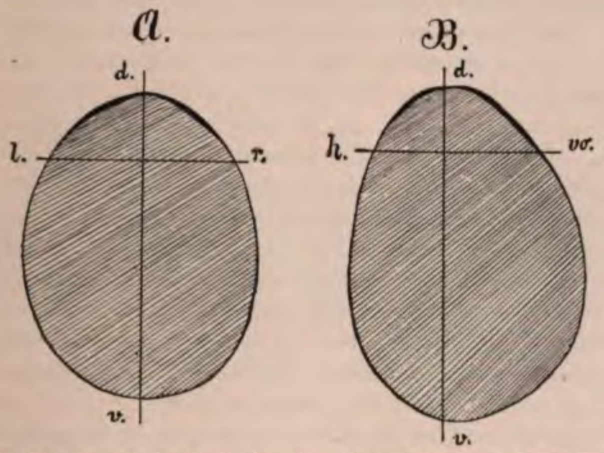

FIG. 106.—Diagrammatic longitudinal sections through the egg of *Loligo Pealii* (after WATASE). *B* is a median sagittal section; *A*, a transverse vertical section at right angles to *B*. The black line on the periphery of the egg represents the formative protoplasm, while the food-yolk is shaded. *d*, dorsal side; *v*, ventral side; *h*, posterior; *vo*, anterior; *l*, left; *r*, right.

A bilateral symmetry can be recognised not only in the early stages of cleavage but even before cleavage sets in; this symmetry bears a definite relation to the later development of the embryo. In the oval eggs of *Loligo Pealii*, it is expressed not only in the form of the egg, but also in the way in which the germ-disc spreads over it (WATASE, No. 50). The eggs of this Cephalopod appear somewhat flattened on one side while, on the opposite side, they are arched (Fig. 106 *B*). The positions of the anus and the mouth in the embryo correspond to these two sides. At the part which becomes the anterior end (*vo*), the protoplasm of the germ-disc extends further down towards the equator than on the opposite side (*h*). The germ-disc, however, spreads to right and left for an equal distance (Fig. 106 *A*, *r* and *l*). A comparison of Fig. 106 *B* with the median sagittal sections of later embryonic stages (Figs. 132, 133, p. 282) shows that the animal pole of the egg (*d*) corresponds to the area of the dorsal surface, the vegetative pole (*v*), on the contrary, to the ventral surface.

In the germ-disc we find the egg-nucleus and later the first cleavage-nucleus. Neither of these, however, quite coincides with the animal pole of the germ-disc (Fig. 105 *A*) but occupies a somewhat excentric position, *i.e.*, it is slightly nearer the posterior edge of the disc. The nucleus appears to be surrounded by a more hyaline zone of protoplasm which passes externally into a more granular protoplasm. The protoplasm of the germ-disc is in any case distinguished by its granular character from the thin protoplasmic layer that surrounds the whole egg. The thickness of the disc appears to vary in different cases, so far as can be gathered from the statements of authors. This is perhaps to be accounted for by the various stages of development at which the disc is represented.

A vitelline membrane is apparently never developed in the eggs of the Cephalopoda. The membrane, which is perforated by the micropyle and is often very tough, is secreted by the follicular epithelium (USSOW, VIALLETON) and may therefore be termed the chorion. Between this egg-shell and the surface of the egg there is a somewhat wide space filled with clear albuminous fluid. This enables the embryo to extend considerably within the chorion, which is itself said to be extensible, and thus to admit of further growth on the part of the embryo.

At the animal pole, in the mature egg, there are two polar bodies, one of which has been observed to divide (*Loligo* and *Argonauta*) and give rise to a third body (Fig. 105, *rk*). Such division is said by VIALLETON not to occur in *Sepia*, but the fact that one of the two polar bodies possesses two nuclei shows that these bodies, even in *Sepia*, are quite normal. VIALLETON denies that there is any constant relation between the polar bodies and the first cleavage-plane, but the deviations from such a relation are very rare, and from his own figures and those of other authors this line of cleavage is seen to occur in the closest proximity to the polar bodies.

2. Cleavage and Formation of the Germ-layers.

The *cleavage of the egg is incomplete*, a fact connected with the great abundance of the food-yolk in it and the distribution of this and of the formative yolk; cleavage is at first limited to the germ-disc. The conditions of this process therefore differ essentially from those in the other Mollusca. The principal features of these processes have been known for many years, being described in Kölliker's famous work on the development of the Cephalopoda (No. 24). These investigations which, from the nature of the case are far from being exhaustive, appeared in 1843, and were followed by observations made by Bobretzky (No. 4), Ussow (Nos. 44-46), Vialleton (No. 48) and more recently by Watase (No. 50). We shall here follow the last-named author, dwelling especially on the detailed descriptions of the processes of cleavage in *Loligo Pealii* as given by him and of *Sepia officinalis* as described by Vialleton. So far as is at present known, cleavage seems to take place in the different Cephalopods in very much the same way.

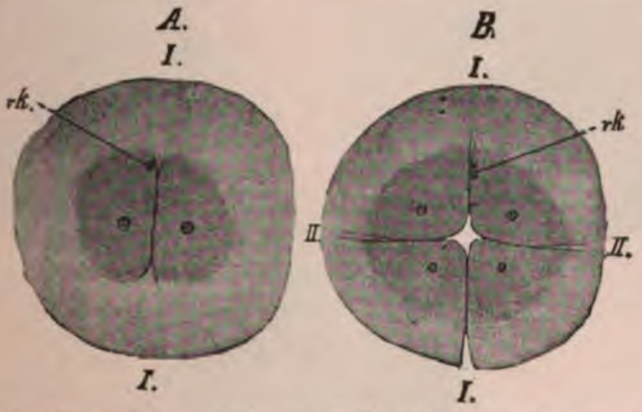

Fig. 107.—Two germ-discs of *Sepia officinalis* showing the first (*I*) and second (*II*) cleavage-planes and the polar bodies (*rk*) (after Vialleton).

The spindle of the first cleavage-nucleus which is preparing for division lies with its longitudinal axis running from right to left (Watase), and therefore in the plane depicted in Fig. 106 *A.** It therefore, curiously enough, does not appear to lie, according to the usually accepted rule, in the direction of the widest extension of the formative protoplasm.

The first line of cleavage runs, in correspondence with the position of the spindle, from before backward, cutting the axis of the spindle at right angles. The first furrow thus lies in the median sagittal

* *Cf.* p. 239 on the bilateral symmetry of the egg before cleavage.

plane of the egg or later embryo, *i.e.*, in the plane given in Fig. 106 *B*. This first furrow (*I*) above which the polar bodies are, as a rule, found (Figs. 107 and 105 *B*, *rk*), starts from the middle part of the germ-disc where the cleavage-nucleus lies and is continued to the periphery of the disc. It cuts deepest in the centre of the disc, dividing the whole of the protoplasm at this point into two segments (Fig. 106 *B*), while, further back and especially beyond the actual disc where it is also prolonged (Figs. 107 and 106 *A*), it forms merely a shallow groove in the formative protoplasm which vanishes towards the equator of the egg. The same is the case with the next furrows which are like the first meridional lines of cleavage (Figs. 107 to 109).

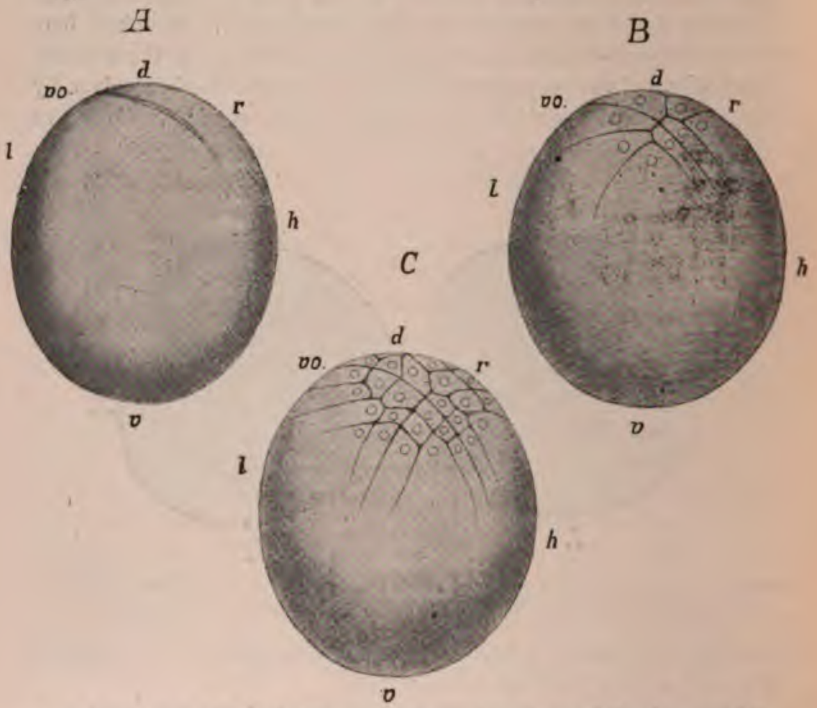

FIG. 108.—Eggs of *Loligo Pealii* representing various stages of the cleavage of the germ-disc, the bilateral symmetry of which can be recognised (after WATASE). *d*, dorsal; *v*, ventral; *vo*, anterior; *h*, posterior; *l*, left; *r*, right.

The second furrow runs at right angles to the first (Fig. 107 *B*, *II*). In consequence of the furrows passing beyond the germ-disc into the thin layer of peripheral protoplasm, these first blastomeres as well as those that follow (Figs. 107 to 109) are not distinctly bounded externally but fade away into the peripheral protoplasm. This is still the case with the peripheral cleavage-cells of later stages (Figs. 108 *C* to 111). VIALLETON defines these as *blastocones* as opposed to the *blastomeres*.

A further step in the cleavage is marked by the breaking up of each of the four segments now present into two new segments (Figs. 109 *A* and 108 *B*). Of these new furrows (*III′* and *III″*) only the anterior ones (*III′*) make an angle of 45° with the median plane and therefore cut the two anterior segments into almost equal halves. The two posterior furrows (*III″*) run somewhat parallel to the median plane (Figs. 108 *B* and 109 *A*), and it thus happens that here, at the posterior part of the germ-disc, two narrow segments bounded by parallel sides are cut off. Through this course of cleavage, concerning

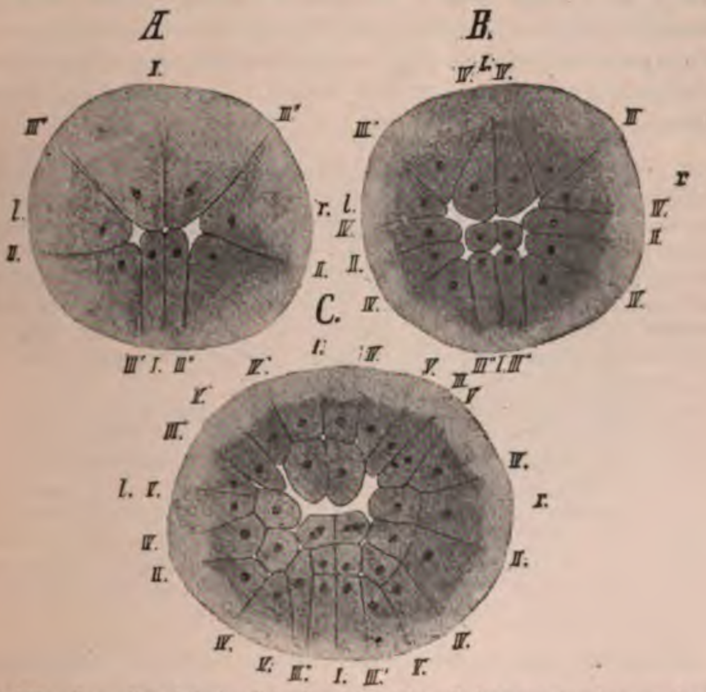

FIG. 109.—Germ-disc of *Sepia officinalis* at the eight-celled stage (*A*) and at two later stages (*B* and *C*) (after VIALLETON). The germ-discs are placed in such a way that the anterior side is directed upwards, and the posterior side downwards. *l*, left side *r*, right side; *I-V*, directions of the first five meridional planes of cleavage.

which observers are agreed, the germ-disc becomes markedly bilateral, a character which is retained in the later stages also (Figs. 108 and 109 *B* and *C*, 110), the two segments mentioned above and the blastomeres that proceed from them retaining their characteristic shape, *i.e.*, retaining their regular position with regard to the median plane, the other cleavage-cells also continuing to be symmetrically arranged with regard to that plane.

The broad segments of the eight-celled stage (Figs. 109 *A* and 108 *B*) are directed forward, the narrow segments, on the contrary, backward (WATASE, USSOW). In this way the bilateral symmetry of the germ-disc after cleavage and the relation to the form of the adult animal are shown still more distinctly than in the egg before cleavage (*cf.* p. 239 and Fig. 106 *A* and *B*).

It should be added that VIALLETON also describes the striking bilateral symmetry of the germ-disc after cleavage which is evident from Fig. 109, but does not assume so definite a symmetry in the shape of the egg before cleavage. It may be more difficult to establish these points with certainty in the spherical egg of *Sepia*. The identity of the median sagittal line of the blastoderm with that of the embryo which is emphasised by USSOW is also apparently assumed by VIALLETON as probable, so that, according to him also, the bilateral symmetry of the germ-disc after cleavage corresponds to that of the embryo.

Since, in consequence of the continuous division of the cells, the shape of the germ-disc is less regular in the later stages (Fig. 111), it is very difficult to prove that the bilateral symmetry of the germ disc passes directly over into that of the embryo: this has, indeed, not yet been exactly proved, so far as we can see. But the bilateral character of the germ-disc found in Cephalopods otherwise very different from one another (*Loligo*, *Sepia*, *Argonauta* *) makes its relation to the form of the embryo appear more than probable, and we must therefore for the present hold to the view of WATASE, although, indeed, this seems to be somewhat conjectural.

As cleavage advances further, an equatorial furrow cuts off from the two narrow posterior segments, towards the middle of the germ-disc, two small blastomeres (Fig. 109 *B*); a continuation of this equatorial furrow cuts off, in *Loligo*, similar blastomeres from the large segments in front (Fig. 109 *C*). In *Sepia*, however, additional meridional furrows appear first and divide these segments into narrower sections (Fig. 109 *B*, *IV* and *V*), after which they become divided by an

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* With regard to *Argonauta*, we have to rely on the statement repeatedly made by USSOW that he saw cleavage taking place, in the forms observed by him, in a similar manner to the above. A confirmation of these statements with respect to the Octopoda is, indeed, very desirable. With reference to the conjectural *Sepiola*, also investigated by USSOW, see the remarks made p. 236.

equatorial furrow. The two narrow posterior segments, so characteristic in shape and position, still remain unaltered even after this division, but two further blastomeres gradually become detached from them by equatorial division and pressed towards the centre (Fig. 109 *C*).

The number of segments increases more and more through the appearance of other furrows, some meridional and others equatorial (Figs. 108 *C*, 110). From the accounts of KÖLLIKER and VIALLETON, it appears that the segments at the middle of the germ-disc are not at first in close contact with each other (Figs. 107 and 109). As cleavage advances, this space in the centre disappears.

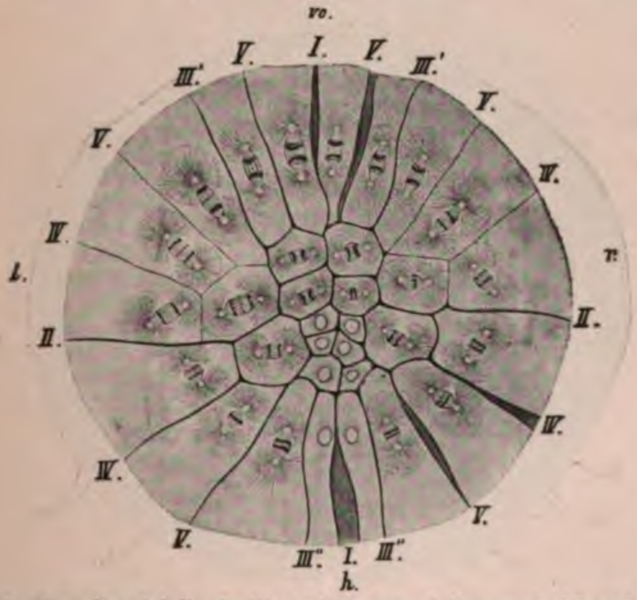

FIG. 110.—Germ-disc of *Loligo Pealii* at a later stage of cleavage, the bilateral symmetry still being evident. The blastomeres and blastocones lie symmetrically to the middle line *I-I* (after WATASE). *ro*, anterior ; *h*, posterior ; *l*, left ; *r*, right ; *I-V*, direction of the first five furrows.

The bilateral symmetry evident up to this time and still visible in somewhat later stages is still further heightened by the division of the cells taking place at somewhat different times, a fact which finds expression in the different conditions of their nuclei. Such a case is represented, for instance, in Fig. 110, in which the posterior cells lying near the middle line contain resting nuclei while the nuclei of all the other cells are found to be dividing. This phenomenon is also frequent in the larger cell-complexes. The almost diagrammatic aspect thus produced corresponds, as WATASE expressly states, to the actual condition of the disc. This is also confirmed by VIALLETON's earlier description (*e.g.*, Figs. 25 and 26, No. 48), in which the various conditions of the nuclei in symmetrical division are given. Further, whole complexes of cells such as the posterior cells or those of a lateral part may advance more rapidly in their division, whilst the division of others may be retarded, this being again visible in the state of their nuclei.

In the germ-disc depicted in Fig. 110 two complexes of segments lying symmetrically and marked off by the planes *II* and *III'*, are distinguished by the fact that the furrows lying between them are less distinct than those in other parts of the germ-disc. These segments are thus shown to be connected together, and have most probably proceeded from the segments bounded by the furrows *II* and *III'* of the stage represented in Fig. 109 *A*, which is passed through in *Loligo* and in *Sepia* in the same way (WATASE). Such a condition also renders the bilateral symmetry specially clear.

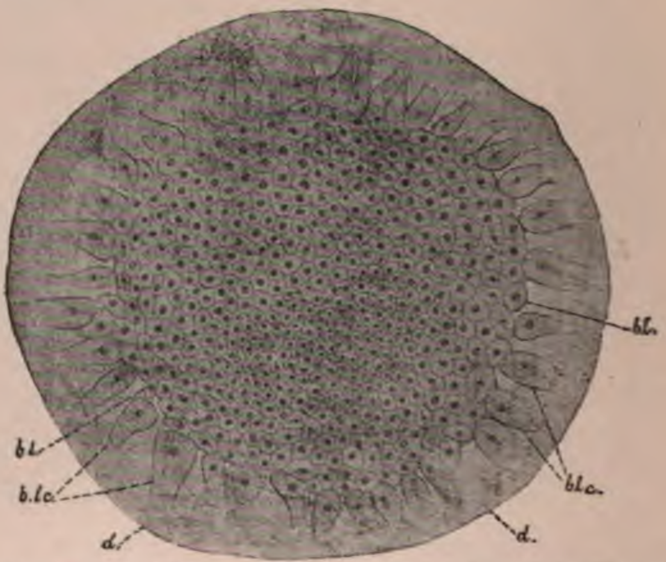

FIG. 111.—Germ-disc of *Sepia officinalis* at a late stage of cleavage (after VIALLETON). *bl*, blastomeres; *blc*, blastocones; *d*, yolk.

Up to this point, the origin of the cells is clearly recognisable in their arrangement; their position with regard to the middle line also is very regular. As cleavage proceeds further, and the blastomeres continually decrease in size, this regularity of form is no longer perceptible in the germ-disc. A certain regularity of position may at first be retained in the peripheral cells, especially in the blastocones, but even this is finally lost as the cells continue to increase in number. The animal pole of the egg now appears covered by a unilaminar "disc"* of polygonal plate-like cells (Fig. 111). The cells at the edge of the disc (blastocones), however, are not polygonal, having no outer edge (Fig. 111, *blc*), but passing over into the remaining mass of formative yolk. In Fig. 111, a certain difference of size can be perceived in the blastomeres, but this apparently cannot yet be related with certainty to the later form of the embryo.

The germ-disc spreads out and increases in size as is evident in Figs. 107-111, at first no doubt chiefly at the expense of the formative yolk in contact with it; only later is the abundant food-yolk utilised as nourishment for the growing embryo.

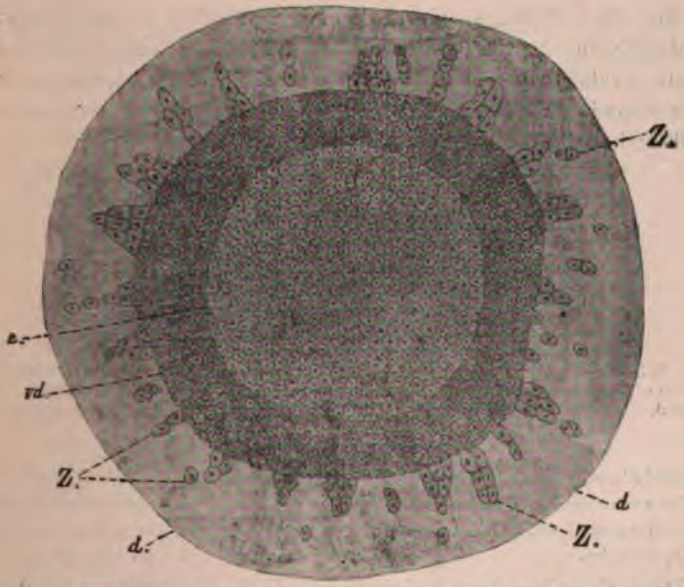

FIG. 112.—Germ-disc of *Sepia officinalis* at the commencement of the formation of the germ-layers (after VIALLETON). *d*, yolk; *e*, unilaminar portion of the germ-disc; *rd*, thickened (multilaminar) portion of the germ-disc (area opaca); *Z*, cells in the act of separating from the germ-disc.

After the cleavage-cells have considerably increased in number, the peripheral cells somewhat change in shape; their free ends narrow and they show a tendency towards becoming detached from the germ-disc (Fig. 112 *Z*). They finally become rounded off and move away from the disc. They are then found scattered round the latter at the surface of the food-yolk. It should here be mentioned that

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* This so-called disc is actually a more or less arched cap.

these cells, according to VIALLETON, wander beneath the cell-material of the germ-disc, there becoming arranged into a connected cell-layer which is said gradually to spread over the whole of the food-yolk. But this brings us to the formation of the germ-layers, and in order to comprehend this, we must first refer to another process and also mention the views which have hitherto prevailed on the subject.

The problem of the formation of the **germ-layers** in the Cephalopoda must be regarded as exceedingly complicated. The fact that the significance of the different cell-layers forming in the germ has not been recognised and that it has not yet been possible satisfactorily to trace back the method of their formation to corresponding processes in the other Molluscs or in the members of other animal groups, is evidently due to the highly modified conditions under which the Cephalopodan egg develops on account of the large amount of food-yolk deposited in it and the marked distinction between the food-yolk and the formative yolk.

FIG. 113.—Longitudinal section through an egg of *Loligo* at the stage in which the edge of the germ-disc becomes thickened (after BOBRETZKY from BALFOUR'S *Text-book*). *c*, peripheral cells; *d* and *ms*, the thickenings of the edge.

The following is a brief statement of the *view hitherto held as to the formation of the germ-layers.* The germ-disc consisting of a single layer of cells which at first covered only a small part of the animal pole of the egg, at a certain time, undergoes at the periphery a thickening of the cell-layer (Fig. 113). The layer which thus arises and which soon gains considerably in size by the active increase in number of its cells, and spreads out beneath the whole of the upper layer of the disc, has been derived either through delamination from the cell-layer already present (METSCHNIKOFF, USSOW) or else through the bending in of this layer (BOBRETZKY).

In contrast to the upper (ectodermal) cell-layer, the massive cell-accumulation has been claimed as chiefly mesodermal although the mid-gut epithelium, which elsewhere is always entodermal in origin, is said to be derived from this accumulation. Beneath the latter which, for the present, we must regard as mesoderm, a new layer is now found which, in its origin and relation to the other layers is of special interest. This is the "*vitelline membrane*" of authors which, starting from the periphery of the germ-disc, no doubt spreads below the disc (and the "mesoderm") as well as over the whole food-yolk, surrounding it as a unilaminar cell-integument.

Ray Lankester assumes, with considerable inherent probability, that the vitelline membrane owes its origin to cells (or nuclei) freely distributed in the yolk, these being at once comparable to the yolk-cells and merocytes in the eggs of the Arthropoda and Vertebrata which are also very rich in yolk. These nuclei are said to shift to the surface, to become surrounded with protoplasm and to unite to form the vitelline membrane.

Other investigators (*e.g.*, Ussow) have been inclined to derive the cells of the vitelline membrane rather from the deeper layers of the germ-disc, and thus from the "mesoderm." In any case, this enveloping membrane of the yolk has the same significance as the vitellophags in the Arthropoda and the Vertebrata. As the terms vitelline membrane and yolk-integument are not specially happy, being commonly used in another sense, we shall give this cellular integument another name (also applied to it by **Ray Lankester**), calling it the yolk-epithelium.

During the formation of the yolk-epithelium, the superficial cell-layer, the ectoderm, has spread over the whole of the food-yolk, which thus, beyond the germ-disc, is covered by two cell-layers. Besides this, there is, as far as the germ-disc extends, the "mesodermal" cell-mass lying between the ectoderm and the yolk-epithelium. The three germ-layers are thus apparently represented, if we may for the time assume the yolk-epithelium to be the entoderm. The difficulty arises, however, that the yolk-epithelium is not found to be connected with the formation of the enteron, which owes its origin rather to the breaking up of the middle layer.

Having now arrived at some comprehension of the germ-layers from which the Cephalopodan body is built up, we must trace the way in which the latter originates, as described in the most recent accounts.

We traced the origin of the germ up to the point at which the animal pole of the egg is covered by a unilaminar plate of polygonal cells, and at which the irregular peripheral cells of this plate begin to detach themselves from it (Fig 112). Almost simultaneously with this process, the thickening of the edge of the plate already mentioned occurs, *i.e.*, the plate here becomes multilaminar through more active increase in number of its cells (Figs. 112, *wd*, and 113). This is the process which was described by earlier authors as the formation (delamination) of the mesoderm.

Before the layer which has formed in this way loses its close connection with the superficial layer of the germ-disc, the cells previously detached from that disc undergo, according to **Vialleton**, an essential alteration. Their cellular character disappears, they are no longer distinctly although irregularly bounded, but now appear as a syncytium, *i.e.*, as nuclei lying in the thin layer of protoplasm that surrounds the food-yolk. There can be no doubt that we have before us, in them, the same nuclei which, according to **Lankester**, give rise to the yolk-epithelium. This last significance actually belongs to these cellular structures which, according to **Vialleton**, arise from the germ-disc; they increase greatly in number and at first unite to form a cell-layer which not only penetrates beneath the disc (Fig. 114 *A-C*, *de*), but also extends beneath the ectoderm over the whole of the yolk. The formation of this yolk-epithelium and the thickening of the edge of the disc which affects the whole of its periphery are clearly illustrated in Fig. 114 *A-C*. These figures show, at the same time, how the yolk-epithelium presses in towards the middle of the disc, as assumed by both VIALLETON and WATASE.

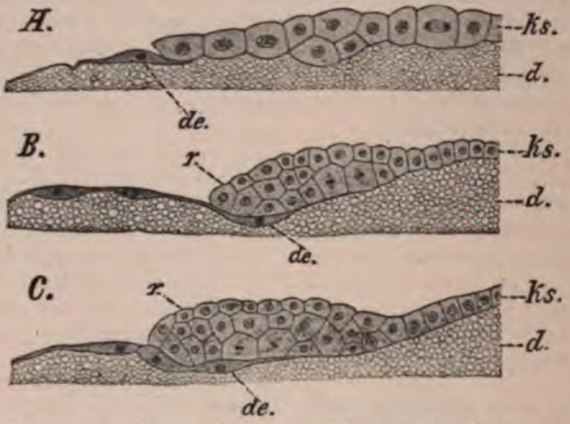

FIG. 114.—Sections through a marginal portion of the germ-disc (*ks*) of *Sepia officinalis* (after VIALLETON). *d*, yolk; *de*, yolk-epithelium; *r*, the thickened edge of the germ-disc.

The separation from the superficial or ectodermal layer of the cell-mass, formed by the thickening of the margin of the disc, gives rise to the layer claimed by earlier authors as the mesoderm. So as to understand the real significance of this layer, we must follow its further fate. Since, to do so, we should have to pass on to somewhat later stages, it will be advisable first to turn our attention to the external changes taking place in the germ-disc or in the whole blastoderm.

3. The Development of the External Form of the Embryo.

While the formation of the yolk-epithelium and the simultaneous thickening of the edge of the germ-disc are taking place, another rapid increase in number of cells occurs in the superficial layer of the disc, and results in the gradual extension of this upper cell-layer over the whole egg. This layer is known as the blastoderm, although this term is not quite correct for, apart from the fact that a differentiation of this layer has already taken place round the animal pole, it is soon followed in its circumcrescence of the egg by a second layer, the yolk-epithelium. Two areas can now be distinguished in the egg. The germ-disc, which forms the embryonic rudiment and which now increases by the thickening of its margins (Figs. 112 and 113) only later extends over the yolk, and a second, the yolk-sac, which at first is bounded by the two cell-layers, the ectoderm and the yolk-epithelium. A middle layer is added to the two cellular integuments which at first cover the yolk-sac, this third layer appearing either simultaneously with them or very soon after them (p. 277).

The extension of the part known as the germ-disc over the yolk varies greatly in different Cephalopods. In the egg of *Sepia*, which is unusually rich in yolk, the embryonic rudiment is represented only by a small cup-shaped region of the spherical egg. Here, therefore, we can best speak of a germ-disc, and the yolk-sac is from the first very large. In other Cephalopods, indeed, so far as is yet known, in the majority, the embryonic rudiment and thus also the so-called germ-disc spread over a much larger portion of the egg (Fig. 115), but as, at a later stage, the embryonic rudiment again draws back more towards the animal pole, a yolk-sac is formed in these cases also (Figs. 116-118). In the Cephalopod investigated by GRENACHER, there is hardly any development of an external yolk-sac (Fig. 126, p. 270) and the yolk-mass which is comparatively small is here found enclosed by the embryonic rudiment at a very early stage. This form would thus have to stand at the end of a series, the starting point of which would be formed by *Sepia* with its unusually large development of yolk. Transitionary forms between *Sepia* and the Cephalopod described but not identified by GRENACHER would be found in such forms as *Loligo*, *Octopus*, *Argonauta*, in which the yolk-sac is more and more reduced and the embryonic rudiment at the first contains the larger part of the yolk.

If we may judge from the large amount of yolk in the egg (p. 237) and the large size of the yolk-sac in older embryos (No. 26) the condition of *Eledone* in this respect may resemble that of *Sepia*.

It should here be mentioned that the cleavage and the formation of the germ-layers in forms which differ somewhat in their later development is, so far as is known, very much alike, and takes place in the way described above.

In forms in which the rudiment of the embryo can early be distinguished from the large yolk-sac, the ectoderm, in the region of the germ-disc consists of cubical cells while in the yolk-region it is formed of flat cells. During its gradual extension over the yolk, the blastoderm becomes *ciliated*. The ciliation may extend over the whole of the blastoderm or may at first be found only at definite parts, appearing, for instance, especially at the growing edge of the blastoderm (Figs. 115 and 116, p. 255). If this ciliation develops strongly and spreads over the whole of the blastoderm which covers the greater part of the yolk, as is the case in *Loligo*, the embryo rotates within the egg-integument, a phenomenon which recalls the free-swimming larvae in other divisions of the Mollusca. In *Argonauta* and *Octopus*, the only movement that takes place in the embryo is the shifting of the pole at which cleavage began away from the micropyle-region to that of the egg-stalk (RAY LANKESTER). Some of the embryos of *Octopus* are, in fact, found lying at the micropyle end of the egg and others at the opposite pole; in the older embryos examined by us the last position was the more frequent.

The ciliation of the embryo either soon disappears, or else is retained for a long time, as, for instance, in *Sepia*, where it is found both in the embryonic region, which is already far developed, and on the yolk-sac. The embryos of *Sepia*, however, notwithstanding this ciliation, do not rotate like those of *Loligo*, a fact evidently due to the large amount of the yolk (KÖLLIKER).

Even before the circumcrescence of the yolk by the blastoderm is completed, indications of the future shape of the Squid appear in the blastoderm or germ-disc (Figs. 115 and 116 *A*). We shall describe the rudiment and further development of the body-form at first in one of those species in which the blastoderm grows round the yolk very early and the embryonic rudiment at first encloses the greater part of the yolk. The ontogeny of such a form, *Loligo Pealii*, was studied in a very thorough manner by BROOKS (No. 7). RAY LANKESTER has also published investigations as to the ontogeny of *Loligo* (No. 30) and representatives of this genus, as has already been mentioned, were studied by earlier zoologists (P. van BENEDEN, No. 3; METSCHNIKOFF, No. 32). Our own investigations, made with very rich material of *Loligo vulgaris*, as well as *Octopus vulgaris* and *Argonauta* have enabled us to supplement the discoveries of earlier observers.

A. Development of the Embryonic Rudiment through its extension over the greater part of the egg with subsequent development of a Yolk-sac.

(a) Loligo.

In the region in which cleavage began, *i.e.*, at the animal pole of the egg, a swelling forms in consequence of the thickening of the cell-layers; this corresponds to the highest point of the dorsal side, as may be seen by a comparison with the later embryonic stages. This swelling, which is the rudiment of the mantle, soon becomes large, and, in the *Loligo* examined by BROOKS, rests like a cap upon the embryo (Fig. 115 *A*), but, in *Loligo vulgaris*, is less distinctly marked at this stage. At the stage depicted in Fig. 115 *A*, the greater part of the circular margin of this cap-like swelling has risen up in the form of a fold from the embryonic body (Figs. 116 and 117, *ma*), the mantle thus forming in the same way as in the other Mollusca. As already mentioned, the swelling lies on the dorsal side and a structure appears here which is comparable with the shell-gland of other Molluscs. This is an ectodermal depression (Fig. 115 *B*, and 116 *A*, *sd*) which at first is shallow but deepens later, and does not flatten out again as in other Molluscs (pp. 34, 92, 126), but becomes a large pouch (Fig. 132, *sd*, p. 282). This peculiarity is connected with the fact that *Loligo* possesses an internal shell.* In those land-Pulmonates that are provided with an internal shell, we also found (p. 187) that such a shell-pouch formed from the shell-gland.

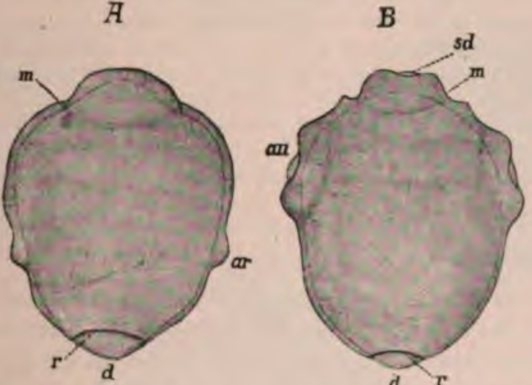

FIG. 115.—Two early stages in the development of *Loligo Pealii* (after BROOKS). *ar*, rudiment of arm; *au*, rudiment of eye; *d*, yolk; *m*, rudiment of mantle; *r*, the ciliated margin of the blastoderm; *sd*, shell-gland.

There is a certain similarity between the swelling which becomes differentiated into the rudiment of the mantle and the shell-gland and the first indications of the eyes which also arise in the form of swellings each carrying a pit-like depression (Fig. 115 *B*). They lie at the two sides of the body below the mantle (Fig. 116 *B*, *au*).

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* *Cf.* p. 287, on the significance of the internal shell of the Cephalopoda.

Other much larger paired prominences are found lower down at the sides of the body in *Loligo Pealii* as the first indications of the arms (Fig. 115 *A*, *ar*, BROOKS). It seems to be specially characteristic of this form that the rudiment of the embryo spreads over a very considerable portion of the egg; in other forms this is not the case, as may be seen by comparing Figs. 115 *A* and 116 *B*.

Orientation of the Cephalopod body. A few words must be said as to the position in which we have represented the embryo, since it is not that formerly ascribed to Cephalopodan embryos, which are generally placed with the head and arms pointing upward. Our orientation of the embryo is in conformity with the now universally accepted view as to morphology of the Cephalopodan body, the ventral side being directed downward as is usual in other animal forms. If we regard the part of the body which lies between the mouth and the anus as the ventral surface, we have to consider by far the greater part of the body as the dorsal surface. That end of the body which, as opposed to the head appears as the posterior end must, according to this view, which was first adopted by LEUCKHART (No. 31), be regarded as the apex of the dorsal surface. In such an assumption, according to which the ventral surface lies in the horizontal line, the embryo ought really to be placed obliquely, but this position was departed from for practical reasons and the head with the arms was simply directed downward. The (ascending) part of the dorsal surface which is directed forward will be called the antero-dorsal, and the (descending) part which is directed backward the postero-dorsal surface. These points are best illustrated by the median sagittal section of an older embryo (Fig. 133, p. 283) which cuts through the mouth and the anus.

In the two ontogenetic stages of *Loligo* (Fig. 115 *A* and *B*) as yet considered, the circumcrescence of the yolk by the blastoderm is not yet completed, although the rudiments of the mantle (*m*), the eyes (*au*) and indications of the arms (*ar*) are present. At a somewhat later stage, the yolk appears completely enclosed by the blastoderm and a number of new structures appear, especially on the ventral surface. Among these, the *oral aperture* deserves special mention; this appears as a transverse oval pit somewhat in front of or between the optic rudiments, this pit arising like those rudiments very early. In Fig. 116 *B* the mouth is seen at a somewhat later stage.

In front of the oral aperture a swelling appears (Fig. 116 *B*, *ar*), which runs right round the embryo, being divided into separate prominences. These latter are the rudiments of the arms which thus appear in *Loligo vulgaris* in a manner somewhat different from that described by BROOKS in the case of *Loligo Pealii*. In the latter, the arms first appear in a very early stage as a pair of prominences, one on each side of the body (Fig. 165 *A*, *ar*), the individual arms appearing later by the breaking up of these. There is no mention of a circular swelling such as foreshadows the development of the arms in *L. vulgaris* (Fig. 116 *B*, *dr*). Further, in *L. vulgaris*, the individual arms develop more distinctly in consecutive order, the first, which appear as button-like prominences, being those which lie next to the funnel. At this period, the rudiments of various other organs are already visible, the most striking of these being the paired *branchial fold* (Fig. 116 *C*, *k*) which lies immediately in front of the mantle

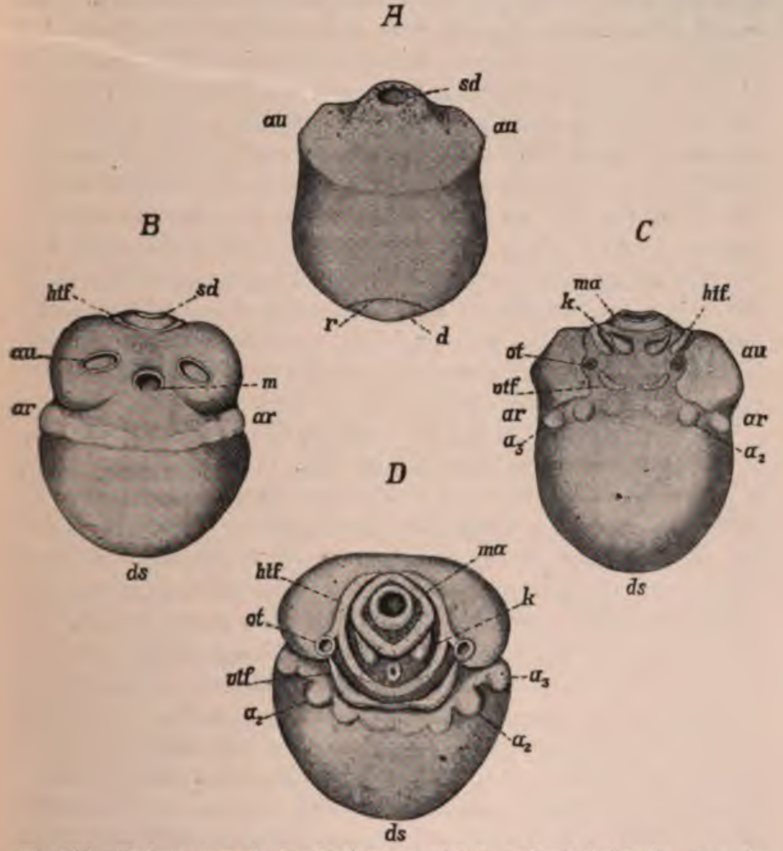

FIG. 116.—Various stages in the development of *Loligo vulgaris* (original). *A*, early stage at which the eyes and the shell-gland appear; *B*, seen from the oral side; *C* and *D*, from the anal side. *D* is seen obliquely from above, and for the sake of clearness, rather more of the yolk-sac is shown in this figure than is actually visible. *ar*, rudiments of the arms; a_1-a_3, first three pairs of arms; *au*, rudiments of eyes, or the swellings that carry the optic pits; *d*, yolk; *ds*, yolk-sac; *htf*, posterior funnel-folds; *k*, gills; between the two branchial prominences lies the rudiment of the anus; *m*, oral aperture; *ma*, mantle; *ot*, otocysts; *r*, edge of the blastoderm; *sd*, shell-gland; *vtf*, anterior funnel-fold.

(*m*). In front of and somewhat laterally to these folds, a rather long paired ridge appears (*C*, *htf*) running at first almost parallel with the branchial folds; it then passes back round the "mantle" at the margin of which it can be seen even on the opposite side of the embryo (*i.e.*, when the embryo is viewed from the oral side, *B*, *htf*). This paired ridge, which appears very early, assists in the formation of the funnel, the chief part of which, however, is derived from a pair of folds which arises somewhat later more anteriorly (*C*, *vtf*). These two pairs of ridges will be distinguished as the posterior (*htf*) and anterior (*vtf*) funnel-folds. At first they are not prominent, and this is still the case with the anterior pair at the stage depicted in Fig. 116 *C*, but they rise up more and more and then become very conspicuous (Fig. 141, *tr*, p. 297). Between the anterior ends of the two posterior folds a slight curved prominence appears, apparently uniting the folds of the two sides (*D*). A very narrow superficial prominence now also connects the anterior folds; this latter fold is the first indication of the complete connection of the two anterior folds which takes place in later stages (Figs. 117 and 118).

When the anterior funnel-folds appear, two vesicular depressions of the surface are seen behind them (Fig. 116 *C*, *ot*; Fig. 141 *A*, p. 297); these are the *otocysts* which, when the posterior funnel-folds shift forward, are found lying near them (Figs. 116 *D* and 117 *A* and *B*). They lie also in the closest proximity to the large swellings which carry the optic pits. These swellings, which are very large even in an early embryonic period (Figs. 116 *A* and 115 *B*, *au*), continue to increase in size, and give the Cephalopodan embryo a highly characteristic appearance at the stage just described and especially in the following stage (Figs. 117 and 118). Only a part of these large projections is yielded by the eyes themselves which first appear on them in the form of depressions (Fig. 116 *B*). These depressions close later, a second depression then forming above the first (primary) optic vesicle, and the lens being secreted inwards at this point (*cf.* Figs. 142 and 143, pp. 298 and 299).

The formative processes hitherto described affect merely a limited part of the egg, for the embryonic rudiment which extended earlier over the larger part of the egg (Fig. 115) has drawn back more towards the animal pole. There is therefore a part entirely free from the rudiments of organs, formed only of the yolk-mass and enclosed by several cellular integuments (Fig. 133, p. 283). This is the yolk-sac, which in later stages is much more distinct, the embryo becoming marked off from it by a constriction (Figs. 117-119). The yolk-sac may contract (KÖLLIKER, METSCHNIKOFF) and, according to RAY LANKESTER, carries out rhythmical movements which are made possible by the fact that its envelopes do not consist, as is generally supposed, merely of a layer of ectodermal cells and another of entodermal cells, but also of a mesodermal layer intercalated between these (Fig. 133) which evidently contains contractile elements. This mesodermal layer, the presence of which in a number of other Cephalopods (*Sepia, Sepiola, Octopus, Argonauta*) has been established through the examination of sections, seems only slightly developed in the forms which have smaller yolk-sacs, but in those with large yolk-sacs as, for instance, *Sepia*, this layer is highly developed, long straight, fibre-like cells here lying one above the other.

It appears that, by the contraction of the yolk-sac, its contents are pressed into the interior of the embryo, extending far into the embryonic rudiment (Figs. 132 and 133, p. 282). A distinction is therefore made between the outer and the inner yolk-sac, the latter extending as far as to the mantle and into the optic swellings. Here also it is enclosed in the "yolk-epithelium" and does not, as has been assumed, stand in direct communication with the intestinal canal of the embryo, so that the yolk-substance can be utilised by the embryo only with the help of the yolk-epithelium. As the yolk-sac extends so far into the embryo, the surfaces are in contact over a very large area, a fact which explains the absorption of the yolk without direct communication existing with the intestine and without the intervention of special vessels. The whole embryo (including the yolk-sac) increases in size during development, the later stages being much larger than the earlier.

Although the great development of the external yolk-sac at first recalls the conditions which prevail in the Vertebrates, some difference is brought about in the Cephalopoda by the fact that the yolk-sac is here devoid of any direct communication with the intestine. Special vessels also seem to be wanting in the yolk-sac, as already mentioned, and it therefore enters far into the embryonic body. Further, the yolk-sac in the Cephalopoda is ventral, its position at the anterior end of the body surrounded by the arms being merely apparent. In reality, it lies ventrally (between the mouth and the anus) and a comparison of Figs. 116 *B* and *D*, and 113, p. 248, shows that the mouth lies at one side of the yolk-sac (the anterior side) and the anus at the other (posterior) side.

It has already been mentioned (p. 254) that the mouth appears as a rudiment at an early embryonic period (Fig. 116 *B*). The anus does not appear until later, sinking in at the middle of a slight prominence, the anal papilla (Fig. 116 *D*); the posterior part of the intestinal canal, starting from this point, runs towards the mantle, its course being externally marked by a slight rising on the surface (Figs. 117 and 118).

In the embryo of *Loligo Pealii*, at a stage intermediate between those depicted in Figs. 116 *B* and *C* we find, in the oral region, starting from the two angles of the mouth and running first to the optic pits and then passing anteriorly, two rows of cilia; these have been compared by BROOKS with the velum, *i.e.*, with the pre-oral ciliated ring of other Molluscan larvae. We should, in this case, have to regard the part including the eyes and the very limited region between them as the pre-oral part of the body.

Among the changes which take place on the dorsal side of the embryo, those that occur in the mantle exercise a special influence on the external form of the animal. The pit representing the shell-gland which, at first, is very wide (Fig. 116, *sd*) narrows with time, and in later stages is only a small aperture (Fig. 117 *B*) and finally closes entirely. The external aperture of the continually deepening pit becomes surrounded by a kind of circumvallation, the surface again sinking in, though not to any great extent (Fig. 116 *D*). The almost rhomboidal swelling (*m*) which surrounds this shallow depression represents the marginal part of the *mantle* which now begins to rise above the rest of the body. At a slightly later stage (Fig. 117 *A*), we find the mantle becoming marked off by the swelling of its margin. The large depression round the circular wall of the shell-gland flattens out again and becomes rounded off like the edge of the mantle itself (Fig. 117 *B*). Two pointed prominences, the rudiments of the fins, are visible upon it (Fig. 117 *A* and *B*).

Another change has taken place in the mantle-region on the dorsal side, the posterior funnel-folds having shifted more towards the middle line, there ending in a kind of plate which is the rudiment of the *nuchal cartilage* (Fig. 117 *B*). The posterior funnel-folds are thus recognisable as the broad muscle-bands (the so-called nuchal muscles) which even in the adult appear as lateral continuations of the funnel. They run to the nuchal cartilage and become attached to it.

In tracing the further development of the funnel, we find that the anterior folds form the essential factor in determining the alterations that take place in its principal parts. These anterior folds, which soon rise much higher than the posterior folds, become united in the ventral middle line (Figs. 116-117). At first they form together merely a slightly undulating line (Fig. 117 *A*), but their lateral ends soon bend back further (Fig. 117 *B*) and as the folds at the same time swell up more, the later form of the funnel becomes indicated (Fig. 118 *A* and *B*). At the same time, the posterior funnel-folds become modified in shape, now appearing forked at the point where they come into contact with the anterior folds (Fig. 118 *A*). This is caused by the rise of a new fold at this point, which runs towards the mantle. This is, like the other folds, an expression of the greater growth of the mesodermal tissue and represents a part of the retractors of the funnel (musc. depressores infundibuli).

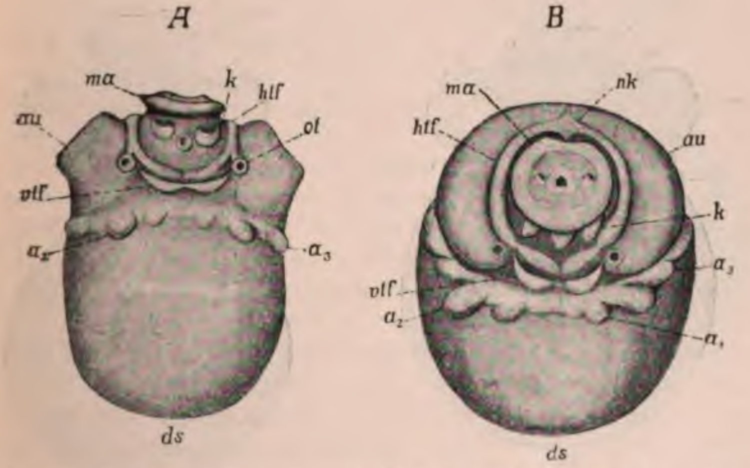

FIG. 117.—Two stages in the development of *Loligo vulgaris* (original). *A*, seen from the anal or funnel-side; *B*, obliquely from above. (The remarks made on Fig. 116 *D* apply to *B*). a_1—a_3, first three pairs of arms; *au*, optic swelling; *ds*, yolk-sac; *htf*, posterior funnel-fold; *k*, branchial folds or gills; *ma*, mantle; *nk*, nuchal cartilage; *ot*, otocysts; *vtf*, anterior funnel-fold. The circular fold out of which the arm-rudiments arise can still be recognised, especially in *A*. In *B*, the long prominences indicating a pair of arms (lying behind a_3) still form part of it. The funnel-folds (*vtf* and *htf*) meet in the middle line. Between the two gills (*k*) lies the unpaired anal papilla; on the mantle, are the two prominences representing the rudiments of the fins (*cf.* Fig. 118, *fl*).

In the adult, these muscles are attached to the funnel laterally, some of them running further forward to end within the funnel and in its dorsal parts. This is perhaps indicated even in the embryo (Figs. 117 and 118) by the course of the anterior folds, but we have hitherto been unable to make any careful examination of the fate of these raised parts which anteriorly become connected with the posterior funnel-folds, and must therefore refrain from conjectures as to their significance.

It is evident from the above that not only do the anterior funnel-folds from the two sides unite to form a common fold but that the posterior folds also fuse with the anterior. At the point of junction of these two sets of ridges, the posterior folds appear as a mere prolongation backward of the anterior (Figs. 118 and 119). By this process and by the simultaneous extension of the anterior folds, the funnel has already approximated closely to its final shape (Fig. 119). The free edges of the two anterior folds become apposed, but do not as yet fuse (Figs. 141, *tr*, p. 297 and 143, *ff*, p. 299) and the funnel has thus attained the stage which is retained throughout life in *Nautilus*. In this primitive Cephalopod the funnel, though acting as a tube, is actually formed by the bending round posteriorly and the overlapping of two distinct folds.

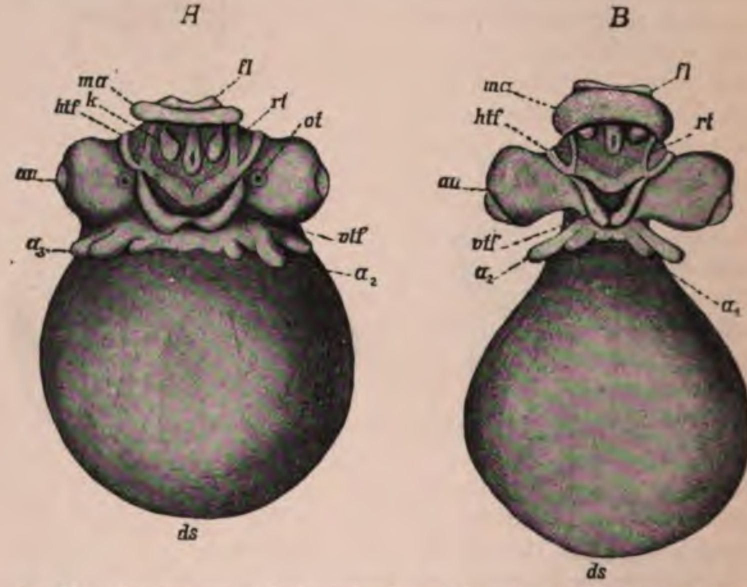

FIG. 118.—Two embryos of *Loligo vulgaris*, seen from the posterior or funnel-side (original). a_1-a_3, arms; *au*, eyes; *ds*, yolk-sac; *fl*, fins; *htf*, posterior funnel-folds; *k*, gills; *ma*, mantle; *ot*, otocysts; *rt*, retractor of the funnel; *vtf*, anterior funnel-folds. Between the two gills (*k*) is the anal papilla.

As development advances, the two half-tubes composing the funnel fuse in the middle line (Fig. 120 *A*); the exhalent aperture, however, which could already be recognised at an early stage, being retained. The formation of the funnel is thus completed in all essential points. Laterally, the posterior funnel-folds run to the nuchal cartilage (Fig.

120 *A* and *B*, *hm*). They continue to increase in breadth and represent the nuchal muscles (musculi collàres) which, together with the retractors (Fig. 120 *A*, *rt*) that run backward direct to the mantle, form a kind of lateral chambers, not communicating with the actual funnel, *i.e.*, with the middle funnel-cavity. The *funnel-valve* appears in the anterior part of the funnel, *i.e.*, in the wall which is in contact with the body, as an unpaired fold (Brooks).

While the changes just described have taken place in the funnel, the mantle also has undergone repeated modifications of form. It now rests like a cap on the end of the body (Fig. 118, *ma*) as its edge has extended forward further and has become raised from the body. The further growth of this overhanging margin leads to the formation of the mantle-cavity, into which the gills are drawn, these not having essentially changed their shape (Fig. 118, *k*). The increase in size of the mantle is now the chief feature of its development (Figs. 118-121). The fins at its upper end also increase in size. The optic swellings have become very large. It has already been pointed out that in this way the embryo acquires a specially characteristic appearance which it retains in later stages also (Figs. 120 *A* and *B*).

Fig. 119.—Older embryo of *Loligo vulgaris*, seen from the posterior or funnel-side (original). *tr*, funnel. The rest of the lettering as in Fig. 118. The gills lie partly hidden by the overhanging margin of the mantle; between them is the anal papilla.

We have so far mentioned only the first stage in the *rise of the arms* (p. 254). From the circular fold which runs round the whole embryo at the boundary line between the embryonic rudiment and the yolk-sac (Fig. 116 *B*, *ar*), the separate prominences which represent the arms become differentiated, each first appearing as a long swelling which soon assumes a button-like form (Fig. 116 *B-D*). The first pairs of arms to become distinct are the two that lie nearest the funnel, the second pair of arms, however, in *Loligo* attains a far higher degree of development than the first and than the one that follows it, a distinction which is retained in later stages. This pair of arms, the prehensile arms, is soon followed by a third pair (Fig. 116 *C* and *D*). When the first three pairs have become distinctly differentiated as button-like prominences, the other two which lie nearest the mouth are still mere transverse swellings; the first of these to become distinct is the fourth, then follows the fifth.* As the embryo continues to develop, the arms grow in length, and the sucking discs appear on them. The change of shape undergone by

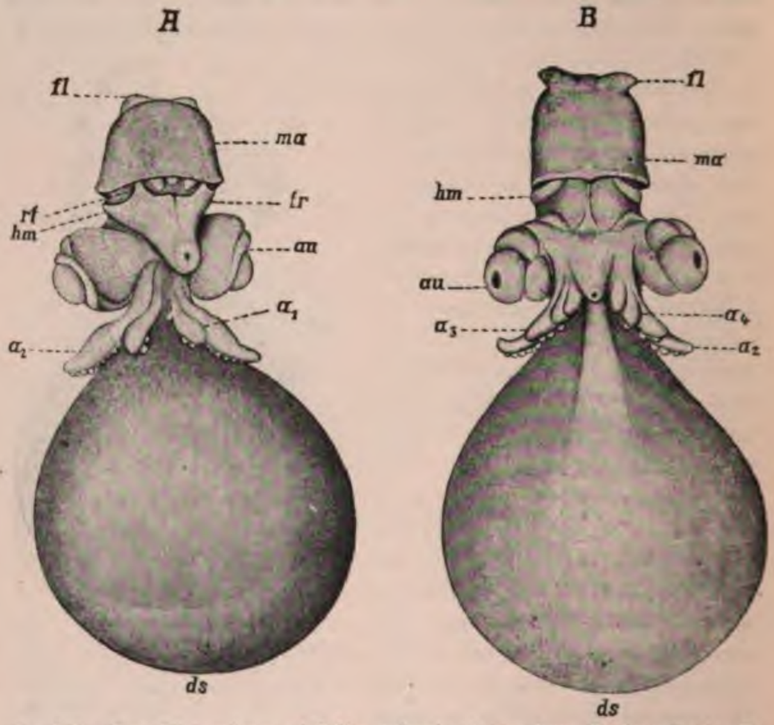

FIG. 120.—Two older embryos of *Loligo vulgaris*, *A*, seen from the funnel side, *B* from the oral side (original). a_1-a_4, arms; *au*, eyes; *ds*, yolk-sac; *fl*, fins; *hm*, nuchal muscle; *ma*, mantle; *rt*, retractor of the funnel (*tr*). In *A*, the gills project below the mantle; between them is the anal papilla.

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* In speaking here of the first to fifth pairs of arms, they are numbered according to the order in which they originate in the embryo, not according to the order sometimes adopted (for which we can see no good reason) in which, on the contrary, the pair of arms which lies furthest dorsally counts as the first and the most ventral pair as the fourth, the prehensile arms being reckoned separately, evidently on account of their different development, which seemed to give them a claim to a special position.

the embryo in rising up from the yolk produces a change in the position of the arms which shift from the funnel-side more towards the oral side (Fig. 117-120).

In *Loligo Pealii*, the three pairs of arms depicted in Fig. 115, *ar*, develop first and only when these have become differentiated, does the pair which lies nearest the funnel appear (BROOKS). The fifth pair seems to form very late. The same is said to be the case in GRENACHER's Cephalopodan embryo (p. 271).

The second pair of arms, the prehensile arms, grow with special rapidity, outstripping in development not only the first but the other arms also (Figs. 119-121); external investigation, however, reveals no special peculiarity in the rudiments of these arms. This corresponds with the adult condition in other more primitive Decapods (*Ommastrephes*). Only later, when the embryo hatches, are the prehensile arms distinguished by the fact that the basal part is free from suckers, this part lying in a depression. In younger embryonic stages and even in older stages (Fig. 120 *A* and *B*), five pairs of arms can easily be made out, but the fifth develops much less than the rest, so that in later stages (*e.g.*, in that depicted in Fig. 121) it appears merely as two small cones which can hardly be made out. This fact no doubt led to the assumption that only four pairs of arms appeared as rudiments in the embryo, the fifth forming later.

FIG. 121.—Older emoryo of *Loligo vulgaris*, seen from the posterior or funnel-side (original). *a*, the arms of the second pair and between them the first pair of arms; *au*, eyes; *ds*, yolk-sac; *fl*, fins; *k*, gills; between the two gills is the anal papilla; *tr*, funnel. The embryo is already covered with chromatophores.

Since the yolk-sac occupies a ventral position (between the mouth and the anus), the same position must be ascribed to the arms that surround it. This is especially noticeable in the younger stages (Fig. 116 *B-D*), although it can also be recognised in older embryos (Fig. 120 *A* and *B*). The mouth here still lies outside of the circle of arms, but soon shifts within it (Fig. 120 *B*) or rather is surrounded by the arms as they shift dorsally. This occurs simultaneously with the degeneration of the yolk-sac that now begins. The mouth finally occupies the place of the yolk-sac, *i.e.*, is surrounded by the arms, a position which, as is well-known, is occupied by it in the adult.

When the yolk-sac begins to degenerate, *i.e.*, in the last stages of development, the embryo approaches ever nearer the form of the adult (Fig. 121). The arms are still rather small, the eyes still remind us of their former condition, but the funnel, the mantle, the gills and the anal papilla have almost attained their final form. The chromatophores have already formed and they also give the embryo a characteristic appearance more like that of the adult. The *chromatophores* appear first on the mantle on the posterior (postero-dorsal) side and are only somewhat later found on the arms and on the head. When the embryo leaves the egg, the external yolk-sac has, to a great extent, disappeared.

(b) Octopus.

Although, systematically, *Octopus* is far removed from *Loligo*, the course of development of the two forms is very similar. The embryonic rudiment extends at first over a larger part of the egg and later withdraws again more towards the animal pole, just as in *Loligo*. The *shell-gland* appears very early, at a time when the blastoderm has not yet grown round the yolk, as a depression at the animal pole. This fact is of special interest, because *Octopus*, like most other Octopoda (*Cirrhoteuthis* perhaps forming an exception?) has no internal shell. The shell-gland in this case, therefore, has the significance of a vestigial organ. At somewhat later stages, when the rudiments of the external organs appear, it can be recognised as a distinct depression at the apex of the rudiment of the mantle, and even later is perceptible (Fig. 122 *A*). According to RAY LANKESTER, it disappears without having closed.

At a stage somewhat earlier than that illustrated in Fig. 122 *A*, a pair of small prominences appear on the mantle, resembling, in shape and position, the fins described in *Loligo*. Indeed, the aspect of the mantle-rudiment in *Octopus* in the younger stages closely resembles that of the mantle-rudiment of *Loligo*. The prominences are retained for some time; they can be recognised in Fig. 122 *A* and *B*, and in later stages are still present, but, finally, they decrease in size and altogether disappear. They cannot be regarded as anything else than the vestiges of a pair of fins, and must be considered as an indication that the Octopoda originally carried fins, like the Decapoda. This fact affords further support to the view which in itself is probable that the Octopoda must be regarded as derived and the Decapoda as primitive forms. The conjecture as to the nature of these prominences is further rendered probable by the fact that fins occur in some adult Octopoda (*Octopus membranaceus*, *Pinnoctopus*, *Cirrhoteuthis*).

The oral aperture appears in *Octopus* at a very early stage and soon takes the shape of a semicircular groove bordering a swelling. The appearance of the rudiments that lie on the ventral side closely resembles that described for *Loligo* and will best be understood by a study of Fig. 122 *A* and *B*, and by comparing this figure with the illustrations of the *Loligo* embryo given in Figs. 117 and 118.

It should be noted that the funnel forms, in the Octopoda, in the same complicated way as in *Loligo* and the other Decapods. A paired posterior fold appears and, in the course of development, unites with an anterior fold which is also paired to form the funnel and its lateral parts (Figs. 122 and 123, *htf*, *vtf* and *vt*).

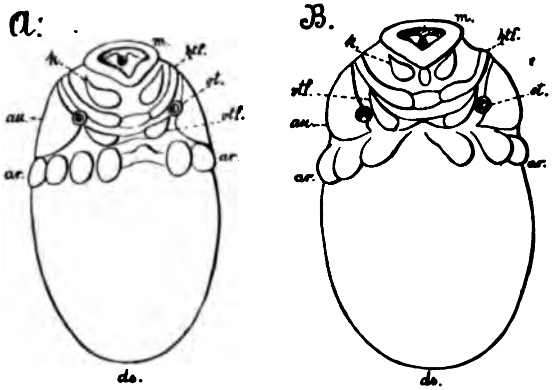

FIG. 122. – Two embryos of *Octopus vulgaris* at different ages, seen from the posterior side (original). *ar*, arms ; *au*, optic swellings ; *ds*, yolk-sac ; *htf*, posterior funnel-fold ; *k*, gills ; *m*, mantle ; *ot*, otocysts ; *vtf*, anterior funnel-fold.

In comparing *Loligo* and *Octopus*, we are struck by the fact that, in the latter, the separate organs appear very early, but do not develop further with corresponding rapidity, so that, as contrasted with organs that appear later, their development is retarded. This peculiarity was pointed out by **Brooks** (No. 7), in comparing the form examined by him (*Loligo Pealii*) with **Grenacher's** Cephalopodan embryo. In *Octopus*, for instance, the rudiments of the arms appear early, their number being complete even earlier than the stage depicted in Fig. 122 *A*, but they then develop very slowly. With regard to the order in which the arms appear, this seemed to us to be the same as in *Loligo*, *i.e.*, from the rudiment of the funnel towards the mouth. Two pairs of arms appear as slight swellings in front of the optic prominences; a third and a fourth pair are soon added; this latter pair, *i.e.*, the one near the mouth, the most dorsal of the arms, is always the least developed. The pairs of arms appear very quickly one after the other, so that the above statements are made with a certain reserve.

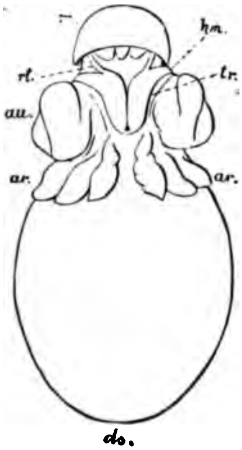

Fig. 123.—Older embryo of *Octopus*, seen from the funnel-side (original). *ar*. arms; *av*, optic swellings; *hm*, nuchal muscle; *rt*, retractor muscle of the funnel (*tr*).

In the development of *Octopus*, it is of special interest that the yolk-sac is somewhat less developed than in *Loligo*, as is evident from a comparison of Figs. 122 and 123 with Figs. 118 and 119, p. 261. In earlier stages, this difference is less marked; later, on the contrary, it is still more noticeable. In itself, this comparatively slight difference in the development of *Octopus* would be hardly worthy of note, but it affords a transition to those forms in which the yolk-sac develops still less (*Argonauta*) or, indeed, is almost altogether wanting (GRENACHER'S Cephalopod).

(c) Argonauta.

Argonauta, in its development, also closely agrees with the forms hitherto considered. Special interest attaches here to the appearance of the shell-gland at an early embryonic stage and to its retention for a long period, although the shell of the adult does not develop in it, having another origin and significance, as will be shown later (p. 294). The *shell-gland*, as in *Octopus*, is said gradually to flatten out again (RAY LANKESTER, No. 29; USSOW, No. 44, p. 352), and the Argonaut shell forms after embryonic life is over, as was shown by KÖLLIKER in opposition to former statements (Nos. 24, 1 and 9).

The embryos of *Argonauta* show, at various stages, in the rise of the different organs, great similarity with the Cephalopods already considered (*cf.*, the late stage depicted in Fig. 124) especially with the embryos of *Octopus* and *Loligo* of about the same age (Figs. 123 and 119), but the small size of the yolk-sac seems to determine a more compact form of body.

As in *Loligo*, the embryonic rudiment at first extends over a large part of the egg, but becomes at a later stage more concentrated, withdrawing more to the animal pole, and rising from the yolk, thus giving origin to an external yolk-sac which, however, is not nearly so large as in cases already mentioned (Fig. 124). As development advances, this yolk-sac decreases in size, and, in mature embryos, at hatching, there is not any trace of it.

FIG. 124. — Embryo of *Argonauta argo*, with funnel still incompletely developed (original). *ar*, arms; *au*, eyes; *ds*, yolk-sac; *hm*, nuchal muscle; *m*, mantle; *tr*, funnel.

The differences in size and shape of body existing between the two sexes of *Argonauta*, also find their first expression during post-embryonic life. No sexual dimorphism could be observed in any of the many embryos examined by us.* This applies also to the striking hectocotylised arm of the male, which in other Cephalopods also, becomes differentiated only as sexual maturity is gradually attained. Mature embryos of *Octopus*, *Loligo* and *Sepia* show no sign of this modification; this is the less strange as the arms are still far from being fully developed in these embryos.

B. Development without actual yolk-sac.

The description of the above forms may best be followed by that of the Cephalopod observed by GRENACHER (No. 14), a form the systematic position of which has not yet been determined. It probably, however, belongs to the large division of the Oigopsida, perhaps to the genus *Teuthis*. STEENSTRUP (No. 42) believes that it resembles *Ommastrephes* (see also p. 236). The eggs, unlike those of the forms hitherto mentioned, are spherical and distinguished by the violet colour of the yolk which elsewhere is yellow. They are about 1 mm. in diameter, and thus much smaller than those of *Argonauta*. This is a remarkable fact since, judging from the quantity of spawn and the number of eggs contained in it (p. 236), this Cephalopod is most probably a large animal. The small size of the eggs, and the small quantity of yolk contained in them afford an indication of the manner of development of this form, which is marked by an almost entire absence of the external yolk-sac.

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* The number of eggs laid by the female Argonaut is very large, so that a considerable number of embryos are to be found in the egg-bunches within the shell. The eggs to which we had access belonged to various females and were at different stages of development, and, although no fully mature embryos were found by us, we were justified in forming the above conclusion from those in a late stage of development.

Since, in GRENACHER'S Cephalopod, we apparently have a comparatively primitive form, it has been thought that paucity of yolk might be regarded as the primitive condition. So long as the first ontogenetic processes are not known, no decided opinion can be given on this point, but the development of this form in general shows such close similarity to that of other Cephalopods that a reduction of the yolk seems more probable. We may also regard the early appearance of the chromatophores which elsewhere appear late as secondary (see below). Although the Oigopsida are very primitive forms among the Cephalopods now living (*Nautilus* and *Spirula* excepted) they themselves appear highly specialised when fossil Cephalopods are taken into account. There is a great gap between them and the forms with chambered shell, and yet *Nautilus* even has large eggs rich in yolk, as is shown by examination of the ovary (OWEN, No. 33). [The egg-capsule measures 45 × 16 mm. and the actual egg is 17 mm. long (WILLEY, No. IV.).—ED.]

The earliest development seems to agree with that of the other Cephalopods. A blastoderm forms which, however, in this case very soon grows round the yolk. Even before distinct rudiments of organs can be seen on the blastoderm, it has grown almost to the vegetative pole, leaving only a small portion of the yolk free (Fig. 125). The growing edge of the blastoderm is beset with cilia, but these do not lead to any rotation of the embryo. The first indication of organs is the appearance at the animal pole of star-like cells containing red pigment, which rapidly increase in number (Fig. 125, *ch*). These are the *chromatophores* which thus form, not as in other Cephalopods, towards the end of the embryonic period (Fig. 121), but, strange to say, arise quite at the commencement of that period. They soon spread over the upper third of the blastoderm, at the edge of which a circular fold now forms. The upper pigmented part of the embryo thus rises from the rest of the body as the *rudiment of the mantle*, this process beginning at the postero-dorsal surface, *i.e.*, in the neighbourhood of the future anal pit, and proceeding towards the antero-dorsal surface. During these differentiations, the originally spherical embryo becomes cylindrical. In Fig. 126 *A* and *B* the

FIG. 125.— Young embryo of GRENACHER'S Cephalopod at the stage in which the blastoderm grows round the yolk (after GRENACHER). *ch*, chromatophores; *d*, yolk; *r*, margin of the blastoderm.

rudiment of the mantle is seen in a later stage thickly covered with chromatophores.

It is curious that GRENACHER makes no mention of a shell-gland, as an internal shell usually occurs in the Oigopsida, and a shell-gland even appears in those Cephalopods which are devoid of the internal shell (*Octopus*, *Argonauta*). The region of the animal pole in general, in GRENACHER'S Cephalopod, differs from the same region in the other Cephalopods considered by us, and it appears probable that the intermediate stages were missed in consequence of the far from favourable conditions under which the observations were carried out. The mantle is rounded at its end, and the fins which, in *Loligo*, form so early, appear only at a later stage.

We have already, in a *Loligo*, seen the arms arise not far from the vegetative pole (Fig. 115 *A*, p. 253). In GRENACHER'S embryo, the rudiments of the first two pairs of arms appear as fold-like prominences directly at the edge of the blastoderm which has not yet completely closed, *i.e.*, quite near the vegetative pole, so that at this stage and still more at a somewhat later stage, when the circumcrescence of the yolk by the blastoderm is completed, the whole yolk with the exception of a small portion is enclosed in the embryonic rudiment. But here also, later, a process takes place similar to that described for some other Cephalopods, *viz.*, the embryonic rudiment withdraws to some extent from the vegetative pole (Fig. 126 *A*) a process which, in the cases before mentioned, led to the formation of a yolk-sac (Figs. 115 and 116, p. 253). Here, indeed, this takes place only to an inconsiderable degree, and thus gives rise to the mere indication of a yolk-sac (Fig. 126 *A* and *B*, *ds*) which, however, becomes somewhat more distinct later (Fig. 127, *ds*). At the time when this swelling, which corresponds to the yolk-sac of other Cephalopods, forms, and in consequence of it, the aperture of the blastoderm, which is still present, undergoes displacement, being pressed further away from the vegetative pole towards the so-called nuchal region. This part is for a long time marked by a ciliated area lying somewhat in front of the disappearing aperture (Fig. 126, *w*). Anteriorly, the oral aperture (*m*) appears as an ectodermal invagination.

When considering the ontogeny of *Loligo*, a ciliated area lying near the mouth was mentioned (p. 258). The ciliation occurring here in GRENACHER'S Cephalopod in the oral region recalls that area which was compared by BROOKS to the velum of other Molluscs. A comparison of the two is, however, inadmissible, since the ciliated area in the present case lies in front of or below the arms, as is evident from Fig. 126 *A*, and still more from GRENACHER'S figures of later stages. The ciliation thus belongs to the region of the yolk-sac and consequently lies ventrally. In *Loligo*, on the contrary, it is found between the rudiments of the arms and the eyes.

The position of the oral invagination in the neighbourhood of the former aperture of the blastoderm might appear remarkable (Fig. 126 *A*), but may possibly be accidental, being caused by the great reduction of the yolk-sac. We shall have to point out later that we are inclined to regard the slight development of a yolk-sac in GRENACHER's Cephalopod as a secondary phenomenon.

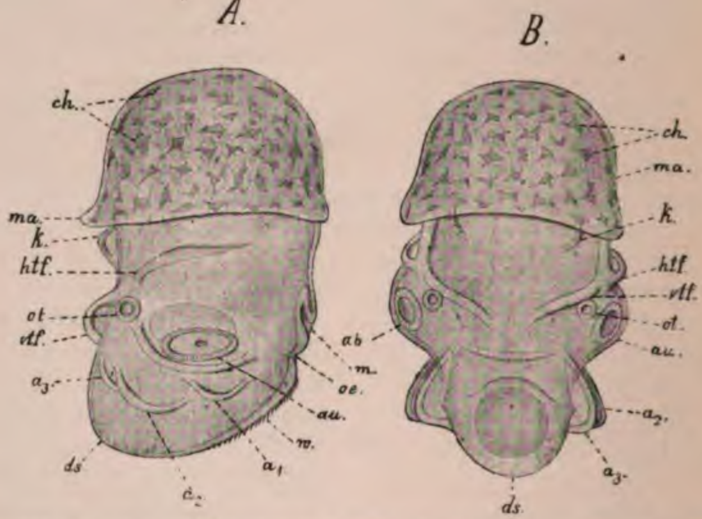

FIG. 126.—Two stages of GRENACHER's Cephalopod embryo. *A*, seen from the side *B*, from the ventral and postero-dorsal surface (after GRENACHER). a_1-a_3, arms; *au* rudiment of eye; *ab*, optic vesicle; *ch*, chromatophores; *ds*, yolk-sac; *htf*, posterior funnel-fold; *k*, rudiments of gill; *m*, mouth; *ma*, mantle; *oe*, aperture of the blastoderm; *ot*, otocyst; *vtf*, anterior funnel-fold; *w*, ciliated area.

About the time when the rudiments of the arms appear, a large swelling arises behind them on either side of the embryo, in connection with a depression, the rudiment of the eyes (Fig. 126 *A*, *au*). Soon after, the rudiment of the funnel appears in the form of two pairs of folds. The anterior, slightly undulating folds are inclined one to the other (Fig. 126 *B*). They unite later, in the way already described for *Loligo*, to form the funnel (Fig. 127). The posterior folds, which were originally distinct from the anterior though running in the same longitudinal direction, fuse later with these latter, and in any case yield the lateral portions of the funnel, that is, the so-called nuchal muscles (Figs. 126 *B* and 127). At the points where the anterior and posterior folds fuse, a process runs inward which gives rise to the retractor of the funnel. We thus see here again that the funnel forms in much the same way in other forms.

The course of development of the other organs, such as the gills and the intestine, the otocysts and the eyes, can be made out by reference to Figs. 126 and 127, as they resemble, in their origin and development, the similar structures in *Loligo*. The *arms*, on the contrary, must be referred to more in detail, since, according to GRENACHER's statement, they appear in an order somewhat different from that seen in *Loligo vulgaris*. We have already mentioned two pairs of arms at an earlier stage, and there was some uncertainty as to the presence of a third pair, which in any case soon follows the others. Of these pairs of arms, those which appeared first are said to be the more dorsal in position. At the base of the subsequent third pair a fourth grows out, diverging to a certain extent from it. A fifth pair has not been observed in this Cephalopod, but probably develops later.

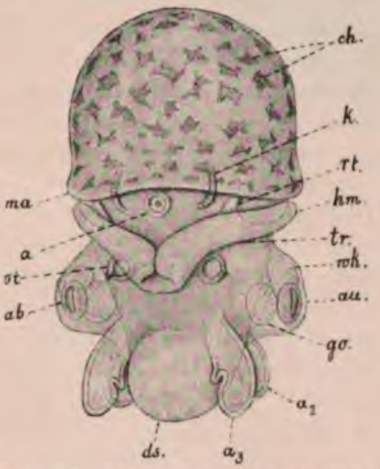

FIG. 127.—Older stage of GRENACHER's Cephalopod embryo, seen obliquely from the anal side (after GRENACHER). *a*, anus; a_2 and a_3, rudiments of the second and the third pairs of arms; on the latter are seen bulgings which perhaps lead to the formation of the fourth pair; *ab*, optic vesicle; *au*, rudiment of eye; *ch*, chromatophores: *ds*, yolk-sac; *go*, optic ganglion; *hm*, nuchal (collar-) muscle; lateral portion of the funnel; *k*, rudiment of gill; *ma*, mantle; *ot*, otocyst; *rt*, retractor of the funnel; *tr*, funnel; *wk*, "white body".

If GRENACHER is correct in his statements, the arms, in this Cephalopod, appear in an order the reverse of that which prevails in *Loligo* and *Sepia*. A certain departure from the accepted order was also found in the *Loligo* examined by BROOKS (p. 263). We must await further observations, made for preference on related forms, to solve this difficulty. We shall not attempt to describe the arms of this Cephalopod embryo, although the difference in size between them and those of the embryos of *Loligo* in younger stages (p. 261) seems to demand examination, and the different result as to the order of appearance of the arms in GRENACHER's embryo might thus be attained.

In consequence of the small amount of yolk they contain, the embryos soon resemble the adult in the shape of the body more closely than do those of other Cephalopods. The embryo depicted in

Fig. 127, for instance, resembles the adult more than do embryos of *Loligo* and *Sepia* at somewhat corresponding stages (Fig. 119, p. 261, and Fig. 129 *C*, p. 275). By the further growth of the mantle, the appearance on it of fins, as well as the closing of the funnel which is grown over by the mantle and, like the gills, partly enclosed in the mantle-cavity, the embryo approaches the adult form more and more. The eyes which, in this embryo, are very large, also decrease in size, as their internal structure gradually develops. The arms grow and become covered with suckers. The swelling between them (the external yolk-sac) gradually disappears, and the internal yolk-sac, which here also fills a large part of the embryo, is gradually but very slowly absorbed. The oral aperture, in consequence of this process of growth, shifts downward to between the arms, to take up its final position at the anterior end of the body. At about this stage, the embryo breaks through the egg-envelopes and, during the period of pelagic life which now ensues, assumes the final form of the adult.

C. Development through the formation of the Embryonic Rudiment on a limited portion of the egg with simultaneous development of a large Yolk-sac.

The type of development now to be considered has only been observed in the egg of *Sepia* (Kölliker, No. 24 ; Vialleton, No. 48), but may occur in other specially large Cephalopodan eggs as well. This form of development is brought about by the abundance of yolk in the egg, and is characterised by the restriction of the embryonic rudiment to a small, cap-like portion of the egg (the germ-disc), the rest of the yolk being enclosed merely by the thin cell-integuments already mentioned (ectoderm, mesoderm and entoderm, p. 257). There is a further difference between this form of development and that in which the embryonic rudiment extends over a considerable part of the egg, inasmuch as the embryo appears on a surface only slightly arched (Fig. 128 *A* and *B*). This makes the processes of development somewhat more difficult to understand, but we are assisted in following them by comparison with the same processes in eggs less rich in yolk.

The first indications of the embryo on the germ-disc take the form of various prominences and swellings which soon show bilateral symmetry in their shape and arrangement. This symmetry most probably corresponds to that already evident in the germ-disc during cleavage (see Fig. 109, and Fig. 110, of *Loligo*). The swellings of the surface which at first are very vague and indistinct, become gradually clearer and can soon be recognised as the rudiments of the different organs, one of the first to grow distinct being a circular depression at the centre of the germ-disc. This becomes surrounded with a flat wall which is more or less pentagonal with rounded corners (Fig. 128 *A*, *sd*, and *ma*). This represents the rudiments of the *shell-gland* and the *mantle*, in the early appearance of which *Sepia* resembles the other Cephalopods already described.

Two broad prominences which, at an earlier stage, occupy almost half of the germ-disc, may, following **Kölliker**, be described as *cephalic lobes*. A large pit appearing on each of them identifies them as those highly developed structures which, in other Cephalopods, we regarded as the optic swellings. In Fig. 128 *A*, they are represented at a somewhat later stage (*kl*). The divergent character of the development of *Sepia* is specially shown in these structures, which here appear on an almost flat surface; elsewhere they form two large and very prominent swellings, one on either side of the body.

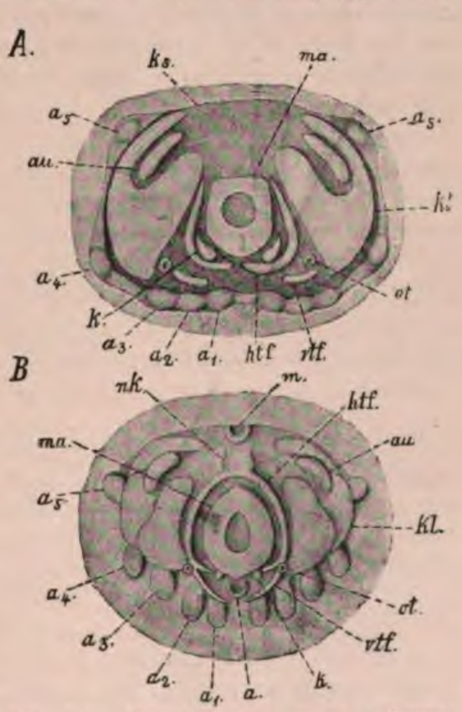

Fig. 128. — Germ-discs with young embryonic rudiments of *Sepia officinalis* (after Vialleton and Kölliker). *a*, anus; a_1-a_5, the five pairs of arms; *au*, rudiments of eyes; *htf*, posterior funnel-fold; *k*, gills; *kl*, cephalic lobes; *ks*, germ-disc; *m*, oral aperture; *ma*, mantle; *nk*, nuchal cartilage; *ot*, otocyst; *vtf*, anterior funnel-fold.

The germ-disc, on the side opposite to the optic swellings, is bordered by a narrow band-like prominence which at first is almost semicircular but soon extends round the greater part of the germ-disc and then resembles an incompletely closed circular swelling. This corresponds to the circular swelling which, in *Loligo*, runs round the whole embryo (Fig. 116 *B*, *ar*, p. 255) and contains, here as there, the rudiments of the arms. Those of the two ventral pairs are to be seen first, becoming differentiated from the circular swelling as rounded prominences. These are followed very soon by a third pair. When these three pairs have become distinct, the swelling containing them is prolonged laterally as a narrow process. As this becomes more massive later, the fourth pair of arms develops from it, this being finally followed by the fifth which lies the most dorsally (Fig. 128 *A*, a_1-a_5). The order in which the arms arise is therefore the same in *Sepia* as in *Loligo vulgaris* (p. 261).* Here also the prehensile arm, as a rudiment, does not seem to be characterised in any special way.

Another characteristic of the germ-disc at this early stage (Fig. 128 *A*) is a pair of rather long, arched folds near the mouth, the later development of which leads us to recognise them as the posterior funnel-folds. Between these and the mantle lie two comma-shaped prominences, the gills. The anterior funnel-folds also (*vtf*) are already present as rudiments. In their neighbourhood, lie the circular otocysts (Fig. 128 *A*, *ot*). These are the organs which KÖLLIKER, as VIALLETON pointed out, regarded as the nuchal cartilages.

We have here, as in former descriptions of the first rudiments of external organs, repeatedly had to speak of folds (*e.g.*, the funnel-folds), but this designation is not altogether justifiable, since, as VIALLETON has shown in sections of young *Sepia* embryos, these and other prominences, are, for the present, mere thickenings of the superficial cell-layer accompanied by slight bulging of the same, but these thickenings soon rise into actual folds. This is especially the case in the further development of the mantle and the funnel in the next stages.

While the organs mentioned have appeared as rudiments, the germ-disc only at first extends slightly over the yolk, occupying merely a small part of it. The blastoderm also does not nearly cover the yolk, but appears in the form of a broad ring beneath the germ-disc. Over the rest of the egg, the yolk lies freely at the surface. The germ-disc and the blastoderm are covered with cilia which are also present in later stages, when the embryo has risen up from the yolk (Fig. 129 *C*).

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* Our statements as to the rise of the arms rest upon our own observations. Since the observations of KÖLLIKER and VIALLETON agree with ours, there would be no need to mention this, especially as only a few *Sepia* embryos at this stage were available, had not the order of development of the arms been less clearly or otherwise described in other cases.

The development of *Sepia* (Fig. 128 *B*) consists for a time in the further growth of the rudiments of the organs already present. The edge of the mantle begins to rise from the germ-disc, and already covers the gills, only parts of which project from beneath it (Fig. 128 *B*, *k*). The rudiment of the anus (*a*) appears between the gills. A depression which at first is crescent-shaped appears on the opposite side of the mantle, quite at the edge of the germ-disc; this is the *oral aperture* (*m*).

The *funnel-folds* also deserve mention. They have now united, and the principal parts of the funnel can already be made out in them, *viz.*, the anterior folds (*vtf*) which yield the chief part of the funnel, the lateral parts (nuchal muscle, *hm*) which run back to the nuchal cartilage (*nk*) and, finally, the retractor-folds (*rt*) which run towards the gills. These parts are, indeed, far less distinct than in *Loligo* (Fig. 117 *A* and *B*, p. 259), but are nevertheless homologous with the similarly named structures found in that genus. The origin of the funnel from two halves is, on the other hand, more distinct, that organ being formed here, as in *Loligo*, through the rising of the two anterior folds which, after obtaining in this way an increase of surface, bend toward one another and fuse (Fig. 129 *C*). The principal part of the funnel derived from two half tubes, thus comes to lie in front of the mantle; its posterior aperture is turned toward the latter and opens into the mantle-cavity after the mantle has grown over the funnel. The narrow anterior aperture is turned away from the mantle.

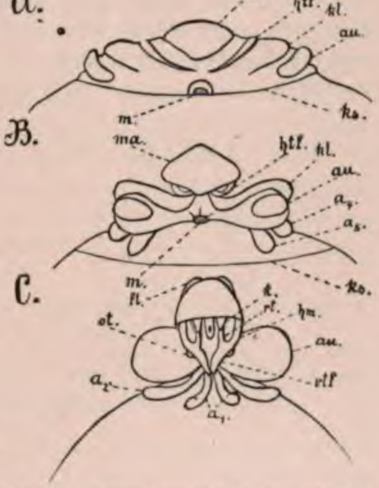

FIG. 129.—Germ-discs and embryos of *Sepia officinalis*, lying upon the yolk-sac. *A* and *B*, seen from the oral side; *C*, from the anal side (after KÖLLIKER). a_1-a_5, arms; *au*, eyes; *ds*, yolk-sac; *fl*, fins; *hm*, nuchal muscle; *htf*, posterior funnel-folds; *k*, gills; *kl*, cephalic lobes; *ks*, germ-disc; *m*, mouth; *ma*, mantle; *ot*, otocysts; *rt*, retractor of the siphon; *vtf*, anterior funnel-folds.

In adult Cephalopods, the efferent aperture of the funnel is directed towards the mouth, for the funnel lies on the ventral surface between the anal and oral apertures (Figs. 120 and 121, p. 262). In the early stages of *Sepia* embryos, this is not self-evident, as apparently different conditions are brought about by the intercalation of the yolk-mass and the superficial extension of the germ. The efferent aperture of the funnel does not appear to be directed towards the mouth but rather turned away from it (Fig. 128 *B*). A comparison with the embryos of *Loligo* shows, however, that quite the same conditions prevail in the two cases. If we imagine a *Loligo* embryo, such as the one seen obliquely from above in Fig. 117 *B*, p. 259, spread out flat, we should find that the anterior aperture of the funnel is here also turned away from the oral aperture which lies on the further side of the mantle and, apart from the modifications peculiar to the *Loligo* embryo, we should have a view something like that given in Fig. 128 *B*.

The further development of the *Sepia* embryo is characterised by the fact that its superficial extension is arrested and it rises up from the yolk-sac, the yolk then pressing in beneath the arched embryonic rudiment; in this way, an internal yolk-sac is formed as already described for *Loligo*. The rise of the embryo from the yolk is very gradual, and has a fairly similar effect on the different organs. Fig. 129 *A*-*C* represents a few stages in this process. In the first two, the embryo is seen from the oral side. The posterior funnel-folds (*htf*) at first still lie rather far from the mantle, but the latter, by extending laterally, soon projects beyond them. At the same time, the mantle bends over and thus begins to assume its final shape. The embryo in its further rise from the yolk is also followed by the cephalic lobes and the eyes, organs which, as in *Loligo*, at this time and even later form the largest part of the embryo (Fig. 129 *B*). Fig. 129 *C*, representing the embryo at a somewhat later stage from the anal side, shows its great resemblance in external shape to the embryos of *Loligo* at about the stage depicted in Fig. 119, p. 261. The gills are not yet completely grown over by the mantle; the

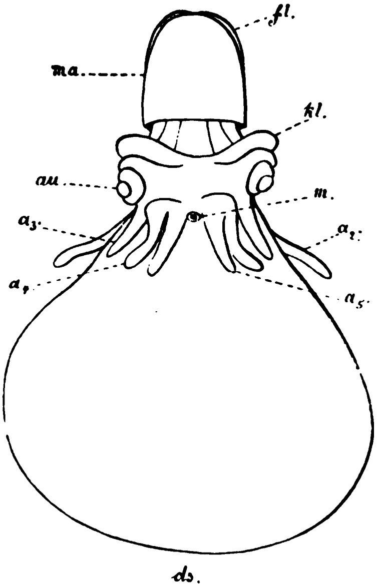

FIG. 130.—Older embryos of *Sepia officinalis*, seen from the oral side (after KÖLLIKER). The yolk-sac, near the embryo ought to be narrower. Lettering as in Fig. 129.

junction of the two posterior funnel-folds has taken place but these folds have not yet fused in the median line. On the mantle, the fins are visible, these apparently forming late in *Sepia*. The mouth lies at the opposite side; its position can be ascertained from Fig. 130 of a later stage. The yolk-sac is still very large, and is directly connected with the internal mass of yolk. As the yolk-sac is gradually absorbed, the large cephalic section decreases in size, approaching the final shape of the adult *Sepia*. By the time that the embryo is mature and ready to hatch, the greater part of the external yolk-sac has been absorbed. Only after its complete reduction can the arms occupy their final position round the mouth. At hatching, they are still rather short, and only attain their full length during free life. The prehensile arms which, as rudiments in *Sepia* also, are not specially distinguished from the others (Figs. 128 and 129), become characterised at later stages not only by their length (Fig. 130, *a*) but also by their bases sinking into the body. The depression thus caused is, in older embryos, visible even externally in the form of a horse-shoe-shaped fold lying above the first pair of arms.

4. The further differentiation of the Germ-layers and the formation of the Organs.

A. The separation of the Germ-layers and the formation of the Yolk-epithelium and the Alimentary Canal.

Only after the external form of the body is known is it possible to enter in detail into the further development of the germ-layers. These, in the Cephalopods, develop very late, or rather, they do not appear so distinctly here as in the other divisions of the Mollusca. As we have already remarked, the great accumulation of yolk in the embryo has, in this direction also, essentially modified the ontogenetic processes.

Our description of the body-layers was interrupted at the stage at which there had formed, at the margin of the germ-disc which covered only a small part of the egg, a peripheral thickened ring (Fig 112, p. 247 and 131 *A*) and cells became detached from the edge which, according to the view adopted by VIALLETON, wandered beneath the superficial cell-layer (Fig. 114, p. 250) there to give rise to a connected layer. This lower cell-layer then extends over the whole yolk, and is followed by a middle layer * so that the yolk is now surrounded

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* See also p. 126, etc.

by three cell-integuments. Yolk-cells are not found in the Cephalopoda, and the yolk thus attains, in them, a greater independence than in the eggs of most Arthropoda and Vertebrata, which are also very rich in yolk.

Very different conclusions have been arrived at as to the significance of these cell-layers. We shall consider first the inner layer, the so-called yolk-epithelium.

The **yolk-epithelium** is formed of large flattened cells which are swollen in the region of their nuclei. The only function of this layer is to yield an envelope for the yolk, and to bring about its utilisation by the embryo. In later stages it is found surrounding the yolk still in the same state as before. The yolk, especially in the typical forms of Cephalopodan development in which it is plentiful, is accumulated principally in the external yolk-sac. This latter is directly continuous with the mass which lies now within the developing embryo (Fig. 132); at a later stage, in consequence of the processes of growth that take place in the embryo, a constriction forms in the region of the arms (Fig. 120, p. 262), and a rather narrow duct here arises connecting the external with the internal yolk-sac (Fig. 133, *a*, *ds*, and *i*, *ds*). In this latter, again, various parts may be distinguished as lying respectively in the cephalic, the pallial, or the nuchal region. The part lying in the head gives off two outgrowths into the optic stalks, the nuchal portion narrows later and leads to the voluminous pallial portion. The embryo no doubt absorbs the yolk in the following way: the external yolk-sac passes on its contents to the internal sac, partly in consequence of the rhythmic contractions of its wall and partly in consequence of the processes of growth in the embryo itself, then the nutritive masses are conducted to the embryo from the inner yolk-sac through the intervention of the yolk-epithelium. Since, so far as we know, there are no vessels in the external sac, its disappearance cannot be accounted for in any other way.

It has already been pointed out that the yolk-epithelium is a closed unilaminar layer of cells extending round the whole yolk. In consequence of its close connection with the yolk, the yolk-epithelium must certainly be regarded as the inner layer of the Cephalopod germ. The question now arises, What is its relation to the *future entoderm?* This latter first becomes perceptible in the following way.

About the time when the first rudiments of organs appear externally on the embryo, there is seen, on the ventral side, contiguous to the yolk, an epithelial plate which at first consists of only a few cells. This is the first indication of the **enteron**, which soon increases somewhat in size (Fig. 131 *D*, *md*) and finally separates from the yolk and appears sac-like (Fig. 132 *A*, *md*). Beneath it, the yolk-epithelium is now seen, which, in earlier stages, was wanting at this spot (KORSCHELT, No. 25).

The sac-like rudiment of the enteron was known long ago and it was assumed, with great probability, that it might be connected with the yolk-epithelium, and thus to a certain extent might be regarded as an outgrowth of the latter (RAY LANKESTER, VIALLETON, BRUCE). The two together would represent the entoderm, the vesicle being regarded as the permanent and the yolk-epithelium as the provisional part of the entoderm. BOBRETZKY, on the other hand, considered that the vesicle arose as a mere differentiation of the lowest cell-layer of the middle layer, *i.e.*, of the so-called "mesoderm." There, indeed, appear to be no yolk-epithelium at the stage when the epithelial plate above described as the first indication of the enteron forms, either beneath that plate or in its near neighbourhood, and this has led to the assumption that the cells of the yolk-epithelium as well as the enteric plate arose as differentiations of a cell-layer which grew from the edge of the germ-disc towards its centre.

This last view seems not without justification because it is very difficult to decide whether the yolk-epithelium presses beneath the germ-disc (Fig. 114, p. 250) or whether these cells are differentiated from the whole cell-mass. The cells which are directly in contact with the yolk actually bear a very close resemblance to those of the middle layer.

These questions are of importance as determining the manner in which the **germ-layers** form. We have to imagine that the cell-mass pressing from the edge towards the centre of the germ-disc (Fig. 131 *A* and *B*) represents the meso-entoderm. The whole process is then to be regarded as a much modified invagination. The edge of the germ-disc corresponds to the blastopore which is filled by the large yolk-plug. The yolk-mass also fills the whole of the archenteric cavity (Fig. 131 *B*).

In the Molluscs considered earlier in this work, especially in the Gastropoda, we have already found the mouth related to the blastopore. In GRENACHER's Cephalopodan embryo, we saw that the oral aperture arises in the neighbourhood of the aperture of the blastoderm which closes only at a very late stage (p. 270). Since we regard the latter as the blastopore, relations between it and the mouth may exist here also.

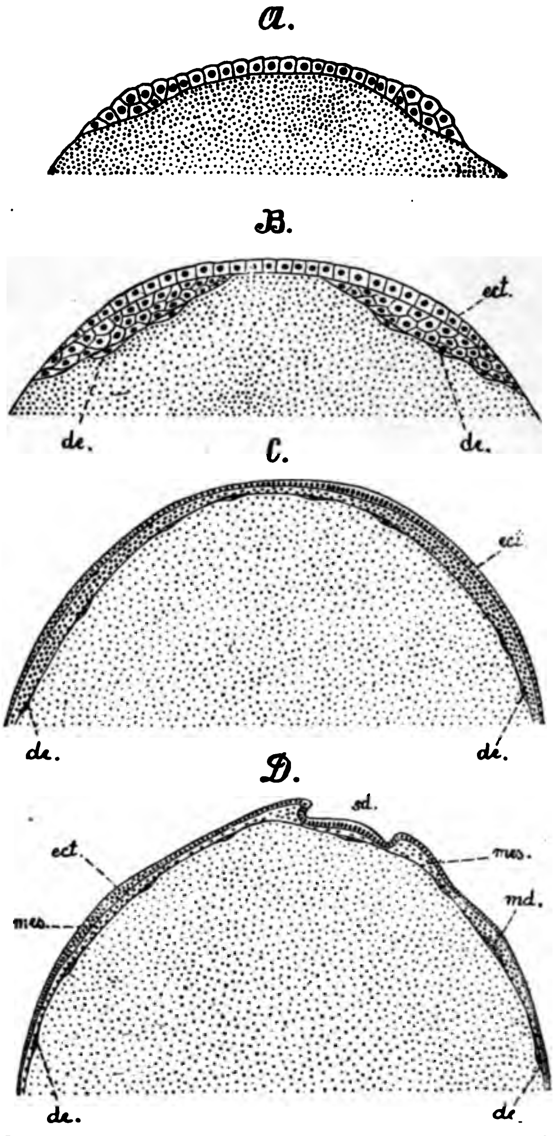

FIG. 131.—Diagrams illustrating the formation of the germ-layers. *A*, thickening of the edge of the germ-disc; *B* and *C*, differentiation of the yolk-epithelium. Further extension of the germ-disc over the yolk. *D*, differentiation of the rudiment of the enteron and the mesoderm; *de*, yolk-epithelium; *ect*, ectoderm; *md*, rudiment of enteron; *mes*, mesoderm; *ect* (in *D*), the rudiment of the cerebral ganglion.

At a later stage, as already described, the lowest cell-layer, that which is in contact with the yolk, becomes differentiated and yields the provisional and the final entoderm (Fig. 171 *C* and *D*, *de*, *md*). The cell-material which remains between these two and the ectoderm corresponds to the mesoderm, which, in its development is, like the entoderm, greatly influenced by the excessive abundance of the yolk. During these processes, the germ-disc has extended far over the egg (Fig. 131 *C* and *D*).

We need hardly point out that the formation of the germ-layers in the Cephalopoda, as compared with that in other Molluscs is much modified; transitions between the two types of formation may, however, be found in the eggs of many Gastropods that are rich in yolk (*e.g.*, *Nassa*, Fig. 95, p. 207) although, in these latter cases, the modifications undergone by the process are not nearly so great. The entoderm, indeed, was there seen forming in a disconnected manner and the rudiment of the enteron was open towards the yolk (Figs. 123-135), as in the Cephalopoda, except that, in the latter, the yolk is still covered by the thin epithelial layer.

The **alimentary canal** now develops, the enteron (Fig. 132 *A*, *md*) increasing in size and soon dividing into two parts, as is seen in Fig. 132 *C* which represents a later stage. The lower part, which appears sac-like (*tb*), represents the rudiment of the ink-sac, and the upper part, which is open towards the yolk-epithelium, the actual stomach and intestine. Where this comes into contact with the ectoderm (*a*), fusion subsequently takes place and results in the anus. There is at this point only an inconsiderable depression of the ectoderm, and there is therefore no proctodaeum of any size, as is evident from the fact that the ink-sac, which originates from the entoderm, opens into the intestine in the adult quite near the anus.

The enteron grows out towards the apex of the yolk-sac, this being still more marked in later stages. It is growing toward the stomodaeum which is approaching it from the other side of the yolk-sac. This latter rudiment arose as an ectodermal depression on the opposite side of the blastoderm and farther down, *i.e.*, more anteriorly.

The positions of the *mouth* and the *anus* have already been mentioned and are made clearer by the sections now before us (Figs. 132 and 133, also Figs. 116-120, pp. 255-262). The oral invagination arises below the ectodermal thickening depicted on the left in Fig. 131 *A*, *vd*. Another depression (*sp*), at first lying outside of the stomodaeum, represents the rudiment of the posterior or large *salivary glands*. At a later stage, the rudiment of the *radular sac* is added (Figs. 132 and 133, *r*), and a tubular depression, the rudiment of the anterior salivary glands, appears farther forward.

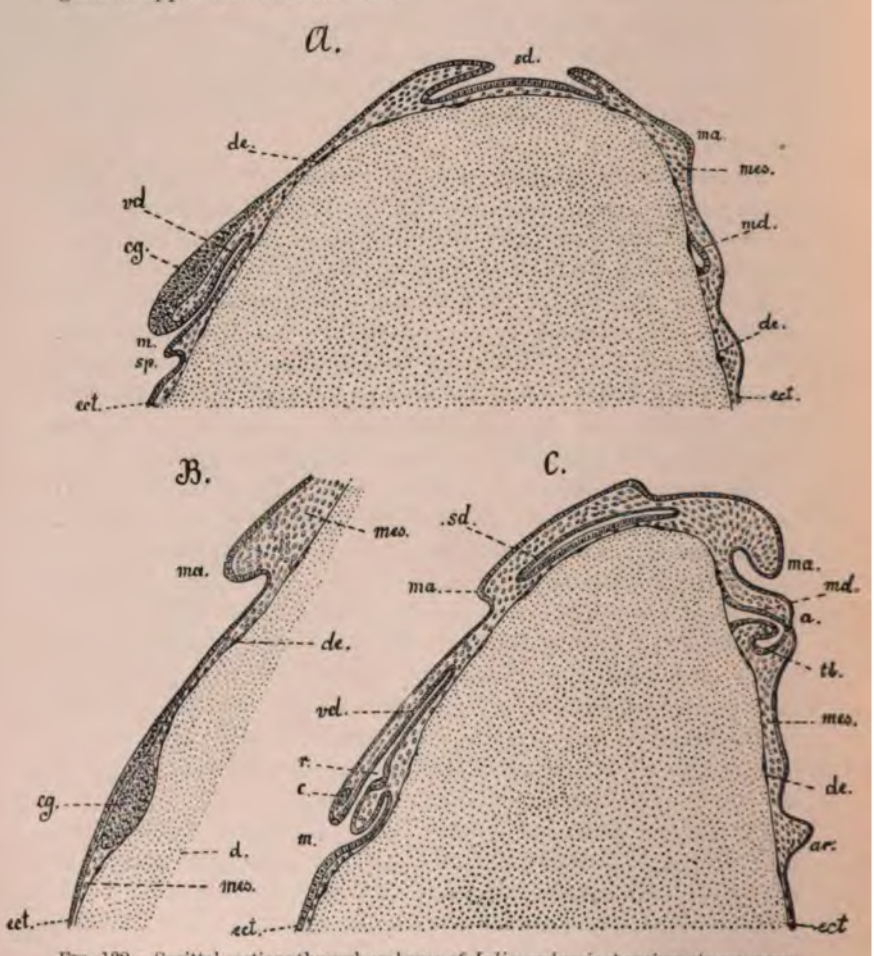

FIG. 132.—Sagittal sections through embryos of *Loligo vulgaris* at various stages, somewhat diagrammatic (original). *B*, section through the region of the mouth. *a*, anal region; *ar*, arm-rudiment; *c*, cerebral commissure; *cg*, cerebral ganglion; *d*, yolk; *de*, yolk-epithelium; *ect*, ectoderm; *m*, mouth; *ma*, edge of mantle; *md*, enteron; *mes*, mesoderm (indicated diagrammatically); *r*, radular sac; *sd*, shell-gland; *sp*, salivary gland; *tb*, ink-sac; *vd*, stomodaeum.

We may here summarise the development of the stomodaeum according to the numerous and careful investigations of GRENACHER, BOBRETZKY, USSOW, WATASE, JOUBIN, as follows. The rudiments of the salivary glands very soon divide into two branches assuming in this respect the final form of the adult organ. The posterior rudiment is specially large. The two branches, which diverge at a wide angle, carry diverticula and thus form the lobed masses of the lower pair of salivary glands (GRENACHER, No. 14; JOUBIN, No. 22). The unpaired part of the rudiment, which corresponds to the common section of the efferent duct, greatly lengthens, for, in the adult, the lower salivary glands lie far back. The rudiment of the radular sac also undergoes modification, the part of its wall which is turned backward and inward thickening and the radula being secreted in the way described above (p. 201 and Fig. 91 *A*).

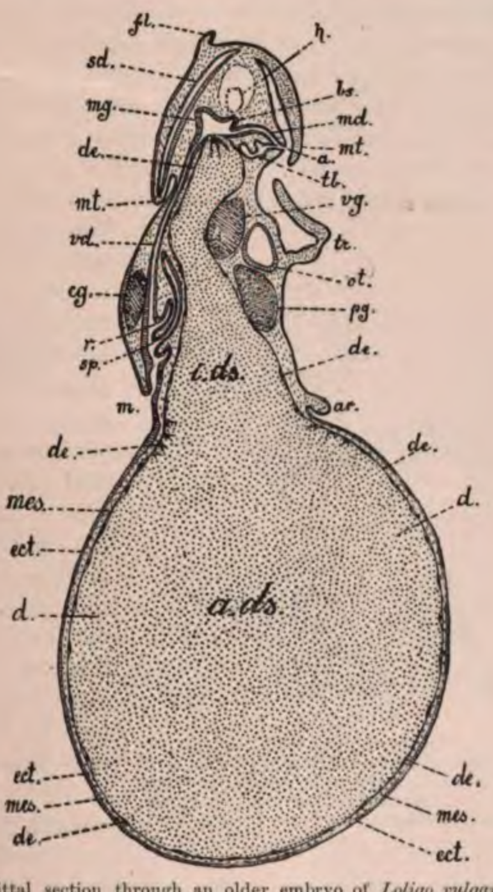

FIG. 133.—Sagittal section through an older embryo of *Loligo vulgaris*, somewhat diagrammatic (original). *a*, anus; *a.ds*, external yolk-sac; *ar*, arm-rudiment; *bs*, caecum of the stomach; *cg*, cerebral ganglion; *d*, yolk; *de*, yolk-epithelium; *ect*, ectoderm; *fl*, fin; *h*, heart; *i.ds*, internal yolk-sac; *m*, mouth; *md*, intestine; *mes*, mesoderm; *mg*, stomach; *mt*, edge of mantle; *ot*, otocyst; *pg*, pedal ganglion; *r*, radular sac; *sd*, shell-sac; *sp*, salivary gland; *tb*, ink-sac; *tr*, funnel; *vd*, stomodaeum; *vg*, visceral ganglion.

Various prominences and folds appear in the epithelium of the stomodaeum near the mouth, and the jaws also arise here as cuticular secretions (JOUBIN, GRENACHER, BOBRETZKY).

Long before the differentiation of the stomodaeum advanced to this point, it became united to the rudiment of the enteron, the two having grown up towards each other from opposite sides of the yolk, and having met near the apex of the inner yolk-sac, there fusing. Fig. 133 represents a later stage, in which the enteron has dilated anteriorly and has thus formed the rudiments of the *stomach* (*mg*) and of the *stomach-caecum* (*bs*).

At a somewhat earlier stage, the rudiment of the enteron shows a remarkable peculiarity, being wide open towards the yolk-epithelium, as is evident in sagittal sections (Fig. 132 *C*) and still more in transverse sections (Fig. 134 *A* and *B*). It here appears as a plate, a large part of which is in close contiguity to the yolk. The infolding of the edges of this plate (Fig. 134 *B*) gives rise to the two hepatic tubes which open into the enteron in the region of the caecum.

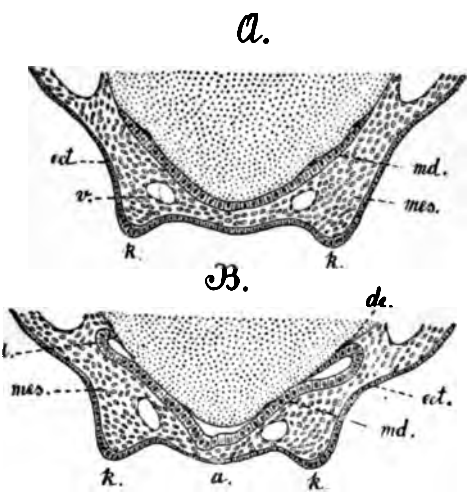

FIG. 134.—The ventral portions of two transverse sections of embryos of *Loligo vulgaris* at different ages (original). *a*, anal region; *de*, yolk-epithelium; *ect*, ectoderm; *k*, branchial rudiments; *l*, liver; *md*, enteron; *mes*, mesoderm; *v*, vascular spaces in the mesoderm.

The wide opening of the enteron towards the yolk-epithelium gradually narrows, but can still be distinctly made out even in later stages (Fig. 133). Below it, large cells of the yolk-epithelium can be seen lying, and sending off lateral processes into the yolk (Fig. 133). The yolk is thus completely covered by the yolk-epithelium even beneath these gaps in the intestinal epithelium, where a connection of the lumen of the intestine with the yolk-sac might be assumed, as well as below the former wide aperture of the enteron. *There is, therefore, no direct communication between yolk-sac and enteron.*

The yolk-material thus does not pass directly into the intestinal cavity, but has first to pass through the yolk-epithelium. The latter consequently promotes the absorption of the yolk by the embryo, this being its principal function. A specially active inception of nutritive substance probably takes place at the open part of the enteron by means of the yolk-epithelium. This view is confirmed by the rise of the liver in this region, this organ showing in other Molluscs also a close relation to the nutritive substance of the egg, and also by the appearance of the large rhizopod-like cells in the yolk-epithelium which separate the cavity of the enteron and the yolk-sac.

When the gap in the intestinal epithelium closes as development advances, the internal yolk-sac appears to lie in the body-cavity quite unconnected with the enteron. The external yolk-sac gradually decreases in size as its contents are transported to the internal sac whence they are absorbed and, when completely taken up, the internal sac itself shares the same fate, the yolk-epithelium being the last to disappear, its function being now fulfilled.

The function of the yolk-epithelium resembles that of the yolk-cells of the Arthropoda and the Vertebrates, described above. This comparison has already been made by RAY LANKESTER, VIALLETON, WATASE and others, and the resemblance is heightened by the fact that the yolk-cells may also appear as a peripheral layer, the outer merocyte-layer of the Selachians or the so-called periblasts of the Teleosteans. Some difference between these and the yolk-epithelium of the Cephalopoda still, however, remains, since, in the Vertebrates, these cells are at first distributed throughout the yolk and then collect into a continuous layer, whereas, in the Cephalopoda, the cells are never found in the yolk, the yolk-epithelium being produced direct from the cells of the germ-disc. The type of the meroblastic egg is thus specially marked in the Cephalopoda.

In order to complete our description of the development of the alimentary canal, some reference must be made to the ink-sac. We have already seen that it arises from the rudiment of the enteron as a vesicular structure (Fig. 132 *C*, *md*). It soon deepens, and grows out as a tube which is surrounded by mesoderm-cells. In this tube, two sections can soon be distinguished, the inner blind end, the walls of which are much folded (GIROD), and the superficial part which opens externally and becomes greatly dilated, but remains lined with a simple epithelial layer. The inner part of the ink-bag represents the glandular secreting part, while the dilated portion which finally, through a long efferent duct, opens into the intestine near the anus, forms the reservoir for the secretion. As has already been pointed out (p. 281), the fact that this entodermal structure opens close to the anus proves conclusively that there is here no long proctodaeum. Nevertheless, a very considerable part of the alimentary canal has actually, by some authors, been attributed to a proctodaeal invagination. Although we considered this view as disproved, we mention it here as having formerly been supported by the majority of authors (METSCHNIKOFF, No. 32; GRENACHER, No. 14; USSOW, No. 44; GIROD, No. 12; WATASE, No. 49).

According to these authors, the structure spoken of as the enteron was already connected with the ectoderm from its earliest development, and, as this gives rise to the intestine, the latter must therefore have arisen in the form of an ectodermal depression, *i.e.*, as a proctodaeum. USSOW, as well as GIROD and WATASE, who later investigated this subject very thoroughly, must be regarded as having adopted this view, the details of which are here unnecessary. The hypothetical proctodaeum grows up over the yolk, becoming differentiated in the way described above for the enteron. As to the point to which the proctodaeum extends forward (or the stomodaeum backward) opinions are divided, but according to this view, the liver, the caecum and the stomach are all derived from the ectoderm, since the whole alimentary canal is produced by the union of the stomodaeum growing backward and the proctodaeum advancing forward. The whole of the entoderm is represented by the yolk-epithelium and is quite transitory (WATASE). Similar statements as to the ectodermal origin of the alimentary canal have been made in connection with other animals (*e.g.*, Insects, GANIN, WITLACZIL, GRABER, HEYMONS), but are, in such cases also, altogether improbable, as is proved by the condition of nearly related forms.

As opposed to the view to which we have just briefly referred, we have given that maintained by RAY LANKESTER (No. 29); VIALLETON (No. 48); BOBRETZKY, (No. 4) and confirmed by ourselves (No. 25) in much earlier stages of development, as, apart from its greater probability, this derivation of the alimentary canal seems much better founded.

B. The Covering of the Body and the Shell.

The ectoderm which covers the body of the embryo seems to pass, with only slight modifications, direct into the body-epithelium (epidermis) of the adult. The shell appears as the secretion of a specially modified part of the ectoderm. In studying the **embryonic formation** of this organ which is of such importance for the comprehension of the Cephalopodan body, we are unfortunately restricted to those forms in which it no longer attains full development. Only in a few recent Cephalopods such as *Nautilus* and *Spirula* * is the shell

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* [It is very questionable if the shell of *Spirula* can be regarded as perfect; it is almost internal and evidently much reduced.—ED.]

found in its perfect form, and the development of these rare animals is not known. The shell of *Argonauta* exemplifies other conditions which will be discussed later (p. 294). In those recent Cephalopods in which the development of the shell has been investigated, it lies, enclosed in the mantle (and is thus internal) on the antero-dorsal surface of the body, and either develops into the so-called pen, of a horny character (*Ommastrephes*, *Loligo*, and others) or consists of numerous calcareous layers built upon a horny foundation (*Sepia*). It forms in an invagination of the ectoderm, the shell-gland.

In a very early embryonic period, a depression appears at the centre of the mantle-rudiment, this being the first indication of the shell-gland (Figs. 115, 116, p. 255, Fig. 131 *D*, p. 280). At first, in *Loligo*, this is a wide, shallow pit, but the margin of the pit soon grows inwards and constricts its aperture, the pit finally assuming the form of a sac connected with the exterior by a small opening. This sac is lined with an epithelium composed of cells which, at its base, are specially long, and is surrounded by mesodermal tissue. The aperture of invagination completely closes at a later stage, and the shell-gland then lies internally as a closed sac, surrounded by the mesodermal tissue (Fig. 132 *C*). It extends later especially anteriorly and then occupies a large part of the antero-dorsal side of the mantle (Fig. 133). The secretion of the shell then takes place within it (Ussow, Bobretzky).

The Interpretation of the Shell in Recent Cephalopods.

There can be no doubt that we have in this case an internal shell, but the question remains, What is its relation to the large external shell met with in the (living) *Nautilus*, in the Ammonites and other extinct forms? This is a point of importance in studying the manner of formation of the Cephalopodan shell and its relation to that of other Molluscs. In solving this question it is necessary to institute comparisons with the shells of various extinct forms.

The shell of the recent Dibranchia is very differently developed in the various forms. It occasionally consists merely of a long, narrow, horny, plate, shaped like a symmetrical bird's feather, but otherwise not specially differentiated (*e.g.*, in *Loligo*). In other cases, the plate is less simply formed, its posterior end forming a hollow cone, the whole shell thus being slipper-shaped (*Ommastrephes*, Fig. 140).

The calcareous shell of *Sepia* (Figs. 137, 138 *A*) is much more complicated in structure, and is composed of many calcareous layers. Its structure is still not fully understood, but it has been compared with the more highly developed Cephalopodan shells. Among the living Dibranchia, the shell which appears to approach most nearly to those of the extinct forms is that of *Spirula;* here we find a spirally coiled and chambered shell which, however, is grown over and enclosed by the mantle. This approximates most nearly to the shell of certain Belemnites which was also an internal shell though, so far as its chambered portion (phragmocone) was concerned, it was less highly developed than that of *Spirula.*

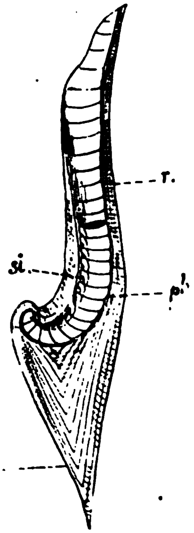

FIG. 135.—Longitudinal section through the shell of a *Spirulirostra* (restoration). *ph*, phragmocone ; *r*, rostrum ; *si*, siphon.

The shell of the Belemnite is not, like that of *Nautilus* or most Ammonites, spirally coiled, but is straight like that of the *Orthoceratidae* (Nautiloidea). It is characteristic of the Belemnite that in addition to the part of it, the phragmocone, that may be regarded as corresponding to the actual chambered Cephalopodan shell (that of the Ammonites and *Nautilus*) there is a calcareous pointed external investing piece, the so-called guard or *rostrum.* A good example of this latter is afforded in the fossil *Spirulirostra* (Fig. 135) the phragmocone of which is curved and thus bears a certain resemblance to that of *Spirula*, but has, in addition, dorsally and late rally, a large conical rostrum. It has also been maintained that traces of such a rostrum are to be found in *Spirula*, although these were not found by us in an examination of a large number of shells.*

The shell of the Belemnite is, as already mentioned, straight. Two parts can be distinguished in it. The chambered part (*phragmocone*) is provided with a siphon and is surrounded by the actual shell-wall (the *ostracum*) ; this latter becomes specially dilated towards the head of the animal as the so-called proostracum, and is not here followed by the phragmocone. This first portion of the shell might be compared with the Ammonite or Nautilus shell, but on the side opposite to the proostracum, surrounding the posterior part of the phragmocone and prolonged in the same direction, there is a second part, a very large rostrum, which is usually the only part of the whole Belemnite to be preserved in a fossil condition. That this shell was internal, *i.e.*, surrounded by the mantle, seems to be highly probable from observations made on forms resembling Belemnites but better

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* The position of *Spirula* as a branch of the Belemnite stock connected to it by forms like *Spirulirostra* seems to us doubtful. While the position of the siphon and the orientation of the shell with regard to the body would seem to favour this view, the constitution of the shell, on the other hand, with its well-retained chambers and the siphon renders it improbable that it has undergone a process of degeneration which led to the total loss of the rostrum. The shells of other recent Cephalopods, in which such degeneration took place, underwent, in consequence, great change of structure. We must, in any case, take into account the view that *Spirula* may have separated from the Decapodan stock before acquiring a rostrum.

preserved, and as is also shown by the so-called vascular impressions on the external surface of the rostrum of many Belemnites.*

Attempts have been made to deduce the constituent parts of the shell of *Sepia* from the above parts of the Belemnite shell (VOLTZ, RIEFSTAHL, No. 39). The shell of *Sepia*, or, as it is generally termed, the cuttlebone, is very complicated. The whole forms an oval shield-like structure, which, for the most part, is biconvex, but in the more dorsal region it becomes concave on its posterior or inner side, its shape is well shown in Figs. 137, 138 *A*. Its antero-dorsal surface is covered externally by a roughly calcified shagreen-like layer, the outer layer, under which is a deposit of horn-like matter (conchyolin), the middle layer, the latter being freely exposed at the margin of the shell (Fig. 137, *mp*). Dorsally, the shell is produced into a small pointed structure (Figs. 137 and 138, *k*, *d*) which consists essentially of a prolongation of the outer calcified layer but has become covered by a secondary development of horny (conchyolin) matter which is quite distinct from the horny middle layer. This calcareous spine may in some species project freely on to the exterior (*S. andreanoides*). On the posterior or internal surface of the shell is a prominent swelling produced by a great deposit of calcareous material arranged in thin oblique layers (Fig. 138 *A*, *w*), separated from one another by air-spaces closed by calcareous supporting trabeculae; this structure which is most developed near the antero-ventral portion of the shell serves as a float. Dorsally this portion of the shell is less developed and consequently the margins of the shield are here much more pronounced. Surrounding the posterior remnant of the calcareous swelling is a modified forked or V-shaped area (Fig. 137, *g*), the two ends of which are directed forward; this ledge,

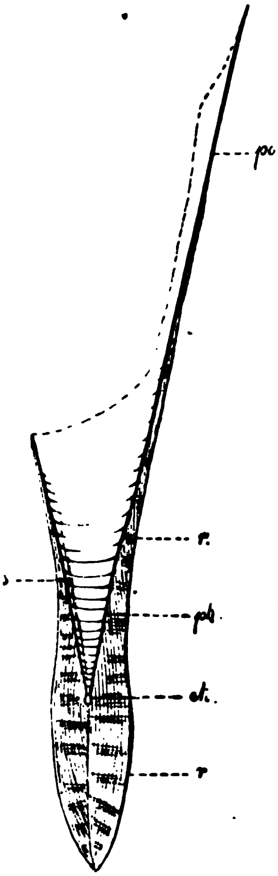

FIG. 136.—Median longitudinal section through the shell of a Belemnite, somewhat diagrammatic. *ek*, embryonic chamber; *ph*, phragmocone; *po*, proostracum; *r*, rostrum; *s*, siphon. The dotted lines indicate the anterior edge of the shell the limits of which are at present not accurately known.

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* We do not here follow out this point, since, for our purposes, it is of no special importance that in certain Belemnites the posterior part of the rostrum projects as a more or less long spine beyond the mantle, giving the posterior end of the animal the shape of an arrow, an adaptation favourable to locomotion.

the posterior part of which is somewhat raised and arched forward, forms a cavity which in some cases (*S. officinalis*) is shallow, but in other species (*S. aculeata*, Fig. 137) tolerably deep.

These parts of the Sepia shell have been homologised with those of the Belemnite shell in the following way. The spine, together with the outer calcareous plate, have been thought to correspond to the rostrum of the Belemnite (*cf.* Figs. 136 and 137) which is continued far on to the actual shell, almost as if the proostracum of the Belemnite were covered by an external calcareous investment connected with the rostrum, as perhaps may actually be the case. A similar condition is found in *Spirulirostra*, in which the rostrum embraces a large part of the shell (Fig. 135, *r*).

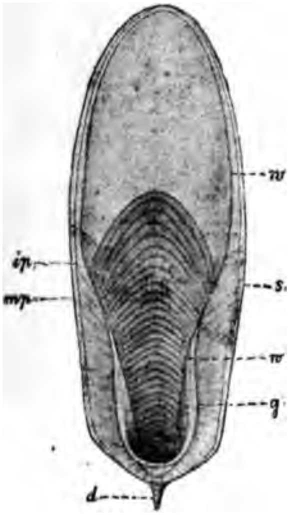

FIG. 137.- Shell of *Sepia aculeata*, seen from the ventral surface (original). *d*, spine; *g*, forked ledge; *ip*, inner layer; *mp*, middle layer of the shield (s); *w*, prominence, showing the free edges of the lamellae.

The actual shell of the Belemnite, *i.e.*, the phragmocone and proostracum, corresponds to the two inner layers of the shield in *Sepia*, the prominence and the fork (Figs. 136-138, *w* and *g*). While the two outer layers are to be regarded as the wall of the shell (ostracum), the lamellae of the prominence may perhaps be considered as partition-walls between the chambers. These lamellae end posteriorly in free edges (Figs. 137 and 138); laterally, however, they are continued into corresponding lamellae of the forked ledge. As this latter rises anteriorly over the posterior end of the prominence and forms a rather deep cavity posteriorly, a structure arises which actually resembles the phragmocone of the Belemnite. If the comparison is carried further, the wide aperture of the posteriorly directed partition-walls of the chambers might be compared to the siphonal spaces in the Ammonites, which, however, have become very wide and in which a considerable part of the body lies.

This view seems to be supported by the condition of a fossil form (*Belosepia*) the shell of which bears a general resemblance to that of *Sepia* but still shows the phragmocone fairly distinctly (Fig. 138 *B* and *C*). In place of the siphon there is, in this form, a wide cavity (Fig. 138 *B*), and this may be regarded as marking a transition to the condition of *Sepia*. The rostrum in these forms resembles that of *Sepia*, but is still more strongly developed (Fig. 138 *A* and *B*).*

If the lamellae are regarded as partition-walls of the chambers, it appears remarkable that these latter extend anteriorly; that is, that the proostracum thus completely disappears, for the whole prominence would then correspond to the phragmocone.

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* We refrain from comparing the anterior part of the shell (of which usually only the hind or dorsal end is retained) with the shell of *Sepia*, but it seems possible that here also resemblance can be found.

The lamellae are connected by numerous delicate calcareous trabeculae, so that the spaces between them are not empty, as one might expect if they represented chambers. But this can hardly be reckoned as an argument against the above interpretation of the Sepia shell, as such a modification of the shell in adaptation to new functions (as a float) is quite explicable.

The development of the different parts of the Sepia shell has been investigated in detail by APPELÖFF, but has, so far as we know, been described only in a short Swedish treatise (No. 2) from which it is impossible to judge whether factors of importance for the morphological interpretation of the shell have been discovered.

Finally, it appears necessary to point out that this whole comparison is still far from being well founded, although it may be considered as extremely plausible.

Other recent Cephalopods, especially those which are universally regarded as more primitive than *Sepia*, have a shell of very simple structure, carrying at its end at the most a hollow cone (*Ommastrephes*, Fig. 140). If this structure is compared with the phragmocone, the rest of the shell would have to be regarded as the proostracum, and this suggests the idea that, in *Sepia* also, the fork which bifurcates anteriorly and the contained cavity may be regarded as such a much-reduced phragmocone. The whole of the part lying anteriorly to it (the prominence) would then have to be considered as the proostracum, which has perhaps attained such a large size in adaptation to its present function, the diminution of the specific gravity of the body. The lamellate structure of the prominence would then be traceable to a secondary modification causing the secretion of the shell in layers, to form the air-cavities of the float; under these circumstances the higher morphological significance could not be ascribed to it. Further light upon the subject of the significance of the shell of *Sepia* and its relation to the shells of the

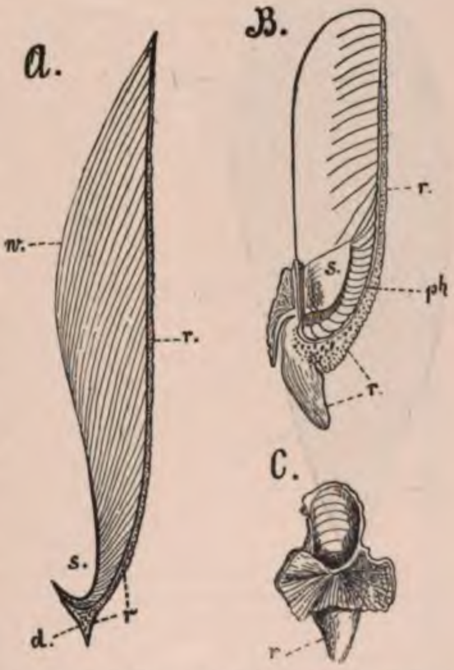

FIG. 138.—*A*, Diagrammatic longitudinal section of the shell of *Sepia*; *B*, shell of *Belosepia Blainvillei*, seen from the side; *C*, posterior part of the same, seen from the ventral side (*B* and *C* after ZITTEL). *d*, spine; *ph*, phragmocone; *r*, rostrum; *s*, siphon; *w*, prominence.

fossil forms may be expected from detailed palaeontological investigations and perhaps also from more comprehensive ontogenetic researches.

A comparison of the shell of *Sepia* with that of *Belemnites*, such as was attempted above, suggests a relation between the Dibranchia in general and the *Belemnitidae*. This indeed seems a bold proceeding, since nothing certain is known of the soft parts of these Cephalopods, but forms like *Belemnoteuthis*, a Cephalopod living in Triassic times with well-preserved phragmocone and arms carrying hooks, as well as *Acanthoteuthis*, a Decapod much nearer the recent Decapods and also armed with hooks (JAEKEL, No. 17), indicate with considerable certainty that the Dibranchia or at least the Decapoda are to be derived from forms resembling the *Belemnitidae*.

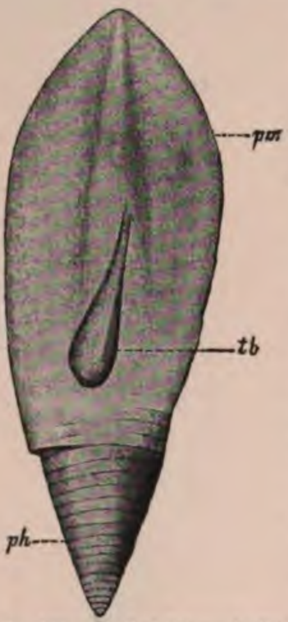

FIG. 139.—Shell of *Belemnoteuthis* from the lower Lias, Lyme Regis, somewhat diagrammatic (original).* The shell is seen from the funnel-side with the ink-sac lying (*tb*) upon it. In the phragmocone (*ph*), the most posterior part is wanting and is indicated by dotted lines. The partition-walls of the chambers are seen on the surface owing to the posterior portion being broken away; *po*, proostracum.

There can be no doubt that the shell of the *Belemnitidae* was internal and was almost completely enclosed in the mantle. Of the transitionary forms, moreover, *Belemnoteuthis* shows on the phragmocone which is still provided with chambers and siphon a large and distinctly bounded proostracum (Fig. 139, *po*) recalling, in its shape, the Sepia shell. The rostrum, in these forms, is either wanting or, when present, is only a slight appendix to the phragmocone. In this respect, these forms would approximate to the recent forms in which the shell has a posterior cup (*Ommastrephes*, *Onychoteuthis*, *Taonius*, *Leachia*).

It is of interest that, in *Ommastrephes*, regular transverse striation is found on the hollow cone (Fig. 140); this is quite distinct from the lines of growth in other parts of the shell and may perhaps be regarded as the last vestige of the chambering of the phragmocone. [*Gonatus Fabricii*, according to STEENSTRUP, has a series of chambers at the end of its horny pen.] Such a view does not appear unjustifiable, as *Ommastrephes* is among the most primitive of the extant Cephalopoda. JAEKEL has already pointed out (No. 17) that *Ommastrephes* also, in the possession of small hooks, shows a primitive character and recalls the hook-bearing transitionary forms mentioned above (*Belemnoteuthis*, *Acanthoteuthis*).

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* Fig. 139 represents a very instructive and as yet undescribed specimen from the collection of Dr. O. JAEKEL, kindly placed at our disposal. Our thanks are due to him also for revising the figure.

The reduction of the shell goes still farther in other recent Cephalopods; the terminal cone, in older specimens of *Dosidicus*, is found to be solid, whereas, in the younger animals, it was hollow (STEENSTRUP). In some *Cranchiidae* the hollow cone is still present at the end of the shell, in others it has disappeared and, in its place, there is mere solid swelling. Finally, a simple horny plate develops, as in *Loligo*. The hollow cone does not even appear ontogenetically, so far as we know at present.

The above comparison seems to show with certainty that the shell in the Cephalopoda is internal, the manner in which it arose from an external shell being still exemplified in a living form, *Spirula*. In *Nautilus*, only a small part of the mantle covers the external shell, but the process of circumcrescence of the shell went farther, until the shell became covered, though incompletely, by the mantle, as in *Spirula*. During this process, the size of the shell as compared with that of the animal became reduced in most cases; at the same time, it changed its position and gradually degenerated, since it no longer functioned in the same way. Externally, new calcareous layers became added to the primitive shell, for we find that only the inner part of the shell of *Belemnites* or *Sepia* corresponds to the shell of *Nautilus*, the rostrum and its continuation as a covering of the proostracum are secondary structures, no doubt secreted by the mantle-sac which surrounded the shell. We are here again brought to the question of chief interest in connection with this subject, *viz*., the manner of formation of the shell.

We saw above that the shell is formed in an ectodermal depression, the shell-gland. It would be well to discover whether this shell-gland is homologous with the organ of the same name in the Lamellibranchia and Gastropoda or not. This question has been raised before now by RAY LANKESTER (No. 28) who maintained the negative because he believed that the shell of *Sepia* corresponds to the Belemnite shell and consequently must be formed in a mantle-sac and not in the primitive shell-gland. RAY LANKESTER was obliged to take up this position decisively since he considered the Sepia shell as homologous with the external part only of the shell of *Belemnites* and left the phragmocone out of account.

In deciding the question as to the significance of the shell-gland in the Cephalopoda, we are inclined from the first to ascribe to this organ which appears so early, in consequence of its position and development, the same significance as is possessed by the shell-gland in the other Mollusca, and thus

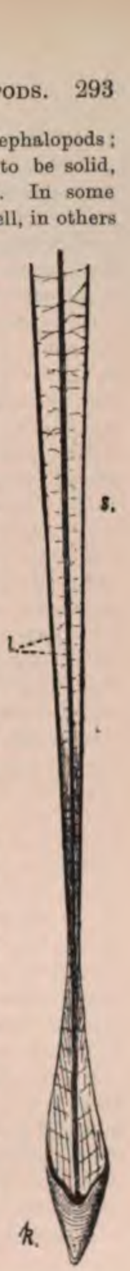

FIG. 140.—Posterior part of the shell of *Ommastrephes* from the Indian Ocean, seen from the posterior surface (original). *k*, conical appendage at the dorsal end; *s*, plate of the shell which narrows dorsally, again broadening out as the conical appendage; *l*, the strong horny ledges between which the shell consists merely of a thin membrane strengthened by ribs.

to consider it as fully homologous with this latter structure. The most natural course is to seek for a confirmation of this view in the ontogeny of those Cephalopods which are provided with an external shell. Since the development of the shell is unknown both in *Nautilus* and *Spirula*, embryos being unobtainable at present, we might turn to the only Cephalopod with external shell which is more accessible, *viz.*, *Argonauta*, if the conditions in this case were not essentially modified.

It has already been shown (p. 266) that a shell-gland does indeed appear in the embryo of *Argonauta*, but that it disappears later and does not give rise to the shell of the adult. The latter is not formed within the egg-shell, as was assumed by a few of the older authors (POLI, DELLE CHIAJE, No. 9) but arises later, as was observed by Mrs. POWER, ADAMS and KÖLLIKER (Nos. 1 and 24). The statements made as to the origin of the shell are somewhat peculiar and obscure. According to the almost universal view, the shell is secreted by the expanded surfaces of the dorsal arms which cover the shell when fully formed. This view, which at first sight is rather improbable, is rendered still more so by the fact that the regeneration of parts of the shell which are lost is said to take place from within. The mantle might also be regarded as a source of the shell, but it is not closely connected with the latter and so this view also has no support.

The disappearance of the shell-gland in the embryo of *Argonauta* shows that the adult shell, in this case, is not a structure which can be homologised with the shells of other Cephalopods. If, as is stated, the shell-gland actually flattens out, the shell may have arisen from a part of the mantle which originally corresponded to the shell-gland. The position of the animal with respect to the shell is the same as in the Ammonites and *Nautilus*, while, in *Spirula*, on the contrary, the orientation is different, the concave and not the convex side of the shell here corresponding to the ventral side.

An attempt has recently been made to derive the Argonaut shell directly from that of *Scaphites*, the external form in the two cases having a certain similarity (STEINMANN, No. 43). We are unable to accept such a view because we do not regard the Argonaut shell as directly homologous with the Ammonite shell, apart from the fact that a long period elapsed between the disappearance of *Scaphites* and the appearance of *Argonauta*, the latter, moreover, belongs to the order Octopoda and is thus closely related to the other living Dibranchia.

If the shell of *Argonauta* is to be derived from that of *Scaphites*, a comparatively quick disappearance of the chambering of the shell without essential modification of the external form must be assumed. The chambering of the shell, however, and the manner in which the animal is connected with it reappears in so marked a manner in all Cephalopoda (in which the shell is well preserved) that we are not warranted in assuming that *Argonauta* relinquished the chambering shell and received sea-water into the living chamber, a change which would involve a complete alteration of the manner of life of the animal.

From what is known of the modifications undergone by the Cephalopod shell, it always appears to take place in the same way as in the forms with internal shells. Although, in them also, the significance of the shell is essentially modified, the chambering is retained (*Belemnites*) and disappears only when the degeneration of the shell has reached its highest limit (horny shell of the Dibranchia). We might presuppose a similar process in the ancestors of *Argonauta*, and thus claim the shell which occurs only in the female and is altogether wanting in the male, as a new formation.*

The only Cephalopod provided with an external shell, the ontogeny of which is at present known, is thus not adapted to assist in the solution of the problem as to the significance of the shell-gland; we are therefore restricted to the embryological facts concerning the forms with internal shell.

Since the invagination known as the shell-gland secretes the whole shell, and therefore also the part of it which corresponds to the rostrum of the Belemnites, and as this is a part added to the primitive (Ammonite or Nautilus) shell, there can be no doubt that the invagination is the equivalent of at least that part of the mantle-sac which covers the internal shell. The extraordinarily early appearance of the invagination indicates, however, that, in the Cephalopoda as in other Molluscs, the original shell owes its origin to a shell-gland. If this is the case, we might assume that in the course of development the shell-gland became connected with this secondary mantle-sac. The position of the primitive invagination is easily reconcilable with this assumption. This question can be satisfactorily answered only when the formation of the shell in recent Cephalopods with external shell such as *Spirula* and above all *Nautilus*, is understood. Since the first of these forms is closely allied with the Decapoda and since, from the examination of the ovaries in the latter (OWEN, No. 33) it is known that, like other Cephalopoda, it has large eggs rich in yolk, it is not too much to assume that similar processes of development took place in these forms also, the conditions of development of the shell especially being similar.

C. The Sensory Organs.

The sensory organs of the Cephalopoda (olfactory, auditory and visual organs) show much similarity in their development, all appearing first as invaginations of the ectoderm. The olfactory organs are, throughout life, mere ectodermal invaginations, but the auditory organs and especially the eyes become partly or altogether separated from the ectoderm and reach a high degree of development. In these cases also, however, traces of the connection with the ectoderm may be retained either as vestigial or specialised structures (as in the auditory organs) or by the retention of the original aperture of invagination, this latter condition being exhibited in the eye of *Nautilus*.

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* *Cirrhoteuthis* is said, unlike other Octopoda, to possess a shell, the nature of which, however, is not well understood. If it is a true shell, it no doubt arises from a shell-gland as in the Decapoda, and we should be justified in assuming that forms like *Octopus* and *Argonauta*, in which a shell-gland occurs, once possessed vestigial shells. The case inhabited by *Argonauta* could then no longer be homologised with a true Cephalopodan shell.

The Olfactory Organs.

These organs, unlike the eyes and the auditory vesicles, appear in the embryo at a very late stage. In *Sepia*, in which they were observed by ZERNOFF (and previously by KÖLLIKER) at a time when all the arms, the funnel and the chromatophores have already formed, there appears, behind each of the eyes, a round prominence. The edges of this rise and curve over towards the centre and thus an invagination of the ectoderm is brought about which at first is rather shallow and sac-like, its floor being much thickened, while the covering consists of thinner cell-layers. Some of the ectodermal elements in the floor of the olfactory sac take the form of spindle-shaped sensory cells produced into stiff setae. This is the condition in the adult *Eledone*, while in *Sepia* and *Loligo* the intermediate and supporting epithelial cells become much lengthened and invested with movable cilia. The organ at a later stage becomes deeper and sac-like this being the usual adult condition.

The papillae which, in *Argonauta*, usually take the place of the olfactory pits, are considered by KÖLLIKER as the equivalent of the prominences which, in other Cephalopods, ontogenetically precede the invagination, this author consequently regarding them as a lower stage of development of the olfactory organ.

These organs cannot be homologised with the osphradial olfactory organs which are so strikingly developed in the Prosobranchia, and in a lesser degree in many other Molluscs, since the latter are found in the mantle-cavity near the gills, whereas the former occur on the head near the eye. In *Nautilus*, true osphradia occur near the gills. [According to WILLEY, two pairs of these organs are present. This author also described two pairs of olfactory tentacles, the pre- and post-occular tentacles.]

Otocysts.

The rise of the otocysts has been observed in most of the forms of which the ontogeny is known, and these organs have already been depicted in many of the figures here given (Figs. 116-118, p. 260, 122, p. 265, 126 p. 270 and 128 p. 273). KÖLLIKER examined in detail their (later) structure, and they were subsequently carefully studied by RAY LANKESTER and GRENACHER.

The position of the otocysts in the embryo may be ascertained from the above-mentioned figures. They form as depressions of the ectoderm (Fig. 141 *A*) which gradually deepen and become vesicular (Fig. 141 *B* and *C*). The aperture of invagination does not close for some time, and its connection with the sac becomes elongated and tubular (*B* and *C*). This appendage, which was described by **Kölliker** and by **Grenacher**, named **Kölliker**'s duct, seems at first to communicate with the exterior, but is said later to become separated from the surface and to end blindly. Its interior is lined with cilia directed towards the aperture of the otocyst which are in constant undulating movement. This appendage is also found in the adult. **Balfour** compares it with the *recessus vestibuli* of the Vertebrates, the blind appendage of the primitive auditory vesicle which represents its former connection with the point of invagination.

In that part of the wall of the auditory vesicle which lies almost opposite to the point at which **Kölliker**'s duct enters, the epithelial cells thicken to form the *crista acustica*, and it is here that the secretion of the *otolith* takes place (Fig. 141 *D*).

The further development of the otocysts is brought about by the differentiation of the *crista acustica* which extends far over the wall of the vesicle. The cells of the *crista acustica* lengthen, the inner free ends developing a number of fine hairs. In this way arise the sensory epithelia which compose the auditory ridges described by **Kowalevsky** and

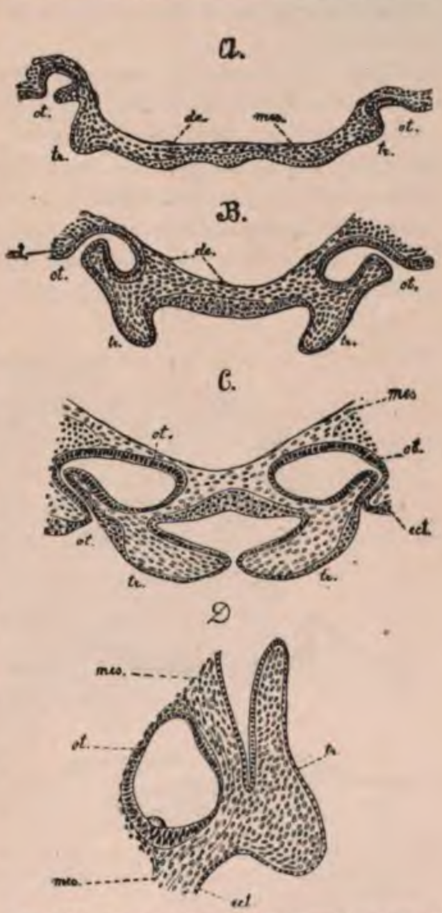

Fig. 141.—Sections through the funnel-region of several advanced embryos of *Loligo vulgaris* (original). *A-C*, transverse sections, *D*, sagittal section, somewhat diagrammatic. The yolk has been omitted. *de*, yolk-epithelium; *ect*, ectoderm; *mes*, mesoderm; *ot*, otocyst; *tr*, funnel-folds.

OWSJANNIKOW (and also probably the auditory plate which only develops later). In examining the formation of this terminal sensory apparatus, GRENACHER thought he could also recognise the nerves which give off branches to the cells in the form of delicate fibrous strands.

While the internal structure of the otocysts is thus developing, the organs change their position, gradually shifting from a lateral position to below the funnel (Fig. 141 *A-C*) where, as large closed sacs, they are found in close contact with the pleuro-visceral ganglia (Figs. 133, *ot*, p. 283 and 143, *ac*). Finally they come into close contact with one another and flatten by mutual pressure, as was observed in GRENACHER'S embryo and in *Sepia*. Their definitive position being attained, the cephalic cartilage develops round them.

The Eyes.

The origin of the eyes in the Cephalopoda has been carefully studied by GRENACHER (No. 14), RAY LANKESTER (No. 29), and BOBRETZKY (No. 4).

Figs. 115-119, pp. 253-261 will help the reader to understand the orientation of the eye-rudiments in the embryo. These organs originate in connection with the large swellings (Fig. 115, *au*) as two large, rather shallow ectodermal depressions (Fig. 142). The floor of each depression soon thickens considerably and its margins grow up and over it towards the centre (Fig. 142 *B*). A vesicle is thus produced with a thin outer and thickened inner wall and this is connected with the exterior by a small aperture. The inner wall of this vesicle yields the retina, while the outer wall yields a part of the lens and the ciliary body.

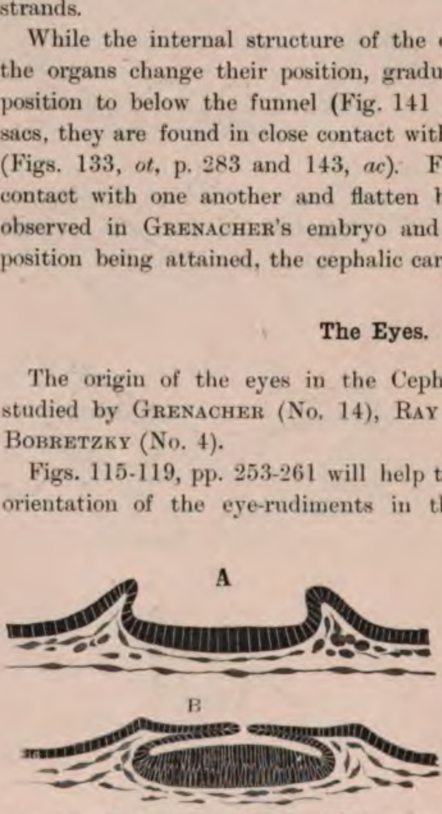

FIG. 142.—Transverse sections through two stages of the eye in *Loligo* (after RAY LANKESTER, from BALFOUR'S Text-book). The ectoderm is represented dark.

It is an interesting fact that this stage of development is retained throughout life in the eye of one Cephalopod, *Nautilus* (Fig. 145). The adult eye, in *Nautilus*, corresponds to the primitive optic vesicle, the cavity of which is lined by the retina, *i.e.*, modified ectoderm, and communicates with the exterior through an aperture. The sensory epithelium is consequently directly bathed by the sea water, and its ectodermal character thus becomes very evident. Eyes thus simply constituted have already been met with in a few primitive Gastropods (Fig. 90, p. 198).

In the Dibranchiate Cephalopoda, the eye reaches a higher grade of development. The first advance is the closing of the primitive optic vesicle and its abstriction from the ectoderm. Mesoderm-cells then press in between the latter and the outer wall of the vesicle, a process the commencement of which is indicated even in Fig. 142 *B*. After the abstriction of the optic vesicle, this stage may be compared to the permanent condition of the eye in the majority of the Gastropoda (Fig. 145 *B*).

FIG. 143.—Transverse section through the head of an advanced embryo of *Loligo* (after BOBRETZKY, from BALFOUR'S Text-book). *ac*, otocyst ; *adk*, optic cartilage ; *ak* and *y*, lateral cartilage and white body ; *cc*, iris ; *ff*, funnel-fold ; *gc*, cerebral ganglion ; *gm*, membrana limitans ; *gls*, duct of the salivary gland ; (*g.op*), optic ganglion ; (*g.vs*), visceral ganglion ; *rt*, retina ; *vc*, vena cava ; *vd*, stomodaeum ; *vk*, ciliary region of the eye ; *x*, thickened ectoderm in the floor of the funnel.

A second circular ectodermal fold now rises above the optic vesicle, enclosing a depression which strongly resembles the primitive optic pit (Fig. 145 *B*). Almost simultaneously, the (cuticular) secretion of a conical structure (Fig. 143) commences on the inner surface of the external wall of the vesicle; this is the first indication of the *lens*. This rudiment increases in size through the deposit of concentric layers (Fig. 144 *A*).

The lens of the Cephalopodan eye is not yielded by the outer wall of the primitive optic vesicle alone, since the floor of the second invagination above the vesicle also takes part in its formation (Fig. 143). From this latter is formed an anterior and smaller section of the lens (Fig. 144 *A* and *B*). The cell-layers formerly lying above the first-formed lens are in this way gradually used up (Figs. 143 and 144).

FIG. 144.—Sections through the eye of *Loligo* in two stages of development (after BOBRETZKY, from BALFOUR'S Text-book). *a* and *a'*, the epithelium lining the anterior optic chamber; *af*, and *if*, iris fold; *aq*, equatorial cartilage; *cc*, small ectoderm-cells of the ciliary body; *gz*, large cells of the ciliary body (*m*); *hl*, inner part of the lens; *ms*, mesoderm-tissue of the ciliary body; *rt*, inner, *rt''*, outer layer of the retina; *st*, rods; *vl*, anterior part of the lens; *x*, epithelium of funnel.

The primitive optic vesicle and the invagination lying above it also yield the ciliary body, the wall of the former, which is directed outward, and the floor of the latter uniting for its formation (Fig. 144 *A* and *B*). The mesoderm present between these two ectodermal cell-layers no doubt gives rise to the musculature of the ciliary body. The anterior or outer part of the invagination (or rather fold) becomes the iris (Figs. 144 and 145). Mesoderm-elements find their way in large numbers into this anterior fold also.

Another circular fold now grows over the eye at this stage of its development and gives rise to the *cornea* (Fig. 145 *C*). This fold, in many Cephalopoda (*e.g.*, Oigopsida) does not close, the cornea retaining its aperture which is often somewhat wide and through which the sea water can enter the external optic chamber, while in others (*e.g.*, the Myopsida among the Decapoda and the Octopoda), the cornea either retains only a minute aperture or else completely closes, thus precluding any communication between the optic chamber and the sea water. Another fold round the eye gives rise to the eyelid found in some Cephalopoda (especially in the Octopoda, Fig. 145 *C*, *Int* ⁴).

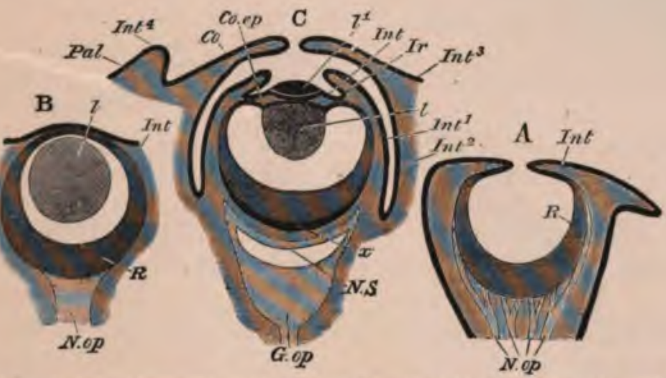

Fig. 145.—Diagrams representing the eyes of *Nautilus* (*A*), a Gastropod (*B*), and one of the Oigopsida (*C*) (after GRENACHER from BALFOUR'S Text-book). *Co*, cornea; *Co.ep*, epithelium of the ciliary body; *G.op*, optic ganglion; *Int-Int*⁴, integument (ectoderm); *Ir*, iris; *l*, lens; *l*¹, outer section of the lens; *N.op*, optic nerve; *N.S*, nerve-layer of the retina; *Pal*, eyelid; *R*, retina; *x*, outer layer of the retina.

The course of development of the Cephalopod eye described above shows that it attains a high degree of perfection, as may indeed be seen from an examination of the adult eye.

D. The Nervous System.

All investigators of the origin of the nervous system in the Cephalopoda were formerly unanimous in tracing it back to the mesoderm (RAY LANKESTER, USSOW, BOBRETZKY). More recently, the formation of the nervous system has been studied by VIALLETON, who found that the ganglia arise through the thickening of the external layer; these thickenings, however, yield at the same time mesodermal tissue. Other similar thickenings of the ectoderm are principally formative centres for the mesoderm.* This view also, therefore, does not establish any sharp distinction between the central nervous system in the process of formation and the mesoderm. At the same time, we have to emphasise the fact that in the Cephalopoda as in other Molluscs, the nervous system is of *purely ectodermal origin* (KORSCHELT, No. 25).

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* See further, p. 307.

The **cerebral ganglion** arises in the form of an ectodermal thickening above the rudiment of the stomodaeum. Before the latter sinks in, the ectoderm above this region becomes multilaminar (Fig. 131 *D*, *ect.*, p. 280). This ectodermal layer, which at first is thin, thickens greatly after the stomodaeum has become invaginated (Fig. 146 *A*, *cg*), and a large ganglionic mass forms at this point, consisting

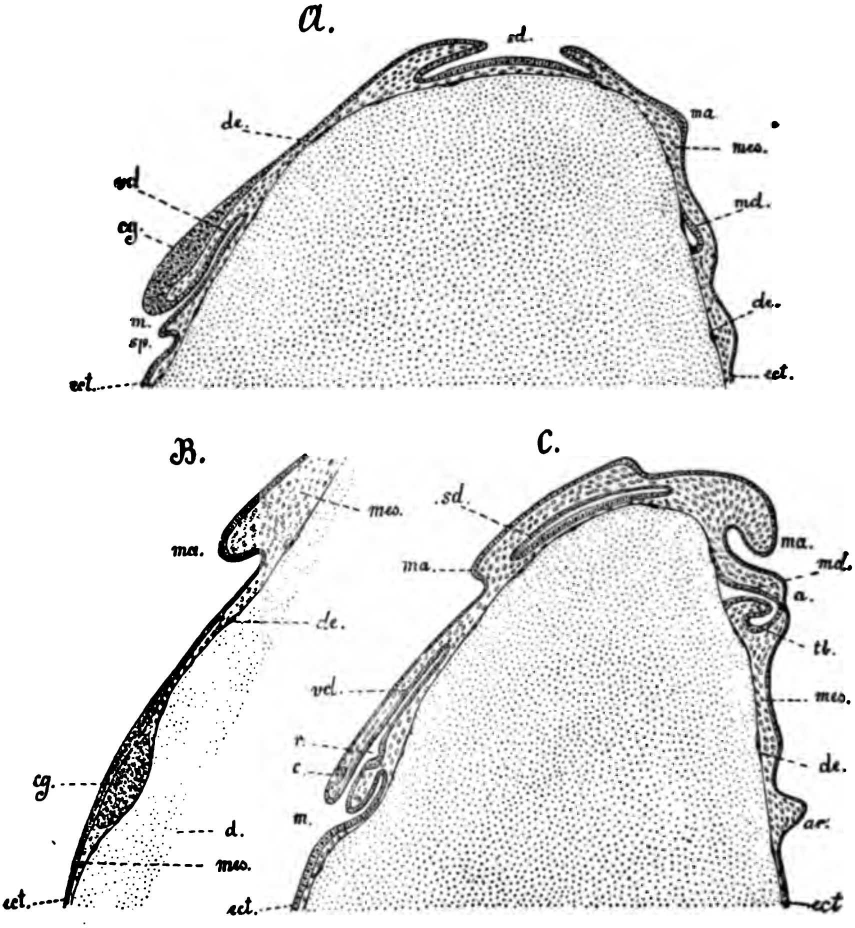

FIG. 146.—Sagittal sections through embryos of *Loligo* of various ages, somewhat diagrammatic (original). Section *B* is made in the region of the mouth. *a*, anal region; *ar*, arm-rudiment; *c*, cerebral commissure; *cg*, cerebral ganglion; *d*, yolk; *de*, yolk-epithelium; *ect*, ectoderm; *m*, mouth; *ma*, mantle-fold; *md*, enteron; *mes*, mesoderm (diagrammatic); *r*, radular sac; *sd*, shell-gland; *sp*, salivary-gland; *th*, ink-sac; *vd*, stomodaeum.

of two parts connected together by a commissure which at first is broad but narrows later; these are the two halves of the cerebral ganglion, which become detached from the superficial ectodermal layer and, in sagittal section (Fig. 146 *B*, *cg*), appear as spindle-shaped bodies. The ectoderm, at the formative centre of the cerebral ganglia (above the mouth) is now again a thin layer (Fig. 146 *B* and *C*). In the median section (*C*), the cerebral commissure (*c*) can here be recognised.

The paired rudiment of the cerebral ganglion was early observed (by the above-named zoologists as well as by GRENACHER). The two ganglia greatly increase in size and finally fuse together. In consequence of processes of growth, the relative position of the cerebral ganglion and the mouth is modified in a striking manner (Fig. 133, p. 283).

The **optic ganglia** also form as massive thickenings of the ectoderm in the cephalic region. They are directly connected with the ectodermal thickenings which become the cerebral ganglia and soon press in below the optic vesicles, a process which evidently gave rise to the statement that the optic ganglion arises on the posterior side of the optic vesicle, from the mesodermal cell-elements there present. The optic ganglion soon shows a close connection with the optic vesicle, a connection which leads to the formation of the optic nerve.

The **pedal** and the **pleuro-visceral ganglia**, like the other ganglia, are said to originate through differentiation of the cell-masses lying between the ectoderm and the alimentary canal. In reality they are due to ectodermal thickenings in the ventral part of the embryo. The pleuro-visceral and pedal ganglia, like the cerebral ganglion, are each composed of two parts of distinct origin. The two cell-masses which yield the pleuro-visceral ganglion lie behind the otocyst, and the masses that produce the pedal ganglion in front of that vesicle (BOBRETZKY, USSOW, Fig. 133, p. 283).

During the course of development, the three ganglia just mentioned gradually shift nearer one another and, as the yolk-sac disappears, move towards the stomodaeum, where they finally fuse, the pleuro-visceral and pedal ganglia uniting to form the sub-oesophageal mass which is connected with the cerebral ganglion by two short commissures, a broad posterior and a narrow anterior commissure.

The anterior section of the sub-oesophageal mass, which is, to a certain extent, marked off from the rest, and into which the narrow commissure enters, is distinguished as the brachial ganglion. This part becomes differentiated from the pedal ganglion at a time when the latter has not yet fused with the visceral ganglion (**Pelseneer**). According to the above author, who is confirmed by **Bobretzky**, the buccal ganglia originate in the same way, becoming abstricted from the cerebral ganglia and shifting forward, but Ussow states that they have a separate origin like the principal ganglia, and unite with these only at a later period. A similar origin is claimed by Ussow for the splanchnic and the stellate ganglia.

The ganglia can easily be recognised by the fact that, soon after their appearance, a differentiation into an outer cellular layer and a central fibrous mass takes place.

The connection of the ganglia with the sensory organs and the peripheral parts of the body takes place only at a somewhat later stage. Ussow assumes that the cells of the layer which produced the ganglia lengthen and thus yield the nerve-fibres, as described above (p. 193) for the Gastropoda.

The above interpretation of the nervous system is not accepted by all anatomists. The anterior part of the sub-oesophageal mass, the brachial ganglion, has been regarded as a part of the cerebral ganglion, which in consequence of the great lateral extension of its anterior section, finally stretched below the oesophagus, fused here in the middle line, the anterior part being constricted off and remaining connected only by a commissure with the cerebral ganglion (v. **Jhering**, **Grobben**, No. 16).

The brachial ganglion supplies the arms with nerves; some of these nerves, however, are said not to arise from the brachial ganglion but to pass into the cerebral ganglion through the anterior commissure (**Dietl**, No. 10). This connection and the conditions found in *Nautilus* have led to the view that the brachial ganglion belongs to the brain. In *Nautilus*, the majority of the tentacle-nerves spring from the part of the middle oesophageal ring which might be indicated as the pedal ganglion, but some originate above the roots of the optic nerves, and are thus thought to be cerebral in origin. According to this interpretation, the part of the oesophageal mass known as the pedal ganglion would then also have to be reckoned as belonging to the cerebral ganglion, since we cannot claim some of the tentacle-nerves as cerebral nerves and the others as pedal nerves.

This question is of importance in connection with the interpretation of the arms which, if innervated from the brain, would have to be regarded as cephalic appendages, while, if they derived their nerves from the pedal ganglion, they would have to be considered as parts of the foot. Some of the facts of ontogeny and comparative anatomy have recently been shown to be opposed to the first of these views and to favour the second. According to **Pelseneer**, as already mentioned, the brachial ganglion at first forms by abstriction from the pedal ganglion, and is thus not in any way closely connected (as assumed) with the cerebral ganglion.

Before the brachial ganglion separated from the pedal ganglion, a nerve-strand ran from the anterior part of the (primitive) pedal ganglion to the arms, a similar strand running from the posterior part of the ganglion to the funnel. The latter, the pedal nature of which can hardly be doubted, thus (according to PELSENEER), at this early stage, receives its nerve-elements from the same ganglion as the arms.

Another argument in favour of the pedal nature of the arms is found in the statement of JATTA (No. 18) that the brachial nerves have their roots in the pedal ganglion and that they do not pass into the cerebral ganglion as has been stated. PELSENEER further rightly points out that the arms in their origin (and also in the manner of their innervation) are clearly ventral organs, and those that assume a dorsal position only reach it in a late stage of development (p. 263). Only as the arms are displaced anteriorly, and to some extent dorsally, does the part of the central nervous system innervating them and originally belonging to the pedal ganglion shift in a dorsal direction (PELSENEER, No. 38). J. STEINER's physiological researches,* according to which the destruction of the pedal ganglion led to paralysis of the arms and thus proved them to belong to the foot-region, are also significant in this connection.

We thus have strong reason for regarding the arms, not as cephalic appendages, but rather as greatly modified parts of the foot (*cf.* Chap. XXXIV.).†

E. The Cartilaginous Skeleton.

The various parts of the cartilaginous skeleton are regarded by some authors (METSCHNIKOFF, USSOW) as ectodermal structures which have gradually shifted inward. BOBRETZKY's figures of the optic cartilage seem to confirm this method of origin which at first sight is surprising. Around each eye (Fig. 143 *ad*, *adk*), the ectoderm is seen to become greatly thickened; these thickenings, in consequence of the development of the folds described above, come to lie deeper. Even if these figures appear convincing, we must not exclude the conjecture that some part of the superficial cell-layers may have already become differentiated, and in this case might be reckoned as mesoderm.

F. The Gills.

The gills were found to arise as papilla-like prominences in front of the mantle near the anal region (Fig. 85 *C* and *D*, *k*, p. 189), to be gradually grown over by the latter (Figs. 87 and 88 *B*, p. 194),

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* Sitz.-Ber. Akad. Berlin, 1890.

† [More recently KERR (No. II.) has opposed the pedal nature of the arms of *Nautilus* and reverted to the older view of GROBBEN that they are cephalic. While advancing several weighty arguments against some of the evidence which has been put forward regarding their pedal nature, he practically gives no striking reasons in favour of their cephalic nature and we think that at present, at any rate, we cannot unhesitatingly accept his conclusions. The question seems to rest on the justification of the attempts to homologise the anterior sub-oesophageal ganglionic mass of the Cephalopoda with one of the highly differentiated ganglia of the Prosobranchia.—ED.]

and thus eventually to lie within the mantle-cavity. They had previously become flattened, and their surfaces folded in such a way as to produce the bipectinate gills characteristic of so many Molluscs (pp. 72 and 208).

The development of the gills in *Sepia* was very carefully studied by JOUBIN (No. 20). Further foldings of the leaflets take place, and as these processes are repeated in the secondary leaflets, a somewhat complicated gill is produced consisting of three systems of folds one above the other; this is peculiar to the Cephalopoda.

According to JOUBIN, the mesoderm is the chief factor in the development of the gills which, by its own increase, determines the growth of these organs and the modifications in their shape. The gill-rudiment, when still papilla-like, was composed of the superficial ectoderm-layer and a massive mesoderm (Fig. 134, *k*, p. 284). The young gill, also, when only slightly differentiated, consists largely of mesodermal tissue, in which, at a later stage, the cavities of the blood-vessels form in the usual way, through the moving apart of the cells. Only the larger vessels develop walls of their own. The afferent (venous) and efferent (arterial) vessels, lying in the axis of the gill (the middle lamella) become connected with the principal blood-vessels of the body, and the afferent vessel of each gill is said at its base to give rise to an auricle. In other Molluscs we saw the auricles form from the coelomic sacs, like the ventricles; we must therefore accept these statements with caution.

G. The Mesodermal Structures.

The rise of the mesoderm, and of the organs derived from it, is still very imperfectly known in the Cephalopoda, and can therefore only be briefly noticed. We shall have to follow chiefly the older researches of BOBRETZKY and USSOW, and shall have repeatedly to refer to the conditions found in the adult animals.

We have already described the first rudiment of the mesoderm as being contained in the peripheral thickening of the germ-disc (Figs. 112-114, p. 247, etc., and Fig. 131, p. 280), and as lying, after the differentiation of the entoderm, between it and the ectoderm. Thus at first it forms a circular thickened layer, which then extends both towards the centre of the germ-disc and towards its edge. In this way it attains a size which, as compared with that of the other layers (ectoderm and entoderm), is very considerable (Figs. 131 and 132).

According to the view of VIALLETON, which has already been mentioned, a delamination of the mesodermal part from the outer layer takes place even at the time when, according to the account here given, the germ-layers have long been differentiated. At a much later stage also, when the rudiments of the organs have appeared and have to some extent developed, the ectoderm continues to yield mesodermal cell-material. VIALLETON compares this process with the development of mesoderm in the Annelida as described by KLEINENBERG (Vol. i., p. 286), and refuses to acknowledge this mesoderm as the equivalent of a distinct germ-layer. Such a view can best be understood in connection with the Cephalopoda in which the formation of the germ-layers is evidently greatly influenced by the large amount of yolk in the egg, the distinction between the layers appearing almost obliterated, but in this case, as in that of the alimentary canal and the nervous system, we must postpone a decision until further light is thrown upon the matter.

In the Cephalopoda, especially in *Nautilus* and the Decapoda, the **secondary body-cavity** (the **coelom**) is very well developed and surrounds the heart with its afferent and efferent vessels, the branchial hearts, the pericardial glands, the genital organs and the stomach, and is connected with the cavities of the nephridia (GROBBEN, No. 15). The last two organs lie in the posterior section of the body-cavity which is incompletely separated from an anterior section by a septum.

In the Octopoda the body-cavity is much reduced, being represented merely by a system of narrow canals formerly claimed as a water-vascular system. In consequence of its slight development, the coelom no longer surrounds the heart, the branchial hearts and the stomach (GROBBEN).

As the condition of the coelom in the Cephalopoda is so primitive, we are led to expect the coelomic sacs to appear distinctly in their ontogeny. But the conditions of the formation of the mesoderm above described seem in this respect to be unfavourable. A splitting of the mesoderm into a somatic and a splanchnic layer has indeed been asserted by USSOW, but is not noticed by other observers and, in any case, does not lead to the formation of coelomic and pericardial sacs such as were met with in the Gastropoda or such as we might expect in connection with the well-developed coelom of the adult Cephalopod. We may observe in passing that there are reasons for believing that structures of this sort may yet be found in the Cephalopoda.

The **kidneys**, in the Cephalopoda, show the same primitive condition as in other Molluscs. In the Octopoda, they are represented by two sacs lying symmetrically; in the Decapoda these have united to form a single sac. The renal sacs open out through ureters on either side of the anus.

A comparison of the Cephalopodan kidney with the nephridia of the segmented animals seems specially suitable on account of two pairs of renal sacs being found in *Nautilus*, each pair opening out through a distinct aperture. One of these pairs, however, is without an aperture into the coelom, and its significance as a true nephridium is therefore doubtful; we must rather imagine it to be a new structure formed from the posterior pair (which alone is originally present). This process may have been connected with the development of four gills, which some believe to be a secondary condition and which has led to the assumption that the Tetrabranchia (*Nautilus*) were derived from Dibranchia (v. JHERING, No. 19). Although *Nautilus* is, without doubt, a very ancient and primitive form, there are certain signs (*e.g.*, the degeneration of the efferent genital duct) that it was already specialised in a definite direction, and thus might have acquired a second pair of gills. The same argument would apply in the case of the kidney. This view would find some support from the fact that, in other Mollusca, only one pair of nephridia and, with the exception of *Chiton*, only one pair of gills are present.

The certain information we possess as to the development of the kidneys is as yet too scanty to enable us to settle this question. It was shown by BOBRETZKY that, in *Loligo*, the kidneys arise directly under the covering of the postero-dorsal surface as two distinct sacs in the mesoderm, and only later unite, and assume the close relation to the veins which they show in the adult. The inner wall of the kidneys is much folded, and thus yields the aciniform structures known as venous appendages (GROBBEN).

Our knowledge of the development of the **genital organs** also is still very incomplete. The genital glands arise as thickenings of the pericardial epithelium near the heart (BOBRETZKY, SCHIMKEWITSCH). This primitive relation to the pericardium or coelom is preserved by them throughout life, but at a later period a (genital) capsule is formed round the glands by a peritoneal fold ; the cavity of this capsule, however, remains permanently in connection with the body-cavity, and thus forms a part of the latter (BROCK, GROBBEN).

The **efferent ducts**, of which there is one pair, are connected with the capsule. When, as in most Dibranchia, there is only one efferent duct, this must be considered as due to degeneration, as is proved by the presence of paired ducts in the Octopoda, in *Ommastrephes* (a Decapod) and in *Nautilus*, this latter form having one functional and one reduced oviduct.

This relation of the efferent genital ducts suggests that they are modified nephridia (see Vol. iii., p. 42 footnote), and the question thus again arises whether the Cephalopoda possessed two pairs of nephridia and in this respect a segmentation (which, however, would be incomplete). Such a view is by no means justified by what is known of those Molluscs which on the whole show conditions more primitive than those of the Cephalopoda. These Molluscs afford no convincing evidence of segmentation. We must therefore regard efferent ducts as having formed independently of the nephridia, or else as derived by fission from nephridia, but cannot consider them as independent nephridia.

The blood-vascular system. Even in the case of this system of organs, so well developed in the Cephalopoda, very little is known ontogenetically,* and

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* BOBRETZKY appears to have studied the development of the circulatory apparatus in detail, but as his work is in Russian, we are limited to the descriptions of the figures and a short abstract in Anat. Jahresb. Hofmann and Schwalbe, Bd. vii., 1878, and this applies also to our former references to his observations.

we must content ourselves with a brief summary of the accounts given of its origin.

According to BOBRETZKY, the arterial heart is derived from two sac-like organs which first appear as cavities in the massive mesoderm near the rudiment of the intestine and the yolk-sac. Round these, the cells become regularly arranged, and the two sacs or vesicles thus produced then unite to form the heart. The formation of the auricles has already been mentioned (p. 306).

The arteries arise as canals in the mesoderm, their limits being marked by the regularity of arrangement in the cells; at a very early period blood is driven through them, in consequence of the commencing pulsations of the heart. After the two sacs have united to form the heart, the two pericardial sacs are said to extend towards the latter, so as to enclose the heart in the same way as in other Molluscs (SCHIMKEWITSCH). The branchial hearts abut on that part of the body-cavity which encloses the heart, and are also covered by the peritoneum. The pericardial glands (the so-called branchial appendage) develop from the latter as growths of the epithelium; these glands are connected with the branchial hearts and are held to be excretory organs. The branchial hearts are said to be differentiated from the mesoderm at the broad bases of the gills, and the whole venous system, the venae cavae (chiefly the anterior vena cava) being specially noticeable in the embryo, arises as lacunar spaces in the mesoderm, some of these spaces changing into actual veins and others into irregular blood-sinuses (BOBRETZKY).

SCHIMKEWITSCH attributes the origin of the blood-corpuscle to the increase in number and migration of cells of the yolk-epithelium in the posterior part of the body, and thus assumes for them an origin similar to that of the blood-cells in the Arachnida, the latter being formed from migrating yolk-cells (Vol. iii., p. 88). We refrain for the present from expressing an opinion on these somewhat improbable statements.

Chromatophores, subcutaneous tissue, musculature. The layers of the mesoderm lying beneath the ectoderm become transformed into the so-called fibrous layer, while the deeper layers yield the connective tissue and muscle-fibres of the cutis and also, in any case, the muscles of the external organs. The chromatophores, also, are said by nearly all authors to originate here, but a somewhat different view of their origin has recently been propounded.

The time of the appearance of the chromatophores in the different forms varies greatly (*cf.* Figs. 120 and 121, p. 263). In *Loligo*, for instance, they appear very late, but in the Cephalopod described by GRENACHER at an early stage, before the circumcrescence of the yolk by the blastoderm is completed and before the organs have appeared (Fig. 125, p. 268). In the last case, a very early differentiation of these mesoderm-layers seems to have taken place.

The chromatophores are said to be derived from mesoderm-cells which are distinguished from the surrounding cells by their large size and by the early deposit of pigment in their protoplasm (GIROD, No. 13). At a later stage, they are covered by a thick envelope; the cells in the neighbourhood stretch out into spindles and become connected with the chromatophoral cells. In this way arises the well-known appearance of the (contractile) fibre-bundles connected radially with the chromatophoral cells. The change of shape in the pigment-cells which is accompanied by change of colour was usually attributed to the contractility of these bundles, *i.e.*, they have been regarded as muscle-fibres, while some authors have ascribed a capacity for contraction to the pigment-cells themselves, the radial fibres being considered as merely connective tissue which, it was assumed, held the actual chromatophores in position (GIROD).

Another account of the origin of the chromatophores has recently been given (JOUBIN, No. 23). According to this view, the ectoderm-cells, which are especially distinguished by their size, sink inwards through a funnel-like depression. In the large cell at the base of the depression, the protoplasm becomes differentiated and, later, pigment appears. The cell then loses its connection with the ectoderm. A number of mesoderm-cells which could be seen even earlier regularly arranged below it, and which soon multiply still further, yield the radial fibres. The chromatophores would thus be due to the combined action of the outer and the middle germ-layers (JOUBIN).

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CHAPTER XXXIV.

General Considerations on the Mollusca.*

In attempting to combine into one general scheme the developmental phenomena described in the preceding chapters, in connection with the different divisions of the Mollusca, we cannot, of course, take into account all the very different ontogenetic processes, but can only select from among them those that are of the more general significance.

Even in the **cleavage of the egg,** great variety prevails. Thus we find, on the one hand, that the meroblastic type of cleavage attains its highest development among the Mollusca (Cephalopoda) but, on the other, that total and, at first equal, but soon after unequal cleavage is still more common in eggs of this phylum (*Chiton*, Gastropoda), and so also is a type of cleavage which from the first is unequal (Solenogastres, Lamellibranchia, Solenoconchae). The cause of this difference is to be sought in the varying amount of yolk contained within the eggs but, even among eggs showing total cleavage, there are some that, through a secondary separation of the yolk-mass from the blastomeres, lead us to the meroblastic method of cleavage (*Nassa*). The latter is to be explained as due to the extraordinarily large amount of yolk in the egg, and this same peculiarity further determines so great a modification of the early ontogenetic phenomena in the Cephalopoda, that this division must be left almost entirely out of account in our comparative review. Within each separate division of the Mollusca, the phenomena of cleavage are very similar and very regular.

The **formation of the primary germ-layers** takes place through the invagination of a blastula with a more or less wide cleavage-cavity, or, where the latter is wanting, and the egg is richer in yolk, through epibole. These two processes are found in nearly related forms, or

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* See note, p. 1.

else an invagination-gastrula appears as a stage following the epibolic gastrula, as, for instance, in *Ostrea* and various Gastropods, in which a cleavage-cavity arises only at a later stage, and the macromeres which are continuing to multiply press in towards it. There is also no essential difference between these two types of formation of the germ-layers. In the Cephalopoda also the germ-layers may be traced back to the same processes, although these are influenced in a marked manner by the large amount of yolk in the egg.

The **middle germ-layer** arises in a very similar way in all those forms in which it has been investigated. It originates in two primitive mesoderm-cells derived from one of the macromeres (primary entoderm). In the Gastropoda, in which this point has been best examined, the formation of the primitive mesoderm-cells from the macromeres was found to be very regular.* The large primary cells of the mesoderm have been discovered to exist in all the following divisions of the Mollusca: the Amphineura, the Lamellibranchia, the Solenoconchae and the Gastropoda. In the Cephalopoda, on the contrary, the development of the mesoderm has been considerably modified by the conditions mentioned above.

The **two mesoderm-bands** arise through the multiplication of the primitive mesoderm-cells. It has repeatedly been stated that mesodermal tissue is not due to the multiplication of these cells, but is yielded later partly by the ectoderm, as described for the Annelida. The first of these views, *i.e.*, the derivation of the mesoderm from the primary cells is, so far, the more probable, but the other view should not be summarily dismissed, and in any case deserves more careful investigation.†

It is very characteristic of the Mollusca that the mesoderm-bands are retained for only a short time. They soon disintegrate, single cells separating from them and becoming distributed in the cleavage-cavity as the so-called mesenchyme. Before this happens, however, or else during this process, a cavity appears in each of the mesoderm-bands: this is bounded by a more or less regular epithelial wall and is thus recognisable as the **coelom**. This process is the same already met with in the Annelida (Vol. i., p. 290), and Arthropoda (Vol. iii., p. 413). In these latter it leads to the formation of two mesodermal layers, one applied to the ectoderm and the other applied to the entoderm; these are the somatic and splanchnic layers. This seems

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* [See footnote, p. 119, Ed.]

† [See p. 29, Ed.]

likewise to be the case in the Chitons which in other respects also appear to be very primitive animals (Fig. 4 *A* and *B*, p. 8); they do not, however, show any suggestion of the segmentation of the mesoderm (formation of the primitive segments) so characteristic of the segmented animals.

The Amphineura, even as adults, show the secondary body-cavity well preserved. It is still very large, and contains the principal organs, such as the alimentary canal, the liver and the heart. In the higher Mollusca (Lamellibranchia and Gastropoda) it is much more reduced in comparison with the primary body-cavity and is even quite small. The primary body-cavity with the mesenchymatous tissue distributed in it is very large and becomes the *definitive body-cavity*, just as in the Arthropoda (Vol. iii., p. 423). In spite of this, the Molluscs have been regarded as typical Schizocoelata, *i.e.*, as forms devoid of a true coelom. Such a true coelom, however, is retained by them, though only slightly developed.

While in the Arthropoda, the coelomic sacs (primitive segments) usually completely disintegrate or at the most persist to a small extent in the genital glands (*Peripatus*, Myriopoda) the coelom of the Mollusca is always retained in the form of the *pericardium* from which the nephridia and the genital glands are formed (Gastropoda) in a manner recalling the primitive conditions in the Annelida. Where the connection between the kidneys, the genital organs and the pericardium has not yet been made evident in the embryo in consequence of insufficient investigation, or else where, in consequence of secondary modifications in the forms examined, it can no longer be demonstrated, the anatomical condition of the systems of organs clearly proves such a connection. In various Molluscs, the cavity of the genital glands is directly connected with the pericardial cavity (Amphineura, Cephalopoda), the nephridia entering the latter through an open funnel, a condition which recalls the open connection existing between the nephridia of the Annelida and the secondary body-cavity (Amphineura, Lamellibranchia, Gastropoda, Cephalopoda). *There can consequently no longer be any doubt that the pericardium of the Mollusca should be regarded as the secondary body-cavity;* and, apart from the absence of segmentation, the resemblance in this point to the Annelida is very great.

The condition of the mesoderm and the structures belonging to it is thus evidently of great importance in interpreting the Mollusca; it has therefore been considered in connection with the early ontogenetic processes. Hardly less important, however, is the *larval* *form* which also in several ways throws light upon the relationships of the Molluscs.

Although the larvae of the different divisions, *e.g.*, those of the Amphineura, the Solenoconchae, the Lamellibranchia, and perhaps also those of the Heteropoda and the Opisthobranchia appear with very different forms, all of them may without any difficulty be traced back to the *Trochophore*, the typical form of which was met with in the Annelida. In some cases, such, for instance, as the larvae of *Dondersia* and *Dentalium* (Figs. 10, pp. 17 and 138, p. 291) as well as in those of a few Gastropoda (perhaps of the Gymnosomatous Pteropoda, Fig. 77, p. 172) this is less evident, while in the larvae of other Gastropods such as *Patella*, *Paludina* and most Lamellibranchia, the resemblance is exceedingly striking (Figs. 51-53, p. 127; 56, p. 135; 14, p. 28; 18, p. 36). But even in larvae in which the resemblance is not so great (Figs. 66 and 67, p. 155; 72, p. 162; 75, p. 168), comparison with other forms or the examination of the younger stages enable us easily to trace back the larval form to the *Trochophore* (Figs. 64 and 65, pp. 153 and 154; see also p. 166). In the greatly modified ontogeny of the Cephalopoda, traces of the larval form have hitherto not been established with certainty.

The *development of the Molluscan Trochophore* closely resembles that of the Annelidan larva. It arises from the gastrula-stage, several rows of cells at the anterior region becoming covered with strong cilia and thus yielding the *pre-oral ciliated ring*, the *velum* of the Molluscan larva. The blastopore, which at first lies at the posterior end, usually becomes slit-like; it probably closes from behind forward and generally, at its anterior end, passes into the mouth through the formation of an ectodermal depression, the stomodaeum. A *post-oral ciliated ring* appearing behind the mouth heightens the resemblance to the typical *Trochophore*, the external form of the Molluscan larva now also agreeing with that of the latter, the anterior end being much widened and the posterior narrowed.

At the posterior end of the body, and thus at the point where the blastopore at first lay and from which its closure commenced, the anus now forms. It thus appears as if it also bore some relation to the blastopore; indeed, an attempt has been made to prove this to be the case in some Molluscs (*e.g.*, the Opisthobranchia), and in another Gastropod, *Paludina*, the direct transformation of the blastopore into the anus has been assumed. We thus find in the Mollusca conditions altogether similar to those met with in the Annelida and the Arthropoda, in which also relations were proved to exist between the mouth and the anus on the one hand and the blastopore on the other.

The intestine, which like the oesophagus, is usually formed by an ectodermal invagination in the Invertebrata, appears to be derived entirely from the entoderm in the Mollusca; thus the enteron usually fuses direct with the ectoderm, without any depression of the latter. This has been regarded as an important peculiarity in the organisation of the Mollusca, and much stress has been laid upon it, but if, as has been stated, an ectodermal intestine actually occurs in a few Molluscs (*Chiton*, *Teredo*, etc., pp. 15, 66, 208), the usual absence of the proctodaeum cannot be considered as a distinctive feature.

At the opposite end of the larval body, *i.e.*, at the cephalic pole, and in the midst of the velar area, an ectodermal thickening known as the *apical plate* is found, occupying the same position as in many other pelagic larvae. In the Annelida, the supra-oesophageal ganglion is thought to originate from the apical plate, and in the Mollusca also the *cerebral ganglion* is said to arise from it (*Chiton*, Lamellibranchia) or else to bear some relation to it (*Dentalium*). In the Gastropoda, indeed, the cerebral ganglia originate as two ectodermal thickenings of the pre-oral part of the body, but these also do not differ much in position from the apical plate, so that even here there may be some relation to the latter.

An organ of special importance in comparing the Molluscan *Trochophore* with other larval forms is the *primitive kidney*. This arises from cells derived from the mesoderm-bands,* in the same way as in the Annelida, as a tubular paired structure. Its relations to the primary body-cavity also seem to be the same as those met with in the Annelida and in the case of the adult excretory organ of the Plathelminthes.

It is evident from the above that the resemblance of the Molluscan larva with the *Trochophore* of other animal phyla, and especially with that of the Annelida is exceedingly striking not only in external form but in internal structure. Attempts have been made to account for this resemblance by the supposition that the larvae of these phyla gradually assumed the same organisation as a consequence of similarity in their manner of life. We do not share this view, and can only explain the remarkable external and internal similarity

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* [See footnote, p. 179. Ed.]

through actual relationship to one another of all those groups which have the *Trochophore* as their larval form.

If we accept this latter view, there can be no doubt as to the significance to be attributed to the larval form. Its reappearance in the development of phyla so different as the Annelida, the Mollusca, and the Molluscoida, points to a racial form having this structure. This brings us to the difficult and much discussed question of the origin of the Mollusca.*

Of the theories as to the origin of the Mollusca, two seem to us to demand our special attention, these being the theory that the Mollusca are derived from Turbellaria-like forms and that which derives them from a *Trochophore*-like ancestor.

The derivation of the Mollusca from Turbellaria-like forms has much in its favour, especially as it affords a partial explanation of the perplexing conditions of the nervous system. The pedal strands, according to this view, would correspond to the ventral longitudinal nerves of the Turbellaria, while the pleuro-visceral strands correspond to the lateral nerves. The resemblance is specially striking in the nervous system of the Amphineura (forms which somewhat resemble the Turbellaria in shape) which consists of four longitudinal strands with connecting commissures. A similar ladder-like nervous system with a ventral and a lateral strand on each side occurs in the Turbellaria (Triclada and especially *Gunda*). The anus, which is wanting in the Turbellaria, was acquired later, and so was the blood vascular system. The coelom is to be explained by the dilation of the genital glands, for the genital products originate, as was shown, from its epithelial wall. The shell, an important component part of the Molluscan organisation, arose for the protection of the body in the form of a cuticular secretion of the dorsal surface in which were deposited calcareous concretions. The foot, an equally essential part of the organism, resulted from the transformation of the ventral surface of the body, which was used for creeping, into a muscular sole, or else is assumed to be a modification of the ventral sucker.†

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* A great deal has been written on the relationships of the Mollusca. We refrain from discussing the different and often opposite views which have been propounded on this subject as they would merely add length to our account and make it the less clear. We shall only allude in passing to the *Trochophore* theory adopted by RAY LANKESTER and still more ardently by HATSCHEK, and to LANG's theory of the derivation from Turbellaria-like forms. A list of the most important works on the subject will be found at the end of this chapter. LANG's view has recently been published in his *Text-book of Comparative Anatomy* (Engl. Trans., Vol. ii.).

† THIELE, like LANG, derives the Mollusca from Turbellaria-like forms and regards the ventral sucker of the Polyclada as the organ from which, without

The above may, on the whole, be described as possible, but this origin has the disadvantage of starting from very highly differentiated animals; and, a point which appears to us as very important, affords no clear explanation of the striking resemblance existing between the larvae of the Mollusca and those of the Annelida. This resemblance is made possible if we go back farther, to a form from which may be derived both the *Trochophore* and the ancestors of the Turbellaria. Since, in such speculations, it is only right to try to start from existing forms, the common ancestral form of the *Trochophore* and the Turbellaria has been sought among the Ctenophora, but it is impossible to construct from them the desired ancestor without unduly forcing the comparisons. It is true that the Ctenophora, on account of their locomotion by means of cilia, their possession of the apical plate and the condition of the entoderm and mesoderm may be brought into relation with the Turbellaria and perhaps even with the *Trochophore*, but it appears to us still more certain that in them we have forms already strongly specialised in a definite direction and thus no longer suited to serve as the ancestral forms of the Mollusca. Instead then of attempting to derive these forms from known and specialised groups, it seems to us simpler and at least equally justifiable to fall back upon some form with a more primitive organisation.

In considering the ontogeny of the Annelida, we started from a gastrula-like form, ciliated all over, which developed at the cephalic pole a ciliated tuft, and in which also the locomotory cilia were specially arranged in the form of a ring running round the body (the later pre-oral ciliated ring or velum). The primitive mouth (blastopore), originally lying at the posterior end of the body, becomes displaced forward owing to the development of a ciliated apparatus in this very limited region; thus the mouth shifts towards the locomotory apparatus which at the same time serves for conducting food to the mouth, as is still seen to be the case with the ad-oral zone and the post-oral ring of the *Trochophore*. In the primary body-cavity of this form, mesodermal elements are already found; among these lie the gonads which no doubt are derived from the entoderm as well as from the mesoderm [probably from distinct blastomeres which are neither mesodermal nor entodermal but are the germ-teloblasts], and which

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doubt, the foot arose (No. 20). The transformation of the sucker into the foot and the relation of the latter to the rest of the body is treated in detail by this author. It may here also be mentioned that THIELE ascribes to the Ctenophora a very important part, not only in the phylogeny of the Mollusca but in that of the bilateral animals generally.

are either still connected with the gastral cavity or already open externally through special efferent ducts (nephridia ?). A specially important organ of this hypothetical form which also lies in the primary body-cavity is the excretory organ, the origin of which is one of the most difficult points to explain. Since we see the excretory organs rising from the mesoderm, and are inclined to derive this latter from the entoderm, we hold it as most probable that the primitive excretory organ was a diverticulum of the entoderm which became secondarily connected with the ectoderm. At a later stage, it loses its connection with the entoderm and thus becomes the structure known as the primitive kidney (protonephridium).

From a form possessing such an organisation, the Plathelminthes also may be derived. Their excretory system remains on the level of the protonephridium, merely branching and extending further through the body. Their larval form corresponds more or less to that described, but does not possess a primitive kidney. The *Pilidium* of the Nemertini already shows a certain similarity to the *Trochophore*, and it has been pointed out that transition forms between it and the MÜLLER's larva of the Turbellaria are to be found (Vol. i., p. 168). The *Pilidium* is distinguished, like the *Trochophore*, by the possession of an apical plate.

Through the concentration of the ciliated apparatus and the acquisition of an anus, the ancestral form ascended to the level of the *Trochophore*, and then became the starting-point for the Rotatoria, the Mollusca, and the Molluscoida. Its relation to the Rotatoria and the Annelida, *i.e.*, its ascent to the level of the latter, has already been discussed (Vol. i., p. 342). The most important features in this process are the appearance of segmentation and the rise of the coelom, the latter being perhaps explicable through the enlargement of the gonads of the primitive form. As already mentioned, the genital products originate from the epithelial wall of the coelom, a fact which favours such an origin. The Mollusca exhibit, on the whole, similar conditions, but show an important difference in the absence of segmentation, remaining in this respect more like the primitive form.

We therefore assume that the Molluscan larva (*Trochophore*) still closely resembles the ancestral form; it already shows, however, some new characters which clearly indicate differentiation in a certain direction, two of these, the shell and the foot, being specially distinctive of the whole organisation of the Mollusca. The first of these, especially, can very early be recognised through the appearance of the shell-gland on the dorsal surface of the larva, and thus gives the larva the special character of the Mollusc without at first affecting its general appearance (Figs. 14, 15, 18, pp. 28, 31 and 36; Figs. 51 and 56, pp. 125 and 135). Somewhat later, but also at a very early stage, the foot appears on the ventral side of the larva. The very early rise of this organ which may in a few cases be found even before the Trochophore form fully develops, must be regarded as a shifting back to an early period of embryonic development of this feature which was only a recent acquisition. It is all the more easy to admit this, as the shell-gland is found to arise exceptionally early in those forms, the development of which show marked specialisation, as, for instance, in the *Unionidae* (Fig. 22, p. 50) and in the Cephalopoda (Figs. 116 *A*, p. 255 and 131 *D*, p. 280). The shifting back of the shell to the earliest possible embryonic period can easily be explained by its importance as a protection to the larva, a fact which may be observed in every Lamellibranch or Gastropod larva whether young or old; the slightest disturbance causes the animal rapidly to retreat into its shell and thus to sink to the bottom of the water.

The larvae of the Amphineura have no true shell-gland, a peculiarity that would increase the resemblance between them and the Annelida if their organisation were better understood. It must at present be confessed that the larvae of the higher Molluscs are far more like those of the Annelida than are the larvae of these more primitive forms, in which we should expect a closer resemblance. The shell-plates of *Chiton*, further, arise in the same region as the typical shell of the higher forms (Fig. 5, p. 9).

The manner in which the shell appears in the embryo favours the view that it is derived phylogenetically from a cuticular dorsal covering, within and beneath which calcareous concretions were deposited. The shell-plates of *Chiton* have, indeed, with some probability, been traced back to the transformed spines of this animal (p. 12), but on the whole it seems more likely that the Chiton shell, which consists of a number of plates, arose in consequence of a secondary distribution (determined by the manner of life of the animal) of an originally continuous dorsal carapace.* From this flattened, bowl-shaped shell

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* The shell has also been regarded as a partly internal dermal skeleton in consequence of its condition in *Chiton*, where it is traversed by strands of connective tissue (Fig. 8, p. 12), and the retractors of the body inserted into it have been thought to play an important part in its development (THIELE, No. 20). This last factor is in any case of importance in connection with the various modifications of the shell (where the latter is already present).

were derived later all the varied shapes of shell met with in the different divisions of the Mollusca.

The protective dorsal covering which became the shell was, in any case, of great significance for the further development of the Mollusca. Since, starting from the back, the shell had to cover a large part of the body so as to be able to shelter it as completely as possible, the locomotory organ could only develop on the ventral surface, the creeping manner of life leading to the *development of the foot*, an equally important organ and one highly characteristic of all the Mollusca.

It has already been mentioned that attempts have been made to derive the foot of the Mollusca from the ventral sucker of the Polyclada, but it appears to us that the exclusive use of the ventral surface as creeping sole, simultaneously with the development of the dorsal shell which necessitated a firmer adhesion to the sub-stratum, alone suffices to explain the greater development of the ventral part of the body into a muscular foot. In a few Annelida and Annelidan larvae, there is a ventral ciliated area extending between the mouth and the anus which evidently assists the animal in creeping. Such a differentiation may in any case be ascribed to the primitive form, and this, together with a strengthening of the ventral musculature, led to the formation of the foot when the primitive form became adapted to a creeping manner of life, an adaptation which, again, was connected with the development of a shell.

In the Solenogastres, which are elongated and evidently very lowly Molluscs, the foot is only slightly developed and appears as a ciliated ridge lying in the ventral longitudinal groove. This groove, which is represented in Fig. 147 *A* and *B*, might be compared with the ciliated area mentioned above as occurring in the Annelida, in some forms becoming depressed in such a way as to produce a ventral ciliated groove. In *Chaetoderma*, there are no signs of either a ventral groove or a foot, and we are much tempted to regard these elongated worm-like creatures (Fig. 147 *A*) which are totally devoid of shell, as worms rather than as Molluscs, a view which has repeatedly been adopted. In any case, it appears possible that they are transition-forms between the Vermes and the Mollusca, this view being supported by the fact that the formation of the spines in the Amphineura shows great similarity to that of the setae in the Annelida.

Although there cannot be any doubt that we have, in the Amphineura, forms which stand very low among the Mollusca, we may hesitate to attribute to them the significance of transitionary forms. We have already pointed out that the spines which cover the body of the Amphineura (Figs. 147 *B*, and 6-8, p. 10) show striking agreement in their origin with the setae of the Chaetopoda and it was mentioned that some authors had regarded this as proving relationship between the Amphineura and the Annelida. We do not attach any great importance to this resemblance, since these spines are found irregularly distributed over the body, while the setae of the Annelida are, as is well known, very regularly and segmentally arranged. Spines also occur in some forms while the related forms show no such structures. As an example of this we would recall the Turbellarian described by v. GRAFF, *Enantia spinifera*. Here we have true cuticular spines which can only be considered as analogous to those of other animals, but in connection with the origin of such structures this illustration is of interest.

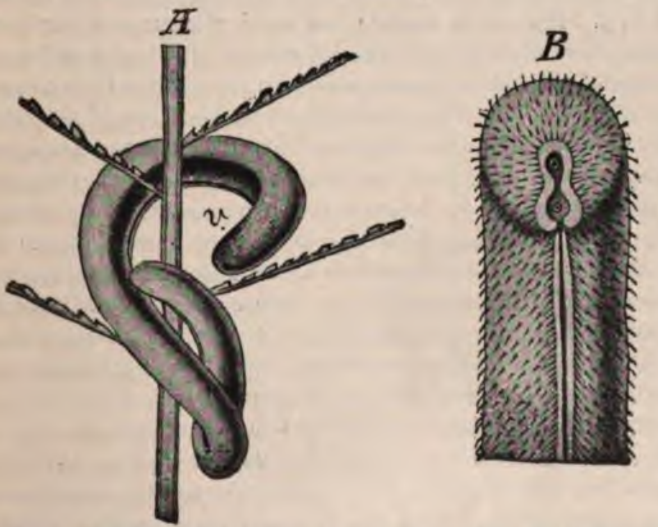

FIG. 147.—*A*, *Proneomenia aglaopheniae*, wound round a branch of *Aglaophenia*; *v*, indicates the anterior end of the body. *B*, anterior end of the same animal seen from the ventral side, and showing the oral aperture and, behind it, the aperture of the pedal gland and the ventral groove (after KOWALEVSKY and MARION).

In comparing the spines of the Amphineura with the setae of the Annelida it must be remembered that we can certainly not derive the Mollusca from such highly developed forms as the Chaetopoda. The most primitive Annelida, however (the Archi-Annelida), have no setae, but even these are certainly too much differentiated to serve as starting points for the Mollusca in which segmentation is altogether wanting.

The temptation is certainly very great to derive the elongate, worm-like Solenogastres which are provided with a coelom and nephridia (Fig. 147 *A*) from the Annelida, but they also show no segmentation. Either segmentation or the distinct remains of it must, however, be found if they are really to be more nearly related to the Annelida. We are thus inclined to regard the elongate form of the Solenogastres rather as a secondary phenomenon and to consider as such also the growing out of the posterior part of the larva into the adult body which recalls similar processes in the Annelida (Vol. i., p. 268). It is possible that the development of the Solenogastres, when better known, will throw further light upon their origin. In the young *Dondersia*, seven calcareous plates are said to cover the back, as in *Chiton*. This stage thus resembles that of *Chiton* and this perhaps supports the conjecture that we have in the Amphineura a less primitive form than was assumed *a priori*. The absence of the shell also would no longer have to be regarded as a primitive feature, nor would the slight development or absence of the foot. We still indeed have to take into account the important fact that the shell is wanting in these forms. The covering of the body with spines and the very primitive internal organisation in any case indicate that the Solenogastres are very primitive forms. If we actually have, in them, merely an aberrant branch of the Molluscan stock, this branch in any case diverged very near the root.

If we are unable to find any direct relations between the Solenogastres and the Annelida, such might perhaps be found between them and other divisions of the Vermes, such as the Turbellaria or the Nemertini. The coelom, that very important part of the internal organisation might, as above shown, with some probability be derived from the dilation of the gonads in these forms. The conditions of the coelom in the Mollusca agree in such a striking manner with those in the Annelida that it is difficult to believe that two structures so remarkably alike arose in different ways; in this case we should have to derive both the Mollusca and the Annelida from Turbellaria or some similar form. This brings us, however, back to our former view as to the racial form of the Mollusca made in connection with the *Trochophore* larva (p. 321) which, however, was not favourable to the derivation of the latter from the Turbellaria.

Starting from a creature still more simple in organisation than the *Trochophore*, we arrived at the form of the latter and traced the acquisition of those characters which determine the typical Mollusc. We then touched chiefly upon features of the outer organisation, but some points of internal organisation were also pointed out, such as the supposed rise of the coelom from the gonads of the primitive form and the primary excretory organ, the primitive kidney. A further important characteristic of the Mollusca is the occurrence of the (adult) nephridia and their connection with the coelom (pericardium).

We believe the origin of the adult nephridia to be the same as in the Annelida, *i.e.*, we derive them from the protonephridium. Although nothing is known ontogenetically on this subject, the adult nephridia, like the primitive kidney, are derived from the middle germ-layer, a fact which, indeed, indicates a common origin, if only because the mesoderm originally distributed in the body-cavity (mesenchyme) and the coelomic mesoderm (the former gonads) had in any case the same origin, *i.e.*, were derived from the entoderm. The connection now existing between the nephridia and the coelom is secondary, for it is wanting in the primitive kidney. The nephridia took over the transmission to the exterior of the genital products, when special efferent ducts for them were not developed.*

The circulatory system of the Mollusca, like the coelom and the nephridia, shows great resemblance to that of the Annelida, a fact which inclines us to ascribe it to the primitive form from which the two stocks are derived. The simplest form of circulatory system was, in any case, that of a contractile sac open at one end and lying dorsally. The heart belonged to the primary body-cavity. Where the coelomic sacs were specially large it was found squeezed in between them and the intestine, dorsally to the latter. The rise of the heart between the entoderm and the splanchnic layer of the mesoderm, still characteristic of many forms, and which, in the Lamellibranchia, even leads to its development round the intestine (Figs. 31-33, p. 75), led some authors to trace back the heart to one of the blood-sinuses which encircles the intestine.† According to this view, the blood-sinus would have to be located dorsally to the intestine. The blood passed into the muscular sac which represented the primitive heart and which carried on rhythmical contractions, by means of which the blood was again driven out. There were no vessels, but the blood ran through spaces and slits in the mesodermal

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* [See footnote p. 179 and GOODRICH, *Quart. Jour. Micro. Sci.* Vol. XXXVII.—ED.]

† This view which was adopted by GROBBEN has been discussed in connection with the formation of the heart in the Lamellibranchia (p. 79).

tissue of the primary body-cavity, a condition which is still passed through by the embryos of the Mollusca, in which the heart arises independently of the vessels (pp. 77 and 216).

The blood-vessels must have first arisen when the gills developed. These later, in any case, arose as very simple leaf-like or tubular outgrowths of the body-wall, such as are found as the most primitive gills in the Annelida, the Arthropoda and the Echinoderma. An increase of surface soon took place and led to the bipectinate gill, the so-called *ctenidium* so characteristic of the Mollusca. This gill was paired, *i.e.*, a ctenidium was found on either side of the body concealed in a cavity formed by a fold of the integument. The fold is the mantle which grew out on each side from the back, and developed simultaneously with the shell and the gills. As the primitive Mollusc we must thus imagine an animal somewhat flattened dorsoventrally, whose back was covered by a bowl-shaped shell while its ventral side formed a muscular and slightly projecting creeping sole. Beneath the lateral parts of the shell lay the mantle enclosing the pallial cavity and within this the gills. On the pre-oral part of the body (the head) there were perhaps also the eyes and two tentacles, corresponding to the cephalic feelers of the Archi-Annelida. In the oesophagus, the radular sac with the radula became differentiated as outgrowths, these occurring even in the most primitive of known Molluscs (Amphineura, Solenogastres). The anus lay at the posterior end, the nephridia opening out at either side of it. These latter opened inwardly into the coelomic sacs with which the genital glands were connected. The two coelomic sacs, dorsally to the intestine, held the heart between them. The primary body-cavity was traversed by mesodermal tissue, which became differentiated into connective tissue and muscles.

From such a simple form of Mollusc can be derived the types represented in the different divisions known to us. Nearest to it stand the Chitones, the characteristics of which have been drawn upon for the above description. The somewhat aberrant conditions of the Amphineura have already been described above (p. 326). After the Chitones come the most primitive Gastropods (Diotocardia), the Chitones themselves being for a long time regarded as Gastropods.

The foot of the Gastropoda, apart from exceptions to be mentioned presently, has the primitive form of the creeping sole. The marked development of the head which carries the tentacles and eyes is characteristic of most Gastropoda. The shell also has attained higher development and is a constant feature of the Gastropoda; where it is wanting, it has evidently degenerated. To the actual shell, the operculum has been added. The position of this latter is like that of the shell itself, *i.e.*, it lies on the dorsal side of the foot at the point where the latter passes over into the back. The shifting of the anus makes it difficult to establish the origin of the operculum. It has been suggested that it arose through abstriction from the shell, but its independent development and position in the embryo point rather to an independent origin.

The simple bowl-shaped shell, assumed by us for the primitive form is no longer retained in this form in the Gastropoda, for the shell has become twisted. This condition is connected with the asymmetry of the body which, again, is the result of the one-sided development of the visceral sac, a feature which is specially characteristic of the Gastropoda. This one-sided development brings about displacements of both external and internal organs, and leads to processes of degeneration (*e.g.*, in the gills, the kidneys, parts of the circulatory and nervous systems); these now occur on one side of the body only and thus still further increase its asymmetry.* In forms which lead a pelagic life, such as the Pteropoda, or in creeping forms that have lost the shell (*Onchidium*, Opisthobranchia, *Limacidae*, etc.) there is a more or less complete return to the symmetrical shape.

In the form of the gills, the paired character of the kidneys and the auricles, the relations of the coelom and of the nephridia, the Diotocardia are among the forms most nearly resembling the primitive Mollusc, but they appear essentially differentiated from it, as the asymmetry of the body is already found in them.

The relation of the Gastropoda to the primitive form is easier to trace than is that of the other great branches of the Molluscan stock (the Solenoconchae, the Lamellibranchia and the Cephalopoda).

The **Solenoconchae** may be derived from the primitive form by the extension of the body in a dorsal direction; the head is much reduced but develops a large number of tentacular filaments. The foot becomes the long burrowing foot, the mantle is found to be influenced by the above-mentioned growth of the body, but on the whole exhibits the usual features, except that it retains an aperture at its dorsal apex. In the same way also we can explain the shape of the shell which resembles a tube open at both ends. According to the most recent investigations as to the structure of *Dentalium* it seems most probable that this form is related to the Gastropoda, the

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* *Cf.* on the asymmetry of the body, Chapter XXXII., p. 143.

supposed relation to the Lamellibranchia and the Cephalopoda being untenable.* The Solenoconchae are an aberrant although insignificant branch of the Molluscan stock, certain resemblances between them and the Lamellibranchia are to be explained by the fact that they both branched off from the same primitive form.

The **Lamellibranchia** also are much specialised, but may still, through their lowest representatives, be related to the primitive form. The Protobranchia, for instance, still possess a foot with a creeping sole, as well as bipectinate gills. The foot and the gills in the higher forms, however, though modified, may still be traced back to the fundamental type. The creeping sole is, in any case, lost in consequence of their burrowing habit, but, on the other hand, one of the pedal glands which are found in the different divisions of the Mollusca develops into the byssal apparatus.

The reduction of the head and absence of the radula, structures which are such constant features in nearly all other Molluscs, are characteristic of the Lamellibranchia. It has been said, no doubt rightly, that the radula has been lost; it is occasionally also wanting in other forms whose relations possess it as, for instance, in various Opisthobranchia (*Phyllidia*, *Doridium*, *Doridopsis*, *Tethys*, etc.).†

The shell of the Lamellibranchia has a specially typical development. At first it is shaped like a shallow bowl, lying upon the back, like the shell assumed to have been possessed by the primitive form; later, however, it bends over on the two sides, calcifies as two pieces, and thus assumes the typical bivalve form. The formation of the mantle corresponds to that of the shell.

Among the internal organs, the nervous system, the circulatory apparatus, the pericardium (coelom) and the nephridia form in the way usual among the Mollusca, and this probably also may be said of these organs in the Cephalopoda.

The **Cephalopoda.** Of the external organs of this class, the mantle and gills also resemble those of other Molluscs. The shell too may be derived from a simpler form, as is evident from the rounded chambers found in the embryo. The highly complicated form of the

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* PLATE, in his recent work on the anatomy of *Dentalium*, gives a detailed account of the relationships of these forms (see Literature to Chapter XXXI., No. 3, p. 98).

† According to SIMROTH (No. 17), *Tethys* (and the related form *Melibe*), for instance, does not require the radula because its food is soft. A Prosobranch also (*Magilus*) has no radula. It lives in a tube covered by corals and feeds on the offal of these animals. [The Prosobranch families *Pyramidellidae* and *Eulimidae* are also devoid of radulae.—ED].

chambered shell of *Nautilus*, the highest development of the Molluscan shell, was attained later.

The head, in the Cephalopoda as in the Gastropoda, is well developed. The arms, which surround the mouth, at first sight appear to belong to it, and yet, according to the results of more recent research, another significance must be ascribed to them, *i.e.*, they must be regarded as parts of the foot. A fact which causes surprise and, at first sight, is unfavourable to this view, is that some of the arms shift to the dorsal side of the head, being here found behind the mouth. This makes it difficult to understand how the foot could have become transformed in this way, but when we see how extremely plastic it is, judging from different transformations which it has undergone in the Lamellibranchia, the Prosobranchia, the Heteropoda and the Pteropoda, further modification is not so inconceivable, especially when we find that the lateral parts of the foot in certain Prosobranchia (Diotocardia) even develop tentacular structures.

Another part of the foot of the Cephalopoda has at any rate become changed into the funnel, which at first is paired. The pedal character of this structure has never been doubtful, its origin being at once betrayed by its position between the mouth and the anus. The change undergone by the foot in yielding the funnel is also very great. We cannot here enter into the question as to whether, as has been assumed, we have in this case to do with epipodia. The comparison of the different parts of the foot known as the propodium, mesopodium, metapodium, parapodium and epipodium becomes very difficult in modified forms, the inter-relationships of which alone present great difficulties. The conditions of transformation and adaptation may, in the various forms, have developed and modified very different parts of the foot.

In the Cephalopoda, the organisation of the Mollusca has attained its highest development. In the structure of the adult the most far-reaching differentiation has taken place and thus also in its ontogeny we have the greatest complications found in the Molluscan stock, the greatest departure being made from those features (total cleavage of the egg, larval forms, etc.) which we have learnt to regard as primitive in the lower as well as the higher representatives of the Mollusca.

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CHAPTER XXXV.

TUNICATA.

Systematic (after **Herdman**) :—

- Order I. Larvacea (*Appendicularia*).
- Order II. Ascidiacea.
    1. Ascidiae Simplices.
    2. Ascidiae Compositae.
    3. Ascidiae Luciae (*Pyrosoma*).
- Order III. Thaliacea.
    1. Cyclomyaria (*Doliolum*).
    2. Hemimyaria (*Salpa*, *Octacnemus*).

I. Sexual Reproduction.

1. Larvacea (*Appendicularia*).

Very little is as yet known as to the development of *Appendicularia*, since the small eggs which are discharged into the surrounding water are not easy to obtain and exceedingly difficult to examine. **Fol** (No. 1) and **Kowalevsky** (treatise on *Amphioxus*) have, however, stated that the development of this form closely resembles that of the Ascidiacea. The paired respiratory tubes of *Appendicularia* are formed in the same way as the first gill-slits of the Ascidian larvae (p. 366), an ectodermal invagination appearing at each side and a diverticulum of the pharynx growing out to meet it until the blind ends come into contact, perforation taking place at the point of junction.

2. Ascidiae Simplices and Compositae.

A. Oviposition, Fertilisation and Egg-envelopes.

The eggs of most of the solitary Ascidians, soon after passing from the oviduct into the atrial (peribranchial) cavity, are ejected into the surrounding water where they pass through their embryonic development, being supported at the surface by the large, foam-like follicle-cells (Fig. 149, *c*). Fertilisation usually takes place either in the peribranchial (atrial) cavity or after the egg is laid, but exceptions to this rule are found in the genera *Cynthia* and *Lithonephrya* (GIARD), these forms passing through their embryonic development within the peribranchial cavity of the mother. In *Clavelina* also, and in all composite Ascidians, development up to the time when the free-swimming, tailed larva is hatched takes place in the peribranchial cavity of the mother, or else in peculiar diverticula of this cavity known as brood-spaces. The composite Ascidians differ from the solitary forms in the large amount of yolk contained in the egg. SALENSKY (No. 49) recently observed in a few *Polyclinidae*

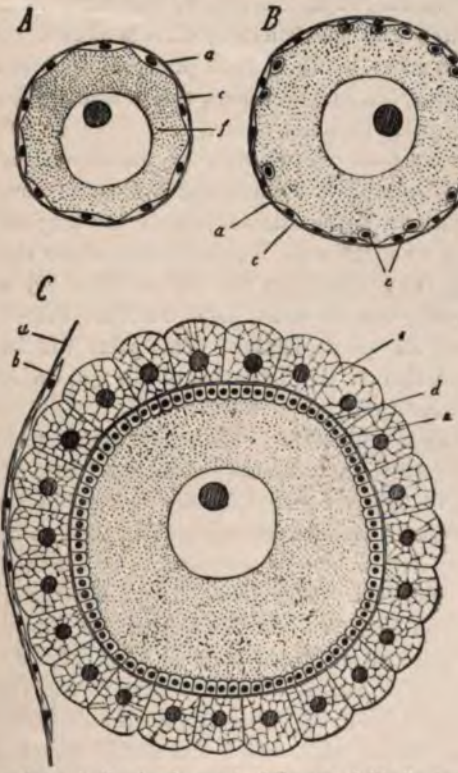

Fig. 148.—Three stages in the development of the egg of *Phallusia mammillata* (after KOWALEVSKY, adapted from KUPFFER, FOL and others). *a*, basal membrane of the follicle; *b*, superficial layer of pavement-epithelium; *c*, follicle-cells; *d*, chorion; *e*, test-cells; *f*, egg-cell.

(*Amaroucium*, *Circinalium*, *Fragarium*) a fusion of the embryo with the atrial wall of the mother. At this spot a thickening, the *placenta*, is formed, derived in part from the atrial wall (*placenta materna*), from the follicle-epithelium enveloping the embryo and from an accumulation of test-cells (*kalymmocytes*).

These Ascidiacea are hermaphrodite. Self-fertilisation seems, indeed, to be prevented, in most cases, by the maturation at different times of the male and the female genital products, but is not impossible in other cases, in which both products ripen simultaneously. [In *Ciona* (Castle, No. II.), although the products ripen at the same time, self-fertilisation does not occur.]

The mature eggs are surrounded, at the commencement of embryonic development, by a complicated system of envelopes, which we are inclined to regard as derivatives of the original egg-follicle. In this respect we agree with Kowalevsky, whose views were confirmed later by Van Beneden and Julin (No. 10) as well as by Morgan (No. 46), but we must point out that the origin of these envelopes is still an open question. This point will be further discussed in the section on the formation of the egg under the heading of general considerations.

Very young eggs, while still in the ovary, appear to be surrounded by a pavement-epithelium consisting of flattened cells (Fig. 148 *A*, *c*). The elements of this *primary follicular epithelium* (*c*) are derived from undifferentiated cells of the ovary (Van Beneden and Julin). A structureless *basal membrane* (*a*) seems to be secreted early at the surface of the follicular epithelium. The follicle-cells multiply by division, and soon lose their flattened form and become cubical; a few of these cells are displaced inwards (Fig. 148 *B*, *e*) in such a way as to become deposited on the surface of the egg into which they may even find their way, passing into the most superficial layer of the vitellus. These cells, which can usually be distinguished by their yellow colour, have been called *test-cells* (*e*) because it was erroneously supposed that they gave rise to the cells of the cellulose mantle (test) of the adult Ascidian, a view which was refuted by O. Hertwig (No. 25).* These test-cells, which soon increase very

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* [These are the abortive eggs (Abortiveier) of Davidoff (No. 14) and the *kalymmocytes* of more recent authors. There seems to be much uncertainty about the fate of these cells. Salensky (No. XXIX.), from his investigations on the compound Ascidians, regards them as giving rise to the test (see p. 356) whereas the similarly named cells of *Salpa* appear to be transitory nutritive structures (Heider, No. XIII.; Korotneff, No. XVIII.; Metcalf, No. XXIV.; Pizon, No. XXVII.), the most recent investigator of the origin of the follicle- and test-cells seems to agree with the account given above.—Ed.]

greatly in number, at first form an inner epithelial layer over the surface of the egg known as the *test-cell-layer* (Fig. 148 *C*, *e*). In later stages they undergo a process of degeneration. They then lose the regularity of their arrangement and are found embedded separately in a gelatinous mass secreted over the surface of the egg. Their original cellular character is then less distinct and has been altogether denied by some authors (SEMPER, FOL). After the development of the test-cell-layer, a structureless membrane (Figs. 148, 149, *d*) is secreted between it and the actual follicular epithelium, and this, being derived from the follicle-cells, may be described as the *chorion*.

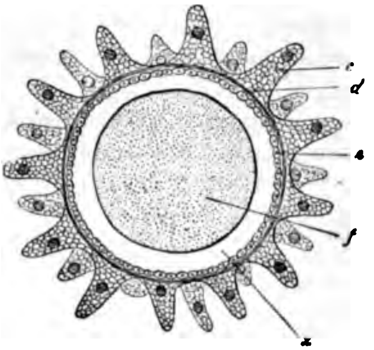

FIG. 149.—Mature egg from the oviduct of *Ascidia canina* * (after KUPFFER). *c*, follicle-cells (foam-like cells); *d*, chorion; *e*, test-cells; *f*, egg-cell; *x*, gelatinous substance.

In the meantime, a delicate *external pavement-epithelium* (Fig. 148 *C*, *b*) has developed on the outer surface of the follicle which is in close contact with the basal membrane: this epithelium is probably to be regarded as an outer layer of follicle-cells. Like the basal membrane, it seems to disappear, not being found in eggs after they have been laid.

In the free eggs of the solitary Ascidians, the cells of the actual follicle-layer, at a later stage, assume a peculiar character. Their protoplasm becomes filled with numerous vacuoles (Fig. 148 *C*, 149, *c*) and thus resembles foam. The cells, which increase in size and form papilla-like structures (Fig. 149, *c*), are concerned in supporting the egg as it floats in the water.

The mature Ascidian egg thus possesses the following envelopes, reckoned from without inwards :—

(*a*) The basal membrane of the follicle.
(*b*) The external pavement-epithelium.
(*c*) The actual follicle-epithelium (layer of foam-like cells).
(*d*) The chorion.
(*e*) The layer of test-cells [kalymmocytes, abortive eggs].

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* [= *Ciona intestinalis*, *var.*—ED.]

According to **Chabry** (No. 13), another fine, structureless membrane covering the external surface of the test-cells should be added to the above. In the solitary Ascidians, after the egg is laid, the interspace between the chorion and the surface of the egg is increased (Fig. 149) through imbibition of water and consequent swelling of the gelatinous matter secreted at the surface of the egg.

We must here briefly allude to views as to the origin of the egg-envelopes which differ from those given above. According to **Sabatier**, **Fol** (No. 21), and **Roule** (No. 47) the follicle-cells are produced by the egg itself. **Fol** and **Roule** think that this is brought about by a process of budding from the germinal vesicle, but **Sabatier** considers that the follicle-cells arise through free cell-formation in the yolk.* It seems to be fairly established that an ejection of chromatin-elements actually takes place from the nucleus of the ovum but we incline to the view that this process has nothing to do either with the rise of the follicle-cells or with that of the test-cells. Such an origin was assumed for the latter by **Roule**, **Davidoff** (No. 14), and **Pizon** (No. XXVII.), while a number of other authors (**Semper**, **Fol**, **Sabatier** and others, following **Kupffer**, No. 34) thought that the test-cells formed freely in the protoplasm of the egg.

It is of interest to note that the eggs of *Appendicularia* also are enveloped while in the ovary by a follicle (A. B. **Lee**, **Davidoff**). When laid, however, they are without covering, and only after fertilisation has taken place in the water do they become surrounded by a delicate vitelline membrane (**Fol**, No. 21).

B. Cleavage.

The free-swimming, tailed Ascidian larvae were known to the older authors and were carefully described by **Milne-Edwards**, P. J. **van Beneden**, and others. Our first knowledge of the embryonic development of the Ascidians, however, was due to the researches of **Kowalevsky** (Nos. 29 and 30), which were soon supplemented by the accounts of **Kupffer** (Nos. 34 and 35) and **Metschnikoff** (No. 41). Among later workers we must mention **Seeliger** (No. 50) and **van Beneden** and **Julin** (Nos. 7-10); the eggs of the Ascidiae compositae which are rich in yolk have been investigated by **Maurice** and **Schulgin** (No. 39) and **Davidoff** (No. 14).†

The cleavage of the Ascidian egg is total, and, seeing that the blastomeres at first differ only to an inconsiderable extent in size and structure, may be described as almost equal. The term "adequal

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* [As we have already stated, free cell-formation is now generally discredited by cytologists.—Ed.]

† [Still more recently, **Salensky** (No. XXIX.) has worked at the development of the Ascidiae compositae. **Castle** (No. II.) has worked at *Ciona intestinalis*. The work of the last-mentioned observer is very important and exhaustive.—Ed.]

cleavage," which was applied by **Hatschek** to the process in the egg of *Amphioxus*, is equally suited to the very similar processes met with in the Ascidians. Certain characteristic irregularities are, indeed, to be observed, and these are referable to the early foreshadowing of certain important differentiations.

The furrow which appears first and divides the egg into two equal halves corresponds to the plane of bilateral symmetry, and the two blastomeres that result from this division represent the right and left halves of the body (**Seeliger**, **van Beneden**, **Julin** and **Castle**). From this stage onward through all the other stages of development, the bilateral symmetry of the embryo is clearly recognisable. The next furrow is also meridional and cuts the first at right angles. The four blastomeres thus produced (Fig. 150 *A*) are not of exactly the same size, two being larger (*h*) and two smaller (*v*).* According to the most usually adopted orientation of the cleavage-stages in these forms, the plane of cleavage now under consideration has a transverse direction so that (according to **van Beneden** and **Julin**) the two larger blastomeres represent the future anterior half of the body and the two smaller the later posterior half, but **Seeliger** takes an exactly opposite view (Fig. 149 *A*). In *Distaplia*, according to **Davidoff**, the four blastomeres are exactly equal in size.

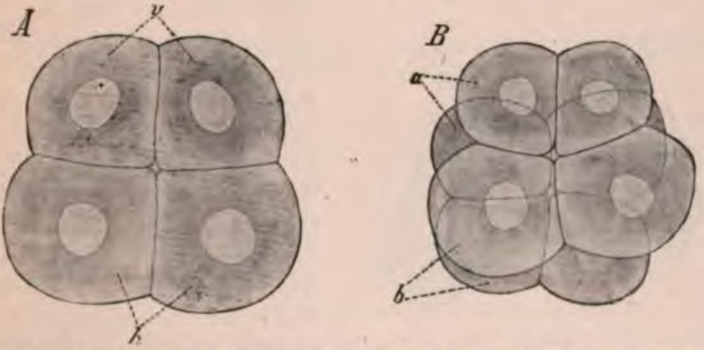

Fig. 150.—Two stages in the cleavage of *Clavelina* (after **Seeliger**). *A*, four-celled stage, seen from above. The two smaller cells *v* represent, according to **Seeliger**, the anterior half of the body, and the larger cells *h* the posterior half. *B*, lateral view of the eight-celled stage ; *a*, blastomeres of the animal half ; *b*, blastomeres of the vegetative half.

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*[In *Ciona* (**Castle**, No. II.) no difference in size is to be seen between the blastomeres at the four-celled stage. The polar bodies are found to correspond to the future vegetative pole.—**Ed.**]

The third plane of cleavage is equatorial and, in the eight-celled stage that follows (Fig. 150 *B*), separates four smaller cleavage-spheres from four larger. According to all observers, the later ventral half of the body is thus divided from the dorsal half. The four smaller spheres (*a*) which lie near the animal pole, and are said to represent the ventral surface of the body, are purely ectodermal in character, while the four larger blastomeres (*b*) which belong to the vegetative half (the future dorsal half) are said by VAN BENEDEN and JULIN to show a mixed character. They give rise, through division, to the large entoderm-cells, smaller ectoderm-elements being simultaneously abstricted from them, these latter then joining with those of the ectodermal half of the body. According to SEELIGER and DAVIDOFF, these cells are, on the contrary, purely entodermal.*

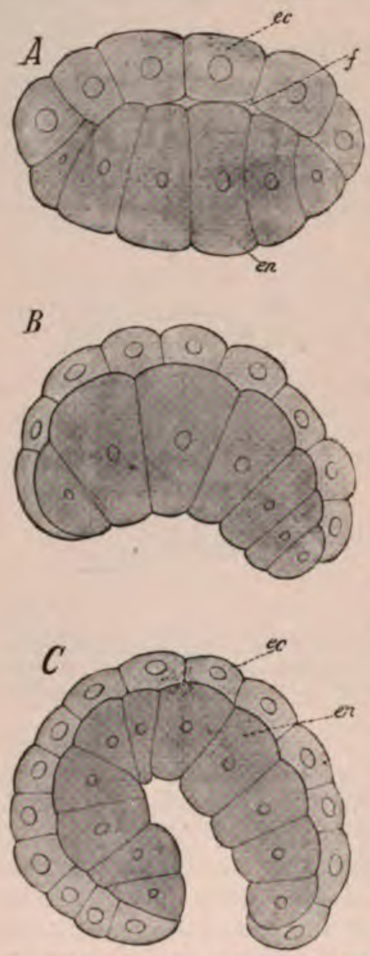

FIG. 151.—Gastrulation in *Clavelina* (after SEELIGER). *A*, placula-stage; *B*, the invagination commencing; *C*, after complete invagination (median section). *ec*, ectoderm; *en*, entoderm; *f*, cleavage-cavity.

Even at this stage, certain displacements of the blastomeres can be observed, and these interfere with the regularity of the later course of the cleavage. This regularity is also disturbed by the fact that the ectoderm-cells, from this time onwards, divide more rapidly than the entodermal elements. It is, however, possible to distinguish a sixteen-cell stage brought about by meridionial furrows, a thirty-two-cell stage caused by equatorial division, and a later

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* [According to both CASTLE (Nos. II. and III.) and SAMASSA (No. XXXII.), VAN BENEDEN and JULIN, together with SEELIGER, were mistaken in their

sixty-four-cell stage. For further details as to the cleavage we must refer the reader to the works of SEELIGER (No. 50), VAN BENEDEN and JULIN (No. 8), CHABRY (Nos. 12 and 13) [and especially CASTLE (No. II.)].

Even at the four-celled stage a cleavage-cavity is found open at both the animal and vegetative poles (Fig. 150). This cavity, at the sixteen-celled stage, appears to be closed on all sides. In later stages it disappears (Fig. 151 *A*, *f*) in consequence of a flattening of the embryo, which begins at the poles and which is specially marked in the entodermal half of the body; this flattening precedes the invagination of the entodermal cell-layer which results in the gastrula-stage.

C. Formation of the Germ-layers. Appearance of the Medullary Tube and the Notochord.

Through the changes just described, the embryo passes from the blastula-stage into a stage which we may, with BÜTSCHLI, call the *placula* (Fig. 151 *A*). The lens-shaped embryo is now composed of two layers, an entodermal layer (*en*) consisting of large high cells and a small-celled ectodermal layer (*ec*) which already covers the former like a cap.* In a fissure (*f*) between these two layers, we recognise the remains of the much compressed cleavage-cavity. The *gastrulation* which now takes place (Figs. 151 *B*, and 152) is due essentially to the curvature of the bilaminar embryo, the flattened area of entoderm-cells becoming invaginated in this process, while the ectodermal layer continues to spread out over the surface of the

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orientation of the Ascidian egg. CASTLE concludes that SEELIGER determined the dorsal and ventral sides of the egg correctly, but reversed the anterior and posterior ends in all his figures of the early stages. VAN BENEDEN and JULIN were correct in their determination of the anterior and posterior ends, but reversed the dorsal and ventral surfaces in all stages prior to the forty-four-celled stage. In consequence, the latter authors state that the four small cells of the eight-celled stage give rise to ectoderm only, while the four larger cells produce both entoderm and ectoderm; whereas, as a matter of fact, neither group produces ectoderm exclusively. It is the four larger, not the four smaller cells, which give rise to the greater portion, perhaps the whole, of the ectoderm. The vegetative pole, which is marked by the polar bodies and the four smaller blastomeres, is dorsal, while the animal pole with the four larger cells is ventral. The future mesoderm arises from both primary layers. CASTLE's work is so complete, and he traces the cell-lineage in such detail, that his interpretation must, we think, be accepted in preference to the above.—ED.]

* [The large cells at this stage would not, according to CASTLE, correspond with the large cells of the eight- and sixteen-celled stage; the latter by their more rapid division have become gradually smaller, whereas the originally smaller cells, by their slower division, have not decreased in size to the same extent and are now the larger of the two.—ED.]

embryo. Gastrulation in the Ascidians has consequently frequently been described as transitional between the typical epibolic and embolic conditions.

The *gastrula-stage* that thus arises (Fig. 151, *C*) is saucer-shaped. The arched surface of the embryo is covered with the small ectoderm-cells, while the flattened side of the body is occupied by the large, round blastopore. This side is said to change into the later dorsal surface of the embryo, while the arched side becomes the ventral surface.

If we take as the principal axis of this gastrula-stage (Fig. 152 *A*) that which connects the animal with the vegetative pole of the egg in the first stages of cleavage (*a-b*), we find that this axis passes through the apex of the arched portion on the one hand and through the centre of the blastopore on the other. The future longitudinal axis of the body, on the contrary, would lie at right angles to this principal axis, since, according to all observers, the blastopore corresponds to the later dorsal surface. We should then have a condition differing from that of other Bilateralia, in which the primary axis corresponds approximately to the longitudinal axis of the adult. It seems probable that the blastopore shifts secondarily from the vegetative pole of the embryo, at which the posterior end of the body now develops to a position on the dorsal surface. According to this orientation, the dorsal and ventral surfaces would, as in the first ontogenetic stages of most of the Bilateralia, occupy a meridional position. After what has been stated above, we may conjecture that, in Ascidians, the displacement of the blastopore to the dorsal side of the body is first brought about by shifting caused by growth in the later gastrula-stages such as is indicated by the orientation adopted in Fig. 152 *A-C*. A comparison with the ontogeny of *Amphioxus* to a certain extent supports this supposition (Chap. XXXVI.). According to this view, the orientation of the cleavage-stages given by some authors, in which the animal pole of the body is said to be related to the future ventral half and the vegetative to the later dorsal half, does not appear altogether suitable, and can only be admitted with certain reservations.*

Bilateral symmetry can be recognised in the gastrula-stage, even at the first, by the distribution of the cells. In later stages this

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*[Castle, in his work on *Ciona*, supports the latter view, that is, he finds that the vegetative pole with the entoderm and blastopore is always dorsal in position. The apparent shifting of the blastopore is due to the fact that it closes more rapidly from the anterior margin and from the sides than from behind. Consequently it comes to lie in the posterior portion of the dorsal surface of the embryo. He is therefore in agreement with Samassa (No. XXXII.) when he states that there is no rotation of the axes during gastrulation as conjectured on theoretical grounds by Korschelt and Heider, but that the primitive axis corresponds with the vertical axis of the larva and the longitudinal axis is at right angles to this. According to this interpretation, the orientation of Fig. 152 is incorrect, since the blastopore, in each of the three stages, is represented on a different surface, whereas it is always dorsal in its position.—Ed.]

symmetry is still more marked, the future anterior end of the body becoming swollen in consequence of the increased curvature of its two layers (Fig. 152 *B*). This arching is connected with the gradual narrowing of the blastopore which takes place on the dorsal side of the embryo in such a way that its last vestige lies near the posterior end of the body (Fig. 153 *C*). Originally, the blastopore is a wide oval aperture, but in later stages it is pear-shaped, and it finally becomes a small posterior aperture (Fig. 153, *b-b''*). This narrowing of the blastopore is caused principally by the inward growth of its anterior and lateral margins, the posterior edge remaining unchanged. We have here conditions exactly similar to those in *Amphioxus*, and we may assume a continuous closure from before backward of the blastopore which originally extended along the whole length of the dorsal surface.

During these stages even, the embryo becomes somewhat elongated in the direction of the longitudinal axis (Fig. 152 *C*). The dorsal side is recognisable by its flatter condition, and shows, at its posterior end, the remains of the blastopore (*p*); the ventral side, on the contrary, is arched. VAN BENEDEN and JULIN have pointed out that the posterior end of the body, at the gastrula-stage, is always marked by the presence of two small wedge-shaped ectoderm-cells lying at the edge of the

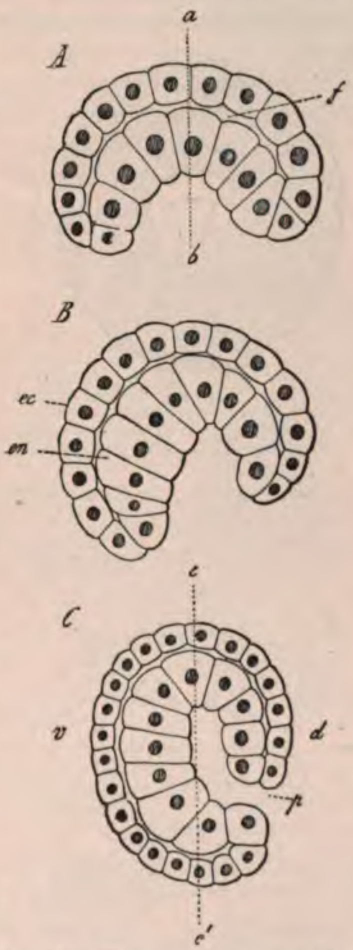

FIG. 152.—Three consecutive gastrula-stages of *Phallusia mammillata* (after KOWALEVSKY). *A*, the invagination commencing; *B*, appearance of the bilateral symmetry; *C*, narrowing of the blastopore; *a-b*, principal axis of the gastrula-stage; *c-c'*, later longitudinal axis of the body; *d*, dorsal side; *ec*, ectoderm; *en*, entoderm; *f*, cleavage-cavity; *p*, blastopore; *v*, ventral side.

blastopore and representing the boundary between the ectoderm and the entoderm (Fig. 154, *x*).

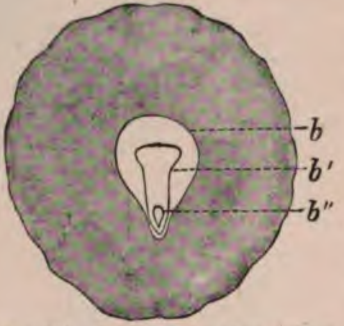

FIG. 153.—Dorsal aspect of an embryo of *Clavelina* (after SEELIGER). *b*, *b'*, *b''*, outlines of the blastopore at three consecutive stages of development.

In these later gastrula-stages the commencement of histological differentiation is already evident. This does not consist merely in the distinction between the ectodermal and the entodermal elements, although the latter are larger, more strongly granular and darker in colour; but differentiations are already to be found within these germ-layers. The ectoderm-cells which bound the blastopore, for instance (Fig. 154 *A*, *n*), are distinguished by the large size of their nuclei, their greater affinity for carmine stain, and their cubical shape from the other ectoderm-cells, which soon become flattened. This ring of cells is the first rudiment of the *central nervous system*, and, as the blastopore closes more and more, changes into the

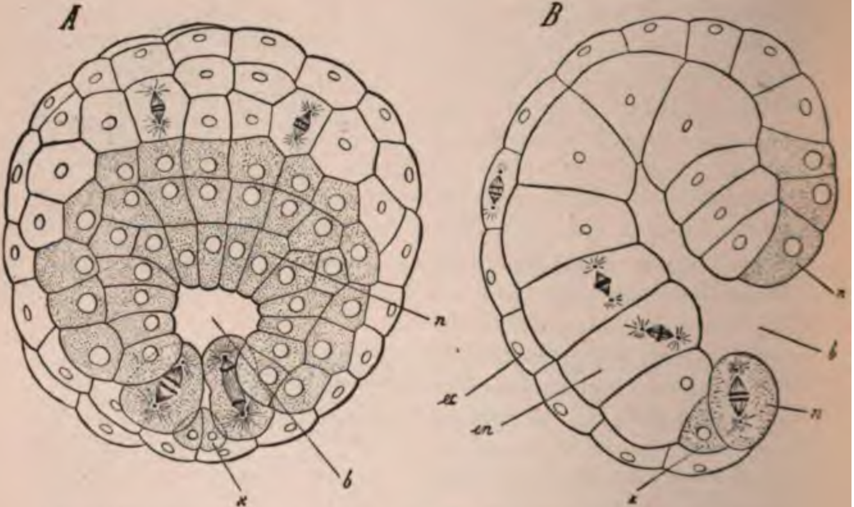

FIG. 154.—Gastrula-stage of *Clavelina Rissoana* (after VAN BENEDEN and JULIN). *A*, dorsal aspect; *B*, median sagittal section. *b*, blastopore; *ec*, ectoderm; *en*, entoderm; *n*, cells of the nerve-ring; *x*, small, wedge-shaped cells.

medullary plate.* This rudiment, when it first appears, consists, at the sides of the still open blastopore, of a single row of cells, while, in front of the blastopore, it is composed of several rows of cells. In later stages (Fig. 154), as the blastopore narrows, the part of the medullary plate in front of it extends more and more, and, at the time when the blastopore is represented by merely a small aperture (Fig. 155), is a large and slightly depressed area. The medullary groove thus formed, which is open anteriorly, is bounded by two lateral swellings (medullary swellings, *m*) which pass into one another behind the blastopore, thus forming a semicircle.

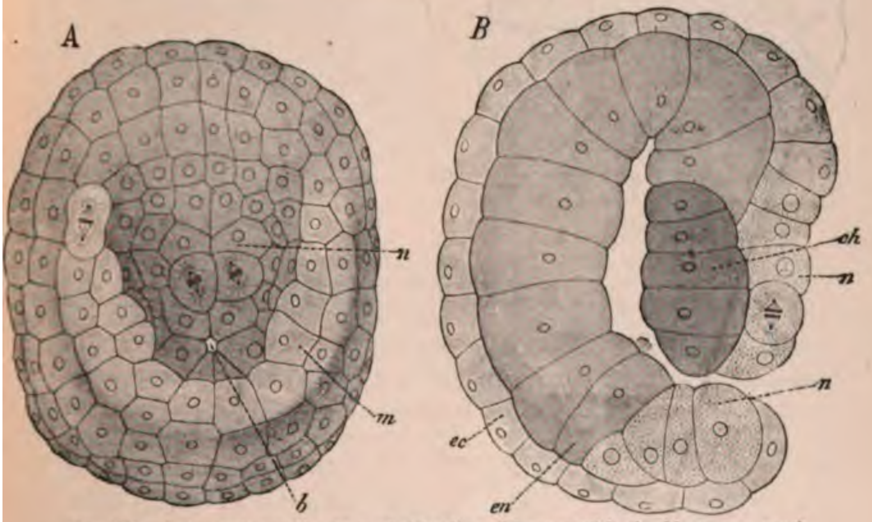

FIG. 155.—Later ontogenetic stage of *Clavelina Rissoana* with the blastopore much narrowed, and the medullary groove appearing (after VAN BENEDEN and JULIN). *A*, dorsal aspect; *B*, median sagittal section. *b*, blastopore; *ch*, rudiment of the chorda; *ec*, ectoderm; *en*, entoderm; *m*, medullary groove; *n*, cells of the nerve-ring.

A differentiation similar to the above is evident in the entoderm (Fig. 158). The cells of the latter, as a rule, are large and turgid, but in the region of the dorsal wall smaller cells appear which are originally arranged so as to form a ring encircling the blastopore, one

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* [According to CASTLE (No. II.), the cells lying behind the blastopore and marked *n* in Figs. 154 and 155 are not part of the rudiment of the central nervous system as stated by JULIN and VAN BENEDEN, but are in reality *muscle*-cells. The rudiment of the nervous system is situated entirely in front of the blastopore. In *Ciona* the posterior margin of the blastopore does not grow forward over the blastopore, covering in the medullary canal, as described by VAN BENEDEN and JULIN in the case of *Clavelina*.—ED.]

side of which, however, as the blastopore narrows, soon extends to form a cell-area in front of it. The whole of this area represents the

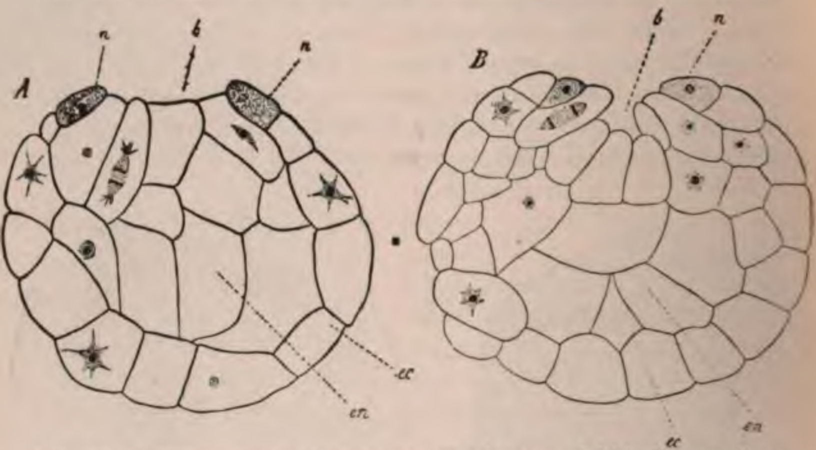

FIG. 156.—Transverse sections through two gastrula-stages of *Distaplia magnilarva* (after DAVIDOFF). *A*, younger stage: *B*, transverse section through the posterior part of an older stage. *b*, blastopore; *ec*, ectoderm; *en*, entoderm; *n*, nerve-ring.

common rudiment of the *mesoderm* and the *chorda*, the "chorda-mesenchyme" ring. The middle cells of this area soon become more distinctly separated from the rest, and represent the plate-like rudiment of the chorda (Fig. 158, *ch*), while the cells that lie laterally give rise to the mesoderm-bands (*ms*).*

FIG. 157.—Transverse section through an embryo of *Distaplia magnilarva* after the closing of the blastopore (after DAVIDOFF). *ec*, ectoderm; *en*, entoderm; *ms*, mesoderm; *n*, neural plate.

In the eggs of the composite Ascidians, which are rich in yolk, the formation of the germ-layers is to a certain extent modified. The cleavage-cavity which, in *Phallusia*, is rather large, is smaller in *Clavelina*, while in *Distaplia* (according to DAVIDOFF) it can only be seen in the first

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*[In *Ciona*, according to CASTLE, the mesoderm-rudiment is made up of cells derived from both hemispheres and all four quadrants, a condition very different from that seen in the Mollusca, where the mesoderm typically arises from the left posterior entodermal macromere.—ED.]

stages as a narrow slit. The entoderm-cells also, in this latter form, do not long retain their unilaminar arrangement, but become distributed in a radial direction, the entoderm thus becoming multilaminar. The gastrula-stage is here in reality reached through epibole (Fig. 156). In the anterior region of the body this overgrowth is especially marked, while in the posterior half, a small pit-like depression (Fig. 156 *B*) indicates the last remains of an invagination-cavity. This cavity, however, completely disappears after the blastopore has closed. The entoderm then represents a solid mass, the cells of which are soon found to vary in size. The position of the blastopore is occupied by the neural plate (*n*).

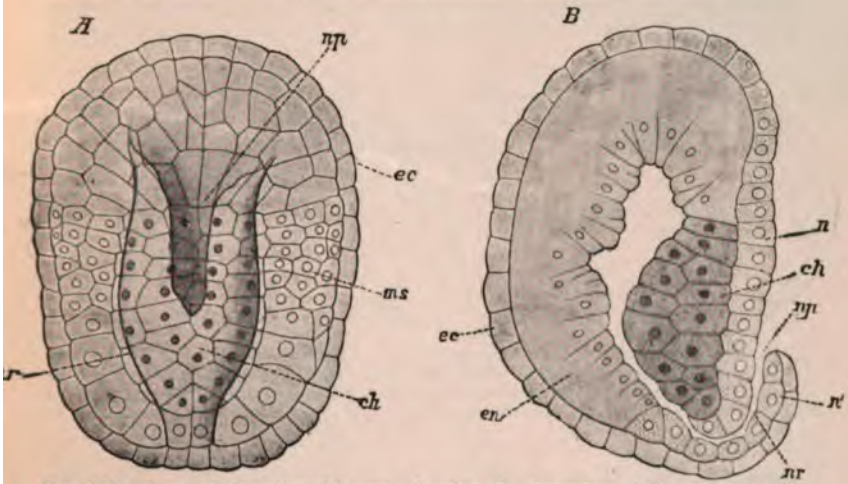

FIG. 158.—Stage of *Clavelina Rissoana* showing the formation of the neural tube (after VAN BENEDEN and JULIN). *A*, dorsal view; the cell-boundaries drawn are those between the cells of the dorsal entoderm-wall; *B*, median sagittal section. *ch*, rudiment of the chorda; *ec*, ectoderm; *en*, entoderm; *ms*, mesoderm; *n*, cells of the neural plate; *n'*, roof of the medullary tube; *nr*, medullary tube; *np*, the neuropore, still very large.

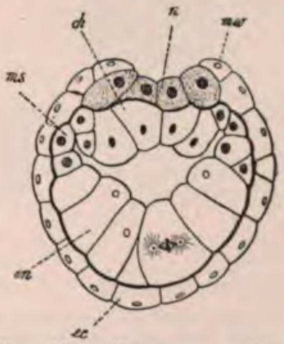

FIG. 159.—Transverse section through an embryo of *Clavelina* (after VAN BENEDEN and JULIN). *ch*, rudiment of the chorda; *ec*, ectoderm; *en*, entoderm; *ms*, mesoderm-diverticulum; *mw*, medullary folds; *n*, medullary plate.

During these stages, the medullary plate, which is already somewhat invaginated, changes into a closed *medullary tube*, its lateral walls, the medullary folds, growing towards one another and fusing (Fig. 160).

The medullary tube develops from behind forward, a special part being taken in the process by the fold which connects the two medullary swellings posteriorly in the form of a semicircle (Figs. 155 and 158). It then appears, especially in longitudinal sections (Fig. 158 *B*), as if the medullary tube was formed solely by the posterior lip of the blastopore growing over the anterior lip. We must, however, bear in mind that, as this posterior medullary fold grows forwards, the lateral medullary swellings are drawn into it, so that the posterior fold does not actually represent the lip of the blastopore, but a purely ectodermal fold lying at this point; in this way, after the medullary tube has developed, its roof (*n'*) which is derived from the inner layer of the folds is also to be regarded as ectodermal. This is a point which deserves to be emphasised in opposition to the view of **Metschnikoff** (No. 42). [*Cf.* footnote, p. 345.]

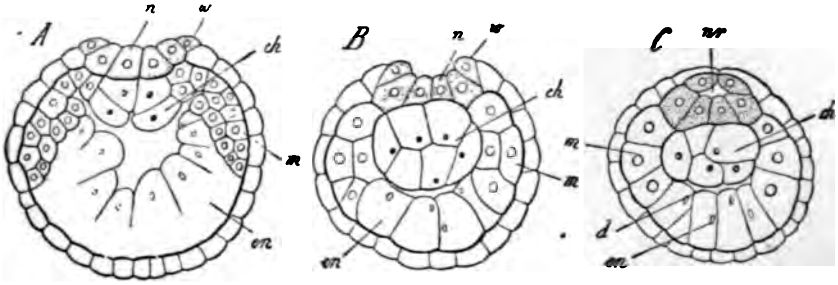

Fig. 160.—Transverse sections through an embryo of *Clavelina Rissoana*, at the same stage as in Fig. 158 (adapted from **van Beneden** and **Julin**). *A*, through the anterior, *B*, through the middle, and *C*, through the posterior part of the body. *ch*, chorda; *d*, lumen of intestine; *en*, entoderm; *n*, medullary plate; *nr*, medullary tube.

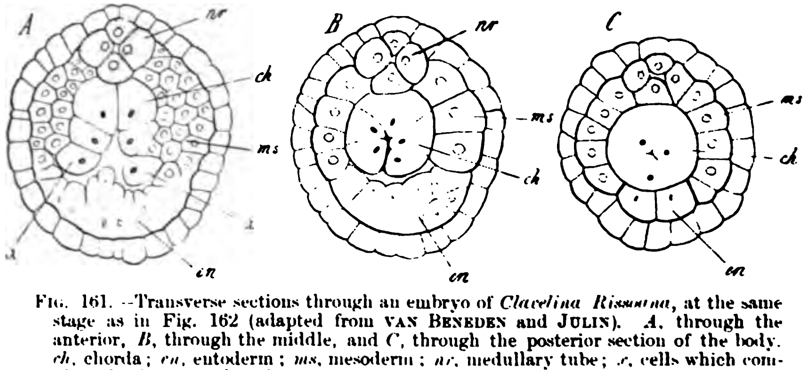

Fig. 161.—Transverse sections through an embryo of *Clavelina Rissoana*, at the same stage as in Fig. 162 (adapted from **van Beneden** and **Julin**). *A*, through the anterior, *B*, through the middle, and *C*, through the posterior section of the body. *ch*, chorda; *en*, entoderm; *ms*, mesoderm; *nr*, medullary tube; *x*, cells which complete the dorsal wall of the intestinal canal.

We shall see (Chap. XXXVI.) that, in *Amphioxus*, the medullary tube forms by the sinking in of the somewhat depressed medullary plate and its separation as such from the ectoderm; hence it is only covered by a single layer of cells. Only at a later stage does the plate curl round under the ectoderm to form a tube. This manner of formation is probably a modification of the origin from folds and is stated by **Seeliger** (No. 50) as occurring in *Clavelina* also, but his observations on this subject were not confirmed by **van Beneden** and **Julin** (No. 10). These latter authors also do not agree in **Seeliger**'s view that the medullary groove, at the time when it appears, lengthens posteriorly beyond the blastopore.

At the time when the medullary tube develops, the blastopore has not completely closed. The remains of it, which originally lie in the floor of the developing medullary groove, are retained for some time longer as the *neurenteric canal* and form a communication between the lumen of the intestine and the central canal of the medullary tube (Fig. 158 *B*).

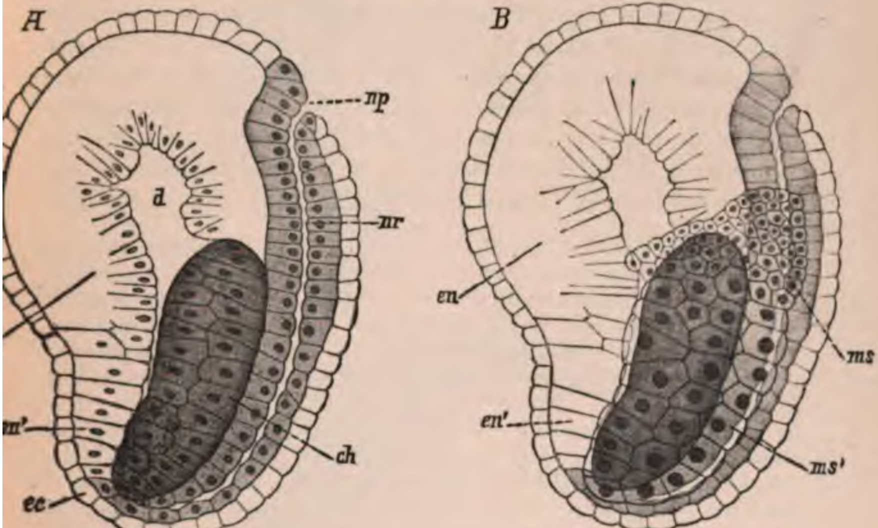

Fig. 162.—Stage at which, in *Clavelina Rissoana*, the trunk-region begins to separate from the caudal region (after **van Beneden** and **Julin**). *A*, median sagittal section; *B*, lateral aspect. *ch*, chorda; *d*, archenteric cavity; *ec*, ectoderm; *en*, entoderm; *en'*, sub-chordal entoderm-strand; *ms*, anterior portion of the mesoderm-bands composed of small cells; *ms'*, posterior portion of the same composed of large cells; *np*, neuropore; *nr*, medullary tube.

As the medullary tube develops from behind forward, the aperture at its anterior end, known as the *neuropore* (Fig. 162, *np*), is retained for a long time. The separation of the *mesoderm* from the *chorda dorsalis* takes place simultaneously with the development of the medullary tube. These two rudiments arise, as may be ascertained from the detailed accounts of **van Beneden** and **Julin**, essentially through the same processes of development as in *Amphioxus*, although the conditions are in this case not so evident, and seem specially modified in the posterior region of the body. The embryo soon assumes a long, pear-shaped form (Fig. 162), the posterior, narrowed region corresponding to the future tail of the larva. In the anterior, dilated region, the mesoderm arises through the development of paired diverticula of the archenteron (Figs. 159, *A*, *ms*), the lumens of these sacs very soon disappear and the cells of their walls, which originally were arranged in two layers (the somatic and the splanchnic layers), then appear irregularly distributed between the ectoderm and the entoderm. Between the two coelomic diverticula, the roof the archenteric wall is completed by entoderm-cells (Figs. 159, 160 *A*, 161 *A*, *ch*) which represent the rudiment of the chorda. At a later stage, these cells become shifted into closer proximity, and thus form a solid strand which, in cross-section, is round. The fact that this strand is to be traced back to a median fold of the archenteron is proved by transverse sections through the most anterior part of the rudiment of the chorda (Figs. 160 *A*, 161 *A*), where the infolding of the cell-plate which represents the rudiment of the chorda can actually be seen (VAN BENEDEN and JULIN, No. 10).

In *Amphioxus*, according to HATSCHEK, the median fold of the intestinal wall is not completely absorbed in the formation of the chorda. Its lateral cells, which are in contact with the coelomic diverticula, yield the cells which complete the dorsal wall of the intestine after the chorda has separated from the mesoderm. VAN BENEDEN and JULIN conjecture that similar conditions exist in the anterior part of the chorda-rudiment in the Ascidians (*cf.* Fig. 161 *A*, *x*).

A certain guarantee of the accuracy of the observations made by VAN BENEDEN and JULIN seems to be afforded by the striking resemblance to the formation of the mesoderm in *Amphioxus*. Their observations, however, have not been confirmed either by DAVIDOFF (No. 14), who investigated the formation of the mesoderm in *Clavelina* and *Distaplia* or by WILLEY (No. 54*a*). According to the former author, the mesoderm-cells become abstricted from definite entoderm-cells at the margin of the blastopore (mesoderm-gonads), and become arranged in an originally single layer below the entoderm. This would be a kind of mesoderm-formation by delamination. DAVIDOFF was unable to find coelomic diverticula. The "mesoderm-gonads" are said to remain in connection with the entoderm, and, after the mesoderm has been produced, some of them are said to take part in the formation of the chorda and others in that of the alimentary canal. *

In the posterior region of the body (the future caudal region), the condition appears to be modified through the early disappearance of the lumen of the intestine (Fig. 160 *C*). The strand-like chorda is

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* [In *Ciona*, the mesoderm-cells form temporarily part of the wall of the archenteron between the chorda and the entoderm. Eventually they become displaced outwardly and the entoderm and chorda come into contact. According to CASTLE (No. II.) there does not appear to be any enterocoelic formation in this genus.—ED.]

here pressed inward by the developing medullary tube, so that it then fills the whole lumen of the intestine. The lateral cells of the wall of the enteron, three of which are usually seen on either side

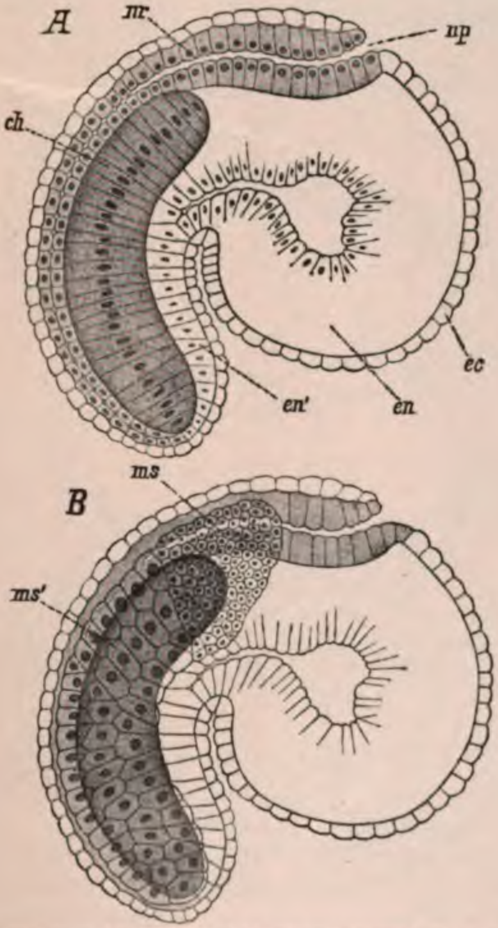

FIG. 163.—Later stage of development of *Clavelina Rissoana* (after VAN BENEDEN and JULIN). *A*, median sagittal section; *B*, lateral aspect. *ch*, chorda; *ec*, ectoderm; *en*, entoderm; *en'*, subchordal entoderm-strand in the caudal region; *ms*, anterior small-celled portion of the mesoderm-bands; *ms'*, posterior large-celled caudal section of the same; *np*, neuropore; *nr*, medullary tube.

in cross-section, pass directly into the large mesoderm-elements which cover the chorda laterally and subsequently yield the caudal musculature. There then still remain the entoderm-cells that lie in the ventral middle line (Figs. 160 *C* and 161 *C*, *en*); these, which are arranged in two parallel rows, retain the character of ordinary entoderm-cells and form a permanent cell-strand connected with the intestine, in which we recognise the vestiges of a caudal section of the alimentary canal (Fig. 162 *A*, 163 *A*, *en'*).

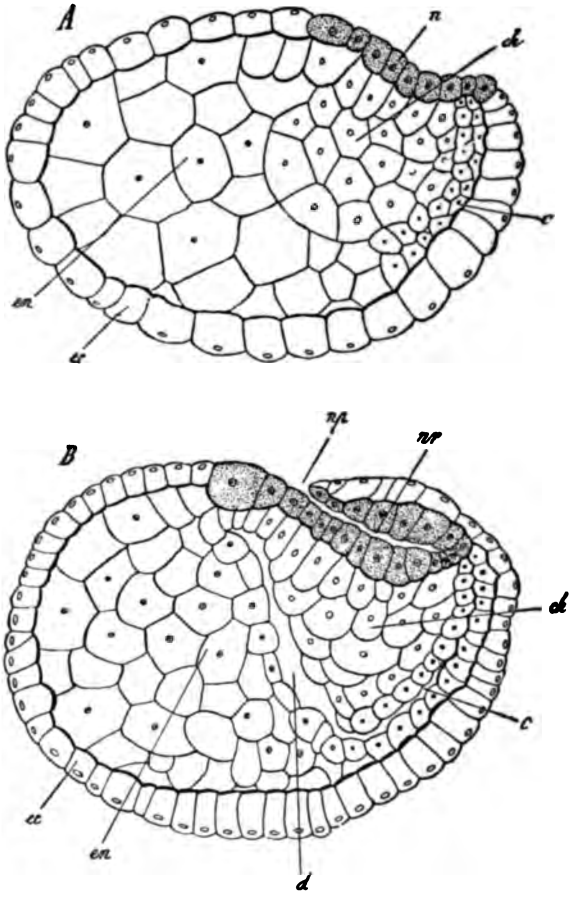

Fig. 164.—Median sagittal sections of two stages of development of *Distaplia magnilarva* (after Davidoff). *c*, rudiment of the caudal section of the intestine; *ch*, rudiment of the chorda; *d*, enteric cavity; *ec*, ectoderm; *en*, entoderm; *n*, medullary plate; *np*, neuropore; *nr*, medullary tube.

In the caudal region, the separation of the mesoderm and the chorda takes place in a very simple way, the archenteron merely breaking up into the two rudiments. These structures, however, are probably to be derived in a way similar to that described above for the anterior region of the body. We shall have here to assume (with **VAN BENEDEN** and **JULIN**) in these regions, the presence of a lumen of the archenteron compressed through the growth of the chorda-rudiment to the shape of a crescent. The question here arises whether the mesoderm-layer of the caudal section is to be referred to the splanchnic or the somatic layer of the former mesoderm-rudiment. **VAN BENEDEN** and **JULIN** incline to the first assumption, and **SEELIGER** (No. 50) has also pointed out the resemblance of the mesoderm-cells of the caudal section to to the cells of the inner layer of the mesoderm in the anterior region of the body.

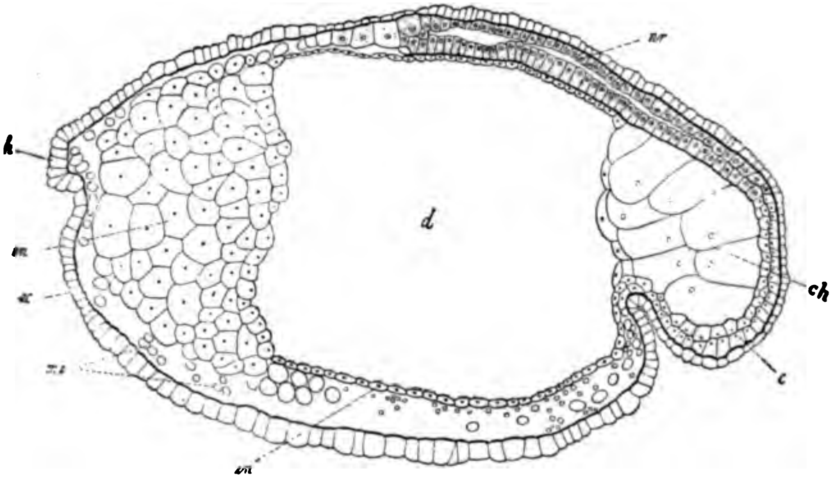

FIG. 165.—A later stage in the development of *Distaplia magnilarva* (after **DAVIDOFF**). *c*, caudal prolongation of the alimentary canal; *ch*, rudiment of the chorda; *d*, enteric cavity; *ec*, ectoderm; *en*, entoderm; *h*, adhesive papillae; *ms*, mesenchyme-cells; *nr*, medullary tube.

The mesoderm and the chorda are therefore derivatives of the primary entoderm.* Their origin can be traced back to the form of folding which is also found in *Amphioxus*. The principal distinction between the process here and in *Amphioxus* seems to be that, in the mesoderm-rudiment of the Ascidians, no trace is to be found of the segmentation which appears so early in *Amphioxus*. In the Ascidians the mesoderm-bands appear composed of two different parts (Figs. 162 *B*, 163 *B*); an anterior part (*ms*), consisting of several layers of small cells, which has arisen through folding in the anterior part of the archenteron, and a posterior part composed of a single layer of large cells (*ms'*) belonging to the caudal region. The anterior part of the mesoderm, at a later stage, forms a mesenchyme filling the

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* [See footnote, p. 340.—ED.]

primary body-cavity (Fig. 167, *ms*) which yields the blood-corpuscles, the connective tissue, the body-musculature, as well as the genital and excretory organs, while the posterior part gives rise to the larval caudal musculature (Fig. 168 *B*, *m*).

In *Distaplia*, in which, after the closure of the blastopore, the entoderm forms a solid cell-mass (Figs. 157, 164 *A*), the enteric cavity arises only later through the shifting apart of these cells (Fig. 164 *B*). In this way a posterior part of the body is marked off; in this the cells of the entoderm separate into the rudiment of the chorda (Fig. 164, *ch*) and into that of the solid sub-chordal enteric process (*c*), while the large entoderm-cells in the anterior region of the body (Fig. 165, *en*) mix later with the mesenchyme and probably disintegrate. In other respects there is no essential difference between the development of *Distaplia* as described by DAVIDOFF (No. 14) and that of other Ascidians. It should be pointed out that the elements of the food-yolk here appear equally distributed in all the tissues (the ectoderm, the mesoderm and the entoderm).

D. Development of the free-swimming larva.

External form of the body. We have already pointed out that, at the time when the medullary tube develops, the embryo becomes elongate and pear-shaped. In this way a broader anterior section is marked off from a narrower posterior section (Fig. 162) which gives rise to the tail of the larva. This latter part of the body next grows greatly in length, less, as SEELIGER points out, by the multiplication than by the elongation of the cells composing it. At the same time, it becomes more distinctly constricted from the anterior section and curves round ventrally (Fig. 163). As the tail, which is now bent downwards and forwards, increases in length, its posterior end not only reaches the anterior end of the body but even grows upwards again at the right side of the latter. In this process, the tail becomes twisted on its longitudinal axis, so that the nerve-tube appears shifted to the left side of the embryo (Fig. 170, p. 368).

The anterior region of the body, which at first appears more or less spherical, lengthens later, and in the larva is ovate (Figs. 167 and 168). Three prominences, arising as thickenings of the ectoderm, can soon be seen at its anterior end; these are the rudiments of the papillae for attachment (Figs. 167, 168, 170, *h*), through which, by means of a secretion yielded by the glandular epithelium, the fixation of the larva takes place.

Balfour has pointed out that, since a similar attaching apparatus is found in Amphibian larvae and (in front of the mouth) in the larvae of many Ganoids (*Acipenser*, *Lepidosteus*) we may perhaps have here an inherited feature common to the Chordata. It seems doubtful, however, to what extent these structures are really homologous and not merely analogous.

After the egg-envelope has burst, the larva straightens out. The tail then forms a direct posterior continuation of the longitudinal axis of the body (Figs. 167 and 173 *A*, p. 375).

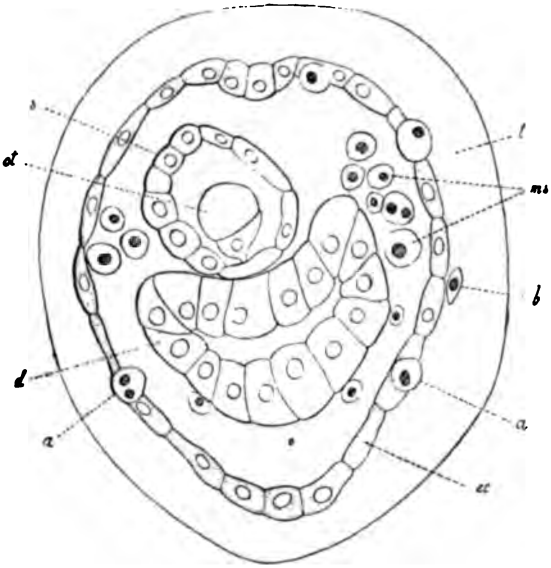

Fig. 166.—Transverse section through an attached larva of *Phallusia mammillata* (after Kowalevsky). *a*, mesenchyme-cells in the act of passing through the ectoderm; *b*, mesenchyme-cells in the cellulose mantle; *d*, alimentary canal; *ec*, ectoderm; *ms*, mesenchyme-cells; *ot*, otolith; *s*, transverse section through the sensory vesicle; *t*, cellulose mantle.

The mantle. The ectoderm-cells, which originally were somewhat cubical but assumed a more flattened form, at the time when the caudal region develops, secrete, at their outer surface, a homogeneous cuticular layer which, from its first appearance, gives a cellulose reaction. This is the first rudiment of the Ascidian test or tunic. In the caudal region, this layer grows out to form a median dorsal and a ventral fin (Fig. 169, *fl*, p. 363). While, in *Doliolum* and *Appendicularia*, such a simple, homogeneous cuticular layer is retained throughout life, in the Ascidiacea and Hemimyaria it is considerably thickened, single cells immigrating into the cellulose layer. It has hitherto been believed that, as O. **Hertwig** (No. 25) maintained, the cells that wandered into the cellulose substance came from the ectoderm, but **Kowalevsky** (No. 32) has recently proved* that the mantle-cells were derived from the mesoderm, being mesodermal cells which traverse the ectoderm and thus migrate outwards (Fig. 166). Subsequently, in the cellulose substance, they assume the character of star-shaped connective-tissue cells. We have to regard the mantle of the Tunicates as a cuticular gelatinous secretion permeated by phagocytes (mesoderm-cells).† When, in the composite Ascidians, some of the individuals disintegrate, the phagocytes of the

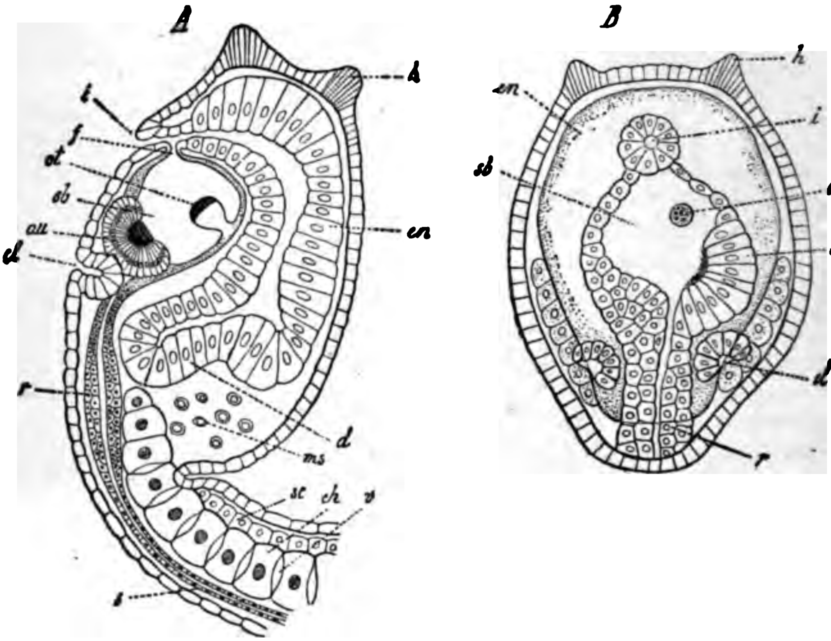

Fig. 167.—Embryos of *Phallusia mammillata* at a later stage (after **Kowalevsky**) *A*, lateral aspect; *B*, dorsal aspect. *au*, eye; *ch*, chorda; *cl*, cloacal vesicle; *d*, rudiment of the alimentary canal; *en*, entoderm-sac; *f*, ciliated pit; *h*, adhesive papillae; *i*, mouth; *ms*, mesenchyme-cells; *ot*, otolith; *r*, trunk-section, *s*, caudal section of the medullary tube; *sb*, sensory vesicle; *sc*, sub-chordal entoderm-strand; *v*, vacuoles between the cells of the chorda.

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* **Salensky's** recent statements as to *Pyrosoma* (No. 74) fully agree with this observation (see below, p. 401).

[† **Seeliger** (No. XXXIII.) agrees with **Kowalevsky** that the true test-cells are mesodermal. In *Oikopleura*, however, the cells of the "Haus" are ectodermal.—**Ed.**]

mantle play an important part in the process (MAURICE, No. 40). The histological character of the mantle-tissue may undergo further modification, such as the vesicular transformation of the mantle-cells in *Phallusia*, and the appearance of fibrillae in the ground-substance in *Cynthia*.

Since the surface of the embryo is, from the earliest stage, surrounded by a gelatinous covering, in which lie embedded the yellow test-cells, it was formerly thought that this layer was to be regarded as the rudiment of the future mantle (KOWALEVSKY, KUPFFER), an error to which the test-cells owe their name. Zoologists were inclined to consider the mantle of the Ascidians as a persisting embryonic envelope. O. HERTWIG first proved that the test-cell-layer is lost and that the mantle arises from the ectoderm. The immigration of the mantle-cells was only recently observed by KOWALEVSKY. SALENSKY, however, in a recent treatise (No. 49, also No. XXIX.) has returned to the older view, ascribing to the test-cells (kalymmocytes) in *Distaplia* the principal part in the formation of the cellulose mantle [see footnote, p. 336.]

The nervous system. The rudiment of the central nervous system which has hitherto been called the *medullary tube*, from the early stages onward, shows a dilatation of its anterior section (Fig. 163, *nr*, p. 351). In the later stages which lead to the development of the free-swimming larva, this dilated anterior part gives rise to a vesicle, the so-called *cerebral* or *sensory vesicle* (Fig. 167, *sb*, *vésicule antérieure ou cérébrale* of VAN BENEDEN and JULIN) while the posterior, narrowed part yields the caudal section (*région caudale*) of the nerve-cord (*s*). These two parts appear connected by a middle part (*r*) with a narrow central canal and thickened wall which KOWALEVSKY (No. 30) has called the trunk-ganglion (*portion viscérale du myelencéphale* of VAN BENEDEN and JULIN). The former connection between the neural tube and the exterior (the neuropore) completely closes even before the appearance of the oral aperture, which lies near the same point.

The *cerebral* or *sensory vesicle* represents the most anterior part of the medullary tube swollen out into a vesicle by the dilatation of its central canal. Its walls consist for the most part of pavement-epithelium, but the dorsal wall is thickened and divided into a right and a left swelling by a median furrow (VAN BENEDEN and JULIN, No. 7). The two organs known as the *eye* and the *otocyst* (*au* and *ot*, Fig. 168) soon appear in the form of accumulations of pigment. The eye, which is derived from the right dorsal swelling (Fig. 168 *B*), is a cup-like deposit of pigment at the inner ends of several radially placed columnar cells, the cavity being occupied by a lens with a superimposed meniscus (Fig. 168).

According to **Seeliger**, the lens and the meniscus develop within a single cell derived from the wall of the sensory vesicle. **Kowalevsky**, on the contrary, believes that they arise from three cells, and this agrees with **Leuckart**'s statement (No. 37) that three biconvex lenses are found within the pigmented eye-cup.

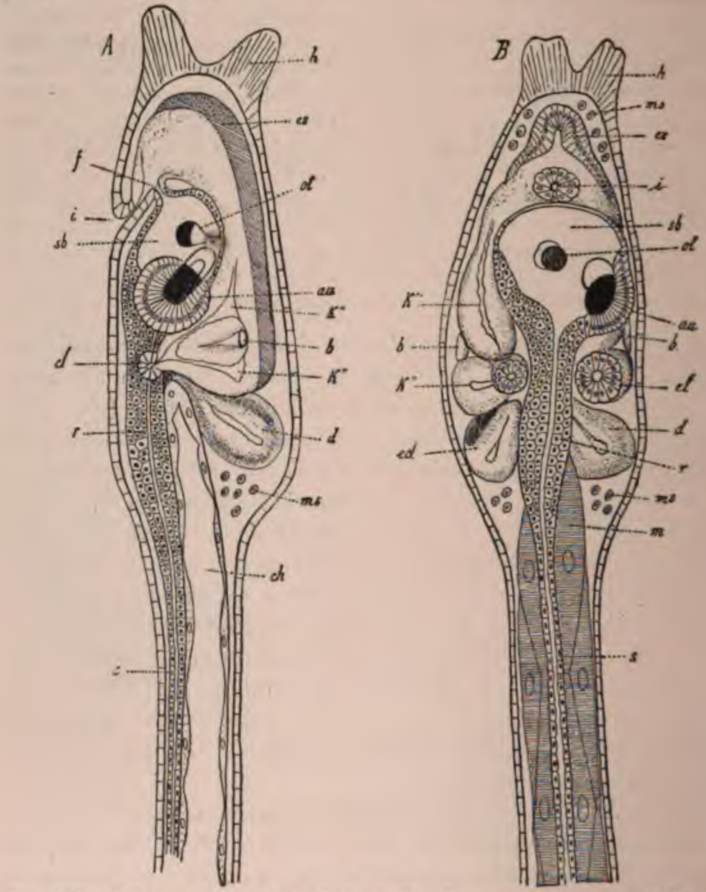

Fig. 168.—Anterior region of the body in the free-swimming larva of *Phallusia mammillata* (after **Kowalevsky**). *A*, lateral aspect; *B*, dorsal aspect. *au*, eye; *b*, blood-sinus between the gill-clefts; *ch*, chorda; *cl*, cloacal aperture; *d*, alimentary canal; *ed*, intestine; *es*, endostyle; *f*, ciliated pit; *h*, adhesive papillae; *i*, mouth (branchial aperture); *k'*, *k''*, first and second gill-slits; *m*, caudal muscles; *ms*, mesenchyme-cells; *ot*, otolith; *r*, trunk-section of the medullary tube; *s*, caudal section of the medullary tube; *sb*, sensory vesicle.

The so-called *auditory organ* (Fig. 168, *ot*) consists of a pear-shaped or conical cell (otolith-cell) projecting into the interior of the sensory vesicle, the narrowed end of which is inserted between the cells of the ventral wall of the vesicle while the free end carries a pigment cap. This view of the formation of the auditory organ is supported by KUPFFER's statement (No. 35) that the cells of the ventral wall of the sensory vesicle which surround the otolith-cell and which differ somewhat in histological character from the rest, are provided with fine, stiff setae projecting towards the otolith-cell. According to KUPFFER, a vesicular cavity is found in the crista acustica directly below the otolith-cell.

According to KOWALEVSKY, the otolith-cell, on its first appearance, is situated on the dorsal wall of the sensory vesicle and only shifts later over its right side to the ventral surface. Our knowledge of the structure and development of both the sensory organs is, however, very inadequate.*

The *trunk-section* of the nervous system (Figs. 167 and 168, *r*) (the trunk-ganglion) is, according to VAN BENEDEN and JULIN, the direct continuation backward of the left dorsal swelling of the sensory vesicle. The cells of the wall of this swelling show the same histological character as those which, in a single layer, line, like an epithelium, the narrow central canal of the trunk-ganglion. On these cells, however, on the ventral side, there is superimposed a great mass of ganglion-cells (Fig. 171). According to the distribution of these cells we can recognise the division of the trunk-ganglion into an anterior and a posterior section, the anterior section being still included by KUPFFER in the cerebral sensory vesicle as a ganglionic portion. In the posterior section, the ganglion-cells enclose a nucleus of nerve-fibrillae. The trunk-region of the nerve-cord lies above the most anterior end of the chorda (Fig. 168 *A*)

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*[According to WILLEY (No. XXXVI.) who has investigated the development of these organs in *Ascidia mentula* and *Clavelina lepadiformis*, the first indication of these sensory organs consists in the deposition of black pigment-granules in the dorsal wall of the *cerebral vesicle*. The most anterior of the cells containing pigment-granules becomes distinguished by the larger size of its granules and the swollen nature of the cell itself. This pigment-cell soon separates itself from the others and becomes gradually transferred by a differential growth of the wall of the vesicle down the right wall to its final position on the ventral side of the vesicle. This cell is the otocyst, and the pigment-granules become consolidated together to form the otolith. The other pigment-cells of the dorsal wall of the vesicle collect themselves together and form a slight protuberance in the right dorso-lateral corner of the vesicle. The pigment-granules become concentrated toward the cavity of the vesicle. Subsequently two or three cells from the adjoining wall of the vesicle take up a position, one above the other, in front of the mass of pigment and by an alteration of their contents give rise to the lens of the eye. The original pigment-producing cells constitute the retina, which retains its primitive position as part of the epithelial wall of the brain. See also SALENSKY (No. XXX.).—ED.]

According to van Beneden and Julin, however, the chorda does not reach so far forward in *Clavelina* as in *Phallusia*.

The *caudal section* of the nerve-cord (Figs. 167 and 168, *s*) is a tube the walls of which consist of a simple pavement-epithelium. In cross-section (Fig. 169, *nr*, p. 363), four cells are usually found, two lying laterally, one dorsally and one ventrally.

This section extends to the posterior end of the body. The reduction of the lumen of the alimentary canal in the caudal region of the embryo is accompanied by the obliteration of the neurenteric canal which represented the posterior continuation of the central canal of the nerve-cord.

Kupffer observed the important fact that, in the larva of *Ascidia mentula*, lateral bundles of fibrillae are given off by the caudal section of the spinal cord; these we may claim as spinal nerves. The first pair of these was found on the boundary between the trunk and caudal regions, and the following two pairs at intervals more or less corresponding to the length of a caudal muscle-cell.

We may regard this as an indication of the segmentation of the caudal region. The same significance may be attributed perhaps to those cell-groups found by Lahille (about ten in number) in the caudal nerve-cord of the *Distaplia* larva, and also occurring in *Appendicularia* (Nogine, Langerhans, and others).

The ciliated pit. In connection with the central nervous system, we must describe a ciliated diverticulum which opens into the dorsal wall of the anterior section of the alimentary canal (branchial sac or pharynx) and which has been claimed as a homologue of the *hypophysis cerebri* of the Vertebrates. In adult Ascidians its form is more complicated. A glandular mass, the sub-neural gland (*glande-hypophysaire* or sub-ganglionic body) can then be recognised in close proximity to the brain, and an efferent duct runs forward to enter the pharynx through a complicated apparatus, the dorsal tubercle, in the dorsal middle line between the two ciliated bands (*sillons péricoronaux*) which run upwards from the endostyle. The opening of this duct has erroneously been assumed to be an olfactory organ (olfactory tubercle, see Julin, Nos. 26 and 27).

According to van Beneden and Julin (No. 7) and Seeliger (No. 50), the first rudiment of this ciliated diverticulum arises quite independently of the nervous system as a pit-like invagination of the entodermal wall of the pharynx. At a later stage, the blind end of this diverticulum is said to become closely applied laterally to the sensory vesicle, always on the side which is turned away from the eye, *i.e.*, as a rule, on the left side, although LAHILLE (No. 37) considers that this condition varies in the different forms.

LAHILLE (No. 37), SHELDON (No. 52), WILLEY, (No. 54), and HJORT (No. 59), on the contrary, have been led by their researches to confirm in almost all points the older observations of KOWALEVSKY as to the rise of the ciliated pit, *i.e.*, to regard it, in its origin, as much more closely connected with the central nervous system. After the neuropore has completely closed, the most anterior section of the cephalic vesicle lengthens and fuses with an ectodermal depression, the stomodaeum (rudiment of the larval mouth, branchial aperture). At this point perforation takes place (Figs. 167 *A*, 168 *A*, *f*), so that now the cephalic cavity, by means of this short tube which represents the rudiment of the ciliated pit, communicates with the most anterior ectodermal section of the alimentary canal. Only in later stages when, after the fixation of the larva, the larval nervous system degenerates, is the connection between the ciliated pit and the nervous system lost. The pit then forms a blind intestinal diverticulum contiguous with the definitive ganglion (Fig. 173 *fl*).*

According to these statements, the ciliated pit opens into the ectodermal or stomodaeal portion of the branchial sac, and we thus have a condition agreeing with that of the hypophysis in the Vertebrata.

The chorda. The chorda arises through the transformation of a plate-like rudiment (Fig. 159, *ch*), which originally formed the roof of the archenteron, into a cell-strand which, in cross-section, is round (*cf.* Figs. 160 and 161, *ch*). We have seen above (p. 348) that we must suppose this to have been brought about by the formation of a groove (as in *Amphioxus*). In cross-section, the chorda-strand is originally composed of several cells. Both in lateral (Fig. 162 *A*) and in dorsal aspect it appears composed of two rows of cells, the ends of which dove-tail with one another. This dove-tailing of the cells denotes the commencement of a change of position which in most cases leads to the chorda-cells appearing arranged one behind the other in a single row like a roll of coins (Fig. 163 *A*). In those

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* [WILLEY (No. XXXVI.) has recently reinvestigated this point both in *Ciona* and *Clavelina*. He is convinced that VAN BENEDEN and JULIN were quite mistaken in their interpretation of the origin of the hypophysial tube in *Clavelina*. The whole is derived essentially from the neural tube, and thus the lumen of the hypophysis is at first in direct communication with the lumen of the central nervous system, the opening of this structure into the pharynx being, according to WILLEY, a reopening of the neuropore.—ED.]

later stages which are connected with a lengthening of the caudal section, the cells of the chorda-strand also lengthen (Figs. 167 *A*, 170, *ch*). The chorda then begins to undergo a transformation which, at its commencement, is comparable to the changes in the chorda of *Amphioxus*, but, in the Ascidians, leads to peculiar modifications in this organ. Between each two consecutive cells there appears a vacuole filled with a gelatinous substance (Fig. 167, *v*; *cf.* also Fig. 170). These vacuoles, which, at first, lie in the axis of the chorda-strand, as they enlarge, compress the chorda-cells in such a way that the latter soon assume the biconcave form of fish-vertebrae and, as the gelatinous mass extends further, can be recognised merely as thin septa between its different sections. These sections soon come into contact and fuse, and in this way a strand of homogeneous gelatinous substance arises which at first resembles a string of beads but is later uniform and cylindrical (Fig. 168 *A*), while the chorda-cells which are pressed out to its surface surround it as a kind of sheath (KOWALEVSKY, KUPFFER, SEELIGER, and others).

The transformation of the chorda is not, in all Ascidians, so complete. According to SEELIGER, in *Clavelina*, it does not advance beyond the stage in which the chorda-cells assume the form of transverse septa.

Mesoderm, body-cavity, musculature. The two mesoderm-bands accompany the chorda along its whole length and project a little beyond it anteriorly. Two parts can be distinguished in them (Figs. 162 *B*, 163 *B*). In the posterior part (*ms'*) where they consist of a single layer of large cells arranged in three longitudinal rows, they yield the musculature of the larval tail. The cells of this part lengthen in later stages of development (Fig. 168 *B*, *m*) becoming hexagonal, while, on their inner and outer surfaces they produce longitudinal fibrils of contractile substance (Fig. 169, *m*) which appear to lie somewhat obliquely to the longitudinal axis of the body in such a way that the fibres of the inner layer cross those of the outer layer at an acute angle (SEELIGER). The caudal musculature of the larva which arises in this way shows indistinct transverse striation.

Anteriorly, in the trunk-region, the mesoderm-bands consist of several layers of smaller cells at first closely crowded together (Figs. 161 *A*, *ms*, 162, 163, *ms*). The innermost layer which lies next to the chorda is evidently a direct prolongation of the myoblast-layer of the caudal region. It undergoes the same transformations as the latter and yields the anterior part of the larval musculature. The connection between the other mesoderm-cells of this region soon becomes somewhat loosened; they assume a spherical form and constitute a mesenchyne which fills the primary body-cavity of the trunk-section (Fig. 168, *ms*).

We have seen (p. 350) that, according to VAN BENEDEN and JULIN, the mesoderm in this anterior part becomes detached from the archenteron in the form of paired coelomic diverticula (Figs. 159 and 160 *A*). The true coelom that arises in this way belongs, however, merely to the earliest embryonic stages, and disappears even as early as the time when the mesoderm completely separates from the entoderm. The mesoderm then fills the space between the ectoderm and the entoderm, which, in later stages, becomes considerably widened and, as it appears, filled with a gelatinous mass; this forms the ground-substance of the mesenchyme that arises through the transformation of this anterior portion of the mesoderm. The lacunae which arise later in this mesenchyme must be regarded, like the blood-vessels (which, according to VAN BENEDEN and JULIN are entirely devoid of an endothelial wall) as the pseudocoele.

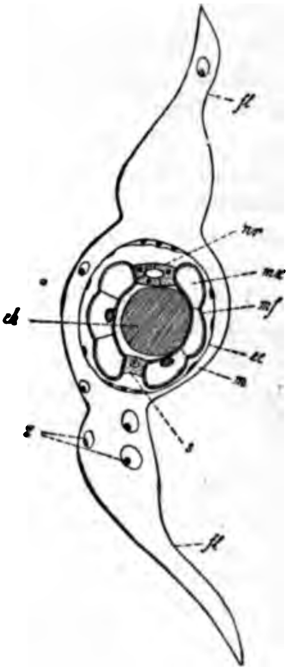

FIG. 169. — Transverse section through the caudal portion of the free-swimming larva of *Clavelina* (after SEELIGER). *ch*. chorda; *ec*, ectoderm; *fl*, median fin; *m*, cellulose mantle; *mf*, muscle-fibrillae in transverse section; *mz*, muscle-cells; *nr*, neural tube; *s*, subchordal entoderm-strand; *z*, mantle-cells.

The mesenchyme of the trunk-region, which is derived in the above way, yields the mesodermal organs of the adult Ascidian. Its histological differentiation gives rise to the connective tissue, as well as to the pigmented elements, and to the body-musculature of the adult which appears arranged in radial and circular muscles surrounding the inhalent and exhalent orifices as well as into longitudinal muscles of the trunk, etc. Single cells of the mesenchyme, which become free and reach the pseudocoele, become changed into blood-corpuscles. We shall see later (p. 380) that the genital organs also, with their efferent ducts, and the urinary organs originate in the mesoderm.

It must be mentioned that at a later stage (especially during the transformation connected with fixation) the mesenchyme becomes apparently enriched by elements which, when the entodermal strand (Fig. 169, *s*) and the larval nervous system disintegrate, become free. KOWALEVSKY thought that these cells became changed into blood-corpuscles, and later, SEELIGER (No. 50) utilised this fact in constructing his theory of the budding in compound forms. It, however, appears doubtful to us whether these elements take any part whatever in the formation of the organs of the adult or of their buds or whether they do not rather, after reaching the blood, undergo degeneration.

The alimentary canal. The rudiment of the alimentary canal is derived from the archenteron by the separation of the mesoderm bands and the chorda-strand. In early embryonic stages (Figs. 162, 163, p. 351) it consists of an anterior pre-chordal dilatation (*en*) and, following this, of a narrowed part lying already below the chorda but still belonging to the trunk-region. This narrowest part is directly continued into the sub-chordal entoderm-strand of the caudal region (*en'*) which must be regarded as the intestinal rudiment of this part of the body.

Since the mesoderm and the chorda (as seen above, p. 350) arise by a process of folding from the dorsal wall of the archenteron, the dorsal wall of the intestine is defective at this point; this gap becomes closed in later stages by certain cells as described above (p. 350). This defect is only found in the trunk-region in the posterior narrowed part of the alimentary canal, as the rudiment of the caudal region undergoes no further advance in form and, on the other hand, the pre-chordal section of the intestine takes no part in the foldings which give rise to the mesoderm and the chorda. This narrowed sub-chordal trunk-portion of the intestine, after the gap just mentioned has closed, forms a blind diverticulum projecting backward (Fig. 167 *A*, *d*, p. 356), the end of which, according to KOWALEVSKY, at those stages in which the caudal section becomes more sharply marked off from the trunk, bends slightly towards the dorsal side, thus severing its connection with the cellular entoderm-band of the caudal region (*se*). In this way is introduced the degeneration of this last part of the intestine mentioned above, which leads to the cells of this band becoming disconnected and assuming a resemblance to blood-corpuscles. We then find, beneath the chorda in the caudal region, a cavity apparently filled with blood-corpuscles and in direct communication with the spaces of the pseudocoele.

According to KOWALEVSKY, with whom the majority of later authors (KUPFFER, SEELIGER) agree, the branchial sac or pharynx is derived from the pre-chordal dilatation of the intestinal rudiment, while the sub-chordal diverticulum, which is directed backward (*d*), yields, through simple growth, the other parts of the alimentary canal (the oesophagus, the stomach and the intestine proper). This diverticulum, as the larva lengthens, is said to form a coil in which we can distinguish a right descending portion, a ventral connecting piece, and a left ascending part which ends blindly. The right portion is said to give rise to the oesophagus, the connecting piece to the stomach and the left ascending portion to the intestine (*cf.* Fig. 168, *d* and *ed* with Fig. 170, *oe*, *m*, and *ed*). The anus only arises later, during larval life, by the blind end of the intestine becoming connected with one of the two so-called cloacal vesicles (that on the left), these latter being ectodermal invaginations which will be described further later.

The account given by VAN BENEDEN and JULIN (No. 10) differs from that given above in so far as they derive only the descending portion of the intestinal coil (consisting of the oesophagus and the stomach) through direct growth from the posterior diverticulum mentioned above, while they believe that the intestine proper arises from the ventral surface of the dilated stomach as a secondary outgrowth. The point of origin of this secondary caecum, which is directed to the left and upward, is said to lie somewhat far forward, *i.e.*, to be almost pre-chordal. We shall see below (p. 521) that these authors ascribe some significance to this observation.

The *oral aperture* of the larva (which gives rise to the inhalent or branchial aperture of the adult) is formed only shortly before the larva hatches. The anterior pointed end of the alimentary canal, just before reaching the sensory vesicle, bends dorsally. It there comes into contact with an invagination which has arisen from a thickened disc of ectoderm-cells. By the apposition of these two structures and a breaking down or separation of the cells, the oral aperture is formed (Figs. 167 and 168, p. 358).

The *endostyle* develops as a ciliated furrow in the antero-ventral region of the branchial sac (pharynx), owing to the formation of two lateral longitudinal swellings. We cannot here enter further into the histological details of this structure, but must refer the reader for these to the treatises of R. HERTWIG, FOL and SEELIGER (No. 50). We may, however, mention that this furrow is not purely ventral in position, its anterior portion extending up towards the dorsally placed oral aperture (Fig. 170, *es*). According to a recent treatise by WILLEY (No. 54*a*), the rudiment of the endostyle originally lies in the most anterior part of the branchial sac in which it has a dorso-ventral position. Only later does it shift farther back and come to lie ventrally. This observation is of importance in connection with the condition of this organ in *Amphioxus*, where it undergoes a similar displacement.

The digestive or pyloric gland arises as a caecal outgrowth at the boundary between the stomach and the intestine; it, however, soon branches repeatedly, and these ramifications extend over the surface of the intestine where, by anastomosing, they form a network (Fig. 175 *A*, *dr*, p. 379). It has been homologised by WILLEY (No. 54*a*) with the hepatic caecum of *Amphioxus*.

Peribranchial, atrial, or cloacal cavity. The first rudiments which lead to the development of the peribranchial cavity are found, shortly before the larva hatches, in the form of a pair of ectodermal invaginations lying dorsally at the boundary between the sensory vesicle and the trunk-ganglion, called by METSCHNIKOFF, who was the first to observe them, the *cloacal vesicles* (Fig. 167, *cl*, p. 356). Two diverticula grow out from the pharynx towards these invaginations, one on each side, and fuse with them, thus giving rise to the first gill-slits (Fig. 168, *k*, p. 358). According to KOWALEVSKY, a second pair of these slits (k'') soon forms in *Phallusia* behind the other in the same way. If the interpretations of KOWALEVSKY and SEELIGER are correct, the cloacal vesicles, by enlarging, give rise to the paired halves of the peribranchial cavity. In this case, the latter would be lined throughout with ectoderm, and the wall of the pharynx, which is perforated by the gill-slits, would on its inner side be covered with entoderm and on its outer with ectodermal epithelium. We should then perhaps be justified in homologising the peribranchial cavity of the Ascidians with the atrium of *Amphioxus*; we can hardly, in any case, doubt the homology of the gill-slits in these two groups. Another view has, however, been adopted by VAN BENEDEN and JULIN (Nos. 9 and 10). According to these observers, the first gill-slit arises through the fusion of a rather long entodermal diverticulum with the cloacal vesicle of the same side which, according to these authors, is never very large. The Ascidian larva at this stage is exactly in the condition in which *Appendicularia* remains throughout life, the pharynx, in the latter, communicating through a branchial passage on either side with the exterior. These passages represent a pair of gill-slits, and this pair, *in the Ascidian as in Appendicularia, remains the only pair.* In the Ascidian, the branchial passages are considerably enlarged secondarily, and in this way the peribranchial or atrial cavity arises. Since these passages, according to VAN BENEDEN and JULIN, are for the most part of entodermal origin, a large although not sharply marked portion of the peribranchial cavity must be lined with entoderm. These observers therefore maintain that these spaces cannot be homologised with the atrial cavity of *Amphioxus*, and the future perforations in their inner walls can in no way be homologised with the gill-slits of *Amphioxus* and the Vertebrates, and are therefore distinguished from true gill-slits by these authors as *branchial stigmata*. We have some hesitation in accepting the view of VAN BENEDEN and JULIN. The origin of the peribranchial cavities in the Ascidians does not appear to us sufficiently understood to justify its utilisation in the formation of such important conclusions. It should be pointed out that, in the embryo of *Pyrosoma*, the purely ectodermal origin of the peribranchial cavities can hardly be doubted (see below, p. 394), and this seems also to apply to *Doliolum* (see the statements as to the *Anchinia* buds, p. 481). Again, we are probably not justified in concluding without further evidence that the condition of *Appendicularia* is primitive. Since an Appendicularian was found by MOSS (No. 5) possessing many gill-clefts like those of *Doliolum*, we may have to regard the apparently simple respiratory organs of other Larvacea as degenerate.

We shall have to speak of the further transformations in the branchial region when describing the metamorphosis of the attached larva, although, in some cases, the multiplication of the gill-slits commences in the free-swimming larva (*Botryllus*, *Distaplia*, Fig. 230, p. 457).

LAHILLE (No. 38) and WILLEY (No. 54*a*) have both recently expressed their belief in the purely ectodermal origin of the peribranchial sacs. According to LAHILLE, they arise, in the *Didemnidae*, through the enlargement of the cloacal vesicles. Their outer aperture then disappears and an unpaired ectodermal invagination appears on the dorsal side; this is the cloacal invagination proper, which only secondarily becomes connected with the peribranchial sacs. WILLEY (No. 54*a*) observed, in *Clavelina*, as the precursor of the cloacal vesicle, a longitudinal furrow, from the posterior end of which the cloacal vesicle develops. WILLEY is therefore inclined to assume that the peribranchial cavity of the Ascidians is homologous with that of *Amphioxus*.

The outer apertures of the two peribranchial spaces (Fig. 231, p. 460) shift continually towards each other and towards the dorsal middle line till they meet and fuse. In this way arises the cloacal, atrial or inhalent orifice (Fig. 230, *e*). VAN BENEDEN and JULIN (No. 9) have pointed out that, during this fusion, the part of the ectoderm which lies between the two apertures becomes depressed and this depression gives rise to the true cloacal cavity, *i.e.*, to the unpaired part which connects the two peribranchial cavities and which is thus lined with ectoderm.

The terminal portion of the intestine which had, at an earlier stage, become connected with the left cloacal vesicle (see above, p. 365) now opens into the common peribranchial cavity.

The heart, the pericardium and the epicardium. We owe to SEELIGER the proof that the heart and the pericardium of the Ascidians are entodermal structures, the first rudiment of which can be recognised in the form of an outgrowth from the pharynx arising between the posterior end of the endostyle and the entrance to the oesophagus. A vesicle which becomes abstricted from this caecum (Fig. 170, *pc*) is the common rudiment of the pericardium and the heart. The remainder of the caecum (*ep*) has been named by VAN BENEDEN and JULIN the *epicardium*.* These authors were able essentially to confirm the statements of SEELIGER, although they repeatedly differ from him in points of detail. They also recognised the significance of the epicardium in connection with budding, and the originally double rudiment of these structures.

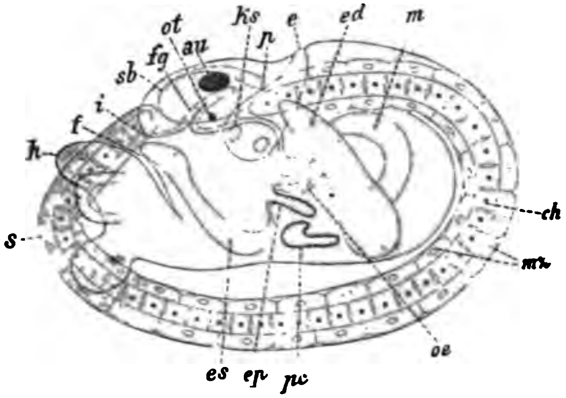

FIG. 170.—Left lateral aspect of a *Clavelina* embryo (after SEELIGER). *au*, eye; *ch*, chorda; *e*, exhalent orifice; *ed*, rectum; *ep*, epicardial outgrowth; *es*, endostyle; *f*, infolding of the body-surface in anticipation of the rotation that takes place after fixation; *fg*, ciliated pit; *h*, adhering papillae; *i*, inhalent orifice; *ks*, gill-slits; *m*, stomach; *mx*, muscle-cells of the tail; *oe*, oesophagus; *ot*, auditory organ; *p*, peribranchial sac; *pc*, pericardium; *s*, larval tail; *sb*, sensory vesicle.

The first rudiment of these organs was observed in the form of two solid cell-strands which run side by side in close contiguity to the

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*[DAMAS (No. IX.) finds that in *Ciona* the epicardium has a paired origin and opens by two distinct orifices into the pharynx.—ED.]

ventral wall of the alimentary canal near the point at which the oesophagus enters the pharynx. The origin of these cell-strands (*procardium*) is less clearly stated. VAN BENEDEN and JULIN have no doubt that they become detached from the entodermal intestinal epithelium. WILLEY has recently (No. 54*a*) made the same observation, finding, however, that the procardial rudiment is unpaired and also not entirely agreeing with VAN BENEDEN and JULIN with regard to its further development. The left procardial strand always appears stronger than the right. The strands soon develop lumina and thus become tubes. In later stages, the posterior ends of these tubes fuse, while, anteriorly, they open into the branchial sac. The whole rudiment now consists of an unpaired posterior caecum (Fig. 171 *B*, *ep* and *pc*), which forks anteriorly into two tubes that open separately into the branchial sac (Fig. 171 *A*, *ep.o*). From the posterior caecum, a vesicle becomes abstricted (Fig. 171 *C*, *pc*) and this represents the common rudiment of the heart and the pericardium.

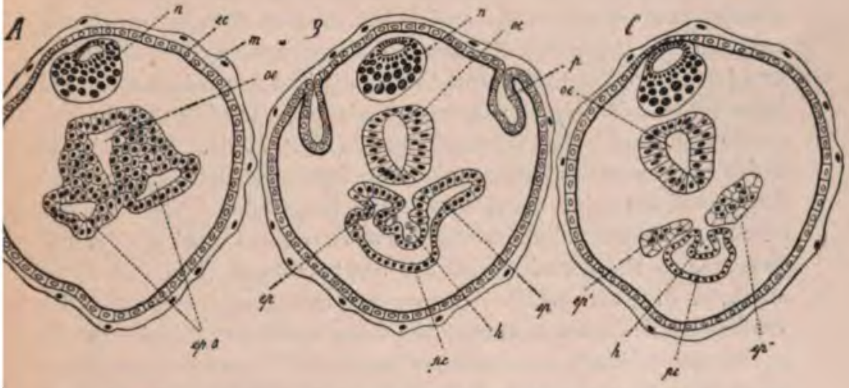

FIG. 171.—Three consecutive transverse sections through the trunk-region of a *Clavelina* larva (diagrammatic, after VAN BENEDEN and JULIN). *A*, shows the posterior blind end of the branchial sac or pharynx with the apertures of the oesophagus and the epicardial tubes (*ep.o*). *B*, shows the connection between the epicardial tubes (*ep*) and the pericardial vesicles (*pc*). *C*, shows the blind ends of the epicardial tubes (*ep*) and the pericaridal vesicle severed from them (*pc*). *ec*, ectoderm: *ep*, epicardial tubes; *ep'*, blind ends of the epicardial tubes; *ep.o*, the epicardial tubes near their openings into the pharynx; *h*, heart; *m*, cellulose mantle; *n*, neural tube; *oe*, oesophagus; *p*, peribranchial sac; *pc*, pericardial cavity.

The lumen of this vesicle (*pc*) is the future pericardial cavity. The form of the vesicle is complicated in consequence of the invagination of its dorsal wall as a furrow running along its whole length; this makes the vesicle crescent-shaped in cross-section. The lumen of this invagination is the future cavity of the heart (*h*). The invaginated part of the wall of the vesicle becomes the wall of the heart while the non-invaginated part changes into the pericardial epithelium.

The lumen of the heart is thus, according to the above description, a cavity which has arisen through the invagination of the outer surface of the pericardial vesicle. This cavity communicates, by means of the long dorsal aperture of invagination, with the lacunar blood-spaces of the surrounding mesenchyme. This communication is partly closed later by a lamella arising from the epicardium; it is, however, retained at the anterior and the posterior ends as the anterior and posterior apertures of the cardiac tube.

That part of the procardial rudiment which remains after the abstriction of the pericardial vesicle is from that time known as the epicardium. It consists, as before, of a posterior unpaired diverticulum (*sac épicardique*) which forks anteriorly into two paired epicardial tubes (*tubes épicardiques*); these, in their turn, entering the pharynx to the right and left of the median line (Fig. 171 *A*). The point at which they enter lies between the posterior end of the hypobranchial furrow and the point of entrance of the oesophagus. The posterior caecum of the epicardium now grows out backward considerably, and thus reaches the dorsal side of the heart-rudiment (Fig. 173 *C*, *ep* and *h*, p. 375) with which it comes into such close contact that its ventral wall is drawn in to close the dorsal aperture of the heart.

The *epicardium* is a structure of great significance in those forms which reproduce asexually, being intimately connected with the production of the buds. By extending farther and farther backward it reaches the stolon (Fig. 173 *C*, *st*) in which it forms a transverse partition. In this process it becomes so much compressed dorso-ventrally that its two layers come into close contact and (in *Clavelina*) fuse completely. The epicardial transverse partition separates, in the stolon, two blood-spaces in which the blood flows in opposite directions. As this partition-wall does not reach quite to the blind end of the stolon (Fig. 229, *x*, p. 456,) the two blood-spaces pass into each other at this point. We shall have to return later (p. 450) to the significance of the epicardium in connection with the development of buds.

The wall of the heart consists of pavement-epithelium directly connected with the pericardium, and bears to the latter the same relation as exists between the visceral and the parietal layers of a vertebrate pericardium. In later stages, the cells of the wall of the heart secrete, on the surface turned to the lumen of the heart, muscle-fibrils in which transverse striation can be distinctly seen. An endocardium is wanting in the Ascidian heart, and its vessels have no endothelial lining.

E. Review of the Organisation of the Free-swimming Larva (Figs. 168-173 A).

It should be mentioned that there is considerable variation in the degree of development attained by the organisation at the moment of hatching in the different species and even in the individuals of the same species.

The form of the larva, the development of which has just been traced in detail, recalls somewhat that of a tadpole. Anteriorly, there is an oral region (cephalic and trunk-region) the end of which carries the three adhesive papillae (Fig. 173, *hp*); this region is followed by a long, flatly compressed swimming tail. This latter, which shows markings like those of fin-rays (Fig. 173 *A*) attains its characteristic form through the great development of the mantle-substance (Fig. 169, *fl*) which further covers the whole surface of the body, even passing over the oral and cloacal apertures.

The axis of the tail is occupied by the chorda which extends anteriorly into the trunk-region. Above it lies the neural tube, while a cell-strand that runs below it and soon disintegrates represents the remains of that part of the intestine which belongs to the caudal region. Running along this part of the body and extending along its whole length, are the massive muscle-bands.

In the anterior region, the neural tube swells out to form a sensory vesicle (Fig. 173, *sb*) and a swollen trunk-section (*r*) immediately following the latter. The primitive enteron gives rise to the pharynx or branchial sac, the oesophagus, the stomach and the intestine. The oral aperture (or inhalent orifice, *i*) is established and is distinguished by its dorsal position. Near it, the ciliated pit (*fl*), which extends as far as the base of the sensory vesicle, opens into the pharynx. The intestine opens into the atrial cavity which has formed by the union of the two originally separate peribranchial sacs. There is now a single atrial aperture (or exhalent orifice, *e*). The number of gill-slits which have at this stage developed varies in different species.

The heart (*h*), the pericardium and the epicardium (*ep*) have developed. The heart already pulsates; the endostyle (hypobranchial groove) has developed. The mesenchyme becomes differentiated into connective tissue, blood-corpuscles and the first rudiments of the future body-musculature.

The free-swimming larva (Fig. 173, *A*) thus already shows the typical organisation of the adult Ascidian. The further transformations which take place after fixation are therefore slight. They consist of the degeneration of the provisional larval organs, the further development of the organs of the adult (especially of the branchial sac) and the development of the reproductive structures (stolon, genital organs).

It should be mentioned that the free-swimming larvae of the various families of Ascidians differ in many respects. On this subject, we must refer the reader to the descriptions and figures of LAHILLE (No. 38) who has also utilised the larval forms for systematic purposes. The above account applies mainly to the larvae of the *Phallusia* and *Clavelina*. The larvae of the *Distomidae* (*Distaplia*) are distinguished by their large size and by the early development and separation from them of several small buds which again divide (Fig. 230, p. 457), while in the larva of the *Didemnidae*, only one large additional individual is at first developed, thus giving rise to the appearance of double individuals (p. 459). The larvae of the *Botryllidae* are devoid of the three adhering suckers; these seem to be represented merely by three conical processes. They are further distinguished by an equatorial ring of dilated mantle-vessels surrounding the body. The *Styelidae* resemble them closely, and such a ring of mantle-vessels also occurs in many Didemnid larvae which otherwise are distinguished from the Botryllid larvae by the development of double individuals and the presence of adhering suckers.

F. Fixation and Retrogressive Metamorphosis.

The transformations which take place after fixation may to some extent be considered retrogressive, as the sensory organs, the nervous system, and the locomotory organs undergo degeneration. The other systems of organs, on the contrary, often become more perfect.

The free-swimming condition does not last for more than a few hours. The larval tail begins to degenerate when attachment takes place. According to KUPFFER, the larva attaches itself by means of only one of the three adhering papillae (Fig. 173 *B, hp*), the other two degenerating. Even the papilla that is utilised for fixation soon disappears, so that the young Ascidian then seems to be attached by the surface of the cellulose mantle. In other cases (*Clavelina*), stolon-like outgrowths from the lower end of the body bring about fixation.

The degeneration of the caudal region is introduced by the detachment of the soft parts of this region from the gelatinous mantle which envelops them and their withdrawal towards the trunk-region

(Fig. 173 *B*), to which they are then appended as a short truncated process. The internal organs of the caudal region are retracted more and more into the trunk (Fig. 172). They there coil up spirally, but the separate elements (the chorda, the muscle-bands, the neural tube) which compose this coiled strand retain for a long time their relative positions (*cf.* Fig. 172 *B*, *x*, where the strand is cut through transversely). The degeneration of the chorda commences, according to Kowalevsky's most recent researches (No. 32), by the disappearance of its gelatinous substance, while its cells (Fig. 172, *ch*) again become

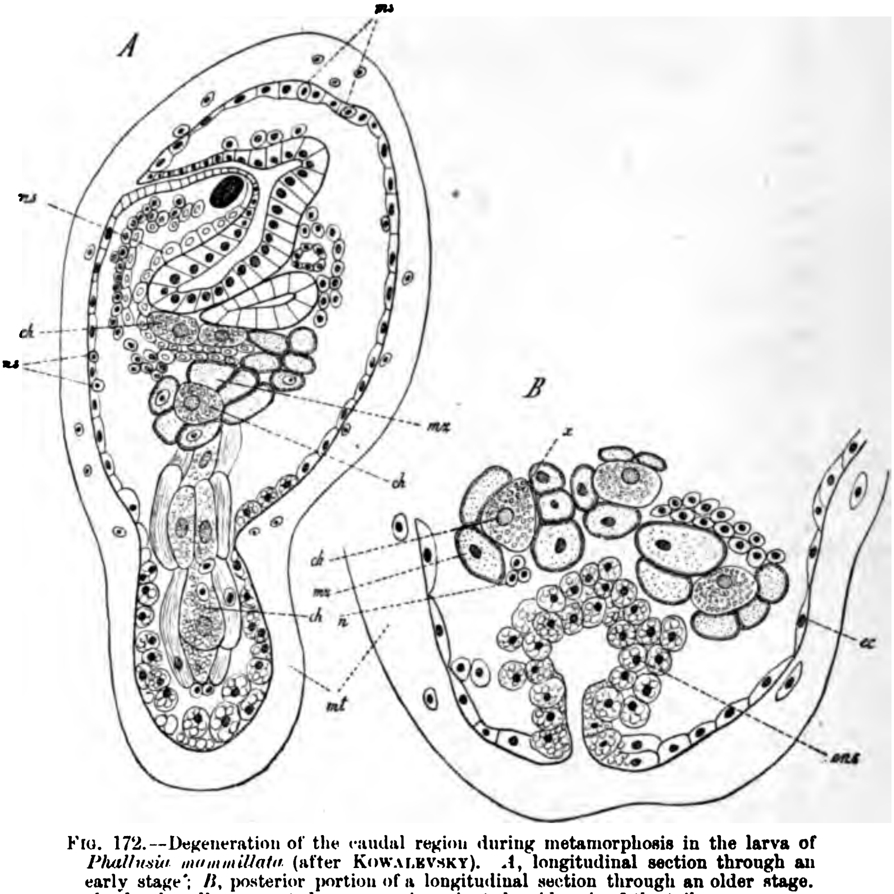

Fig. 172.—Degeneration of the caudal region during metamorphosis in the larva of *Phallusia mammillata* (after Kowalevsky). *A*, longitudinal section through an early stage; *B*, posterior portion of a longitudinal section through an older stage. *ch*, chorda-cells; *ec*, ectoderm; *ens*, invaginated epidermis of the tail; *ms*, mesenchyme-cells in the act of passing through the ectoderm; *mt*, cellulose mantle; *mz*, muscle-cells of the tail; *n*, nerve-cells of the caudal section; *ns*, neural tube.

arranged into a simple strand. The degeneration of the chorda-cells which are distinguished by their granular contents, is finally brought about by phagocytosis. This is also the case with the muscle-cells. The ectoderm-cells, as the caudal section shortens, become larger (Fig. 172 *A*), and spherical, strongly refractive bodies appear in them, so that they come to resemble the so-called granulated spheres of the pupa of the *Muscidae* (Vol. iii., p. 379). When the internal organs of the caudal section have been completely taken up into the body-cavity of the trunk, the ectoderm is invaginated (Fig. 172 *B*, *ens*). This invagination soon becomes completely abstricted from the epidermis of the larva and then forms a closed vesicle lying within the body-cavity; the cells of this vesicle soon lose their cohesion, the lumen disappears, and finally nothing remains but a mass of detached and gradually disintegrating granular cells. The gelatinous envelope (Fig. 173 *C*, *ss*) of the caudal region is, finally, lost either by being simply absorbed according to KUPFFER'S observations, or thrown off, as SEELIGER and MILNE-EDWARDS agree in maintaining.

Since the attachment of the larva is accomplished by means of the anterior end of the body, the oral aperture (inhalent orifice) appears to lie near the point of attachment (Fig. 173 *B*). In the adult Ascidian, on the contrary, the oral aperture lies at the end of the principal axis of the body opposite to the point of attachment (Fig. 173 *C*). This shifting of the position of the oral aperture is the result of a rotation made by the body round its transverse axis after attachment, during which the part of the body between the mouth and the point of attachment lengthens. This lengthening, in *Clavelina*, according to SEELIGER, is made possible by the development of a deep infolding of the surface of the body (Figs. 170, 173 *A* and *B*, *f*) which slightly separates a pre-oral portion carrying the adhering papillae from the rest of the body. This pre-oral region represents the basal section of the young *Clavelina* from which the branching stolon soon grows out. The folding just mentioned renders it possible for the *Clavelina*, which originally was placed with its longitudinal axis at right angles to the basal plane (surface of attachment), first to bend sharply towards this plane and then to lie with its longitudinal axis parallel to it, finally however, to rise up from it in such a way that the oral aperture comes to lie opposite to the point of attachment. During this rotation round the transverse axis, which was pointed out first by KUPFFER and later by SEELIGER, the angle passed through is one of almost 180.°

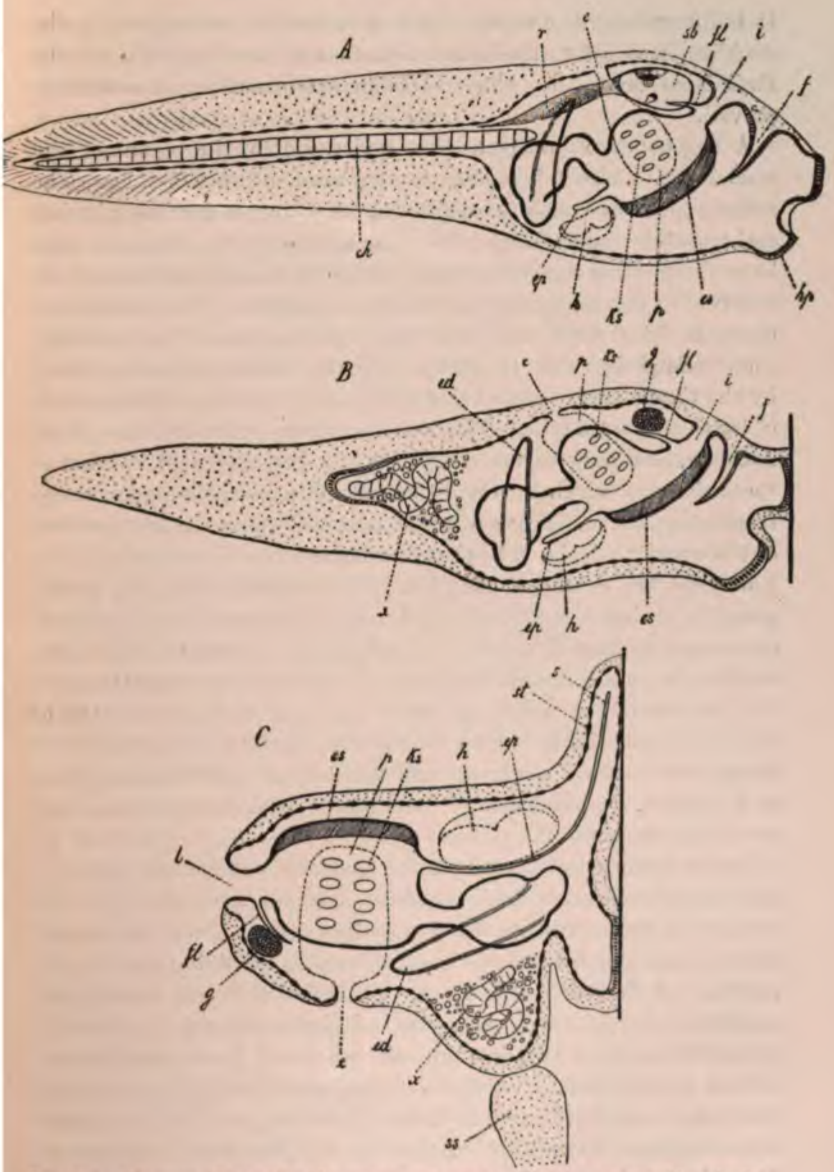

FIG. 173.—Diagram illustrating the metamorphosis of the larva of *Clavelina* during and after fixation (mainly after SEELIGER). *A*, free-swimming larva; *B*, larva just attached; *C*, older metamorphosed stage. *ch*, chorda; *e*, atrial aperture; *ed*, intestine; *ep*, epicardial process; *es*, endostyle; *f*, ectodermal fold; *fl*, ciliated pit; *g*, ganglion; *h*, heart; *hp*, adhering papillae; *i*, branchial aperture; *ks*, gill-slits; *p*, atrial cavity; *r*, trunk-portion of the medullary tube; *s*, partition-wall of the stolon; *sb*, sensory vesicle; *ss*, the cast cellulose envelope of the tail; *st*, stolo prolifer; *x*, the larval tail in course of degeneration.

It is interesting to compare the transformations undergone by the Ascidian larva after attachment with that of the Cirripedia and the *Pedicellina* larvae, in which to some extent analogous conditions prevail.

A degeneration similar to that undergone by the organs of the caudal region also takes place in the larval nervous system. The anterior sensory vesicle breaks down, its elements become spherical and lose their connections. For some time after the sensory organs have disappeared a mass of pigment remaining from them may be observed in the body-cavity of the young Ascidian. The degenerated elements later reach the circulatory system, where they probably completely disintegrate (p. 364). A similar disintegration is suffered by the tissue on the ventral side of the trunk-ganglion which consists of large ganglionic cells. The central nervous system of the young Ascidian, according to VAN BENEDEN and JULIN (No. 9), consists of those elements which surround the central canal in the region of the trunk-ganglion, and are continued anteriorly on to the left swelling of the sensory vesicle. The elements derived from the cephalic vesicle thus yield the definitive ganglion, while the elements of the trunk-ganglion produce a ganglionic cell-strand (*cordon ganglionnaire viscéral*) discovered by VAN BENEDEN and JULIN, which, first running backward in the dorsal median line, becomes applied to the dorsal wall of the pharynx but then diverges to the left, runs along the left side of the oesophagus and ends between the two hepatic diverticula. After the gelatinous cover has been perforated by the apertures of ingestion and egestion, the admission of water and of food into the alimentary canal becomes possible.

In the further development of the *branchial network*, the chief importance attaches to the appearance of new slits, each of which, as a rule, arises through the fusion of a shallow diverticulum growing out from the entodermal wall of the pharynx with the lining of the atrial cavity. At the point of fusion, the slit is first visible as a very small aperture. In this way, according to KOWALEVSKY, in *Phallusia mammillata*, after the first gill-slit has formed, a second appears behind it (Fig. 168, *k''*) this being apparently of the same size as the first. Later, according to KROHN (No. 33), two new slits appear between these two and behind the last slit (the second in order of formation) one more. In this way five primary gill-slits form in a longitudinal row. Each of the trabeculae between every two gill-slits contains a blood-sinus (branchial vessel, Fig. 168, *b*). Above and below this primary row of slits, other rows are said to form later, the number being then further increased by the intercalation both of new slits and new rows between those already formed. The gill-slits are at first elongated in the transverse direction, but their shape changes later, as they lengthen longitudinally.

According to van Beneden and Julin (No. 9) the formation of the additional gill-slits in *Phallusia* (*Ascidiella*) *scabroides* follows an entirely different rule. A longitudinal row of six primary slits here first forms (Fig. 174 *A*, 1-6). Of these, the fourth (4) in the row is said to appear first, the first in position (1) being the second to form. The fifth (5) forms next and then the second (2), while those that occupy the third and sixth positions (3 and 6) form last. These six primary gill-slits are markedly elongate transversely (Fig. 174 *B*) and each becomes divided by projecting outgrowths of the trabeculae lying between them. In this way the six primary slits give rise to six rows of secondary slits. In later stages, new slits are said to break through between these.

In *Clavelina*, according to Seeliger, two transverse rows of gill-slits are found even in the free-swimming larva (Fig. 173 *A*). A new row forms in front of these and behind them another is added after fixation. In this case the number of slits is increased by the appearance of new independent perforations (and thus not by the division of those already present). This is also the case, according to Garstang (No. 21*a*) with the buds of *Botryllus*, while, in the larva, the number of slits is increased through the division of those formed first. According to this author also, *Pyrosoma*, with its transversely elongated slits in a single row, represents a specially primitive condition.

The rise of the six primary gill-slits (Fig. 174 *A*, 1-6) has recently been carefully examined in *Ciona* by Willey (No. 54*a*). Slits 1 and 4 arise first, simultaneously and apparently independently of one another. Willey is inclined to regard these two as parts of a single slit separated as in *Amphioxus* by a tongue-bar. The next slits to appear (2 and 3) form by abstriction from 1 and 4, while 5 and 6 arise independently. Willey thus regards slits 1-4 as parts of a single primary slit separated by abstriction. The stage depicted in Fig. 174 *A* would then possess only three actual primary slits. As the six slits present divide in the manner stated by van Beneden and Julin, six transverse rows of slits are formed, these all at first being elongated transversely but later lengthening longitudinally (parallel to the endostyle). Further division of the apertures leads to the intercalation between these six rows of other transverse rows (Willey).

Even at an early stage, an entodermal fold can be seen projecting inward on the inner side of the branchial region between every two primary slits (Fig. 174, *tr*). These folds are the rudiments of the transverse bars; prominences (p) form on them both anteriorly and posteriorly and give rise to papillae. The papillae on the consecutive branchial arches lie so near each other as to come into

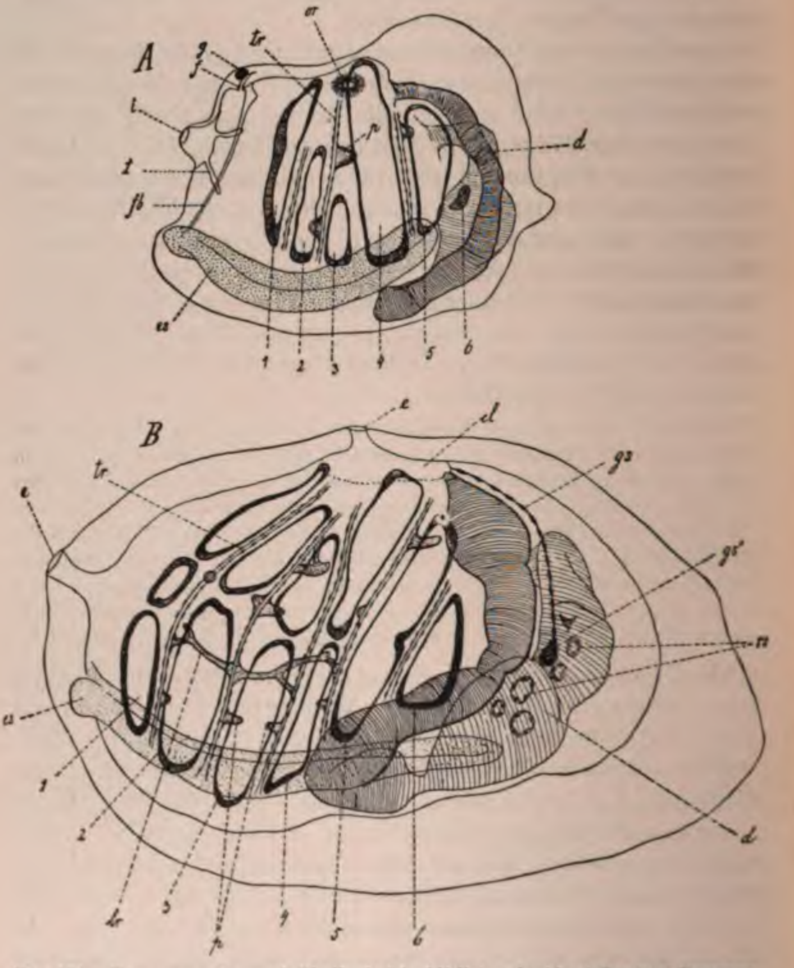

FIG. 174.—Two young stages of *Phallusia* (*Ascidiella*) *scabroides* (after VAN BENEDEN and JULIN, somewhat altered). 1-6 in *A*, the six primary gill-clefts, in *B*, the series of gill-clefts derived from them. *cl*, atrial cavity; *d*, intestinal loop; *e*, atrial aperture; *es*, endostyle; *f*, ciliated pit; *fb*, ciliated arch; *g*, ganglion; *gs*, genital strand; *gs'*, genital vesicle; *i*, inhalent orifice; *lr*, internal longitudinal bars; *or*, paired rudiment of the atrial aperture; *p*, papilla-like rudiment of the longitudinal ribs; *rs*, renal vesicles; *t*, ring of tentacles; *tr*, transverse ribs of the branchial network.

contact and fuse, giving rise to the internal longitudinal bars (*lr*) of the branchial region.

At an early stage, the first rudiment of the pericoronal circle (peripharyngeal bands, ciliated arch, Fig. 174 *A*, *fb*), as well as that of the coronal circle, which lies in front of it and is beset with tentacles, can be seen. The arrangement of the tentacles when they first appear is bilateral.

The development of the **genital organs** has still to be described. In the compound Ascidians, the individual that develops from the egg has no genital organs, but multiplies exclusively through budding. This is also the case with the social Ascidians (GANIN). In studying the development of the genital organs we are consequently restricted to the simple Ascidia if we wish to study their origin in a sexually produced embryo, otherwise we must trace their rise in the asexually produced buds of other Ascidians. The course of development in these two cases is, however, so uniform that we may take as our example the buds of *Perophora* which were examined with special reference to this point by VAN BENEDEN (No. 10).

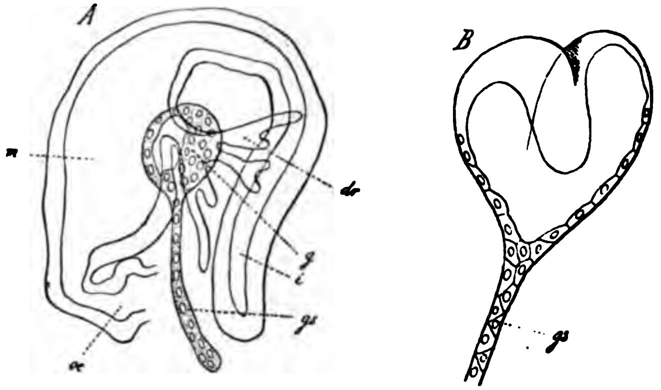

FIG. 175.—*A*, dorsal aspect of the intestinal coil in the bud of *Perophora Listeri* with the rudiment of the genital organs; *B*, somewhat older genital vesicle (after VAN BENEDEN and JULIN). *g*, genital vesicle; *gs*, genital strand; *dr*, digestive gland; *oe*, oesophagus; *m*, stomach; *i*, intestine.

The Ascidians are hermaphrodite. The male and female genital rudiments, however, are derived from a common rudiment which is always unpaired and lies on the intestinal loop medianly and dorsally (Figs. 174 *B*, *gs'*, 238 *E*, *g*). This is found at the point at which the efferent duct of the digestive gland first branches (Fig. 175 *A*). It consists of an accumulation of cells indistinguishable from ordinary mesenchyme-cells, and of a uniserial cell-strand which runs forward and reaches the atrial aperture (genital strand, Fig. 175 *B*, *gs*). In the next stage, a cavity appears in the cell-accumulation (Fig. 175 *A*). This vesicular rudiment of the genital glands is soon divided into two diverticula by a transverse constriction (Fig. 175 *B*), one of these representing the rudiment of the male gland and the other that of the female gland and its efferent duct. Of these two diverticula, the inner one, that which lies ventrally, develops first and becomes flask-shaped. Its dilated terminal swelling (Fig. 176 *A*, *h*) becomes the testis, and in this an external flat epithelial layer can soon be distinguished from an inner layer of spermatogonia. The narrowed efferent duct (vas deferens, *vd*) opens at first into the female genital vesicle. In this latter also considerable elongation can be noticed (Fig. 176). While, near the blind end, the germ-epithelium (*k*) becomes differentiated, the remaining elongated part of the rudiment becomes the oviduct (*od*). At the time when this oviduct elongates, the genital strand (*g*) which functions as gubernaculum becomes correspondingly shortened. It is probable that the oviduct develops to some extent at the expense of the latter. In this way, the end of the oviduct approaches the atrial wall more and more till, after the complete disappearance of the genital strand, it

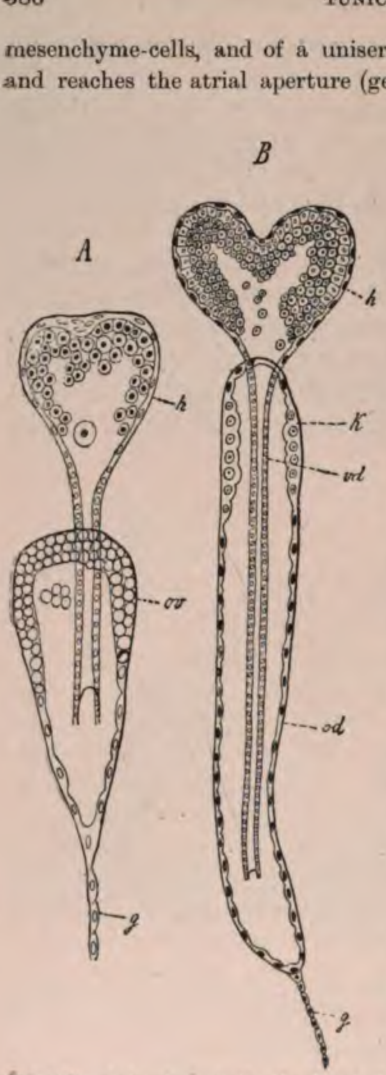

Fig. 176.—Later stages in the development of the genital organs in the bud of *Perophora Listeri* (after van Beneden and Julin). *g*, genital strand; *h*, rudiment of the testis; *k*, germ-layer of the ovary; *od*, oviduct; *ov*, rudiment of the ovary; *vd*, vas deferens.

comes into contact with it. At the same time, the vas deferens has been gradually split off from the oviduct so that finally the two canals enter the cloaca separately. The male and female genital rudiments have thus become altogether distinct. The further development of the genital glands manifests itself chiefly in the continuous formation of lobes. In the epithelium lining the ovary, the eggs can soon be distinguished from the surrounding undifferentiated cells, which form the follicular epithelium. As the eggs increase in size, they shift, enveloped in their respective follicles, into the surrounding stroma, so that, finally, they are only connected, like the grapes on a bunch, by means of the thin efferent ducts of the follicles with the ovarian epithelium.

The *urinary vesicles* (Fig. 174 *B*, *rs*) form in the same way as the first rudiment of the genital organs as accumulations of mesenchyme-cells in which a cavity appears, containing at first only serous fluid, but, later, urinary concretions (VAN BENEDEN and JULIN, No. 9).

G. The Abbreviated Development of the Molgulidae.

The development of those forms the eggs of which up to the time when the tailed larva hatches remain within the body of the mother (Ascidiae compositae, *Cynthia*, *Lithonephria*) is, in many ways, somewhat modified and abbreviated. One of the *Molgulidae* which lays its eggs affords us, however, curiously enough, the most marked example of abbreviation of development. The caudate larval stage, in this case, is altogether omitted (LACAZE-DUTHIERS, No. 36; and KUPFFER, No. 35); even the chorda does not appear to develop. In other respects, the ontogeny of this form, so far as it is known, does not seem essentially to differ from that of other Ascidians. After the cleavage of the very opaque egg has taken place, the thick-walled primary enteric vesicle can be recognised inside the embryo, and near it an accumulation of large cells filled with reserve nutritive material. This accumulation can be seen for a long time, as development proceeds, lying near the posterior end of the body (Fig. 177, *r*). It may perhaps be regarded as the equivalent of the suppressed larval tail and may be compared to the elaeoblast of *Pyrosoma* and *Salpa*. As the internal organs develop, five finger-shaped outgrowths appear on the surface (Fig. 177, *f*); these vary greatly in size and position and degenerate later. They do not serve, as might be supposed, for the fixation of the embryo. The nervous system (*n*) seems to develop from an ectodermal depression. The primary enteric vesicle represents the rudiment of the branchial sac (pharynx). The rest of the alimentary canal (*d*) develops as an outgrowth at the posterior dorsal

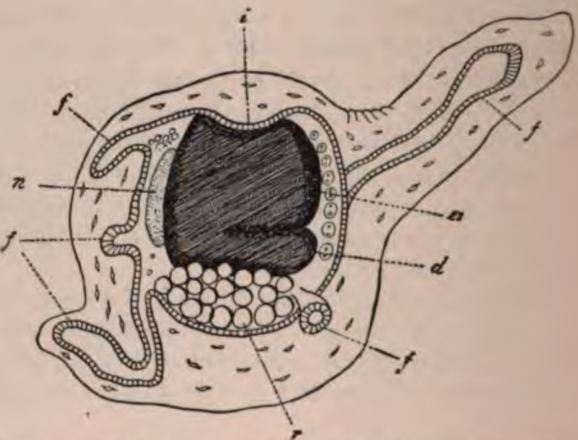

FIG. 177.—Embryo of *Molgula macrosiphonica* (after KUPFFER). *d*, rudiment of the alimentary canal; *es*, endostyle; *f*, body-processes; *i*, rudiment of the inhalent orifice; *n*, nervous system; *r*, spherules of reserve nutriment.

angle of the primary enteric vesicle. The inhalent and exhalent orifices, the endostyle, the gill-slits, etc., develop as in other Ascidians.

3. Doliolum.

The development of the egg in *Doliolum* seems to form a direct sequence to that in other Ascidians. As in the latter, a larval form occurs which propels itself by means of a swimming tail. This larva was first described by KROHN (No. 85), and later by GEGENBAUR (No. 78), KEFERSTEIN and EHLERS (No. 81), GROBBEN (No. 79), and ULJANIN (No. 86). To the latter author we owe, further, almost the only statements we have as to the embryonic development of *Doliolum*, which is very insufficiently known.

The mature egg of *Doliolum*, surrounded by follicle-cells, reaches the atrial cavity of the mother from which it is soon ejected into the surrounding water. Occasionally, however, part of the embryonic development seems to take place within the atrial cavity. As a rule, the egg is fertilised only after its expulsion, and then surrounds itself with a homogeneous membrane. This membrane (Fig. 178, *m*) which soon rises up from the surface of the egg in such a way that a space filled with fluid can be seen between it and the egg, has been called the *vitelline membrane* by **Uljanin**, and for a long time shows, on the external surface, remains of the original follicular epithelium (*f*). Since, however, both **Grobben** and **Fol** (No. 21) observed within this membrane cells which without doubt correspond to the test-cells of the Ascidiacea we may perhaps rather regard it as the equivalent of the chorion of the Ascidian egg.

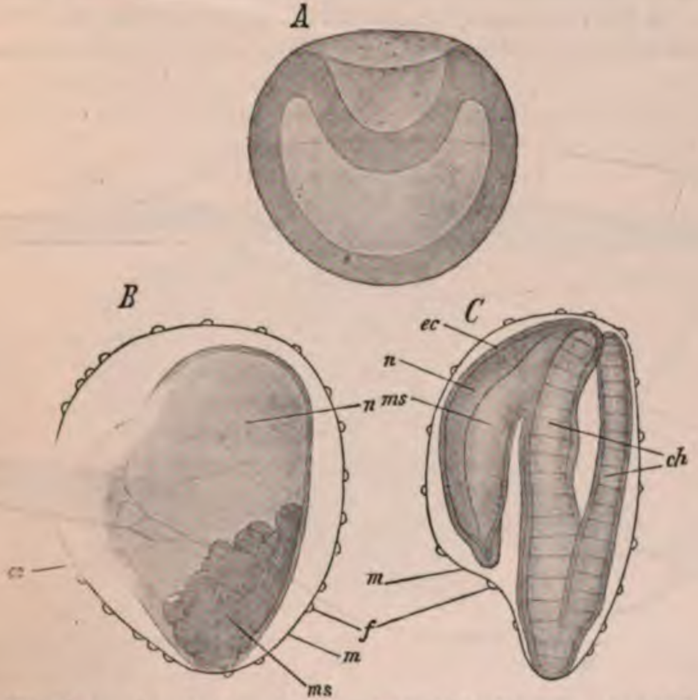

Fig. 178.—Three embryonic stages of *Doliolum Mülleri* (after Uljanin). *A*, gastrula-stage; *B* and *C*, embryos at later stages of development. *ch*, chorda; *ec*, ectoderm; *f*, follicle-cells; *m*, egg-shell (chorion); *ms*, mesoderm; *n*, rudiment of the nervous system.

Cleavage is total and almost equal, and closely resembles that described above in connection with the solitary Ascidians. The blastula and invagination-gastrula (Fig. 178 *A*) observed by **Uljanin** were comparable to the similar stages in the Ascidiacea.

We have very incomplete accounts of the subsequent stages. At the next stage observed by **Uljanin** and depicted in Fig. 178 *B*, the embryo is pear-shaped, and within it we can see three distinct rudiments. A large dorsal cell-mass (*n*) is regarded by **Uljanin** as the rudiment of the central nervous system, which here does not take the form of a tube but of a solid ectodermal growth, while a ventral cell-mass (*ch*) is assumed to be the rudiment of the chorda and a posterior mass the mesoderm (*ms*). According to ULJANIN, the archenteron is used up in the formation of the chorda and the mesoderm; the rudiment of the adult intestine on the contrary owes its origin to an independent ectodermal invagination which occurs later.

In the next stage (Fig. 178 *C*), the embryo appears to be folded several times within the egg. A dilated anterior region principally occupied by the large ganglionic rudiment (*n*) can be distinguished from a caudal region bent back upon itself, in which the chorda (*ch*) is seen to be already developed. Two lateral mesoderm-bands (*ms*) run along the whole length of these two regions of the body. Similar stages were also observed by FOL (No. 21).

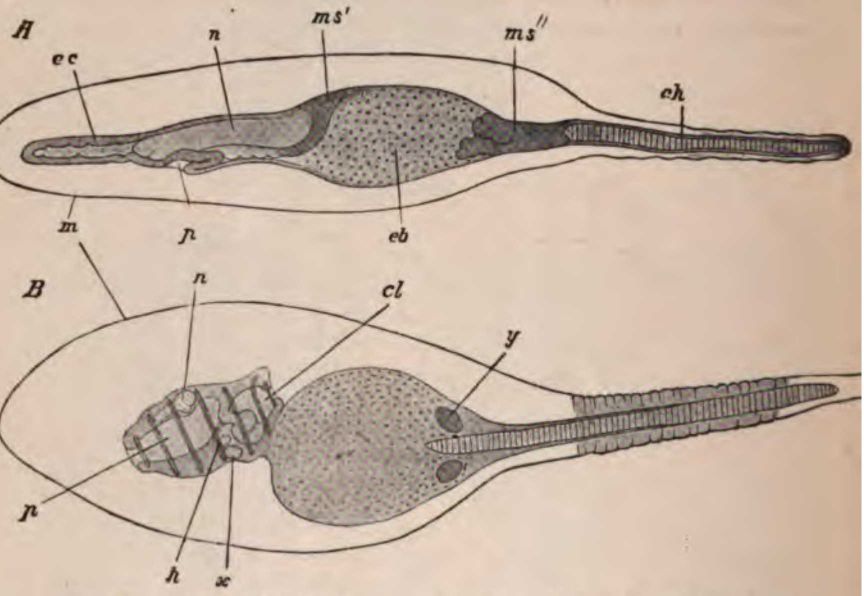

FIG. 179.—Two so-called larval stages of *Doliolum Mülleri* (after ULJANIN). *A*, younger stage; *B*, older stage. *ch*, chorda; *cl*, atrial cavity; *eb*, ectodermal vesicle; *h*, heart; *m*, egg-shell; *ms'*, anterior mesoderm-rudiment; *ms''*, posterior mesoderm-rudiment; *n*, nervous system; *p*, pharynx; *x*, mesodermal rudiment of the stolon; *y*, mesoderm-masses.

In the stages which follow (Fig. 179 *A*), the embryo straightens itself out within the egg-shell and is now able to raise itself from the bottom of the sea on which the egg rests and to swim about by means of its long caudal region, and is therefore usually called a *larva* although it is still enveloped in the much-distended egg-shell (*m*) in which traces of the follicle-cells can be found. We do not know for certain when this egg-shell is cast off. During these pelagic ontogenetic stages in which the *Doliolum* resembles the Ascidian larva, the body is elongate (Fig. 179 *A*) and the middle of it is occupied by a vesicular ectodermal swelling (*eb*) caused by the accumulation of a clear fluid. This vesicle divides the body into a posterior and an anterior region. The anterior develops into the young *Doliolum* (the first asexual or "nurse" form, the *blastozooid*) while the ectodermal vesicle and the caudal region must be regarded as provisional larval organs and degenerate later (Figs. 179 *B*, and 180). The structure of the caudal region corresponds to that of the same region in the Ascidian larva. It consists of a chorda and, laterally, of muscle-plates derived from the mesoderm-bands. At the anterior end of the caudal region, a part of the mass of mesoderm-cells (Fig. 179, *ms''*) is not transformed into spindle-shaped muscle-fibres. Two cell-masses (*y*) are subsequently given off from this into the ectodermal vesicle, where they break up and change into blood-corpuscles.

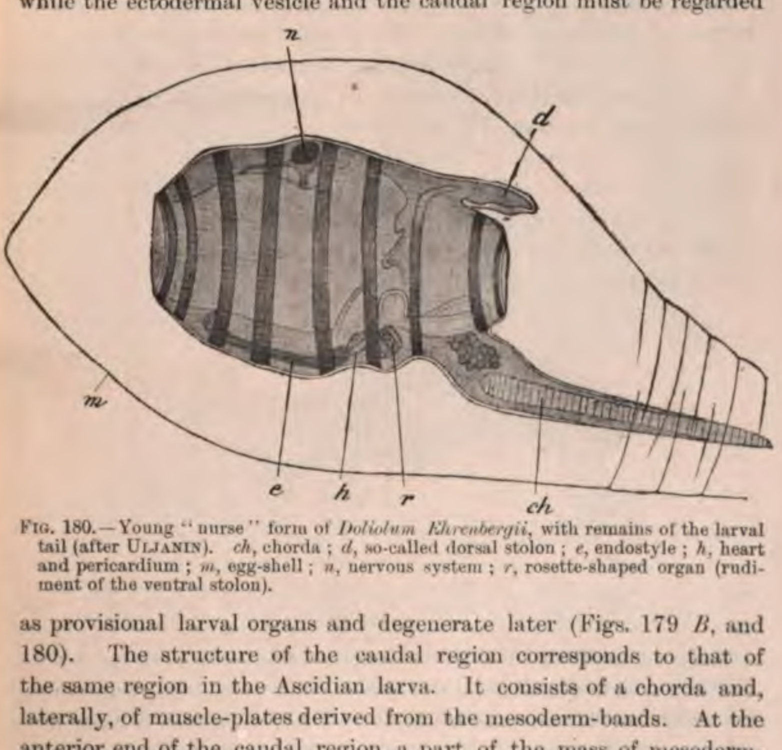

FIG. 180.—Young "nurse" form of *Doliolum Ehrenbergii*, with remains of the larval tail (after ULJANIN). *ch*, chorda ; *d*, so-called dorsal stolon ; *e*, endostyle ; *h*, heart and pericardium ; *m*, egg-shell ; *n*, nervous system ; *r*, rosette-shaped organ (rudiment of the ventral stolon).

The anterior region of the body contains the very large rudiment of the central nervous system (Fig. 179 *A*, *n*) and the anterior portion of the lateral mesoderm-bands (*ms*) which also give off into the ectodermal vesicle from their posterior ends elements that change into blood-corpuscles. An ectodermal invagination can also be seen forming ventrally (*p*) and from this is derived the whole intestine of the "nurse" form. This invagination first gives rise by its dilatation to the pharyngeal cavity (Fig. 179 *B*, *p*), while the intestine proper is derived from a solid cone of cells which develops at the base of the invagination. This cone very soon develops a lumen at first closed at both ends, and this becomes differentiated into the oesophagus, the stomach and the intestine, the rudiment of the digestive gland also becoming visible. The rudiment of the intestine opens only later into the atrial cavity (*cl*). The latter develops later than the pharyngeal cavity from an independent dorsal ectodermal invagination (Fig. 181, *cl*) which, as it enlarges, comes into close contact with the posterior wall of the pharynx. In this way the transverse and somewhat diagonally-placed branchial lamella arises, in which the four pairs of gill-clefts found in this generation (Fig. 245, p. 475) soon appear in the form of small round perforations. According to ULJANIN, the two pairs that lie dorsally develop before those that lie ventrally.

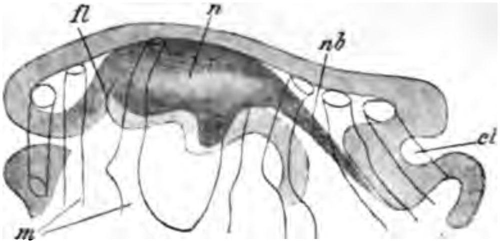

FIG. 181. -Dorsal region of an older larva of *Doliolum Mülleri* (after ULJANIN). *cl*, atrium; *fl*, ciliated pit; *m*, muscle-hoops; *n*, ganglion; *nb*, branchial nerve.

Only the middle part of the rudiment of the central nervous system (Fig. 181, *n*) retains its original massive character, while the anterior and posterior ends soon become narrower In the anterior narrowed portion, an irregular cavity develops and breaks through into the pharynx. At this point, the ciliated pit (*fl*) appears and a delicate canal connects it with the sub-ganglionic body (the homologue of the "*glande hypophysaire*" of the Ascidians). From the middle swelling of the neural rudiment, the actual ganglion and the sub-ganglionic body develop, while the posterior narrowed portion gives rise to an unpaired nerve which runs backwards (*nervus branchialis*, *nb*.

ULJANIN) in which we perhaps have the homologue of the ganglionic cell-strand discovered by VAN BENEDEN and JULIN in the Ascidians (p. 376). The peripheral nerves and the sensory organs develop later, and among these the vesicular auditory organ which belongs to the left side of the body deserves special mention (Fig. 245 *A*, *ot*); the vesicle itself arises as an ectodermal invagination into which a cell wanders and develops into the otolith. According to ULJANIN, the auditory organ of *Doliolum Mülleri* remains throughout life a mere cup-shaped ectodermal invagination.

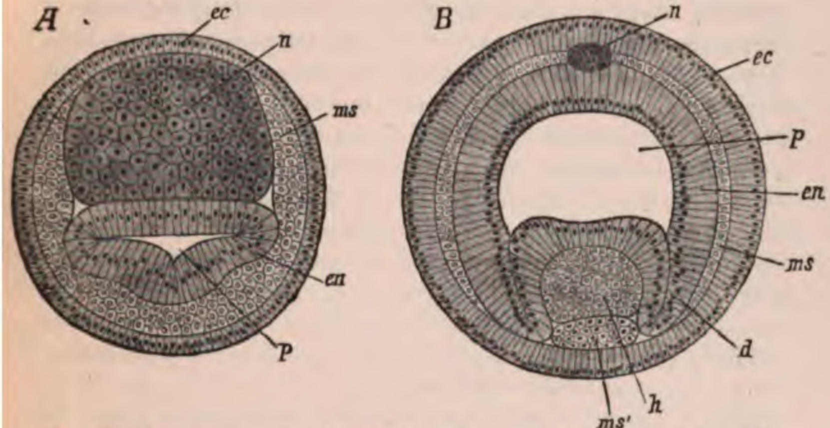

FIG. 182.—Transverse section through two ontogenetic stages of *Doliolum* (after ULJANIN). *A*, section through anterior region of the body at a stage somewhat holder tan that depicted in Fig. 179 *A*; *B*, section through an older stage. *d*, paired pharyngeal outgrowth, which takes part in the formation of the ventral stolon; *ec*, ectoderm; *en*, entoderm; *h*, rudiments of the heart and pericardium; *ms*, mesoderm; *ms'*, mesoderm of the ventral stolon; *n*, rudiment of the nervous system; *p*, pharynx.

The mesoderm of the anterior region of the body gives rise principally to the muscle-hoops (Fig. 181, *m*), the pericardial rudiment (Fig. 182 *B*, *h*) and the mesoderm-mass (*ms'*) of the ventral proliferating stolon of the "nurse" stage (the *rosette-shaped organ* of KEFERSTEIN and EHLERS). Two cell-groups become separated posteriorly and ventrally from the mesoderm-layer which envelops the pharyngeal cavity like a mantle; one of these, in close contact to the ectoderm, becomes the mesoderm of the ventral stolon (*ms'*), while the other, near the rudiment of the alimentary canal, changes into the pericardial vesicle (*h*), a cavity appearing within it round which the cells become arranged into an epithelium. As in other Tunicates, the heart is derived from a dorsal invagination of this vesicle.* It should here be mentioned that the dorsal closure of the cardiac tube is brought about by a histologically differentiated lamella (the "*mittelfeld*" of **GROBBEN**) as to the development of which, however, we have no detailed information, but we are reminded of the participation of the epicardial lamella in the formation of the heart in the Ascidians (**VAN BENEDEN** and **JULIN**, p. 370).

The muscle-hoops develop in the way described by **LEUCKART** for *Salpa democratica* (see p. 431), through the fenestration of the mesodermal lamella, these perforations separating one muscle-hoop from another.

In this way, the general course of the most important systems of organs occurring in the first "nurse" generation is indicated (Figs. 180, 243, 245, p. 475). To these, *two stolons* connected with the formation of buds have to be added. One of these (Figs. 180, *r*, and 245 *A*, *rs*) lies behind the fifth muscle-hoop, close to the posterior end of the pericardial vesicle; this we shall call the *ventral stolon* (the rosette-shaped organ). The second or *dorsal stolon* (Figs. 180, *d*, 245, *ds*) † arises from the dorsal surface in the seventh intermuscular space and forms a geniculate process pointed posteriorly, into the base of which an open coil of the seventh muscle-hoop extends (Fig. 243, *st′*). We shall have to enter into the details of the structure and development of these stolons and of their relation to the formation of the subsequent generations later (p. 470).

After the young barrel-shaped "nurse" has developed fully, the provisional larval organs gradually atrophy. While the internal parts undergo fatty degeneration and the cells become mixed with the blood, the ectodermal envelope gradually shortens so that the ectodermal vesicle and the larval tail soon form merely a rounded prominence on the body of the "nurse". This outgrowth strikingly resembles an embryonic organ consisting of reserve nutrition found in the Thaliacea, the so-called *elaeoblast*, a fact which makes the derivation of the latter from the transformed tail of the Ascidian larva, attempted by **SALENSKY**, appear somewhat probable (see below p. 432)

The first "nurse" generation of *Doliolum*, at a later period, as **FOL** first pointed out, undergoes a remarkable metamorphosis, the

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* **GROBBEN'S** statements as to the formation of the heart in the larval *Doliolum* have been misunderstood and misrepresented by **ULJANIN**.

† [This is better termed the dorsal outgrowth, as it does not itself give rise to buds, but receives those structures in rudiment from the ventral stolon and only gives attachment to them (pp. 472-476).—ED.]

gills, the endostyle and the whole of the alimentary canal degenerating completely, while the muscle-hoops considerably increase in size, and the nervous system develops correspondingly. The "nurse" then, like a swimming bell of a Siphonophoran stock, carries out the locomotory function, while the nutritive and respiratory functions of the whole stock are fulfilled by certain laterally-placed buds (*trophozooids*) on the dorsal outgrowth.

4. Pyrosoma.

The development of *Pyrosoma* from the egg resembles in many respects that of the Thaliacea. Embryonic development takes place, as in them, within the body of the mother and is consequently direct or abbreviated. It even takes place, as at first in the Thaliacea, within the egg-follicle. *Pyrosoma* is, however, specially distinguished : (1) by the large amount of food-yolk in the egg, which leads to a discoidal cleavage and the development of a germ-disc and (2) by the early asexual multiplication of the embryo. The primary individual which develops from the embryo and which has been called the *Cyathozooid* by HUXLEY, at an early embryonic stage, gives rise by a kind of transverse fission to four more individuals, the first *Ascidiozooids* of the colony (Fig. 193, etc).

We owe our knowledge of the embryonic development of *Pyrosoma* chiefly to HUXLEY (No. 72), KOWALEVSKY (No. 71), and SALENSKY N. 74).

A. Cleavage and Formation of the Germ-Layers.

Only a single egg matures in the genital rudiment of the Ascidiozooid which has arisen through budding, as also is the case in the Thaliacea. Part of the remaining cell-material of the so-called genital strand becomes arranged round the egg as the follicle, while another part is used up in forming the rudiment of the testes and of the oviduct which appears as an outgrowth of the follicle. The egg grows greatly by the addition of food-yolk, so that finally the formative yolk and the germ-vesicle within it form a mere prominence upon the large yolk-sphere (Fig. 183 *A*). After the oviduct has become connected with the atrial cavity, spermatozoa pass into it and remain in it until the egg is ready for fertilisation, while the oviduct partly degenerates. At the same time, an active immigration of follicle-cells takes place into the space extending between the surface of the egg and the follicular epithelium (Fig. 183 *A*, *fz*).

These cells, which have been called by **Kowalevsky** inner follicular cells and by **Salensky** kalymmocytes, and as to the derivation of which from the follicle-cells there can be no doubt, are homologous with the test-cells of the Ascidians and the inner follicle-cells of the Thaliacea (**Salensky's** gonoblasts). According to **Salensky**, they take a certain part in the formation of the embryo here as in the Thaliacea. The statements on this subject, however, appear to us somewhat inconclusive.

An epithelial lamella further becomes separated from that part of the inner surface of the follicle which lies next the oviduct (Fig. 184, *ds*); this covers the germ-disc like a cap and represents a secondary germ-envelope that takes no further part in the development of the embryo. This has been called by **Salensky** the covering layer.

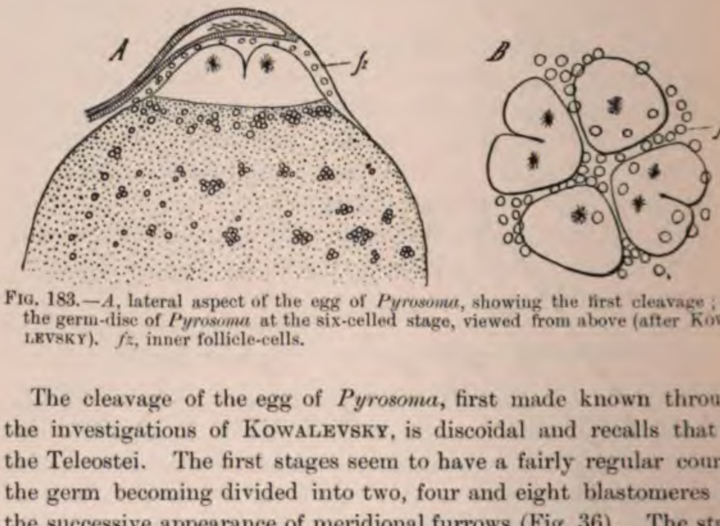

FIG. 183.—*A*, lateral aspect of the egg of *Pyrosoma*, showing the first cleavage; *B*, the germ-disc of *Pyrosoma* at the six-celled stage, viewed from above (after **Kowalevsky**). *fz*, inner follicle-cells.

The cleavage of the egg of *Pyrosoma*, first made known through the investigations of **Kowalevsky**, is discoidal and recalls that of the Teleostei. The first stages seem to have a fairly regular course, the germ becoming divided into two, four and eight blastomeres by the successive appearance of meridional furrows (Fig. 36). The stage of three blastomeres observed by **Salensky** and that of six found by **Kowalevsky** (Fig. 183 *B*) must be regarded as accidental irregularities. We have no further details as to the course of cleavage, but its result is a so-called *morula-stage* (Fig. 184 *B*) in which the germ-prominence is composed of blastomeres apparently irregularly arranged and already forming several layers.

The numerous inner follicle-cells (kalymmocytes) wander by means of amoeboid movements into the spaces between the blastomeres (Fig. 184 *A*, *fz*) and are even able to penetrate the cell-substance of the latter. This seems to be the case, however, only in the first stages of cleavage and to have no further significance, since the follicle-cells, as it appears, do not remain inside the blastomeres. Many inner follicle-cells, as cleavage advances are, however, found scattered between the blastomeres (Fig. 184 *B*, *fz*) and, as the distinction of size between the two kinds of cells disappears when the blastomeres divide further, and the original histological character of the inner follicle-cells can also no longer be recognised, it is finally impossible to distinguish the follicle-cells from the actual germ-cells or blastomeres. For this reason, and because SALENSKY was unable to find follicle-cells showing the commencement of disintegration, this author concluded that the inner follicle-cells take part in the formation of the embryo, a view resembling that held by him in connection with the Thaliacea (p. 420). We consider it to be more probable that the embryo here, as in the Thaliacea, is produced solely by the blastomeres, and that the follicle-cells which wander in between the blastomeres undergo final disintegration. [See footnotes, pp. 420 and 421].

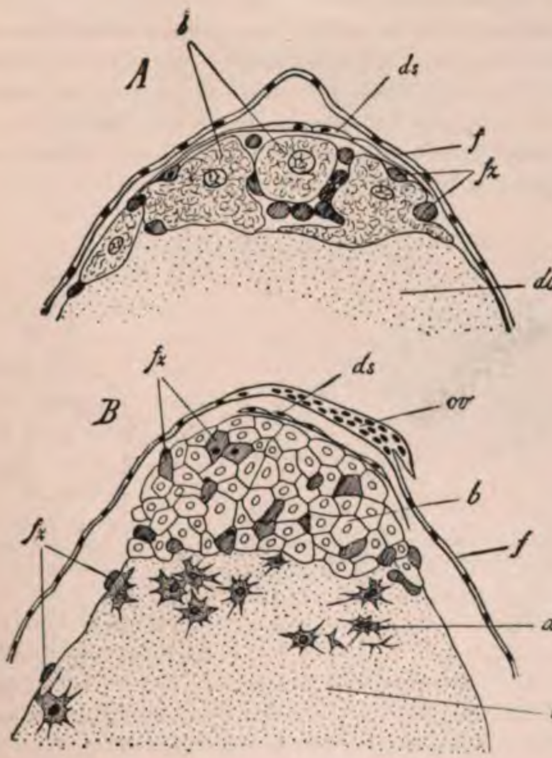

FIG. 184.—Sections of two germ-discs of *Pyrosoma* (diagrammatic after SALENSKY). *A*, eight-celled stage; *B*, older stage. *b*, blastomeres; *do*, food-yolk; *ds*, covering layer; *dz*, yolk-cells; *f*, egg-follicle; *fz*, immigrated follicle-cells; *ov*, oviduct.

Mention must now be made of cells which, in the later stages of cleavage, are found in large numbers in the yolk, near the point at which the germ-disc lies on it, and which may be called *yolk-cells* (Fig. 184, *dz*). SALENSKY, who traced back these cells to follicle-cells that had immigrated into the yolk, has named them the *yolk-kalymmocytes*. Since, however, as we shall see below (p. 395), these yolk-cells take part in the formation of the intestinal wall, we are inclined to regard them as blastomeres belonging to the entoderm-part of the germ-mass. We here have a repetition of the conditions found in the meroblastic egg of the Vertebrata, in which also yolk-cells (to be considered as entoderm) are said to take a similar part in the formation of the intestinal gland-cells.

For information as to the formation of the germ-layers in *Pyrosoma* we are dependent entirely on SALENSKY's statements. The embryo, after a number of cell-divisions, lies on the yolk as a prominence composed of uniform polygonal cells which are irregularly distributed. This prominence soon becomes bilaterally symmetrical, the largest mass of cells collecting in the posterior half of the germ-disc, so that the posterior slope is more abrupt than the anterior (Fig. 185). According to SALENSKY, the separation of the germ-layers takes place through delamination, the most superficial cell-layer (*ec*) first becoming arranged into an epithelium (ectoderm); the mass that remains (the meso-entoderm) then undergoes a similar transformation, the lowest layer, that in contact with the yolk, becoming separated as the intestinal epithelium (entoderm). Between the ectoderm and the entoderm the mesoderm extends, being greatly developed in the posterior half of the germ-disc while, in the anterior half, it is wanting or else is represented merely by a few cells (Fig. 186 *A* and *B*).

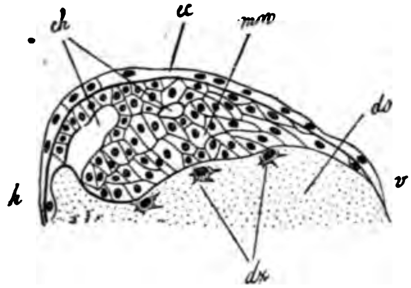

FIG. 185.—Median section through a germ-disc of *Pyrosoma* (after SALENSKY). *ch*, cavities of the chorda; *do*, food-yolk; *dz*, yolk-cells; *ec*, ectoderm; *mn*, meso-entoderm; *h*, posterior; *v*, anterior.

Taking into account the process of formation of the germ-layers in the meroblastic eggs of the Vertebrata, we may perhaps be allowed to conjecture that in *Pyrosoma* also the separation of the germ-layers is not an actual delamination, but an invagination or infolding of the posterior edge of the germ-disc, such as, for instance, occurs in the Selachians.

At the time when the separation of the germ-layers takes place three systems of cavities appear in the mesoderm (Salensky) these being connected with invaginations on the lower (entodermal) surface of the germ-disc. One of these invaginations is rather large and lies near the posterior edge of the germ-disc (Fig. 185, *ch*). It is connected with a system of cavities running forward in the median line of the disc. The two other (paired) invaginations (Fig. 186 *A*, *c*) lie laterally and somewhat in front of the first and probably communicate with the lateral system of cavities.* These are regarded by Salensky as the rudiments of the coelomic sacs, and the axial system of cavities as the equivalent of the chorda. Salensky was unable to decide whether there are here a number of separate spaces serially arranged or a continuous, but somewhat bent longitudinal canal.

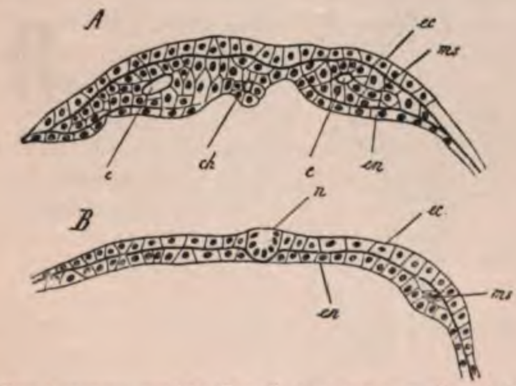

Fig. 186.—Two transverse sections through a young germ-disc of *Pyrosoma* (after Salensky). *A*, through the posterior, and *B*, through the anterior region. *c*, coelom; *ch*, cavity of the chorda; *ec*, ectoderm; *en*, entoderm; *ms*, mesoderm; *n*, nervous system.

B. Development of the Cyathozooid.

The next changes to be noticed in the germ-disc are the appearance of the rudiment of the nervous system of the Cyathozooid and the development of the peribranchial sacs. The nervous system arises as an ectodermal thickening in the anterior part of the germ-disc (Fig. 187, *n*), which later becomes depressed as a furrow, and in this way

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* [Salensky figures the paired coelomic invaginations at an earlier stage than that shown in Fig. 186 *A*, and further he regards the depression seen on the right of the swelling containing *ch* as the coelomic invagination, and in his figure, of which the above is a copy, letters it as such.—Ed.]

orms the vesicular rudiment of the ganglion. In cross-sections this anterior part of the germ-disc is seen to be bilaminar (Fig. 186 *B*), as the mesoderm of the germ-disc does not extend so far forward.

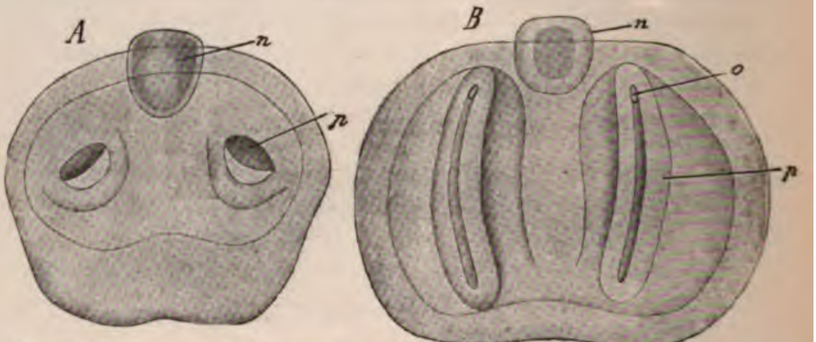

Fig. 187.—Two germ-discs of *Pyrosoma* (after Kowalevsky). *n*, rudiment of the nervous system; *o*, aperture of one of the peribranchial tubes; *p*, peribranchial cavity (tube).

The two peribranchial sacs or tubes appear as ectodermal invaginations (Fig. 187 *A*, *p*) directed from before backward, which soon lengthen (Fig. 187 *B*) and show, at the anterior end, the original aperture of invagination (*o*). The two anterior ends with their apertures unite in front of the rudiment of the nervous system (*n*) (Kowalevsky), and thus give rise to the atrial aperture (Fig. 189, *cl*) of the Cyathozooid. According to Salensky, on the contrary, the latter is produced by an unpaired ectodermal invagination with which the anterior ends of the peribranchial tubes come into contact, the original apertures of these tubes having closed before the formation of the cloaca (Salensky).

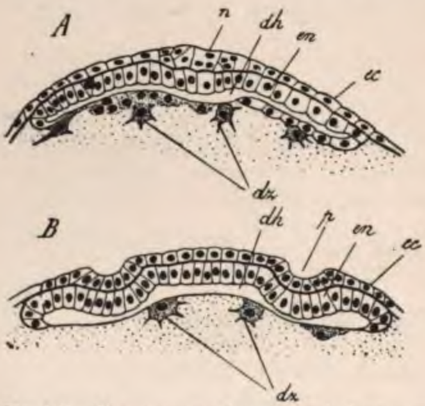

Fig. 188.—Transverse sections through the germ-disc of *Pyrosoma*, at the stage depicted in Fig. 187 *A* (after Salensky). *A*, through the anterior part of the disc, with the rudiment of the nervous system; *B*, through the middle part with the peribranchial sacs. *dh*, enteric cavity; *dz*, yolk-cells; *ec*, ectoderm; *en*, entoderm; *n*, rudiment of the nervous system; *p*, invaginations of the peribranchial sacs.

In the meantime the germ-disc has separated somewhat from the surface of the food-yolk (Fig. 188). The cavity thus formed is the enteric cavity, which originally appears covered by the entoderm (*en*) only on its upper surface. At a later stage the entoderm covers the whole of the cavity, its lateral edges bending downward and growing towards one another (KOWALEVSKY). According to SALENSKY, the yolk-cells also take part in this ventral closure of the enteric rudiment (Fig. 188, *d₂*) by coming to the surface of the food-yolk and changing into epithelial cells of the entoderm (p. 392). While the enteric rudiment in this way becomes a tube closed on all sides (Fig. 190), a median infolding, the rudiment of the *endostyle* (*es*) becomes visible in the posterior half of its upper wall.

FIG. 189.—Germ-disc of *Pyrosoma* with the atrial orifice developed (after KOWALEVSKY). *cl*, cloaca; *en*, endostyle; *n*, nervous system; *p*, peribranchial tubes; *pc*, pericardial sac; *pc'*, the posterior tubular continuation of the same.

FIG. 190.—Transverse section through the posterior region of a germ-disc at the stage depicted in Fig. 189 (after SALENSKY). *dh*, enteric cavity; *ec*, ectoderm; *en*, entoderm; *es*, rudiment of the endostyle; *ms*, mesoderm; *pb*, peribranchial tubes; *pc*, pericardial tube.

The transformations undergone, in the further course of development, by the paired coelomic sacs, the lumina of which had become connected posteriorly, are of importance. Only the right coelomic sac is retained (Fig. 191, *rc*), while the left * undergoes degeneration (Fig. 191 *A-C*), its lumen becoming smaller and its cells losing their

FIG. 191.—Three germ-discs of *Pyrosoma*, diagrammatic (after SALENSKY). *d*, enteric cavity; *es*, endostyle; *lc*, left coelomic sac; *n*, rudiment of the nervous system; *p*, peribranchial tubes; *pc*, pericardial sac = *rc*, right coelomic sac.

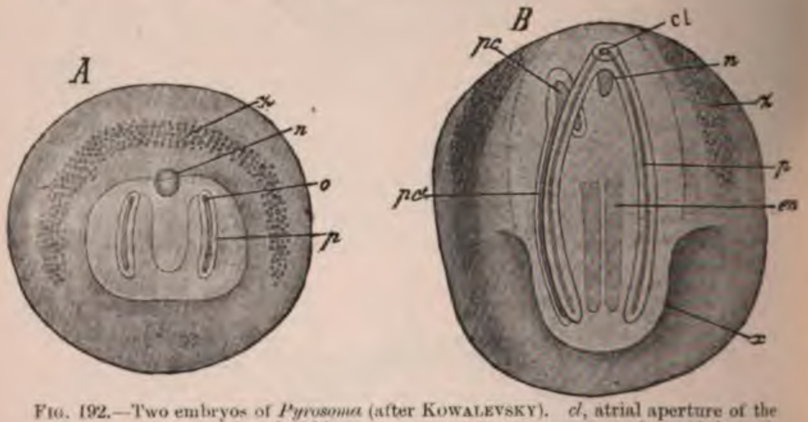

FIG. 192.—Two embryos of *Pyrosoma* (after KOWALEVSKY). *cl*, atrial aperture of the Cyathozooid. *en*, endostyle-folds; *n*, nervous system; *o*, aperture of one of the peribranchial tubes; *p*, peribranchial tube; *pc*, pericardial sac; *pc'*, posterior tubular continuation of the pericardial sac; *x*, posterior part of the germ-disc raised up from the surface of the egg (rudiment of the stolon); *z*, cell-zone.

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* The terms "right" and "left" refer to the arrangement of the organs in the adult Cyathozooid, in which the atrial aperture denotes the posterior end of the body. As, in our orientation of the germ-disc, the atrial aperture lies at the anterior edge of the disc, the right and left organs appear to be reversed. Our orientation of the germ-disc is, however, intentional (p. 404), having been retained, in accordance with the views of authors, since the opposite orientation would also lead to certain difficulties in describing the processes (especially in connection with the development of the Ascidiozooid).

epithelial continuity, so that finally, only a mass of irregularly arranged cells remains to take part in the formation of the mesenchyme which is developing in the primary body-cavity. A similar disintegration is undergone by the median strand which was regarded as the equivalent of the chorda, and which, after the disappearance of its lumen, retains its independence only for a short time, and is called by **Salensky** the axial mesoderm-strand. The right coelomic sac gives rise to the pericardial rudiment (Figs. 192 *C*, 189, 190, *pc*),

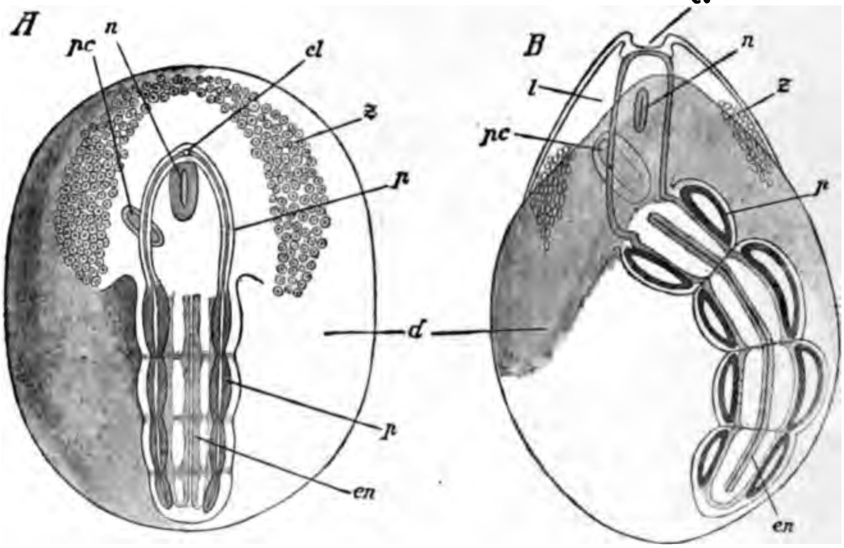

Fig. 193. Two Cyathozooids with their first-formed buds (after **Kowalevsky**, somewhat altered). *A*, with straight stolon; *B*, with curved stolon; the Cyathozooid is commencing to rise from the surface of the food-yolk (*d*). *cl*, atrial aperture; *d*, food-yolk; *en*, rudiment of the endostyle; *l*, body-cavity of the Cyathozooid; *p*, peribranchial tubes; *pc*, pericardial sac of the Cyathozooid; *z*, cell-zone.

which soon becomes club-shaped, a dilated, anterior, sac-like part changing into the pericardial vesicle of the Cyathozooid, while the tube that runs backward from this part does not develop further but soon loses its lumen: the connection of its cells then becomes loosened. It appears that these elements then mingle with the mesenchyme and assist in the formation of the mesoderm of the Ascidiozooid. In the pericardial sac of the Cyathozooid the surface adjacent to the intestinal wall is seen to thicken, this part then becoming invaginated and forming the rudiment of the heart proper.

The germ-disc appears surrounded by a semicircular *zone of cells* lying on the surface of the yolk (Fig. 192, *z*); **Kowalevsky** believes that this zone consists of immigrated cells, the so-called inner follicle-cells or kalymmocytes, but **Salensky** holds that mesodermal elements (corresponding to the disintegrated left coelomic sac) also contribute largely to it. When, at a later stage, the surface of the yolk is grown over by the continually extending germ-disc, this cell-zone also passes under the ectoderm of the disc and thus into the primary body-cavity of the Cyathozooid (Fig. 193 *B*, *z*). It then soon breaks up into separate islands (Fig. 194, *z*) which are still for a long time visible near the surface of the food-yolk. **Kowalevsky** thought that the elements of this cell-zone took no further part in the formation of the embryo, or at the most changed into blood-corpuscles, but **Salensky** ascribes to them a very important part in the development of the mesoderm of the Ascidiozooid (see below, p 410).

C. The Development of the Primary Tetrazooid Colony.

The edge of the germ-disc, by continually extending, overgrows the yolk-sphere (Figs. 193 *B*, 194), which was originally covered merely by the follicular epithelium. The food-yolk in this way comes to lie inside the Cyathozooid, *i.e.*, in its body-cavity. No part is taken in this circumcrescence, however, by the posterior region of the elongated disc (Fig. 192 *B*, *x*). This soon protrudes and grows out into a long sac-like appendage (Fig. 193) which is cut up by transverse furrows into four sections (recalling the strobilation of the tape-worm); these sections are the rudiments of the first four Ascidiozooids. This chain of Ascidiozooids, which is known as the *stolon*, and is evidently homologous with the ventral stolon of *Doliolum* and *Salpa*, is originally straight, lying parallel to the principal axis of the Cyathozooid (Fig. 193 *A*). Later, however, as it lengthens, it curves and finally lies equatorially (Figs. 194, 195, 196) so that the Ascidiozooids form a ring surrounding the gradually diminishing Cyathozooid. The individual Ascidiozooids at the same time alter their positions; at first they lay with their longitudinal axes in the same direction as that of the whole stolon (Fig. 194), but later there is a tendency for these axes to lie parallel to the principal axis of the Cyathozooid (Fig. 196). The stolon then, as a whole, forms a series of zig-zags, as the thin, drawn out trabeculae (Fig. 196, *s*, *s'*) connecting the individual Ascidiozooids lie obliquely, ascending from the posterior end of one zooid to the anterior end of the next.

While the four Ascidiozooids continue to increase in size and develop the structure of the adult individual (Figs. 194-196), the Cyathozooid which lies in the midst of them gradually atrophies (Fig. 196, *c*). Only now (Fig. 196 *B*) does the colony, which is enveloped in a large, common cellulose mantle, attain an independent existence. It passes out of the parental brood-sac into the cloaca of the colony, and thence to the exterior. The youngest free colonies of *Pyrosoma* are only found at considerable depths (CHUN), but older and larger stocks are met with at the surface of the water.

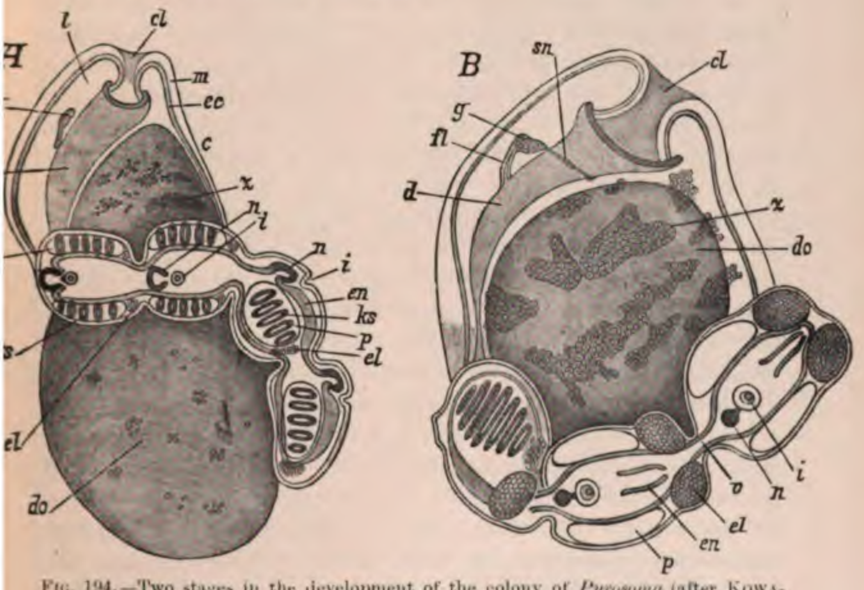

FIG. 194.—Two stages in the development of the colony of *Pyrosoma* (after KOWALEVSKY). In *A*, the yolk-mass (*do*) is partly surrounded by the Cyathozooid (*c*), while, in *B*, it lies entirely within the body-cavity of the latter. *c*, Cyathozooid; *cl*, atrial pore of the Cyathozooid; *d*, alimentary canal of the Cyathozooid; *do*, yolk; *ec*, ectoderm; *el*, elaeoblast; *en*, endostyle of the Ascidiozooid; *fl*, ciliated pit; *g*, ganglion of the Cyathozooid; *i*, inhalent orifice of the Ascidiozooid; *ks*, gill-slits; *l*, body-cavity of the Cyathozooid; *m*, cellulose mantle; *n*, nervous system of the Ascidiozooid; *p*, peribranchial cavity; *sn*, lateral nerve; *v*, entodermal canal connecting the Ascidiozooids with one another; *z*, remains of the cell-zone.

The organ-rudiments of the young Ascidiozooid chain are, originally, direct continuations of the imperfectly developed organ in the Cyathozooid (Figs. 192 *B*, 193). The ectoderm of the chain is in continuity with that of the germ-disc. The intestine of the Cyathozooid is continued into the enteric rudiment of the Ascidiozooid, and the endostyle-fold also proceeds direct from the rudiment of this fold in the germ-disc (Figs. 192, 193, *en*). In a similar way the peribranchial tubes (*p*) on either side of the intestine, and, on the right side of the body, the pericardial tube (Fig. 192, *pc*), are continued direct from the Cyathozooid into the chain of Ascidiozooids. The central nervous system, on the contrary, arises independently in the Ascidiozooids (SALENSKY). From this point the development of the Cyathozooid and that of the Ascidiozooids will be treated separately.

D. Further Development of the Cyathozooid.

The structure of the Cyathozooid is fairly simple. One of the poles of the body is marked by the presence of an ectodermal invagination, the atrial invagination (Fig. 193 *B*, 194, *cl*) which occupies the most anterior end of the germ-disc (Fig. 189, *cl*), and the origin of which has already been discussed (p. 394). This invagination originally communicates with the peribranchial tubes (Figs. 189, 192 *B*, 193 *A*, *p*). Very soon, however, that part of these tubes which lies in the Cyathozooid degenerates and completely disappears (Fig. 193 *B*). The atrial invagination, on the contrary, in which a narrow thick-walled portion can be distinguished later from a thin-walled portion, the actual cloaca, becomes connected with the alimentary canal of the Cyathozooid, the lamellae that separate the two cavities being perforated (Fig. 194). The alimentary canal (Fig. 194, *d*) of the Cyathozooid is a simple thin-walled sac, narrowed in the shape of a funnel posteriorly, which adopts a somewhat curved position in accordance with the curving of the stolon in later stages. Its posterior, narrowed end passes over into the enteric rudiment of the Ascidiozooids. There is no sign of endostyle-folds in the intestine of the Cyathozooid, that part of the organ in which, in the germ-disc, the rudiments of these folds appeared (Fig. 189 *en*) being used up in the formation of the Ascidiozooids (Fig. 193, *en*).

The rudiment of the *nervous system* of the Cyathozooid, which is derived from an ectodermal invagination lying close behind the atrial rudiment near the anterior margin of the germ-disc (Fig. 189, *n*) is originally a somewhat long and completely closed vesicle which, when the alimentary canal changes its position, in consequence of the curvature of the stolon, also shifts from its original position. The posterior end of the neural vesicle now enters into open communication with the enteric cavity (Figs. 194 *B*, *g*, and 197). This is the rudiment of the ciliated pit (*fl*). The anterior part of the vesicle now becomes divided by a furrow from that part which is used for the formation of the ciliated pit: it swells and changes into the rudiment of the ganglion (*g*). This part gives off two lateral processes, the rudiments of the lateral nerves (*sn*) which clasp the enteric canal (*d*) laterally and end in the lower wall of the atrial invagination. Within the ganglionic rudiment of the Cyathozooid there is never any development of punctated nervous tissue (Punktsubstanz).

The development of the *heart* has already been described (Fig. 193, *pc*).

The ectoderm of the Cyathozooid yields the cellulose test of the young colony. The secretion of this layer begins even before the circumcresence of the yolk-sphere by the Cyathozooid is fully completed (Fig. 194 *A*, *m*). The area occupied by the Cyathozooid is then indicated by the extension of the cellulose mantle which, at a later period, encloses the four primary Ascidiozooids (Figs. 194, 195). The ectoderm of the Ascidiozooids does not, according to SALENSKY, take part in the formation of the cellulose investment of the young colony, which is yielded exclusively by the Cyathozooid. The process by which this mantle is secreted agrees pretty closely with that described by KOWALEVSKY for the Ascidiacea (p. 355). According to SALENSKY, single mesoderm-cells (mesenchyme-cells), wandering through the ectoderm, come to lie on its external surface (Fig. 198, *ms*) and are the cells found later in the test. The secretion of the latter which now takes place proceeds from the ectoderm-cells (*ec*), each cell giving off externally a perpendicular plate-like process, so that the cellulose layer which is secreted seems broken up by these processes into separate prisms. At the same time, the mantle-cells

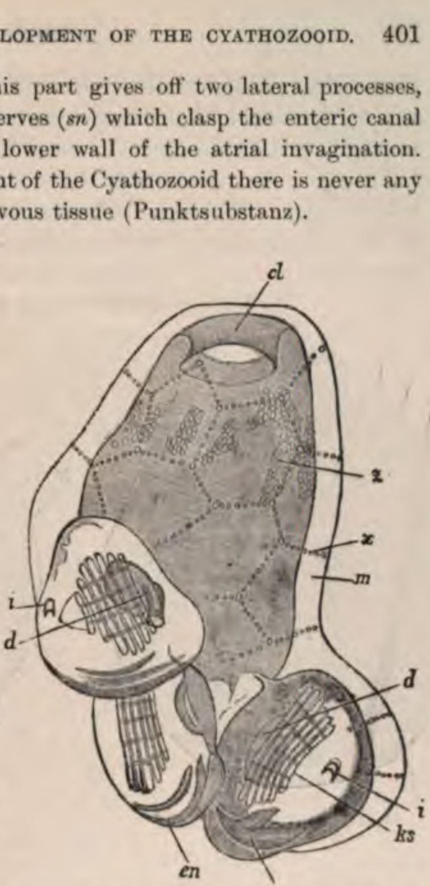

FIG. 195.—Later ontogenetic stage of a tetrazooid colony of *Pyrosoma* (after SALENSKY). The greater part of the food-yolk has been absorbed. The cellulose mantle of the Cyathozooid has grown round the Ascidiozooids. *cl*, atrial aperture of the Cyathozooid; *d*, alimentary canal; *en*, endostyle; *i*, inhalent orifice; *ks*, gill-clefts; *m*, mantle; *x*, cell-lamellae of the cellulose mantle; *z*, remains of the cell-zone.

(wandering mesoderm-cells) become arranged in a very characteristic way in *Pyrosoma*. They form rows, which are connected in such a way as to produce hexagonal areas (Figs. 195, 196, and 198, *ms'*). In later stages the processes of the ectoderm-cells which traverse the test are again withdrawn. The hexagonal pattern which is produced by the arrangement of the mesoderm-cells is, however, retained for some time.

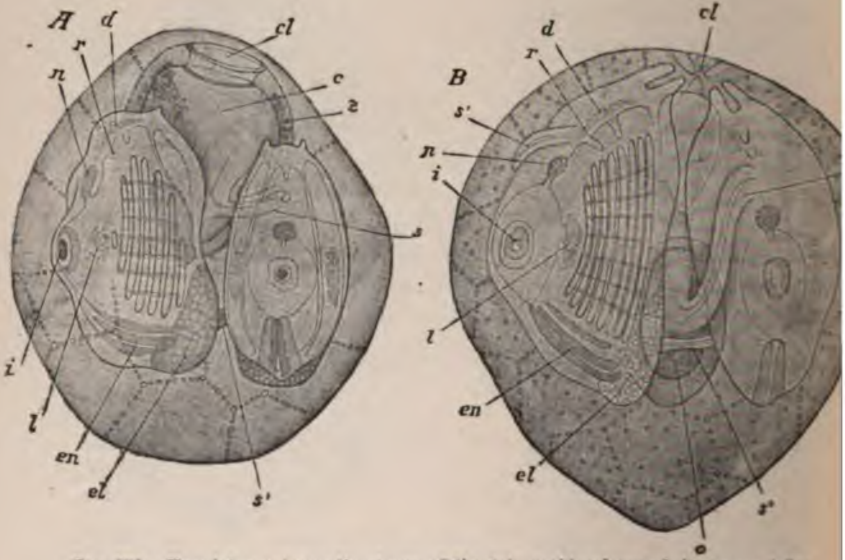

FIG. 196.—Two later ontogenetic stages of the tetrazooid colony of *Pyrosoma* (after KOWALEVSKY). *c*, Cyathozooid; *cl*, atrial aperture of the Cyathozooid, cloacal aperture of the young colony; *d*, dorsal elongated cell-mass; *el*, elaeoblast; *en*, endostyle; *i*, inhalent orifice; *l*, lens-shaped cell-mass; *n*, central nervous system; *r*, languets; *s*, connective strand between the Cyathozooid and the first Ascidiozooid; *s'* and *s"*, connective strands between the separate Ascidiozooids; *z*, remains of the cell-zone.

According to SALENSKY, the ectoderm of the Cyathozooid is also capable of secreting cellulose substance on its inner surface, and this accounts for the fact that the ground-substance of the mesenchyme which fills a part of the primary body-cavity is cellulose. Through the development of this intermediate layer, the alimentary canal becomes removed a considerable distance from the ectoderm of the Cyathozooid.

The simplicity of structure of the Cyathozooid is explicable when we consider that its sole function is to give rise by budding to the four primary Ascidiozooids. As soon as these have attained a certain degree of development, the Cyathozooid begins gradually to degenerate. It can then be seen as an oval body (Fig. 196, *c*) gradually decreasing in size, at the centre of the young tetrazooid colony. Its atrial aperture (*cl*) closes, and it is gradually absorbed till not a trace of it is left. **Kowalevsky** thought that the atrial cavity of the Cyathozooid persisted as the common cloacal cavity of the whole colony; this, however, is in opposition to the above account by **Salensky**. In accepting the latter account we must assume that the common cloacal cavity of the colony represents a depression of the surface of the cellulose mantle which appears later.

Fig. 197.—Later stage in the development of the central nervous system of the Cyathozooid (after Salensky; *cf.* Fig. 194 *B*, *g*). *d*, wall of pharynx; *dh*, enteric cavity; *fl*, ciliated pit; *g*, ganglion; *sn*, lateral nerves.

We have still briefly to describe the way in which the structure of the Cyathozooid is to be interpreted and to compare it with that of a typical Tunicate (Fig. 199), and in connection with this we must explain why, together with **Kowalevsky** and **Salensky**, we regard the ectodermal depression in the Cyathozooid just mentioned as the atrial cavity (*c*). The fact that the peribranchial tubes open into this cavity is in favour of interpreting it in this way, and this view is still further confirmed by the position of the nervous system with relation to this invagination. If it is to be regarded as the inhalent aperture, the ciliated pit (*fl*) of the central nervous system would have to be directed towards it, but this is not the case. The ciliated pit forms the part of the central nervous system (*g*) which is turned away from the invagination. A comparison of a diagram illustrating the relative positions of the most important organs in the body of a solitary Salp (Fig. 199 *B*) with a diagram of a Cyathozooid

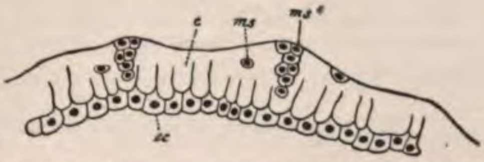

Fig. 198.—Transverse section through the developing test of the Cyathozooid in the stage depicted in Fig. 195 (after Salensky). *c*, cellulose substance; *ec*, ectoderm; *ms*, mesenchyme-cells; *ms'*, mesenchyme-cells forming hexagonal pattern in test (*cf.* Fig. 196).

(Fig. 199 *A*) shows that the inhalent aperture is wanting in the latter. The point at which we should expect it to lie is indicated by *i*. It is evident that the whole of the area which corresponds to the inhalent aperture and the endostyle is much abbreviated in the Cyathozooid. The stolon which, in comparison, is very highly developed, thus appears to be shifted forward. We also find that the atrial invagination which appeared quite at the anterior edge of the germ-disc, actually corresponds to the most posterior end of the body of the Cyathozooid and consequently the terms "anterior" and "posterior" are applied arbitrarily to the germ-disc and have nothing to do with the orientation of the Cyathozooid.

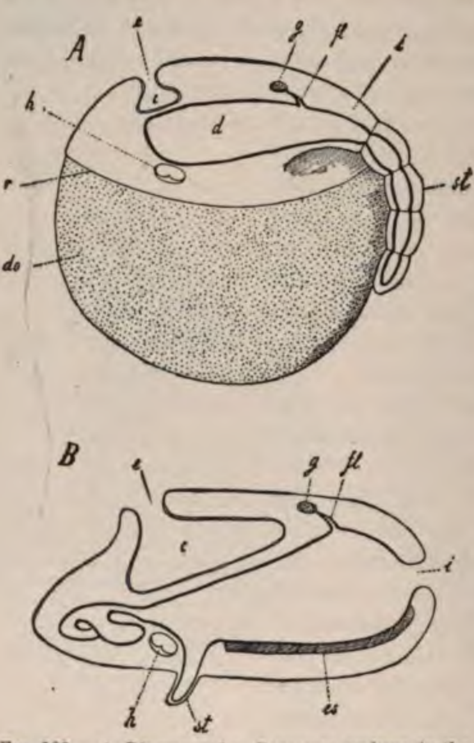

FIG. 199.—*A*, Diagram of a *Pyrosoma* embryo in the stage of Fig. 193 *A*; *B*, diagrammatic median section through a Salp (a solitary form). *c*, atrium; *d*, alimentary canal of the Cyathozooid; *do*, food-yolk; *e*, cloacal or exhalent orifice; *es*, endostyle; *fl*, ciliated pit; *g*, ganglion; *h*, heart; *i* (in *B*), inhalent or branchial orifice, in *A*, the point at which it may be conjectured to lie; *r*, edge of the germ-disc growing over the yolk; *st*, ventral stolon.

E. Development of the four primary Ascidiozooids.

The chain of Ascidiozooids, from the time it forms, contains within it three longitudinal parallel tubes (Fig. 193), the middle one representing the intestinal tube, the enteric rudiment of the consecutive individuals, and the two lateral ones the peribranchial tubes (*p*). These tubes are originally nothing more than direct prolongations of the corresponding organs in the Cyathozooid (Fig. 192 *B*). When, at a later period, the individual Ascidiozooids become more markedly constricted from one another, these rudiments also are cut up into sections corresponding to the different individuals. The peribranchial tubes become completely dissevered at the boundaries of the individuals (Fig. 193 *B*), each Ascidiozooid then containing a pair of lateral closed sacs, the *peribranchial cavities* (*p*). The remains of the peribranchial tubes in the Cyathozooid, as already mentioned (p. 400) then atrophy. The enteric rudiment, however, does not at first undergo such complete constriction between the individual Ascidiozooids, but a canal is retained in the connecting trabeculae which establishes communication between the consecutive individuals (Fig. 194 *B*, *v*). This canal does not disintegrate until the Ascidiozooids separate completely on attaining their full development. A vestige of it plays an important part in the later development of buds, changing into the so-called endostyle-process or entoderm-process of the stolon (SEELIGER, p. 486).

The rudiment of the *endostyle-furrow* was recognisable in the primary enteric rudiment of the Cyathozooid even before the chain of Ascidiozooids began to form (Figs. 189, 190, *en*). That part of the alimentary canal of the Cyathozooid which was distinguished by the presence of the endostyle-rudiment was the part which, by lengthening, changed into the common enteric rudiment of the four primary Ascidiozooids. Consequently, the endostyle-rudiment originally runs through all the four Ascidiozooids (Fig. 193, *en*). At a later stage, however, only the posterior part of it is retained in each individual (Figs. 194, *en*, 200, *es*), becoming the definitive endostyle of the zooid. In cross-section, the endostyle-rudiment originally has the form of a broad fold projecting into the lumen of the intestine (Fig. 203 *A*), the lateral part of which shows epithelial thickenings which, in a surface view, appear as dark bands. The depression between them flattens out later, but, on either side, the paired endostyle-folds project inwards (Fig. 203 *B*, *es*). It is not yet clearly understood in what way these lateral endostyle-folds together with the middle part yield the endostyle of the adult.

In front of the anterior end of the endostyle-rudiment there is, in the developing Ascidiozooid, a pit-like ectodermal depression (Figs. 194, 200, *i*), the rudiment of the inhalent or branchial aperture. The space in front of this is occupied by the rudiment of the central nervous system (Figs. 194, 200, *n*).

The lateral walls of the branchial sac of the Ascidiozooid are in contact with the peribranchial tubes (Fig. 193, *p*). Here the *gill-slits* (*ks*) break through (Fig. 200), a small entodermal outgrowth fusing on either side with the wall of the peribranchial sacs, and the perforation then taking place in the base of the outgrowth. The entodermal lamella thus takes a more active part in the development of the gill-slits than does the ectodermal wall of the peribranchial sac. The vertical bars between the adjacent gill-slits which, in cross-section, are almost quadrangular, are not merely covered on their inner surfaces with entoderm, but their lateral surfaces also which are turned towards the slits belong to the entoderm. Only the covering of the external surface is derived from the ectodermal wall of the peribranchial cavities. The gill-slits in *Pyrosoma*, according to **Salensky**, appear in order from before backward, the most anterior slit forming first. After the gill-slits have broken through, they very soon lengthen ; those of *Pyrosoma*, indeed, are distinguished for their length. The internal longitudinal bars, which cross the slits at right angles and give rise to the characteristic lattice-like appearance of the branchial wall, develop later as independent ingrowths from the vertical bars which become secondarily connected.

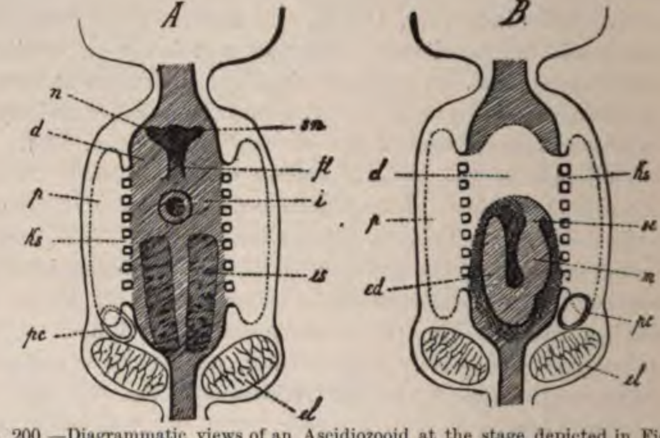

Fig. 200.—Diagrammatic views of an Ascidiozooid at the stage depicted in Fig. 194 (following **Salensky**). *A*, viewed from above ; *B*, from below. *cl*, atrium ; *d*, pharynx (branchial sac) ; *ed*, rectum ; *el* elaeoblast ; *es*, rudiment of endostyle ; *fl*, ciliated pit ; *i*, inhalent or branchial aperture ; *ks*, gill-slits ; *m*, stomach ; *n*, nervous system ; *oe*, oesophagus ; *p*, peribranchial sacs ; *pc*, pericardial vesicle ; *sn*, rudiment of the lateral nerves.

The gill-slits, as **Seeliger** has pointed out, seem always to lie at right angles to the endostyle (Fig. 201, *ks* and *es*). Since the endostyle of the Ascidiozooids originally runs horizontally, as may be seen in the diagram Fig. 201 *A*, and then later adopts a vertical position (Fig. 201 *C*) the gill-slits pass gradually from a vertical to an oblique position and finally lie horizontally. This leads us to the general changes of form which characterise the development of the Ascidiozooid. The longitudinal axis of the adult Ascidiozooid (Fig. 201 *C*) seems to be marked by the branchial and atrial apertures (*i*); in the bud, however, these two apertures do not lie at the ends

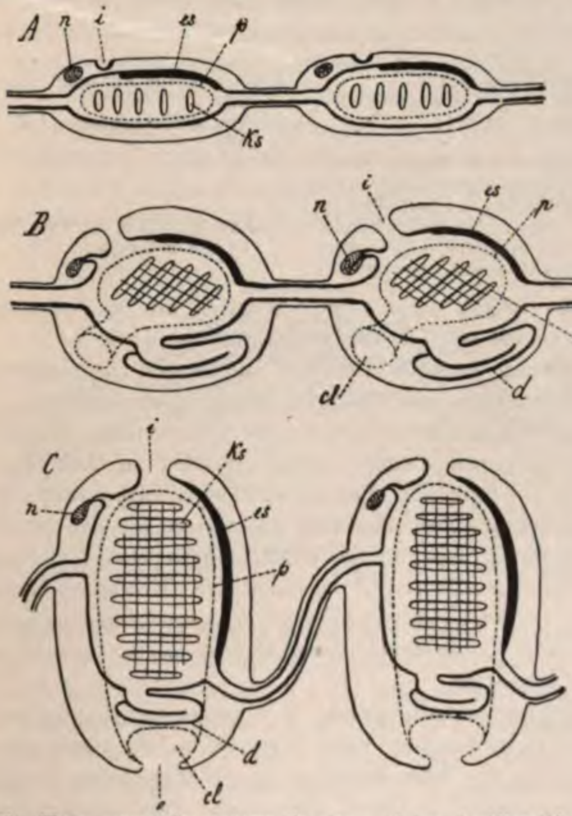

FIG. 201.—Three consecutive ontogenetic stages of two Ascidiozooids, side view, diagrammatic (following SALENSKY). *cl*, atrium; *d*, alimentary canal; *e*, atrial aperture; *es*, endostyle; *i*, branchial aperture; *ks*, gill-clefts; *n*, nervous system; *p*, peribranchial cavity.

of the longitudinal axis (Fig. 201 *A*). This shows that through the changes brought about by growth during the course of development, the longitudinal axis of the bud is replaced by a new one running at right angles to it. The longitudinal axis of the young Ascidiozooid, the two poles of which are represented by trabeculae joining one Ascidiozooid to another becomes, later, the transverse axis of the adult Ascidiozooid. The upper surface of the body in the Ascidiozooid thus contains one half of the later dorsal side and the corresponding half of the later ventral side. The boundary between these two halves is marked by the position of the branchial aperture (Fig. 201 *A*, *i*). In comparing the adult with the young Ascidiozooid, we must bear in mind the distinctions, which may be tabulated as follows :—

YOUNG.		ADULT.
Upper surface of the body.	=	Surface of the anterior half of the body.
Lower surface of the body.	=	Surface of the posterior half of the body.
The anterior part of the embryo from the branchial aperture to the corresponding point of the lower side.	=	Neural surface of the body.
The posterior part of the embryo, from the branchial aperture to the corresponding point on the lower side.	=	Haemal surface of the body (marked by the endostyle).

The terms "right" and "left," however, are applicable to the same sides of the body in the young and the adult.

As the gill-slits increase in number and in size, the peribranchial sacs, the epithelium of which flattens, enlarge correspondingly. Each of them gives off a diverticulum to the lower surface of the body which, by fusing with a corresponding diverticulum from the other side, leads to the formation of an unpaired atrial cavity (Fig. 200, *cl*).

The branchial aperture (Fig. 200, *i*) is derived from an ectodermal invagination on the upper surface of the embryo between the nervous system and the anterior end of the endostyle. We cannot here enter further into the somewhat complicated processes which, according to Salensky, lead to the development of this aperture and its valve-like closing apparatus.

The branchial aperture appears at a rather early stage, but the exhalent or atrial aperture only forms at a late stage after the development of the Ascidiozooid is, in other respects, completed. The common cloacal cavity of the colony, into which the atrial apertures of the individuals open, was traced back by Kowalevsky to the atrial cavity of the Cyathozooid. Salensky on the contrary, observed that, when the Cyathozooid degenerates, its atrial aperture closes, and consequently atrophies with the rest of the body. We must therefore assume that the common cloacal cavity of the *Pyrosoma* colony is a new structure which arises later, though its development has not so far been described (p. 403).

The primary enteric rudiment in the Ascidiozooids gives rise first directly only to a pharyngeal cavity which functions as a respiratory cavity. The rudiment of the stomach and intestine is found on the lower surface of the entoderm-tube in the form of a blind horseshoe-shaped diverticulum (Fig. 200 *B*) closely bent upon itself, the free ends being directed anteriorly. The two limbs of the horseshoe are seen cut through in the cross-section given in Fig. 204 (*oe* and *ed*). One limb (*ed*) of this rudiment separates early from the entoderm-sac and, as a blind diverticulum, represents the rudiment of the intestine, while the other gives rise to the stomach and oesophagus. The communication between this latter limb and the pharyngeal cavity is retained as the entrance to the oesophagus (*oe*). Only in later stages does the blind end of the intestine become connected with the atrial cavity and the alimentary canal attains complete development with the appearance of the so-called digestive gland.

FIG. 202.—Transverse section through the anterior region of an Ascidiozooid of *Pyrosoma* with the rudiment of the nervous system (after SALENSKY). *ec*, ectoderm; *en*, entoderm; *ms*, mesoderm-cells; *n*, rudiment of the nervous system; *p*, peribranchial tube.

The **central nervous system** arises in the most anterior region of the Ascidiozooid as an ectodermal invagination (Fig. 202, *n*) on the upper surface of the body, which soon becomes separated from the ectoderm as an elongate closed vesicle. This, at a later stage, becomes triangular (Fig. 200, *n*). The anterior part * of this vesicle forms the rudiment of the ganglion proper principally by a growth of its upper wall. From this region, two lateral hollow processes arise (Fig 200, *sn*) which, at a later period, grow and embrace the sides of the alimentary canal. These are the rudiments of the lateral nerves which thus arise here in a way similar to that described by SEELIGER for the later buds of *Pyrosoma*. The narrowed portion of the neural rudiment which is directed towards the branchial aperture becomes connected with the ectoderm of the alimentary canal, and, by a per-

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* [Anterior in relation to the long axis of the bud, posterior in the adult.—ED.]

foration which takes place between the neural and the enteric cavities, becomes the rudiment of the so-called ciliated pit (Fig. 200, *fl*). According to **Salensky**, the lumen of the neural tube is obliterated later, through the encroachment of the cells forming its walls, as the ganglion develops further. The lumen of the embryonic ciliated pit is also said to disappear; the similarly-named organ of the adult is thought to arise anew from the enteric wall. The blind end of the ciliated pit changes later into a large sac lying beneath the ganglion which probably forms the rudiment of the sub-neural gland.

Since the chain of Ascidiozooids arose as an outgrowth from the body of the Cyathozooid, its primary body-cavity, which extends from the enteric tube and the peribranchial cavities to the ectoderm, is in open communication with the primary body-cavity of the Cyathozooid. It is therefore possible for mesenchyme-elements to pass over from the Cyathozooid into the chain of Ascidiozooids. According to **Salensky**, this actually happens to a great extent, large numbers of the elements of the cell-zone passing over into the chain. According to this author, the cell-zone which was described above (p. 398), and which is to some extent derived from inner follicle-cells (kalymmocytes), but for the greater part from elements of the disintegrated left coelemic sac, is the principal source of the whole of the mesoderm in the Ascidiozooids. It must indeed be pointed out that the pericardial tube which is derived from the right coelomic sac and extends posteriorly as a prolongation of the pericardial rudiment of the Cyathozooid, after breaking up into separate cells, may also contribute to the formation of the mesenchyme in the Ascidiozooids, and this may also be the case with the so-called axial mesoderm-strand which arose from the tube interpreted as the remains of the chorda. The later fate of these structures is difficult to make out from **Salensky's** account. This author in any case seeks the origin of the mesoderm of the Ascidiozooids in the cell-zone which, in its turn, is derived principally from the elements of the disintegrated left coelomic sac. The immigration of the mesoderm into the germ-stock (the chain of Ascidiozooids) takes place first in the form of an ingrowth of crowded cell-masses. Later, when the cell-zone has broken up into separate islands, detached cell-groups or single elements pass over into the body-cavity of the Ascidiozooids.

The mesodermal elements become distributed in the primary body-cavity of the Ascidiozooids. Two groups of them, however, soon take up a definite position in the posterior region of the zooid at either side of the body, and their elements are found to be arranged in two layers, the external layer (Fig. 203 *A*, *el*) being the rudiment of the *elaeoblast*, and the inner that of the so-called pericardial strands, which must not be confounded with the pericardial tube mentioned above, an organ that disappears at an early stage (Fig. 203 *A*, *pc* and *pc'*). The cells of the elaeoblast-rudiment soon increase in size and form a rather high cylindrical epithelium. At a later stage, they are less regular in their arrangement, vacuoles develop within them and they change into large elements, resembling vegetable parenchyma-cells, and thus assume the features characteristic of the elaeoblast-tissue (Fig. 203 *C*). The elaeoblast is here at first paired and consists of rounded groups of cells lying in the posterior part of the body which cause the surface of the body to bulge out somewhat (Figs. 194 and 200 *el*).

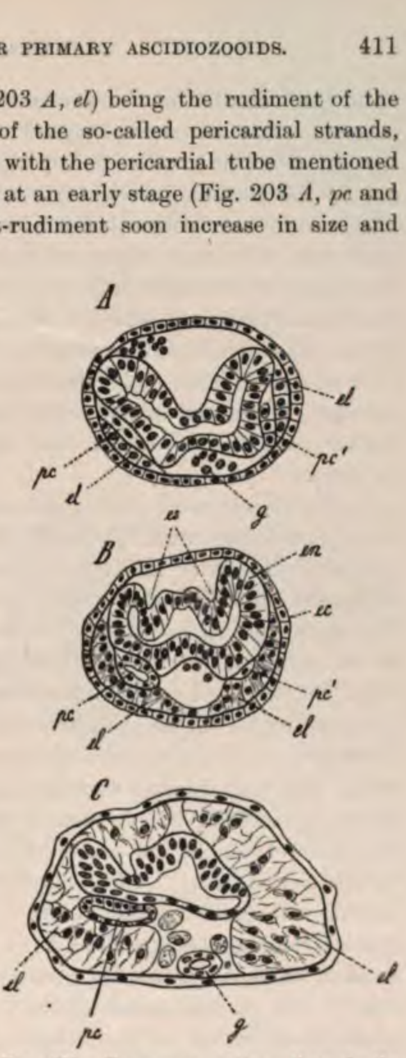

FIG. 203.—Transverse sections through the distal region of an Ascidiozooid of *Pyrosoma* in three consecutive stages of development (after SALENSKY). *ec*, ectoderm; *el*, rudiment of elaeoblast; *en*, entoderm; *es*, paired endostyle-folds; *g*, genital strand; *pc*, right pericardial strand, or pericardial vesicle; *pc'*, left pericardial strand.

The inner layer of the paired mesodermal rudiment just described gives rise to two cell-strands which develop differently (Fig. 203, *pc*, *pc'*). The strand to the right extends somewhat further forward than the other, and its anterior end becomes transformed into a closed vesicle, the *pericardial vesicle* (Fig. 203 *B* and *C*, *pc*). The *heart* develops through the thickening of that wall of the vesicle which is in contact with the alimentary canal and its invagination into the vesicle. The heart consequently forms here in the same way as in all other Tunicates.

The right pericardial strand (Fig. 203, *pc*) is not completely used up in the formation of the pericardial vesicle, but is continued posteriorly. This mesodermal strand and the corresponding strand of the left side (the so-called left pericardial strand, Fig. 203, *pc'*) do not for the present develop further, but at a later stage, when the Ascidiozooid has become independent and prepares to give rise to fresh buds, these strands pass over into the proliferating stolon which is developing and, on either side of the endostyle-process (entoderm-tube) that is also continued into the stolon, form the mesoderm-rudiment of the latter structure (Salensky). According to Salensky, therefore, *the paired pericardial strands of the Ascidiozooid give rise, on the right, to the pericardial vesicle of the Ascidiozooid, and, in their further course, to the two mesoderm-strands of the proliferating stolon* (p. 486).

By the development of the peribranchial sacs and the above-mentioned mesoderm-formation in the lateral parts of the embryo, the primary body-cavity is divided into two longitudinal sinuses, one above and the other below the alimentary canal (Fig. 203), called by Salensky the *supra-intestinal* and the *sub-intestinal blood-sinuses*. In the region of the sub-intestinal sinus the mesenchyme-cells collect (Fig. 203 *A*, *g*) and unite to form the *genital strand* belonging to the posterior region of the Ascidiozooid. In later stages, according to Salensky, a lumen appears in this strand (Fig. 203 *C*, *g*), round which the cells become arranged like an epithelium, but the lumen disappears again in the course of further development. The genital strand not only represents the genital rudiment of the Ascidiozooid in which it appears, but gives rise to the genital strand of the proliferating stolon of this zooid, as will be described later (p. 484). The rise of the genital organs in the first four Ascidiozooids has recently been described in detail by Seeliger (No. 76*a*). As it resembles that of the corresponding organs in the zooids that develop later we must refer the reader to the description given on p. 493, merely adding here that, in the first four Ascidiozooids, the ovary degenerates. It was well-known to

Fig. 204.—Transverse section through an Ascidiozooid of *Pyrosoma* (after Salensky). *db*, diapharyngeal band; *ed*, intestine; *i*, rudiment of the branchial aperture (ectodermal thickening); *oe*, oesophagus; *p*, peribranchial cavities.

KOWALEVSKY that the small *Pyrosoma* colonies contained only male zooids, females being found in the large colonies.

Anteriorly the supra-intestinal blood-sinus surrounds the rudiment of the central nervous system. Further back it is continued into the furrow which seems to be formed by the infolding of the endostyle-rudiment. Since, between the nervous system and the endostyle-rudiment the branchial aperture occurs, the stream of blood would be interrupted but for a peculiar adaptation for conducting it further, the upper wall of the intestine becoming folded in at this point somewhat in the manner of a typhlosole (Figs. 204, 205, *db*). This fold within which the blood now runs becomes completely separated from the dorsal wall of the intestine, and then forms a tube running freely through the intestine from the neural rudiment (Fig. 205, *n*) to the beginning of the endostyle-furrow (*en*). This peculiar structure, which has been called by SALENSKY the *pharyngeal blood-sinus*, and by HUXLEY the *diapharyngeal band*, may be compared with the gill of the Thaliacea with which SALENSKY even homologises it, although topographically it is clearly only an analogous structure. The diapharyngeal band is merely a provisional adaptation which atrophies in the further course of development.

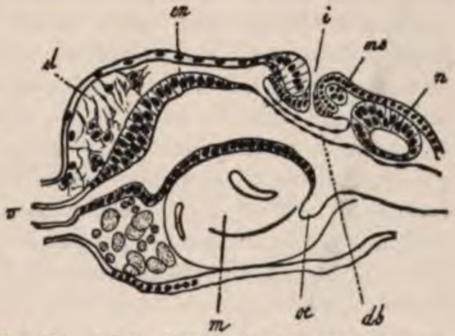

FIG. 205.—Longitudinal section through an Ascidiozooid of *Pyrosoma* (after SALENSKY). *db*, diapharyngeal band; *el*, elaeoblast; *en*, endostyle; *i*, branchial aperture; *m*, stomach; *ms*, sphincter muscle; *n*, rudiment of the ganglion; *oe*, oesophagus; *v*, connective strand.

Two structures, the significance of which is obscure, the *elongate* and the *lenticular cell-masses* (KEFERSTEIN and EHLERS) are to be traced back to the mesoderm. The lenticular masses are paired and symmetrical accumulations of cells lying at the entrance to the branchial sac between the wall of the peribranchial cavities and the entoderm (Figs. 196, *l*, and 106, *lm*, *p*). SALENSKY considers that they are to be derived from the kalymmocytes (inner follicle-cells). They are said to be phosphorescent organs. The elongate masses, which lie on the neural side "near the gills in the blood-sinus," form later from an unpaired accumulation of mesoderm-cells which originally lies below the so-called languets of the entoderm (Figs. 196, *d*, 106, *dm*).

The body-musculature, which is only slightly developed in *Pyrosoma*, arises from mesenchyme-cells arranged in bands. The fibrils of contractile substance are arranged round the periphery of these cell-bands which, in cross-section, appear triangular and extend in a radial manner towards the interior of the muscle-bundle.

As may be seen from Fig. 196, p. 402, the four primary Ascidiozooids of the young colony are placed radially to the principal axis in such a way that their branchial apertures appear to lie equatorially on the outer surface. The centre of the colony is at first occupied by a Cyathozooid but later by the common cloacal cavity which opens externally at the pole marked *cl* in Fig. 196. The dorsal surface of each Ascidiozooid is turned towards the cloacal cavity; its ventral surface, on the contrary, seems turned towards the opposite pole. Since it is here (at the end of the endostyle) that the first buds become abstricted, it might be expected that the oldest Ascidiozooid of the colony would lie nearest to the common cloacal aperture, while the younger Ascidiozooids would occupy the posterior part of the colony, that turned away from the cloacal aperture. According to SEELIGER, however, this is not the case; but the young buds, after becoming separated from the parent individual, wander to its dorsal side so that they become intercalated between it and the common cloacal aperture. Each Ascidiozooid gives off towards the cloacal aperture two mantle-vessels which, in Fig. 196 *B*, can already be seen as dorsal processes in the neighbourhood of *cl*. In large colonies, the four primary zooids surround the posterior pole of the colony, that turned away from the cloacal aperture and their mantle-vessels must consequently have the longest course.

5. The Hemimyaria (Salpidae).

The embryonic development of the *Salpidae* stands in somewhat sharp contrast to that of other Tunicates. The fact that the developing embryo fuses with the wall of the atrial cavity of the mother and that, at the point of fusion, there develops a nutritive organ known as a placenta derived in part from the remains of the egg-follicle, has brought about divergent ontogenetic conditions. The development is abbreviated, as it usually is where it takes place within the body of the mother. Neither the larval tail nor the chorda develops. It must be at once admitted that our knowledge of the embryonic development of the *Salpidae* must not be regarded as in any way complete. Even with regard to the most important points, such as the cleavage, the formation of the germ-layers and the development of the placenta, the recorded investigations are incomplete and contradictory, and we have statements which we must hesitate to accept because they are at variance with all that is known of the development of other Tunicates (and of animals in general). In our account we shall have these difficulties to contend with and must restrict ourselves to giving a brief survey of what at the present time seems to be fairly well established. We cannot enter upon the many contradictory and obscure points in connection with this subject.

Among the *Salpidae*, the sexual individuals (the forms belonging to the chain) are hermaphrodite, but the time of maturation of the male and female products differs. The individuals of the young chain set free from the stolon of the "nurse" generation (solitary form) are at first female; they are fertilised by the individuals of another chain, and each develops one embryo. Only as this develops, do the testes become functional.

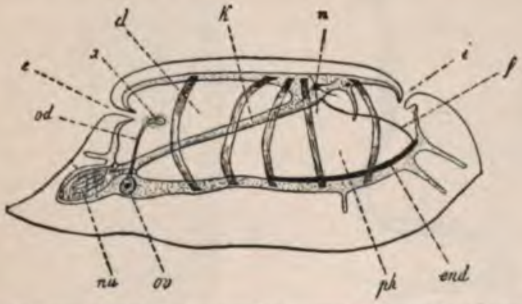

FIG. 206.—Side-view of *Salpa democratica-mucronata* (combined after CLAUS and SALENSKY). *cl*, atrial cavity; *e*, atrial aperture; *end*, endostyle; *f*, peripharyngeal band; *i*, branchial aperture; *k*, gill; *n*, nerve-ganglion; *nu*, nucleus; *od*, oviduct; *ov*, ovary (consisting of a single egg-follicle); *ph*, pharyngeal cavity; *x*, aperture of the oviduct.

The *Salpidae*, as a rule, develop only one egg. The whole ovary (Fig. 206, *ov*) consists, in such cases, of a single follicle which contains the egg and is connected with the epithelium of the atrial cavity * by a strand-like oviduct in which two portions can be dis-

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* [Owing to the peculiar relations existing between the pharynx and the atrial cavity in *Salpa*, it becomes extremely difficult to decide their limits; the term respiratory cavity (Athemhöhle) is commonly loosely applied to the greater part of this chamber. We have, however, thought it advisable to drop this word and to use in its stead the more specific terms atrial cavity and pharyngeal cavity in those cases in which we were able to determine the portion of the general cavity which was being referred to.—ED.]

tinguished (Fig. 207). One of these (*st*) is directly connected with the follicle and consists of a single row of cells (the so-called stalk of the follicle) and the other is a dilated efferent portion (*od*), with a distinct lumen. The egg-follicle lies at the base and to the right

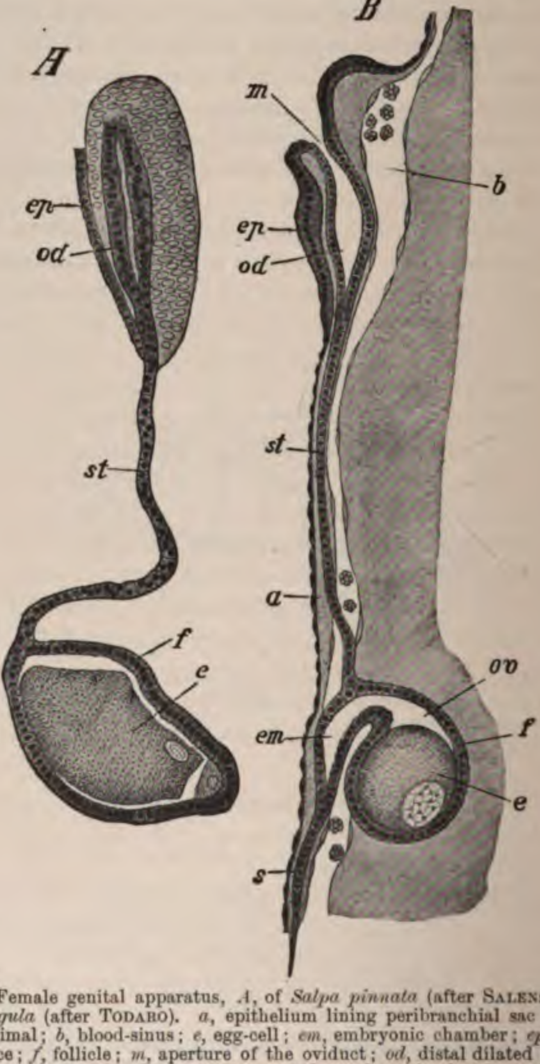

FIG. 207.—Female genital apparatus, *A*, of *Salpa pinnata* (after SALENSKY); *B*, of *Salpa virgula* (after TODARO). *a*, epithelium lining peribranchial sac (atrium) of parent animal; *b*, blood-sinus; *e*, egg-cell; *em*, embryonic chamber; *ep*, epithelial prominence; *f*, follicle; *m*, aperture of the oviduct; *od*, distal dilated part of the oviduct; *ov*, ovarian chamber; *s*, process of the embryonic chamber; *st*, narrowed part of the oviduct (so-called stalk of the follicle).

of the nucleus near the oesophagus (Fig. 206) and is surrounded by ramifications of the circumvisceral network of blood-vessels. The oviduct also appears to be accompanied until near its aperture by a vascular network (Fig. 207 *B*, *b*). The point at which the oviduct opens (Fig. 206, *x*) is found on the right side of the body behind the penultimate muscle-hoop above the nucleus. Round the aperture, the epithelium of the atrial cavity is thickened into a shield (Fig. 207 *A*, *ep*) and projects slightly inward (Fig. 207 *B*, *ep*). This swelling is the rudiment of the *epithelial prominence* of **SALENSKY** which **TODARO** calls the *uterus*.

The question now arises whether the members of a Salpa-chain, after the birth of the mature embryo, remain sterile or are able to produce a new ovary which may yield a new embryo. Some of **SALENSKY'S** observations seem to favour the latter view. The individuals composing a chain grow considerably in size while the embryo is developing within them, so that the largest individual contains the most advanced embryo. **SALENSKY**, in such a large individual, found the remains of a placenta which indicated the previous expulsion of an embryo and, side by side with this, a mature egg or a quite young embryo.

Exceptions to the rule that each individual of a chain produces only one embryo are found in *Salpa zonaria* (**CHAMISSO** and **ESCHRICHT**), *S. Thilesii* (**KROHN**) and *S. hexagona* (**TRAUSTEDT**), in which several embryos develop simultaneously, although they are not all at the same stage of development. In consequence of this and of the presence of a special point of attachment for each embryo, **LEUCKART** (No. 98) concluded that several egg-follicles with distinct ducts must be present. These forms have recently been united to form the genus *Iasis* (**LAHILLE**, No. 38), the above feature being one of its generic characters.

In many of the *Salpidae* (*S. maxima*, *S. pinnata*, *S. punctata*) the follicle appears to be incompletely divided by a longitudinal furrow (Fig. 207 *B*), into two chambers, one of which (the *ovarian sac*, *ov*) contains the egg during the stages of its maturation, while the other (the *embryonic sac*, *em*) receives it during the first embryonic stages. In many forms (*e.g.*, *S. maxima*) the embryonic sac is continued into a pointed process (*s*) which soon degenerates. The remains of this process, in later stages, when the

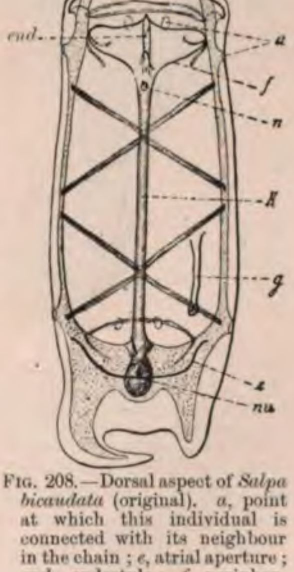

FIG. 208.—Dorsal aspect of *Salpa bicaudata* (original). *a*, point at which this individual is connected with its neighbour in the chain; *e*, atrial aperture; *end*, endostyle; *f*, peripharyngeal band; *g*, genital tube; *i*, branchial aperture; *k*, gill; *n*, nerve-ganglion; *nu*, nucleus.

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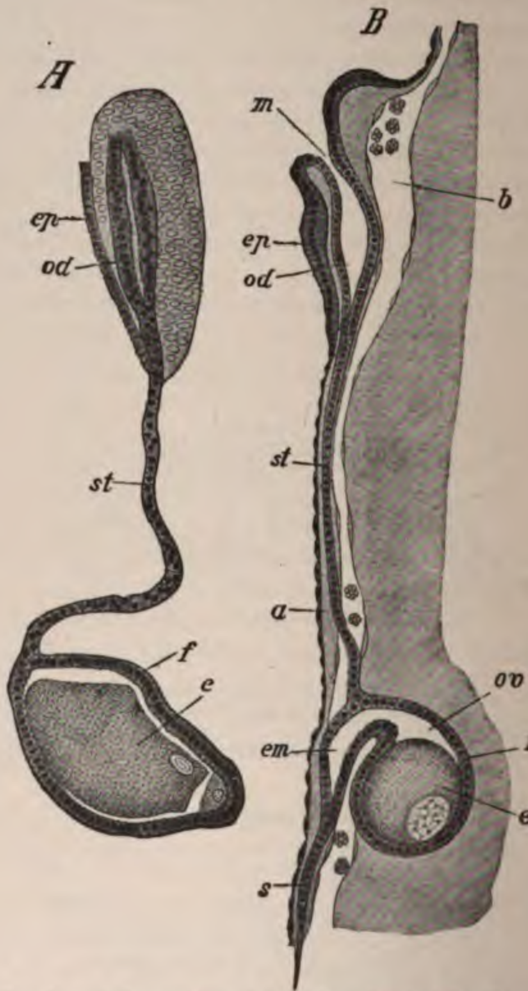

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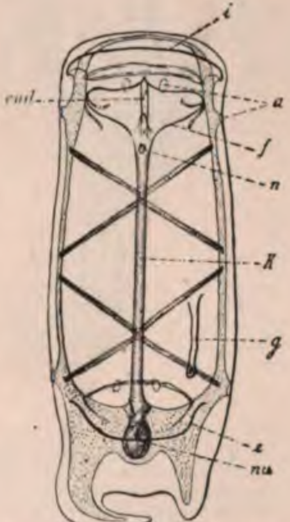

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The development of the female genital apparatus of *Salpa* (*Pegea*) *bicaudata* is quite exceptional. Here (Fig. 208) at about the middle of the body of the individual of the chain, at the right side, there is an outgrowth of the body-wall with a somewhat curved end (*genital tube*, *g*. SALENSKY. No. 104).

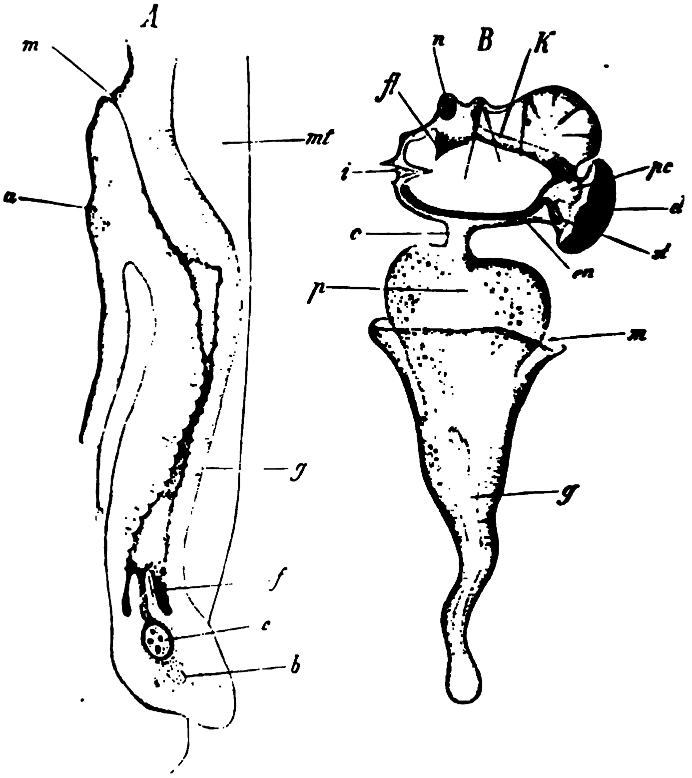

FIG. 209. -Two stages in the development of *Salpa bicaudata* (after SALENSKY). In *A* (a combined figure after SALENSKY), the embryo *e* still lies at the base of the genital tube (*g*) within the dilated oviduct. In *B*, the embryo, at a more advanced stage, has passed out of the tube together with the placenta. *a*, wall of the respiratory cavity; *b*, blood-forming bud (remains of the follicle); *c*, umbilical cord (connection between the embryo and the placenta); *e*, embryo in the dilated oviduct; *el*, elaeoblast; *en*, endostyle; *f*, genital fold; *fl*, ciliated pit; *g*, genital tube; *i*, branchial aperture; *k*, gill; *m*, aperture of the genital tube; *mt*, mantle; *n*, nerve-centre; *p*, placenta; *pe*, pericardium; *st*, stolon.

The lumen of this tube communicates with the atrial cavity (Fig. 209 *A*). The short oviduct opens far back in the base of this tube between two epithelial folds projecting into the lumen of the genital tube (incubatory folds, *f*). In spite of this peculiar arrangement, which must be regarded as a modification of the part of the atrial wall surrounding the aperture of the oviduct, it seems

(SALENSKY) that the embryonic development of *Salpa bicaudata* does not, in essentials, diverge greatly from that of other forms. The greater the increase in size of the embryo and of the placenta which has attached itself at the base of the tube, the shorter does the tube become. The embryo finally passes into the atrial cavity of the parent through the opening of the tube (Fig. 209 *B*).

The first change in the genital apparatus which precedes the fertilisation of the egg, occurs in quite young Salps, in the act of detaching themselves from the stolon of the "nurse" or just after detachment. It consists of a continuous shortening of the oviduct, especially affecting the part that has been described as the stalk of the follicle, the cells of which shift towards each other in such a way that they soon form several layers, while a lumen appears, so that the oviduct is now hollow throughout its whole length. During this abbreviation of the oviduct (Fig. 210) the egg, together with the follicle, shifts continually nearer the aperture of the duct, the process suggesting that seen in the descent of the mammalian testes.

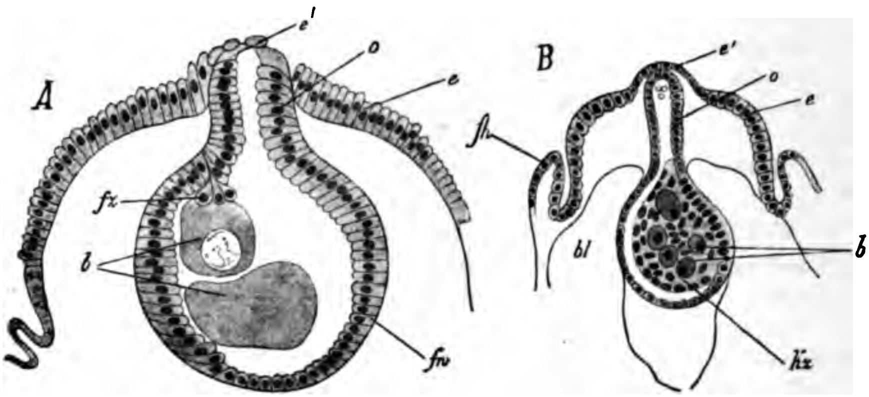

FIG. 210. –Two ontogenetic stages of *Salpa pinnata* (after SALENSKY). In *A*, the embryo consists of four blastomeres, two of which are cut through in the section. In *B*, it consists of a larger number of blastomeres and of numerous smaller cells, *kz*. *b*, blastomeres ; *bl*, blood-sinus ; *e*, epithelial prominence ; *e'*, modified part of the epithelial prominence (SALENSKY'S ectoderm-germ) ; *fh*, enveloping fold ; *fw*, follicle-wall ; *fz*, immigrating follicle-cells, kalymmocytes ; *kz*, smaller cells of the embryo (SALENSKY'S gonoblasts) ; *o*, shortened oviduct.

Through the now open oviduct the spermatozoa obtain access to the *follicle*, and fertilisation takes place. According to TODARO (No. 112), the spermatozoon enters the egg and the male pronucleus develops after the expulsion of the first polar body and before the development of the second.

Cleavage is total (Figs. 210 *A*, 211 *A* and *B*). Eggs have been observed divided into two and into four and also in the later stages of cleavage; we are, however, far from having obtained a clear insight into the details of the process. In individual cases, cleavage seems to be unequal. Salensky figured the embryo of *Salpa mucronata* in the four-celled stage consisting of four equal blastomeres, but both he and Todaro observed an inequality of the blastomeres in *S. pinnata* and *S. punctata* at this stage. [Judging from recent investigations (Nos. XIII. and XXI*a*.), unequal segmentation is the rule rather than the exception in *Salpa*.]

The processes of cleavage are here specially difficult to follow in detail because of the cells which become detached from the wall of the follicle and become applied to the embryónic mass (Fig. 210 *A*, *fz*), and even wander in between the blastomeres; these cells are known as the follicle-cells or kalymmocytes. This immigration of cells, which we may compare to the test-cells of the Ascidiacea (p. 336) and the inner follicle-cells of *Pyrosoma* (p. 390), is so profuse that the blastomeres at the later stages of cleavage seem actually enveloped in them (Fig. 210 *B*), appearing to be embedded in a matrix of *gonoblasts* (as Salensky terms them, No. 104). Todaro, who was the first to notice this multiplication and immigration of the follicle-cells (Nos. 108 and 109), described them as yolk-cells (*cellules lécitiches*) and holds that they serve for the nourishment of the embryo which forms from the blastomeres. They are said to undergo granular disintegration, to be taken in and assimilated by the blastomeres, and, finally, to disappear altogether. Salensky (No. 104), on the contrary, sees in these cells the actual constituent elements of the future embryo and therefore calls them gonoblasts.* According to him, the large blastomeres, the protoplasm of which soon becomes divided up in a peculiar way, do not subdivide further and are, in general, incapable of any special further development. They are said finally

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* [The recent and exhaustive investigations made by Brooks (No. I.), Heider (No. XIII.), Korotneff (Nos. XVIII.-XXI*a*.), and Metcalf (No. XXIV.), prove undoubtedly that Salensky was in error when he ascribed a formative rôle to the kalymmocytes, since, however much these observers differ from one another in detail, they were all agreed that the organs of the embryo are eventually wholly formed from the blastomeres, the view of the majority being that the kalymmocytes play an entirely passive rôle in the development of the embryo, being merely nutritive structures.

The account given in the following pages is largely based upon Salensky's work on the development of *Salpa*. Unfortunately, the conclusions arrived at by this observer have, in many cases besides the one mentioned above, not been confirmed by subsequent investigators. This renders our account incomplete and, in some particulars, inaccurate, so that the reader will do well to consult the original monographs of Heider, Korotneff and Brooks. We have, however, endeavoured, in footnotes, to draw attention to the most serious errors.—Ed.]

to disintegrate, while the embryo is built up by the gonoblasts which form the greater part of all the later rudiments of organs. SALENSKY, therefore, considers the embryonic development of the *Salpidae* as a process intermediate between the development of an egg and budding, beginning with a regular cleavage, but the resultant blastomeres play no further part in the development, the embryo being for the greater part built up out of derivatives of the egg-follicle. SALENSKY consequently describes the embryonic development of the Salps as *follicular budding*. *A priori*, SALENSKY'S view as to the part taken by the follicle cells in the embryonic development of the *Salpidae* must be regarded as extremely improbable; it is also by no means proved by what SALENSKY says of the decisive stages. We must therefore for the present accept TODARO'S views as the more probable.*

We have already seen (p. 390) that SALENSKY also ascribes a considerable part in the building up of the embryo of *Pyrosoma* to the immigrated follicle-cells or kalymmocytes, and he has recently attributed to these cells a share in the development of the cellulose mantle of *Distaplia* (No. 49, see also p. 357).

The shortening of the oviduct mentioned above (Fig. 210) is not due merely to the dilation of its lumen and the consequent shifting of the cells of its wall, but is also directly connected with the immigration of cells already described. In this way, a large amount of cell-material is given off by the wall of the oviduct and the follicle to the embryo. In its abbreviated condition, the oviduct forms a short wide chamber (Fig. 211 *A*) communicating with the follicle through a narrow aperture which, however, soon widens. The two cavities finally unite to form a single capsule, the lumen of which is almost

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* [According to BROOKS and METCALF (Nos. I. and XXIV.) these kalymmocytes first block out the embryonic tissues and organs, but are eventually replaced by blastomeres, after which the former degenerate and probably serve as food-material for the latter cells. Even at an early stage kalymmocytes degenerate and their nuclei migrate into the large blastomeres, forming the so-called yolk-particles. HEIDER (No. XIII.), while agreeing that the kalymmocytes are taken up by the blastomeres, thinks that the entire cell, not merely its nucleus, enters the protoplasm of the latter. KOROTNEFF (Nos. XX*a*. and XXI*a*.), however, regards the masses seen in the blastomeres as true yolk-masses and not degenerating kalymmocytes. The last two observers regard the latter cells as playing a passive rôle in the development and do not agree with BROOK'S view that the embryonic organs are blocked out in kalymmocytes. According to these two authors, the embryo is made up of large and small blastomeres and kalymmocytes, the small blastomeres being indistinguishable from the latter and hence, they suppose, BROOKS' and SALENSKY'S error arose, the cells which the latter took to be kalymmocytes being in reality small blastomeres.—ED.]

completely filled by the embryo (Fig. 211 *B*). The wall of this capsule, which is produced by the union of the oviduct and the follicle is from this time called (although not very accurately) the *follicular epithelium*.

During the above changes, the shield-like thickening of the epithelium round the aperture of the oviduct has risen up more and more, and now forms a mound-like swelling (*epithelial prominence*, Fig. 210, *e*, 211, *a*) projecting into the posterior portion of the atrial cavity. As the oviduct continues to shorten, the follicle, with the embryo, is brought into ever closer proximity to this prominence and finally passes into it. At later stages, the prominence becomes constricted at its base (Fig. 213), remaining connected with the wall of the atrial cavity only by a thin stalk. The embryo now, enclosed in a kind of brood-sac, projects into the interior of the atrial cavity.

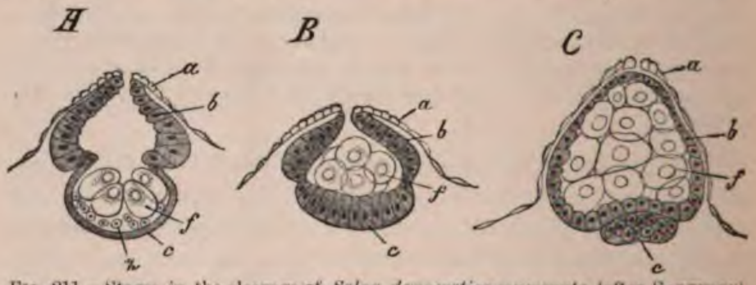

FIG. 211.—Stages in the cleavage of *Salpa democratica-mucronata* (after SALENSKY). In *A*, the embryo undergoing cleavage still lies in the egg-follicle (*c*). In *B*, the embryo has passed into the cavity of the oviduct (*b*). The follicular epithelium has contracted (*c*) and represents the first rudiment of the placenta. *C* shows a later stage. *a*, so-called epithelial prominence = outer lamella of the brood-sac; *b*, shortened oviduct = inner lamella of the brood-sac; *c*, follicular epithelium = rudiment of placenta; *f*, blastomeres; *z*, immigrated follicle-cells (not represented in *B* and *C*).

The wall of this brood-sac, which, as we shall see, is merely provisional, is double. The external wall (Fig. 211 *C*, *a*) is a modified portion of the epithelium of the atrial cavity, and, in the inner wall (Fig. 211 *C*, *b*) we recognise the follicular epithelium. It appears that, in this stage, the opening of the oviduct into the atrial cavity has completely closed.

After cleavage has ended, the embryo forms a solid, rounded body composed of numerous cells which, according to SALENSKY, are mostly derived from the follicular epithelium, but, according to TODARO, have been produced by fission from the blastomeres. We shall for the present adopt the latter view as the more probable.*

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* [See editorial note, p. 421].

According to **Todaro**, the cells derived from the follicle-epithelium which are fated to disintegrate, can still be distinguished between these embryonic cells. It should, indeed, be mentioned that **Salensky** was able to find within the embryo, long after cleavage had ended, at a time when the first rudiments of organs grow distinct, a few large blastomeres definitely arranged. The significance of these is obscure, and we are altogether in the dark as to those stages in the development of *Salpa* which lie between cleavage and the beginning of the formation of the organs, *i.e.*, the stages in which we should expect the germ-layers to form.* The cleavage-cavity appears to be wanting in all *Salpidae* [**Salensky, Heider** and **Korotneff**]. **Brooks**, however, suggests that the follicular cavity may be thus interpreted.

Certain divergencies are found in the different species of *Salpa* in the further processes of development, but these apparently are not due to any fundamental difference. The development of most species being as yet only very partially known, we shall restrict ourselves to a closer account of the two forms which have been best investigated, *viz.*, *S. democratica-mucronata* and *S. pinnata*. These represent two types of development which are to be distinguished by the absence or presence of a covering fold and by the structure of the placenta.†

A. Forms without Covering Folds.

The embryo of *Salpa* (*Thalia*) *democratica-mucronata*, in the stages that mark the completion of the cleavage-processes (Fig. 211 *C*) projects in the form of a cone into the atrial cavity of the parent. It lengthens later and becomes more cylindrical, its end being rounded (Fig. 212 *B*). It is still surrounded by the two walls of the brood-

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* [Recent investigations tend to show that germ-layers, as we understand them in other animals, cannot be said to exist in *Salpa*, since the various germ-cells, which give rise to the different organs, appear to be mixed in an irregular way throughout the germ-mass. Gradually, however, certain of the blastomeres take up definite positions, and, from what is known of their subsequent history, can now be definitely stated to give rise to certain tissues. The first of these rudiments to be recognised is the ectoderm; this takes the form of certain large blastomeres which migrate to the surface opposite the placenta and there give rise to the ectoderm and its derivatives. Other large blastomeres which remain nearer the placenta have been found to give rise to the entoderm and possibly some mesoderm; the latter layer, however, appears to arise largely from the smaller blastomeres which, with the kalymmocytes, make up the main mass of the germ.—Ed.]

† [**Korotneff** (No. XVIII.) expresses grave doubts as to the advisability of this subdivision, and there can be no doubt from recent investigations that the developmental differences between these two divisions have been greatly exaggerated.—Ed.]

embryonic sac, in consequence of the shortening of the oviduct, shifts towards the epithelial prominence, serves for attaching the sac to the epithelium.

The development of the female genital apparatus of *Salpa* (*Pegea*) *bicaudata* is quite exceptional. Here (Fig. 208) at about the middle of the body of the individual of the chain, at the right side, there is an outgrowth of the body-wall with a somewhat curved end (*genital tube*, *g*, SALENSKY, No. 104).

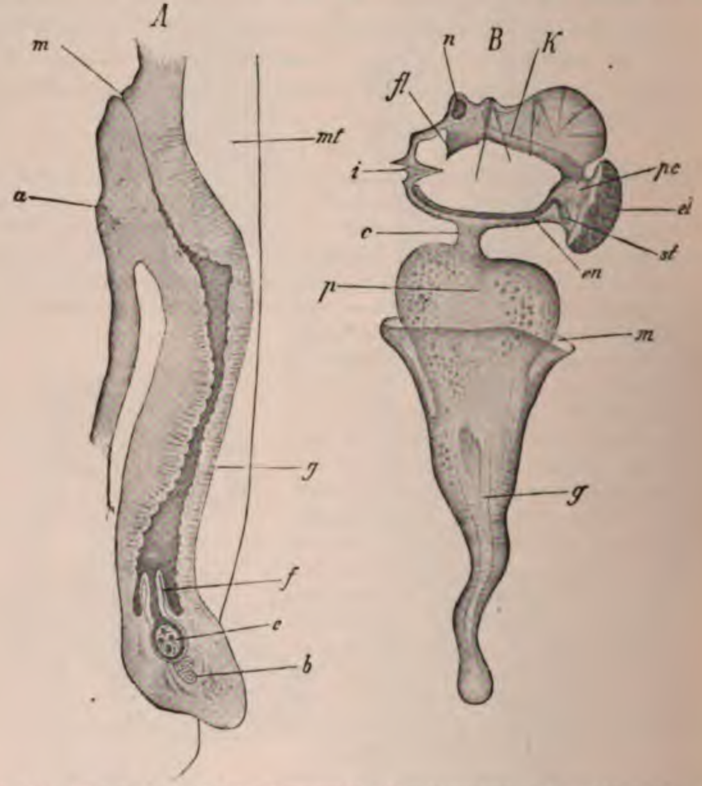

FIG. 209.—Two stages in the development of *Salpa bicaudata* (after SALENSKY). In *A* (a combined figure after SALENSKY), the embryo *e* still lies at the base of the genital tube (*g*) within the dilated oviduct. In *B*, the embryo, at a more advanced stage, has passed out of the tube together with the placenta. *a*, wall of the respiratory cavity; *b*, blood-forming bud (remains of the follicle); *c*, umbilical cord (connection between the embryo and the placenta); *e*, embryo in the dilated oviduct; *el*, elaeoblast; *en*, endostyle; *f*, genital fold; *fl*, ciliated pit; *g*, genital tube; *i*, branchial aperture; *k*, gill; *m*, aperture of the genital tube; *mt*, mantle; *n*, nerve-centre; *p*, placenta; *pc*, pericardium; *st*, stolon.

The lumen of this tube communicates with the atrial cavity (Fig. 209 *A*). The short oviduct opens far back in the base of this tube between two epithelial folds projecting into the lumen of the genital tube (incubatory folds, *f*). In spite of this peculiar arrangement, which must be regarded as a modification of the part of the atrial wall surrounding the aperture of the oviduct, it seems

It appears that the inner lamella of the brood-sac is very soon reduced (Fig. 212 *B*) and completely degenerates. This degeneration at first affects a zone running obliquely round the embryo, leaving only a cap of the lamella covering the anterior end of the embryo and a posterior cup-like portion connected with the rudiment of the placenta, which completely unites with the latter at a subsequent period; the anterior cap appears soon to disintegrate. The embryo is then covered by only one envelope, the outer lamella of the brood-sac (*a*).

The above is in accordance with SALENSKY'S earlier description of the fate of the inner lamella (No. 100). The more recent statements of this author suggest that the inner lamella does not disintegrate, but enters into close connection with the embryo, finally changing into the ectoderm of the latter. The ectoderm in *S. democratica-mucronata* would then have to be traced back to the transformed epithelium of the oviduct, a view which is *a priori* improbable, and less in accordance with our own investigations than the older statements. [The ectoderm, like the other embryonic organs, is now generally regarded as arising from the blastomeres. See footnote, p. 424, and KOROTNEFF (No. XVIII.) on *S. democratica*.]

In the next stage (Fig. 212 *B*) important differentiations are evident in the embryo. The mesoderm (*m*) has appeared between the ectoderm and the entoderm in the form of a cell-accumulation, which spreads out like a germ-layer to right and left over the sides of the embryo. The central nervous system (*n*) is also found as a cell-growth proceeding from the ectoderm. Its position marks the plane of symmetry and the anterior end of the body in the embryo.* Diametrically opposite to it is another cell-accumulation (*l*), which SALENSKY also traces back to the ectoderm, and which seems to be the first rudiment of the elaeoblast. That part of the ectoderm which is in contact with the rudiment of the placenta is already distinguished by the large size and the height of its cells (*x*). This is the rudiment of the lamella, which takes part in the formation of the epithelium covering the placenta.

The fundamental features of the organisation of the embryo of *Salpa*, which are thus already sketched out, appear still more distinctly in the following stage (Fig. 213), in consequence of the development of a system of cavities. The inner cell-mass severs

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* [KOROTNEFF believes that the nervous system is formed as a closed vesicle, which lies at first quite independently in the mesoderm without any relation to the ectoderm or to the pharynx. The elaeoblast also arises from the embryonic blastomeres and not from follicular cells, as SALENSKY stated.—ED.]

of cleavage; we are, however, far from having obtained a clear insight into the details of the process. In individual cases, cleavage seems to be unequal. SALENSKY figured the embryo of *Salpa mucronata* in the four-celled stage consisting of four equal blastomeres, but both he and TODARO observed an inequality of the blastomeres in *S. pinnata* and *S. punctata* at this stage. [Judging from recent investigations (Nos. XIII. and XXI*a*.), unequal segmentation is the rule rather than the exception in *Salpa*.]

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* [The recent and exhaustive investigations made by BROOKS (No. I.), HEIDER (No. XIII.), KOROTNEFF (Nos. XVIII.-XXI*a*.), and METCALF (No. XXIV.), prove undoubtedly that SALENSKY was in error when he ascribed a formative rôle to the kalymmocytes, since, however much these observers differ from one another in detail, they were all agreed that the organs of the embryo are eventually wholly formed from the blastomeres, the view of the majority being that the kalymmocytes play an entirely passive rôle in the development of the embryo, being merely nutritive structures.

The account given in the following pages is largely based upon SALENSKY'S work on the development of *Salpa*. Unfortunately, the conclusions arrived at by this observer have, in many cases besides the one mentioned above, not been confirmed by subsequent investigators. This renders our account incomplete and, in some particulars, inaccurate, so that the reader will do well to consult the original monographs of HEIDER, KOROTNEFF and BROOKS. We have, however, endeavoured, in footnotes, to draw attention to the most serious errors.—ED.]

to disintegrate, while the embryo is built up by the gonoblasts which form the greater part of all the later rudiments of organs. Salensky, therefore, considers the embryonic development of the *Salpidae* as a process intermediate between the development of an egg and budding, beginning with a regular cleavage, but the resultant blastomeres play no further part in the development, the embryo being for the greater part built up out of derivatives of the egg-follicle. Salensky consequently describes the embryonic development of the Salps as *follicular budding*. *A priori*, Salensky's view as to the part taken by the follicle cells in the embryonic development of the *Salpidae* must be regarded as extremely improbable; it is also by no means proved by what Salensky says of the decisive stages. We must therefore for the present accept Todaro's views as the more probable.*

We have already seen (p. 390) that Salensky also ascribes a considerable part in the building up of the embryo of *Pyrosoma* to the immigrated follicle-cells or kalymmocytes, and he has recently attributed to these cells a share in the development of the cellulose mantle of *Distaplia* (No. 49, see also p. 357).

The shortening of the oviduct mentioned above (Fig. 210) is not due merely to the dilation of its lumen and the consequent shifting of the cells of its wall, but is also directly connected with the immigration of cells already described. In this way, a large amount of cell-material is given off by the wall of the oviduct and the follicle to the embryo. In its abbreviated condition, the oviduct forms a short wide chamber (Fig. 211 *A*) communicating with the follicle through a narrow aperture which, however, soon widens. The two cavities finally unite to form a single capsule, the lumen of which is almost

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* [According to Brooks and Metcalf (Nos. I. and XXIV.) these kalymmocytes first block out the embryonic tissues and organs, but are eventually replaced by blastomeres, after which the former degenerate and probably serve as food-material for the latter cells. Even at an early stage kalymmocytes degenerate and their nuclei migrate into the large blastomeres, forming the so-called yolk-particles. Heider (No. XIII.), while agreeing that the kalymmocytes are taken up by the blastomeres, thinks that the entire cell, not merely its nucleus, enters the protoplasm of the latter. Korotneff (Nos. XX*a*. and XXI*a*.), however, regards the masses seen in the blastomeres as true yolk-masses and not degenerating kalymmocytes. The last two observers regard the latter cells as playing a passive rôle in the development and do not agree with Brook's view that the embryonic organs are blocked out in kalymmocytes. According to these two authors, the embryo is made up of large and small blastomeres and kalymmocytes, the small blastomeres being indistinguishable from the latter and hence, they suppose, Brooks' and Salensky's error arose, the cells which the latter took to be kalymmocytes being in reality small blastomeres.—Ed.]

completely filled by the embryo (Fig. 211 *B*). The wall of this capsule, which is produced by the union of the oviduct and the follicle is from this time called (although not very accurately) the *follicular epithelium*.

During the above changes, the shield-like thickening of the epithelium round the aperture of the oviduct has risen up more and more, and now forms a mound-like swelling (*epithelial prominence*, Fig. 210, *e*, 211, *a*) projecting into the posterior portion of the atrial cavity. As the oviduct continues to shorten, the follicle, with the embryo, is brought into ever closer proximity to this prominence and finally passes into it. At later stages, the prominence becomes constricted at its base (Fig. 213), remaining connected with the wall of the atrial cavity only by a thin stalk. The embryo now, enclosed in a kind of brood-sac, projects into the interior of the atrial cavity.

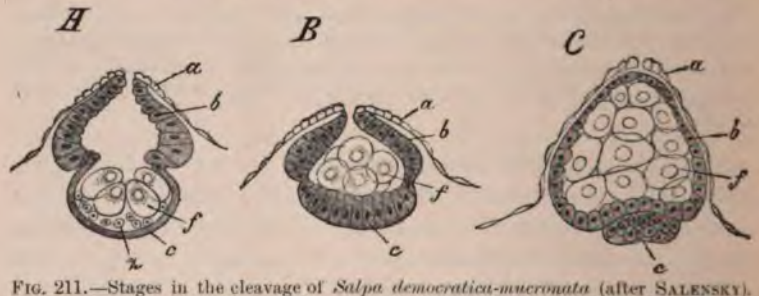

FIG. 211.—Stages in the cleavage of *Salpa democratica-mucronata* (after SALENSKY). In *A*, the embryo undergoing cleavage still lies in the egg-follicle (*c*). In *B*, the embryo has passed into the cavity of the oviduct (*b*). The follicular epithelium has contracted (*c*) and represents the first rudiment of the placenta. *C* shows a later stage. *a*, so-called epithelial prominence = outer lamella of the brood-sac; *b*, shortened oviduct = inner lamella of the brood-sac; *c*, follicular epithelium = rudiment of placenta; *f*, blastomeres; *z*, immigrated follicle-cells (not represented in *B* and *C*).

The wall of this brood-sac, which, as we shall see, is merely provisional, is double. The external wall (Fig. 211 *C*, *a*) is a modified portion of the epithelium of the atrial cavity, and, in the inner wall (Fig. 211 *C*, *b*) we recognise the follicular epithelium. It appears that, in this stage, the opening of the oviduct into the atrial cavity has completely closed.

After cleavage has ended, the embryo forms a solid, rounded body composed of numerous cells which, according to SALENSKY, are mostly derived from the follicular epithelium, but, according to TODARO, have been produced by fission from the blastomeres. We shall for the present adopt the latter view as the more probable.*

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* [See editorial note, p. 421].

According to TODARO, the cells derived from the follicle-epithelium which are fated to disintegrate, can still be distinguished between these embryonic cells. It should, indeed, be mentioned that SALENSKY was able to find within the embryo, long after cleavage had ended, at a time when the first rudiments of organs grow distinct, a few large blastomeres definitely arranged. The significance of these is obscure, and we are altogether in the dark as to those stages in the development of *Salpa* which lie between cleavage and the beginning of the formation of the organs, *i.e.*, the stages in which we should expect the germ-layers to form.* The cleavage-cavity appears to be wanting in all *Salpidae* [SALENSKY, HEIDER and KOROTNEFF]. BROOKS, however, suggests that the follicular cavity may be thus interpreted.

Certain divergencies are found in the different species of *Salpa* in the further processes of development, but these apparently are not due to any fundamental difference. The development of most species being as yet only very partially known, we shall restrict ourselves to a closer account of the two forms which have been best investigated, *viz.*, *S. democratica-mucronata* and *S. pinnata*. These represent two types of development which are to be distinguished by the absence or presence of a covering fold and by the structure of the placenta.†

A. Forms without Covering Folds.

The embryo of *Salpa* (*Thalia*) *democratica-mucronata*, in the stages that mark the completion of the cleavage-processes (Fig. 211 *C*) projects in the form of a cone into the atrial cavity of the parent. It lengthens later and becomes more cylindrical, its end being rounded (Fig. 212 *B*). It is still surrounded by the two walls of the brood-

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*[Recent investigations tend to show that germ-layers, as we understand them in other animals, cannot be said to exist in *Salpa*, since the various germ-cells, which give rise to the different organs, appear to be mixed in an irregular way throughout the germ-mass. Gradually, however, certain of the blastomeres take up definite positions, and, from what is known of their subsequent history, can now be definitely stated to give rise to certain tissues. The first of these rudiments to be recognised is the ectoderm; this takes the form of certain large blastomeres which migrate to the surface opposite the placenta and there give rise to the ectoderm and its derivatives. Other large blastomeres which remain nearer the placenta have been found to give rise to the entoderm and possibly some mesoderm; the latter layer, however, appears to arise largely from the smaller blastomeres which, with the kalymmocytes, make up the main mass of the germ.—ED.]

†[KOROTNEFF (No. XVIII.) expresses grave doubts as to the advisability of this subdivision, and there can be no doubt from recent investigations that the developmental differences between these two divisions have been greatly exaggerated.—ED.]

sac (Figs. 211 *C*, 212 *A*, *a* and *b*). The first differentiation in the embryo consists in the appearance of a continuous superficial cell-layer, in which we recognise the ectoderm of the embryo (Fig. 212 *A*, *ec*).* Important changes in the brood-sac take place at the same time, its outer lamella, which represents a layer continuous with the epithelium of the atrial-cavity of the parent (Fig. 212, *a*) soon changing into an extremely thin pavement-epithelium. The inner lamella of the brood-sac (Fig. 212, *b*) represents the modified epithelium of the oviduct and the follicle. In it we can distinguish a simple cell-layer which at first completely encircles the embryo. This is the inner lamella of the brood-sac in the strict sense of the term, and is no doubt derived from the modified oviduct. To the base of the sac formed by the inner lamella is attached a cell-accumulation (*p*) which probably represents the modified cell-material of the follicle; this forms the first rudiment of the placenta. [The placenta, including the basal plate, according to KOROTNEFF (No. XX*a*.) is wholly maternal in origin.]

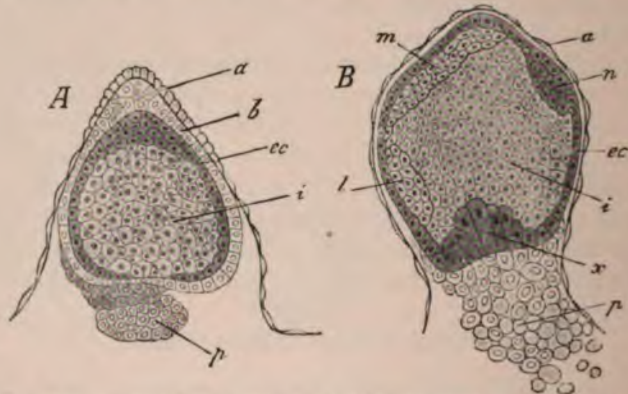

FIG. 212.—Two sections through embryos of *Salpa democratica-mucronata* (diagrammatic, after SALENSKY). *A*, younger stage; *B*, sagittal section through an older stage. *a*, outer lamella of the brood-sac; *b*, inner lamella of the same; *ec*, ectoderm [layer of kalymmocytes, ectoderm not yet formed, KOROTNEFF]; *i*, inner cell-mass (entoderm, mesoderm ?); *l*, rudiment of elaeoblast; *m*, mesoderm (?); *n*, rudiment of the nerve-centre; *p*, remains of the follicle = rudiment of the placental tissue; *x*, ectodermal thickening, from which the covering of the placenta is derived [this is follicular, *i.e.*, maternal in origin according to KOROTNEFF].

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* [According to KOROTNEFF (No. XVIII.) the embryo becomes covered in the first instance by a layer of kalymmocytes; these SALENSKY mistook for the ectoderm. The latter layer forms later by a rupture in the layer of kalymmocytes covering the embryo and a discharge of blastomeres through the gap into the follicular cavity, where they become arranged as a layer, the future ectoderm between the follicle and the embryo. Mesenchyme-cells are also discharged into this cavity, and arrange themselves under the ectoderm.—ED.]

It appears that the inner lamella of the brood-sac is very soon reduced (Fig. 212 *B*) and completely degenerates. This degeneration at first affects a zone running obliquely round the embryo, leaving only a cap of the lamella covering the anterior end of the embryo and a posterior cup-like portion connected with the rudiment of the placenta, which completely unites with the latter at a subsequent period; the anterior cap appears soon to disintegrate. The embryo is then covered by only one envelope, the outer lamella of the brood-sac (*a*).

The above is in accordance with Salensky's earlier description of the fate of the inner lamella (No. 100). The more recent statements of this author suggest that the inner lamella does not disintegrate, but enters into close connection with the embryo, finally changing into the ectoderm of the latter. The ectoderm in *S. democratica-mucronata* would then have to be traced back to the transformed epithelium of the oviduct, a view which is *a priori* improbable, and less in accordance with our own investigations than the older statements. [The ectoderm, like the other embryonic organs, is now generally regarded as arising from the blastomeres. See footnote, p. 424, and Korotneff (No. XVIII.) on *S. democratica*.]

In the next stage (Fig. 212 *B*) important differentiations are evident in the embryo. The mesoderm (*m*) has appeared between the ectoderm and the entoderm in the form of a cell-accumulation, which spreads out like a germ-layer to right and left over the sides of the embryo. The central nervous system (*n*) is also found as a cell-growth proceeding from the ectoderm. Its position marks the plane of symmetry and the anterior end of the body in the embryo.* Diametrically opposite to it is another cell-accumulation (*l*), which Salensky also traces back to the ectoderm, and which seems to be the first rudiment of the elaeoblast. That part of the ectoderm which is in contact with the rudiment of the placenta is already distinguished by the large size and the height of its cells (*x*). This is the rudiment of the lamella, which takes part in the formation of the epithelium covering the placenta.

The fundamental features of the organisation of the embryo of *Salpa*, which are thus already sketched out, appear still more distinctly in the following stage (Fig. 213), in consequence of the development of a system of cavities. The inner cell-mass severs

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[*] [Korotneff believes that the nervous system is formed as a closed vesicle, which lies at first quite independently in the mesoderm without any relation to the ectoderm or to the pharynx. The elaeoblast also arises from the embryonic blastomeres and not from follicular cells, as Salensky stated.—Ed.]

itself from the ectoderm, giving rise to a cleft which gradually widens to form the rudiment of the *primary body-cavity* (*l*). A cavity rises in a similar way within the entodermal cell-mass, this being the first rudiment of the alimentary canal, especially of the *branchial sac* (pharnyx, Fig. 213, *d*). This chamber, when it first appears, consists of two lateral cavities connected across the middle line by a narrower part (Fig. 213 *B*, *k*).* The dorsal ingrowth that partly separates the two halves of the enteric cavity must be regarded as the rudiment of the gill (Fig. 213 *B*, *k*). It becomes separated from the enteric rudiment, by the fusion of the atrial cavity, which develops between it and the ectoderm, with the projecting lateral diverticula of the pharyngeal cavity. The atrial cavity of *Salpa* is derived by TODARO (No. 113) from an ectodermal invagination. The gill, which is originally a solid ingrowth of cells, changes later into

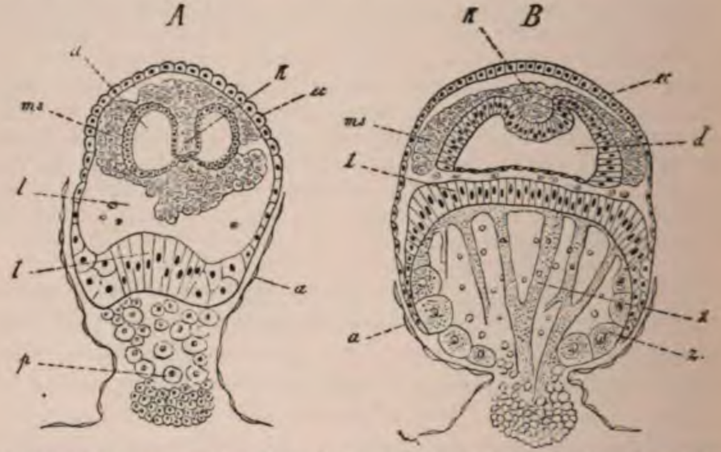

FIG. 213.—Transverse sections through two ontogenetic stages of *Salpa democratica-mucronata* (schematic, original). *a*, outer lamella of brood-sac; *d*, rudiment of the alimentary canal; *ec*, ectoderm; *k*, rudiment of the gill; *l*, primary body-cavity; *ms*, mesoderm; *p*, rudiment of the placenta (remains of the follicle); *l*, the epithelial covering (basal plate) of the placenta; *x*, tissue of the placenta; *z*, large marginal cells of the placental tissue.

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* [Investigations both on this and other species show that, in every case, the atrial cavity is the first to appear. HEIDER and KOROTNEFF agree in describing it as a single cavity from its earliest origin, while BROOKS ascribed a paired origin similar to that found by SALENSKY for the atrium and, on this account, BROOKS concludes that SALENSKY mistook the atrium for the pharynx. The pharynx appears below this as either a single or paired cleft in the embryonic mass, and the gill arises from the horizontal septum between these two cavities (atrium and pharynx), by the appearance in it of a pair of laterally placed longitudinal slits.—ED.]

a tube, the inner cells being transformed into blood-corpuscles which pass into the blood.

Before passing on to describe the other changes that take place in the embryo we must dwell for a moment on the degeneration of the brood-sac and the development of the placenta. After the inner lamella of the brood-sac has degenerated as described above, the embryo remains surrounded solely by the very thin epithelium of the outer lamella (Fig. 212 *B*, *a*), which consists of a differentiated part of the atrial epithelium of the parent. This outer lamella is unable to keep pace with the further increase in size of the embryo; it becomes ruptured at the point at which the aperture of the oviduct was originally situated and shrinks downwards over the embryo (Fig. 213). In consequence of this contraction of the outer lamella the embryo, which originally lay in the follicle (Fig. 211 *A*), and then shifted forward into the dilated oviduct (Fig. 211 *B*), protrudes into the atrial cavity of the parent, in which from this time it lies freely.

We have already seen (p. 424) that a compact cell-mass is attached to the lower surface of the embryo (Fig. 212, *p*); this, which represents the first rudiment of the placenta, is derived from the transformed cell-material of the egg-follicle. The outer lamella of the brood-sac now shrinks completely back over this cell-mass, and finally, as a constricted funnel-like annulus, surrounds and strengthens the connection between the rudiment of the placenta and the parent (Fig. 214, *a*). The placenta-rudiment would lie exposed, after the withdrawal of the outer lamella, were it not covered by a thin ectodermal layer of the embryo (Fig. 214, *ec*), which develops as the brood-sac is withdrawn. Through this circumcrescence of the placenta by an ectodermal lamella, which was not observed by SALENSKY, but of which we were able clearly to convince ourselves, the placenta is incorporated in the embryo and then appears enclosed in a capsule derived from the ectoderm of the embryo. The lateral walls of this capsule are formed by the thin lamella just mentioned; its upper wall or the so-called roof (Fig. 213, *t*), on the contrary, is yielded by the thick ectoderm-layer, the origin of which was traced above (p. 425). [This is of follicular origin according to KOROTNEFF (No. XX*a*.).] On its under side the ectodermal capsule of the placenta possesses an aperture through which the placental cavity communicates with the blood-vascular system of the parent. The placental cavity arises in the form of gaps or clefts in the placental tissue, which thus assumes a loose structure. Some of the cells of this originally compact tissue now form a layer of large, swollen cells in contact with the ectodermal capsule, while others form a granulated trabecular network traversing the cavity of the placenta (Figs. 213 *B*, 214, *x* and *z*). The cavity of the placenta, therefore, as **Leuckart** rightly pointed out (No. 98), communicates with the blood-vascular-system of the parent, but never with the body-cavity of the embryo, from which it is always divided by the continuous ectodermal capsule of the placenta. Our own researches have here led us to differ from **Salensky**, according to whom the placental cavity appears as a part of the body-cavity of the embryo.

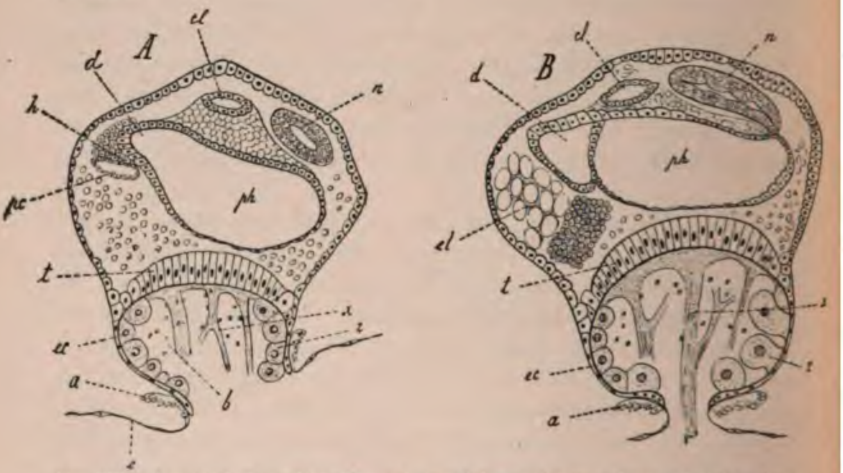

FIG. 214.—Longitudinal sections through two later embryonic stages of *Salpa democratica-mucronata* (after **Salensky**, somewhat altered). *a*, contracted outer lamella of brood-sac; *b*, blood-sinus within the placenta; *cl*, atrium or peribranchial cavity; *d*, rudiment of the alimentary canal; *e*, epithelium of the atrial cavity of the parent; *ec*, ectodermal covering of the placenta; *el*, elaeoblast; *h*, rudiment of the heart; *n*, nervous system; *pc*, pericardial vesicle; *ph*, pharyngeal cavity; *t*, so-called roof of the placenta (basal plate); *x*, tissue of the placenta; *z*, marginal cells of the placental tissue.

The placenta is concerned in the nourishment of the embryo. In later stages it attains greater independence, its connection with the embryo becoming constricted (Fig. 216). The point at which the placenta is inserted lies on the ventral side of the embryo, between the two endostyle-folds. When the embryo separates from the parent, the placenta remains hanging to it; in the free-swimming solitary forms, a vestige of this organ is long visible as a small stalked body enclosed in the mantle-substance (**Leuckart**). The wound formed in the wall of the respiratory cavity of the parent when the embryo detaches itself is, according to **Leuckart**, closed by the remains of the brood-sac which can still be recognised for some time as a kind of corpus luteum. The embryo, at birth, passes out through the atrial aperture of the parent.

The development of the final shape of the body goes hand in hand with the development of the placenta. The embryo at first formed a cone projecting into the atrial cavity of the mother (Fig. 212), its principal axis corresponding to the future dorso-ventral axis. It now lengthens at right angles to this axis, *i.e.*, in accordance with its future longitudinal axis (Fig. 214). It soon becomes cylindrical and, after the *cellulose mantle* has developed, resembles a tetragonal prism. The mantle-substance develops in just the same way as in the Ascidians (p. 355). It arises on the outer surface of the ectoderm as a secretion into which single cells soon wander. Finally, the two conical processes characteristic of *Salpa democratica* (solitary form) develop (Fig. 262, p. 495).

The **nervous system** has been seen to arise as a solid ingrowth of the ectoderm.* This soon severs its connection with the latter, a cavity develops within it, and it becomes a vesicle characterised by its size and the thickness of its walls (Fig. 214, *n*). KOWALEVSKY (No. 96) was aware of the fact that this vesicle lengthens later and is indistinctly divided by constrictions into three consecutive parts which show a certain resemblance to the primary cerebral vesicles of the vertebrate embryo (Fig. 214 *B*, *n*). The anterior vesicle becomes closely connected anteriorly with the adjacent wall of the pharynx, and this connection which is at first solid soon develops a lumen which puts the neural cavity into communication with the pharyngeal cavity. The canal thus formed is the first rudiment of the future ciliated pit (Fig. 216, *fl*). While this organ develops further, the walls of the ganglionic vesicle thicken, it shortens, its lumen disappears and the vesicular rudiment thus gradually assumes the character of the definitive ganglion of the adult. A conical process rising on the dorsal side of the ganglion on which three accumulations of pigment appear represents the rudiment of the eye.

Further details as to the development of the **eye** have recently been published by METCALF (No. 99) and BÜTSCHLI (No. 94).† The eyes seem to develop differently, not only in the different species but also in the solitary and the colonial forms of the same species. According to BÜTSCHLI, the simplest form

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* [See footnote, p. 425.—ED.]

† [See also METCALF in Brooks' Monograph (No. I.), and GÖPPERT No. 94*a*).—ED.]

of eye is a mound-like swelling of the brain (Fig. 215 *A*); at the sides of this swelling are arranged the pigment-cells while, from the centre, closely packed rod-bearing cells are found radiating towards the surface, the nerve-fibres being connected with the inner ends of the rods. In this eye, the rods are therefore turned directly towards the source of light. In other forms, the rudiment of the eye becomes differentiated into three parts which either remain united in the shape of a horse-shoe, or form three entirely distinct eyes, the unpaired median eye retaining the original simple condition (Fig. 216 *B*, *a*) while the two lateral eyes are formed on the plan of an inverse eye (*b*), *i.e.*, the rods are directed away from the surface and the nerve-fibres are connected with their outer ends. BÜTSCHLI, assuming an optic vesicle which cannot be observed, homologised the median non-inverted eye with the cephalic eye of the Vertebrates, and the lateral inverted eyes with the paired eyes of the Vertebrates, but, independent of this theoretical vesicle, the structure of the lateral eye of the Ascidian larva seems directly to suggest the paired vertebrate eyes by the fact that the rods are directed towards the cerebral cavity (see, however, the objections raised by METCALF, No. 99*a*, and GÖPPERT, No. 94*a*).

FIG. 215.—Diagram of the eye of a Salp (after BÜTSCHLI). *A*, typical single eye; *B*, typical tripartite eye. *a*, median part, *b*, lateral part of the tripartite eye; *n*, nerve-fibres; *p*, pigment-cells; *r*, retina.

The first rudiment of the **pharynx** and the development of the gill have already been described (p. 426). The wall of the pharyngeal cavity is formed by a simple epithelium, the cells are either cubical or somewhat flattened. The rudiment of the *endostyle* (hypobranchial furrow) appears in the form of paired folds of this epithelium originating at some distance from each other (Fig. 216, *es*); these shift towards one another later and then form the boundaries of a hypobranchial furrow which runs from the peripharyngeal bands to near the entrance of the oesophagus. The rudiments of the peripharyngeal bands which run towards the anterior end of the gill from the anterior end of the endostyle, encircling the aperture of the respiratory cavity, first appear as similar prominences. The rudiments of the branchial and atrial apertures (Fig. 216, *i* and *e*) appear only in later stages in the form of transverse depressions of the ectoderm which break through into the pharynx and atrial cavities. The rudiment of the atrial aperture originally lies almost at the centre of the dorsal side of the body (Fig. 216), but later, as the part of the body known as the nucleus decreases in size, it shifts further back.

The rudiment of the **alimentary canal**, in the strict sense of the term (Fig. 214 *B*, *d*), originally forms a posteriorly directed diverticulum of the pharynx. This caecum becomes divided later by two folds rising into it from below into three spaces (Fig. 216, *oe*, *m*, *ed*), the anterior space being the rudiment of the oesophagus, while the posterior space represents the intestine. The middle space is the rudiment of the stomach-caecum. The intestine curves upward towards the left, till its blind end comes into contact with the atrial wall, perforation leading later to the formation of the anal aperture.

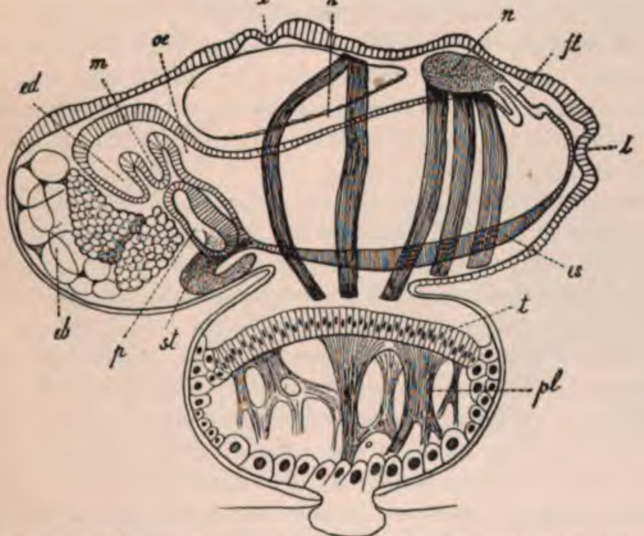

FIG. 216.—Later embryonic stage of *Salpa democratica-mucronata* (after SALENSKY). *e*, atrial aperture; *eb*, elaeoblast; *ed*, intestine; *es*, endostyle; *fl*, ciliated pit; *i*, branchial (oral) aperture; *k*, gill; *m*, stomach-caecum; *n*, ganglion; *oe*, oesophagus; *p*, pericardial sac; *pl*, placenta; *st*, stolon; *t*, so-called roof of the placenta (basal plate).

It has been shown that the mesoderm (Fig. 213 *B*, *ms*) spreads out over the right and left sides of the embryo in the form of two lamellae in close contact with the entoderm. These lamellae, according to LEUCKART, yield the *muscle-hoops*, a kind of fenestration taking place in the lamellae and separating the mesoderm-bands which correspond to the different hoops. The transversely striated contractile substance develops later in the muscles. The *heart* also, according to SALENSKY, owes its origin to the mesoderm, *i.e.*, to the lamella lying on the right side of the body, which is continued back over the posterior end of the wall of the branchial cavity, and there forms a vesicle (Fig. 216, *p*) in which we recognise the first rudiment of the pericardial vesicle.* A swelling of the thickened dorsal wall of the vesicle, which projects into its lumen, and which, though at first solid becomes hollow later, is the rudiment of the heart proper; this consequently develops in just the same way as in the Ascidiacea (p. 370). The blood-vessels apparently arise as spaces within the gelatinous connective-tissue which, in later stages, fills the primary body-cavity. It should be mentioned that, in the *Salpidae*, as TODARO has pointed out and figured, the blood-vessels seem to be lined throughout with a cellular intima (Fig. 207 *B*, *b*). In this respect this group would seem to differ from the Ascidiacea, in which, according to VAN BENEDEN and JULIN, such an intima is wanting (*cf.* pp. 363 and 371).

The *elaeoblast* (Fig. 216, *eb*), the rudiment of which has already been described (p. 425), attains its full development only in the later stages of embryonic life, and, after the birth of the embryo, undergoes gradual degeneration [by phagocytosis, according to KOROTNEFF (No. XIX.)]. It is a mass of large polygonal cells, which are filled with reserve nutrition. The remarkable resemblance between the elaeoblast and the degenerating larval tail of *Doliolum* (p. 388) caused SALENSKY to assume that this problematical organ is the homologue of the tail and the chorda of the Ascidian larva. But the presence of the rudiment of the elaeoblast, as we shall see in the buds of the *Salpidae* and of *Pyrosoma*, is not very favourable to this view. Physiologically, the elaeoblast is probably, as LEUCKART suggests, a reservoir of food-material, which is gradually used up as the embryo develops.

At a later stage of development the rudiment of the stolon can be seen (Fig. 216, *st*). This consists first of a diverticulum of the pharyngeal wall lying at the posterior end of the endostyle, and is turned toward the left side of the body. The ectoderm soon bulges over this entodermal diverticulum. The space between the two layers is, according to SEELIGER (No. 105), filled with mesenchyme-cells, the short conical stolon thus consisting of three germ-layers (p. 495).

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* [According to KOROTNEFF (No. XVIII.), the pericardium arises as in other Tunicates as a diverticulum of the pharynx.—ED.]

B. Forms with Covering Folds.

The development of the forms belonging to this type (*S.* (*Cyclosalpa*) *pinnata*, *S. africana-maxima*, *S. runcinata-fusiformis*, *S. punctata*) differs in many essential points from that of *S. democratica-mucronata*. The principal distinction consists in the presence in the former of an external covering which after the degeneration of the primary brood-sac (present also in *S. democratica-mucronata*), forms a secondary sac investing the embryo, and in the peculiar development of the placenta. The development of the organs also appears to follow another type.* The forms just mentioned seem to agree fairly well in their development, which has been studied by many zoologists, especially by Todaro, Barrois and Salensky, and more recently by Brooks (No. I.), Heider (No. XIII.), and Korotneff (Nos. XX., XX*a*., and XXI*a*.). The following account relates chiefly to *S. pinnata*, a comparatively well-known form.

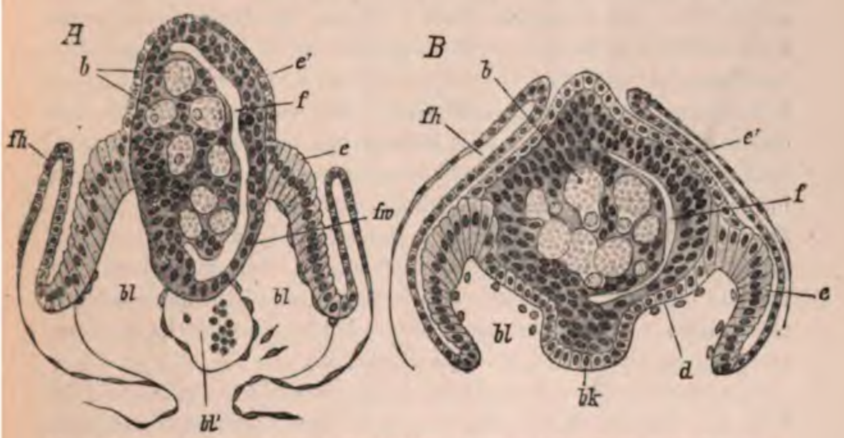

Fig. 217.—Two ontogenetic stages of *Salpa pinnata* (after Salensky) forming a sequence to Fig. 210 *B*. *b*, blastomeres; *bk*, "blood-forming bud"; *bl*, blood-cavities in the placenta; *bl'*, median blood-sinus; *d*, roof of the placenta (basal plate); *e*, lower part of the epithelial prominence, known later as the placental membrane; *e'*, upper part of the epithelial prominence (Salensky's ectoderm-germ); *f*, follicular cavity; *fh*, covering fold; *fw*, follicle-wall.

Starting with the embryonic development of *S. pinnata* at the stage depicted in Fig. 217 *A*, we find conditions in fairly close agreement with those described in connection with *S. democratica*. The embryo consists of large and of small cells. The protoplasm of the large cells (*b*) breaks up in a peculiar way into polygonal portions

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* [See footnote, p. 423 and p. 445.—Ed.]

which must be regarded as the direct descendants of the blastomeres. These seem to multiply little, but, up to the stage at which the organs begin to develop, continue to be seen in the embryo (Fig. 219 *A*, *b*). The significance of these parts and their further fate are obscure. The numerous small cells which form the greater part of the embryo are all regarded by SALENSKY as immigrated follicle-cells, but we think ourselves justified in assuming, with TODARO, that they are partly derived from the blastomeres and are only partly immigrated follicle-cells. The latter cells disintegrate, while the former take an essential share in the formation of the embryo (p. 420 and footnote, p. 421).*

The embryo lies in a sac (Fig. 217 *A*, *fw*) which is derived from the union of the follicle and the dilated oviduct. The wall of this sac has been described in *S. democratica-mucronata* as the *inner lamella of the brood-sac*. At the posterior end of this sac a thickening is soon seen in the forms now under consideration; this becomes more and more distinct (Fig. 217 *B*, *bk*), and is to be traced back to the transformed wall of the follicle. While, in *S. democratica-mucronata*, this thickening forms the rudiment for the whole of the placenta, in *S. pinnata* and related forms it represents a comparatively small part of that organ, which does not develop further but, in later stages, breaks up into its elements and mingles with the blood of the parent (or of the embryo ?). This part has been called by TODARO the *blood-bud* (*bottone ematogene*, Figs. 217 *B*, and 218, *bk*).

The embryo almost entirely fills the cavity of the brood-sac (Fig. 217, *f*). On one side, it appears to be continuous with the inner lamella of the sac. According to SALENSKY, this side represents the later haemal side of the body, so that we are able, even at this stage, to orient the embryo. [According to BROOKS (No. I.), this, on the contrary, marks the middle dorsal line of the embryo.]

The outer lamella of the brood-sac (Fig. 217, *e* and *e'*) is derived from the thickened part of the atrial epithelium of the parent, which is pushed out into the atrium by the growth of the embryo beneath it, and which is called by SALENSKY the epithelial prominence (p. 417). Two parts can soon be distinguished in it. The upper part (*e'*), which covers the greater part of the embryo, consists of rather small low cells, while the lower part (*e*) is composed of deep columnar cells. This latter yields later the lateral walls of the placenta, and is called

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* [It is now generally believed that the embryo at the end of cleavage consists of two kinds of blastomeres, *i.e.*, large and small, the latter being in appearance indistinguishable from the kalymmocytes.—ED.]

by TODARO the *placental membrane* or *germoblastica* [the supporting ring of the placenta (BROOKS)].

A differentiation somewhat resembling that just described in the outer lamella is also found in the inner lamella (splanchnic layer of the follicle) which represents the transformed epithelium of the oviduct and follicle. The lower half of the lamella (Fig. 217 *B, d*), in this case, becomes connected with the thickened epithelium of the atrial cavity known as the placental membrane or supporting ring of the placenta (*e*), and forms the roof of the placenta (Fig. 218 *A*, *dp*), in the centre of which the "blood-bud" is attached. The placenta is thus hollow, its lateral walls (supporting ring, Fig. 218 *A*, *mp*) being yielded by the epithelial prominence of the atrium, and its roof (*dp*) by the inner lamella of the brood-sac, *i.e.*, by the follicle (placental portion of the follicle). The "blood-bud" (*bk*) hangs from the roof into the cavity which is part of one of the blood-channels of the parent. SALENSKY distinguishes in this cavity two communicating sinuses, an afferent and an efferent sinus, and, between these two, a third vascular space round the "blood-bud" (Fig. 217 *A*, *bl'*), the relations and significance of which are unknown.

The placenta, which, from the first, is a greatly swollen structure, now becomes constricted at its base (Fig. 218), and thus forms a stalked structure on the upper surface of which the embryo rests. It becomes saddle-shaped later, the parts lying at the sides of the embryo growing upward. This is why, in a horizontal section (Fig. 219) only the lateral parts of the placenta (*p*) are seen cut through. The actual relations of this organ are still very obscure.

While, in this way, the primary brood-sac undergoes essential alteration, a circular fold of the atrial epithelium grows up from the base of the epithelial prominence (Figs. 210 *B*, and 217, *fh*) and completely overgrows the placenta and the embryo (Fig. 218, *f*), and thus forms a new secondary brood-sac (embryo-sac) such as is not found in *S. democratica-mucronata*. This is known as the *covering fold* or *amnion*. It continues to grow upwards as a circular fold round the embryo, over which, however, it never fuses, but remains separated by a variable aperture through which the embryo eventually passes out into the atrium.

There are, in the different species, characteristic variations in the form of this fold. In *S. africana-maxima*, the aperture is elongate and the margins of the fold project and take the form of a semicircular crest; this is seen in cross-section in Fig. 221, *c*; in *S. fusiformis*, this crest is abruptly truncated. In *S. pinnata* and *S. punctata*, on the contrary, such a crest is wanting.

We have seen that the placenta is formed from the lower parts of the primary brood-sac, the upper halves of the outer and inner lamellae taking no part in it (Figs. 217 and 218). We are still quite in the dark as to the future fate of these latter parts, which cover the embryo like a cap. According to Barrois (No. 87) and Todaro (No. 110), they are cast off and disintegrate.

According to Salensky, on the contrary, they are retained by the embryo, becoming closely connected with it and participating in its formation. That part of the outer lamella (Fig. 217, *e'*) of the primary brood-sac, derived from the maternal atrial wall, which is not concerned in the formation of the placental membrane, is said to yield the ectoderm of the embryo (Fig. 218, *ec*),[*] and the upper half of the outer lamella, which consists of flat cells, has therefore been called by Salensky the *ectoderm-germ*. The inner lamella (Fig. 217, *fw*), on the other hand, which can be traced back to the transformed epithelium of the oviduct, is said to yield, together with those parts that are not used up for forming the roof of the placenta, chiefly the mesoderm-tissue of the embryo (Fig. 218); the enteric rudiments, however, are also said to originate in this layer. We must admit that we feel sceptical as to these statements. According to them, the embryo results from separate rudiments derived from various parts of the body of the parent. The epithelium of the atrial cavity of the latter would yield the ectoderm, the oviduct, a part of the mesoderm and the enteric rudiments, while the rest of the embryo would be derived from immigrated follicle-cells (for, according to Salensky, the blastomeres take no part in the building up of the embryo, p. 421). We are inclined to think that errors of observation or of interpretation must here have crept in. [See editorial notes, pp. 420-425].

At the stage when we should expect the development of the germ-layers,[†] and the first rudiments of the organs, there is a considerable gap in our knowledge. We, at least, have been unable, from the very fragmentary statements of the stages that follow those described above, to obtain any clear idea of these processes of development which we desire to compare with the facts known in connection with the ontogeny of the other Tunicates or that of other animals.

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[*] [This layer, (*e'*) the epithelial capsule of Brooks, is apparently only a temporary protective membrane which disintegrates at a later stage. It takes no part in the formation of the ectoderm, which is, on the contrary, derived from the blastomeres (Brooks, Heider and Korotneff).—Ed.]

[†] In connection with the formation of the germ-layers in the *Salpidae*, special stress is to be laid on a "gastrula-stage" observed by Barrois (No. 87), in which an invagination is found on the lower side of the embryo, that turned towards the placenta.

[According to Brooks, the stage in *Salpa* corresponding to the gastrula of the Ascidians is to be sought in a stage like that given in Fig. 217, the cavity of the follicle, which becomes the body-cavity, being the cleavage-cavity, and the blastopore coinciding with the attachment of the central mass of blastomeres and follicle-cells to the inner layer of the brood-chamber. The segmentation of the egg is much retarded, but the gastrula is planned out in follicle-cells. This view is not accepted by other observers.—Ed.]

In the next stages we find ourselves on firmer ground (Fig. 218 *A*), the most important organs having already developed. This stage is characterised by the appearance of a cavity which, from its relations to the rudiments of organs (corresponding with those described for *S. democratica-mucronata*), we may regard as the body-cavity. Into this cavity, a club-shaped mass of cells, the early rudiments of the organs, hangs down from the upper surface of the embryo. The pericardial rudiment (*pc*) is, however, distinguished by being further attached at its lower end.

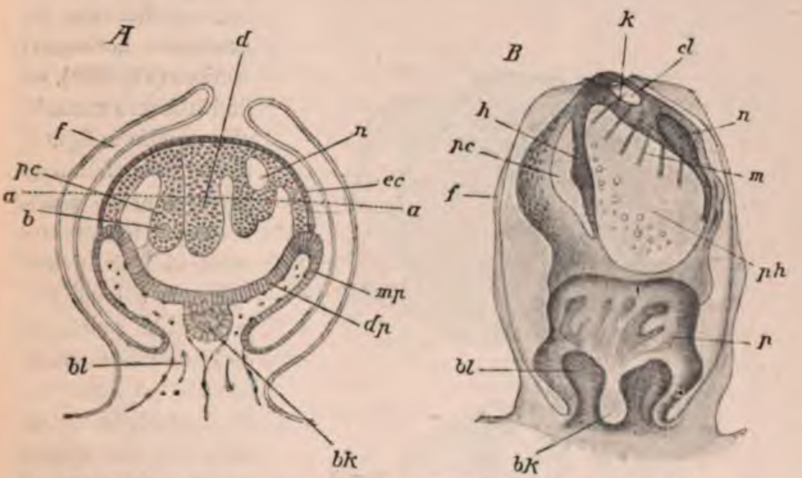

FIG. 218.—Two ontogenetic stages of *Salpa pinnata* (after SALENSKY). *A*, diagrammatic median section of a younger stage combined from various figures by SALENSKY; *B*, older stage. *b*, blastomeres; *bk*, "blood-forming bud"; *bl*, blood-spaces in the placenta; *cl*, atrial cavity; *d*, enteric rudiment; *dp*, roof of the placenta; *ec*, ectoderm; *f*, covering fold; *h*, rudiment of heart; *k*, gill; *m*, muscle-hoops; *mp*, placental membrane; *n*, rudiment of the nervous system; *p*, placenta; *pc*, pericardial rudiment; *ph*, pharyngeal cavity.

This cavity has been called by SALENSKY the *secondary follicle-cavity*. Since, according to this author, only some of the rudiments of the internal organs (the nervous system and the pericardial rudiments) are formed from the inner cell-mass of the embryo, the body-wall (together with the rudiment of the intestine) being derived from the wall of the primary brood-sac; this cavity has, for SALENSKY, the same significance as the original cavity of the primary brood-sac (Fig. 217, *f*). The latter, which is called by SALENSKY the *primary follicle-cavity*, is said completely to disappear in those obscure stages which lead up to the stage now being considered, and to be replaced by a secondary follicle-cavity that appears in the same place.*

The **body-cavity** (SALENSKY'S secondary follicle-cavity) separates the rudiments of the organs laterally and ventrally from the body-wall. In the latter we can now distinguish an external layer, the ectoderm (Fig. 218 *A*, *ec*), from an inner layer, the cells of which wander into the body-cavity, filling it with a mesenchyme. We are consequently enabled to recognise in this inner layer a part of the mesoderm-rudiment.

If, in order to obtain a correct idea of the relative positions of the organ-rudiments, we examine horizontal sections (Fig. 219), we find in them a remarkable cruciform figure, the enteric rudiment (*d*) forming the transverse portion of the cross, while the neural rudiment (*n*) and the pericardial rudiment (*pc*) form the longitudinal portion. It is characteristic of the Salps now under consideration that the enteric rudiment (*d*) originally appears to develop chiefly in a transverse direction. At the same time, it is evident that the first parts of the enteric rudiment (pharynx) to develop are its future lateral portions so that there

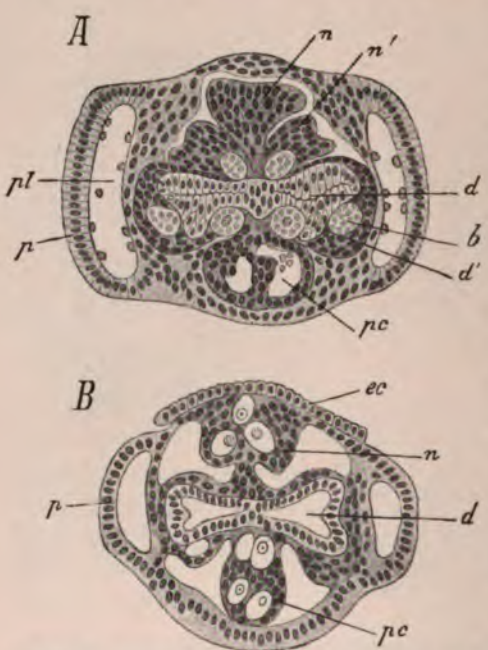

FIG. 219.—Horizontal sections through two embryos of *Salpa pinnata*, made in the direction of the line *a-a* in Fig. 218 *A* (after SALENSKY). *b*, the blastomeres; *d*, enteric rudiment; *d′*, layer covering the intestine; *ec*, ectoderm; *n*, middle part, *n′*, lateral parts of the nerve-rudiment; *p*, lateral parts of the placenta; *pc*, pericardial rudiment; *pl*, blood-cavities of the placenta.

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* [BROOKS considers that this second cavity is probably the original cavity of the follicle opened a second time by the growth of the surrounding parts. He would thus derive the body-cavity in *Salpa* from the primary follicular cavity, the latter he believes to represent the cleavage-cavity of the Ascidiacea. —ED.]

is at first a paired rudiment of the pharynx only slightly connected in the median line. According to SALENSKY, the first recognisable rudiments of this system of organs are found as two entirely distinct accumulations of cells derived from the wall of the primary brood-sac (wall of the follicle).* In a similar way, in *S. democratica-mucronata* also, the rudiment of the pharynx develops in the form of paired cavities (p. 426). Two layers may be distinguished in the enteric rudiment; an inner layer consisting of deep cylindrical cells (entoderm) and an external layer, the so-called covering layer of the intestine (*d'*), in which a few larger blastomeres (enteric blastomeres, Fig. 219 *A*, *b*) can still be recognised and which may perhaps be considered as belonging to the mesoderm.

In horizontal sections the rudiment of the nervous system has at first a curious trilobate form (Fig. 219 *A*), but this is less marked in later stages. TODARO (No. 107) has given to the two paired lobes (*n'*) the name of the *dorsal disc*, and regards them as belonging to the mesoderm. He considers them to be provisional and homologous to the chorda. The pericardial rudiment (*pc*) is distinguished by the regular arrangement of the blastomeres found in it, two columns of the latter in which the cells are arranged in pairs running through it. Both the pericardial rudiment and the neural rudiment project slightly at their upper ends above the surface of the embryo (pericardial and neural projections, Fig. 220, *n'*); in later stages a dorsal longitudinal furrow runs between them, but as to the significance of these structures we are still in the dark.

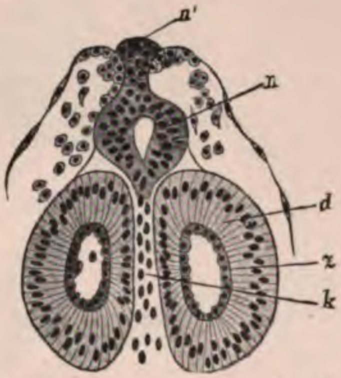

FIG. 220.—Horizontal section through an embryo of *Salpa pinnata* (after SALENSKY). *d*, the two atrial diverticula of the enteric rudiment (gill-slits of BROOKS); *k*, rudiment of gill; *n*, neural rudiment; *n'*, so-called neural projection; *z*, cells within the lumen of the intestine (invaginated somatic layer of the follicle, BROOKS).

In these stages the embryo lies like a flat disc on the placenta (Fig. 218 *A*). Only its upper surface appears covered by the cap-like ectoderm-layer (Fig. 221, *ec*). It is not clear in what way the basal

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* [See footnote, p. 426. The above account of the origin of the pharynx appears to be quite inaccurate. In all probability the cavity described by SALENSKY was the atrial cavity, but even that structure is not derived from the wall of the follicle but from the ectodermal blastomeres.—ED.]

boundary between the embryo and the placenta arises. In the stage now being considered the body-cavity seems to be separated from the placental cavity only by the lamella which was mentioned above as the roof of the placenta (*dp*), but we do not know to what extent this lamella participates in the formation of the embryo.

Further development leads to the complete disappearance of the primary body-cavity which becomes filled in the way mentioned above by a mesenchyme (Fig. 222, *ms*), the elements of which give origin not only to the connective tissue but also to the blood-corpuscles, the

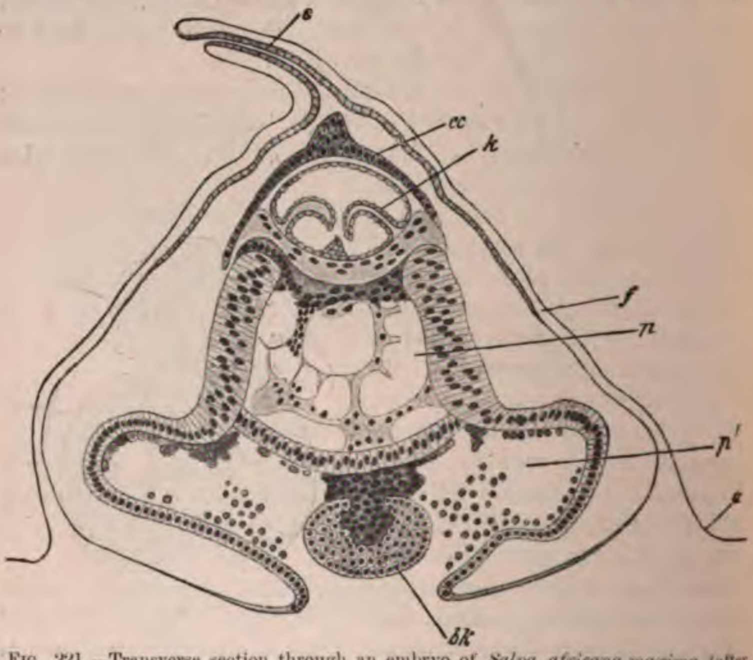

FIG. 221.—Transverse section through an embryo of *Salpa africana-maxima* (after SALENSKY). *a*, epithelium of the respiratory cavity of the parent; *bk*, "blood-bud"; *c*, crest of the covering fold; *ec*, ectoderm of the embryo; *f*, covering fold (embryo-sac); *k*, paired fold-like rudiment of the gill; *p*, upper cavity between the placenta and the embryo; *p'*, actual placental cavity.

body-musculature and the elaeoblast. As the embryo grows further a marked increase in length takes place, and it thus approaches the adult form, whereas at first its transverse diameter was greater than its longitudinal diameter (*cf.* Fig. 218 *B* with Fig. 224). This change in shape is specially connected with the change both in shape and relation of the pharyngeal cavity. This rudiment, which may be sidered as consisting of two sacs connected by a narrow transverse bridge, first elongates. The trabecula, which is retained between the two diverticula of the developing respiratory cavity (Figs. 220, *d*, and 222, *cl*) that run upward, represents the rudiment of the gill (*k*) which, when the diverticula unite over it, becomes detached from the dorsal wall of the respiratory cavity.*

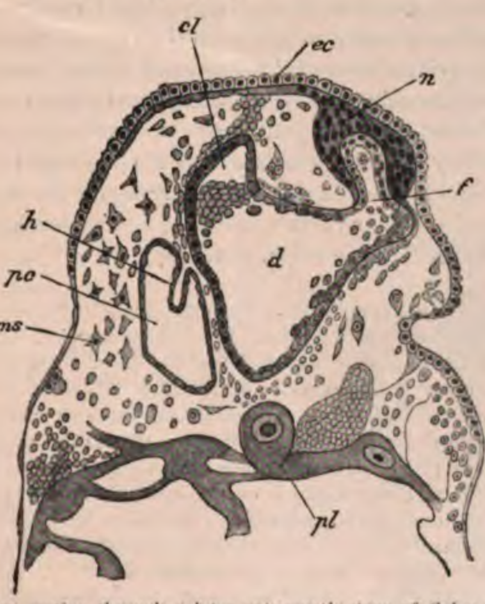

FIG. 222.—Median section through a later ontogenetic stage of *Salpa pinnata* (after SALENSKY). *cl*, atrial diverticulum of the enteric rudiment; *d*, enteric rudiment (rudiment of the respiratory cavity); *ec*, ectoderm; *f*, ciliated pit; *h*, rudiment of heart; *ms*, mesenchyme; *n*, ganglion; *pc*, pericardium; *pl*, tissue of the placenta.

The part of the respiratory cavity which is to be regarded as the cloacal cavity is not, consequently, according to SALENSKY, derived from an independent rudiment, but arises through the formation of diverticula from the rudiment of the pharyngeal cavity. TODARO

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* [The recent observations of BROOKS, HEIDER and KOROTNEFF are so absolutely antagonistic to those of SALENSKY, that we must now regard the above account of the origin of the pharyngeal and atrial cavities and of the gill as inaccurate. HEIDER and KOROTNEFF are fairly in agreement, and together they differ in some important points from BROOKS. All three are, however, agreed that the atrium develops first, and is probably ectodermal in origin. The pharynx, on the other hand, appears as a cleft in the embryonic mass which becomes lined with entodermal blastomeres. The gill arises from the septum between these two cavities by the breaking down of the lateral parts of this septum, the clefts thus formed being the gill-slits. SALENSKY'S view that the gill and atrium of *Salpa* are not homologous with the similarly named structures in the other Tunicates may be regarded as disproven.—ED.]

(No. 113), on the contrary, states that, in *Salpa*, the cloacal cavity is derived independently from the ectoderm, two ectodermal invaginations that develop one after the other taking part in its formation. An ectodermal growth first develops on the dorsal side, behind the cerebral vesicle, and this then becomes hollow and forms a vesicle which is the rudiment of the primary cloacal vesicle. This vesicle becomes applied laterally to the epithelium of the respiratory cavity (pharyngeal cavity), but remains separated from the latter medianly by a mass of mesenchyme. The median part becomes the future gill, and in the lateral part, at a later stage, the two large gill-clefts break through. Only after the gill is completely developed does a second ectodermal invagination appear and bring about the communication of the cloacal vesicle with the exterior (*cf.* the development of the cloacal cavity in *S. democratica*, p. 426).*

According to SALENSKY, the development of the gills varies considerably in the different species of the *Salpidae*. In *S. africana* and *S. fusiformis* the gill develops through a median fusion of two horizontal folds which rise from the lateral walls of the respiratory cavity (Fig. 221, *k*).† The figure of *S. africana*, in which this is depicted, serves at the same time to illustrate some other peculiarities occurring in this species. We see the upright crest (*c*) of the covering fold (p. 435) in cross-section, and may observe that the connection of the embryo with the placenta is here brought about in a manner different from that in *S. pinnata*, a large cavity (*p*) here being intercalated between the embryonic rudiment and the roof of the placenta. The origin and significance of this cavity are, however, still somewhat obscure.

According to SALENSKY, the rudiment of the pharyngeal cavity is not closed completely, but, at a certain stage, shows a dorsal aperture through which a considerable number of mesenchyme-cells wander into the respiratory cavity [probably entodermal blastomeres]. These partly fill the latter and become applied to the wall of the intestine from within; later, however, they disintegrate and are absorbed (Fig. 220, *z*).

The development of the actual enteric canal (as an outgrowth of the pharyngeal cavity), that of the endostyle, and of the oral and atrial apertures, seem to take place here in the same way as in *S. democratica-mucronata* (p. 430).

The rudiment of the nervous system (Fig. 218, *n*), which arises, as we have seen (p. 439), as a trilobed cell-strand (Fig. 219 *A*, *n*, *n'*), now

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* [TODARO's account, in its most essential features, is in accord with that of BROOKS.—ED.]

† [KOROTNEFF (No. XXI*a*.) supports SALENSKY in his account of the origin of the gill in *S. africana-maxima*.—ED.]

begins to assume a simpler form (Fig. 219 *B*, *n*); at still later stages it is found as a cell-mass running obliquely downwards and forwards; within this mass a cavity appears which communicates anteriorly with the respiratory cavity (Fig. 222). The part lying nearest to the aperture of the central canal represents the rudiment of the ciliated pit (*f*), while the blind end that is directed backward and upward forms the ganglion proper (*n*). In the course of development these two sections of the neural rudiment become more sharply marked off from one another by a constriction. At the same time, in the ganglionic part of the rudiment, the central canal becomes segmented, breaking up into three consecutive cerebral vesicles, a condition first noticed by **Kowalevsky**, and similar to that seen in *S. democratica* (p. 429). In later stages the cerebral rudiment becomes completely separated from the ciliated pit, and the two rudiments shift apart, although they seem still to remain connected by a nerve-strand that runs forward from the brain to the ciliated pit. The central cavity of the cerebral rudiment disappears, and the interior of the rudiment then seems filled with punctate nervous tissue (**Leydig**'s "Punktsubstanz"). A process running towards the surface leads to the development of the eyes, in which single cells of the ganglion become changed into elements sensitive to light, while other cells of the most superficial layer become filled with pigment (p. 430). No details are known of the development of the paired auditory vesicles which lie in contact with the brain, and were first observed by H. **Müller** and further described by **Todaro** (No. 107). The ciliated pit, by the folding of its walls, assumes a complicated form approaching that of the same organ in the adult (Fig. 214, *B*, *fl*).

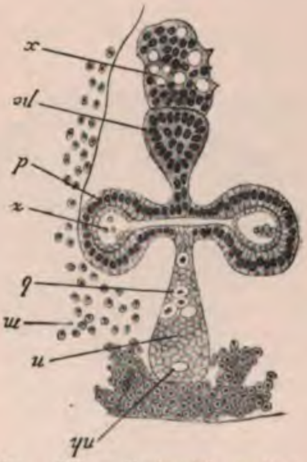

Fig. 223. — Horizontal section through an embryo of *Salpa pinnata* (after **Salensky**). *b*, blastomeres; *d*, enteric rudiment; *m*, mesenchyme-cells; *n*, rudiment of the nervous system; *nh*, neural cavity; *pc*, pericardial rudiment; *x*, sub-pericardial cell-strand; *z*, cells in the lumen of the pharynx (atrium, **Brooks**).

The pericardial rudiment (Figs. 218, 219 *pc*), which is originally a cell-strand running from above downward, divides into two parallel strands (Figs. 223, 224 *A*); the anterior strand, near the enteric rudiment, is known as the pericardial rudiment (*pc*) in the strict sense of the term, while the posterior strand has been called by SALENSKY the *sub-pericardial strand* (Fig. 224 *A*, *x*, *sp*). In the further course of development, the posterior strand breaks up into its elements, which are probably transformed into blood-corpuscles. The pericardial rudiment proper, which was originally a solid strand, becomes a tube known as the pericardial sac, the superficial cells uniting to form an epithelial wall, while the inner cells lose their cohesion and, as it appears, disintegrate. The heart (Fig. 222, *h*) develops in a way similar to that described for the other Tunicates, as an invagination of the wall of the pericardial sac (*pc*). The lumen of this invagination then becomes the cavity of the heart.

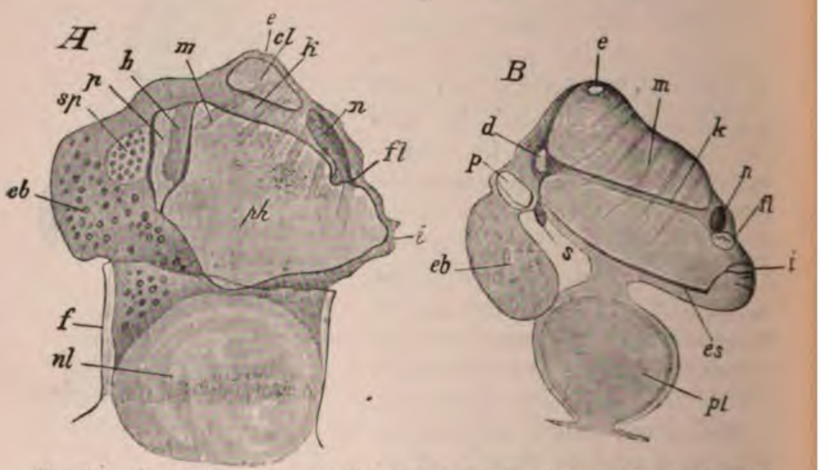

FIG. 224.—Two older embryos of *Salpa pinnata* (after SALENSKY). *cl*, cloaca; *d*, enteric rudiment; *e*, atrial aperture; *eb*, elaeoblast; *es*, endostyle; *f*, covering fold; *fl*, ciliated pit; *h*, heart; *i*, branchial aperture; *k*, gill; *m*, muscle-hoops; *n*, nervous system; *p*, pericardial sac; *ph*, pharynx; *pl*, placenta; *s*, proliferating stolon; *sp*, sub-pericardial cell-strand.

The muscle-hoops arise from the mesenchyme-cells present in the primary body-cavity. Some of these become arranged on the outer surface of the wall of the respiratory cavity to form a layer (muscle-plate) in which, at an early stage, thicker and thinner transverse zones can be distinguished. The fenestration observed by LEUCKART (p. 431), by means of which the hoops are separated from one another (Fig. 224, *m*) takes place in the thinner zones. The muscle-layer is said first to develop on the dorsal side of the body and to proceed thence towards the ventral side. It should be mentioned that a cavity appears within each of the developing muscle-hoops and these cavities have been compared by SALENSKY with those in the primitive muscle-plates of the Vertebrates (cavities of the primitive segments).

The *elaeoblast* (Fig. 224, *eb*) seems to be derived from cells of the mesenchyme.

The development of the other species of *Salpa* that are provided with the enveloping fold (*S. africana*, *S. fusiformis* and *S. punctata*) seems to follow essentially the same course as that of *S. pinnata*. Judging from the very fragmentary statements as to the ontogeny of these forms (BARROIS, No. 87, SALENSKY, No. 104), however, there appears to be considerable variation in points of detail [see HEIDER (No. XIII.) and KOROTNEFF (Nos. XX., XX*a*., and XXI*a*.)].

General Considerations on the Embryonic Development of the Salpidae.

[The embryonic development of the *Salpidae* is still, in spite of the recent investigations of BROOKS, HEIDER and KOROTNEFF, anything but satisfactorily understood. The confusion arising from the immigration of the kalymmocytes and the difficulty of discriminating between these cells and the smaller formative blastomeres of HEIDER and KOROTNEFF, still requires to be swept away before we can make any satisfactory comparisons of the development of *Salpa* with that of other Tunicates. When, further, we compare the monographs of the two last authors with that of BROOKS, we must feel that additional confirmation of one or other of the views put forward by these writers is necessary before one of them is finally accepted. It is obvious, however, that we are dealing with a highly specialised form of development which has possibly arisen in connection with the viviparous habit of *Salpa* and has been further complicated in connection with the peculiar life-history of this form.]

The embryo undergoes direct development in accordance with its retention during the whole embryonic and larval periods within the body of the parent. We have already seen a similar omission of metamorphosis among the Ascidiacea in the *Molgulidae*. The *Salpidae* in this respect show a more specialised condition in so far as the embryo becomes closely connected with the tissues of the parent, and a placenta develops for its nourishment. Since we may, with some probability, derive the *Salpidae* from the attached Ascidia-like forms, we might be tempted to trace back the fixation of the embryo on the wall of the respiratory cavity of the parent to this original attached manner of life.

[Considerable stress was formerly laid upon the ontogenetic differences described by SALENSKY as occurring in the various species of *Salpa*, especially on the presence or absence of covering folds and on the structure of the placenta. According to SALENSKY, the covering folds were completely wanting in *S. democratica*, which form was further peculiar in the structure and origin of its placenta, inasmuch as this organ was said to arise, in part at least, from the ectoderm of the embryo, whereas, in other Salps, the embryo was covered by protective folds and the placenta was purely follicular, *i.e.*, maternal. Recent researches, especially those of BROOKS (No. XIII.) and KOROTNEFF (No. XVIII.), tend to show that this distinction was greatly overrated by SALENSKY, and that in all probability traces of covering folds exist in *S. democratica*, as BROOKS has shown is the case in *S. hexagona*. Further, when we remember that the folds are extremely transitory even in those forms in which they are best developed, it will be agreed that the division of the *Salpidae* into two groups on this character is inadvisable, since such a division does not appear to involve any fundamental difference between the embryos.

In the matter of the placenta also, SALENSKY appears to have been in error and in all probability that organ is entirely follicular (maternal) in origin in every case (even in *S. democratica*, KOROTNEFF). Neither does there appear to be any essential difference in the structure of this organ in the two groups. Consequently, the more recent writers have ceased entirely from considering the development of the *Salpidae* as taking place along two distinct lines, regarding the differences rather as slight and unimportant modifications of one and the same type.]

The changes which occur towards the end of embryonic development have been well described in *S. pinnata*. When the embryo is approaching its final form, it passes through the dilated aperture of the enveloping fold into the respiratory cavity of the parent. The enveloping fold then draws back more and more (Fig. 224 *A*, *f*), soon leaving the placenta also free. The latter, at this stage (Fig. 224 *B*), becomes sharply marked off from the embryo, being finally connected with it merely by a narrow umbilical cord. This cord, as a rule, is short, but, in *S. scutigera*, it attains a considerable length. Finally, after the embryo has, for some time, carried on independent respiratory movements, it detaches itself altogether, with the placenta connected with it, from the respiratory wall of the parent and passes out at birth through the atrial aperture of the latter. Vestiges of the placenta and of the covering fold are retained for some time on the wall of the atrial cavity of the parent. The placenta attached to the embryo gradually decreases in size, but, even in somewhat well developed young Salps, can be recognised as a small stalked mass embedded in the mantle-substance and attached to the posterior half of the endostyle.

It has been pointed out that the development of the *Salpidae* is direct; a tailed larval stage such as is characteristic of the Ascidian does not develop. With this is connected the apparently complete absence of the chorda dorsalis. The absence of this provisional structure, although explained by the direct nature of the development, is nevertheless very remarkable, this organ having been considered as the typical feature of the Tunicate plan of organisation. To explain this fact, we might be tempted to assume that there are, among the Tunicates, forms only slightly removed from some primitive ancestor which did not possess a chorda, and in which, consequently, the development of this organ is not sufficiently established as a constant feature.*

SALENSKY holds that a rudiment of the larval tail is found in the Salp embryo in the elaeoblast, that problematical provisional organ (p. 432) to which TODARO (No. 107) no doubt erroneously attributes such a great significance in connection with the development of the proliferating stolon. The significance of this structure as a vestige of the larval tail seems to be rendered somewhat probable by a comparison with the tailed embryos of *Doliolum*. [During the development of this organ, however, there is no suggestion of an entodermal origin, if anything an ectodermal one is suggested. Functionally, the elaeoblast appears to be nutritive.]

Turning to the rudiments of organs, we must first trace the development of the respiratory cavity. In this we can always distinguish two separate cavities divided from one another by the gill which runs between them obliquely (Fig. 224, *k*). The anterior and ventral cavity known as the pharyngeal cavity (*ph*) is considered as the equivalent of the respiratory cavity of the Ascidian, while the posterior cavity which lies dorsally to the gill is regarded as the atrial cavity (*cl*). The two large apertures through which these two cavities communicate on either side of the gill are regarded as unusually dilated gill-clefts. In this view, which is favoured by the condition of the gill in *Doliolum*, this one pair of gill-clefts occurring in the *Salpidae* has been thought to arise by the fusion together of several smaller clefts. This view is opposed by VAN BENEDEN and JULIN (No. 10), according to whom only one pair of true gill-clefts develops in the Ascidians also, the many perforations of the wall of the gill which develop later being secondary structures (branchial stigmata, p. 367). The *Salpidae* in this case would, like the Larvacea, exhibit a very primitive character in the presence of a single pair of gill-clefts. TODARO (No. 113), who adopts this view on the whole, has extended it by explaining certain ciliated invaginations which are found arranged in rows at the sides of the gill in some Salps

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* We must, however, bear in mind that the body of the Thaliacean represents principally the pre-chordal region of the Ascidian larva.

(*S. pinnata*, *S. bicaudata*, etc.), as the homologue of the secondary gill-clefts in the Ascidians (branchial stigmata). We do not think there are sufficient grounds for such an explanation, since these invaginations, which were already known to FOL, may also be secondary acquisitions resulting from the need for increasing the respiratory surface. We have pointed out above that the condition of *Appendicularia* is probably not to be regarded as primitive.

Some statements as to the occurrence of a true coelom in the embryos of the *Salpidae* have still to be noticed. TODARO (No. 107) considers that the coelomic sacs originated through dehiscence taking place in a mesodermal layer surrounding the intestine. According to SALENSKY, a cavity first arises in each of the already distinct muscle-hoops, and this cavity also is considered as the equivalent of the coelom in the Vertebrates (*i.e.*, of the cavities in the primitive segment plates, p. 445).*

The origin of the pericardial sac may perhaps, according to SALENSKY, be traced back to the mesoderm, whereas, in the Ascidiacea, it is of entodermal origin (p. 368). [Entodermal according to KOROTNEFF, see footnote, p. 432].

II. Asexual Reproduction.

Asexual reproduction, both by fission and budding, is of wide occurrence among the Tunicata, and frequently leads to the formation of stocks. Before describing these reproductive processes, we must point out that the capacity for regeneration also occurs to a large extent in this class. The experiments made by LOEB and continued by MINGAZZINI have shown that solitary Ascidians (*Ciona intestinalis*) are capable of regenerating distinct portions of the body. If, for example, the central nervous system is removed artificially, it can be regenerated. In some cases, similar processes of regeneration seem to occur normally. This was observed by DELLA VALLE (No. 70) in colonies of *Diazona violacea*, in which, under unfavourable conditions, the anterior part of the body (the branchial sac and other organs) degenerate in the individuals of the colony. There is then found in this region an accumulation of yellow mesoderm-cells filled with nutritive material. The organs of the posterior half of the body

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* [BROOKS (No. I.) considers the transitory body-cavity of *Salpa* as a re-opening of the follicular cavity, and this latter he attempts to homologise with the cleavage-cavity of the normal gastrula. He thus regards the body-cavity of *Salpa* as the equivalent of the primary body-cavity (cleavage-cavity), and not as the secondary body-cavity (coelom proper). The cavity becomes filled later with mesenchyme-cells from which the muscle-hoops arise.—ED.]

(the intestinal loop and the heart) remain unaffected by degeneration, and, should the conditions of existence again become more favourable, this posterior half is able to regenerate the anterior part. An increase in the number of individuals forming the colony, by means of division, may even be connected with this regeneration. The yellow body then becomes lobate, and divides into several parts, each of which develops into a new Ascidian. The details of these interesting processes are, however, still unknown.

The occurrence of such far-reaching regenerative processes and the capacity for asexual reproduction in the Tunicata at first sight seems surprising, when we take into account their comparatively complicated organisation and their near relationship to the Vertebrata. We must, however, remember that the same capacity is found in the Annelida and the Echinoderma, groups which, in the condition of their organisation, may at least be compared with the Tunicata.

1. Social and Composite Ascidians.

The asexual reproduction which takes place in these groups is usually called budding. In the *Polyclinidae*, however, asexual multiplication takes place through the segmentation of the post-abdomen. This kind of reproduction, therefore, must, strictly speaking, be defined as transverse fission, and must be considered as distinct from budding.

A. Reproduction through Transverse Fission.

This is the kind of multiplication which was defined by GIARD (No. 57) as "bourgeonnement ovarien" and which has become better known through the researches of KOWALEVSKY (No. 61) in connection with *Amaroucium proliferum*.

[Since this description was published, further investigation of the budding processes in the composite and the social Ascidians has shown us that, while the account given in the following pages is correct in so far as it derives all the important internal organs from the inner sac, yet it obscures the actual state of affairs by always speaking of this structure as entodermal. While it is probably true that this inner sac is derived from the entoderm in most cases, yet, in one group, the *Botryllidae*, if the observations of HJORT (No. XIV.) and PIZON (No. XXVI.) are correct, this does not appear to be the case. These observers find that the stolon is purely ectodermal, the epicardia arising from the peribranchial sacs of the parent which, in the first instance, *i.e.*, in the larva, are of ectodermal origin. From this ectodermal epicardium, the bud arises much in the way described above. Thus we find that, in one family, all the organs of the bud are of ectodermal origin, while, in the majority, they arise from the entoderm.—ED.]

In the Mediterranean the larvae of *Amaroucium* hatch out in winter (Maurice and Schulgin, No. 39). After becoming attached, they multiply by transverse fission, and throughout the whole summer produce a succession of generations exclusively asexually, and in this way the colony grows. Towards the beginning of winter the youngest zooids cease to reproduce in this manner and develop sexual organs. The older asexual individuals of the colony die off, and their disintegrated remains are, according to Maurice's observations on *Fragaroides* (No. 40), taken in and digested by the mantle-cells which function as phagocytes (p. 356).

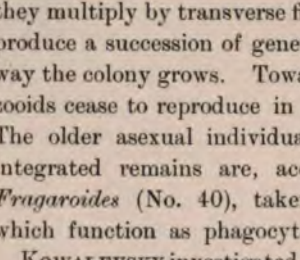

Fig. 225. — Transverse section through the post-abdomen of *Amaroucium* (after Kowalevsky). *b*, upper, *b′*, lower blood-sinus; *ec*, ectoderm; *m*, muscle-fibres in transverse section; *ms*, mesoderm-cells; *s*, partition-wall (epicardial sac).

Kowalevsky investigated the asexual reproduction that takes place in the primary individuals of the colony which result from the larva. He found in them (Fig. 227 *A*) three body-regions; thorax (*a*), abdomen (*b*) and post-abdomen (*c*). The post-abdomen is the elongated posterior region of the body in which the genital organs develop in the hermaphrodite individual (hence the term "bourgeonnement ovarien"). In a cross-section (Fig. 225) through the post-abdomen of an individual about to commence multiplying asexually, beneath the ectoderm, longitudinal muscle-bundles (*m*) are seen embedded in an extensive layer of mesoderm-cells (*ms*), these latter seeming to be filled with reserve nutritive material. The primary body-cavity (*b*, *b′*) which is continued upward into the thorax and the abdomen, appears divided by a transverse partition-wall (*s*) into a dorsal half (*b*) and a ventral half (*b′*). The partition-wall itself is hollow, and is nothing more than a flat diverticulum of the branchial sac arising from the latter immediately behind the posterior end of the endostyle, between it and the entrance of the oesophagus, which runs back through the whole of the post-abdomen and ends blindly near its posterior end. Here lies the heart (Fig. 227 *A*, *h*) curved into a crescent round the posterior end of the entodermal process just mentioned. This entodermal diverticulum is identical with the tube in *Clavelina* called by van Beneden and Julin (No. 10) the epicardial tube (see Fig. 173 *C*, *ep*, p. 375). It is also evidently the homologue of the entodermal or endostyle-process in the proliferating stolon of the *Salpidae* and *Pyrosoma*, but the relative position of the heart distinguishes this so-called epicardial tube in the *Polyclinidae* from the similar tube in the above-mentioned forms. The finer anatomical features of this tube have been described by MAURICE (No. 40) in *Fragaroides*. The tube forks at its anterior end; the two prongs of this fork have been distinguished by VAN BENEDEN and JULIN as epicardial tubes from the posterior undivided epicardial sac (see above, p. 370). The two epicardial tubes arise on either side of the median line behind the posterior end of the endostyle from the pharynx. The posterior end of the sac is, according to MAURICE, also forked (Fig. 226 *A* and *D*, *ep*). It embraces the crescent-shaped pericardial vesicle (*p*). In *Clavelina*, the epicardial tube enters into close relation to the heart (p. 370), completing the dorsal wall of that organ, but this is not the case, according to MAURICE, in the *Polyclinidae*. The heart-tube (*h*) in these latter is an invagination of the outer wall of the U-shaped pericardial vesicle (Fig. 226 *C* and *D*).

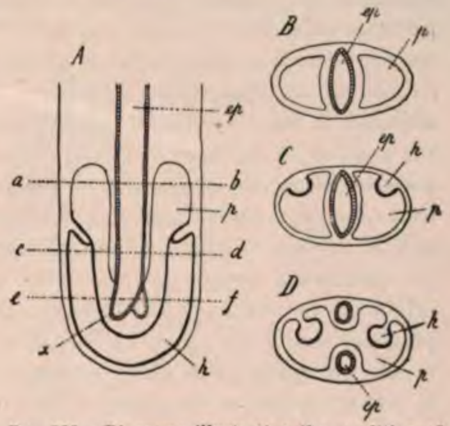

FIG. 226.—Diagrams illustrating the condition of the posterior end of the post-abdomen in *Fragaroides* (after MAURICE). *A*, side view; *B*, transverse section at the level *a-b*; *C*, at the level *c-d*; *D*, at the level *e-f*. *ep*, epicardial sac; *h*, heart; *p*, pericardial sac; *x*, forked end of the epicardial sac.

It should be mentioned that the paired apertures of the two epicardial tubes can be recognised only in larvae and in quite young asexually-produced individuals. They could not be found by KOWALEVSKY in the adult zooid, and MAURICE also has recently stated that the two epicardial tubes, although they approach close to the wall of the branchial sac, seem no longer to communicate with its cavity.

The epicardial sac in the *Polyclinidae* divides the body-cavity into a dorsal and a ventral half (Fig. 225, *b*, *b'*). Through each of these halves a blood-stream flows, but, in the dorsal half, the direction of the stream is opposed to that in the ventral half, the blood flowing in the one half towards the heart and in the other from the heart to the body. Similar conditions are found in the proliferating stolon of other Tunicates (*e.g.*, *Clavelina*, p. 370). In this form also, in the stolon, a dorsal blood-current is separated from a ventral current flowing in the opposite direction by the epicardial sac which forms a partition extending almost to the end of the stolon (Fig. 229, *x*). A transverse section through the proliferating stolon of *Clavelina* shows, on the whole, remarkable agreement with one through the post-abdomen of the *Polyclinidae*, though important variation is found in the position of the heart. In the *Polyclinidae*, the heart lies at the posterior distal end of the post-abdomen (Figs. 226 and 227), which, consequently, contains important organs belonging to the organisation of the parent (the heart and the genital organs). In *Clavelina*, the pericardial vesicle and the heart have shifted to the point of origin of the stolon (Fig. 173 *C*, p. 375). The heart lies at the proximal end of the epicardial sac, on the ventral side of the latter, so that the epicardial lamella, as shown above (p. 370), can be utilised in the formation of the dorsal wall of the heart. The proliferating stolon of *Clavelina* does not contain any important organ of the parent body, but is a process of the body dedicated exclusively to a sexual reproduction. The same is the case with the stolon of other Tunicates (Thaliacea and *Pyrosoma*, etc.). We might imagine the proliferating stolon as derived from the post-abdomen of the *Polyclinidae*, if we chose to assume that the genital organs and the heart withdrew to the proximal end of the post-abdomen, which then became dedicated exclusively to the function of reproduction. Such an assumption would satisfactorily explain the remarkable divergence in the position of the heart above alluded to. While, in *Clavelina*, the heart lies on the ventral side of the epicardial sac, in *Pyrosoma* it is found on the dorsal side of the so-called endostyle-process (Fig. 253, *hz*, p. 485). If, then, we assume that in these two groups the heart originally lay, as in the *Polyclinidae*, at the distal end of the stolon, it is not difficult to imagine that secondary shifting took place, in the *Clavelina* to the ventral and in *Pyrosoma* to the dorsal side.

The ontogeny of the *Pyrosoma* would, indeed, rather lead us to consider the change of position of the heart as the consequence of lateral shifting of the organs. The heart there lies originally on the right side of the entoderm-process, and only later shifts to the dorsal side (SEELIGER) ; *cf.* p. 493.

It is evident from the above that the asexual reproduction of the *Polyclinidae* (through the segmentation of the post-abdomen) and the stolonic budding found, for instance, in *Clavelina*, are related one to the other. GIARD (No. 57) has already pointed out that the elongated, branched post-abdomen of many *Polyclinidae* (*e.g.*, *Circinalium*), part of which creeps horizontally along the substratum, is remarkably like the stolon of *Clavelina*. These two methods of reproduction are thus connected with each other by transitional forms.

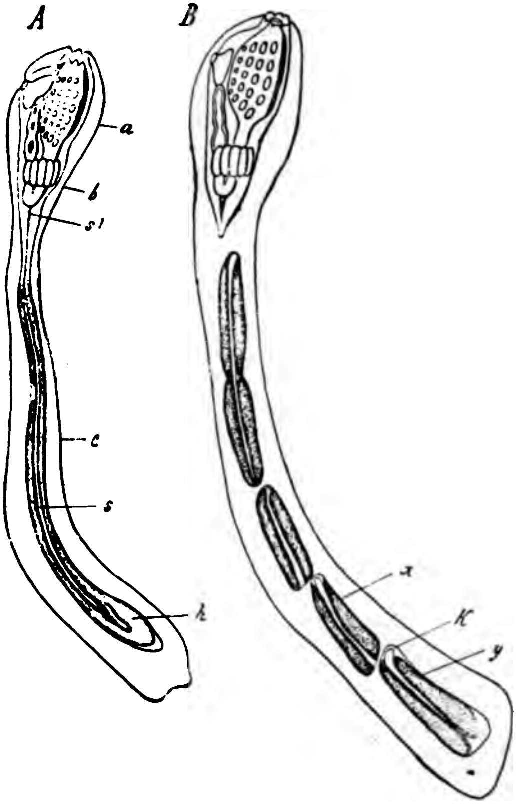

FIG. 227.—*A*, young *Amaroucium* before the commencement of asexual reproduction; *B*, *Amaroucium* with segmented post-abdomen (after KOWALEVSKY). *a*, thorax; *b*, abdomen; *c*, post-abdomen; *h*, heart; *s*, partition-wall; *s'*, anterior part of the partition-wall; *x*, *y*, separated portions of the post-abdomen; *k*, anterior swollen end of the partition-wall in the posterior separated portion.

The commencement of asexual reproduction in the post-abdomen of *Amaroucium* is marked by its elongation and the abstriction of its soft part from the point of attachment to the rest of the body. The heart continues to beat after the separation of the post-abdomen from the abdomen is accomplished. Soon after, the post-abdomen (Fig. 227 *B*) breaks up, through transverse fission, into a varying number of parts, each of which develops into a young Ascidian. The first sign of development is shown in a widening of the proximal end (K) of the ectoderm-tube (segment of the epicardial sac) which lies in every segment. This proximal dilation is the rudiment of the whole alimentary canal of the young animal. The non-dilated part of the entoderm-tube becomes the epicardial tube of the young individual. The heart of the parent-animal that has remained in the distal segment now degenerates. Somewhat older colonies (Fig. 228) are of a different shape. The young animals, which originally lay in a row one behind the other, show a tendency to shift upward within the test towards the parent-individual, and the whole colony thus becomes broader and shorter. The parent-individual now begins to develop, through regeneration, a new heart and post-abdomen (Fig. 228 *A*, *a*). The daughter-individuals in the figure seem to be at different stages of development. One of them (*b*) exhibits the almost perfect organisation of the adult Ascidian, while the three others show the rudiments of the different parts of the body, but these are very slightly developed. In all these young individuals the post-abdomen is still comparatively short. Only later (Fig. 228 *B*) does it grow out to a greater length, and come

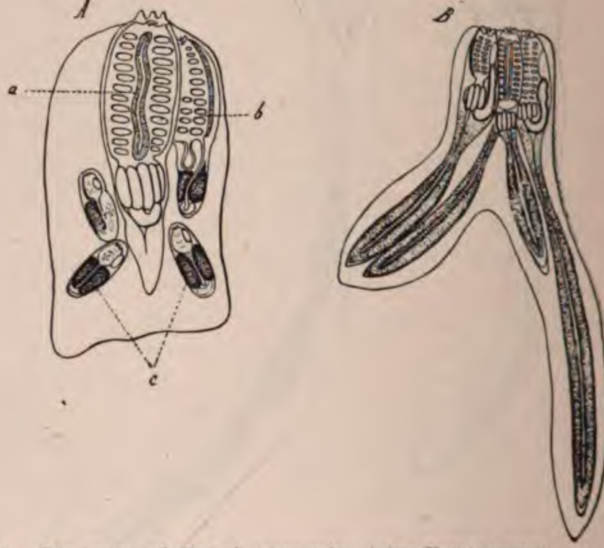

FIG. 228.—Two young colonies of *Amaroucium* (after KOWALEVSKY). *A*, younger, *B*, older stage. *a*, parent-animal; *b*, an advanced bud; *c*, younger buds.

to resemble more and more the post-abdomen of the parent before the commencement of asexual multiplication. The anterior part of the body of the young individual has shifted upward. The branchial and atrial apertures have broken through, and reproduction by means of tranverse fission now takes place in the daughter-individuals that have arisen as described above.

We thus find, in this case, the first rudiments of the young animal in the portion of the post-abdomen, which becomes separated by transverse constriction, and which, through processes of regeneration, is able to develop into a perfect new individual. For details of these processes, see p. 470.

Whether, in the segmentation of the post-abdomen in the *Polyclinidae*, we actually have a more primitive form of asexual multiplication, from which the stolonic gemmation of other Tunicates is to be derived, must still be regarded as doubtful. It is also possible that the transverse division of the *Polyclinidae* is to be derived from stolonic budding. A comparison with the conditions of development of *Pyrosoma* shows that caution must be exercised in such speculations. At first sight we should feel inclined to describe the rise of the first four Ascidiozooids in the *Pyrosoma* embryo as transverse fission (Fig. 193, p. 397), but more careful examination reveals the fact that the later longitudinal axis of the Ascidiozooid is at right angles to that of the proliferating stolon. We have, consequently, to regard the rise of these first Ascidiozooids also as stolonic budding, which is not essentially distinguished from the budding of the zooids that are produced later (see pp. 404 and 484).

B. Stolonic Gemmation.

The typical form of stolonic gemmation is found in the so-called social Ascidians, in *Clavelina* and *Perophora*. The single individuals here send out a creeping proliferating stolon which branches repeatedly (Fig. 229), and at the end of which the buds appear as club-shaped swellings. In structure the stolon closely resembles the post-abdomen of the *Polyclinidae*. Here also we find, as has already been shown, the blood-space of the stolon (primary body-cavity) divided by the extension of the epicardial sac (stolonic septum, *s*) into a dorsal and a ventral half, the blood circulating through these in opposite directions. Since the partition-wall does not reach quite to the distal end of the stolon (*x*) the two sinuses communicate at this point, where also the stream of blood changes from the one direction into the other.

The buds here originally appear in the form of bilaminate vesicles (*kn*). The outer layer of the vesicle, the ectoderm of the bud, is continuous with the ectoderm of the stolon and of the parent-individual. The inner layer, the entoderm, arises as was first proved by **Kowalevsky** (No. 60) for *Perophora*, as a diverticulum of the stolonic septum (epicardial sac) with which it long remains connected. Between the ectoderm and the entoderm, the primary body-cavity of the bud appears filled with mesenchyme - cells. We shall presently, following the accounts of **Kowalevsky** (Nos. 60 and 61), **Seeliger** (No. 66), and **van Beneden** and **Julin** (No. 10), describe more in detail the further development of the bud. We can here merely mention that, in *Clavelina*, the connection of the bud with the stolon, and through the latter with the other individuals of the colony, is usually retained even in the adult.

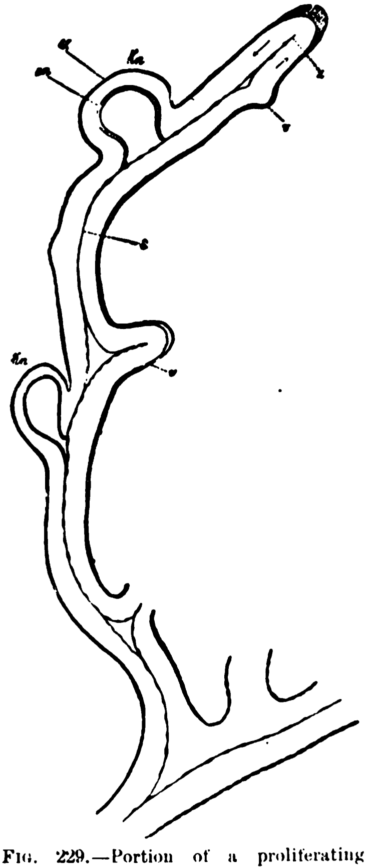

Fig. 229.—Portion of a proliferating stolon of *Perophora* (after **Kowalevsky**). *ec*, ectoderm of the bud; *en*, entoderm of the bud; *kn*, buds; *s*, stolonic septum (epicardial lamella); *r*, ramification of the stolon.

Not all the root-like processes of *Clavelina* seem to be capable of producing buds. Many of the ramifications seem intended merely for attachment or to serve as reservoirs of blood (**Seeliger**). The latter then have no epicardial process extending into them. A sharp distinction must be made between these sterile body-processes, which may be compared with the mantle-vessels, and the ramifications of the actual proliferating stolon.

Among the Composite Ascidians the family of the *Distomidae* belongs to the type just described, the entoderm-vesicle of the bud here also becoming abstricted from a process at the posterior end of the endostyle. In the *Botryllidae*, the *Didemnidae*, and the *Diplosomidae*, on the contrary, budding of another type occurs.

The family of the *Distomidae* seems to be distinguished by the fact that its buds separate very early from the proliferating stolon. They are then found within the common cellulose mantle scattered between the separate individuals as small, rounded bodies, each provided with a cavity. In individual cases a longer proliferating stolon seems to occur, as in the stalked colony of *Colella pedunculata*, in which **Herdman** found that each individual gave off into the common stalk a body-process (evidently the proliferating stolon). On this, then, the young buds arise and detach themselves, shifting upward in the common mantle-substance in proportion as they develop further. In another form belonging to this group, described by **Kowalevsky** as *Didemnum styliferum*, but which, according to **Della Valle** (No. 68), belongs to the genus *Distaplia*, the small buds which early become independent, arise, as **Kowalevsky** conjectured, on a process directed posteriorly, which must evidently be regarded as a proliferating stolon. This is also the case, according to **Lahille** (No. 38), with the individuals of *Distaplia magnilarva*, but **Della Valle** (No. 68) assumes that these processes are merely mantle-vessels. The special characteristic of the *Distomidae* is the early detachment of the small buds within the still free-swimming larva (Fig. 230). The large larvae of *Distaplia magnilarva*, in which, according to **Della Valle**, the organisation of the adult Ascidian is almost perfectly attained while the animal swims about freely, also show, between the endostyle and oesophagus, a short proliferating stolon (*st*), from which small buds that multiply by division (*k*, *k'*) are abstricted.

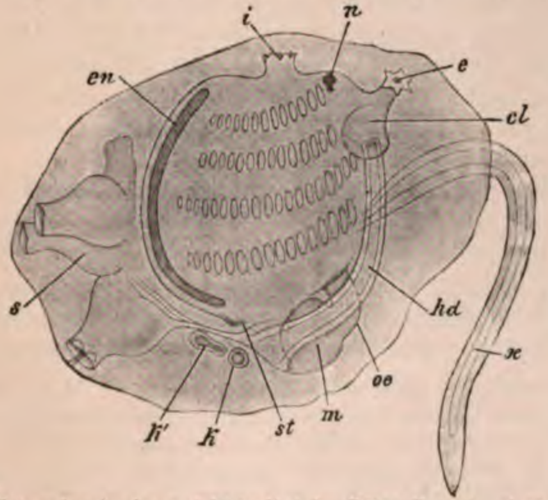

Fig. 230.—Free-swimming larva of *Distaplia* (after **Della Valle**). *cl*, atrial cavity; *e*, atrial aperture; *en*, endostyle; *hd*, intestine; *i*, branchial aperture; *k*, detached bud; *k'*, bud in the act of dividing; *m*, stomach; *n*, ganglion; *oe*, oesophagus; *s*, adhering organ; *st*, stolon; *x*, larval tail.

C. Pallial Gemmation of the Botryllidae.

In the *Botryllidae* also, the buds early show a certain independence, the entoderm-vesicle * found in each of them becoming separated from the parent-animal, and the connection between them and the parent-animal consisting later merely of a hollow, stalk-like ectodermal process. In this case, the buds are not produced from a stolon arising at the above-mentioned point, but as simple outgrowths of the body-wall at the sides of the branchial sac. DELLA VALLE on this point agrees with the older authors (METSCHNIKOFF, GANIN, KROHN, GIARD, and others), and this view has been quite recently confirmed by HJORT (No. 59) and OKA (No. 64*a*). This is the type of budding described by GIARD (No. 57) as "bourgeonnement palléal". There is usually only one bud on one side of the body about on the level of a line cutting off the upper third of the branchial sac. Occasionally, however, two buds are found, one to the right and the other to the left.

The first rudiment of the bud consists of a bilaminate outgrowth of the body-wall (DELLA VALLE, HJORT and OKA, who confirm METSCHNIKOFF'S statements on this point). The outer layer is formed by the ectoderm, the inner layer, on the contrary, which yields the entoderm-vesicle of the bud, is said to originate as an outgrowth of the wall of the peribranchial sac in the parent.

It was formerly thought (by M. SARS, KÖLLIKER, and others), that, in the *Botryllus* larva, budding commences during the free-swimming stage, and that eight processes, which surround the anterior end of the larva in a circle, represent the rudiments of a similar number of buds. In this way, the first cycle of individuals were said to arise surrounding a common cloaca. The later researches of METSCHNIKOFF (No. 41), KROHN (Nos. 62 and 63), and GANIN (No. 55), have shown that so-called mantle-vessels have in this case erroneously been regarded as buds. Budding begins only after attachment, a single bud forming first. While this bud grows, the primary individual of the colony disintegrates. The daughter-individual then produces two buds, one on the right and the other on the left side of its body. These two individuals of the third generation continue to grow, while the individual that produced them dies. By a repetition of the process in the third generation, a colony consisting of four individuals (of the fourth generation) arises. The four

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* [According to HJORT (No. XIV.) and PIZON (No. XXVI.), the inner vesicle is not derived from the entoderm of the parent, but from the peribranchial cavity which arises in the larva as a pair of ectodermal invaginations. Consequently these observers conclude that all the organs of the bud in *Botryllus* are formed from the ectoderm. This condition, if true, is very remarkable, as it differs *in toto* from what is known of the development of the inner organs in the buds of other Ascidians.—ED.]

individuals are arranged in such a way that their atrial apertures turn towards each other. In this way commences the union of the individuals round a common cloaca (KROHN, No. 63). This young tetrazooid colony shows considerable resemblance to the youngest *Pyrosoma* colonies. The individuals which are produced later by budding are always given off by the parent laterally, and thus occupy the spaces between the parent-individuals. They themselves are very soon capable of multiplying in their turn. The daughter-individuals at first lie somewhat away from the common cloaca, towards which they only shift later. Systems consisting of two concentric cycles may thus develop, the inner cycle containing the parent-individuals and the outer the daughter-individuals. While the latter shift to positions round the common cloaca, the individuals of the inner cycle disintegrate (JOURDAIN). The common cloaca is nothing more than a pit-like depression of the outer surface of the common cellulose mantle. This is also the case with the common cloaca in *Pyrosoma* (*cf.* p. 403).

New circular systems are produced in the *Botryllidae*, when one of the buds belonging to a cycle does not shift towards the common cloaca, but moves away from it. This individual, by reproducing itself through budding, becomes the founder of a new cycle.

D. Budding of the Didemnidae and the Diplosomidae.

The conditions of budding in the families of the *Didemnidae* and the *Diplosomidae* are very peculiar. Since, in these families, the buds remain connected with the parent until fully developed, remarkable double individuals are produced which long since attracted the attention of zoologists. Since, further, in the *Diplosomidae*, the first budding process takes place during larval life, free-swimming and still caudate larvae are found in which two branchial sacs are well developed. On closer inspection, it is not difficult to distinguish the branchial sac of the larva from that of the bud. In the brain of the primary individual, moreover, the larval sensory organ can be recognised, while in the bud it is wanting.

Budding, in these two families, follows the type defined by GIARD (No. 57) as "bourgeonnement pylorique." According to GEGENBAUR, GANIN (No. 55), DELLA VALLE (No. 68) and other authors who have investigated this method of budding, the newly formed individual here arises through the concrescence of two originally distinct buds (Fig. 85), one of which (the *thoracic bud*, *k'*) yields the branchial region with its organs, the peribranchial sacs, and the pharynx, while the other (the *abdominal bud*, *k*) gives rise to the intestinal loop, the genital organs and the heart. The first rudiment of the abdominal bud (Fig. 232 *A*, *k*) is found as an outgrowth of the oesophagus of the parent; the thoracic bud, on the contrary (*k'*) lies further down on a level with the stomach, on the right side of the body and, according to **Della Valle**, is derived from a simple outgrowth of the body-wall (consisting of ectoderm and the parietal layer of the wall of the peribranchial sac), and thus arises in the way described above for the buds of the *Botryllidae*. **Jourdain** (No. 64) has recently stated that these two buds (the thoracic and the abdominal buds) arise through the division of an original single bud, and that the connection between the two halves is still maintained for some time. No further details, however, are known on this point. **Giard** (No. 58) holds that the first rudiment of the bud can here also be traced back to the epicardial tube.

The *abdominal bud* (Fig. 232 *A*, *k*) is thus at first apparently an outgrowth of the oesophagus of the parent which, however, soon becomes more sharply marked off (Fig. 231 *A* and *B*) in such a way that it then forms a caecum connected with the oesophagus only at its anterior end (Fig. 231 *C*), this becomes U-shaped and can now be recognised as the rudiment of a new intestinal loop, in which the various parts (oesophagus, stomach, intestine) become differentiated. The oesophagus of the newly-formed intestinal loop is connected with the oesophagus of the parent (*oe*). The intestine of the bud becomes applied to that of the parent (Fig. 232 *B*, *b*) and enters into communication with it. The parent-individual now possesses two fully developed intestinal loops, with continuous lumina. It is not yet clearly known how the heart and the genital rudiments of the bud develop, but **Della Valle** believes that the latter are perhaps derived direct from the genital rudiments of the parent.

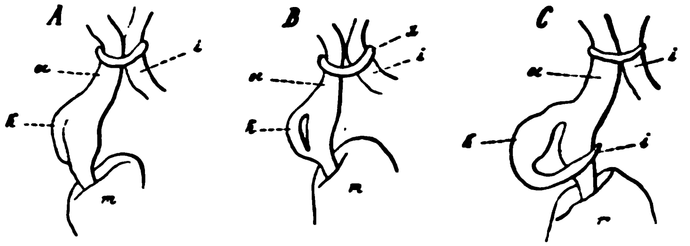

Fig. 231.—Three ontogenetic stages of the oesophageal bud of *Tridideminum** (after **Della Valle**). *i*, intestine; *i'*, intestine of the bud; *k*, bud; *m*, stomach; *oe*, oesophagus; *r*, constricting ectoderm-ring.

At the same time, the *thoracic bud* (Fig. 232 *A*, *k'*) also develops fully (Fig. 232, *B*). We cannot here enter in detail into the some-

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*[The genus *Tridideminum* is included by **Herdman** in the genus *Didemnum* Savigny.—Ed.]

what unsatisfactory statements of authors as to the way in which the organs develop in this bud, but may mention that peribranchial sacs develop at the sides of the central enteric cavity, that gill-clefts break through, and that the ganglion, and the branchial and atrial apertures, appear as rudiments. An oesophageal tube and a short rectum seem also to appear. The former (Fig. 232 *B*, *a*) now becomes connected with the oesophagus of the parent (*oe*) near the point at which the oesophageal tube of the abdominal bud (*a*) enters it. At this one point, therefore, three oesophageal tubes seem to be connected, viz., that of the parent and those of the two buds. This is also the case with the rectum, the short rudiment of that organ belonging to the thoracic bud (*b′*) entering the rectum of the parent (*i*) at the point at which the rectum of the abdominal bud (*b*) joins it. If, now, the oesophagus of the thoracic bud became more closely connected with that of the abdominal bud, and such connection were also to be established between the intestines of the two buds, the two halves of the daughter organism would then at last be united. But although the alimentary canal of the bud is now completed, it still, for a long period, remains connected with that of the parent, both in the oesophageal region and through the rectum (Fig. 233).*

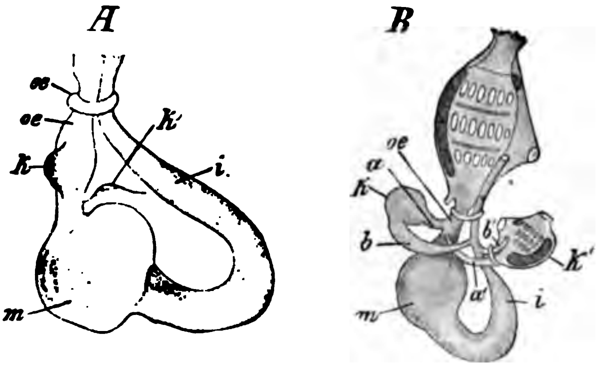

FIG. 232.—Budding in *Trididemnum* (after DELLA VALLE). *A*, intestinal loop of the parent-individual with the rudiment of the abdominal (*k*), and thoracic (*k′*) buds; *B*, individual with the two buds at a later stage of development. *a*, oesophageal rudiment of the bud *k*; *a′*, oesophageal rudiment of the bud *k′*; *b*, rudiment of the intestine in the bud *k*; *b′*, the same rudiment in the bud *k′*; *i*, intestine of the parent-individual; *k*, abdominal bud; *k′*, thoracic bud; *m*, stomach; *oe*, oesophagus; *x*, constricting ectoderm-ring.

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* [For further details concerning the development of the complex buds of the *Diplosomidae* and *Didemnidae*, see the recent works of CAULLERY (Nos. V.-VII.) and SALENSKY (No. XXIX.). CAULLERY finds epicardial tubes in the adults, and from these he derives the thoracic and abdominal buds.—ED.]

The thoracic and the abdominal buds do not always develop equally. In some cases only the abdominal bud develops. This leads to an abnormality, consisting of one branchial region with two fully developed intestinal loops (Fig. 234 *B*). In such cases the intestine of the parent may degenerate later. This condition is regarded by **Della Valle** as a rejuvenescence, and consists in the development of an individual, the anterior half of which belongs to the parent, while its posterior half develops anew (see also **Oka**, No. 64*b*). A similar process may occur in the anterior part of the body, when the thoracic bud alone develops (Fig. 234 *A*). The process is often still further complicated by the appearance of the bud-rudiments of a third generation arising from the not yet fully developed bud. In this way remarkable combinations of the various halves of the body are produced.

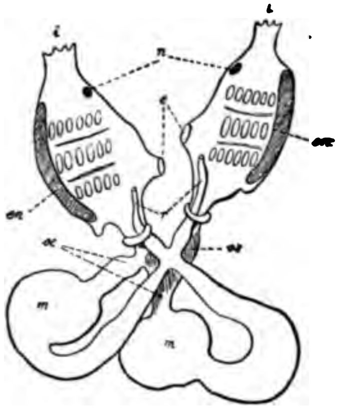

Fig. 233.—Late stage in the budding of *Trididemnum* (after **Della Valle**). The alimentary canal of the perfectly developed bud still remains connected with that of the parent. *e*, atrial aperture; *en*, endostyle; *i*, branchial aperture; *m*, stomach; *n*, ganglion; *oe*, oesophagus; *r*, rectum.

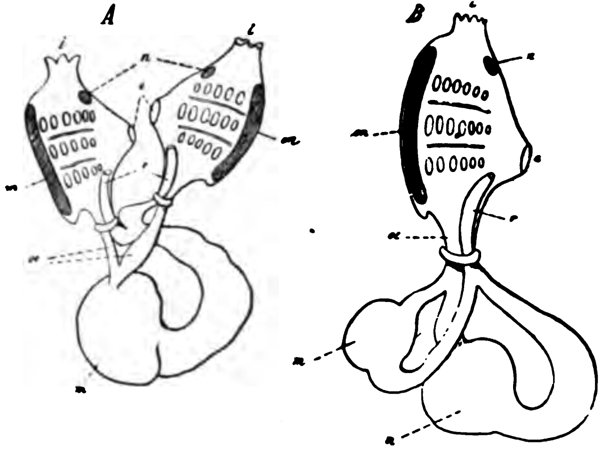

Fig. 234.—Abnormal forms resulting from the development of one half of the bud in *Trididemnum* (after **Della Valle**, simplified). *A*, two branchial regions connected with one intestinal loop; *B*, two intestinal loops connected with one branchial region. *e*, atrial aperture; *en*, endostyle; *i*, branchial aperture; *m*, stomach; *n*, ganglion; *oe*, oesophagus; *r*, rectum.

In the *Diplosomidae* the process of budding and the formation of double individuals begins even in the free-swimming larva, but in the *Didemnidae* this is not the case.

But for the statements made by Jourdain we might be tempted to derive the remarkable budding processes in these two families from a primitive longitudinal fission of the parent.

E. Development of the Organs in Asexually Produced Individuals.

The development of the inner parts of the bud has been described by Metschnikoff (No. 41), Ganin (No. 55), Kowalevsky (Nos. 60 and 61), Giard (No. 57), Della Valle (No. 68), Seeliger (Nos. 66 and XXXIV.), van Beneden and Julin (Nos. 10 and XVII.), Hjort (Nos. 59 and XVI.), Oka (No. 64*a*), and in the still more recent works of Caulery (No. IV.), Lefèvre (No. XXII.), and Ritter (No. XXVIII.). In our account of these processes we have followed Kowalevsky, whose careful researches have been confirmed with regard to the development of the nervous system and the pericardial vesicle by van Beneden and Julin.

The bud is at first a hollow body consisting of two or three layers (Fig. 229, *kn*). The outer layer is the ectoderm (*ec*) which is in continuous connection with the ectoderm of the stolon. The inner layer, the entoderm (*en*), encloses the primary enteric cavity of the bud, which, in *Clavelina* and the *Distomidae*, originated as a diverticulum of the epicardial sac (entodermal stolonic septum, "cloison").* The connection between the entoderm-vesicle of the bud and the epicardial sac is retained in the social Ascidians (*Clavelina* and *Perophora*) for a very long time, often throughout life. According to van Beneden and Julin, the stalk-like portion which connects the bud with the stolonic septum represents the rudiment of the epicardial sac and of the pericardial vesicle of the budding individual. The primary body-cavity extends between the ectoderm and the entoderm of the bud; into it mesoderm-elements soon immigrate, and these are the first rudiment of the mesoderm of the bud. In many cases (especially in the buds of the *Distomidae* and the *Botryllidae*) the

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* [In *Perophora*, according to Ritter (No. XXVIII.) and Lefèvre (No. XXIII.), the developing blastozooid (bud) is connected with the stolonic septum, not by its branchial sac but by the left peribranchial sac. Ritter expresses some doubt concerning the origin of the pericardium; he thinks that it arises from the inner vesicle, but even if it is produced by the aggregation of mesenchyme-cells, as Lefèvre states, it is still probable that its ultimate source is the entoderm, since the mesenchyme-cells are probably produced from that layer.—Ed.]

genital rudiments can also be distinguished at an unusually early stage.* The above is the case in the buds of ***Distaplia*** (**Kowalevsky's** ***Didemnium styliferum***), which, as free bodies detached from the stolon, are found scattered in the cellulose substance of the colony. In the genital strand (Fig. 235, *g*) of the youngest of these buds, several young egg-cells can always be recognised. These buds, however, are capable of multiplying by fission (Fig. 235 *B*), and in this case the eggs become distributed so that one occurs in each portion of the original bud. **Kowalevsky** is, therefore, inclined to regard the buds which form first as stolons which have separated from the Ascidiozooids, the parts resulting from fission alone representing the true buds, and **Lahille** has recently adopted this view.

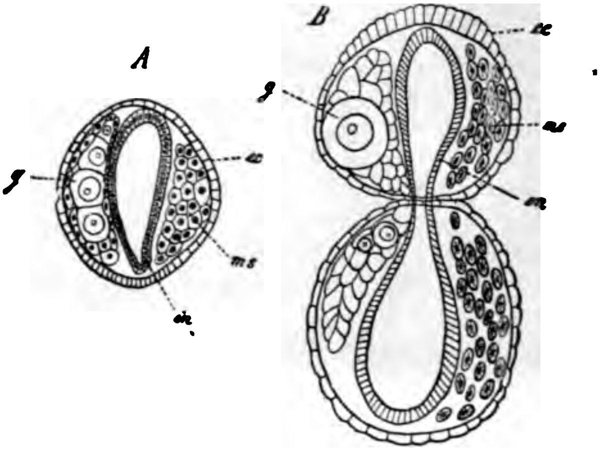

Fig. 235.—*A*, younger, *B*, older stage of development of *Distaplia stylifera* (after Kowalevsky). In *B*, the bud is dividing into two. *ec*, ectoderm; *en*, entoderm; *g*, genital strand; *ms*, mesoderm.

The entoderm-sac is the seat of the most important transformations through which the bud develops into the young Ascidian. This sac increases in size and its anterior margin becomes trilobed (Fig. 236). The middle lobe must be regarded as the rudiment of the branchial sac (pharynx), while the two lateral parts represent the rudiments of the peribranchial sacs. These sacs are, therefore, in the bud of *Distaplia*, distinctly entodermal in their origin.

The peribranchial sacs grow round the sides of the middle vesicle and, at the same time, a process grows from each sac towards

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* [In the *Didemnidae* (Pizon, No. XXVI*a*.) the sexual cord is continued from the parent into the bud.—Ed.]

the dorsal middle line (Fig. 236 *B*, *p*). These processes grow towards each other and fuse, and thus the single atrial cavity arises (Fig. 237, *cl*). In the meantime the two peribranchial sacs have become completely disconnected from the central cavity.

The peribranchial sacs arise in a slightly different manner in *Perophora* (KOWALEVSKY, RITTER), in which form, instead of separating as two distinct sacs and fusing together at a later period, a single bilobed sac separates from the inner vesicle; thus the definitive atrial cavity is formed at an earlier period, the development being apparently abbreviated. SEELIGER also states that, in *Clavelina*, an unpaired vesicle becomes abstricted from the dorsal side of the enteric sac, which persists as the atrium and, growing round the sides of the pharynx, forms the peribranchial sacs. HJORT (No. 59) again, recently stated that, during the budding of *Botryllus*, a saddle-shaped vesicle becomes separated from the inner vesicle of the bud and gives rise to the atrial cavity and the paired peribranchial sacs.

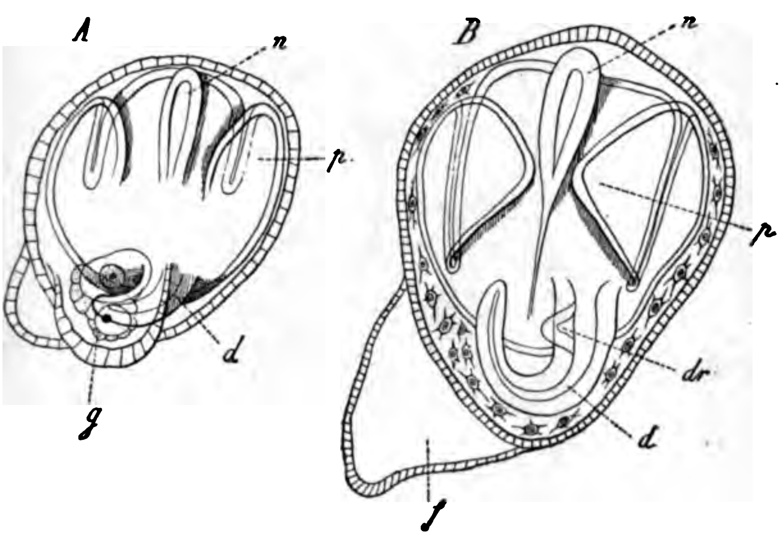

FIG. 236.—Two stages in the development of the buds of *Distaplia stylifera* (after KOWALEVSKY). *A*, younger, *B*, older stage. *d*, alimentary canal; *dr*, digestive gland; *f*, rudiment of the stolon; *g*, genital rudiments; *n*, nerve-tube; *p*, right peribranchial sac.

At the time when the peribranchial sacs form, an unpaired caecum grows out from the posterior end of the entoderm-vesicle (Fig. 236 *A*, *d*); this soon bends to the left and thus becomes the rudiment of the intestinal loop (Fig. 236 *B*, *d*) in which latter the different sections (oesophagus, stomach and intestine) can be more distinctly made out. A diverticulum (*dr*), rising from the pyloric region, develops into the rudiment of the so-called digestive gland (Fig. 237).

The rudiment of the genital organs appears dorsally to the intestinal loop immediately below the nerve-strand (Figs. 238 *E*, *g*, and 237, *g*). The strictly median position of this rudiment is specially distinct in the buds of *Clavelina*, where it appears only in later stages. It apparently takes its rise as an agglomeration of closely crowded mesenchyme-cells, in which a cavity nevertheless soon appears; this is the primary genital cavity round which the cells become grouped like an epithelium. For the development of the male and female genital organs from this uniform rudiment we must refer the reader to p. 379.

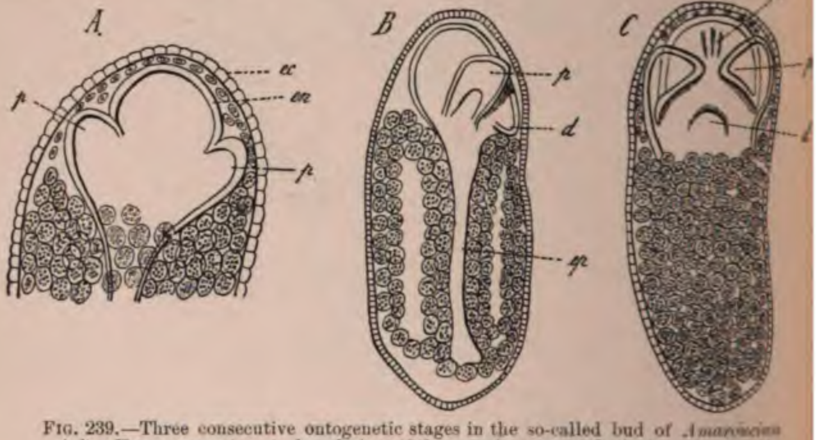

FIG. 239.—Three consecutive ontogenetic stages in the so-called bud of *Amaroucium* (after KOWALEVSKY). *A*, dorsal view of the anterior part of the body; *B*, side view of an older stage; *C*, dorsal view of a still more advanced stage. *d*, enteric rudiment; *ec*, ectoderm; *en*, entoderm; *ep*, epicardial process; *n*, rudiment of the nervous system; *p*, peribranchial sac.

Important observations on the condition of the pericardial vesicle and the epicardial tube have been made by VAN BENEDEN and JULIN. Following these authors, we shall first describe the condition of a more fully developed bud traced in a series of cross-sections. The last section of this series (Fig. 238 *F*) passes through the base of the U-shaped intestinal loop (*i*) and, ventral to this, the stolonic septum (*st*) is seen. In anterior sections, we find that the latter is in direct connection with the pericardial vesicle (Fig. 238 *D*, *pc*). The heart (*h*) here also has arisen through the invagination of the wall of the pericardial sac (*pc*). A section cut further forward (Fig. 238 *D*) shows the double or forked end of the epicardial sac (*ep*) of the bud, in close contact with the pericardial vesicle. Further forward, the pericardial vesicle decreases in size (Fig. 238 *C*, *pc*) and finally disappears (Fig. 238 *B*), while the epicardial sac (*ep*) can be followed forward to the point at which its wide paired aperture (Fig. 238 *A*) enters the pharynx (branchial sac). In other words, the epicardial sac arises from paired apertures situated ventrally to the entrance of the oesophagus and extends backward, its forked, blind end becoming applied to the pericardial vesicle. The latter is continued direct into the stolonic septum. At an earlier stage, the forked end of the epicardium is found to be continuous with the wall of the pericardial vesicle, and the cavity of the epicardium of the bud communicates at this point with the pericardial cavity. Consequently, the cavity of the stolonic septum, the pericardial sac and the epicardium are merely differentiated portions of one and the same system of cavities. In the larva, however, according to VAN BENEDEN and JULIN, the relation of the parts is different (p. 368).*

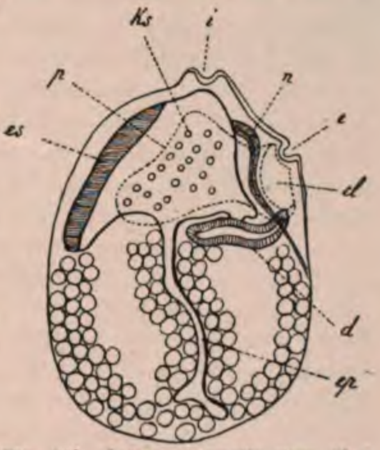

FIG. 240.—Later ontogenetic stage of a so-called bud of *Amaroucium* (after KOWALEVSKY). *cl*, atrium; *d*, alimentary canal; *e*, atrial aperture; *ep*, epicardium; *es*, endostyle; *i*, branchial aperture; *ks*, gill-clefts; *n*, nervous system; *p*, peribranchial cavity.

With regard to the further development of the bud, we can merely briefly mention that the gill-clefts appear as perforations of the contiguous walls of the pharyngeal sac and the peribranchial sacs; that the muscles are derived from strands of mesenchyme-cells, and that the branchial and atrial apertures owe their origin to ectodermal invaginations which become connected with the pharynx and the atrium. The endostyle appears in the form of a fold of the ventral wall of the pharynx.

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* [JULIN (No. XVII.) has recently investigated the origin of the pericardium in *Distaplia*, and finds a condition which differs somewhat from that described above as occurring in *Clavelina*. As in *Clavelina*, a pair of epicardial (procardial) tubes grow out from the pharynx on either side of the oesophageal aperture; of these the left becomes divided transversely into an anterior portion, which then fuses with the left epicardial tube to form the epicardial sac, and a posterior portion which gives rise to the pericardium and heart. From the recurved end of the right sac the primary bud is given off before the tube fuses with that on the left to form the median epicardial sac.—ED.]

Ontogenetic processes altogether similar to those just described are found in cases where the detached parts of the post-abdomen in the *Polyclinidae* regenerate (Fig. 239). Here also the central entoderm-vesicle is the first seat of transformation. As has already been mentioned (p. 454), the first change to occur is a widening of the proximal end of the epicardial septum (Fig. 239 *B*). An entoderm-vesicle is in this way formed in the proximal part of the young individual, and this is continued backward into the part of the stolonic septum which did not widen. The proximal dilatation is the rudiment of the whole alimentary canal of the new individual, while from the non-widened part are derived the epicardial sac (Fig. 239 *B*, *ep*) and probably also the pericardium. The entoderm-vesicle here also divides up in the same way as in the bud into three lobes (Fig. 239 *A* and *B*), the middle lobe being the rudiment of the branchial sac and the two lateral lobes the rudiments of the peribranchial sacs. The complete abstriction of the latter, their interconnection (Fig. 239 *C*) to form a median unpaired dorsal part (atrium), and the development of the gill-clefts all occur in the same way as in the formation of buds. The rudiment of the alimentary canal is here also a small, unpaired caecum (Fig. 239 *B*, *d*), which grows out at the dorsal side in the posterior part of the entoderm-vesicle and curves into the shape of the letter U. In the development of the more important systems of organs, we thus have here complete agreement with the processes of gemmation.

2. Doliolidae.

We have already mentioned (p. 388) that two stolons are apparently found in the "nurse" (blastozooid) generation of *Doliolum*, one ventral (*vs*) and the other dorsal (*ds*), the dorsal outgrowth developing to a much greater size than the true ventral stolon, and finally giving rise to heteromorphous individuals known as lateral and middle buds (the gastrozooids and phorozooids). The two stolons vary greatly in structure. As will be seen later, the so-called dorsal stolon is merely a dorsal outgrowth of the body which receives and gives attachment to the buds derived from the true ventral proliferating stolon, hence it is better to restrict the term stolon to the ventral structure and to speak of the dorsal structure as the dorsal outgrowth.

The *ventral stolon* (Figs. 180, *v*, p. 385; 243, *v*; 245 *A*, *vs*), formerly known as the rosette-like organ, and first recognised by GROBBEN (No. 79) in its true character as proliferating stolon, appears as a pear-shaped projection rising from an ectodermal depression; in cross-section, this is found to be composed of seven parallel cell-strands (Fig. 242) four of which (*k* and *p*) are arranged symmetrically in two pairs, while the other three (*n*, *z*, and *m*) are unpaired. GROBBEN and ULJANIN differ considerably as to the origin and significance of these seven strands which, with the ectoderm that envelops them, form the primary rudiment of the buds. These two authors agree that two cones grow downwards from both the pharyngeal and the atrial cavities of the "nurse" (Fig. 241, *ph* and *cl*), enclosing between them a mesoderm-mass (*m*), the origin of which has already been traced (p. 387; see also Fig. 182 *B*, *d* and *ms'*, p. 387). According to ULJANIN, the stolon is thus originally composed of five strands, two pharyngeal and two atrial strands and a middle mesoderm-strand (Fig. 241). The number of these strands becomes augmented to seven when the atrial strand (*cl'*) becomes bent on itself, its reflexed end giving rise to a new pair of strands (*cl''*). The fusion of this pair, according to ULJANIN, yields the future neural rudiment (*n*), while the pharyngeal strand (*p*) yields, by dehiscence, an unpaired middle strand (*x*) in which this author sees the rudiment of the pharyngeal cavity of the bud. The unpaired strand (*m*) is said to represent the pericardial rudiment, while the pharyngeal strands (*p*) change into the genital rudiment, and the atrial strands (*k*) into those of the muscle-plates.

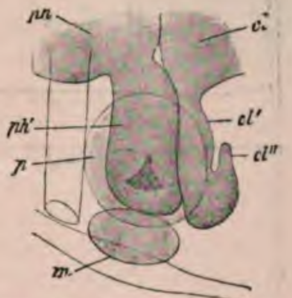

FIG. 241.—Young stage of development of the proliferating stolon (rosette-like organ) of *Doliolum Mülleri* (after ULJANIN). *cl*, atrial wall of the parent-animal; *cl'*, out-growth of the atrial wall; *cl''*, bent portion of the same; *m*, aggregation of mesoderm forming part of the rosette-like organ; *p*, pericardial vesicle; *ph*, pharynx of the parent; *ph'*, outgrowth of the wall of the pharynx.

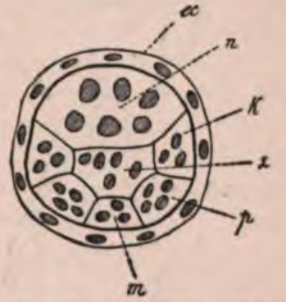

FIG. 242.—Transverse section through the ventral stolon or a primitive bud of *Doliolum* (diagram after GROBBEN and ULJANIN). *ec*, ectoderm; *k*, muscle-rudiments; *m*, pericardial rudiment; *n*, neural rudiment; *p*, genital rudiment; *x*, pharyngeal rudiment (ULJANIN).

According to GROBBEN, on the contrary, the pharyngeal strands (*p*) represent the rudiment of the pharyngeal cavity and intestine of the bud, the atrial strands (*k*) the later rudiment of the atrium, and the unpaired mass *x* (resulting from the fusion of paired strands) is assumed to be the genital rudiment. The unpaired strand *m* is regarded as the rudiment of the pericardial sac, and the mass *n*, which from the first is unpaired, as that of the nervous system.

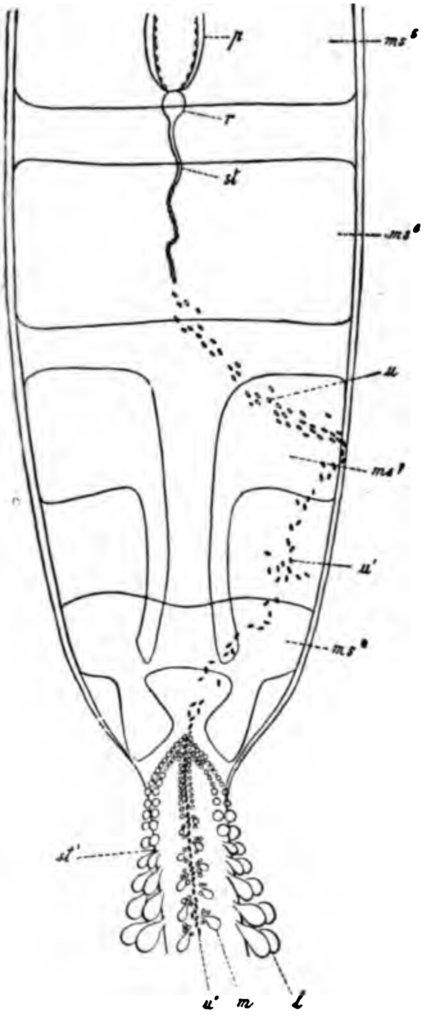

FIG. 243.—Dorsal view of the posterior part of the body in a large "nurse" (blastozooid) *Doliolum* (after BARROIS). *l*, lateral buds (gastrozooids); *m*, median buds (phorozooids); ms^5-ms^8, four posterior muscle-hoops; *p*, pericardium; *r*, rosette-like organ; *st*, ventral stolon; *st'*, dorsal outgrowth; *u*, primitive buds wandering to the ventral side of the "nurse"; *u'*, primitive buds wandering to the dorsal side; *u''*, primitive buds on the dorsal outgrowth.

The buds are produced through the transverse constriction of the *ventral stolon* (Fig. 243, *r* and *st*), from which they eventually become completely detached. In structure, they resemble the stolon itself, being composed of an ectodermal envelope and the seven strands above described. They are not capable, however, of developing further on the ventral stolon. GROBBEN has therefore regarded the ventral stolon, which is evidently homologous with the proliferating stolon of the other Tunicates, as a vestigial stolon, and considers the buds produced by it as abortive.

A cross-section of the *dorsal outgrowth* (Fig. 243, *st'*) of the "nurse" generation (blastozooid) reveals an essentially different structure (ULJANIN). Like the ventral stolon, it is covered superficially by a layer of ectoderm, thickened on the dorsal side, but the interior of this outgrowth is occupied merely by two blood-vessels separated by a partition-wall of connective tissue. The transverse section of this outgrowth, indeed, strikingly recalls sections through the stolon of certain Ascidians, although it must be noted that, in these latter, the partition-wall is formed by an entodermal lamella (epicardial lamella) of which nothing can be seen in *Doliolum*.

The buds which develop from the dorsal outgrowth as lateral and median buds (Fig. 243, *l*, *m*) do not arise independently from this structure. GROBBEN conjectured that they were all abstricted from a "primitive bud" found at the base of the stolon. ULJANIN, on the other hand, observed that the parts which become abstricted from the ventral stolon are capable of wandering along the surface of the body of the parent, and in this way reach the dorsal outgrowth (*u*, *u'*). These wandering cell-masses are the primitive buds, from which the lateral and median buds of the dorsal outgrowth arise by constriction. The primitive buds that first reach the dorsal outgrowth remain at its base and, through fission, produce buds which become arranged along each side of the stolon, developing into the lateral buds or gastrozooids (*l*); consequently the buds towards the distal end of the row are more highly developed than those near its base. Those primitive buds which reach the dorsal outgrowth later are distributed along the whole of the middle dorsal line (*u''*), and by gemmation give rise to the median buds or phorozooids (*m*). These buds are arranged in groups alternating on either side of the row of primitive buds (*u''*). The buds of each group develop unequally, but here also there is an advance in development towards the distal end of the stolon.

According to ULJANIN, the ventral stolon is thus the only proliferating stolon of the "nurse" generation; the dorsal outgrowth cannot be regarded as a true proliferating stolon, but is merely a body-process serving for the nourishment of the buds attached to it, which can be traced back to the mantle-vessels of the Ascidians.

The *Doliolidae* thus show an early detachment of the buds from the proliferating stolon such as takes place in the *Distomidae* (pp. 456 and 468), in which family also the detached buds are able to multiply further through fission. The wandering of the primitive buds and the development of their descendants in their secondary position in the *Doliolidae* are very remarkable. The statements made on this subject have been confirmed for *Doliolum* by BARROIS (No. 77), and similar processes have been observed in *Anchinia* and *Dolchinia*, so that little room is left for doubt on this point. According to ULJANIN, the buds are able to move by means of pseudopodia-like processes of their ectoderm-cells. According to BARROIS, on the contrary, there are, on each side of the ventral stolon of *Doliolum*, large amoeboid cells, arranged in such a way that one pair becomes attached to each primitive bud as it separates from the stolon (Fig. 252 *A*, p. 483). While these large, amoeboid cells are attached to the surface of the primitive buds, they do not seem to belong directly to the bud itself. According to Barrois, they are modified test-cells concerned in the transportation of the primitive buds. Similar cells are found on the buds of *Anchinia* and the primitive buds of *Dolchinia*.

The median buds differ essentially from the lateral buds in form and function. The *lateral buds* or gastrozooids (Fig. 244) are asymmetrical, short-stalked individuals in which, through increase in length, the characteristic barrel-shape disappears. They may be likened to spoons with deep concavity and short handle. The concavity of the spoon is formed by the pharyngeal cavity with its wide aperture, the dorsal wall being formed by the somewhat swollen branchial lamella. The atrial cavity of the bud and its aperture are so dilated as altogether to disappear. The gill-clefts therefore lead from the pharyngeal cavity direct to the exterior. The alimentary canal (*d*) is well developed, the muscle-hoops are vestigial, and the genital rudiment found in the bud degenerates in the further course of development. The lateral buds are not able, after their detachment from the dorsal outgrowth, to lead an independent life, and they do not multiply in any way. Their sole functions are the taking in of food and respiration; they obtain the nutritive material for the other buds of the dorsal outgrowth as well as for the blastozooid ("nurse") which has lost its alimentary canal (p. 388). They correspond to the nutritive polyps of a Siphonophoran stock (Fol) and have therefore been called nutritive forms or trophozooids.

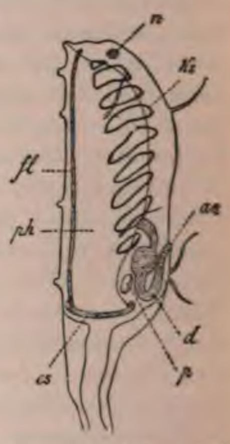

Fig. 244.—Lateral bud (gastrozooid) of *Doliolum Mülleri* (after Grobben). *an*, anal aperture; *d*, alimentary canal; *es*, endostyle; *fl*, ciliated arch; *ks*, gill-clefts; *n*, ganglion; *p*, pericardial vesicle and heart; *ph*, pharynx.

The *median buds* (phorozooids), on the contrary, after attaining their full development, become detached from the dorsal stolon of the first "nurse" (blastozooid) generation and lead a free pelagic life. These individuals (Fig. 245 *B*) in the development of their body, closely resemble the barrel-shaped sexual generation, from which they are only distinguished by the absence of the genital organs (which here degenerate at an early period in the bud) and by the presence of a ventral process (*st*) near the posterior end of the body; this process is derived from the peduncle connecting the median bud with the

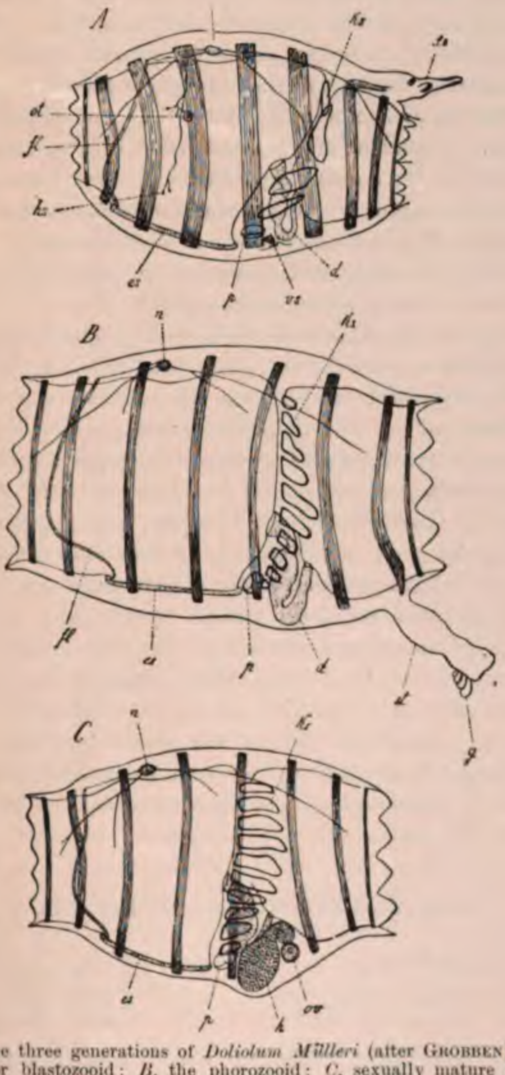

FIG. 245.—The three generations of *Doliolum Müllieri* (after GROBBEN). *A*, young "nurse" or blastozooid; *B*, the phorozooid; *C*, sexually mature individual or gonozooid. *d*, alimentary canal; *ds*, dorsal outgrowth of the "nurse" form; *es*, endostyle; *fl*, peripharyngeal band; *g*, buds of the sexual generation; *h*, testis; *hs*, integumental sensory organ; *ks*, gill-clefts; *n*, ganglion; *ot*, auditory organ; *ov*, ovary; *p*, pericardial vesicle and heart; *st*, peduncle for the attachment of the gonozooids (*g*) to the phorozooid; *vs*, ventral stolon of the "nurse" form (so-called rosette-like organ).

dorsal outgrowth of the "nurse," and carries the buds of the sexual generation or gonozooids (*g*). The latter was formerly thought to be produced from the phorozooid itself, and these buds, when free, were consequently known as the second "nurse" generation. The sexual generation, however, is produced from a primitive bud which has become attached to the base of the peduncle of the phorozooid. This bud, according to Uljanin, is not yielded by the phorozooid itself, but is a direct descendant of the primitive buds (Fig. 243, *u''*) which wandered over to the dorsal outgrowth of the first "nurse" generation. Uljanin therefore regards the median bud merely as the foster-mother of the buds which develop into sexual animals.

There is thus, according to Uljanin, in the whole cycle of generations of *Doliolum*, only a single true proliferating stolon, viz., the ventral stolon, which alone is capable of producing primitive buds. All the individuals derived from these primitive buds which attain development represent, according to this author, only the heteromorphous forms of one and the same generation, the sexual generation either, as nutritive animals or as foster forms, losing their genital organs, or else changing into actual sexual animals (Fig. 245 *C*).

According to Grobben, on the contrary, who practically follows Gegenbaur, the cycle of generations of *Doliolum* consists of two successive asexual generations and one sexual generation. Grobben consequently regards the form yielded by the egg, which differs essentially from the sexual animal, as the first "nurse" form *A*. This gives rise to the two heteromorphous forms (lateral buds *L*, and median buds *M*): of these, the median buds, in their capacity of second "nurse" generation, produce the sexual generation *G*. The abortive buds yielded by the ventral stolon represent a lateral branch of the cycle of generations (*K*). These two opposite views may be tabulated as follows:—

Alternation of Generations in Doliolum.

Grobben's view:	Uljanin's view:
A (first "nurse" form)	A ("nurse" form)
K	
L + M (second "nurse" form)	L + M + G (sexual generation)
G (sexual individual)	

We see from the above that if Uljanin's view is confirmed, the alternation of generations in *Doliolum* closely resembles that in the

Salpidae, consisting in both cases of an asexual generation followed by a sexual generation. The only difference between the two would be that the primitive buds produced by the asexual generation, in *Doliolum*, multiply by fission, and that the sexual generation develops in three different forms (*L*, *M* and *G*). In this way also the fact that the median buds entirely agree in structure with the sexual generation would be explained (Fig. 245 *B* and *C*).

We have still to describe the development of the young buds after their detachment from the primitive buds. According to ULJANIN, all these buds, whether lateral, median or sexual, develop more or less in the same way, so that an account of the development of the lateral buds will suffice. The young buds, immediately after abstriction, resemble in structure the primitive bud and the ventral stolon, consisting of an external layer of ectoderm and of the seven strands mentioned above. We have already mentioned (p. 471) the different views held by GROBBEN and ULJANIN as to the significance of these seven strands in connection with the further development of the bud. We have as yet comparatively few statements as to the way in which the young bud develops out of these seven primary rudiments, and further investigation of this point is very desirable.

The young bud (Fig. 246 *A*), from the time when it becomes detached from the primitive bud, is a completely independent organism enclosed in ectoderm, but attached externally, like a parasite, to the body of the "nurse" or to the foster form. This attachment is brought about by means of a thickening of the ectoderm (*ec*). In the youngest buds observed by ULJANIN, the body was already elongated, and the organs, as compared with the seven cell-strands, had already changed their positions. The dorsal side can now be distinguished by the presence of the large rudiment of the nervous system (*n*), while, on the ventral side, the pericardial rudiment (*p*) is to be observed. Between these two, the pharyngeal rudiment (*ph*) can be seen, while the paired genital rudiment, forming a common cell-mass, has shifted into the neighbourhood of the point of attachment of the bud. The ectodermal invagination (*cl*), behind the nervous system, represents the rudiment of the atrium. This is one of the principal points in which ULJANIN's description differs from that of GROBBEN. According to the latter author, the atrium arises from paired rudiments (the strands *k* in Fig. 242) already present in the primitive bud. At the two sides of the body, the muscle-plates (*m*), lying in close contact with the ectoderm, have extended considerably.

In the course of further development a cavity forms in the pharyngeal rudiment and gradually enlarges (Fig. 246 *B*, *ph*); this soon opens externally through an aperture (branchial aperture, *i*) resulting from an ectodermal invagination which forms opposite to the atrial aperture. The muscle-hoops which lie in the neighbourhood of the atrial and branchial apertures now become separated from the muscle-plates. The pharyngeal cavity gives off a pair of flat lamella-like diverticula (*l*) towards the dorsal side, and these, as **Grobben** had already observed, embrace the neural rudiment (*n*) laterally. According to **Uljanin**, these diverticula are concerned principally in the formation of the branchial lamellae. A process (*d*) running back from the pharyngeal cavity develops into the intestine of the bud, its blind end becoming applied to the wall of the dilating atrial cavity (*cl*). The latter extends specially towards the sides of the body, so that, as **Grobben** observed, at a certain stage it resembles a pair of spectacles. Its lateral extensions become applied to the wing-like processes of the pharyngeal cavity (*l*). This juxtaposition of the atrial and pharyngeal walls gives rise to the branchial lamellae (Fig. 246 *C*, *k*), in which the gill-clefts then break through. The rudiment of the central nervous system undergoes a transformation closely

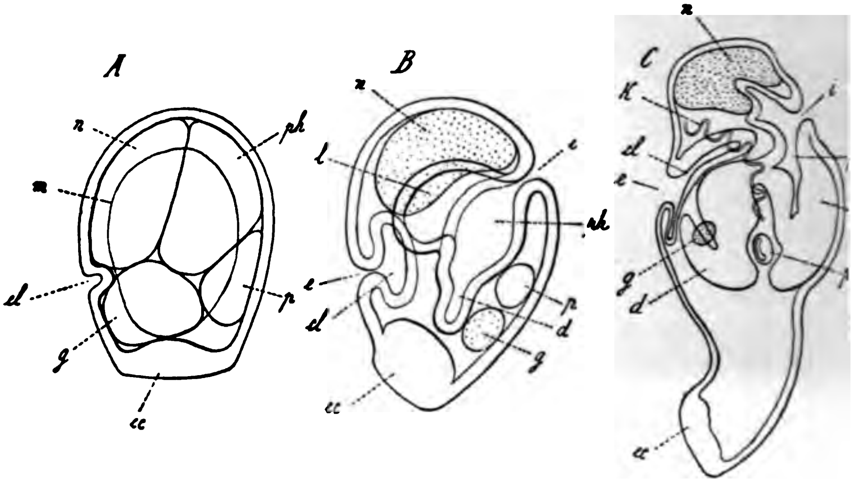

FIG. 246—Diagrams illustrating three stages in the development of the lateral buds of *Doliolum*, seen from the side (*A* and *B*, after **Uljanin**; *C*, after **Grobben**). *cl*, atrium; *d*, enteric rudiment; *e*, atrial aperture; *ec*, basal ectodermal thickening; *es*, endostyle-rudiment; *g*, genital rudiment; *i*, branchial aperture; *k*, gill; *l*, lateral outgrowths of the pharyngeal cavity; *m*, outline of the muscle-plates; *n*, neural rudiment; *p*, pericardial rudiment; *ph*, pharyngeal rudiment.

resembling that described above for the larva on leaving the egg (p. 386). An anterior narrowed portion becomes the ciliated pit, a posterior process changes into an unpaired nerve running from the ganglion, while a third part of the rudiment develops into the ganglion and the sub-ganglionic body. The pericardial sac (*p*) and the heart seem, as in the larva, to develop according to the type prevalent among all Tunicates. The genital rudiment (*g*) degenerates in the lateral buds. It can still be recognised for some time to the left side of the intestinal loop as a mass of cells. In the buds which become sexual individuals this rudiment breaks up into two unequal portions, the anterior smaller part developing into the ovary and the posterior larger portion into the testis.

The later differences found in the lateral and median buds and the sexual individuals are explained by the varied forms which these finally attain. The median buds and the sexual individuals tend to assume the characteristic barrel-shape, while the lateral buds increase in height and, as mentioned above, adopt the somewhat asymmetrical spoon-shape, owing to the dilation of the atrial aperture and cavity.

Two more remarkable and insufficiently understood genera, *Anchinia* and *Dolchinia*, which, in the structure of their gills, form a transition between *Pyrosoma* and *Doliolum*, have still to be added. In these genera only parts of detached stolons are known, the asexual "nurse" form, developed from the egg which produced the stolon, being still undiscovered. We shall have to compare these stolons with the dorsal outgrowth of the first "nurse" generation of *Doliolum*. As a rule the stolon, in *Anchinia* and *Dolchinia*, consists of a tube which, in cross-section, is round (the colonial tube, Fig. 247, *c*), and seems to be formed of a single layer of flat ectoderm-cells. The interior of the tube is filled with a gelatinous mass, in which are embedded mesoderm-cells varying in shape. The external surface of the ectodermal tube which is covered by a cellulose mantle carries the various buds (*z*) which, in later stages of their development, seem to grow out on stalks from thickened parts of the ectoderm. The buds are thus here, as in *Doliolum*, only attached to the exterior of the so-called stolon. They appear irregularly arranged along the stolon, quite young buds being found among others half-developed, and others again fully developed. In a transverse section of a stolon, however, the

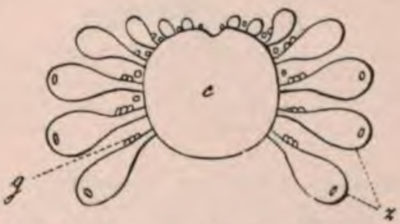

FIG. 247.—Diagrammatic cross-section through the colonial tube (dorsal outgrowth) of *Dolchinia* (after KOROTNEFF). *c*, colonial tube; *g*, buds giving rise to the sexual individuals; *z*, zooids.

youngest buds are found to occupy the dorsal middle line, while the older buds shift to the sides of the stolon (Fig. 247).

Three different forms have been found in the colonies known of *Anchinia*, but these are regarded by **Barrois** (No. 77) as fragments of the same stolon in different stages of development.

I. There are fragments with zooids which, even when developed, remain comparatively small, which are without genital organs and are incapable of reproducing themselves by budding. These zooids are distinguished from those of the sexual generation (III.) by the absence of the three pigment-spots and of the papilla-like processes above the apertures of the body. An accumulation of pigment is found, on the other hand, at the base of the peduncle (Fig. 248 *A*, *pd*). On the dorsal side of the tube which bears these zooids a slightly coiled thread is found running longitudinally (Fig. 249, *st*); this consists apparently of ectoderm and entoderm (Fig. 249 *B*), and is assumed by **Barrois** to be the actual proliferating stolon, from which the buds of this generation grow out laterally.

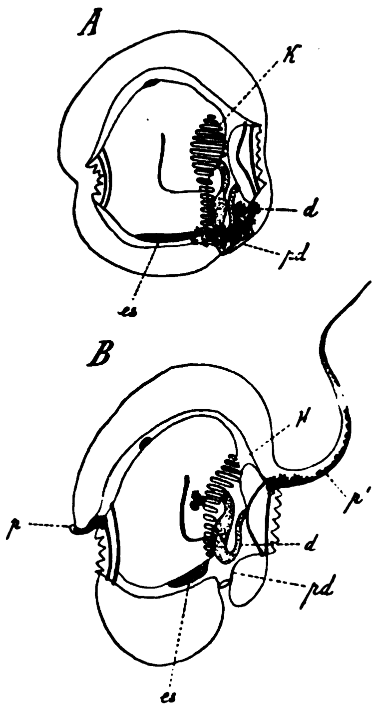

Fig. 248.—*A*, first asexual generation of *Anchinia*; *B*, sexual generation (after Barrois). *d*, alimentary canal; *es*, endostyle; *k*, gill; *p*, papilla above the branchial aperture; *p'*, papilla above the atrial aperture; *pd*, peduncle.

II. Fragments with zooids resembling in shape the sexual forms (III.) in which also the rudiments of genital organs appear. These rudiments, however, degenerate later. These zooids, which may be compared to the phorozooids of *Doliolum*, do not seem to reproduce themselves either sexually or asexually. They do not, however, directly nourish the buds of the sexual generation, for these grow out independently on the colonial tube. In the tube on which these zooids are found, the structure above described as the proliferating stolon is no longer to be seen; but there are clusters of very small buds which **Barrois** holds to be derived from the disintegrated proliferating stolon.

III. Fragments with sexually mature zooids (Fig. 249 *B*). Each of these zooids is distinguished by the possession of a papilla-like process (*p*, *p'*) above the branchial and atrial apertures, that over the latter being specially large. On these processes, there are accumulations of pigment; a third pigment-spot occupies the middle of the body. These zooids are further distinguished by the great depth of the body and the abbreviation of the endostyle (*es*). The young buds from which they are derived are found scattered between the developed zooids on the colonial tube.

Barrois compares the zooids of type I. to the lateral buds of *Doliolum*, and those of the second type to the phorozooids or foster forms of *Doliolum*. The three different forms of the asexually produced generation are believed to develop in succession in the colony of *Anchinia*, the one replacing the other. On the youngest stolons, zooids of the first type develop; later, when the proliferating stolon proper breaks up into portions, only zooids of type II. develop, and these finally are replaced by the sexually mature forms.

The budding of *Anchinia* has been described most in detail by **Barrois** (No. 77) and is in many respects of great interest. It appears that the development of the three types of buds takes place as a rule in a very uniform manner, although considerable variety prevails in the time and manner of development of the organs into which we cannot here enter further. In *Doliolum*, the proliferating stolon is composed of a number of longitudinal strands and, consequently, even the youngest buds show the separate rudiments of the most important organs, but the stolon of *Anchinia* (Fig. 249 *B*) is composed merely of ectoderm and an inner cell-mass called by **Barrois** entoderm. The same structure is exhibited by the very small or youngest buds in which an ectodermal layer and a central cell-mass can be distinguished. The latter becomes differentiated, in a way as yet insufficiently known, into the nervous system, the enteric canal (pharynx + intestine), the pericardial vesicle and (in types II. and III.) into the rudiment of the genital organs which appears very early. Certain features of the later development of type I. are of special interest, as showing close resemblance to the manner of development of the Ascidian embryo. The nervous system is found in the form of a tube running along the whole dorsal side of the bud (Fig. 250 *A*, *n*). The anterior part of this tube gives rise to the ganglion and the ciliated pit, while the posterior part changes into an unpaired nerve-strand (Fig. 250 *B*) which runs backward and ends in a visceral ganglion. This nerve no doubt corresponds to the strand observed by **Uljanin** in *Doliolum* and called the branchial nerve. It may be regarded as the homologue of the "cordon ganglionnaire viscéral"

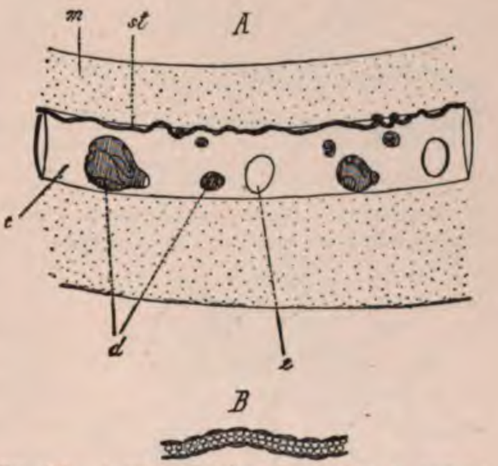

FIG. 249.—*A*, part of a stolon of *Anchinia*; *B*, part of the proliferating stolon, more highly magnified. *c*, colonial tube; *d*, younger buds; *e*, points of attachment of older individuals; *m*, cellulose mantle; *st*, proliferating stolon.

found by **van Beneden** and **Julin** (No. 7) in Ascidians. The peribranchial sacs arise from paired ectodermal invaginations (*cl*) which in all respects recall the atrial vesicles of the Ascidian larva and the corresponding rudiments in the embryo of *Pyrosoma*. These paired ectodermal invaginations increase in size and come into contact with two lateral, wing-like outgrowths of the pharynx. The close apposition of the walls of these outgrowths and those of the peribranchial sacs leads to the formation of the branchial lamellae in which the gill-clefts soon break through. The atrial cavity proper results from a fusion of the two ectodermal invaginations resembling that which takes place in the Ascidians (p. 366). A further agreement with the course of development in the Ascidiacea is found in the manner in which the pericardial vesicle develops (Fig. 250 *B*, *p*), this vesicle being here also a derivative of the entoderm. It is originally a solid outgrowth of the pharynx in the centre of which a lumen soon forms which becomes connected with the pharyngeal cavity, so that the whole rudiment now represents a diverticulum of the pharynx corresponding in position to the posterior end

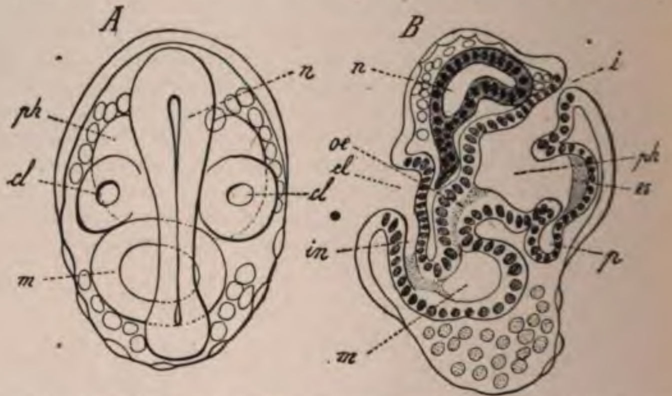

Fig.—250.—*A*, dorsal aspect of a bud of the first asexual type of *Anchinia*; *B*, median section through an older stage (after **Barrois**). *cl*, atrial rudiment (paired in *A*); *es*, endostyle; *i*, branchial aperture; *m*, stomach; *n*, nervous system; *oe*, oesophagus; *p*, pericardial rudiment; *ph*, pharynx.

Fig. 251.—Portion of a colonial tube of *Dolchinia* with its zooids (after **Korotneff**). *a*, points of attachment of older zooids; *c*, colonial tube; *g*, buds giving rise to the sexual individuals; *g'*, primitive bud of the sexual gemmae; *u*, wandering primitive buds; *z*, zooid.

of the endostyle (*es*). From this diverticulum, the pericardial vesicle becomes separated in late stages. It is probable that a part of the diverticulum is retained here as an epicardium (p 368.).

Of the form known as *Dolchinia* (KOROTNEFF, No. 82), the only colonies which have been found have zooids corresponding to types II. and III. of *Anchinia* (*i.e.*, foster-forms and sexual gemmae, Fig. 251). The individuals belonging to type II. (phorozooids) are here closely crowded on the common colonial tube, while the sexual gemmae (*g*) develop on the peduncles of the foster forms (in the same way, therefore, as in *Doliolum*). These foster forms (phorozooids) of *Dolchinia* (*z*) become very easily detached from the colony and then lead an independent pelagic existence. In the same way, the sexual individuals sever themselves from the phorozooids. Migrating primitive buds (*u*) may be seen on the colonial tube. These are able to move from place to place (as was stated by BARROIS for *Doliolum* and *Anchinia*) by means of large, amoeboid cells (*c*) adhering externally to the bud on each side (Fig. 252 *A*, *a*). Small secondary portions (*b*) become detached from the primary primitive buds by fission, and these either attach themselves to the colonial tube itself and grow into foster forms (phorozooids), or else settle on the peduncle of one of the developing foster forms and there change into primitive buds of the sexual gemmae carried by that individual (Fig. 251, *g*). The primitive bud seems to produce only sexual gemmae, and does not itself develop further. For the further development of the buds, which has not been made out quite clearly, we must refer the reader to the statements of KOROTNEFF (No. 82). Here also only an outer and inner layer of cells can at first be distinguished. In the latter, a mass of large cells (Fig. 251 *B*, *x*) soon separates from a mass of small cells. The large cells are said to be the rudiment of the nervous system and the genital organs, while the mass composed of small cells breaks up into three strands, the median strand (*ph*) representing the rudiment of the pharynx, while the lateral strands are thought to represent the muscle-rudiments. The atrium arises as an ectodermal invagination, and the pericardial vesicle as a diverticulum of the pharynx.

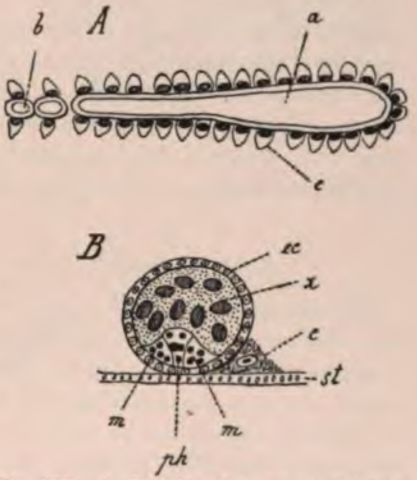

FIG. 252.—*A*, Primitive bud (*a*) of *Dolchinia* with two detached buds (*b*); *B*, Transverse section through an attached bud of *Dolchinia* (after KOROTNEFF). *a*, primitive bud; *b*, detached buds; *c*, amoeboid transporting cells; *ec*, ectoderm; *m*, muscle-rudiments; *ph*, pharyngeal rudiment; *st*, epithelium of the colonial tube; *x*, mass of large cells.

3. Pyrosoma.

Since the development of the four primary Ascidiozooids of the *Pyrosoma* colony is closely connected with that of the Cyathozooid, and takes place almost entirely within the period of embryonic life, it has already been described above. It still remains for us to describe the process of budding by which the other individuals found in the adult colony are produced. These processes have been described by Huxley (No. 72) and Kowalevsky (No. 71), and later by Joliet (No. 73) and Seeliger (No. 76). The first development of the proliferating stolon has also recently received some attention from Salensky (No. 74). The chief point which we shall have to consider is the origin of the primary organs in the proliferating stolon. The further development of the zooids agrees so closely with that of the four primary Ascidiozooids described above that we need only refer to it briefly. The following account is based mainly on the detailed observations made by Seeliger.

A. Development of the Proliferating Stolon.

The individual zooids of *Pyrosoma* start budding very early, even at a time when their individual independence is not fully attained, as they are still connected with the stolon from which they were produced. In such a stolon (Figs. 253 and 267) the individuals increase in size from its proximal to its distal end, those lying furthest from the parent (Fig. 253 *III*) being the most developed and exhibiting the almost perfect organisation of a *Pyrosoma* zooid and the first rudiments of the future proliferating stolon.

The first indication of this organ is an outgrowth (*d*) of the branchial or pharyngeal sac directed toward the ectoderm; this lies at the posterior end of the endostyle (*es*), ventrally to the heart (*hz*), and appears surrounded by elaeoblast-tissue (*eb*). This structure is known as the *entoderm-tube*, the *entoderm-process*, or, on account of its close relation to the endostyle of the parent, the *endostyle-process*. It seems probable that the stolon in every case is nothing more than the remains of the entodermal tube which connects the entoderm-sacs of two neighbouring buds (Fig. 253, *v*).

Another element which enters into the formation of the proliferating stolon is a group of closely crowded mesoderm-cells (*ms*) embedded in the elaeoblast. This must be regarded as the *rudiment of the genital strand* of the budding stock. Even earlier one or more large cells are seen in it which can be recognised as young egg-cells. The rudiment of the genital strand has, in its turn, become abstricted from the genital rudiment (*o*, *h*) of the parent (*cf.* *ms*, in individuals *II* and *III*).

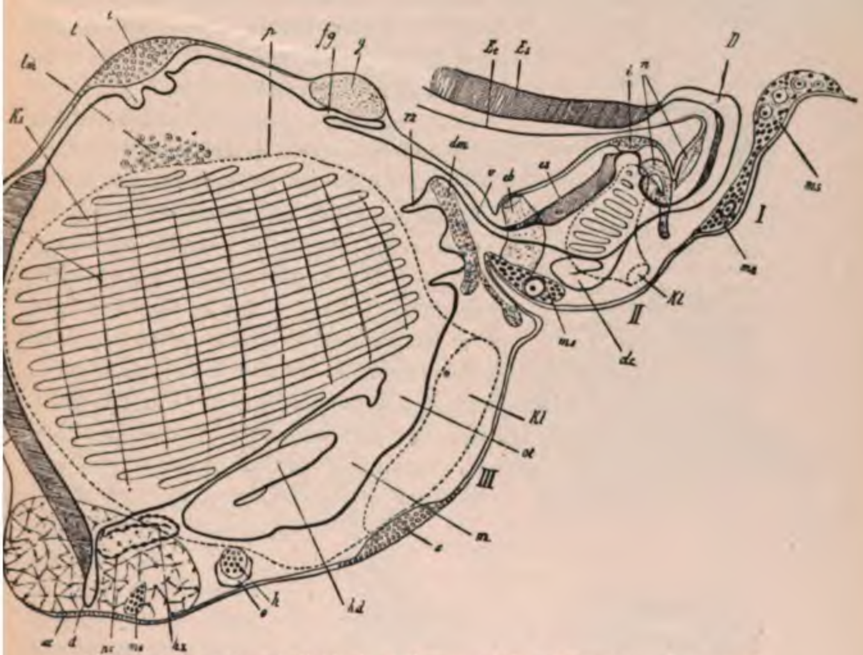

FIG. 253.—A chain of three individuals of *Pyrosoma* (after SEELIGER). *I*, youngest, proximal bud; *II*, middle and *III*, oldest, distal bud (nearly fully developed). *D*, point at which the endostyle-process of the parent enters; *d*, endostyle- or entoderm-process; *dc*, rudiment of the alimentary canal; *dm*, elongate cell-mass; *e*, rudiment of the atrial aperture; *eb*, elaeoblast; *Ec*, ectoderm of the parent; *ec*, ectoderm-plate of the stolon-rudiment; *Es*, endostyle of the parent; *es*, endostyle; *fg*, ciliated pit; *g*, ganglion; *h*, testis; *hd*, intestine; *hz*, heart; *i*, rudiment of the branchial aperture; *kl*, atrium; *ks*, gill-clefts; *lf*, internal longitudinal gill-bars; *lm*, lenticular phosphorescent organ; *m*, stomach; *ms*, genital strand; *n*, rudiment of the nervous system; *o*, ovary (egg-follicle with egg); *oe*, oesophagus; *p*, dotted line indicating the boundary of the peribranchial sacs; *pc*, pericardium; *rz*, languets; *t*, tentacle-rudiment; *v*, duct connecting the enteric cavity of the second individual with that of the third.

These two rudiments (those of the entoderm-process and the genital strand) can also be recognised in a transverse section through this region of the body of the parent (Fig. 255). We then also see that the entoderm-process is still accompanied by isolated mesenchyme-cells (Fig. 254, *ms*). At the two sides of the process especially, mesenchyme-cells can be seen arranged in two strands (*ms*). The strand on the right is continued as far as the pericardial vesicle of the parent. These strands are the so-called mesoderm-strands of the proliferating stolon mentioned above, the development of which in the four primary Ascidiozooids was followed by **Salensky** (No. 74). The part played by these mesoderm-strands in the further development of the proliferating stolon and of the buds is still obscure, and therefore no further note will be taken of it.

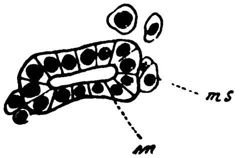

Fig. 254.—Transverse section through the entoderm-process (*en*) of a very young stolon-rudiment of *Pyrosoma* (after **Seeliger**). *ms*, surrounding mesenchyme-cells.

That part of the *ectoderm* towards which the entoderm-process is directed (Fig. 253, *ec*) seems somewhat thickened even in the early stages. The actual stolon now begins to form in this region as a rapidly increasing swelling. The conical process that results (Fig. 256 *A*) is the stolon at the distal end of which transverse constrictions soon lead to the abstriction of individuals (Fig. 256 *C*).

In transverse sections through a developing stolon (Fig. 255), the rudiments of the *peribranchial tubes* (*p*) can already be seen at either side of the entoderm-process. How these rudiments arise is not yet accurately known, but as they are found connected by their distal ends in a certain way with the genital strand, **Seeliger** is inclined to derive them from the latter. He therefore regards the peribranchial tubes in the buds of *Pyrosoma* as mesodermal structures, although, in the Cyathozooid and in the first four Ascidiozooids, they are undoubtedly derived from the ectoderm. [Judging by what is known of the development of these organs in other Tunicates, and of the relations of the genital rudiment in all other animals, it appears to us in the highest degree improbable that there is any connection between the two structures, *i.e.*, peribranchial tube and genital strand, or between the latter and the nervous system].

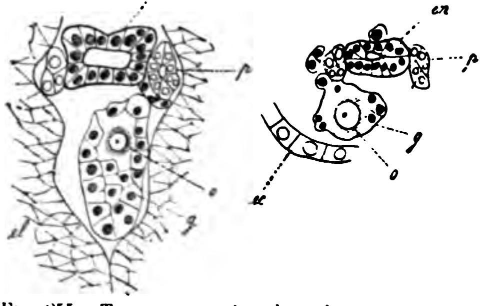

Fig. 255.—Transverse section through two very young stolons of *Pyrosoma* (after **Seeliger**). *ec*, ectoderm; *el*, elaeoblast-tissue of the parent; *en*, entoderm-process; *g*, genital strand; *o*, young egg-cell; *p*, peribranchial tubes.

The rudiment of the *nerve-tube* of the stolon also, according to **SEELIGER**, is derived from the genital strand. In very young stolons (Fig. 256 *A*) the distal end of the latter appears to bend round to the upper side. (The lower side of the stolon is marked by the position of the genital strand *g*). This upper part of the genital strand becomes, in the further course of development, separated from the lower part, and, according to **SEELIGER**, becomes the rudiment of the neural tube (Fig. 256 *C*, *n*), a lumen very soon appearing inside it.

SEELIGER thus holds that not only the genital organs of the bud but also its peribranchial tubes, and a large part of all its mesodermal structures, are derived from the genital strand. The group of cells, which we described as the simple rudiment of the genital strand, has thus, in his eyes, a far wider significance in the development of the proliferating stolon. He has therefore designated it as the *germ-strand* or the *mesodermal germ-mass.*

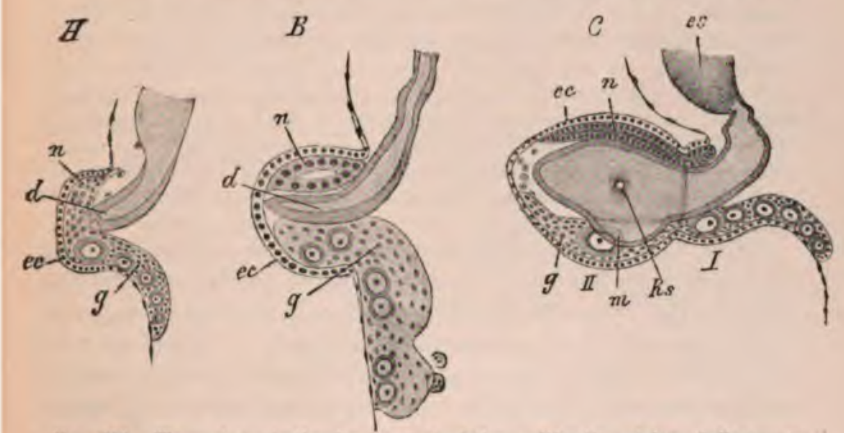

FIG. 256.—Three stages in the development of the proliferating stolon of *Pyrosoma* (after SEELIGER). In *C*, the separation of the two individuals (*I* and *II*) is already indicated. *d*, entoderm-process; *ec*, ectoderm; *es*, endostyle of the parent; *g*, genital strand; *ks*, first gill-slits; *m*, rudiment of the alimentary canal proper; *n*, rudiment of the neural tube.

The fact that SEELIGER traces back the peribranchial tubes and the neural tube in the buds of *Pyrosoma* to the mesoderm cannot fail to awaken surprise when it is remembered that the rudiments of these organs are undoubtedly derived from the ectoderm, not only in the Cyathozooid but also in the four primary Ascidiozooids. In our attempts to interpret the structure and significance of the proliferating stolon, we naturally seek for agreement between the development of its buds and that of the first four Ascidiozooids. When we consider that the proliferating stolon must evidently be traced back to the remains of the duct connecting each zooid with its neighbours (Fig. 196, *s*, p. 402; Fig. 253; *v*), and when we remember that in the four primary Ascidiozooids continuations of the peribranchial tubes also are originally contained in these ducts, we shall be led to ask whether, after the abstriction of those parts of the peribranchial tubes that belong to the separate Ascidiozooids from the ducts, remains of the tubes may not be retained in the form of inconspicuous cell-groups which might easily be mistaken for mesoderm, and from which the peribranchial tubes of the stolon that develops later are derived. The rudiment of all the peribranchial tubes which form later could in this way be traced back to the peribranchial tubes in the Cyathozooid. Indeed, an extension of this way of viewing the matter might perhaps lead us to conjecture that the explanation of the many conflicting statements as to the rise of the primary organs in the proliferating stolon in the various groups of Tunicates is perhaps to be found in the theory that *no primary organs originate afresh in the proliferating stolon, but that they can all be traced back to corresponding organs in the embryo from which they become abstricted.* Such a conjecture receives special support from the condition of the ventral stolon in *Doliolum*.

We might well feel inclined to find some genetic relation between the peribranchial tubes of the *Pyrosoma* bud and the so-called mesoderm-strands of the stolon mentioned above. After SALENSKY's statements as to the rise of these strands (No. 74), such an assumption seems to us improbable, and we prefer to derive the mesodermal structures of the bud from these strands.

When the stolon is perfectly developed, the typical aspect presented by it in cross-section (which recurs also in the *Salpidae*) is that depicted in Fig. 257. The entoderm-tube (*en*) is cruciform, two limbs of the cross extending upwards and two downwards; the fold between the former gives rise to the endostyle, while the two latter may already be considered as the rudiment of the stomach and intestine. In the spaces between the four outgrowths of the entoderm-tube are four strands, three of which already possess lumina. The dorsal strand (*n*) is the nerve-strand, the lateral strands are the peribranchial tubes (*p*), and the ventral space is occupied by the genital strand (*g*). In later stages, by the development of the primary body-cavity, these strands become separated from the entoderm-tube; the mesoderm (*ms*), at the same time, appears both as isolated mesenchyme-cells and as cell-masses which, according to SEELIGER, must to some extent be traced back to the genital strand (Fig 255 *B*, *g*).

The breaking up of the stolon into separate individuals takes place by means of constrictions (Fig. 256 *C*). Through the development of these, the peribranchial tubes, the neural tube and the genital strand of each individual become completely separated from the corresponding rudiments of the adjacent buds. The enteric tube retains its continuity longer; even in highly developed buds we find the enteric rudiment still connected with that of the next bud (Fig. 258, *v*). The distal individual of the stolon is always the most developed (*cf.* also Fig. 267). When five individuals have become marked off on the stolon through the appearance of constrictions, the distal individuals always seems to become detached. More than five individuals are consequently never found on one stolon.

B. Further Development of the Buds.

A fact already pointed out in connection with the development of the four primary Ascidiozooids (p. 407) must again be emphasised here, viz., that the longitudinal axis of the stolon does not coincide with the later longitudinal axis of the developing buds, but rather appears to lie at right angles to it (Figs. 258, 267). The longitudinal axis of the segments of the stolon changes into the dorso-ventral axis of the developed bud. The axis which becomes the later longitudinal axis of the body is one which we may imagine as cutting the longitudinal axis of the stolon at right angles, *i.e.*, from the neural side to that of the genital strand. The ends of such an axis would be indicated by the rudiments of the branchial and atrial apertures.

From the ectoderm of the stolon is developed the *integument* of the bud which, on its outer surface, secretes the cellulose mantle. According to SEELIGER, this secretion takes place here in the way described for other Tunicates by SEMPER, HERTWIG and others. When, therefore, SALENSKY emphasises the fact that the first rudiment of the cellulose mantle is yielded by the Cyathozooid, the four primary Ascidiozooids at first taking no part in the secretion of the cellulose substance, his remark applies only to the first stages of development. The further enlargement of the cellulose envelope proceeds from the Ascidiozooids.

The branchial and atrial apertures (Figs. 253, 259, *i*) first appear as simple ectodermal invaginations. These invaginations fuse with the wall of the branchial sac or atrial cavity, the apertures breaking through later at the points of fusion. Near the point at which the branchial aperture forms, the branchial sac (*i.e.*, the entoderm) gives off the first bud-like rudiments of the crown of tentacles that encircles the entrance to this part of the alimentary canal (Fig. 253, *t*).

The entoderm-sac of the bud first forms the *branchial sac* or pharynx. It has already been mentioned (p. 488) that this is cruciform in transverse section (Fig. 257), two of the outgrowths being directed upward and two downward. The upward outgrowths are separated from each other by a median fold in which can be recognised the first rudiment of the *endostyle* (Fig. 259, *es*). The latter is completed later through the rise of two lateral folds, the median groove becoming the base of the endostyle-furrow. The condition here, according to JOLIET and SEELIGER, corresponds perfectly with that described for the four primary Ascidiozooids (p. 406). The rudiment of the endostyle originally occupies the upper or neural wall of the branchial sac, its proximal end corresponding to the later anterior end. The endostyle-rudiment, according to JOLIET (as described on p. 413), here passes over into the remarkable provisional structure known as the *diapharyngeal band*, which runs towards the ganglion below the branchial aperture.

The two lower outgrowths of the branchial sac, as seen in transverse section, are the rudiment of the *alimentary canal* proper (*i.e.*, oesophagus, stomach and intestine). These two outgrowths communicate at the distal end of the bud. This rudiment, which soon becomes abstricted from the branchial sac, is thus horse-shoe-shaped. The right portion, which retains a connection with the branchial sac, gives rise to the oesophagus and stomach, while the left portion becomes the intestine, which ends blindly at first and later opens into the atrial cavity (Fig. 253). SEELIGER's account agrees fairly well with SALENSKY's description given above (p. 408). The digestive gland, which originates as an outgrowth, arises at the boundary between the stomach and the intestine.

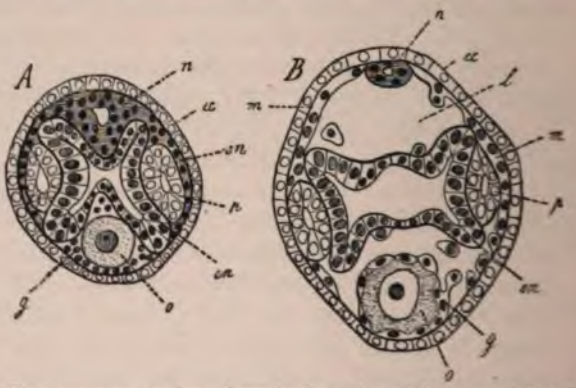

FIG. 257.—Two transverse sections through the stolon of *Pyrosoma* (after SEELIGER). *ec*, ectoderm; *en*, entoderm; *g*, genital strand; *l*, body-cavity; *m*, mesoderm; *n*, neural tube; *o*, young egg-cell; *p*, peribranchial tubes; *sn*, rudiment of the lateral nerves.

The lateral walls of the branchial sac are occupied by the *gill-clefts*. These are at first (Fig. 256 *C*, *ks*) more or less round perforations of the contiguous walls of the entoderm-sac and the peribranchial sacs (Fig. 258, *p*), but they very soon become elongate (Fig. 259) The inner longitudinal bars of the branchial sac (Fig. 253, *lf*) now develop at right angles to the clefts. As the slits break through chiefly in consequence of an outgrowth of the entoderm-sac, they appear to be lined with entoderm.

The two peribranchial sacs, which early lost their connection with those of the adjacent bud, by growing towards each other on the lower side of the stolon and fusing, give rise to the unpaired *atrial cavity* (Figs. 253, *kl*, 259, *cl*).

Finally, the outgrowths of the dorsal wall of the branchial sac known as the *languets* (Fig. 253, *rz*) develop.

The rudiment of the *central nervous system* appears at first as a tube running along the whole length of the upper side of a stolon-segment (Fig. 256, *n*); later, however, the proximal part of this tube develops into a large vesicle, while the thinner, distal part disappears. Two lateral outgrowths of the proximal part of the neural tube (Figs. 258, *s*, 259) can be seen very early (Fig. 257 *A*, *sn*); these soon change into hollow processes which encircle the alimentary canal and unite on its lower side. These are the rudiments of the so-called *lateral nerves*. A growth of the cells on the dorsal wall of the cerebral vesicle yields the rudiment of the *ganglion* proper, which later gives off the lateral nerves that run backward along the dorsal surface of the adult in the form of solid strands with terminal ganglionic swellings. The remains of the cerebral vesicle develop a connection with the branchial sac and become transformed into the *ciliated pit*

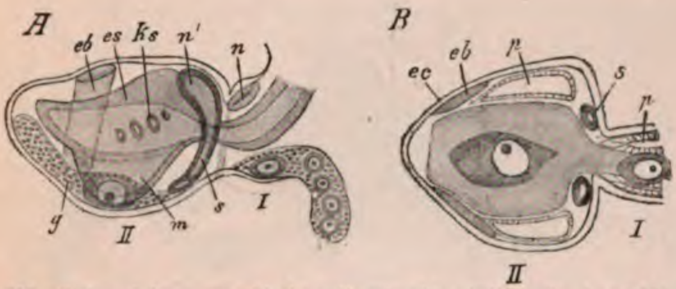

FIG. 258.—Stolon of *Pyrosoma* with the rudiments of two individuals, *I* and *II* (after SEELIGER). *A*, side view; *B*, seen from the side on which the genital strand is situated. *eb*, rudiment of elaeoblast; *ec*, ectoderm; *es*, endostyle-rudiment; *g*, genital strand; *ks*, gill-clefts; *m*, rudiment of the stomach and intestine; *n*, nervous system of bud *I*; *n'*, nervous system of bud *II*; *p*, peribranchial tubes; *s*, rudiment of the lateral nerves (in *B*, seen in transverse section).

(Fig. 253, *fg*). The posterior blind end of this tube gives rise to the *subneural gland.*

Isolated mesenchyme-cells are early met with in the primary body-cavity of the stolon (Fig. 257). **Seeliger** traces these to a great extent to cells of the genital strand that have become independent (Fig. 255 *B*). Some of these mesenchyme-cells become transformed later into connective tissue-cells and blood-corpuscles. Others take part in the formation of the *lenticular* and *elongate cell-masses.* The elongate mass which belongs to the dorsal region (Fig. 253, *dm*) seems to be connected with the formation of blood-cells. The cells of the lenticular masses (Fig. 253, *lm*), on the contrary, contain oil globules in their protoplasm in later stages, and are regarded as phosphorescent organs. The *elaeoblast* also (Figs. 253, *eb*, 258, 259) arises from an

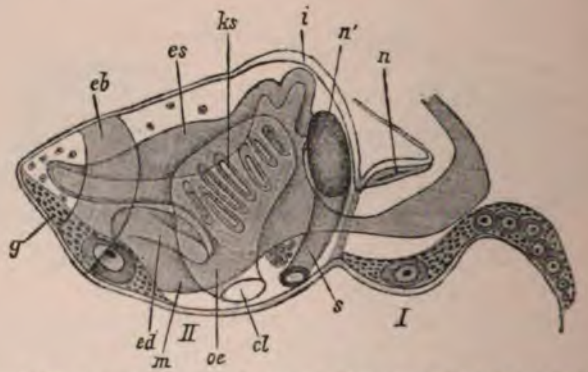

Fig. 259.—Stolon of *Pyrosoma* with the rudiments of two individuals, *I* and *II* (after **Seeliger**). *cl*, atrium; *eb*, elaeoblast; *ed*, intestine; *es*, endostyle; *g*, genital strand; *i*, branchial aperture; *ks*, gill-clefts; *m*, stomach; *n′*, neural tube of bud *I*; *n*, rudiment of ganglion of bud *II*; *oe*, oesophagus; *s*, lateral nerves.

originally paired accumulation of mesenchyme-cells lying immediately below the entoderm in the distal region of the stolon-segment. The two halves of the elaeoblast-rudiment unite later at their upper and lower surfaces, a perfect circle being thus formed which soon, through deposits of nutritive material, develops the typical character of elaeoblast-tissue.

The *musculature* also which, in *Pyrosoma*, is reduced to a few slight strands running round the branchial and atrial apertures and in the outer wall of the peribranchial cavity, is derived from the mesenchyme-cells. These at first unite to form cell-strands in the peripheral parts of which the fibrils of contractile substance first appear. As these fibrillae increase in size, they become band-like. In transverse section, they then appear radially arranged, while the centre of the muscle-bundle is occupied by the undifferential protoplasm and nuclei of the cells.

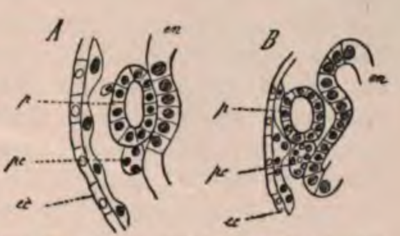

FIG. 260.—Two early stages in the development of the pericardial vesicle in the buds of *Pyrosoma* (after SEELIGER). *en*, entoderm (wall of the enteric rudiment); *ec*, ectoderm; *p*, peribranchial sac; *pc*, rudiment of the pericardial vesicle.

The first rudiment of the *pericardial vesicle* is also traced back, by SEELIGER, to a small group of mesenchyme-cells which can be seen beneath the distal end of the right peribranchial tube. In this cell-group (Fig. 260, *pc*) a lumen soon appears which is the *pericardial cavity;* at a later stage, the rudiment of the heart (*hz*) arises through the invagination of that part of the wall of the pericardial vesicle which is in contact with the wall of the intestine (Fig. 261). The pericardial vesicle originally lies on the right side of the bud, but wanders later towards the median plane and thus reaches the dorsal side of the endostyle, process (Fig. 253, *hz*). It has therefore in *Pyrosoma*, a position unlike that occupied by it in the other Ascidiacea, where, as described above (p. 370), the heart lies on the ventral side of the endostyle-process (epicardium) in such a way that the epicardial lamella brings about the closure of the cardial tube.

FIG. 261.—Two later stages in the development of the pericardial vesicle in the bud of *Pyrosoma* (after SEELIGER). *ec*, ectoderm; *el*, elaeoblast; *en*, entoderm (wall of intestine); *pc*, pericardial vesicle; *hz*, rudiment of heart.

In each bud, the genital strand (Fig. 259, *g*) gives rise to the *genital organs* of the individual and to the genital strand of the stolon produced by that individual. At an early stage, the genital strand is found to break up into a distal and a proximal part. The distal part, which is embedded in the elaeoblast-tissue (*eb*), becomes abstricted and gives rise to the *genital strand of the stolon.* In the proximal part, which represents the rudiment of the *genital organs*, lies the egg-cell surrounded by smaller undifferentiated cells from which the follicular epithelium is derived. A cell-mass attached to the follicular epithelium and lying proximally to the left of the egg-cell represents the rudiment of the testis (Fig. 253, *h*). In the young rudiment of this organ, a superficial epithelium-like layer of cells can be distinguished from a central mass of cells. The seminal duct forms as an outgrowth of the peripheral epithelial layer. The oviduct arises in a similar way from the egg-follicle, and both ducts open into the atrium. In later stages, the rudiment of the testis becomes lobate. Two eggs occasionally occur in the egg-follicle, one being larger than the other. The smaller egg seems to disintegrate later, so that only one egg is maturated in each individual in *Pyrosoma* as in the *Salpidae*.

4. Salpidae.

The processes of budding in the *Salpidae* early attracted the attention of zoologists and have been repeatedly investigated. Eschricht, Huxley (No. 95), Leuckart (No. 98), and Vogt laid the foundations of our knowledge of this subject, and in more recent times it has been increased through the application of modern methods by Kowalevsky (No. 96), Todaro (No. 107), Salensky (Nos. 101 and 102), Seeliger (No. 105) and Brooks (Nos. 92 and I.). No very satisfactory comprehension of the ontogenetic processes has, however, as yet been attained. Brooks was able to trace back the budding of the *Salpidae* to the type observed in *Pyrosoma*, pointing out that the biserial arrangement of the buds on the stolon of the former is the result of lateral shifting and the simultaneous rotation of the buds round their longitudinal axis. Since this latter point was overlooked by the other authors, we must regard with some doubt their statements as to the rise of the organs in the buds.

In *Salpa*, the buds arise on a proliferating stolon (Fig. 262, *st*) which must be regarded as in every way homologous with that of *Pyrosoma*. In older embryos (Figs. 216, *st*, 224 *B*, *s*) this can be seen as a conical outgrowth at the posterior end of the endostyle growing out between it and the opening of the oesophagus rather to the left side of the body. When the stolon grows longer, it appears embedded in the cellulose mantle of the solitary individual. A cavity containing the stolon develops, however, in the mantle-substance (Fig. 262, *h*) and this finally opens externally (*o*), so that the distal end of the stolon from which the mature buds are abstricted, projects out freely. The position of the stolon differs in the various species.

In *Salpa pinnata*, *S. affinis and S. dolichosoma*, it is more or less straight and runs forward along the ventral side of the body. In *S. runcinata-fusiformis* and *costata-Tilesii*, it at first runs forward on the ventral side, but then bends round and runs backward on the left side of the nucleus, and only passes out behind this organ. In *S. democratica - mucronata*, *S. scutigera - confederata* and *S. cordiformis - zonaria*, the stolon winds spirally round the nucleus (Fig. 262).

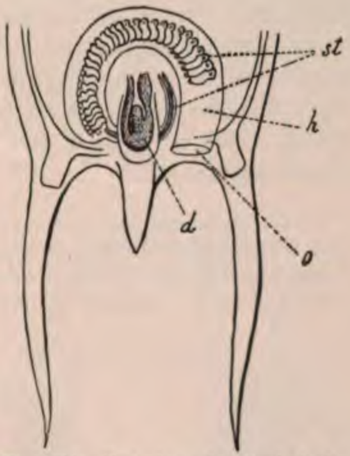

FIG. 262.—Posterior end of the body in a solitary form of *Salpa democratica-mucronata*, from the dorsal side (after LEUCKART). *d*, alimentary canal; *h*, brood-cavity; *o*, aperture of the same; *st*, proliferating stolon.

The individual buds here, as in *Pyrosoma*, become marked off by transverse constrictions which appear on the stolon. While, however, in *Pyrosoma*, the separate parts of the stolon remain in a single row, in the *Salpidae*, secondary shifting leads to a bi-serial arrangement. A large number of buds consequently can be crowded on to a short piece of the stolon.

A. Structure and Development of the Proliferating Stolon.

Our knowledge of the earliest stages of the development of the stolon is due chiefly to SEELIGER (No. 105). The stolon, as already mentioned, is at first a small, conical outgrowth on the left side of the body near the posterior end of the endostyle. Three layers can be distinguished in it; ectoderm, mesoderm and entoderm. The ectoderm of the stolon passes direct into that of the parent. The entoderm-sac of the stolon (Fig. 263, *en*) is a diverticulum of the wall of the parent's branchial sac arising immediately behind the endostyle. This diverticulum exactly corresponds to the organ known

FIG. 263.—Youngest stage of development of the stolon in *Salpa* (after SEELIGER). *b*, blood-sinus; *ec*, ectoderm; *en*, entoderm-process; *m*, mesoderm; *mz*, mesenchyme-cells.

in the other Tunicates as the entodermal, endostylic, or epicardial process. Between the ectoderm and the entoderm of the stolon, the primary body-cavity extends, being directly connected with that of the parent. In it we find an accumulation of mesoderm-cells (*m*) completely enveloping the entoderm-process; these, according to SEELIGER, are produced by the simple immigration of mesenchyme-cells from the parent. Such cells (*mz*) are found in large numbers at the point of origin of the stolon in the neighbourhood of the elaeoblast-tissue.

While SEELIGER considers that the mesoderm of the stolon results from the immigration of a large number of mesenchyme-cells, TODARO (No. 107) regards it as arising from the division of certain large germ-cells (germoblasts) derived from the placental membrane (membrana germoblastoca, p. 435) at the cleavage of the original egg which gave rise to the solitary form. Since, according to TODARO, the whole bud is derived exclusively from the descendants of these cells, the ectoderm and entoderm of the stolon taking no part in the formation of the buds, these latter are to be traced back to a form of sexual reproduction. TODARO regarded the buds (in Salpa-chains) as younger members of the generation to which the solitary form belongs.

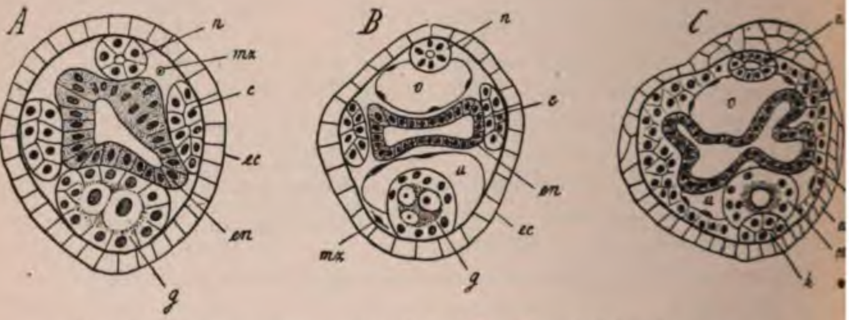

FIG. 264.—Three transverse sections through the stolon of *Salpa democratica-mucronata* at consecutive stages of development. *c*, peribranchial (cloacal) strands; *ec*, ectoderm; *en*, entoderm-tube; *g*, genital strand; *h*, rudiment of testis; *mz*, mesenchyme-cell; *n*, neural tube; *o*, upper blood-sinus; *ov*, ovarian rudiment; *u*, lower blood-sinus.

Transverse sections through older stolons (Fig. 264) reveal a condition deviating somewhat from that above described, but showing great agreement with the stolon of *Pyrosoma* (Fig. 257, p. 490). In the primary body-cavity, four regularly-arranged strands have appeared. The uppermost of these, which we will call the *neural strand* or *neural tube* (Fig. 264, *n*) contains a distinct lumen. The paired lateral strands also (*c*) are said by authors to have lumina round which the cells are arranged like an epithelium (Fig. 265, *c*), although SEELIGER was not able to come to a definite conclusion on this point. He called these strands the *lateral strands*, whereas the other authors speak of them as the peribranchial, perithoracic or cloacal tubes. They correspond to the peribranchial tubes in the stolon of *Pyrosoma*. In the fourth, lower strand (*g*), young egg-cells early appear, and it must therefore be called the *genital strand*. Besides these strands, scattered mesenchyme-cells are found in the primary body-cavity (Fig. 264, *mz*).

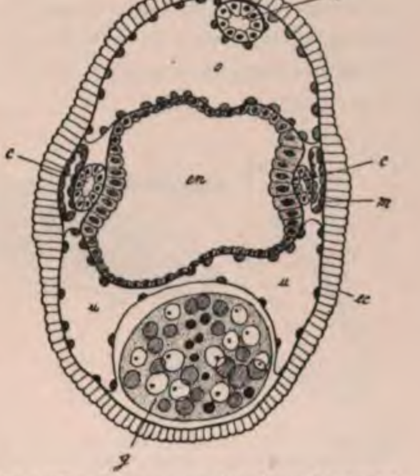

FIG. 265.—Transverse section through a young stolon of *Salpa* (after BROOKS). *c*, peribranchial tubes; *ec*, ectoderm; *en*, entoderm-tube; *g*, genital strand; *m*, muscle-tubes; *n*, neural tube; *o*, upper, and *u*, lower blood-sinus.

In later stages of development of the stolon (Figs. 264 *B* and *C*, 265), we find, further, two large blood-sinuses lined with an endothelium, one lying above (*o*) and the other below (*u*) the entoderm-tube. Since this tube does not reach as far as to the end of the stolon, communication between the two sinuses is possible. At this point the blood flows from one sinus to the other.

Another constituent element of the stolon in *Salpa* has been pointed out by BROOKS, who found, on either side of the stolon, between the peribranchial tubes and the ectoderm, another tube which, he considers, gives rise to the muscular system. These tubes BROOKS calls the *muscular tubes* (Fig. 265, *m*).

In these six longitudinal strands running through the stolon we have the rudiments of the most important organs of the buds. The central entoderm-tube (*en*) yields the rudiment of the branchial sac (pharynx) and of the alimentary canal; the neural tube yields the ganglion and the ciliated pit, while from the peribranchial tubes (*c*) the single atrial cavity arises, from the genital strand (*g*) the genital organs, and from the muscle-tubes (*m*) the body-musculature. When, later, through transverse constriction, the separate individuals (buds) begin to detach themselves from the stolon, the longitudinal strands break up into segments corresponding to the buds. The neural tube, genital strand and peribranchial and muscular tubes early break up into such segments, but the entodermal and ectodermal parts of the distinct buds remain connected together (Fig. 268, *en*) until a late stage of development.

We are still somewhat in the dark concerning the first origin of these six longitudinal strands that appear in the body cavity. According to SEELIGER, they are derived through simple differentiation from the mesoderm-mass (Fig. 263, *m*) of the first stolon-rudiment. This breaking up of the mesoderm into distinct longitudinal strands seems to be determined to some extent by the form of the entoderm-tube, which early assumes, in cross-section, a quadrangular form (Fig. 264), its projecting edges, by approaching the ectoderm, causing the mesoderm-mass to divide up into an upper, a lower and two lateral strands. In this case, the neural tube and the peribranchial strands would originate from the mesoderm, a derivation which from our knowledge of the development of other Tunicates is not very probable. On this point we refer the reader to our account of the budding of *Pyrosoma* (p. 487). Other authors have attributed a different origin to the peribranchial strands at any rate. These, according to KOWALEVSKY, arise as independent growths from the atrial region of the parent, while SALENSKY holds that they grow out of the pericardial vesicle of the solitary individual. It is possible that SALENSKY'S view was founded on a confusion of these strands with BROOKS' muscle-tubes. In any case, it is possible that some of the longitudinal strands of the stolon in *Salpa* are direct outgrowths of the corresponding systems of organs in the parent. An independent origin from the

FIG. 266.—Proliferating stolon of *Salpa* (after TODARO). *b*, blood-vessels of the stolon; *ec*, ectoderm; *en*, entoderm-tube of the stolon; *es*, endostyle of the parent (solitary form); *s*, stolon.

ectoderm of the stolon must, however, be considered probable for the neural tube. We should add that the examination of these ontogenetic processes in the stolon is exceedingly difficult.*

B. Development of the Buds on the Stolon.

It has already been shown (p. 495) that the buds arise through transverse constriction of the stolon (Fig. 266). The stolon is in this way cut up by a kind of transverse fission into a series of consecutive individuals which continuously increase in size while remaining connected together by the narrowed parts of the stolon. The buds thus arise in *Salpa* in exactly the same way as in *Pyrosoma* (Figs. 253 and 256 *C*). Only in later stages do the buds of the *Salpidae* undergo important changes of position which lead to their biserial arrangement on the stolon. In order clearly to understand these changes, we must first recall the condition of the Pyrosoma stolon. According to the more detailed account given on p. 484, the individuals are arranged on the Pyrosoma stolon in a single row, one behind the other. The orientation of each individual resembles that of the parent. The haemal or ventral side of the buds (marked by the position of the endostyle, *es*) is directed towards the distal end of the stolon. The right half of the body of every individual agrees in position with the right side of the parent; the left half of the bud corresponds to the left half of the parent and has been produced by the left half of the stolon, just as the right half of the bud has been produced by the right half of the stolon.

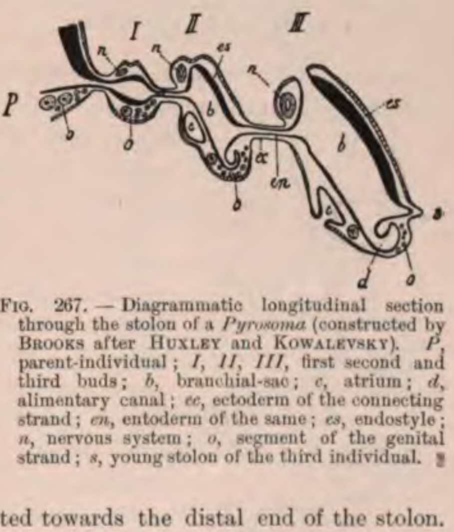

FIG. 267. — Diagrammatic longitudinal section through the stolon of a *Pyrosoma* (constructed by BROOKS after HUXLEY and KOWALEVSKY). *P*, parent-individual; *I*, *II*, *III*, first second and third buds; *b*, branchial-sac; *c*, atrium; *d*, alimentary canal; *ec*, ectoderm of the connecting strand; *en*, entoderm of the same; *es*, endostyle; *n*, nervous system; *o*, segment of the genital strand; *s*, young stolon of the third individual.

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* [According to BROOKS (No. I.), the nerve-tube and the two peribranchial tubes are probably derived from the ectoderm of the stolon; the upper blood-sinus is continuous with the cavity of the heart, and the lower sinus with the body-cavity of the nurse-form.—ED.]

If, now, the individuals of the Salpa stolon remained in the same position as those of the Pyrosoma stolon, the stolon of the *Salpidae*

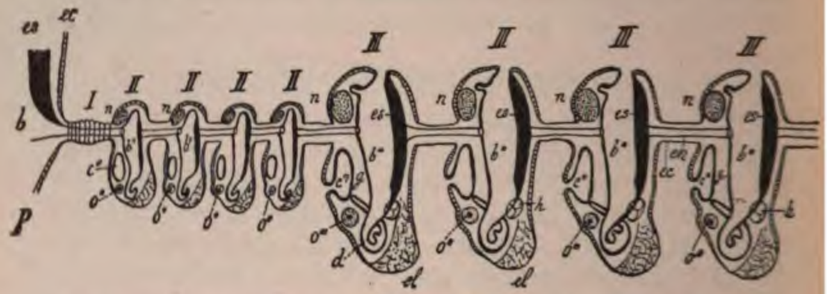

FIG. 268.—Diagram representing a stolon of *Salpa* as it would appear if no secondary shifting of the individuals were to take place (after BROOKS). *P*, solitary form (parent-individual); *I*, *II*, *III*, first, second and third group of individuals; *b*, *b''*, *b'''*, branchial sac (pharynx); *c''*, *c'''*, atrium; *d*, alimentary canal; *ec*, ectoderm; *el*, elaeoblast; *en*, entoderm (of the connecting strands); *es*, endostyle; *g*, gill; *h*, heart; *n*, nervous system; *o''*, *o'''*, ovary.

would be accurately represented by BROOKS' diagram (Fig. 268). Here also the individuals are still arranged in a single row one behind the other, their orientation being that of the parent. The median plane of the stolon and of all the individuals on it coincides with that of the solitary form (*P*). The only distinction between this stolon and that of *Pyrosoma* is the larger number of individuals here present. The Pyrosoma stolon has only a limited number of individuals (five), but the stolon of *Salpa* consists of several consecutive groups, each comprising 50 to 100 individuals all at the same stage of development. The most distal group (*III*) is the oldest, and contains the most highly developed individuals. (For the sake of clearness, the groups depicted in the diagram are composed of not more than four individuals). These groups, further, are not sharply marked off from one another. Between every two groups there are always a few individuals which, in the degree of their development, form transitions between the two groups. We also find, especially in the

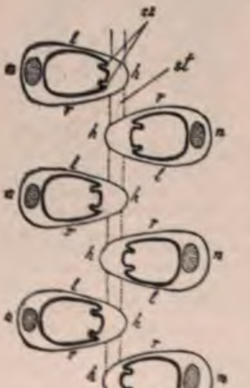

FIG. 269.—Diagram illustrating the position of the individuals on the stolon in the Salpa-chain. *es*, endostyle-folds; *h*, haemal or ventral side of the buds; *l*, left side; *n*, nervous system and neural or dorsal side; *r*, right side; *st*, remains of stolon.

younger stages, that the distal individuals of a group are somewhat further developed than the proximal individuals of the same group.

The individuals are in reality arranged on the stolon in two alternate rows (Fig. 269) in such a way that the corresponding individuals of the two rows turn their ventral (haemal) sides (*h*) to each other, while their dorsal (neural) sides (*n*) are directed outward. This arrangement can be clearly made out in the transverse section (Fig. 275) through an older part of a stolon. We thus have an arrangement of the individuals like that depicted in the diagram (Fig. 269). The median plane of the individuals does not coincide with that of the stolon, but lies at right angles to it. This biserial arrangement of the buds results from a lateral shifting of the segments of the stolon which move alternately to the right and left side. Each bud at the same time rotates round its longitudinal axis, passing through an angle of 90°; consequently, the dorsal side of the bud which originally (Fig. 268) was directed

FIG. 270.—Horizontal longitudinal section through an advanced stolon of *Salpa* (after BROOKS). The individuals are cut through obliquely, the longitudinal section passing through them in such a way that, in those placed most distally (1, 2, etc.), the most anterior region of the body is seen and, in the most proximal individuals (20, 21, etc.), the posterior region of the body. *D*, distal; *P*, proximal; *R*, right; *L*, left. *a*, anal aperture; *c*, atrium; *el*, elaeoblast; *es*, endostyle; *g*, gill; *h*, heart; *hs*, haemal side of the bud; *i*, intestine; *lb*, left half of the branchial sac; *m*, opening of the oesophagus; *n*, nervous system; *ns*, neural side of the bud; *o*, ovary; *rb*, right half of the branchial sac; *s*, stomach.

towards the proximal end of the stolon is now turned toward the outer side of that structure (Fig. 269), while the ventral side has passed from its original distal position and is turned toward the median line of the stolon. This rotation, which was pointed out by BROOKS, does not take place simultaneously throughout the whole of the bud, but affects the posterior or ab-oral end at which the elaeoblast lies earlier than the anterior or oral end. If, therefore, we carefully examine a somewhat oblique longitudinal section through the stolon, like that given in Fig. 270, we shall be able to follow the process of shifting, since the individuals are in consequence cut through at different planes. We find that individuals 16-21, the posterior ends of which are cut through, are already in their final position, their arrangement being distinctly biserial. The individuals of the left row (16, 18, 20) have their dorsal side directed to the left, but the ventral side turned to the middle line of the whole stolon. The individuals of the right row show an opposite arrangement. When, however, we examine the buds the anterior part of which is cut through (7-11), we find that the biserial arrangement is here not fully carried out, the individuals of the left row lying partly on the right and those of the right row partly on the left of the stolon. The rotation also is not complete. The endostyle (*es* in individuals 8) which marked the ventral (haemal) side, is still directed distally (*D*). The neural side, which is marked by the position of the ganglion (*n* in individual 11), still to a certain extent retains its primary position, *i.e.*, is still turned towards the proximal end (*P*) of the stolon. We here see very clearly the way in which the final biserial arrangement of

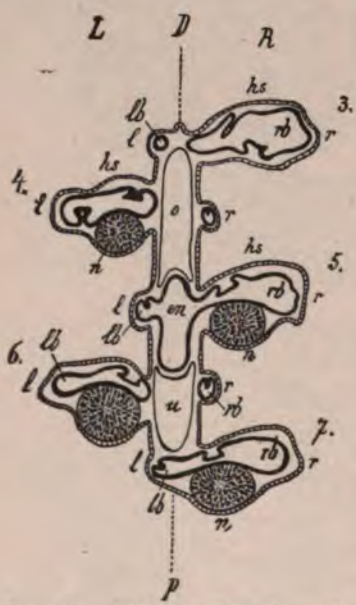

FIG. 271.—Diagram illustrating the relative position of the individuals 3-7 depicted in Fig. 270 (after BROOKS). *D*, distal; *P*, proximal; *R*, right; *L*, left (with regard to the stolon). *en*, entoderm-tube of the stolon; *hs*, haemal side of the bud; *l*, left side of the bud; *lb*, left half of the branchial sac; *n*, neural side of the bud; *o*, upper blood-sinus in the stolon; *r*, right side of the bud; *rb*, right half of the branchial sac; *u*, lower blood-sinus in the stolon.

the individuals on the stolon of *Salpa* can be traced back to the original monoserial arrangement which is retained in the stolon of *Pyrosoma*.

Special interest attaches to the condition of individuals 3-7 of Fig. 270, diagrammatically illustrated in Fig. 271. We can here clearly see the relation of the buds to the stolon. The stolon itself is cut through obliquely, the section being intermediate between a longitudinal and a transverse section. We can see the entoderm-tube of the stolon (*en*), anteriorly, the upper blood-sinus (*o*) and posteriorly the lower blood-sinus (*u*, *cf.* Figs. 264 and 265). In individual 5, we can trace the connection between the right (*rl*) and the left (*lb*) halves of the branchial sac with the entoderm-tube (*en*) of the stolon. All the other individuals are cut through at a different level. In individuals 4 and 6, for instance, the two blood-sinuses are intercalated between the right and left halves of the respiratory cavity.

We have reproduced other diagrams by BROOKS (Figs. 272 and 273) which still further illustrate this condition. Fig. 272 gives the upper or oral aspect of a stolon as it would appear if the primary position of the buds had been retained unaltered (*cf.* Fig. 268). The right half of each bud is seen to have arisen from the right side of the stolon and the left half of the bud from the left side of the stolon. Fig. 273 shows the buds shifted alternately to the two sides of the stolon, a condition attained through the repetition of the process taking place in individual 5 in Figs. 270 and 271. The buds 1, 3 and 5 have moved toward the right side of the stolon while 2, 4 and 6 have moved toward the left side. The rotation of the individuals, however, is not yet visible.

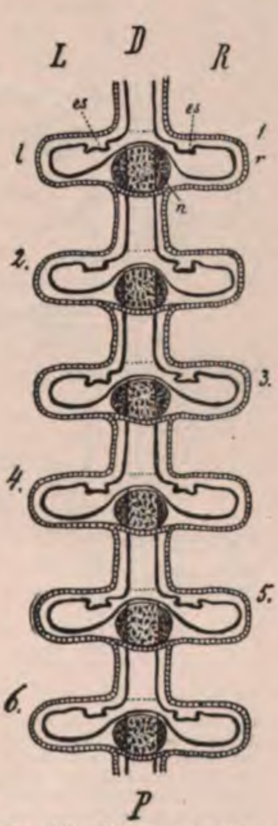

FIG. 272.—Diagram of a stolon of *Salpa* as it would appear if no secondary shifting of the individuals were to take place (after BROOKS). *P*, proximal; *D*, distal; *R*, right; *L*, left of the stolon; *r* and *l*, right and left sides of the individuals; *es*, endostyle-folds; *n*, ganglion.

Originally, therefore, the rudiments of the individuals (buds) are nothing more than the consecutive segments of the stolon marked off one from the other by transverse furrows. These furrows, as seen from above or below, are soon no longer transverse, but run somewhat obliquely (Fig. 274), in alternating directions, so that furrows 1, 3 and 5 are parallel on the one hand, and furrows 2, 4 and 6 on the other. In this oblique course of the furrows, we see the first preparation for the later biserial arrangement; it is the expression of the lateral displacement of the tissues of the buds forming the different segments of the stolon. When, therefore, in later stages, the segments shift to the two sides, it appears as if the buds arose as lateral outgrowths from the stolon. This erroneous view of the budding of the *Salpa* is actually adopted by many of the older authors. **Brooks** was the first to trace back the origin of the buds to the transverse division of the stolon.

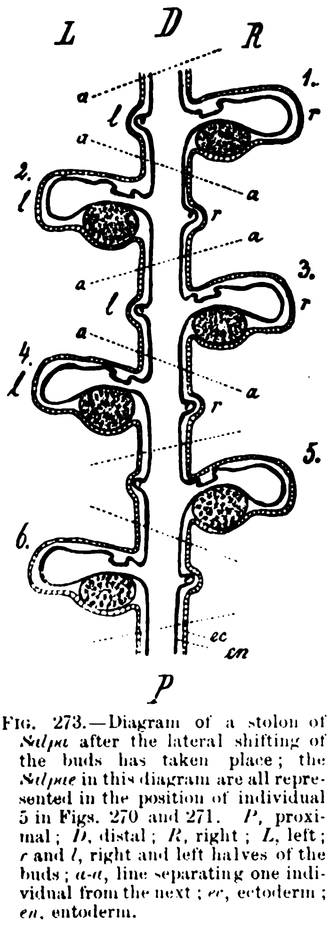

Fig. 273.—Diagram of a stolon of *Salpa* after the lateral shifting of the buds has taken place; the *Salpae* in this diagram are all represented in the position of individual 5 in Figs. 270 and 271. *P*, proximal; *D*, distal; *R*, right; *L*, left; *r* and *l*, right and left halves of the buds; *a-a*, line separating one individual from the next; *ec*, ectoderm; *en*, entoderm.

The individuals become more and more sharply marked off from one another in proportion as they assume their lateral positions and project out from the stolon. They then appear to be hanging on to the remains of the stolon like grapes on a bunch (Fig. 275 *B*). The remains of the stolon (*st*), however, are nothing more than the consecutive strands which connect the individuals. These, as may be seen from the diagram (Fig. 272), originally ran from the haemal side of each individual to the neural side of the next older bud. They are originally inserted at the middle of the body. In later stages, when the individuals have taken up the lateral position and have undergone rotation, the connective strand forms a continuous longitudinal tube to which the buds adhere laterally. The blood-vessels running in this strand, and the entoderm-tube which persists within it and connects the branchial sacs of the individuals, are of importance for the nourishment of the buds. This longitudinal strand may be called the *remains of the stolon.* Its position with relation to the buds changes, as its points of attachment wander more and more upward, *i.e.*, toward the branchial aperture of the individual (Fig. 275), while the individuals sink downward on either side of it. This change of position can be most distinctly traced in the ganglia. The neural tube of the stolon originally lies above the entoderm-tube as is seen in Fig. 264. The ganglia derived from the neural tube must consequently seem to lie in the median line above the entodermal connective canals (see diagram, Fig. 268). When, later, the buds become marked off laterally, the ganglia sink lower down, and come to lie at the sides of the connecting canals; indeed, in the diagram (Fig. 268) they appear alternately to cover the canals and to be covered by them. Later, the ganglia and, with them, the individuals, sink still farther down.

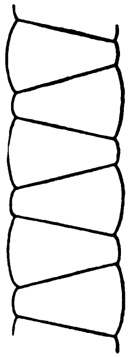

FIG. 274. — Diagram illustrating the course of transverse furrowing in the stolon of *Salpa*, seen from above.

The sinking down of the buds on either side of the remains of the stolon solves a difficulty which apparently presents itself in connection with their rotation. In examining individual 5 in Fig. 271, and still more in considering the diagram Fig. 273, it may occur to the observer to wonder in what way the endostyle-fold which, in individual 5, lies on the left side, passed over to the right, since it appears separated from the right side of the body by the entoderm-tube of the stolon. We have tried to make this process clear by the diagrams given in Fig. 276. The connecting strand *ab*, which represents the remains of the stolon, originally runs from the neural side of each individual to the haemal side of the next (proximal) individual. After rotation has taken place, these strands would assume a zig-zag course, as indicated in Fig. 276 *B.* Later, as the buds sink down, the connecting strands, which are already attached near the anterior region of the body, shift further forward to a position quite near the branchial aperture, whereas the endostyle-folds, which remain unaffected by this change, do not extend so far forward. There is therefore no obstacle in the way to prevent the union of the connecting strands; by this union these strands appear as a continuous tube in which we recognise the remains of the stolon (Fig. 276 *C*).

Even in later stages, the two principal blood-sinuses (Figs. 264, 275, *o* and *u*) which appeared at an early stage within the developing stolon (Fig. 264 *B*) are still to be found in the remains of that structure. These vessels are bounded by distinct epithelial walls and have no connection with the bud, the blood-vascular system of which arises quite independently. The blood from the body of the parent therefore does not pass over into the body of the bud.

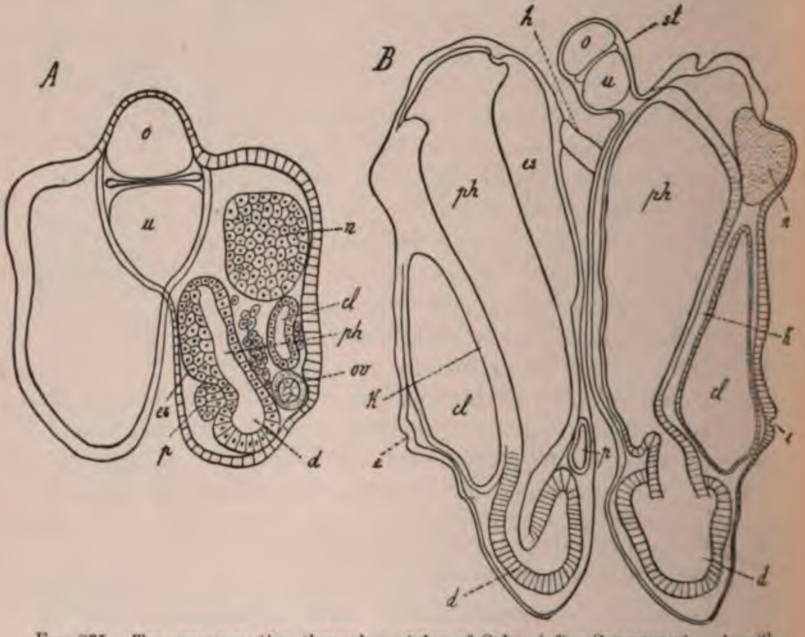

FIG. 275.—Transverse section through a stolon of *Salpa* (after SALENSKY). *A*, with younger, and *B*, with older buds. *cl*, atrium; *d*, enteric canal; *e*, atrial aperture; *es*, endostyle; *h*, connecting process (couplings); *k*, gill; *n*, nervous system; *o*, upper blood-sinus; *ov*, ovary; *p*, pericardial vesicle; *ph*, pharynx; *st*, remains of stolon; *u*, lower blood-sinus.

When the buds are fully developed the remainder of the stolon degenerates, breaking up into segments which are drawn in by the buds and absorbed by them. The connection between these (the individuals of the chain), originally brought about by the stolon, is now maintained by means of integumental processes derived from buds (the so-called connecting processes or couplings, Fig. 278, *hf*), which originate as outgrowths of the integument. These processes are hollow, and each of them contains a blood-vessel. These might be compared to the mantle-vessels of the Ascidians. The final connection between the individuals is formed by the processes of neighbouring individuals growing out towards one another and fusing. Each of the individuals belonging to a chain possesses, as a rule, eight of these processes placed in four longitudinal rows; two ventral and two lateral. The lateral couplings serve for attachment to the individuals lying in the same longitudinal row, while the ventral processes establish a connection between the two parallel rows of individuals seen in the diagram (Fig. 277 *A*). The long axes of the individuals are inclined somewhat obliquely to that of the chain, a position which results from the fact that the couplings are not inserted at the same level on the right and the left sides of the body (Fig. 277 *B*). This oblique position may have given rise to the horizontal one seen in *Salpa fusiformis*. In *S*. (*Cyclosalpa*) *pinnata* the individuals are found arranged in the form of a rosette, each of the buds giving off a single process only from the ventral side which runs towards the centre of the rosette, where all the processes meet

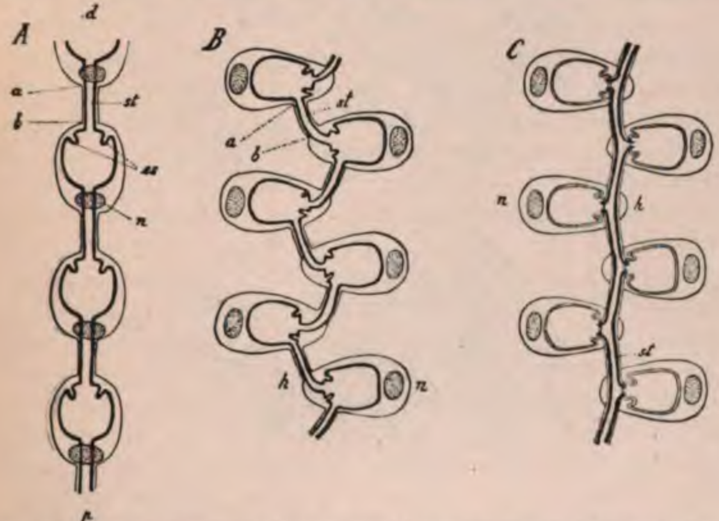

FIG. 276.—Diagram illustrating the relations of the connecting strand (*st*) to the buds on the stolon of a *Salpa*. *A*, represents the stolon from Fig. 268 viewed from above; *B*, shows the condition after rotation has taken place; *C*, the condition after the buds have sunk downward. *a*, distal end of the connecting strand, *b*, proximal end of the same; *d*, distal part of stolon; *es*, endostyle-folds; *h*, haemal or ventral side; *n*, nervous system and neural or dorsal side; *p*, proximal part of stolon; *st*, connecting strands.

together like the spokes of a wheel. Such an arrangement is characteristic of the genus *Cyclosalpa*.

This union between the individuals of the Salpa-chain must be regarded as colony-formation. Whereas, in the composite Ascidians and in *Pyrosoma*, the individuals which arise through budding remain connected by means of a common cellulose mantle, connection here takes place through special connecting organs.* This connection is not very close. When the fully developed chain passes out from the cavity in the cellulose mantle of the parent and separates from the proliferating stolon, it very easily breaks up into smaller portions; individuals even become detached from the chain and continue their existence independently.

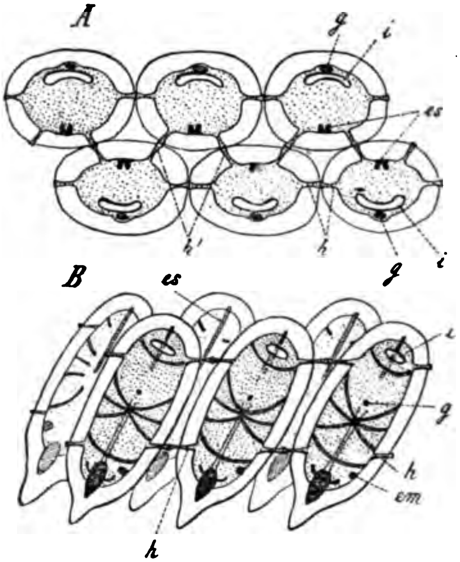

FIG. 277. – Diagram illustrating the interconnection existing between the individuals of a Salpa-chain. *A*, the chain seen from above; *B*, lateral view. *es*, endostyle; *em*, embryo; *g*, ganglion; *h*, lateral connecting processes; *h*, ventral processes; *i*, branchial aperture.

C. Development of the Organs in the Bud.

In the above account of the relation of the buds to the stolon we have in all points followed the short but important description given by BROOKS (No. 92). The most important investigations made in

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* See LEUCKART's description, No. 28.

connection with the development of the organs in the bud are those of **Salensky** (Nos. 101 and 102) and **Seeliger** (No. 105). Although the researches of these investigators yield much valuable material for working out the organogenesis of the buds of *Salpa*, yet, owing to the fact that these observers did not recognise the rotation of the bud round its longitudinal axis, as made out by **Brooks**, their observations are somewhat vitiated through the adoption of an erroneous orientation of the bud, taken from its later stages and applied in describing the earlier stages. **Salensky** and **Seeliger** hold that the buds arise simply by the lateral shifting of the segments of the stolon. According to them the dorsal part of the bud develops from one of the lateral surfaces of the stolon, while its ventral side corresponds to the opposite side of the stolon. According to **Brooks**, on the contrary, the right side of the stolon gives rise to the right half of the body of the bud and the left side of the stolon to the left half. In the following account we shall merely give a brief outline of the genesis of the organs in *Salpa* which probably closely resembles that in *Pyrosoma*.*

It must once more be pointed out that we have the first rudiment of the bud in a transverse segment of the stolon. The proximal parts of this segment become the dorsal side of the bud, and the distal parts its ventral side. From the upper region of the stolon is developed the anterior part of the body of the bud, while its posterior end develops from the lower region (see diagram, Fig. 268). The organs of the bud are formed from sections of the tubes and longitudinal strands which are to be seen in the transverse section of the stolon (Fig. 265).

That part of the central *entoderm-tube* found in each segment of the stolon gives rise to the pharynx of the bud. The entoderm-tube, in a cross-section through the stolon, bears some resemblance to the expanded wings of a butterfly (Fig. 264 *C*), an upper and a lower indentation and two lateral indentations being found in it. Its form, in cross-section, later resembles that of the letter H, also found in a similar section of a Pyrosoma bud (Fig. 257). In the latter, the two portions of the tube that point upward are connected with the development of the endostyle-folds, while those that extend downward, yield the stomach and intestine (p. 490). It is at present impossible to say whether similar conditions prevail in the Salpa bud.

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* [**Brooks**' memoir on the genus *Salpa* (No. I.) should be consulted in this connection; he gives a full and detailed account of the development of the chain-form, including its organogenesis.—**Ed.**]

In any case, the rudiment of the endostyle grows out as paired folds projecting inward, while the intestinal loop (Fig. 268, *d*) is derived from the lower end of the entoderm-vesicle, from which it grows out as a blind diverticulum on the right side.

The atrial cavity of the bud (Fig. 269, *c*) arises, according to Brooks, through the union of the paired peribranchial tubes (Fig. 265, *c*). The cavity which thus arises then occupies a dorsal position in the posterior part of the bud. Two lateral perforations which occur in the partition-wall extending between the atrial cavity and the pharynx represent the rudiment of the two gill-clefts, and the trabecula remaining between the clefts is the rudiment of the *gill* (Fig. 268, *g*), the ventral and lateral covering of which is derived from the entoderm, while the covering of the dorsal side is yielded by the epithelium of the atrial cavity [ectoderm, Brooks]. Only at a later stage do the pharyngeal and atrial cavities open externally, ectodermal invaginations leading to the formation of the *branchial and atrial apertures.*

The neural tube of the stolon becomes broken up into segments, each of which, in the form of a spherical vesicle with thick walls, gives rise to the central nervous system of a bud. In the young buds, these appear remarkably large (Figs. 270, 275, *n*), but decrease in size later. The vesicular rudiment which lies on the dorsal side of the bud in the anterior region of the body, becomes divided into two parts by a transverse furrow; these parts at first remain connected with each other, but are later completely separated. The anterior part becomes connected with the entodermal wall of the pharyngeal cavity and, after its lumen has broken through into that cavity, it may be recognised as the rudiment of the ciliated pit. The posterior part of the vesicle which soon loses its lumen is the rudiment of the ganglion proper, in which a peripheral layer of ganglionic cells and a central accumulation of punctate tissue (Leydig's Punktsubstanz) develop. The peripheral nerve-strands also soon grow out. A dorsal outgrowth from the ganglionic rudiment forms the rudiment of the eyes which, in the buds, develop somewhat otherwise than in the embryo. [See on the development of the eyes, Seeliger (No. 105) and Metcalf (Nos. 99, 99*a*, and I.).]

The *mesoderm* of the stolon, which is represented by a mesenchyme filling the primary body-cavity and by the Brooks' muscle-tubes, gives rise to the connective tissue, the blood-vessels, the pericardial vesicle, the elaeoblast and the body-musculature. We are not in a position, however, to make any more definite statements as to the origin of these organs. According to **Brooks**, the muscle-tubes give rise to the body-musculature. We may no doubt assume that the paired segments of these tubes spread out on either side of the bud and thus yield muscle-plates, which become fenestrated and then break up into the muscle-hoops.

The rudiment of the genital organs is yielded by the genital strand (Figs. 264, 265, *g*). We have already seen (p. 497) that young egg-cells can early be recognised within this strand. These at first are very plentiful, but many of them disintegrate later and seem to serve as food for the developing eggs. When the genital strand is ready to break up into segments, the eggs become arranged in such a way that only one occurs in each division. The smaller peripheral cells of the genital strand yield the egg-follicle, the oviduct and (according to **Seeliger**) probably also the rudiment of the testis. Even in early stages, it is evident, in cross-sections through the stolon, that a group of cells becomes detached in each segment from the lower part of the genital strand, and this probably is to be regarded as the rudiment of the testis (Fig. 264, c, *h*).

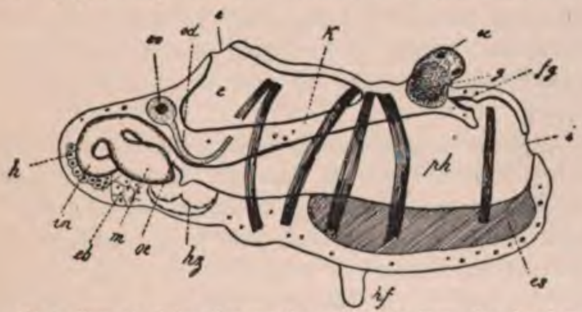

FIG. 278.—Chain-form of *Salpa democratica-mucronata* from the distal part of an advanced stolon (after **Seeliger**). *c*, atrium; *e*, atrial aperture; *eb*, elaeoblast; *es*, endostyle; *fg*, ciliated pit; *g*, ganglion; *h*, rudiment of testis; *hf*, connecting process; *hz*, heart; *i*, branchial aperture; *in*, intestine; *k*, gill; *m*, stomach; *oc*, eye; *od*, oviduct; *oe*, oesophagus; *ov*, egg-follicle; *ph*, pharynx.

The rudiment of the genital organs originally lies at the posterior end of each bud. Later the egg-follicle shifts farther forward on the dorsal side and then lies above the intestinal loop in the dorsal median line. From this point the oviduct turns to the right with an S-shaped curve and becomes connected on the right side of the body with the epithelium of the atrial cavity (Fig. 278, *ov* and *od*). The watch-glass-shaped rudiment of the testis (*h*) remains longer at the posterior end of the body curved round the posterior end of the intestinal loop. At a later stage it breaks up into separate tubes which unite to form a common efferent duct that opens out into the atrial cavity between the intestine and the stomach on a papilla-like prominence (see SALENSKY, Nos. 101 and 102, and SEELIGER, No. 105). The testis develops comparatively late in the chain-form.

5. The Interpretation of the Alternation of Generations in the Tunicates.

Alternation of generations is found among the Tunicates in a marked form in *Pyrosoma*, *Doliolum* and *Salpa*. This fact has long attracted the attention of zoologists, who have attempted to explain it in many different ways. We shall adopt the view first put forward by LEUCKART (No. 98) and accepted later by CLAUS* and GROBBEN (No. 79) that alternation of generations in the Tunicates must be regarded as having arisen in consequence of the formation of stocks through division of labour, and we shall follow GROBBEN's clear exposition of this view. Among more recent descriptions we may specially mention those of ULJANIN (No. 86) and SEELIGER (No. 106).

The Larvacea, which are conjectured to be the most primitive of all existing Tunicates, develop through sexual reproduction. This seems to suggest that the capacity for asexual reproduction (by means of buds) was acquired as a consequence of the attached manner of life. Asexual reproduction is indeed very common among attached animals. We may, with GROBBEN, suggest as the cause that the abandonment of locomotion left a larger proportion of the substance of the body available for reproduction, so that it was possible for attached animals to introduce a new method of multiplication into the cycle of their development. It may also, however, be added that when, in consequence of attachment, cross-fertilisation became more difficult, the capacity for asexual reproduction would become of special importance for the maintenance of the species.

It is evident that, originally, all the individuals of forms which had developed this character were equally able to reproduce themselves either sexually or asexually.

Asexual multiplication led to the formation of stocks, the buds being either altogether incapable of separating from the parent or else able to do so only incompletely. All individuals were thus at first capable, by asexual multiplication, of increasing the size of the colony to which they belonged, or else by sexual multiplication of

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* Grundz. d. Zool. 4 Aufl.

founding new colonies. Such a condition is found, for example, in the Ascidiozooids of *Pyrosoma*, which produce stolons and also maturate genital products.

The distribution of these two kinds of reproduction among various individuals of the colony must be regarded as a later, derived condition through which the first individuals arising in a colony then became adapted exclusively for increasing the colony by budding, while the lateral individuals formed new colonies by sexual reproduction. Such an arrangement, in which we see the first commencement of alternation of generations, is found in the composite Ascidians. **Ganin**, following the investigations of **Krohn**, established that, in this case, the individuals developing from the egg are capable of asexual reproduction only, and in this way lay the foundation of the colonies, while the descendants of these individuals, produced by budding, again develop genital products.

In *Salpa* we find this condition more marked, and established as a regular alternation of two generations, one reproducing only asexually and the other only sexually. At the same time the two generations vary to a certain degree in the structure of the body. **Grobben** has rightly pointed out that these variations may be explained by the different conditions of life and the different work to be carried out by the two generations. The points that project at the posterior end of the "nurse" of *Salpa democratica-mucronata* (Fig. 262) serve as a protection for the proliferating stolon which occurs in that region of the body. This "nurse" of *S. democratica-mucronata* further possesses one muscle-hoop more than the sexual animal, and this is explained on the ground that, owing to the presence of the massive proliferating stolon, greater muscular power is required in this case to enable the animal to swim with equal rapidity. On the other hand, the form of the sexual individua (that belonging to a chain) may be explained by the crowding of the buds on the chain.

It follows from the above that the solitary form and all the individuals of the chain produced by it must be regarded as members of one and the same colony. The solitary ("nurse") form is the founder of the colony, while the individuals of the chain produced asexually give rise to the foundation of new colonies in producing sexually new solitary forms.

The heteromorphous development of the individuals of the Salpa colony recalls the polymorphism of the Siphonophora. Polymorphism is still more strongly marked in the *Doliolidae*, where we have, in the barrel-shaped "nurse," the lateral and the median buds of differently formed individuals of one and the same stock (pp. 388 and 474).

In *Pyrosoma*, the alternation of generations consists of successive generations of Cyathozooids and Ascidiozooids. The Cyathozooid corresponds to the solitary form of *Salpa*, but remains in an undeveloped condition, its development being restricted to the embryonic period. It reproduces itself only asexually. The Ascidiozooids, on the contrary, besides multiplying sexually, have retained the capacity for budding, and therefore, in the cycle of generations of *Pyrosoma*, one generation (Cyathozooid) produced from the egg, alternates with several generations (Ascidiozooids) which have arisen through budding.

The alternation of generations which takes place in the *Doliolidæ* has already been described in detail (p. 474).

The alternation of generations in the Tunicates must therefore be derived from colony-formation and must be regarded as a case of division of labour (LEUCKART). The only difficulty that remains to be explained is in what way the hypothetical ancestors of the Tunicates which became attached acquired the capacity for reproduction by budding. It is not easy to understand how an animal which had always reproduced itself sexually should come to produce buds. There is considerable evidence tending to show that, in the Tunicates, budding developed out of fission. The asexual reproduction of *Amaroucium* especially must be regarded as an actual process of division (p. 449). We are therefore justified in assuming that the hypothetical ancestors of the Tunicates, besides their sexual multiplication, at first reproduced themselves through fission, and that the later budding and stolon-formation developed out of this manner of reproduction.

BALFOUR * and ULJANIN (No. 86) have tried to remove the difficulty which arises if we regard the capacity for multiplication by fission as acquired only after attachment, by suggesting that this process appears first in the embryos. According to this view, the Tunicates first acquired a capacity for dividing in the first embryonic stages, as is the case in *Lumbricus trapezoides* (Vol. I., p. 281), a capacity which was only secondarily passed on from the embryonic stages to the adult form. But when we remember the great capacity for regeneration possessed by the Tunicates (p. 448) we shall hardly find it necessary to fall back on such an hypothesis. There is no

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* Text-book of Comp. Embr., Vol. II., p. 34 (footnote) 2nd edit., 1885.

reason why we should not assume that the capacity for division was not possessed by the adults from the first, indeed, this capacity may possibly have been inherited directly from older pelagic ancestors of the Tunicates. For, even if the circumstance that the Larvacea do not multiply asexually seems to indicate that this form of reproduction was acquired only after attachment, we are not sure that this was the case.

SEELIGER, who attributes to the mesoderm the principal part in the development of the proliferating stolon, and who derives the mesoderm of the stolon, at any rate in *Pyrosoma*, from the genital tissues of the parent, finds in the limitation of sexual reproduction the cause for the development of buds, the material left in the ovary after the production of a single egg is utilised in its plastic capacity as the mesoderm of the stolon. But even if we make this assumption, the manner in which budding was acquired remains obscure.

Further confusion has been introduced into the views as to the alternation of generations in the Tunicates by the fact that the egg-cells frequently maturate very early in the buds. They can even be distinguished in the genital strand of the stolon in *Pyrosoma* and *Salpa*. This has, in many cases, led to the view that the ovary actually belongs to the solitary form and is merely deposited in the forms composing the chain. This view, which is adopted by BROOKS (Nos. 88-91) does not seem justifiable to us. We prefer SEELIGER'S view that the egg with its follicle is just as much an organ of the individual of the chain as are all the other organs. The early differentiation of the egg-cells is to be traced back to the effort on the part of the organism to arrive at sexual maturity as early as possible. The same hastening of sexual maturity is found in the Hydroids and, indeed, in the parthenogenetic Cladocera and *Aphidae* and also in the Diptera (polar cells).

BROOKS regards all the ovaries of the individuals of a Salpa-chain taken together as the germ-gland of the solitary form shifted into the stolon. He considers the solitary forms not as sexless but as females, while he regards the individuals of the chain as males which have arisen from the females as buds. The solitary form deposits an egg in each male, and this, when fertilised, develops into a female. BROOKS therefore reduces the alternation of generations of *Salpa* to a kind of sexual dimorphism.

We have already stated (p. 496) that TODARO, by deriving all the buds from certain embryonic germ-cells (germoblasts), and by tracing these latter directly to the blastomeres of the embryo, regards the individuals of a Salpa-chain not as the descendants of the solitary form but merely as younger members of the same generation. TODARO would, however, strictly speaking, not be justified in assuming an asexual multiplication of the embryo in early stages of embryonic development.

SALENSKY (Nos. 74 and 102) traces back the alternation of generations of the Tunicates to metamorphosis. The acquisition of the capacity for asexual reproduction by the larvae of the Tunicates, or, in other words, the shifting back of this capacity originally belonging to adult forms to larval stages, made it possible to spread out over several generations the series of transformations which constitute metamorphosis. In this way we can explain the dimorphism of the generations. SALENSKY consequently regards the solitary form as a larval stage and the individuals of the chain as the adults. We, however, with LEUCKART (No. 98), hold on the contrary that we are justified in regarding the solitary form just as much as the individual of the chain as a fully developed individual.

III. General Considerations on the Tunicates.

If we attempt to draw from the ontogeny of the Tunicates conclusions of a more general nature, we are at once struck by the difference of opinion prevailing among the various investigators of this subject. As an example of this, we may mention that the central nervous system in the larvae of the Ascidiacea is traced back to an ectodermal invagination ; in the buds of the composite Ascidians, on the contrary, according to statements made by KOWALEVSKY and recently confirmed by HJORT (No. 59), it is derived from the entoderm of the bud.* In the Cyathozooid of *Pyrosoma*, and probably also in the first four Ascidiozooids, it is derived from the ectoderm, whereas SEELIGER, in all the later-developed Ascidiozooids of the colony, as in the buds of the *Salpidae*, traces it back to the mesoderm. Similar uncertainty prevails with regard to the development of the peribranchial cavities and the atrium. We are also in doubt as to how far the ectoderm and entoderm take part in their formation in Ascidian larvae, but in the Cyathozooid of *Pyrosoma*, in any case, they are derived exclusively from the ectoderm. Nearly all authors, however, are agreed that the peribranchial sacs become abstricted from the central entoderm-sac in the buds of the Ascidiacea. In the buds of the *Salpidae* and in the later Ascidiozooids of *Pyrosoma*, SEELIGER derives the peribranchial tubes from the mesoderm. It is difficult to decide how far this difference of opinion can be accounted for by errors of observation or to what extent actual differences exist. We, for instance, find it difficult to assume that the buds of *Pyrosoma* develop in a totally different way from those of the nearly related

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* [See footnote, p. 466.—ED.]

composite Ascidians. We must await the result of further researches before coming to any definite conclusion.

In any case, the *development of the buds* must always be considered quite apart from embryonic development, since these two methods of development are to be traced back to different principles. In the embryo, the primary organs arise anew from an originally undifferentiated mass of blastomeres, while in budding, which is evidently deducible from division, parts of the most important primary organs are taken over from the organisation of the parent into the bud. Although the literature on the budding of the Tunicates at present is far from supporting the statement that all the more important organs in the bud or the stolon are to be derived by abstriction from the corresponding organs of the parent, indications are not wanting that the solution of the problem as to the origin of the organs of the bud is to be sought in this direction (p. 487). It appears, for instance, that the strands which compose the rosette-like organ of *Doliolum* are direct continuations of all the more important organs of the parent. In the four primary Ascidiozooids of *Pyrosoma* also, the peribranchial tubes and the pericardial rudiment of the Cyathozooid are directly continued. It may be mentioned further that, according to KOWALEVSKY, the peribranchial tubes in the stolon of *Salpa* are derived from the atrium of the parent. These statements which, however, are in direct contradiction to many observations on other forms suggest that *none of the more important organs arise anew in the bud, but that all the more important rudiments of organs pass over from the parent into the stolon and thence into the buds, while the actual new formation of organ-rudiments takes place only in the embryo.* The nervous system would probably have to be considered as an exception to this rule. Since we know that the brain of the Ascidian can be regenerated after excision, it appears possible that it arises anew also in the buds, though probably only from the ectoderm.

Turning to the *embryonic development*, we find that the different divisions of the Tunicata here also vary greatly. The embryonic development of the *Salpidae* is, indeed, so little understood that we are hardly in a position to say anything definite about it. When we see that, according to SALENSKY, all the species examined show important variation in their methods of development, it is evident that there is here an ample field for further research.* We may,

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[* See footnote, p. 423 and pp. 445-446.—ED.]

however, say that in *Pyrosoma*, as well as in the *Salpidae*, the embryonic development has undergone great coenogenetic variation. In *Pyrosoma*, the accumulation of food-yolk, and, in *Salpa*, the fusion of the embryo with the body of the parent as well as other conditions have brought about such variations. In both cases, development is direct, and, as compared with the development of the Ascidians, much abbreviated. The suppression in the embryonic development of the *Salpidae* of so important an organ as the chorda dorsalis is of interest. In the Cyathozooids of the *Pyrosoma*, also, this organ does not develop distinctly, although **Salensky** thought that he found a trace of its rudiment. The chorda-rudiment is also wanting in the buds of all Tunicates. **Salensky**, indeed, regarded the elaeoblast, that provisional organ of the Salp embryo, as the rudiment of the chorda, but the fact that the elaeoblast also occurs in the buds of *Pyrosoma* and *Salpa*, while other provisional larval organs are not found as rudiments in these buds, throws doubt upon this view. It is found, for example, that the nervous system in the second individuals produced by budding in the larval *Diplosoma* no longer show the larval character (p. 459). The elaeoblast is wanting in the buds of the composite Ascidians and the *Doliolidae*, nor does its rudiment appear in the Cyathozooids of *Pyrosoma*.

Salensky maintains that, in the chief groups of the Tunicata, the follicle-cells take part in the formation of the embryo. We are somewhat sceptical as to these statements, which will be found more in detail on pp. 357, 392 and 421 and think that this supposed participation may be reduced to the absorption of the follicle-cells as nourishment by the blastomeres [see footnote, pp. 420 and 421].

It is evident from the above that, in judging of the systematic position and phylogeny of the Tunicates, we are dependent almost entirely on the embryonic development and metamorphosis of the Ascidiacea. Among these, the solitary forms and *Clavelina* have yielded the most valuable material, while the eggs of the composite forms, which are rich in yolk, show a derived condition.

Among the Tunicates now living, *Appendicularia* is regarded as showing in its organisation the most primitive conditions. We must, however, raise the question as to how far these conditions are really primitive. The Larvacea show remarkable resemblance in their structure to the free-swimming tailed Ascidian larvae, from which they are distinguished chiefly by the absence of a common atrial cavity, the anus and the two peribranchial tubes opening out independently on the ventral side of the body. Since the abbrevia-

tion of the dorsal region found in the Ascidians and the approximation of the branchial and atrial apertures thus brought about is traced back to attached forms, the position of the anus in the Larvacea, which must evidently be regarded as primitive, would indicate that these animals are descendants of those hypothetical Tunicate ancestors which still retained the original pelagic life. On the other hand, we find in *Appendicularia* a series of unmistakable degenerative phenomena tending to support the assumption that we must regard the racial form of the Larvacea as an attached Tunicate. It is evident that they must be considered as sexually mature larval forms, sexual maturity being shifted continually further back to earlier stages so that, finally, the mature adult form no longer developed. What form can we imagine this latter to have assumed? Was it a free-swimming Ascidian form intermediate between *Amphioxus* and the Ascidian larva, or an already attached Ascidian form? The last assumption seems the more probable. The appearance of the cellulose mantle and hermaphroditism and the indistinctness of the segmentation of the body must be regarded as features acquired as a consequence of attached manner of life. As these characters are found in the Larvacea, we are to a certain extent justified in considering them as the sexually mature larvae of an already attached form of Tunicate.* In any case, however, all phylogenetic speculations concerning the Tunicates must rest upon careful consideration of the structure of *Appendicularia* and the Ascidian larvae.

Among the Ascidiacea the solitary forms are probably the more primitive. The composite forms lead on to *Pyrosoma*, which may be regarded as a composite colony that has not become attached and that is distinguished by a large common cloaca. In the interesting family *Coelocormidae* we see the development of the whole colony in a similar direction. Here also the colony is not attached but, on the other hand, the internal cavity cannot be compared to the common cloaca of *Pyrosoma* (see HERDMAN, No. 24). *Pyrosoma* forms a transition to the free-swimming *Doliolidae*. This was pointed out by HUXLEY with reference to the structure of the gill and the opposite position of the two apertures of the body (*cf.* also GROBBEN, No. 79). The *Doliolidae* (Cyclomyaria), among which *Doliopsis* (*Anchinia*) exhibits the most primitive characters, must be regarded as phylogenetically the oldest Thaliacea. The *Salpidae* (Hemimyaria) must be considered as derived from them. We shall, therefore, have

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* WILLEY (No. 54*a*) also has lately maintained that the Larvacea are degenerate forms.

to derive the condition of the gill in the *Salpidae* from that in the *Doliolidae*, and not compare it, as a primitive structure, directly with that of the *Appendicularia*, as was done by VAN BENEDEN and JULIN (see p. 566). The curious transformations of which the organisation of the Tunicates is capable is shown by the extraordinary *Octacnemidae* which live at the bottom of the sea at great depths: these star-like creatures, which resemble *Lucernaria* in form, must probably be regarded as modified *Salpidae* (HERDMAN, No. 29, Pt. III.).

Since KOWALEVSKY laid the foundations for our knowledge of the ontogeny of the Ascidians and of *Amphioxus* there has been no room for doubting that the two branches of the Tunicate stock and the Cephalochorda are intimately related. Later researches have entirely confirmed this conviction. The agreement found in the most important points of organisation and of development can only rest on true homology. Among these are: the presence of a dorsal neural tube which, in early stages, opens externally through the neuropore; the possession of a chorda dorsalis extending between this and the alimentary canal; the transformation of the anterior part of the alimentary canal into a respiratory region perforated by lateral gill-slits, the ventral side of which region is occupied by the hypobranchial groove (endostyle); and, finally, the transformation of the posterior part of the body into a locomotory organ provided with an unpaired marginal fin, while the intestinal rudiment at this part degenerates. The first stages of development in these two forms are also strikingly alike. Only recently VAN BENEDEN and JULIN (p. 349), who, however, are not supported by DAVIDOFF, have made statements as to the development of the mesoderm and the chorda dorsalis which would render the agreement between these two groups almost complete. We are, therefore, justified in regarding the Tunicata and the Cephalochorda which lead on to the Vertebrates, as members of a large common group, the Chordata, and to derive them from a common racial form (the Protochordata). We must imagine this racial form as a pelagic, segmented animal, provided with gill-slits and a chorda. The Tunicates, as compared with such a form, are to some extent degenerate, this being due, on the whole, to their attached manner of life, while, in another direction, their organisation is more highly developed. This is the case, for instance, in the pharyngeal region which has undergone considerable enlargement and specialisation.

Among the indications of degeneration found in the body of the Tunicates we should first mention the loss of the coelom and the

disappearance of the segmentation of the body. Only in the caudal region of the Ascidian larvae and of *Appendicularia* are there any traces of the segmentation which must have been present in their ancestors. In the caudal portion of the nervous system in the Ascidian larva, spinal nerves are given off segmentally, as KUPFFER first noticed. In *Appendicularia* these are connected with paired ganglionic swellings in the dorsal cord. LANGERHANS (No. 2), by the use of reagents, was further able to prove that the caudal musculature breaks up into ten consecutive muscle-segments (myomeres) which are provided with segmentally arranged pairs of motor nerves. In individual cases LANGERHANS (No. 2) found that, in the posterior caudal region of *Appendicularia*, the spinal nerves of the left side have shifted somewhat forward as compared with the corresponding nerves of the right side. A similar condition is found in *Amphioxus*. In the anterior region of the body, on the contrary, no traces of segmentation are retained.

Although we must recognise a great general agreement in structure and development between *Amphioxus* and the Tunicates, it is very difficult to establish exactly in detail the homologies between the organs of the two groups. A special attempt of this kind was made by VAN BENEDEN and JULIN, but we are not able to regard all their deductions as convincing. Starting from the view that, in the Tunicates, a large part of the alimentary canal (in the caudal section) has degenerated, VAN BENEDEN and JULIN regard the rectum and the anal aperture of the Tunicates as new acquisitions which are not homologous with the homonomous structures of *Amphioxus*. They find the homologue of the rectum of the Tunicates in the "club-shaped gland" of *Amphioxus*, which belongs to the first trunk-metamere (p. 549) and opens out near the mouth.* Consequently the whole of the precaudal part of the body in the Ascidian larva corresponds to only the small anterior region of *Amphioxus*, viz., to the anterior cephalic part—the first trunk-segment. This view leads these authors further logically to deny the strict homology of the endostyle with the hypobranchial groove of *Amphioxus*. Since, however, in the Cephalochorda and the Vertebrata also, the anal aperture has evidently undergone a secondary shifting forward and the caudal section of the alimentary canal degenerates, there is nothing which compels us to doubt either the homology of the rectum throughout the Chordata,

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* [WILLEY (No. XXXVII.) regards the club-shaped gland as the right primary gill-slit.—ED.]

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Among the Tunicates now living, *Appendicularia* is regarded as showing in its organisation the most primitive conditions. We must, however, raise the question as to how far these conditions are really primitive. The Larvacea show remarkable resemblance in their structure to the free-swimming tailed Ascidian larvae, from which they are distinguished chiefly by the absence of a common atrial cavity, the anus and the two peribranchial tubes opening out independently on the ventral side of the body. Since the abbrevia-

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Among the Ascidiacea the solitary forms are probably the more primitive. The composite forms lead on to *Pyrosoma*, which may be regarded as a composite colony that has not become attached and that is distinguished by a large common cloaca. In the interesting family *Coelocormidae* we see the development of the whole colony in a similar direction. Here also the colony is not attached but, on the other hand, the internal cavity cannot be compared to the common cloaca of *Pyrosoma* (see HERDMAN, No. 24). *Pyrosoma* forms a transition to the free-swimming *Doliolidae*. This was pointed out by HUXLEY with reference to the structure of the gill and the opposite position of the two apertures of the body (*cf.* also GROBBEN, No. 79). The *Doliolidae* (Cyclomyaria), among which *Doliopsis* (*Anchinia*) exhibits the most primitive characters, must be regarded as phylogenetically the oldest Thaliacea. The *Salpidae* (Hemimyaria) must be considered as derived from them. We shall, therefore, have

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Since KOWALEVSKY laid the foundations for our knowledge of the ontogeny of the Ascidians and of *Amphioxus* there has been no room for doubting that the two branches of the Tunicate stock and the Cephalochorda are intimately related. Later researches have entirely confirmed this conviction. The agreement found in the most important points of organisation and of development can only rest on true homology. Among these are: the presence of a dorsal neural tube which, in early stages, opens externally through the neuropore; the possession of a chorda dorsalis extending between this and the alimentary canal; the transformation of the anterior part of the alimentary canal into a respiratory region perforated by lateral gill-slits, the ventral side of which region is occupied by the hypobranchial groove (endostyle); and, finally, the transformation of the posterior part of the body into a locomotory organ provided with an unpaired marginal fin, while the intestinal rudiment at this part degenerates. The first stages of development in these two forms are also strikingly alike. Only recently VAN BENEDEN and JULIN (p. 349), who, however, are not supported by DAVIDOFF, have made statements as to the development of the mesoderm and the chorda dorsalis which would render the agreement between these two groups almost complete. We are, therefore, justified in regarding the Tunicata and the Cephalochorda which lead on to the Vertebrates, as members of a large common group, the Chordata, and to derive them from a common racial form (the Protochordata). We must imagine this racial form as a pelagic, segmented animal, provided with gill-slits and a chorda. The Tunicates, as compared with such a form, are to some extent degenerate, this being due, on the whole, to their attached manner of life, while, in another direction, their organisation is more highly developed. This is the case, for instance, in the pharyngeal region which has undergone considerable enlargement and specialisation.

Among the indications of degeneration found in the body of the Tunicates we should first mention the loss of the coelom and the

disappearance of the segmentation of the body. Only in the caudal region of the Ascidian larvae and of *Appendicularia* are there any traces of the segmentation which must have been present in their ancestors. In the caudal portion of the nervous system in the Ascidian larva, spinal nerves are given off segmentally, as KUPFFER first noticed. In *Appendicularia* these are connected with paired ganglionic swellings in the dorsal cord. LANGERHANS (No. 2), by the use of reagents, was further able to prove that the caudal musculature breaks up into ten consecutive muscle-segments (myomeres) which are provided with segmentally arranged pairs of motor nerves. In individual cases LANGERHANS (No. 2) found that, in the posterior caudal region of *Appendicularia*, the spinal nerves of the left side have shifted somewhat forward as compared with the corresponding nerves of the right side. A similar condition is found in *Amphioxus*. In the anterior region of the body, on the contrary, no traces of segmentation are retained.

Although we must recognise a great general agreement in structure and development between *Amphioxus* and the Tunicates, it is very difficult to establish exactly in detail the homologies between the organs of the two groups. A special attempt of this kind was made by VAN BENEDEN and JULIN, but we are not able to regard all their deductions as convincing. Starting from the view that, in the Tunicates, a large part of the alimentary canal (in the caudal section) has degenerated, VAN BENEDEN and JULIN regard the rectum and the anal aperture of the Tunicates as new acquisitions which are not homologous with the homonomous structures of *Amphioxus*. They find the homologue of the rectum of the Tunicates in the "club-shaped gland" of *Amphioxus*, which belongs to the first trunk-metamere (p. 549) and opens out near the mouth.* Consequently the whole of the precaudal part of the body in the Ascidian larva corresponds to only the small anterior region of *Amphioxus*, viz., to the anterior cephalic part—the first trunk-segment. This view leads these authors further logically to deny the strict homology of the endostyle with the hypobranchial groove of *Amphioxus*. Since, however, in the Cephalochorda and the Vertebrata also, the anal aperture has evidently undergone a secondary shifting forward and the caudal section of the alimentary canal degenerates, there is nothing which compels us to doubt either the homology of the rectum throughout the Chordata,

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or the derivation of the anterior region of the body in the Tunicate larva through fusion from a large number of trunk-metameres.

We have already mentioned (p. 367) that van Beneden and Julin deny the homology of the branchial slits and the peribranchial or atrial cavity in the Tunicates with those of other Chordata. Only the two clefts which form first in the Tunicates are really to be regarded as true gill-slits. This view results from the ascription by these authors to the entoderm of a considerable part in the development of the peribranchial sacs. In the same way, van Beneden and Julin doubt the homology of the heart in the Tunicates with the heart of the Vertebrata. We shall only be able to judge of this last view, which indeed receives decided support from the absence of the heart in the *Amphioxus*, when the way in which this organ arises in the Tunicates is fully established. While Seeliger, like van Beneden and Julin, derives the pericardial sac in the Ascidian larva from the entoderm, most of the statements of other writers seem to render its mesodermal origin probable. We must, however, constantly bear in mind that an actual endocardium is altogether wanting in the heart of the Tunicata.

This view, shared by many of the more recent writers (Balfour, van Beneden and Julin, Hatschek) that the Tunicates and the Cephalochorda, to which the Vertebrates are allied, represent distinct branches of the Chordate type connected together only at their roots, is opposed to that of Dohrn (Nos. 15-19), who regards the Tunicates as degenerate fish. The Cyclostoma and *Amphioxus* are by this author thought to represent distinct stages in the series of degenerative processes through which the organisation of the Tunicates is to be derived from that of the fishes. This view rests principally upon the proof which Dohrn attempted to establish that the hypobranchial groove (endostyle) as well as the peripharyngeal ciliated bands of the Tunicates, the homologue of which was discovered by Schneider in *Ammocoetes*, are to be regarded as transformed gill-clefts, and the thyroid-gland, the homology of which with the hypobranchial groove had been maintained by W. Müller was said to represent a branchial sac lying between the spiracle and the first branchial cleft, while the ciliated arch is the homologue of the spiracular cleft (the pseudobranch of the Teleosteans).* The endostyle and the ciliated arch

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* [Dohrn stands alone in his belief that the pseudobranch of the Teleosteans is formed from the anterior wall of the original spiracular cleft and that, by the later suppression of the cleft, the pseudobranch comes to lie in the first branchial cleft. Most vertebrate morphologists regard this pseudobranch as

would thus be met with in the Tunicates in a secondarily modified form. This view rests especially on observations of the development of the homologous structures in *Ammocoetes*.

Even though it appears to us that DOHRN carries these homologies too far, since we are not inclined to assume direct genetic relations between the Fishes and the Tunicata, and still less to regard the two groups as independent branches derived from a common, primitive racial form (Protochordata), we consider that it entirely justifies the conviction that the Tunicates cannot be utilised to bridge over the gap existing between the Chordata and the other branches of the animal kingdom. HAECKEL and GEGENBAUR have been specially prominent in their advocacy of this view. The hypothetical primitive form of the Tunicates is represented as a typical Chordate with all the features generally ascribed to that type. But no characteristics are to be found either in the anatomy or the ontogeny of the Tunicata which ally them directly to any one branch of the Invertebrata. The Tunicates appear to us no more nearly related to the Invertebrata than are *Amphioxus* or the Vertebrata. The specially striking features in the Tunicates, viz., the absence of segmentation, of the coelom and the nephridia, the occurrence of asexual reproduction are all characters which we cannot regard as primitive. They have been newly acquired in connection with the attached manner of life. The way in which we have to reconstruct for ourselves the primitive Chordata (the common hypothetical racial form of the Tunicata, the Cephalochorda and the Vertebrata) can only be discovered through careful comparison of the ontogeny and anatomy of these three groups, and in this we are convinced that the chief stress must be laid on *Amphioxus*. Such a reconstruction is at present specially difficult, indeed is rendered almost impossible by the fact that our knowledge is as yet too fragmentary to enable us to establish exactly the homologies of the different organs in the three groups of the Chordata. In illustration of this it may be mentioned that our knowledge of the origin of the peribranchial cavities in the Tunicates is still incomplete, and the question as to the homology of the ciliated pit in the Tunicates with the hypophysis cerebri and other problems are as yet also insoluble.

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a development of the anterior wall of the first branchial cleft in no way connected with the spiracular cleft or with the pseudobranch of Elasmobranchs. Consequently, if there is any truth in the comparison given above it would be more in accordance with the generally accepted homologies to read pseudobranchiae of Elasmobranchs for pseudobranchiae of Teleosteans.—ED.]

however, say that in *Pyrosoma*, as well as in the *Salpidae*, the embryonic development has undergone great coenogenetic variation. In *Pyrosoma*, the accumulation of food-yolk, and, in *Salpa*, the fusion of the embryo with the body of the parent as well as other conditions have brought about such variations. In both cases, development is direct, and, as compared with the development of the Ascidians, much abbreviated. The suppression in the embryonic development of the *Salpidae* of so important an organ as the chorda dorsalis is of interest. In the Cyathozooids of the *Pyrosoma*, also, this organ does not develop distinctly, although SALENSKY thought that he found a trace of its rudiment. The chorda-rudiment is also wanting in the buds of all Tunicates. SALENSKY, indeed, regarded the elaeoblast, that provisional organ of the Salp embryo, as the rudiment of the chorda, but the fact that the elaeoblast also occurs in the buds of *Pyrosoma* and *Salpa*, while other provisional larval organs are not found as rudiments in these buds, throws doubt upon this view. It is found, for example, that the nervous system in the second individuals produced by budding in the larval *Diplosoma* no longer show the larval character (p. 459). The elaeoblast is wanting in the buds of the composite Ascidians and the *Doliolidae*, nor does its rudiment appear in the Cyathozooids of *Pyrosoma*.

SALENSKY maintains that, in the chief groups of the Tunicata, the follicle-cells take part in the formation of the embryo. We are somewhat sceptical as to these statements, which will be found more in detail on pp. 357, 392 and 421 and think that this supposed participation may be reduced to the absorption of the follicle-cells as nourishment by the blastomeres [see footnote, pp. 420 and 421].

It is evident from the above that, in judging of the systematic position and phylogeny of the Tunicates, we are dependent almost entirely on the embryonic development and metamorphosis of the Ascidiacea. Among these, the solitary forms and *Clavelina* have yielded the most valuable material, while the eggs of the composite forms, which are rich in yolk, show a derived condition.

Among the Tunicates now living, *Appendicularia* is regarded as showing in its organisation the most primitive conditions. We must, however, raise the question as to how far these conditions are really primitive. The Larvacea show remarkable resemblance in their structure to the free-swimming tailed Ascidian larvae, from which they are distinguished chiefly by the absence of a common atrial cavity, the anus and the two peribranchial tubes opening out independently on the ventral side of the body. Since the abbrevia-

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CHAPTER XXXVI.

CEPHALOCHORDA.

Amphioxus.

The earlier statements concerning the development of *Amphioxus* made by **Max Schultze** (No. 18), **Leuckart** and **Pagenstecher** (No. 15) referred merely to a few of the later larval stages; our knowledge of the ontogeny of this form is, therefore, founded principally on the investigations of **Kowalevsky** (Nos. 10 and 11), and was extended by **Hatschek** (Nos. 4 and 8). The metamorphosis of *Amphioxus* has recently been described by **Ray Lankester** and **Willey** (No. 13) and by **Willey** alone (No. 23). The development of the genital organs has been investigated by **Boveri** (No. 3). This last author (No. 2) as well as **Spengel** (No. 19), **Ray Lankester** (No. 12) and **van Wijhe** have also published treatises on the anatomy of the adult *Amphioxus* to which we shall have occasion to refer.*

A. Oviposition, Cleavage and Gastrulation.

The mature genital products of *Amphioxus* pass from the genital chambers, through rupture of their walls, into the atrial cavity and thence they were said to pass through the gill-clefts into the pharynx and to be ejected through the mouth (**Kowalevsky**, **Hatschek**). According to **Ray Lankester** and **Willey**, however, they are, in most cases, ejected through the atriopore. Fertilisation takes place in the surrounding water. The newly laid egg is surrounded by a vitelline membrane at first only slightly separated from it, but, under the influence of the sea water, the interval between the egg and the

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* [More recently, **Sobotta** (No. XI.) and **Sticht** (No. XII.) have reinvestigated the maturation and fertilisation of the egg, and the former, **Klaatsch** (No. IV.) and **Macbride** (No. VIII.) have re-examined the formation of the germ-layer.—Ed.]

membrane becomes greater. There is no micropyle. The spermatozoa pass through this elastic membrane to reach the egg.*

The first stages of development closely resemble those of the Ascidians. Cleavage is total and almost equal (adequal type of HATSCHEK). The first furrow is meridional and appears first at the animal pole, where for some time it is deepest; it eventually divides the egg into two exactly equal parts (Fig. 279 *B*). The second furrow, which is also meridional, is at right angles to the first and leads to the rise of four blastomeres of equal size which leave free between them a cavity open above and below; this is the cleavage-cavity (Fig. 279 *C* and *D*). The eight-celled stage (Fig. 279 *E*) is brought about by an equatorial furrow which lies somewhat nearer the animal than the vegetative pole and leads to the first differentiation between the blastomeres of the animal and vegetative halves. The embryo consists of a circle of four smaller blastomeres near the animal pole and another circle of four larger blastomeres belonging to the vegetative pole. Further meridional furrows divide these eight cleavage-spheres into sixteen, the sixteen-celled stage then consisting of a circle of eight smaller and another of eight larger blastomeres (Fig. 279 *F*).

Even at this sixteen-celled stage, according to WILSON, certain individual differentiations are found which influence the further course of cleavage. The regular stage described by HATSCHEK, in which the eight cells of the upper circle are found resting regularly on the eight cells of the lower circle, was comparatively rarely observed by WILSON. The blastomeres of the upper circle often appear shifted spirally in relation to those of the lower, as is found to be the case in the Annelida and Mollusca. Most frequently, however, at the sixteen-celled stage a bilateral (or strictly speaking a biradial) symmetry is evident in the arrangement of the blastomeres, the eight cells of the vegetative half being divided into four larger and four smaller cells. The four larger cells surround the vegetative pole in regular order, while the four smaller cells are grouped in two pairs symmetrically to the median plane. This median plane, according to WILSON, corresponds to the first cleavage-plane. A similar arrangement of the blastomeres was seen in the sixteen-celled stage of the Ascidians.

The thirty-two-celled stage arises, according to HATSCHEK, in consequence of further equatorial furrows. It consists of four rows of eight cells each, one super-imposed above the other. The [illegible] cleavage-cavity, which was hitherto open at the animal and vegetative poles, now becomes closed at these points. In the further course of

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* Only one polar body is generally said to be present at this stage (Fig. 279), but SOBOTTA (No. XI.) has recently discovered the presence of a second one.—Ed.

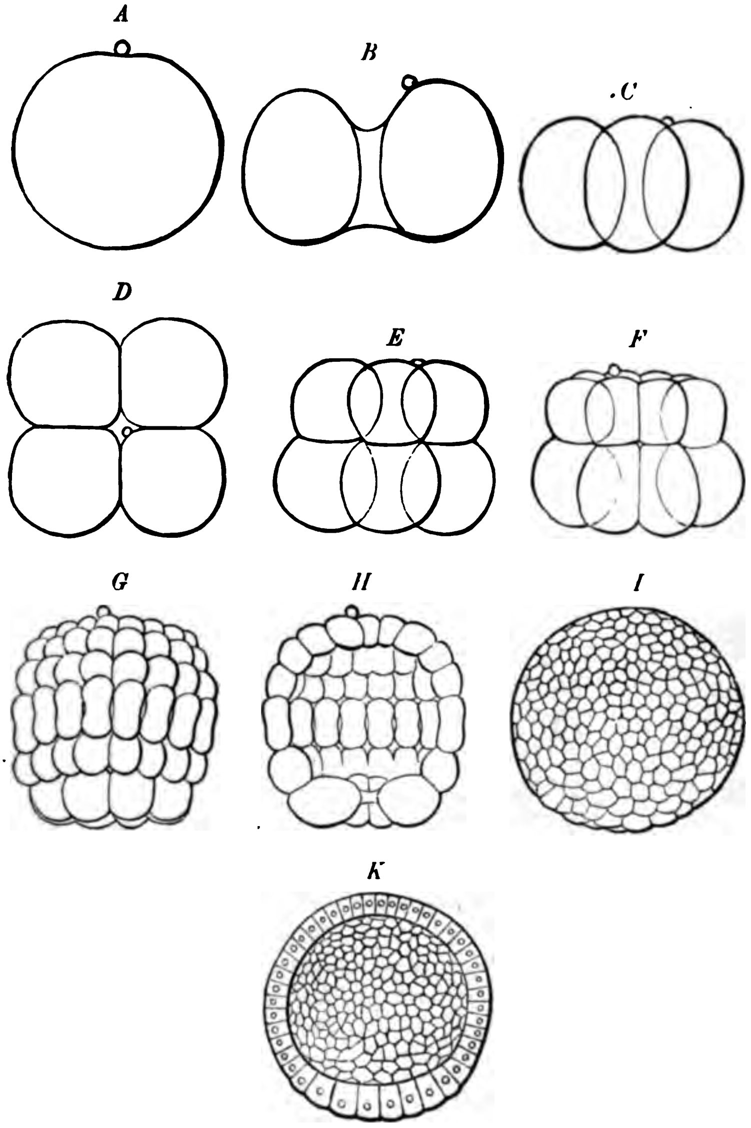

FIG. 279.—Cleavage of *Amphioxus* (after SALENSKY). *A*, egg before cleavage, with the polar body; *B*, division into two, the two cells being still connected by a band of protoplasm; *C*, four-celled stage; *D*, the same seen from the pole; *E*, eight-celled stage; *F*, sixteen-celled stage; *G*, stage showing more rapid division at the animal pole: one of the circles of cells is in the act of dividing; *H*, the same stage in section; *I*, blastula, surface view; *K*, blastula, in section.

cleavage, the circle of small blastomeres divides more rapidly, while the circle of eight larger cleavage-spheres surrounding the vegetative pole remains longer undivided (Fig. 279 *G*). In later stages, the regular arrangement of the blastomeres in circles is obliterated and the cells form an epithelium surrounding the cleavage-cavity, the *blastula-stage* being reached in this way (Fig. 279 *I*, *K*). The egg, at this stage, is lengthened in the direction of the future gastrula axis, and the wall at the vegetative pole, *i.e.*, the posterior third of the egg, is composed of somewhat larger cells richer in yolk-granules. This represents the entodermal region of the embryo. In it flattening occurs, and this soon passes into an invagination (Fig. 280 *A*) which leads to the development of a cap-shaped gastrula. The invagination causes the cleavage-cavity to decrease in size and finally completely to disappear, the two primary germ-layers coming into close contact (Fig. 280 *B*).

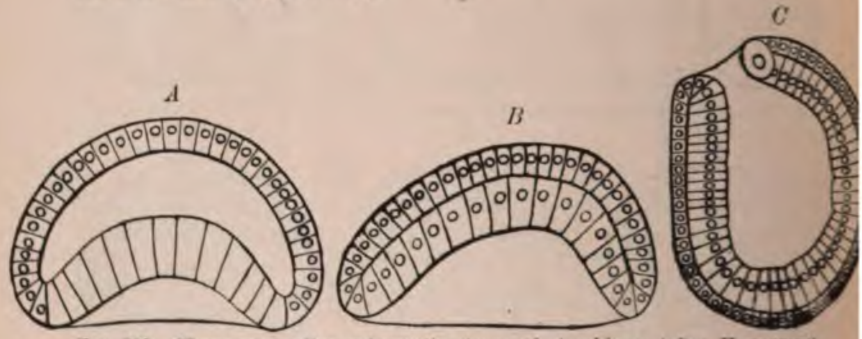

FIG. 280.—Three consecutive ontogenetic stages of *Amphioxus* (after HATSCHEK), showing the invagination of the entoderm. *A*, during invagination; *B*, after the completion of invagination, right dorsal side, left ventral side; *C*, with narrowed gastrula-mouth, orientation as in *B*.

The gastrula-stage now passes through certain phases by means of which the bilateral symmetry which, according to WILSON, is already evident in the stages of cleavage, becomes more distinct, while at the same time, the embryo elongates in the direction of its definitive longitudinal axis. The apex of the ectoderm of the gastrula corresponds to the animal pole, while the vegetative pole may be said to coincide with the centre of the at first circular aperture of invagination. This latter soon becomes oval, and the plane of symmetry is thus established. These later stages, seen in profile (Fig. 280 *B*), show a point at which the curve is more abrupt; this point does not coincide with the animal pole but lies somewhat excentrically, corresponding to the anterior end of the later principal axis, the posterior end coinciding with the posterior edge of the blastopore. The definitive principal axis thus forms an acute angle with the primary axis. The blastopore has undergone shifting to the dorsal side of the embryo; it now gradually decreases in size, chiefly through a backward growth of its dorsal or anterior border. The posterior (ventral) edge of the blastopore, on the contrary, remains stationary during this narrowing process. It is always marked by two larger entoderm-cells lying symmetrically to the median plane (Fig. 280 *C*); these are claimed by HATSCHEK as pole-cells of the mesoderm.* Finally, the embryo becomes more elongated. The ventral surface is distinguished by being arched, while the dorsal side, which was originally occupied by the blastopore, is distinctly flattened. The posterior end of the dorsal side is occupied by the now very small vestige of the blastopore (Fig. 280 *C*). Even at this stage, the external surface of the embryo is covered with short flagella which enable it to rotate within the egg-envelope.

In the position of the blastopore and the conditions under which it closes, there is close resemblance between *Amphioxus* and the Ascidia (*cf.* p. 342).

In our description of the transformations undergone by the gastrula-stage, we have for the most part followed HATSCHEK. A rather divergent account has recently been given by LWOFF (No. 17) who, in dealing with the closure of the blastopore, lays the chief stress on the independent and rapid growth of the ectoderm at its dorsal margin. (Stress should also be laid on the protrusion of the lateral edges of the blastopore, a point which was overlooked by LWOFF). From this rapidly growing dorsal edge, ectodermal elements are said to be invaginated dorsally into the gastrula-cavity and there finally to force the proper entodermal elements from the dorsal to the ventral side of the cavity. According to this view, the cells forming the dorsal wall of the archenteron are ectodermal and it is from this cell-layer that LWOFF derives the chorda. LWOFF was not able to convince himself of the presence of the primitive cells of the mesoderm which HATSCHEK found marking the posterior end of the longitudinal axis of the embryo.

B. Development of the Medullary Tube, the Primitive Segments and the Notochord.

The next ontogenetic stages of *Amphioxus* are characterised by the increase in length of the whole body. The median part of the dorsal surface, at the same time, sinks in somewhat (Fig. 281), and this

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* [SOBOTTA (No. X.) agrees with LWOFF (No. 17) in denying that the blastopore closes from before backward. They believe that it gradually diminishes on all sides. SOBOTTA was unable to find the pole-cells and does not believe that they exist, at any rate at the early stages figured by HATSCHEK.—ED.]

depression leads to the development of the medullary tube. The latter is here formed, not, as in the Ascidia and many Vertebrates, through the fusion in the middle line of two lateral medullary folds, the process, although it may be deduced from the above type, being somewhat modified. It might be described as lateral overgrowth. The medullary plate (Fig. 282 *A*, *mp*) sinks down somewhat and its lateral edges become detached from the rest of the ectoderm. The ectoderm (*hb*) now grows inward from either side above the medullary plate and unites in the middle line before the plate has become curved into a tube (Fig. 282 *B*). "The dorsal groove, although completely covered externally, is still open within, under the integument" (Fig. 283). Only later does the medullary plate curve round dorsally, and, through the fusion of its lateral edges, form a closed tube, the medullary tube (Fig. 284).

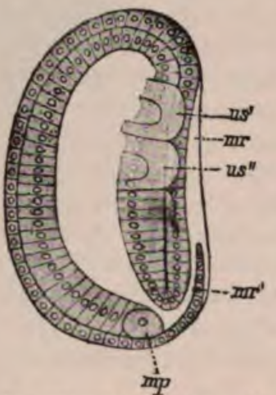

Fig. 281.—Embryo of *Amphioxus* with the rudiment of two primitive segments (after HATSCHEK). *mp*, pole-cells of the mesoderm; *mr*, medullary groove; *mr'* medullary tube; *us'*, first primitive segment; *us''*, second primitive segment.

The union of the lateral ectodermal growth above the medullary plate takes place from behind forward, commencing near the remains

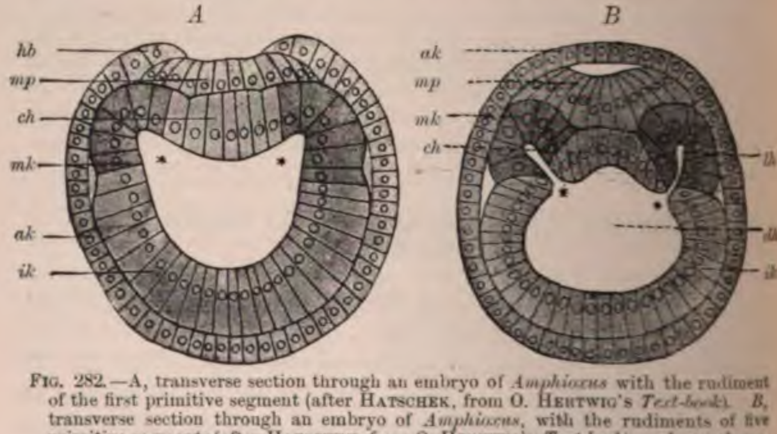

FIG. 282.—A, transverse section through an embryo of *Amphioxus* with the rudiment of the first primitive segment (after HATSCHEK, from O. HERTWIG'S *Text-book*). *B*, transverse section through an embryo of *Amphioxus*, with the rudiments of five primitive segments (after HATSCHEK, from O. HERTWIG'S *Text-book*). *ak*, ectoderm; *ch*, chorda-rudiment; *dh*, archenteric cavity; *hb*, layer of the ectoderm that grows over the medullary plate; *ik*, entoderm; *lh*, body-cavity; *mk*, primitive segment; *mp*, medullary plate.

of the blastopore, which thus becomes covered by a layer of ectoderm (Fig. 281). The blastopore thus does not open externally but into the neural canal; this connection between the intestine and the neural tube is long retained, being known as the *neurenteric* canal. [See Kopsch, No. V.]

The medullary plate does not reach the most anterior end of the embryo, but extends for about three-quarters of its length. At the point where it stops, which lies somewhat in front of the anterior edge of the first primitive segment, the medullary tubes retain an external aperture which is at first wide but gradually narrows later (*neuropore*, Figs. 285, 286, *np*). As we shall presently see, the neuropore in *Amphioxus* only closes in a very late stage (Kupffer). The cells of the medullary tube, like the other ectodermal cells, carry flagella. These, which are long and exceedingly fine, project into the lumen of the tube and are directed backward.

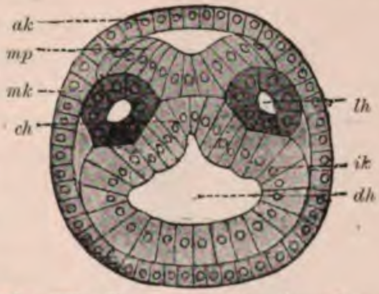

Fig. 283.—Transverse section through an embryo of *Amphioxus* with five well-developed primitive segments (after Hatschek, from O. Hertwig's *Text-book*).

The development of the medullary tube leads to a pressing inward of the middle part of the dorsal wall of the entoderm-sac (Fig. 282 *A*). This median swelling is accompanied by two latero-dorsal outgrowths of the entoderm-sac (Fig. 282 *B*, *mk*). These paired longitudinal folds, the so-called mesoderm-folds, yield the material which becomes the mesoderm and can be traced posteriorly as far as to the neighbourhood of the two primitive mesoderm-cells,* although the most posterior part of the folds is indistinctly marked off from the rest of the entoderm-sac. Segmentation very soon appears in the anterior region, the mesoderm-folds becoming cut up by transverse indentations, into consecutive portions, the primitive segments (Fig. 281, *us'*, *us''*). The segments which, owing to their origin, must be regarded as archenteric diverticula, develop regularly from before backward. We thus see, in Fig. 281 two, in Fig. 285 five, and in Fig. 286 nine segments distinctly marked off. Later, the primitive segments become completely cut off from the entoderm-sac, and they

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[* See footnote, p. 539.—Ed.]

then form paired coelomic sacs closed on all sides (Fig. 283, *mk*). The coelom consequently here forms as in *Sagitta*, *Balanoglossus*, the Echinoderma and the Brachiopoda, through abstriction of pouches (enterocoeles) from the walls of the archenteron; the coelomic cavity is derived from a part of the primary archenteric cavity. While the anterior primitive segments develop more and more, new segments are constantly becoming severed from the contiguous, unsegmented part of the mesoderm-folds.

LWOFF has recently described the formation of the coelomic sacs in a way differing from that of KOWALEVSKY and HATSCHEK. According to him, the development of the two mesoderm-folds has no direct connection with the rise of the coelomic sacs, but results merely mechanically as a consequence of the sinking in of the medullary tube between them. The primitive segments, indeed, arise through abstriction from these folds, but the cavities found in them disappear, while the coelom of the adult rises only later through the shifting apart of the cells composing the temporarily solid primitive segment. Even if LWOFF's observations should be confirmed, the way in which the primitive segments here develop would still have to be regarded as a modification of development by evagination or out-folding of the archenteron in the sense given above.*

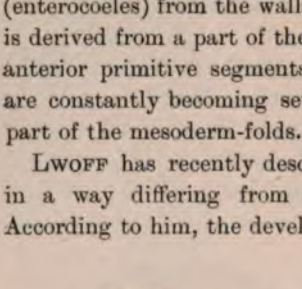

FIG. 284. — Transverse section through the middle of the body of an embryo of *Amphioxus* with eleven primitive segments. On the left, only one primitive segment has been cut through, but on the right, two consecutive segments are seen. *ak*, ectoderm; *ch*, rudiment of chorda; *dh*, enteric cavity; *ik*, entoderm; *lh*, body-cavity; *mk*^{1}, somatic, *mk*^{2}, splanchnic layer of the mesoderm; *n*, neural tube; *us*, primitive segment.

The *notochord* or *chorda dorsalis* develops somewhat later than the first rudiment of the medullary tube and the primitive segments, arising through a folding in of that part of the dorsal wall of the entoderm-sac which extends between the mesoderm-folds (Fig. 282, *ch*). This median entoderm-mass lying beneath the medullary plate at first bulges into the archenteron dorsally (Fig. 282 *B*), but later changes into an outgrowth (Fig. 283), the lumen of which is finally a mere slit. Even this slit disappears later, and the cells which come into

[* MACBRIDE's recent investigations (Nos. VIII. and VIII. *a*) show that the mesoderm arises as a series of true gut-pouches.—ED.]

contact in the median line dove-tail into one another. The rudiment of the chorda is then a solid strand-like thickening of the dorsal entoderm-wall, from which it soon becomes severed as an independent strand (Fig. 284, *ch*). In the meantime the cells of this rudiment press between each other in such a way that each cell finally extends transversely across the entire rudiment.

The chorda develops, on the whole, from before backward. It commences to develop in the region of the primitive segments. The anterior part of the chorda, which extends above the first primitive segment towards the anterior end of the body, only develops later, and then not through the independent growing out of the already developed rudiment, but through a separation of cells at the most anterior part of the archenteron from which no primitive segment is abstricted.

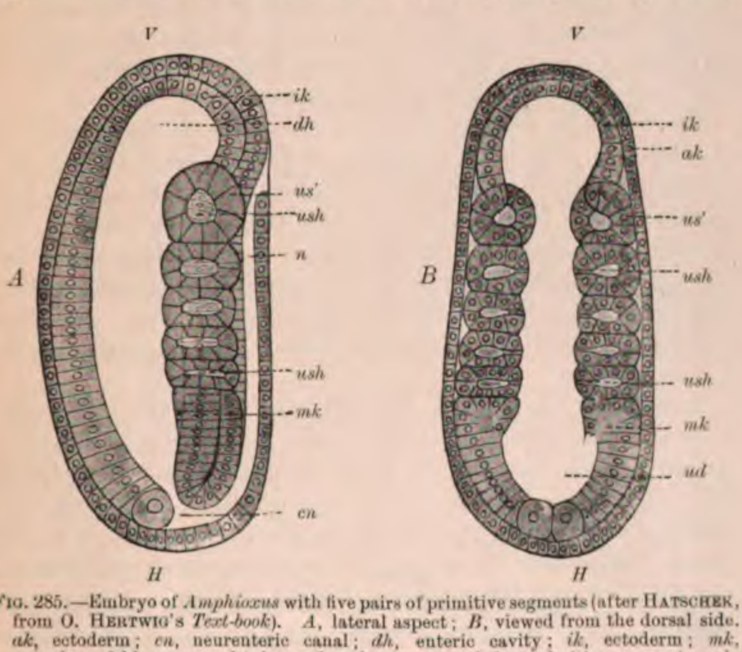

FIG. 285.—Embryo of *Amphioxus* with five pairs of primitive segments (after HATSCHEK, from O. HERTWIG's *Text-book*). *A*, lateral aspect; *B*, viewed from the dorsal side. *ak*, ectoderm; *cn*, neurenteric canal; *dh*, enteric cavity; *ik*, ectoderm; *mk*, mesoderm-fold; *n*, neural tube; *ud*, archenteron; *us'*, first primitive segment; *ush*, cavity of primitive segment; *V*, anterior, *H*, posterior.

The whole of the entoderm-plate which lies between the mesoderm-folds is not, however, used up for the formation of the chorda, but only the median part of it, the lateral parts, according to **HATSCHEK**, being utilised for the completion of the dorsal wall of the alimentary canal, viz., the filling up of the gap in the entoderm-sac which arises through the abstriction of the chorda and the primitive segments. On this point, however, LWOFF (No. 17) does not agree with HATSCHEK.

C. Further Development up to the Time when the Mouth and the First Gill-cleft Form.

The embryo quits the egg-envelope very early, usually at about the stage in which the rudiments of two pairs of primitive segments can be recognised (Fig. 281). The young larva then swims about freely by means of its cilia, its movements recalling those of many invertebrate larvae. As the body moves forward it rotates round its longitudinal axis, thus taking a spiral course.

The transition from embryonic to larval life is very gradual in *Amphioxus*. The larva is capable of feeding independently only in comparatively late stages. Up to that time it is nourished by particles of the food-yolk derived from the egg which, in the form of spherical granules, fill all the tissues of the embryo, but do not disintegrate simultaneously in the different layers of the body. They disappear most quickly in the external epithelium, then in the mesoderm, then in the medullary plate, and are retained longest in the entoderm.

In an aquarium, the newly hatched larva for the first few hours of its free-swimming existence keeps rigidly to the surface of the water. At later stages, however, the larva frequently rests at the bottom, lying on one side. Thus, during metamorphosis, *Amphioxus* leads a pelagic life. The young *Amphioxus*, when metamorphosis is completed, buries itself in the sand in an upright position (WILLEY), like the adult, only the anterior end of the head projecting above the surface.

In the gastrula-stage, the embryo becomes ellipsoidal, the dorsal side at first flattening or curving in (medullary groove, Fig. 280 *C*, 281). Later, the embryo increases in length, the body at the same time becoming laterally compressed (Fig. 286). As the anterior end of the body lengthens out into a snout, and the posterior end becomes marked by a caudal fin, it bears a general resemblance to a fish (Figs. 288, 290).

As the body increases in size the ectodermal cells change, as a rule, into flattened, ciliated cells, only remaining columnar at the anterior and posterior ends of the body. The larval (primary) caudal fin (Figs.

288, 290, *c*) does not arise as an epithelial fold, but as a simple thickening due to the ectoderm-cells increasing greatly in height.

The medullary tube (Fig. 288, *mr*), in the central canal of which backwardly directed cilia can still be seen, has an anterior swelling, in which not only are the walls thicker but the central canal wider. Even in very young stages a pigment-spot is found in the ventral wall of the medullary tube in the fifth metamere (Fig. 288). Later, a similar spot, functioning as an eye-spot, appears at the anterior end of the cerebral swelling (Figs. 289, 290). The posterior end of the medullary tube appears dilated (Fig. 288), and this swelling contains the undifferentiated material which, as growth advances, continually produces new parts of the medullary tube. This dilated, posterior end is bent round the posterior end of the chorda. At this point the communication with the alimentary canal is found (*neurenteric canal*, Fig. 288, *cn*).

In cross-sections, the medullary tube is found to consist of a single layer of cells (Fig. 234, *n*), the first perceptible nerve-fibres being found in the ventro-lateral corners, in contact with the chorda.

The rudiment of the *mesoderm* consists of the series of consecutive *primitive segments* (Fig. 286, *us*′, *us*″) and of a posterior unsegmented region, the *mesoderm-folds* (*mf*) which (according to HATSCHEK) terminate in the pole-cells of the mesoderm (*mp*). In this posterior region, the coelom is still for a time in communication with the enteric cavity. Later, however, the mesoderm-folds become completely separated from the entoderm-sac, and, as the posterior end of the chorda-rudiment becomes similarly abstricted from the alimentary canal, the neurenteric canal, in later stages, forms a simple communication between the ventrally-curved posterior end of the medullary tube and the most posterior end of the intestine.

Even in the stage with eight primitive segments, we find indications of that asymmetry which affects the later development of the body. The primitive segments of the right side of the body lie somewhat further back than those of the left (*cf.* the boundaries of segments fully outlined with those in dotted outline in Fig. 287). This asymmetrical shifting of the primitive segments takes place to such an extent that the junction between two segments on one side coincides with the centre of a segment on the opposite side.

In the stage with nine primitive segments, the most anterior segment sends off dorsally, at the side of the chorda-rudiment, a hollow process (Fig. 286, *m*) which gradually grows forward to the anterior extremity of the body. This cephalic process of the mesoderm yields the mesodermal structures in the anterior region of the body. It has recently been regarded by **Hatschek** (No. 8) as the rudiment of an independent pair of primitive segments, in which case, the segment hitherto called the first would actually be the second.

The walls which separate the consecutive segments, the so-called *dissepiments*, at first run straight from the dorsal to the ventral side (Fig. 285, *A*). Later, they curve backward (Fig. 286) and finally they develop the characteristic angulation at the level of the upper part of the chorda dorsalis (Figs. 287, 288).

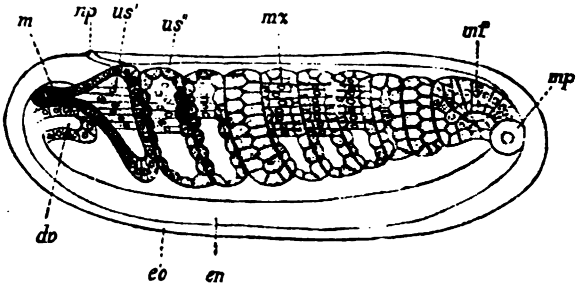

Fig. 286.—Stage in the development of *Amphioxus* in which there are nine primitive segments (after **Hatschek**). In the fifth, sixth and seventh primitive segments, the muscle formative cells (*mz*) are clearly marked. *dv*, anterior entoderm-diverticulum; *ec*, ectoderm; *en*, entoderm; *m*, cephalic process of the first primitive segment; *mf*, mesoderm-folds; *mp*, pole-cells of the mesoderm; *mz*, muscle formative cells; *np*, neuropore; *us'*, first primitive segment; *us"*, second primitive segment.

The primitive segments originally lie dorsally above the alimentary canal (Fig. 283, *mk*). Later, they extend ventrally and thus grow round the alimentary canal (Fig. 284). Those parts of the coelom also which surrounded the canal are originally distinct from one another, but at the stage in which the mouth forms, the ventral part of the dissepiments degenerates, and consequently the originally distinct coelomic cavities run together and form the *splanchnocoele*, which, enclosed by the lateral plates, runs through the whole length of the body as a continuous cavity. The right half of the splanchnocoele is in open communication with the left half below the alimentary canal. According to **Hatschek**, previous to this union of the ventral part of the primitive segments that grow down on either side, a simple ventral lamella is formed which extends between the ectoderm and the alimentary canal. In this ventral lamella the rudiment of the first recognisable blood-vessel, the *sub-intestinal vessel* appears, a vessel which lies later on the ventral side of the alimentary canal covered by the splanchnopleure. The first rudiment of this vessel can be followed forward from the posterior end of the body as a clear canal (Figs. 288, 289, *sv*). Near the second segment it is deflected to the right side of the body by the first gill-rudiment forming in the ventral median line, and ends, apparently blindly, near the club-shaped gland. The origin of this vessel is still obscure. KOWALEVSKY derives it from cells lying free in the body-cavity which form a solid strand that becomes hollowed out later.

As the cavities of the primitive segments gradually increase in size the cells of their walls become more and more flattened. This does not apply, however, to the cells in contact with the sides of the notochord which, on the contrary, become greatly elongated as columnal or club-shaped cells and form the rudiment of the lateral trunk-muscles (Fig. 284). These cells contain nuclei in their free club-shaped ends, while the basal portion, that is turned to the chorda, becomes transformed into muscular tissue. Each of these muscle-cells traverses the whole length of the primitive segment to which it belongs (Fig. 286, *mz*), and its axis lies in a line with the corresponding cells of the neighbouring primitive segments. The muscle-fibres formed by these cells fuse together and run continuously through the consecutive segments. Each muscle-fibre is thus formed from a series of consecutive muscle-cells. Transverse striation can early be made out in the fibres. The fact that the walls of the primary gut-pouches (enterocoeles) give rise not only to the lining of the body-cavity but also to the trunk-muscles, has caused some observers to speak of the primary cavities as the myocoelomic pouches. At an early period after the ventral extension of the mesodermal somite described above, its cavity becomes divided into two by the formation of a horizontal partition which separates a ventral splanchnocoele from a dorsal myocoele (see pp. 564 and 565).

FIG. 287.—Stage of *Amphioxus* with thirteen primitive segments (after HATSCHEK). The boundaries of the segments of the left side are indicated by uninterrupted lines, and those on the right by dotted lines. *cn*, neurenteric canal; *dr*, rudiment of the club-shaped gland. *dv'*, right, *dv''*, left, anterior entoderm-diverticulum; *np*, neuropore.

The principal change to be noted in the notochord is the great development of its anterior end (Figs. 287, 288). It now extends to the anterior end of the body, a feature in which *Amphioxus* is distinguished both from the Tunicata and from the Vertebrata. We have already mentioned that the posterior end of the chorda-rudiment in later stages becomes abstricted from the enteric wall in the same way as the mesoderm-folds, and is then independent. In the meantime, histological differentiations take place which foreshadow the final condition of the chorda. In transverse section the chorda is seen to be composed of about four cells one above the other (Fig. 284). Small, round vacuoles now appear in the protoplasm of these cells. These vacuoles in the uppermost and undermost rows of cells remain small, but in the two middle rows they run together to form large vacuoles, the order at the same time becoming changed in such a way that a large vacuole compressed from before backward alternates with a cell. The cells of the middle layers then form partitions between the successive large vacuoles. A similar stage of development was described above for the chorda of the Ascidians. According to Lwoff's researches (No. 16), the chorda-tissue of *Amphioxus*

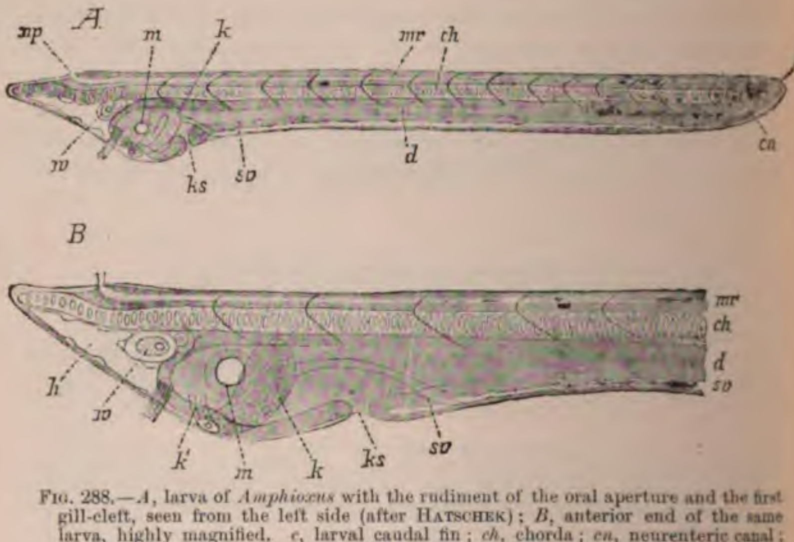

Fig. 288.—*A*, larva of *Amphioxus* with the rudiment of the oral aperture and the first gill-cleft, seen from the left side (after Hatschek); *B*, anterior end of the same larva, highly magnified. *c*, larval caudal fin; *ch*, chorda; *cn*, neurenteric canal; *d*, alimentary canal; *h*, cavity caused by the transformation of the right anterior entoderm-sac; *k*, club-shaped gland; *k'*, efferent portion of the same; *ks*, gill-cleft; *m*, mouth; *mr*, medullary tube; *np*, neuropore; *sv*, sub-intestinal vein; *w*, ciliated organ (pre-oral pit).

essentially agrees with that of the Vertebrates, consisting of vesicular flattened cells. The structures that were described as chorda-plates appear to be a kind of artifact.

Great changes also take place in the *entoderm*. Two lateral diverticula first become abstricted from that anterior part of the entoderm-sac which lies in front of the first primitive segment; these diverticula lie beneath the cephalic process of the first primitive segment (Fig. 286, *do*), and are called by HATSCHEK the *anterior entoderm-sacs*. This author has recently claimed them as an anterior pair of branchial sacs (No. 8). The future fate of these two diverticula, which at first resemble each other, differs greatly. The one on the right (Fig. 287, *dv*) increases considerably in size and, pressing back the anterior end of the alimentary canal, completely fills the anterior cavity beneath the chorda in the snout-like prolongation of the body (Fig. 288, *h*). The left diverticulum (Fig. 287, *dv*), on the contrary, remains small and does not shift forward. In later stages it lies transversely beneath the chorda and opens outward in front of and above the oral aperture (Fig. 288, *w*). A strongly ciliated efferent portion can be distinguished from a smaller blind portion lying to the right. This vesicle to which, later, a nerve runs, was regarded by KOWALEVSKY as a peculiar sensory organ of the larva. The pre-oral pit becomes enclosed by the developing oral hood and thus comes to lie within the adult mouth; the ciliated epithelium lining its efferent section increases in extent and gives rise to the so-called wheel-organ (Räderorgan), while its sensory organ persists in the adult as the groove of HATSCHEK.

The two anterior entoderm-diverticula have been interpreted in many different ways. We have already mentioned that HATSCHEK (No. 8) regards them as the most anterior pair of branchial sacs. VAN WIJHE (No. 22) recently claimed the aperture of the left entoderm-vesicle as the primary mouth (autostoma) of *Amphioxus*, homologous with the mouth of the Tunicata. The ciliated organ which develops from the entoderm-vesicle, together with HATSCHEK'S pit, has been compared by VAN WIJHE to the ciliated pit of the Tunicata. The right entoderm-vesicle, on the contrary, which is not morphologically the antimere of the left, corresponds to the anterior cephalic somite of the Selachians, from which are developed the optic muscles innervated by the oculo motorius. BATESON (No. 26) has compared the two anterior vesicles to the proboscis-coelom of *Balanoglossus* and the aperture of the left vesicle to the proboscis-pore, a conclusion with which WILLEY (No. XIII.) agrees.

A further derivative of the entoderm is found in the so-called *club-shaped gland* first seen by M. SCHULTZE and later by LEUCKART and PAGENSTECHER (Figs. 288, 289, *k*). This lies near the first primitive segment and arises as a transverse groove in the floor of the enteron (Fig. 287, *dr*) specially distinct on the right side of the body and running thence ventrally to the left side. This groove deepens and becomes constricted off from the enteron to form an independent tube, and then represents the club-shaped gland. the right, blind portion of which is dilated, while the narrowed left section opens externally in front of the oral aperture (Fig. 288, *k*). In later stages, the right, blind end of this gland enters into communication with the lumen of the intestine (RAY LANKESTER and WILLEY).

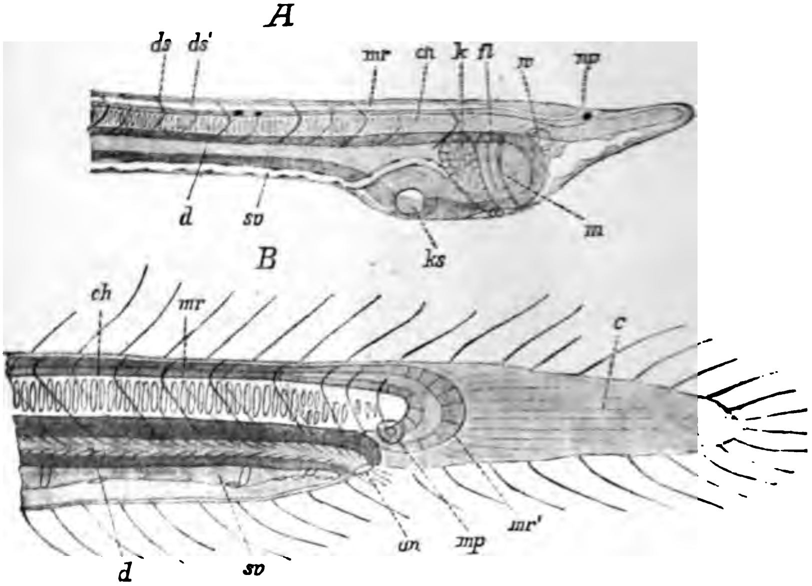

FIG. 289. *A*, anterior end of a larva somewhat older than that depicted in Fig. 288, seen from the right side; *B*, posterior end of the same seen from the left side. *an*, anus; *c*, larval caudal fin; *ch*, chorda; *d*, alimentary canal; *ds*, dissepiments of the side turned to the spectator; *ds'*, dissepiments of the other side; *fl*, ciliated band (rudiment of the endostyle); *k*, club-shaped gland; *ks*, gill-cleft; *m*, mouth; *mp*, pole-cells of the mesoderm; *mr*, medullary tube; *mr'*, posterior end of the medullary tube; *np*, neuropore; *sv*, sub-intestinal vein; *w*, ciliated organ (pre-oral pit).

Immediately in front of the club-shaped gland there is a transverse ciliated band (Fig. 289 *A*, *fl*) which, according to WILLEY, is the first rudiment of the *endostyle*.

The *oral aperture* (Fig. 289, *m*) forms on the left side of the body in the region of the first segment. A disc-like thickening of the ectoderm first appears, to the inner side of which the intestine becomes closely applied, since, in this region, the mesoderm does not extend so far ventrally. In the middle of this ectodermal thickening, the larval oral aperture forms at first as a narrow perforation which, however, soon widens. Consequently, the oral aperture is surrounded by a thickened ectoderm-wall.

The *first gill-cleft* forms soon after (Fig. 289, *ks*) in the ventral region of the second body-segment. A small outgrowth of the entoderm here forms, round which the entoderm-cells become elongated and less granular. An annular entodermal thickening is thus formed in the middle of which is the above-mentioned depression, the cells of which soon fuse with the ectoderm, and a perforation, the first gill-slit, takes place. Round the first gill-cleft, the ectoderm is not thickened, but the entoderm forms a circular wall representing the inner edge of the gill-cleft. The first primary gill-cleft which arises in this way soon shifts to the right side of the body (Fig. 289 *A*).

After the mouth and the first gill-clefts have broken through, the ciliated organ, the pre-oral pit (derived from the left enteric vesicle), and the club-shaped gland also open externally.

The *anal aperture* breaks through at the most posterior end of the alimentary canal on the left side of the body. At the same time, the communication between the intestine and the ventrally curved end of the medullary tube (neurenteric canal) (Fig. 289 *B*) is lost.

After all these apertures have formed, the larva is capable of taking in food.

D. Later Larval Stages.

The further development of the larva falls into three periods :—

I. Behind the first gill-slit, a series of other so-called *primary gill-slits* (as many as fourteen, Willey) develop ; most of these shift to the right side of the pharynx. The metapleural folds arise and the atrium begins to form and to close from behind. The primitive segments increase in number till the condition of the adult is in this respect reached (sixty-one segments forming in *Amphioxus lanceolatus*). The unpaired fin of the adult with its cavity develops (Figs. 290, 291).

II. On the right side, above the row of primary gill-clefts, a second row forms (*secondary clefts* of Willey). After the atrium has closed, the primary gill-clefts shift to the left side, while the secondary remain on the right side. The larval mouth becomes changed into the velum, and the definitive mouth-aperture arises as a consequence of the formation of paired folds, the oral hood, round the larval mouth. The mouth shifts into the ventral median line. The oral cirri develop and the club-shaped gland degenerates. In consequence of the development of tongue-bars in connection with the gill-slits, the number of the latter is doubled. The hepatic caecum forms (Figs. 292, 293, 296).

III. The larva, which in essential points now closely resembles the adult, has given up pelagic life and buries itself in the sand. The gill-clefts already formed, which at first were arranged metamerically, shift nearer together, and their number is further increased by the addition of paired *tertiary clefts* (WILLEY). These tertiary clefts continue to increase in number throughout life.

It has already been mentioned (p. 551) that the first primary *gill-cleft* which arose in the ventral median line of the second trunk-segment soon shifts to the right side of the body. In an exactly similar way, new gill-clefts form successively in the body-segments that follow (Figs. 290, 291), these clefts also lying in the ventral median line and shifting later to the right side of the body. The row of *primary* clefts now lying on the right side is destined later to take up its final position on the left side. The number of primary clefts which thus arise one after the other varies from twelve to fifteen, and is usually fourteen. *They have a strictly metameric arrangement* and, according to HATSCHEK (No. 8), are intersegmental. The gill-clefts thus correspond to the boundaries of the segments.

HATSCHEK (No. 8) regards the above-mentioned entoderm-vesicles as the most anterior pair of gill-clefts. These vesicles correspond to the posterior boundary of the first metamere (represented by the cephalic process of the mesoderm which HATSCHEK regarded as an undeveloped pair of primitive segments). The peribranchial groove (the anterior ciliated arch, which is homologous with the ciliated arch of the Tunicates) was regarded by him as the second pair of gill-clefts. The clefts which were described above as the first true gill-clefts would, according to this interpretation, represent the third pair. This pair is on the right somewhat smaller than the others; the clefts which follow the ninth are also at first smaller than the rest and do not deviate from their median position to the right.

The median ventral blood-vessel which, in the pharyngeal region, constitutes the branchial artery, turns somewhat to the right in the branchial region and then runs forward above the row of primary gill-clefts (Figs. 292, *si*). We have already seen (p. 547) that the course of this vessel is diverted to the right by the rudiment of the most anterior pair of gill-clefts. The course of this vessel marks the future ventral median line of the pharynx.

A longitudinal ridge now soon arises above the branchial artery on the right side of the body (Fig. 292, *k*); this is composed of con-

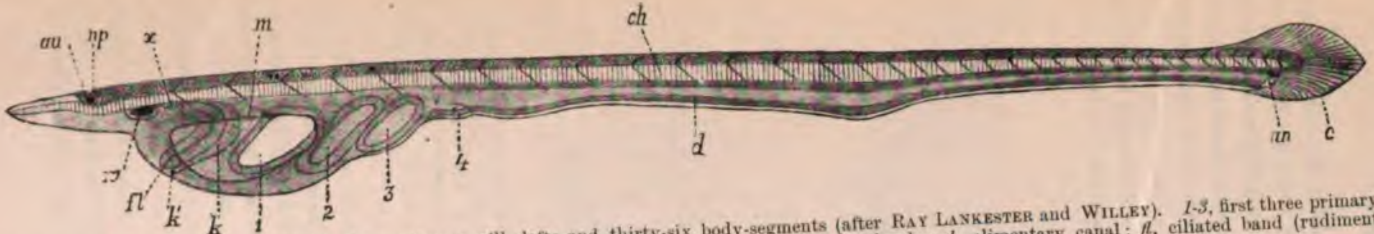

FIG. 290.—Larva of *Amphioxus* with three primary gill-clefts and thirty-six body-segments (after RAY LANKESTER and WILLEY). *1-3*, first three primary gill-clefts; *4*, rudiment of the fourth cleft; *an*, anus; *au*, eye-spot; *c*, larval caudal fin; *ch*, chorda; *d*, alimentary canal; *fl*, ciliated band (rudiment of endostyle); *k*, club-shaped gland; *k'*, aperture of the same; *m*, mouth; *np*, neuropore; *w*, pre-oral pit; *x*, HATSCHEK's nephridium.

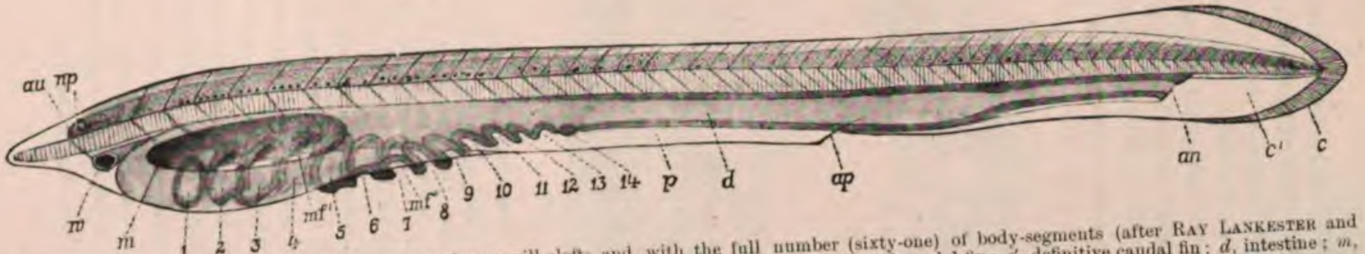

FIG. 291.—Larva of *Amphioxus* with fourteen primary gill-clefts and with the full number (sixty-one) of body-segments (after RAY LANKESTER and WILLEY). *1-14*, first fourteen primary gill-clefts; *an*, anus; *ap*, atriopore; *au*, eye-spot; *c*, larval caudal fin; *c'*, definitive caudal fin; *d*, intestine; *m*, mouth; *mf'*, edge of the right metapleural fold; *mf''*, edge of the left metapleural fold; *np*, neuropore; *p*, atrial cavity; *w*, pre-oral pit.

secutive connected oval thickenings. This ridge, which represents a thickening of the pharyngeal wall, is the rudiment of a new row of gill-clefts, the *secondary clefts* of WILLEY which remain on the right side of the body. Their true character is soon announced by fusion of the entodermal thickenings with the ectoderm and by the appearance of small elongated perforations in the middle of the ovals (Fig. 292 *B*, *I-VII*). The rudiments of six secondary clefts usually first appear, alternating in position with the primary clefts in the way described above in connection with the primitive segments of the right and left sides of the body (p. 545). The most anterior of these six secondary gill-rudiments lies between the third and fourth primary clefts. The number of secondary clefts increases later, one more forming anteriorly, and several being added posteriorly, so that, finally, they number in all seven to nine, eight being the most common number.

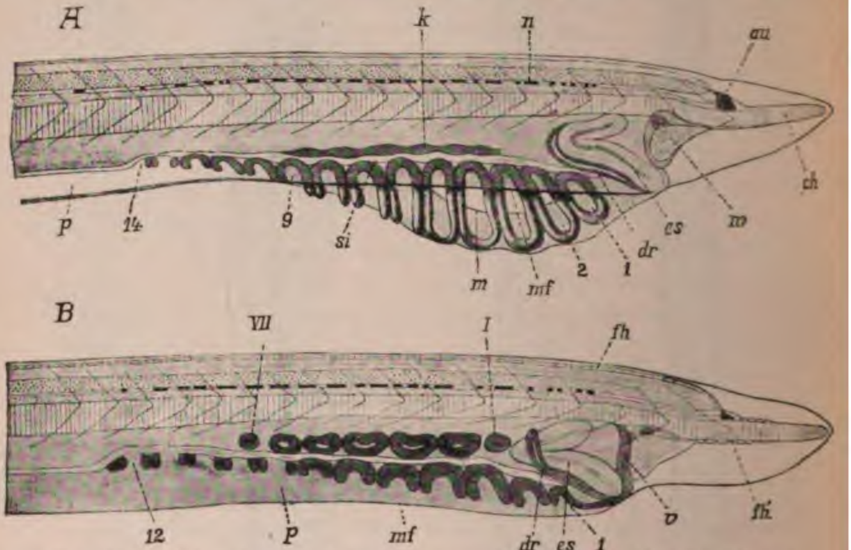

FIG. 292.—Two larval stages of *Amphioxus*, seen from the right side (after WILLEY). *1*, *2*, *9*, *12*, *14*, first, second, ninth, twelfth and fourteenth primary gill-clefts. *I-VII*, first seven secondary gill-clefts; *au*, eye-spot; *ch*, chorda; *dr*, club-shaped gland; *es*, rudiment of endostyle; *fh*, dorsal fin-cavities; *fh'*, ventral fin-cavities; *m*, margin of the mouth; *mf*, edge of the right metapleural fold; *k*, rudiment of the secondary gill-clefts; *n*, medullary tube; *p*, atrial cavity; *si*, branchial artery; *v*, velum; *w*, pre-oral pit.

The later changes in the branchial region consist of the shifting of the row of primary gill-clefts over the ventral surface of the pharynx from the right side of the body to the left. The oral aperture has meanwhile shifted from the left side and taken up a more anterior and ventral position. The branchial artery, which lies beneath the rudiment of the endostyle, now occupies the ventral middle line, while the secondary gill-clefts remain on the right side of the body (Fig. 293). A reduction in the number of the primary clefts takes place at the same time, the most anterior and some of the most posterior closing and completely disappearing (twelfth in Fig. 293), so that finally the number of clefts on the right equals that on the left. These changes have been defined as the process of symmetrisation of the branchial region or the equalisation of the gill-slits. They lead to a final stage in which an equal number of clefts (seven to nine, usually eight) is found on each side. This stage, which marks a long pause in development during which only the endostyle-rudiment grows further posteriorly and the clefts increase in height, has been named by WILLEY the *critical stage* of larval development. WILLEY points out that the number of clefts at this stage approximately agrees with the typical number of gill-clefts in Vertebrates.

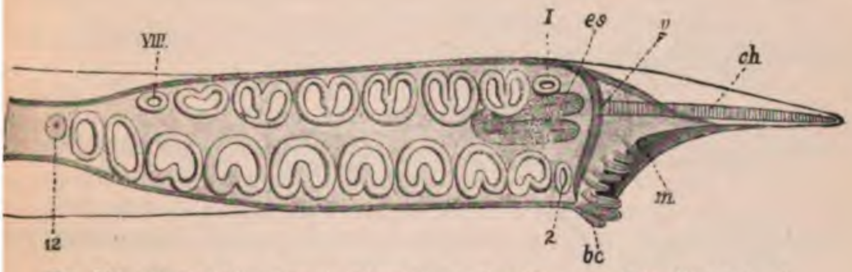

FIG. 293.—Ventral side of an *Amphioxus* larva at a later stage (after WILLEY). *2*, second, *12*, vestige of twelfth primary gill-cleft; *I-VIII*, first eight secondary clefts; *bc*, buccal cirri; *ch*, chorda; *es*, endostyle; *m*, mouth; *v*, velum.

The gill-clefts hitherto present were segmentally arranged, but this relation to the body-segments is lost in the *tertiary clefts* which are added later in pairs behind the clefts already formed. The most anterior, originally segmental clefts (primary and secondary) are also then displaced forward.

The primary clefts become early lengthened in the transverse direction of the body, *i.e.*, vertically (Figs. 292, 293). The secondary clefts, on the contrary, are, when they first appear, lengthened at right angles to this direction and consequently parallel to the longitudinal axis of the body (Fig. 293). Only in later stages do they also extend vertically.

While the above changes are taking place in the branchial region, the number of gill-clefts is doubled, each cleft being cut up into two halves by the down-growth of a conical process from its dorsal edge (Fig. 293). So long as this process (the rudiment of the secondary or tongue-bar) does not reach the lower edge of the cleft, the latter is horse-shoe-shaped, recalling in appearance the gill-clefts of *Balanoglossus*. The process finally fuses with a prominence which rises to meet it from the lower edge and each gill-cleft is thus divided into two. In consequence of the clefts having developed in this way, we are able to distinguish in the adult alternate series of primary and secondary gill-bars, between which an essential anatomical distinction exists, as has recently been pointed out by RAY LANKESTER (No. 12), SPENGEL (No. 19), and BOVERI (No. 2).* Here we can only mention that the primary bars enclose a coelomic canal which is wanting in the tongue-bars. The cross-bars or synapticula (Fig. 312, *s*), running in an obliquely horizontal direction from one primary bar to the next, only develop comparatively late.

While the changes just described are gradually leading to the perfection of the pharynx, a cavity develops round this region, the peribranchial or atrial cavity. In accordance with KOWALEVSKY and ROLPH, this was formerly thought to arise through two longitudinal folds growing completely over the region of the branchial clefts like the branchiostegite in the Crustacea and fusing in the ventral median line so that, finally, of the original wide aperture between the peribranchial folds only a small median postero-ventral opening is left. This aperture, the atriopore, serves to put the atrial cavity into communication with the exterior. Our view of the development of the atrial cavity has, however, recently been modified through the researches of RAY LANKESTER and WILLEY. The first rudiment of this cavity is, indeed, found in the form of two folds (Fig. 294 *A*), known as the *lateral* or *metapleural folds* (*lf* and *rf*). Within these folds a cavity develops (Fig. 311, *of*, p. 572), which, according to KOWALEVSKY, represents an isolated part of the body-cavity. This cavity, which is known as the metapleural canal (HATSCHEK'S *Oberfaltenhöhle*), is not reckoned as belonging to the coelom by RAY LANKESTER and WILLEY, but is regarded as a lymph-sinus (pseudocoele). According to HATSCHEK, on the contrary, it should be considered to belong to the myocoele.

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* [See BENHAM'S more recent work, No. I.—ED.]

The *lateral folds* at first lie very near together on the ventral side of the larva (Fig. 294). They are found in larvae in which nine or ten primary gill-clefts have developed. Behind this region, the lateral folds are bilaterally symmetrically placed at the sides of the median line. Near the gill-clefts, on the contrary, they diverge to the right (Fig. 294). The right lateral fold (*rf*) runs forward along the right side of the body above the clefts, in front of which it again bends toward the median line. It covers externally the upper part of the clefts. The left lateral fold (*lf*) is at first only slightly developed anteriorly and runs almost along the median line in the branchial region.

The lateral folds border a groove running along the ventral side which is the first rudiment of the atrial cavity. The posterior part of this groove closes first (Fig. 294 *B*), closure being effected by the appearance of two solid ridge-like projections of the inner opposed faces of the metapleurs (sub-atrial ridges of Ray Lankester and Willey); these ridges grow out towards one another (Fig. 295 *A*, *sl*) and fuse (Fig. 295 *B*). Through the fusion of the sub-atrial ridges, the floor of the atrial cavity is formed, in which later that part of the body-cavity called by Hatschek (No. 8) the *cavity of the lower folds* appears (Fig. 311, *uf*, p. 572). The atrial cavity, which is at first tubular and open at both ends, gradually extends farther forward (Fig. 294 *B* and *C*), till, finally, the anterior part of the atrial cavity is completely closed towards the exterior. Only in the posterior part of it do the metapleurs still remain separate. The aperture here

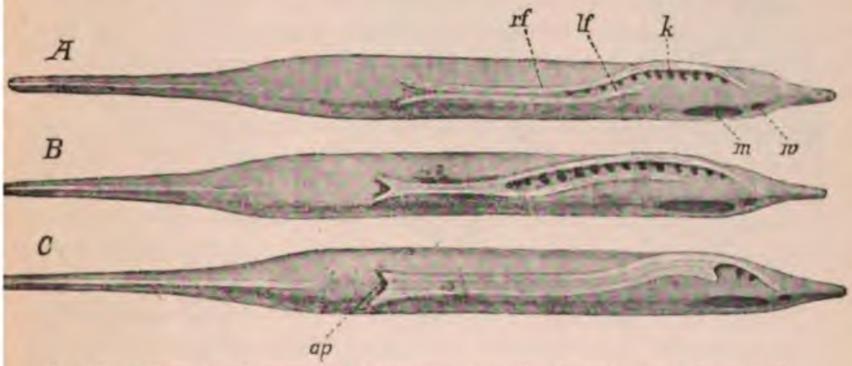

FIG. 294.—Three larval stages of *Amphioxus*, from the ventral aspect (after Ray Lankester and Willey). *A*, the atrium is still entirely open; *B*, the atrium is partially closed posteriorly; *C*, the atrium is almost completely closed. *ap*, atriopore; *k*, gill-slits; *lf*, left metapleural fold; *m*, mouth; *rf*, right metapleural fold; *w*, pre-oral pit.

retained is the atriopore (Fig. 294, *ap*). The lateral folds are also found in the adult as projecting ridges of the body-wall, running from the mouth to the atriopore.

The atrial cavity thus formed is at first a tube with a comparatively narrow lumen (Fig. 295 *B*) which only secondarily widens; this widening, which is accompanied by a shifting apart of the metapleural folds, is brought about by the lateral growth of the atrial cavity between the wall of the intestine and the body-wall pressing into the coelom so as almost completely to grow round the alimentary canal (Fig. 311, p. 572), the coelom being proportionately reduced as the atrium enlarges. Part of the outer wall of the atrial cavity (the epipleura of **Ray Lankester**) therefore does not arise through the formation of folds, but is a modified portion of the body-wall which has undergone no displacement. [See also **MacBride**, No. VIII. *a*.]

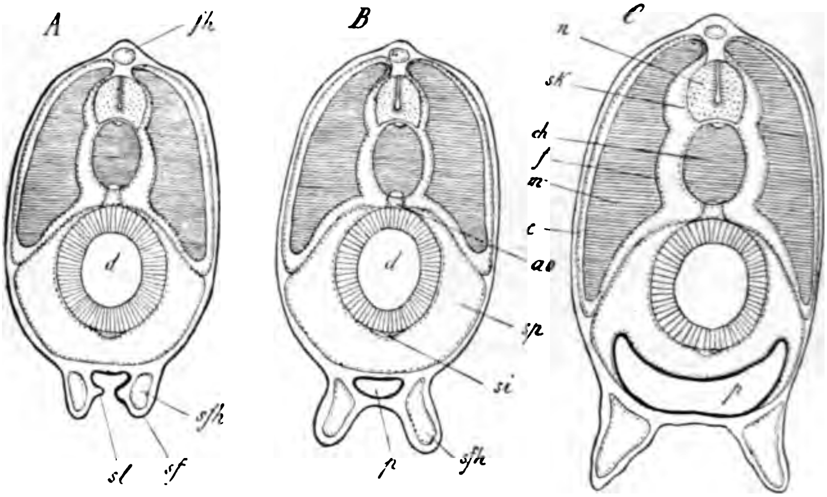

Fig. 295.—Three diagrammatic transverse sections through older larval stages of *Amphioxus* to illustrate the development of the atrial cavity (after Ray Lankester and Willey). *ao*, aorta; *c*, cutis; *ch*, chorda; *d*, enteric canal; *f*, muscle-fascia; *fh*, dorsal fin-cavity; *m*, myomere; *n*, neural tube; *p*, atrial cavity; *sf*, metapleur; *sfh*, metapleural cavity; *si*, sub-intestinal vein; *sk*, sclera-layer; *sl*, sub-atrial ridge; *sp*, coelom.

The formation of the atrial cavity in *Amphioxus* recalls to some extent that of the similarly placed cavity in the Ascidians which, as we have seen, originated in the form of paired invaginations (p. 366) which also only secondarily grow round the pharynx.

The outer wall of the atrial cavity cannot be homologised with the operculum of the fishes, the latter being a fold which belongs exclusively to the hyomandibular arch.

The metapleural folds have frequently been homologised with the primary paired lateral fins of the Vertebrata (RAY LANKESTER and WILLEY, HATSCHEK). According to HATSCHEK (No. 8), they are merely special parts of a system of ventral folds which in the most anterior part of the body develops as the unpaired ventral fin of the rostrum, in the oral region forms the lateral buccal wall, in the branchial region the metapleural fold, and, finally, behind the atriopore, the unpaired ventral fin which extends in front of and behind the anus. The "cavities of the lower folds" which develop in the sub-atrial ridges are said to be the cavities of the unpaired ventral fin.

We have already alluded (p. 550) to a ciliated band lying on the right side of the pharyngeal wall in front of the club-shaped gland (Fig. 289, *fl*). This ciliated band, in which a somewhat clearer inner zone can be distinguished, resembles in shape the club-shaped gland, so that, in the illustration, it looks like a shadow or a reduplication of the latter. It is the rudiment of the endostyle and, even in early stages, appears bent on itself (Fig. 292 *A*, *es*), being divided into a shorter upper and a longer lower half. The endostyle-rudiment then proceeds backward (Fig. 292 *B*) passing over the club-shaped gland into the space between the primary and secondary clefts. It thus comes to overlie the branchial artery. During the shifting mentioned above as taking place in the branchial region, the endostyle-rudiment passes from the right side of the body to the ventral median line (Fig. 293, *es*). The upper half of the bent rudiment becomes the right and the lower half the left part of the endostyle of the adult. At an early stage, two ciliated arches, the peripharyngeal bands, are to be seen ascending from the anterior end of the endostyle-rudiment to the dorsal side of the pharyngeal wall (Fig. 296, *fl*), and then continue backward on either side of the dorsal middle line as the ciliated hyperpharyngeal (epipharyngeal) bands. The proximal part of them corresponds to the ciliated arches (pericoronal arches or peripharyngeal bands) of the Ascidian (WILLEY).

The formation of the definite oral aperture has been described in detail by WILLEY. The oral aperture shifts from the left side of the body forward and ventralwards, so that it finally occupies a median symmetrical position on the ventral side. At the same time, it becomes grown over by a secondary fold of the body-wall (Fig. 296, *mr*), the stomodaeum or oral hood being thus formed. The primary oral aperture of the larva shifts to the back of the buccal cavity and its lips are retained as the velum (*v*) ; here the first rudiments of the velar tentacles soon appear. There are at first four of these, two lateral, one upper and one lower; later, the number increases to twelve. In the lower of the two secondary oral folds, the first rudiment of the cartilaginous skeleton that supports the oral cirri (Fig. 296, *bc*) soon appears in the form of rounded thickenings of the mesodermal tissue. Each of these cartilaginous spherules corresponds in later stages to an outgrowth of the edge of the mouth which gives rise to a cirrus. New cirri form in the lower lip in front of and behind those already formed, while, from the condition of the adult, **Ray Lankester** concluded that the median cirri of the ventral edge of the mouth were the last to arise.

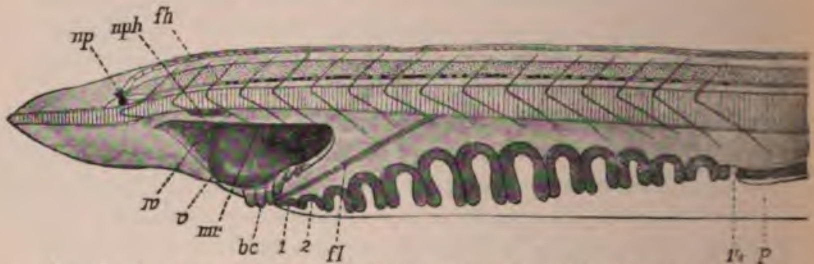

Fig. 296.—The same stage as in Fig. 292 *B* seen from the left side (after **Willey**). *1*, *2*, *14*, first, second, and fourteenth primary gill-clefts. *bc*, buccal cirri; *fl*, peri-pharyngeal ciliated band; *fh*, dorsal fin-cavities; *mr*, oral fold; *np*, neuropore; *nph*, nephridium of **Hatschek**; *p*, atrial cavity; *v*, velum; *w*, wheel-organ (part of pre-oral pit).

After the oral hood has formed, those organs which opened in the immediate proximity of the larval mouth have to open into the secondary oral cavity. These are the club-shaped gland and the pre-oral pit which marks the aperture of the sensory organ derived from the left anterior entoderm-vesicle.

The lower of the two folds which form the definitive oral aperture is continued forward without break into the unpaired fin (**Ray Lankester**). **Ray Lankester** interprets the oral folds as the anterior continuation of the so-called epipleura (lateral walls of the atrial cavity) and **Hatschek** (No. 8) has also adopted this view. According to **Willey**, the right half of the oral hood arises essentially in continuity with the right metapleur. The left half, however, is entirely independent of the left metapleur. The latter condition, **Willey** thinks, may possibly be secondary.

Another view has recently been adopted by **van Wijhe** (No. 22), who maintains that both the halves of the oral hood belong exclusively to the left side of the body. This conclusion was arrived at from a consideration of their innervation as well as from the fact that only the cavity of the left lateral fold is continued into the lip on the outer side of the massive external lip-muscle. The definitive mouth of *Amphioxus* is thus, according to **van**

WIJHE, like the larval mouth, an organ belonging to the left side of the body, in spite of its apparently symmetrical position.

It is difficult, from WILLEY'S description, to gain a clear idea of the shiftings which occur in the oral region. According to this author, the longitudinal axis of the slit-like larval mouth rotates about a vertical axis through an angle of 90°. Originally it lies parallel to the axis of the body, but is at right angles to it later. Consequently, the anterior part of the larval mouth sinks in and passes to the right side to give rise to the right half of the velum, while the left half of that organ is derived from the posterior corner of the mouth. Similar shifting of the labial folds takes place.

VAN WIJHE maintains that the mouth of *Amphioxus* is not homologous with that of the Craniata. He also doubts the homology of the velum of *Amphioxus* with that of the Cyclostomi. According to him the mouth of *Amphioxus* is a gill-cleft lying on the left, and the club-shaped gland is the corresponding organ on the right side of the body. VAN WIJHE homologises it with the left spiracle of the Selachians and with the left gill-cleft of *Appendicularia* (?).

In the later larval stages, when eight secondary gill-clefts have already developed and the tongue-bars have begun to form, the *club-shaped gland* degenerates, and finally, as it appears, reaches the interior of the alimentary canal where it is perhaps absorbed. The aperture of the gland into the intestine which was mentioned above (p. 550) seems to withstand disintegration longer than any other part of the organ (WILLEY).

In these later stages an organ is found which was discovered by HATSCHEK (No. 5) and was figured and described both by him and by RAY LANKESTER and WILLEY (Nos. 12 and 23) as the *kidney* (*nephridium*, Fig. 290, *x*). This is developed only on the left side in the form of a mesodermal ciliated funnel and canal lying in front of the mouth in the region of the first metamere (between the pre-oral pit and the mouth). It lengthens posteriorly later and is found, in the adult, as a strand extending on the left side beneath the chorda from the anterior edge of the mouth to immediately behind the velum. HATSCHEK conjectured that this canal opened into the pharynx. [See MACBRIDE, No. VIII. *a*.]

This last observation has recently been confirmed by VAN WIJHE (No. 22) who considers this organ, which he calls the oesophageal process, as the remains of the original communication between the intestine and the left anterior entoderm-diverticulum.

We have already mentioned that, in the larval stages which follow the stage with one primary gill-cleft, the number of primitive segments is continually increasing through the formation of new segments from the mesoderm-folds at the posterior end of the body. At the time when the mouth and the first gill-clefts form (Fig. 288), the larval *Amphioxus* has fourteen primitive segments, the cavities of which, when they arise, are in communication with the archenteric cavity. The primitive segments that form later are yielded by the mesoderm-folds after these have become separated from the entoderm (p. 545). The cavities of these segments are thus from the first quite distinct from the archenteron. The number of body-segments of the adult *Amphioxus* is approximately sixty-one, and this number is attained even before the appearance of the secondary gill-clefts (Fig. 291).

The unpaired fin of the adult develops simultaneously with the increase in number of the primitive segments. While the larval fin (Figs. 288, 289, 290, *c*) consists of a simple thickening of the ectoderm (see p. 544), the cells of which had a columnar form, the adult fin (Fig. 291, *c*′) consists of an ectodermal-fold, into which special parts of the body-cavity (the fin-cavities) extend (Fig. 302 *I*, *II*). Within these fin-cavities the fin-rays develop in consequence of a thickening of the mesoderm which grows up into the cavity from its floor, and these project freely into the cavity (RAY LANKESTER).

The unpaired fin extends along the whole of the dorsal side (Fig. 291). In consequence of its development, the neuropore (*np*) is pressed out of its original median position to the left side of the body The anterior end of the unpaired fin passes round the anterior end of the chorda, so that, in the rostral region, the fin is continued also on to the ventral side. This anterior ventral section of the fin, according to RAY LANKESTER (No. 12), is continued without break into the right oral fold. In passing round the posterior end of the body the unpaired fin is widened and then runs forward along the ventral side of the body as far as to the atriopore, the anal aperture being displaced by the developing caudal fin to the left. side of the body (Fig. 291).

While, in the dorsal region, the fin-rays are unpaired, in the ventral region, between the atriopore and the anus, they are paired, though, according to RAY LANKESTER, they develop in unpaired fin-cavities. The presence of these paired fin-rays has been regarded as an indication that this part of the unpaired fin arose from the fusion of paired folds which represent the backward continuation of the epipleural folds (RAY LANKESTER, HATSCHEK).

The fin-cavities are divided into consecutive compartments (Figs. 292, 296, *fh*), about five of which in the dorsal fin, according to RAY LANKESTER, belong to one muscle-segment, although a definite relation of these compartments to the segmentation of the body cannot be made out.

The anal aperture which originally lay at the posterior end of the body shifts later further forward (Fig. 291), and this leads to the development of the post-anal region of the body characteristic of the Vertebrates.

We have seen above (p. 545) that the anterior end of the *medullary tube*, which lies in the region of the first true primitive segment and the so-called cephalic process of the mesoderm (anterior primitive segment of HATSCHEK) is widened (Figs. 288, 289). This part, according to HATSCHEK's recent statements (No. 8), becomes differentiated, in the young *Amphioxus*, into three consecutive sections which correspond to the three primary cephalic vesicles of the Craniata.

FIG. 297.

FIG. 297.—*A*, transverse sections through the brain of a young *Amphioxus* (after HATSCHEK). *I*, through the (primary) first ventricle; *II*, through the (primary) second ventricle (*aquaeductus Sylvii*); *III*, through the (primary) third ventricle (*fossa rhomboidalis*). *B*, transverse section through the spinal cord.

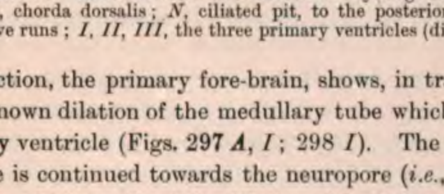

FIG. 298.

FIG. 298.—Brain with the most anterior nerve-roots of a young *Amphioxus* (after HATSCHEK). *Ch*, chorda dorsalis; *N*, ciliated pit, to the posterior wall of which the olfactory nerve runs; *I*, *II*, *III*, the three primary ventricles (diagrammatic).

The anterior section, the primary fore-brain, shows, in transverse section, the well-known dilation of the medullary tube which constitutes the first primary ventricle (Figs. 297 *A*, *I*; 298 *I*). The anterior end of this ventricle is continued towards the neuropore (*i.e.*, towards the ciliated olfactory pit) into the infundibulum (the *lobus olfactorius* of LANGERHANS) which, in *Amphioxus*, is curved upward. The second part of the brain (the mid-brain) contains within it the second primary ventricle, which is represented by a narrowed portion of the medullary canal (*aquaeductus Sylvii, II*). In the third part (the hind-brain) the central canal shows a narrow ventral tube, while its dorsal portion is independently dilated so as to form a vesicle covered by a thin membrane, the *fossa rhomboidalis* of HATSCHEK (*III*).

The medullary tube originally opens externally through a neuropore bordered by closely crowded flagella. This is pressed out of the middle line to the left through the development of the dorsal fin. An epithelial depression forms later at this point; this is KÖLLIKER'S *olfactory or ciliated pit* (Fig. 298, *n*), at the base of which the neuropore opens. The ciliated pit is the homologue of the olfactory organ and of the hypophysis of the Craniata. The short, unpaired olfactory nerve discovered by LANGERHANS runs from the brain to the posterior wall of the ciliated pit. The continuation of the first ventricle towards the neuropore corresponds, as above mentioned, to the infundibulum of the Craniata. In *Ammocoetes*, the hypophysis and the olfactory organ are still connected together, and the external aperture of the hypophysis still retains its original dorsal position. The inner end of the hypophysis, on the contrary, and the infundibulum have moved to the ventral surface of the brain.

In identifying the anterior end of the medullary tube of *Amphioxus* with the infundibulum of the Craniata we have followed HATSCHEK. It should, however, be mentioned that KUPFFER has recently been led by his researches on *Acipenser* (No. 38) to homologise the anterior end of the cranial axis of *Amphioxus* with his *lobus olfactorius impar* which lies near the lamina terminalis above the anterior commissure, and indicates the point where the medullary tube remained longest in direct connection with the ectoderm precisely as in *Amphioxus*, and to regard the infundibulum as a secondary outgrowth of the ventral side of the brain.

It should here be pointed out that KOHL (No. 9) occasionally noticed, on the right side of the head of *Amphioxus*, a pit resembling the olfactory pit of the left side. KOHL is inclined to consider this as the half of an originally paired olfactory organ in a vestigial condition. The relations of the neuropore to the olfactory pit were denied by KOHL. The remains of the neuropore are said to be found in an ectodermal depression lying somewhat behind the olfactory pit.

Our knowledge of the important transformations that take place in the primitive segments and the body-cavity is due chiefly to HATSCHEK (No. 7). Each primitive segment becomes divided by a transverse partition into two portions, as has already been stated (p. 547), viz., a dorsal portion (proto-vertebra) and a ventral part (lateral plate, Fig. 300, *I* and *II*). Only in the dorsal portion is the primitive segmentation retained, the adjacent walls of the segments persisting as the transverse septa (myosepta). In the region of the lateral plates, the septa disappear and the segmental cavities enclosed by them flow together to form a common cavity surrounding the intestine (splanchnocoele). The disappearance of the ventral mesentery leads to intercommunication between the right and left halves of the splanchnocoele.

The proto-vertebrae enclose segmentally-arranged cavities which, however, are not quite symmetrical in relation to the median plane (p. 545). These are the cavities of the proto-vertebrae or the myocoeles (Fig. 153, *I*). The walls of each proto-vertebra consists of a parietal (*1*) and an inner (*2*) layer. The parietal layer (*1*), which consists of flat cells, applies itself closely to the ectoderm, and since

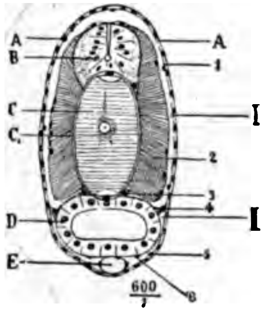

Fig. 299.—Transverse section from the middle of the body of an *Amphioxus* larva with five branchial clefts (after Hatschek).

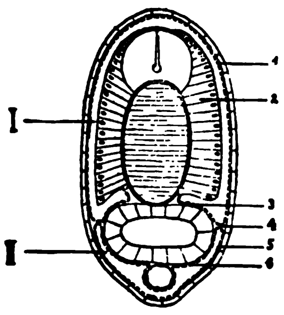

Fig. 300.—Diagrammatic rendering of the same section.

A, epidermis; *B*, medullary tube; *C*, chorda; C_1, inner chorda-sheath; *D*, intestinal epithelium; *E*, sub-intestinal vessel. *1*, cutis-layer; *2*, muscle-layer (lateral trunk-muscle); *3*, sclera-layer; *4*, boundary cells of the proto-vertebra; *5*, somatopleure; *6*, splanchnopleure. *I*, myocoele; *II*, splanchnocoele.

it yields the cutis of the adult, is sometimes termed the cutis-layer. The cells of the inner layer, at the sides of the chorda and of the medullary tube, elongate transversely and longitudinally, as described above (p. 548), and, as they give rise to the muscle-fibres of the myotome, this part is spoken of as the muscle-plate.

At first, each muscle-cell contains only one fibrilla, but as the number of fibrillae increases later they are arranged in regular order one above the other. Several such groups of fibrillae occur in each muscle-cell. The nuclei of the muscle-cells lie on the outer side of the muscle-layer that turns towards the myocoele. Towards the ventral side, the muscle-layer is continued into a pavement-epithelium in contact with the intestinal wall; this is known as the *sclera-layer* and this portion of the coelom as the *sclerotome* (*3*). At the point at which it passes over into the cutis-layer, there is a large boundary cell (*4*) which, according to **Boveri**, is probably to be regarded as a primitive genital cell.

In the lateral plates also, a parietal layer (*5*) can be distinguished from a median (visceral) layer. The parietal layer (*somatopleure*) at first lies on the inner side of the ectoderm; the visceral (*splanchnopleure*) forms the dorsal mesentery, in connection with which the aortae develop later, and surrounds the intestine and the sub-intestinal vessel, running along the ventral surface of the latter. This layer yields the unstriped muscle-layer of the alimentary canal.

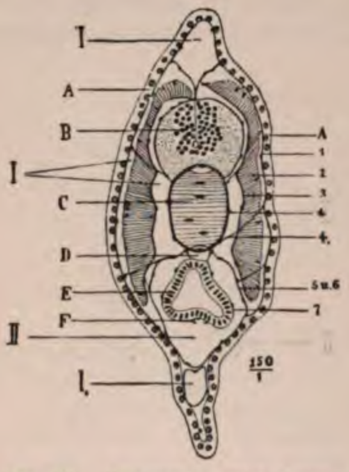

Fig. 301.—Transverse section through a young *Amphioxus*, immediately after metamorphosis, through the region between the atriopore and the anus (after Hatschek).

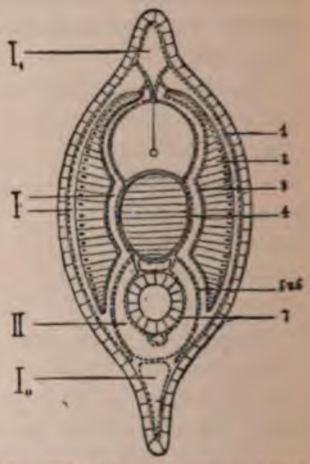

Fig. 302.—Diagrammatic rendering of the same section.

A, epidermis; *B*, medullary tube; *C*, chorda; *D*, aorta; *E*, intestinal epithelium; *F*, sub-intestinal vessel. *1*, cutis-layer; *2*, muscle-layer; *3*, fascia-layer; *4*, outer chorda-sheath; *4'*, muscle-septum; 5, gastral continuation of the skeletogenous layer (intercoelic membrane); *6*, somatopleure; *7*, splanchnopleure; *I*, myocoele; $I_{,}$ dorsal, $I_{,,}$, ventral fin-cavity; *II*, splanchnocoele.

In later stages (Figs. 301, 302) the muscle-plate becomes completely separated from the chorda dorsalis and the nerve-tube, in consequence of the development of an outgrowth of that part of the myocoele termed the sclera-layer which grows up from below (*sclerotome*). The muscle-plate is then connected merely at its dorsal edge by means of a mesentery-like band to the wall of the proto-vertebra and otherwise hangs quite freely into the cavity of the same. Its chief points of attachment are to the dissepiments. The inner wall of the sclerotome becomes applied to the chorda and the medullary tube, and here forms the *skeletogenous layer* which yields the outer sheath of the chorda (*4*) and the neural continuation of the latter. The outer layer of the *sclerotome* becomes applied to the inner side of the muscle-layer and forms the internal sheath or *fascia-layer* (*3*). The lateral trunk-muscle of *Amphioxus* is not entirely surrounded by fascia, since this layer only develops on its inner side.

All these layers, derived through differentiation from the wall of the proto-vertebra, shift ventrally, pressing in between the ectoderm and the somatopleura. The cutis-layer in this way comes to lie in the ventral middle line, where it yields the lining of the cavity of the ventral fin ($I_{,,}$), and the dorsal fin-cavities ($I_{,}$) seem in the same way to be lined by the cutis-layer. From the floors of these cavities, the fin-rays grow up later. The skeletogenous and the muscular layers also shift ventrally.

The method of formation of the layers agrees in all essential points with that of the Craniata. In this type, beneath the epidermis, lies the cutis-layer (*1*) which, in *Amphioxus*, retains its simple epithelial character throughout life. This is followed by the myocoele, which also here persists throughout life. Then comes the muscle-layer (*2*) and on the inner side of the latter lies the fascia-layer (*3*); in the Craniata the fascia is also developed on the outer surface of the muscles; then comes the cavity of the sclerotome, and, finally, the skeletogenous layer (*4*). The latter (as chorda-sheath) encloses the chorda and also the medullary tube in the dorsal half of the body; in the lower half, it becomes applied to the somatopleure. The two layers (skeletogenous layer and somatopleure) here form a delicate partition-wall, the intercoelic membrane (*5* and *6*) which separates the cavity of the primitive vertebrae from the splanchnocoele. On the inner side of the splanchnocoele lie the splanchnopleure and the entodermal intestinal epithelium.

In the branchial region (Fig. 311) the condition of the body-cavity is complicated through the development of the atrial cavity (*p*), which presses in between the splanchnocoele and the ventral part of the myocoele. The latter then lies in the peribranchial fold and breaks up into sections called by HATSCHEK (No. 8) the upper and lower fold-cavities. The cavity of the upper fold (*of*) lies in the metapleural folds and is also known as the metapleural cavity. In its inner wall, which is in contact with the outer wall of the atrial cavity, the transverse or sub-atrial muscle (*mt*) develops. The cavities of the lower folds (*uf*) are regarded by HATSCHEK as the equivalent of the ventral fin-cavities in that part of the body which lies behind the atriopore. The splanchnocoele is divided by the gill-clefts into an upper paired cavity (*sc*, *epi-branchial*, *supra-pharyngeal* or *sub-chordal coelom*) and an unpaired ventral cavity (*ec*, *endostylar coelom*). These two are connected by means of canals running within the gill-bars (*cf.* p. 556 and Fig. 311, on the right side of which a primary gill-bar with its coelomic canal is represented as cut through longitudinally).

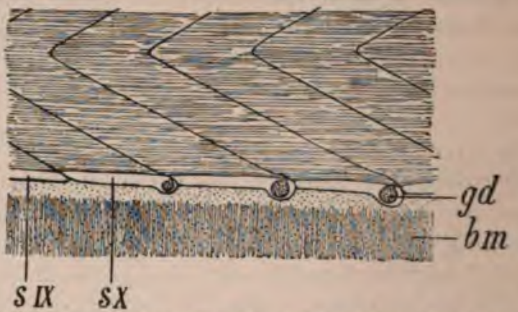

FIG. 303.—Side view of the lower edges of the proto-vertebrae in a young *Amphioxus*, 9 mm. long (after BOVERI). *bm*, ventral muscle; *gd*, genital gland; *S IX*, *S X*, ninth and tenth mesodermal somites.

The development of the **genital organs** has recently been described by BOVERI (No. 3). The genital vesicles which develop in each mesodermal somite from the tenth to the thirty-fifth, are abstricted portions of the somites which may be compared to the nephrotomes or gononephrotomes (RÜCKERT) of Selachian embryos. BOVERI, therefore, regards the genital chambers of *Amphioxus* as the homologues of the canals of the primitive kidney in the Craniata. The development of these chambers can be observed in the quite young *Amphioxus* four to twelve millimetres long. In cross-sections, at the

FIG. 304.—Side view of the genital rudiment in a young *Amphioxus*, 5 mm. long (after BOVERI).

part along the ventral edge of the protovertebrae where the cutis-layer passes into the skeletogenous layer, small cells filled with deeply staining nuclei can be made out. These are accumulations of primitive genital cells which represent the rudiment of the genital gland, and which may perhaps be traced back to **Hatschek**'s large boundary cells mentioned above (Fig. 299, *4*, p. 565). These agglomerations of cells are repeated at definite intervals in series of cross-sections. Since they are related to the dissepiments between the mesodermal somites, they are affected by the asymmetry of those structures and, like them, alternate on the right and left sides of the body. In superficial views of later stages (Fig. 303), the rudiments of the genital gland can be seen as rounded knobs (*gd*) lying in small outgrowths in the posterior lower angles of the myocoeles (rudiments of the genital pouches).

FIG. 305. FIG. 306.

FIG. 305 and 306.—Later stages of development of the genital rudiment in *Amphioxus* (after (**Boveri**).

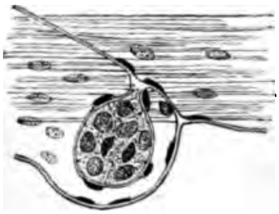

FIG. 307.—Genital rudiment in an *Amphioxus*, 8 mm. long (after **Boveri**).

Examination of the genital rudiment in the youngest stages reveals that it arises as a modified part of the epithelium on the anterior wall of each myocoele (Fig 304). This epithelial growth then forms a hernia-like invagination into the cavity of the preceding segment (Figs. 305, 306), and in this way constitutes a knob which at first is hollow but is provided later with a lumen (Fig. 307), and which is covered superficially with an epithelium derived from the posterior wall of the segment into which the knob projects, the latter being connected with this wall by means of a stalk-like prolongation of the epithelium. Consequently the genital gland does not originate in the segment in which it lies later, but is derived from the anterior wall of the segment immediately following.

FIG. 308.—Transverse section through a stage corresponding to that depicted in Fig. 307 (after BOVERI). *bm*, ventral muscle; *g*, blood-vessel; *gd*, genital gland.

Fig. 308 shows a transverse section of the genital rudiment approximately at the stage represented in Fig. 307. The fusion of the rudiment with the inner wall of the somite is visible, a connection which is permanently retained. The genital rudiment, at this stage, still lies in the myocoele. Figs. 309 and 310 illustrate the way in which the part of the myocoele which corresponds to the genital rudiment becomes severed to form a distinct genital chamber. This takes place through the formation of a fold (*w*) which grows backward from the anterior apex of the genital pouch till, finally, in individuals 16 mm. long, the communication between the genital chamber and the myocoele is entirely lost. The genital pouches at first corresponded merely to the posterior angle of the myocoele to which they belonged, but they extend so far forward secondarily that each chamber comes to lie in contact with the posterior end of the one next in front of it.

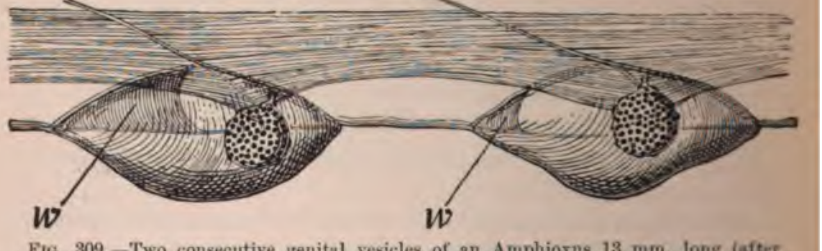

FIG. 309.—Two consecutive genital vesicles of an Amphioxus 13 mm. long (after BOVERI).

So as to complete our description of the organisation of *Amphioxus* we must, in conclusion, briefly describe the **renal canals** discovered by BOVERI (Nos. 1 and 2) in the adult animal. These are short tubes found in the region of the pharynx which connect the sub-chordal coelom (Fig. 311, *sc*) with the atrial cavity (*p*). They lie on the mesial side of the sub-chordal coelomic sac, and open into the atrial cavity at the uppermost angle where the wall that covers the outer side of the gill-bars bends outward to form, together with the wall of the sub-chordal coelomic sac, the thin partition-wall known as the ligamentum denticulatum (*ld*). This latter, in the primary gill-bars, extends further down than in the secondary (Fig. 312, *I* and *II*). The nephridial canals recur regularly in the pharyngeal region and open on the tongue-bars (Fig. 312). In each canal (*nk*) an anterior ascending branch can be distinguished from a short posterior branch. Each of these branches opens at its end into the sub-chordal coelomic cavity (*nc*, funnel), and in the course of the canal three or four other apertures occur. Round these apertures (*nc*) the cells of the walls of the sub-chordal coelom are peculiarly modified. Highly refractive spherical cells are found in the body-cavity connected with the apertures by means of delicate filaments (thread-cells). Round the nephridial canals, the upper ends of the branchial vessels, by anastomosing, form a vascular network which we may call the glomerulus (Fig. 311, *gl*).

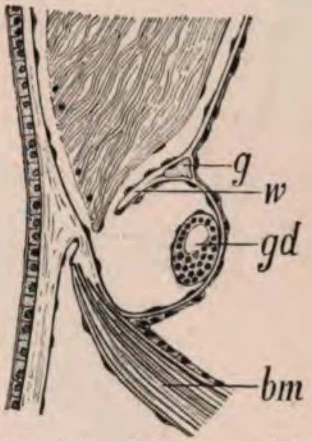

FIG. 310. — Transverse section through the genital rudiment of the stage represented in Fig. 309 (after BOVERI). *bm*, ventral muscle; *g*, blood-vessel; *gd*, genital gland; *w*, fold separating myocoele and gonadic pouch.

BOVERI regarded these canals as homologues of the pronephros of the Craniata, and the atrial cavity of *Amphioxus* as the homologue of the pronephric duct of the Vertebrata. For further details on these points we must refer the reader to the works of this author. Nothing is as yet known of the development of these renal canals. We are also in the dark as to their relation to the larval organ mentioned above and described by HATSCHEK as the nephridium, but it should be mentioned that the figure of this organ given by HATSCHEK (No. 14) shows a certain similarity to the canals discovered by BOVERI. Objections have recently been raised to BOVERI's generalisations by SEMON and VAN WIJHE (No. 22).

General Considerations.

With regard to the systematic position of *Amphioxus*, we adopt the view now accepted by most zoologists that this animal is to be regarded as the representative of a very primitive group which served as a starting-point for the Vertebrate phylum. In most of its organs, *Amphioxus* exhibits conditions so extraordinarily simple and yet so much in agreement with the fundamental plan of the vertebrate type, that we may well regard it as the "primitive Vertebrate," or at least as a form standing remarkably near the hypothetical ancestor of the Vertebrata. We need here only refer to the primitive con-

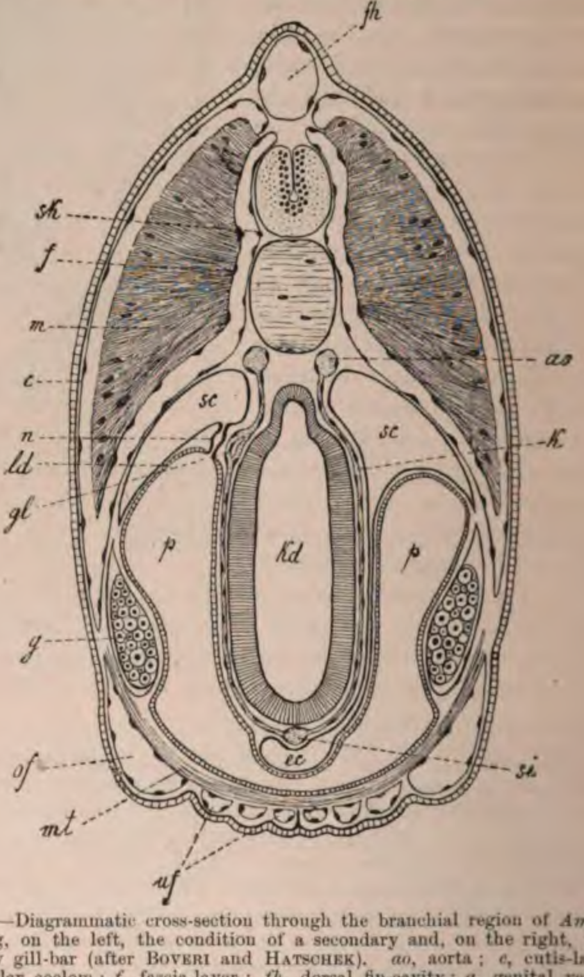

FIG. 311.—Diagrammatic cross-section through the branchial region of *Amphioxus*, showing, on the left, the condition of a secondary and, on the right, that of a primary gill-bar (after BOVERI and HATSCHEK). *ao*, aorta; *c*, cutis-layer; *ec*, endostylar coelom; *f*, fascia-layer; *fh*, dorsal fin-cavity; *g*, genital vesicle; *gl*, glomerulus; *k*, branchial vessel; *kd*, pharynx; *ld*, ligamentum denticulatum; *m*, muscle-plate; *mt*, transverse muscle; *n*, renal canal; *of*, metapleural cavity; *p*, atrial cavity; *sc*, sub-chordal coelom; *si*, truncus arteriosus (branchial artery); *sk*, sclera-layer; *uf*, cavities of the lower folds.

ditions of the blood-vascular system, and especially to the development of the body-cavity which, as made known by **Hatschek**, yields the key for understanding the formation of the layers in the Vertebrates. It must further be pointed out that the development of *Amphioxus* without doubt shows very primitive characters, a view to which however, objections have been raised by **Dohrn**. The occurrence of free-swimming ciliated larvae, nevertheless, can hardly be interpreted in any other sense.

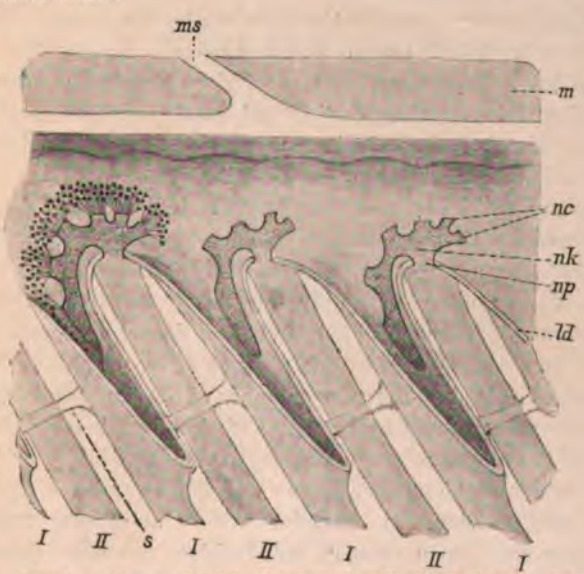

Fig. 312.—Dorsal portion of the left pharyngeal wall of *Amphioxus*, showing three renal canals, seen from the side (diagrammatic, after **Boveri**). *ld*, ligamentum denticulatum; *m*, myotome; *ms*, myoseptum; *nc*, openings of the renal canal into the body-cavity; *nk*, renal canal; *np*, opening of the renal canal into the atrial cavity; *s*, synapticulum; *I*, primary gill-bar; *II*, tongue-bar.

Considering the agreement prevailing between *Amphioxus* and the Vertebrates, it is important to emphasise the distinctions between the two forms. *Amphioxus* is specially distinguished by the rostrum-like prolongation of the notochord, by the secondary increase in number of the gill-clefts, and by the duplication of such primary clefts through division (development of the tongue-bars), this last characteristic recalling the multiplication of the gill-clefts in the Ascidia. With regard to the condition of the urogenital system, we must refer to the accounts of **Boveri** (No. 2), according to which the renal canals of *Amphioxus* are to be considered as the homologue of the pronephric canals of the Vertebrata, and the atrial cavity of

Amphioxus as that of the pronephric duct in the Craniata, while the genital vesicle of *Amphioxus* is homologous with the gononephrotomes of the Craniata and consequently also of the canals of the primitive kidney in the latter. Even if we adopt BOVERI's homologies, we must still recognise certain distinctions between the development of the urogenital system of *Amphioxus* and that of the Vertebrata, which, however, would not then be of a fundamental character. Through the great development of the atrial cavity which, according to BOVERI, is represented in the Craniata by the pronephric canals, *Amphioxus* is linked on to the Tunicates. Among the further peculiarities of *Amphioxus*, we must reckon the development of the so-called anterior entoderm-vesicle and the club-shaped gland, organs as to the morphological significance of which we are at the present time unable to state anything with certainty.

The peculiarities just mentioned seem to indicate that *Amphioxus*, as contrasted with the Craniata or Vertebrata, shows, in the strict sense of the term, a certain independence in its position. It would be difficult to find an explanation for this if we were to adopt the assumptions of DOHRN (p. 522), that *Amphioxus* is a degenerate form derived from the Craniata. We do not deny that *Amphioxus*, in consequence of its half-sedentary manner of life (burying in the sand) may have undergone a certain degree of simplification and degeneration. Above all, we might in this way explain the slight development of the brain and the sensory organs and also the locomotory system. It is naturally difficult to determine how far the simple structure of *Amphioxus* rests upon primary peculiarities or to what extent upon peculiarities secondarily acquired through degeneration. The majority of the facts known to us as to the ontogeny and the anatomy of *Amphioxus* seem to indicate that we have in this case actually to do with a very primitive form.

Among the peculiarities which we regard as secondarily acquired is the remarkable asymmetry in the structure of the body which is specially marked in the larval forms, but is also retained to some extent in the adult (position of the olfactory pit, of the anus, and of the hepatic caecum, conditions of the innervation of the velum and the definitive mouth according to VAN WIJHE). WILLEY's observation that the *Amphioxus* larva lies when at rest at the bottom of the sea on the right side of the body seems to indicate that this asymmetry is acquired in the same way as in the *Pleuronectidae*.*

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* [According to WILLEY, our authors have misunderstood his observations on this point. The fact that the young when kept in a glass jar sink to the

We therefore regard *Amphioxus* as a very primitive chordate form very closely related to the hypothetical ancestor of the Craniata, but somewhat more distantly related to the Tunicates. Every speculation as to the origin of the Vertebrates and the Chordata must necessarily take account of *Amphioxus* as the most primitive representative and the starting-point of the whole series. Among all the hypotheses* which have hitherto been advanced as to the origin of the Chordate stock, that which derives it from the Annelida has at present most adherents. As the founders and most eminent upholders of this hypothesis we must name **SEMPER** (No. 46) and **DOHRN** (Nos. 30 and 31), while, more recently, a whole series of renowned zoologists have taken part in its further development. The view that the Vertebrates are descended from Annelids rests chiefly on the similarity in the segmentation of the body and in the production of new segments at the posterior end of the body; further, on the agreement in the position of the more important organs, if we assume that the hypothetical Annelid ancestor of the Vertebrata underwent such a rotation round its longitudinal axis that the former ventral side became the dorsal side, an assumption which lay at the root of **GEOFFROY ST. HILAIRE**'s statement that "Insects are Vertebrates running on their back." When such a rotation is assumed, the ventral ganglionic chain of the Annelida corresponds to the medullary tube of the Chordata, the ventral longitudinal vessel of the Annelida becomes the aorta, while the dorsal vessel corresponds to the sub-intestinal vessel. The Annelidan hypothesis obtained its strongest support when **SEMPER** discovered a remarkable

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bottom and fall on one side, is due to the physical impossibility to rest in any other position, and not to a pressing desire or instinct to assume this position. The asymmetry of Amphioxus is of a totally different character to that of the *Pleuronectidae*. For a full account of these views, see **WILLEY**, *Amphioxus and the Ancestry of the Vertebrates*. Columbia Univ. Biol. Series, 1894.—ED.]

* We have no intention of entering upon the much-disputed point of the origin of the Chordata except in a passing way. A detailed investigation of this difficult problem would require a study of vertebrate embryology which does not fall within the scope of the present work. We have already, in the foregoing chapter (p. 523), stated that the Tunicates contribute little to the solution of this question. They are to be considered as degenerate members of the Chordate stock, of which *Amphioxus* is to be regarded as the most primitive form. Of the many theories on the subject of the relationship of the Chordata we have here alluded only to those two which appear best founded on actual morphological facts, viz., the derivation of the Chordata from Annelids and the assumption of relationship between the Chordata and *Balanoglossus*. The hypothesis of the relationship to the Nemertines has been briefly alluded to above (vol. i., p. 231). We do not consider it necessary to refer to the relationship of the Vertebrata to the Arthropoda which has recently been again assumed.

similarity of structure between the primitive kidney-tubules of the Selachian embryo and the segmental organs of the Annelida. Our acceptance of this homology, however, has been recently made impossible by the researches of **van Wijhe** (No. 48), **Rückert** (No. 44), and **Boveri** (No. 2) which cause us to doubt the serial homology of the pronephros with the primitive kidney and to regard the latter as a secondary acquisition which in any case has nothing to do with the segmental organs. From this point of view it would be the pronephros which requires consideration.

The derivation of the Vertebrates from the Annelida is, in fact, accompanied by certain difficulties which are not insurmountable. The most important of these is the position of the mouth. While, in the Annelida, the oesophagus perforates the central nervous system at the oesphageal ring in such a way that the supra-oesophageal ganglion comes to lie above and the ventral cord below the gut, no such relation between the stomodaeum and the central nervous system is to be found in the Vertebrates. The most varied hypotheses have been suggested to obviate this difficulty. **Schneider** thought that he could discover in the connection of the hypoglossal and trigeminal nerves an equivalent for the oesophageal ring. **van Beneden** and **Julin** (No. 29) have assumed that, in the primitive ancestors of the Vertebrates, the oesophagus shifted forward in the median plane between the still unconnected cephalic lobes of the brain, while other zoologists like **Kleinenberg**, **Beard**, No. 27, v. **Kennel** (No. 35*a*) believe that the supra-oesophageal ganglion atrophied and that the brain and the dorsal chord of the Vertebrates only are the equivalents of the ventral cord of the Annelida. In connection with this idea, we have the question as to the primitive mouth of the Vertebrates. Under the assumption that the pro-cephalon of the Vertebrates corresponds to the supra-oesophageal ganglion of these Annelida, we should have to conjecture that the original vertebrate mouth, which perforated the oesophageal ring, has disappeared. The definitive mouth of the Vertebrates would have to be regarded as a secondary formation, and is by many zoologists thought to have arisen through the fusion of gill-slits. There is actually much to support the view that the mandibular arch is a branchial arch which has been drawn into the mouth. This, however, does not decide the question of the derivation of the vertebrate mouth from gill-clefts. In the case of *Amphioxus*, there is no ontogenetic indication of the derivation of the mouth from gill-clefts. The mouth here arises in a different manner from the gill-slits (p. 550) and in a different position.

Hatschek (No. 8) has therefore maintained that the velar opening of *Amphioxus* is not to be regarded as a gill-slit.

The attempt has often been made, in following out these ideas further, to discover vestiges of the primary vertebrate mouth, which has been sought in the rhomboidal fossa, the pineal gland and the hypophysis. Only recently, **Beard** (No. 27) and **Kupffer** (No. 38) have pointed to the hypophysis as the primary mouth (palaeostoma) of the Vertebrata.

An altogether satisfactory solution of the difficulties connected with all these questions is, however, at present wanting.

Attempts have been made in other directions also to find the connection between the Vertebrates and the Annelida. We may recall the discovery by **Eisig** of organs in the *Capitellidae* comparable to the lateral line of the Vertebrata, the homologising of the spinal ganglia of the Vertebrates with the parapodial ganglia of the Annelida by **Kleinenberg** (No. 36), the derivation of the unpaired fin of the Selachians from fused Annelidan parapodia by P. **Mayer** (No. 39), the attempt to derive the vertebrate eye from the Annelidan eye by v. **Kennel** (No. 35*a*), etc. For its support, the Annelidan hypothesis has required a number of sub-hypotheses. Nevertheless, we must admit that the gap which divides the Annelida from the Chordata is even now very considerable, and, as **Balfour** pointed out, the two most typical organs of the Chordata, the notochord and the gill-clefts, are not foreshadowed in the Annelids. Attempts have not been wanting, it is true, to find the equivalents of these organs in the Annelids. The origin of the mouth from paired rudiments in the buds of *Nais* and *Chaetogaster* (**Semper**) was compared to the formation of gill-clefts, while the most varied structures in the Annelida were regarded as homologues of the chorda. With regard to this latter point, the view that most deserves attention is that of **Ehlers** (No. 32) and **Eisig** (No. 33), who see in the so-called accessory intestine of the *Capitellidae* and the *Eunicidae* (and in similar structures in the Gephyrea) the homologue of the notochord. On the other hand, it should be mentioned that the researches of **Kleinenberg** (No. 36) on this point did not lead to satisfactory results. "In the development of most Annelids," says **Kleinenberg**, "there is no trace of the accessory intestine; I found it only in the larvae of those forms which possess it when adult, viz., the *Capitellidae* and the *Eunicidae*. In a larva belonging to the last of these families it hangs as a somewhat short loop beneath the principal intestine and opens both anteriorly and posteriorly into the latter.

In the *Capitellidae*, a diverticulum forms early at the most posterior part of the archenteron and grows out anteriorly. I believe that this is the rudiment of the accessory intestine, but am not quite certain on this point." With regard to the origin of the gill-clefts, we may assume that the originally blind intestinal diverticula secondarily acquired external openings, so as to allow of the outflow of the respiratory water. The assumption that such perforations occur is supported by the actual presence of pores of communication at the ends of the tentacles in the Actinia, and in the hepatic tubes of some *Aeolidae*.

We are not, however, able to regard the Annelidan hypothesis as resting on altogether certain foundations. It seems to us that we have no convincing proof that the many points of agreement which actually exist between the Annelida and the Chordata rest upon true homology. The crucial point of the whole question lies in the decision as to whether it is necessary for us to refer the similar method of segmentation of the body in the two groups to their derivation from a common ancestor. It is evident that, as Bateson (No. 26) has shown, it is not a decisive objection to this assumption that the characteristic segmentation in each of the two groups (the Annelida and the Chordata) has arisen separately, or, in other words, that the common ancestor of the two groups was still unsegmented. Balfour (No. 25) in this connection wrote "that we must look for the ancestors of the Chordata, not in allies of the present Chaetopoda, but in a stock of segmented forms descended from the same unsegmented types as the Chaetopoda, but in which two lateral nerve-cords, like those of Nemertines, coalesced dorsally, instead of ventrally to form a median nerve cord."

If, after what has just been said, we do not regard the derivation of the Chordata from the Annelida as certainly proved, and institute comparison with the other invertebrate groups, we are confronted first of all by *Balanoglossus* which, in the possession of gill-clefts in the pharyngeal region and the nerve-strand running dorsally shows striking agreement with the type of the Chordata. This form was formerly thought to be nearly related to the Chordata by Gegenbaur and Huxley and more recently by Bateson, Haeckel, Schimkewitsch, Morgan, Roule and others. We are far from regarding as established the various homologies assumed by Bateson between *Balanoglossus* and *Amphioxus*, and on this point refer the reader to the detailed criticism of the best qualified judge in this matter—Spengel (No. 47, p. 721, etc.) who denies all relationship between the Chordata and *Balanoglossus*. **Bateson** (No. 26) homologises the dorsal nerve-strand in the collar region of *Balanoglossus* (the so-called collar-cord) with the medullary tube of the Vertebrates. The anterior intestinal diverticulum (the so-called proboscis-intestine) of *Balanoglossus* (Vol. i., Fig. 165, *di*, p. 375), according to him and to **Koehler**, is the homologue of the notochord. The rudiment of the so-called proboscidal coelom is homologised with the anterior unpaired entoderm-diverticulum of *Amphioxus* (Fig. 285 *B*). The external aperture of the left anterior entoderm-diverticulum of *Amphioxus* is assumed to correspond to the proboscis-pore of *Balanoglossus*. A posterior fold in the collar-region, called by **Bateson** the "operculum," is said to correspond to the epipleura of *Amphioxus*. Finally, even **Gegenbaur** compared the ventral nutritive section of the pharynx in *Balanoglossus* (Vol. i., Fig. 166, *d*, p. 377) to the endostyle of the Tunicates. **Spengel** (No. 47) has pointed out the difficulties that stand in the way of such a homology, and lays special stress on the great difference in the position of the gills which, in *Balanoglossus*, are dorsal, and, in *Amphioxus*, ventral—the development of the blood-vascular system and the genital organs in the two groups. The bare fact of the presence of gills in *Balanoglossus*, indeed, and their remarkable and detailed agreement in structure and arrangement with those of *Amphioxus* (U-shaped form in consequence of the growth of tongue-bars, chitinous skeletal structures in the form of prongs, presence of synapticula) seem to us of such significance that we cannot avoid the thought that we have, in *Balanoglossus*, the only living form of Invertebrate which is closely related to the Chordata. But, if we adopt this assumption, the Chordata naturally become somewhat more remote from the Annelida, since *Balanoglossus* is only distantly related to this last group. How far it is possible to remove the difficulties which now lie in the way of establishing a stricter homology between *Balanoglossus* and *Amphioxus* must be decided by further research.

The problem of the derivation of the Chordata is not solved by assuming a relationship between them and the Enteropneusta, since the latter themselves occupy an unusually isolated position. Only through the structure of the *Balanoglossus* larva is an indication given of remote connection with the Echinoderma. We must resign ourselves to the thought that we are not at present in a position to state from what primitive form the Chordata and, with them, *Balanoglossus* are to be derived. The origin of the Vertebrates is lost in the obscurity of forms unknown to us.

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