The Development of Haliotis tuberculata, with Special Reference to Organogenesis during Torsion

Doris R. Crofts

Phil. Trans. R. Soc. Lond. B 1937 **228**, 219-268
doi: 10.1098/rstb.1937.0012

V—THE DEVELOPMENT OF *HALIOTIS TUBERCULATA*, WITH SPECIAL REFERENCE TO ORGANOGENESIS DURING TORSION

By DORIS R. CROFTS, M.Sc.

(*Communicated by F. J. Cole, F.R.S.—Received* 26 *May* 1936, *Read* 29 *April* 1937)

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Introduction

Investigation of the development of *Haliotis tuberculata*, Linnaeus, was undertaken as a natural sequel to an examination of the bionomics and anatomy of *Haliotis* (Crofts 1929, p. 159). It is an attempt to elucidate the organogenesis during the changing larval habits, in the hope of adding to the scanty ontogenetical evidence available towards solving the problems of gastropod evolution.

Vol. CCXXVIII.—B 552 (Price 11*s*.) 28 [Published October 15, 1937

Excellent accounts of the embryonic phase, including patiently worked out details of the cleavage and of gastrulation, have been published for *Crepidula* (Conklin 1897), *Patella* (Patten 1886; Wilson 1904; and Smith 1935), *Trochus* (Robert 1902), *Physa* (Wierzejski 1905), *Dentalium* (Wilson 1904). The only comprehensive accounts of gastropod larval development already published are of *Paludina* (Erlanger 1891; Tonniges 1896; Drummond 1902; Andersen 1924) and of *Patella* (Patten 1886; Smith 1935). The accounts of *Paludina* elucidate the details of development of the coelom and its derivatives. The viviparous habit and consequent loss of free larval life in *Paludina*, however, make it a very unsuitable example of gastropod development. Evolutionary stages are more likely to be traced from the development of less specialized gastropods, an adequate selection of whose free-living larval stages can be obtained. The larval development of *Patella*, *Acmaea*, *Trochus* and *Haliotis* has been described, in varying completeness for the different genera. Patten's work on *Patella coerulea* (1886) gives a description only of the beginning of organogenesis. After a lapse of fifty years a more detailed account of the development of *P. vulgata* has been given by Smith (1935). This work gives a new interpretation of the development of the mesoderm, of the muscles and of the nervous system. The dorsal retractor muscle of the larva, which Patten indicated for *P. coerulea*, is shown in *P. vulgata* to be placed asymmetrically and torsion takes place "under the action" of this muscle.

Robert (1902) gives an excellent account of the development of *Trochus*. His description, however, does not extend to the development of internal organs. In his account of the development of *Acmaea* and *Haliotis*, Boutan (1899) also confines his attention to external characters and habits, but the age of the stages described for *Haliotis* was unknown and he was unable to determine at what age the swimming larvae begin to creep. Boutan's claim to have observed complete 180° torsion in the rapid twist of the pelagic *Acmaea* and *Haliotis* larvae, upon which various theories have been based, is not confirmed by the account given in the following pages, which, unlike his account, is based on the examination of serial sections and reconstructions. Boutan's drawings and descriptions of the external features of the post-veliger creeping stage are of interest. Stephenson (1924), when undertaking a short economic investigation of *Haliotis*, kept larvae alive only for 62 hr. after fertilization.

Murayama (1935) gives a superficial account of the development of the Japanese abalone, *Haliotis gigantea*, which adds but little to Boutan's description for *H. tuberculata*.

Additional information concerning the details of organogenesis and metamorphosis of primitive gastropods is still highly desirable before the various theoretical views concerning the peculiarities of this group can be either substantiated or modified.

The Haliotidae (Flemming) is a somewhat more primitive family of the Archaeogastropoda (Thiele) than the Patellidae (Guilding). In addition to the retention of paired kidneys and osphradia, *Haliotis* possesses paired auricles, hypobranchial glands and ctenidia; the rectum, as in lamellibranchs, is ensheathed by the heart. The following description concerns mainly the post-embryonic development of the Sarnian species *tuberculata*, in which the full complement of these adult paired characters is acquired only after 2 months of development.

My thanks are due to M. Charles Perez and M. Georges Teissier of the Biological Station at Roscoff and to Dr. Philippa Esdaile of King's College of Household and Social Science, London University, for the provision of excellent facilities for the investigation.

To the Royal Society of London I am indebted for a Government Grant for the purchase of a high-power binocular microscope for use during the investigation.

Methods

Haliotis eggs were fertilized artificially at the Roscoff Biological Station throughout the summer of 1929 (p. 223).

Pelagic life lasted less than 2 days, so that the plunger-jar method for rearing larvae (Allen and Nelson 1910) proved less useful than was anticipated. Feeding began only in the benthic veligers, and they were so minute that *Nitzschia* was too large for food until the late veliger stage was reached. A mixed culture containing *Pleurococcus*, started from a culture supplied by the Plymouth Laboratory, was useful for the early veligers. The post-veligers were supplied with small stones bearing young stages of various red sea-weeds.

A few post-veligers lived fairly successfully in bowls with aerated and circulating sea water. Although stages up to a fortnight old were sometimes healthy, it was more difficult to rear the larvae through the post-veliger metamorphosis. Specimens of five different post-veliger stages were preserved for section cutting, including a solitary specimen, which had remained healthy for 2 months. The shell was then 2 mm. long and the final metamorphosis had taken place. Several minute specimens were collected from the rocks off Sark, and the smallest of these was completely metamorphosed and was the same size as the artificially reared specimen.

Smith also found great mortality at the beginning of metamorphosis in *Patella vulgata* (1935). He was able to rear a few specimens as far as the first stage of metamorphosis and to observe the complete process only in one specimen. In *Haliotis*, as in *Patella*, mortality appeared to be due to feeding difficulties, sudden changes of temperature, and sometimes to the presence of pathogenic Protozoa.

As Boutan remarked, the larvae are extremely sensitive. Observation therefore involved considerable time and patience and, except in the very early stages, it seemed impossible to fix the larvae without contraction. Various methods of narcotizing were used, but they proved unreliable. Lo Bianco's method for extending molluscs was sometimes successful for older stages, but it was useless for the early days of development because it involved leaving the larvae in 1% absolute alcohol in sea water for at least a day. A trace of magnesium chloride was more generally used.

Segmentation stages were followed in living specimens. These and the gastrulation process were observed after treatment according to Wilson's method for *Patella* (1904). The specimens were preserved in a few drops of acetic acid in a watch-glass of sea water. Glycerine was added gradually until the specimens were quite transparent. The non-permanence of these preparations is the only disadvantage. Permanent preparations were made after placing the specimens for 3 min. in Perenyi's fluid or in Kleinenberg's picro-sulphuric acid mixture. Some of these were stained in haemalum, but the best results were obtained by staining in undiluted acetic-acid alum-carmine, used by Southwell (1930) for Cestoda. They were left for 4 hr. in this stain, then rinsed and taken up to 90% alcohol, after which they were mounted in Gurr's euparal, which has a suitable refractive index. The method used by Wierzejski (1905) for *Physa* was also valuable for gastrulation stages. Complete dehydration was followed by clearing in clove oil and mounting in a fluid mixture of Canada balsam and clove oil.

At first difficulty was found with the orientation and sectioning because of the minuteness of the larvae, the earliest veligers being approximately 130μ long. The best series of sections were obtained after fixation in either Bouin's fluid or in corrosive sublimate with acetic acid; both were used hot. The larvae were tinged with eosin to facilitate orientation. The celloidin-paraffin method of embedding was employed to minimize contraction and, to aid orientation, the celloidin block was made transparent in cedar oil. Occasionally it was found difficult to obtain a complete series of sections by this method, and subsequently simple paraffin embedding proved to give quite satisfactory results. Orientation was performed, after the manner suggested by Professor Graham Cannon, in molten wax under a high-power binocular dissecting microscope. Sections were cut at 6μ, except with the gastrulae and trochophores, for which a thickness of 9–12μ was employed. Transverse sections of larvae, starting from the posterior end, proved to be the most useful, because it was essential to know the exact spatial relations of the pallial cavity in connexion with the torsion phases.

The first sets of serial sections were stained with Weigert's iron haematoxylin or borax-carmine with picro-indigo carmine. Excellent results were obtained later with cotton red-aniline blue (gossypimine and aniline picrate).* For recommendation of this stain thanks are due to Miss S. Lockyer and to Mr. S. Garside. The best results were obtained after leaving the sections for 40 min. in gossypimine. They were then rinsed in distilled water and placed for 2 min. in aniline picrate, after which they were again rinsed and rapidly dehydrated so that the gossypimine remained only in chromatin and food vacuoles. This double staining facilitated the discrimination of the developing nervous system.

Reconstructions were found to be essential to an understanding of the serial sections. Twelve reconstructions of various stages, magnified approximately 900 diameters, were made from plywood of carefully selected thickness. For the accurate fret-sawing, from the author's camera lucida drawings of serial sections, indebtedness is acknow-

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* The formulae for this stain were first published by Flatters (1905).

ledged to Mr. N. Davey. Models held together by veneer sprigs were studied. The sections were then separated and the important muscles, the nervous system and parts of the digestive system were cut out and reconstructed separately.

Age at Maturity and Method of Spawning

Spawning takes place probably only in specimens which have attained 5 cm. in length and are about 3 years old. Stephenson (1924) describes the spawning of a captured specimen, and Crofts (1929) gives an account of spawning in the sea. The spawning period undoubtedly extends from June to September, but it probably continues into late autumn. The latter would account for the discovery in the Channel Islands of specimens only a few millimetres long in March and April (Crofts). The present account shows that the post-larval metamorphosis is complete at the end of about 2 months of development.

Haliotis tuberculata is dioecious. Murayama (1935) states that *H. gigantea* is also normally dioecious, but he describes one hermaphrodite specimen. My examination of large numbers of *H. tuberculata* of all sizes in the Channel Islands did not lead to the discovery of a hermaphrodite specimen. Among 280 specimens of marketable size the sexes were almost equally distributed, so that it seems unlikely that *H. tuberculata* is a protandrous hermaphrodite.

In both sexes the genital products escape via the cavity of the definitive right renal organ through the shell perforations. In the late stage of spawning some of the genital products escape from under the shell margin. In the male the spermatozoa are emitted from the shell holes in puffs like white clouds, but in the female the grey-green ova are less conspicuous. The ova are puffed upwards and then sink. The egg membrane has a thin albuminous layer and there is no protective gelatinous layer, such as is present in *Trochus*. The egg membrane has a micropyle and fertilization takes place in the sea. Inclusive of the egg membrane the diameter of the egg is about 180μ.

Development up to the Trochophore Stage

The method used by Wilson with *Patella coerulea* for assisting artificial fertilization by placing the ova and spermatozoa separately for an hour in sea water made slightly more alkaline by the addition of about five drops of a 5% solution of caustic soda to 500 c.c. of sea water proved to be very successful for *Haliotis*. Although fertilization was hastened, the proportion of abnormal larvae was as small as when caustic soda was not added. The fertilizations were made from specimens which had commenced to spawn in aquarium tanks. After the specimens had been placed in separate bowls, the ova were collected as they were liberated. An emulsion of spermatozoa was used in the manner described by MacBride (1914) for echinoderm fertilizations.

The development of cleavage planes was not followed in detail, but it appears to follow closely that of *Trochus*, which is described in great detail by Robert (1902). From artificial fertilizations of *Haliotis* started at 2.30 p.m. on 22 July, four blastomeres had formed at 6.30 p.m. After the third cleavage, which is spiral, there are four very large macromeres because of the presence of much deuteroplasm. The macromeres appear to be larger than in *Patella coerulea* (Wilson 1904) and *P. vulgata* (compare endoderm cells in Smith 1935, fig. 2*a* and *Haliotis*, fig. 39*b*). The macromeres separate off micromeres towards the animal pole to form the three ectoderm quartettes. Thus the blastula, with a very reduced blastocoele, is formed.

Gastrulation is by epibole. From optical sections of specimens cleared by Wilson's method, it appeared that this process closely resembled that described for *Patella coerulea* (Wilson 1904), for *Trochus* (Robert 1902), for *Littorina* (Pelseneer 1911) and for *Crepidula* (Conklin 1897). These authors describe division of the macromere of the quadrant *D* giving a cell 4*D*, which together with the macromeres of quadrants *A*, *B* and *C* forms the endoderm, and a cell 4*d*, which is the mesoderm mother cell. Since my attention has been called to the recent careful reinvestigation of the gastrulation of *Patella* (Smith 1935), an examination of serial sections of gastrulae of *Haliotis* has been carried out. The conclusion arrived at is that the formation of endoderm and mesoderm takes place as Smith has shown for *Patella vulgata* and not in the manner described by Conklin, Robert and Wilson. The macromere 4*D* divides equally to form two cells which are almost spherical, in contrast with the still undivided macromeres *A*, *B* and *C*, which are irregular and much elongated in the polar direction. When first observed, the two derivatives of 4*D* are in the region of the blastopore (fig. 39*a*, *pr.mes.*). At this time large portions of each of the three other macromeres are already pressed into the obliterated segmentation cavity. The two cells formed from

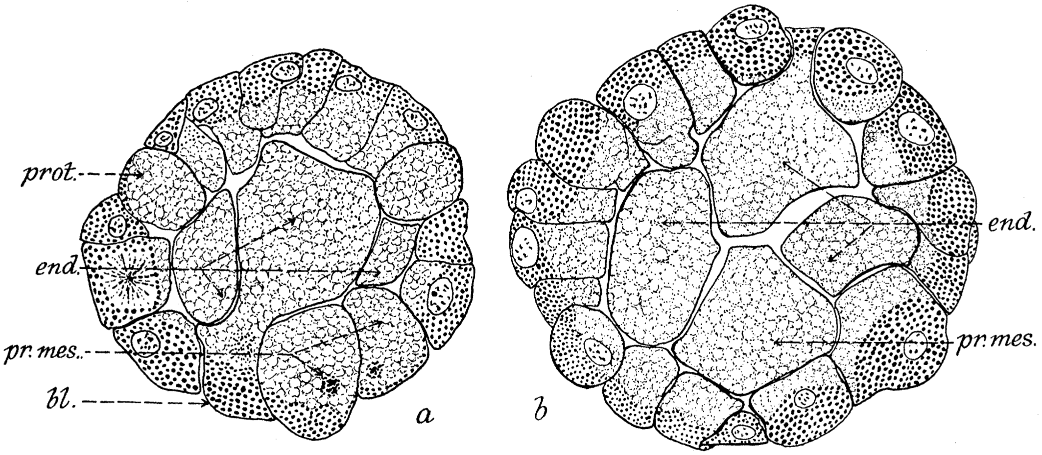

Fig. 39—*a*, parasagittal section of 7-hr. embryo, seen from left side, showing endoderm cells and two primitive mesoderm cells. *b*, transverse section of 8-hr. embryo, showing primitive mesoderm cell nearer animal pole than its partner, which is seen in fig. 40*a*. ×450 linear approx.

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4*D* appear to correspond with the primitive mesoderm cells of *P. vulgata* (Smith 1935). Unfortunately a stage was not found with the division of the macromere in progress, which Smith describes for *Patella*. During invagination of these primitive mesoderm cells, one of the pair is pushed nearer to the apical plate than the other, so that in transverse sections in that region four invaginated cells are seen which, on first examination, suggest that four macromeres take part in the formation of the endoderm (fig. 39*b*). A transverse section nearer the blastopore of the same embryo, however, shows five internal cells, two of which are primitive mesoderm cells (fig. 40*a*). It seems, therefore, probable that in *Haliotis* the whole of the macromere 4*D* gives rise to mesoderm and three macromeres only take part in the formation of the endoderm, as in *Patella* (Smith 1935). It may be significant that in *Trochus* that member of the pair of cells formed from 4*D*, which Robert (1902) describes as taking part in the formation of endoderm, does not divide at the time division of the endoderm cells *A*, *B* and *C* takes place.

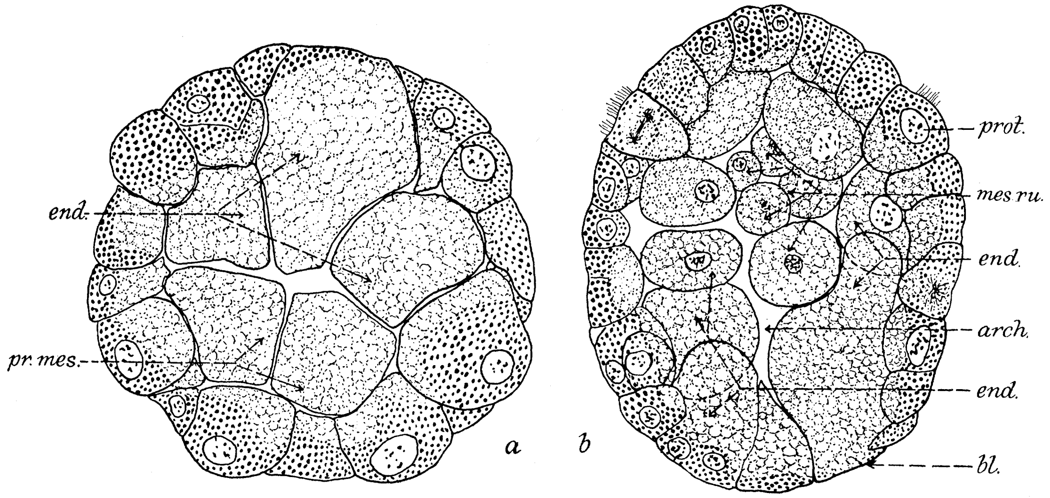

Fig. 40—*a*, transverse section of 8 hr. embryo nearer blastopore than that of fig. 39*b*, showing two primitive mesoderm cells and three endoderm cells. *b*, frontal section of 11 hr. embryo, showing division of endoderm cells and further division of mesoderm elements. ×450.

In *Haliotis* the invaginated cells are so large that there is no room for an archenteron, and it can be discovered only after further division of these cells (fig. 40*b*).

During gastrulation there is elongation in the direction of the axis through the centre of the apical plate (fig. 40*b*). Gradual shifting of the axis of the invaginated elements takes place as the unclosed blastopore migrates towards the prototroch. The migration appears to be due to the rapid formation of mesoderm cells accompanied by rapid divisions of the ectoderm cells in the dorsal region of the embryo. Robert's method of indicating the migration of the axis in *Trochus* has been adopted in the figures of *Haliotis* embryos (fig. 41).

At about 8 hr. after fertilization the embryo rotates within the vitelline membrane by movements of the cilia of the prototrochal girdle (fig. 41*a*). Derivation of the velum was not followed. As in *Trochus* it is monotrochal, unlike that of the trochophore of *Patella* (Patten 1886; Smith 1935). *Haliotis* also differs from *Patella* in the absence of apical cilia and telotroch in the trochophore. The refractive cells and the fine cilia of the embryo cap of *Patella* (Patten 1886; Smith 1935) are also lacking in *Haliotis*.

The larvae are freed at times varying from 8 to 13 hr. after fertilization when they are about 130μ long (fig. 41*b*). They have the trochophore characters, and the rudiments of the molluscan characters have scarcely begun to appear. According to Stephenson (1924) many *Haliotis* trochophores left the egg membrane and were swimming actively at 44–48 hr.; at 60 hr. "there was little difference in general form". Since Stephenson was unfortunate in the lack of suitable facilities, it seems probable that his larvae were arrested in development. *Patella* trochophores are freed at about 24 hr. after fertilization (Patten 1886). Robert (1902) states that *Trochus magus* larvae were freed at about 14 hr., but in other species of *Trochus* they were not freed until a much more advanced stage of development.

The primitive mesoderm cells have given rise, at the time the trochophore is freed, to ten mesoderm cells situated at the opposite end of the larva to the apical plate. There are no mesoderm pouches such as are described for *Paludina* (Erlanger 1894). The mesoderm cells of *Haliotis* spread on either side of the primitive gut and form the mesoderm bands, which are symmetrical in arrangement only in the anterior region (fig. 23, Plate 25).

Early Veliger Prior to Torsion

Bionomics of the Early Veliger

This phase begins at about 9 hr. and ends not earlier than 27 hr. after fertilization.

The larvae are pelagic up to about 60 hr. after fertilization. The freed post-trochophores are positively phototropic and swim near the surface of the water with the velum directed upwards and the shell below. As in other gastropod larvae, the velum is the only swimming organ. Rotation about the axis in the field of the velum is produced by the lashing of the long cilia. It appears to be usually counter-clockwise, when the veliger is regarded from the posterior end (fig. 2, Plate 21). Occasionally the direction of rotation is reversed and now and then, especially when the water is disturbed, the cilia stop lashing and converge anteriorly over the centre of the velar field (fig. 1, Plate 21). This causes the larvae to sink to the bottom of the water, where they rest motionless for a time and then resume their rapid revolutions. Feeding has not yet begun.

Beginning of Organ Formation

The velum of the *Haliotis* veliger retains the simple character of the pre-oral ciliated ring or prototroch of the trochophore, as in *Patella* (Patten 1886) and *Trochus* (Robert

1902). When the ciliated cells have become arranged in a circle, there are sixteen cells cut off from the rest of the body by a constriction (fig. 41*b*). The velum gets very little larger, increasing to twenty-four cells only in the older veliger (figs. 1–6, Plate 21).

The blastopore has now closed and, when first the invagination for the shell gland rudiment appears, there is a groove indicating the direction of migration of the blastopore towards the velum from its original position on the axis of the velar field (fig. 41*a*). This migration is completed in *Haliotis* before the proctodaeal and stomodaeal invaginations are formed. The stomodaeal invagination is well developed by 17 hr. after fertilization, in the region where the blastopore has closed just posterior to the velum (fig. 41*b* and *c*). In veligers not younger than 27 hr. old, in which 90° of torsion has been accomplished, the mouth has developed from this invagination and the foregut communicates with the endodermal part of the digestive system.

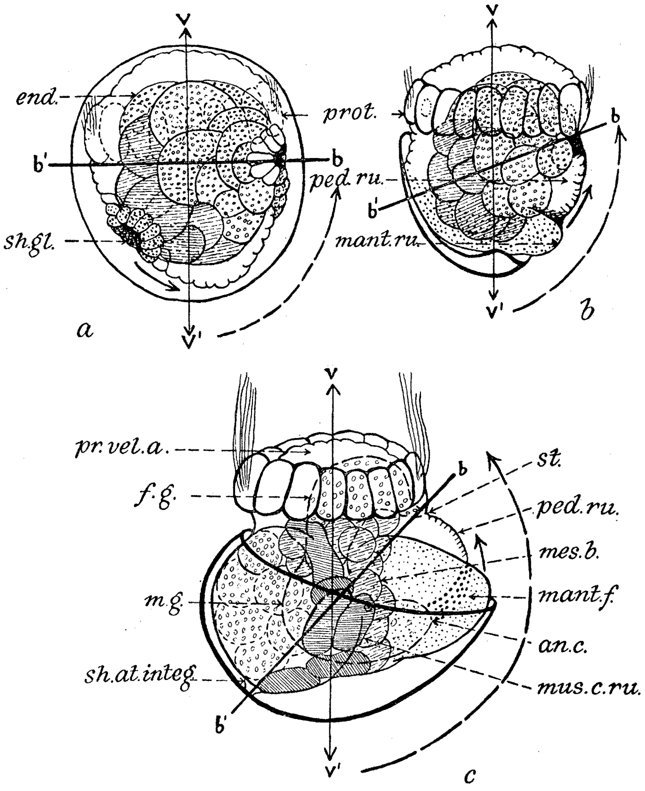

Fig. 41—Late embryo and early veligers seen from right side, drawn from whole mounts and models. ×170. *a*, 11 hr., immediately before larva freed, showing rudiment of shell gland and stomodaeum in region of closed blastopore. *b*, 16 hr., showing shell rudiment and "ano-pedal flexure" begun. *c*, 19 hr., showing further stage in development of shell and flexure of primitive gut. Mesoderm cross-hatched, endoderm with small circles; *bb'* indicates axis of invaginated elements; *st.* stomodaeum; *vv'* indicates axis in field of velum.

At the time the larvae are freed the foot originates as a median swelling below the united ventral lips of the blastopore.

As in *Patella vulgata* (Smith 1935), *Trochus* (Robert 1902), *Crepidula* (Conklin 1897) and *Ischnochiton* (Heath 1899), the pedal protuberance begins only after fusion of the blastopore lips so that the foot rudiment is never bilobed as Patten (1886) described it for *Patella coerulea*, although at 15 hr. it has a slight anterior groove in *Haliotis*. Smith points out how easy it is in *Patella vulgata* to mistake enlargements due to growth of the two mesoderm bands for two pedal rudiments.

The shell gland can be recognized in *Haliotis* at about 10 hr. It is an invagination giving a slight depression on the dorsal side of the body, and it is slightly to the right side (fig. 41 *a*).

Eversion of the shell gland is due to rapid multiplication of the cells of the gland combined with the enlargement of the primitive midgut and mesoderm bands. It occurs at 14 hr. after fertilization, or sometimes a little later, and at about 15 hr. a delicate shell of watch-glass shape has been secreted (fig. 41 *b*). At about 18 hr. the shell gland rudiment has spread over most of the dorsal region of the body, the shell has increased round its margin into a deep saucer shape, tilted somewhat towards the right side. The body is now contracted away from the central part of the shell. This space may contain air, and in other veligers it has been thought to serve a hydrostatic purpose (fig. 41 *c*). The shell is attached to the body at its periphery, and rapid multiplication of cells of the mantle margin, particularly at the right ventral edge of the shell, produces a thickening which is the mantle fold. For several days the shell is of transparent conchiolin and without calcareous spicules.

Ano-pedal Flexure and Subsequent Changes

Ano-pedal flexure occurs, as in all gastropod larvae, at a stage prior to torsion and, as Amaudrut (1898) and Robert (1902) point out, it must be considered as a process distinct from torsion. It involves curvature of the digestive system into a U shape so that the anus, instead of pointing posteriorly as in Amphineura and Annelida, travels round in a ventral direction; this is a result of the enlarging visceral hump, which becomes dome-shaped (fig. 41). At the completion of ano-pedal flexure, the rectum points anteriorly and lies ventrally to the stomodaeum, with the enlarging pedal mass between. In *Haliotis*, the flexure begins before the proctodaeum has formed and is complete before the stomodaeal invagination has established its connexion with the endodermal elements, which change their orientation and form the midgut, consisting of cells filled with yolk (fig. 42).

The mantle cavity originates as a result of the enlargement of the visceral mass, which causes the mantle fold, in which cells are multiplying very rapidly, to spread and encroach over the foot (fig. 41 *c*). A gulley, which will become the pallial cavity, is thus formed between the foot and the mantle fold. In *Haliotis*, it is not at first quite in the mid-ventral position as Robert describes for *Trochus* and Patten (1886) and Smith (1935) for *Patella*. Nor are there separate right and left mantle cavity rudiments behind the prototroch, such as Drummond (1902) describes for *Paludina* and Smith

(1935) for *Patella*. The mantle fold is first developed on the ventral right side of the body (fig. 42*b*). This may be a result of the asymmetry at the gastrula stage, when there is slight swelling on the right side in *Haliotis*, as is also described by Robert for *Trochus*. The mantle fold spreads over the pedal mass from its ventral and right sides (figs. 41*c* and 42). In one specimen sectioned and modelled 19 hr. after fertilization, the left side of the foot is still not covered at all by the mantle fold, but a few hours later the margin of the mantle fold has spread to the left side and most of the foot is now enveloped (fig. 43*a*).

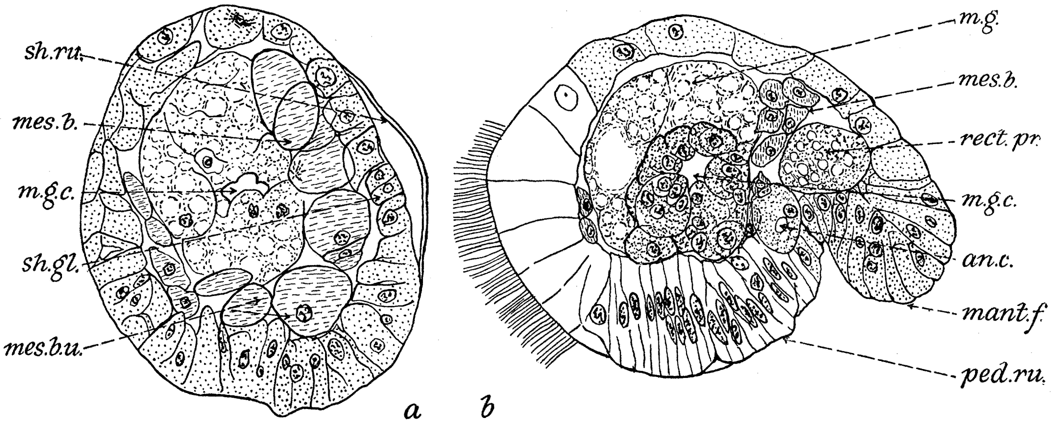

Fig. 42—Transverse sections of early veligers. ×450. *a*, 17 hr., passing through shell gland and shell rudiment on right side, showing union of mesoderm bands ventrally and larger mesoderm band on right side. *b*, 19 hr., passing through mantle fold, anal cell and pedal rudiment; mesoderm cells of right band pass between midgut and primitive rectum.

At 29 hr. transverse sections show that the deepest part of the pallial cavity is mid-ventral (fig. 46A and fig. 31, Plate 26). The anal cell is seen on the mantle side of this region (fig. 42*b*), but it is less obvious than in *Patella* (Smith 1935). There is scarcely any invagination when the proctodaeum forms after the first half of torsion has taken place (fig. 43).

Early in the second day the shell has changed considerably in shape; it has a wide aperture, due to rapid additions from the ventral parts of the mantle fold, and it is drawn in dorsally following the constriction between the visceral enlargement and the velum (fig. 1, Plate 21). Thus a nautiloid form with typical exogastric curvature is begun. There is also much elongation in the direction of the axis of the velum. This is due to increase in length of the visceral dome as the digestive system becomes more developed (fig. 43).

The digestive gland rudiment is a massive left dorsal swelling at about 27 hr. after fertilization (fig. 25, Plate 25), but in *Paludina*, Drummond (1902) describes it as a left ventral diverticulum. The small larval stomach is lined by cubical cells which have extended to meet the invaginated ectoderm cells of the stomodaeum; the cells of the short primitive rectum are considerably larger than those of the larval stomach (figs.

25 and 27, Plate 25). Although, according to Drummond (1902) for *Paludina* and Patten (1886) and Smith (1935) for *Patella*, a radular sac rudiment is present at this stage, there is no sign of it in *Haliotis* until sometime after the first phase of torsion (compare fig. 30, Plate 26 with fig. 44).

The mesoderm mother cells give rise anteriorly to the mesoderm bands while ano-pedal flexure is being accomplished (fig. 41*c*; fig. 23, Plate 25). At 17 hr. the right mesoderm band is larger than the left (fig. 42*a*). Some of the more anterior cells group themselves around the dorsal and lateral parts of the ectodermal foregut, as in *Patella coerulea* (Patten 1886). At this time mesoderm cells of the left band have migrated into the developing foot and others of the right mesoderm band have passed into the foot and the mantle fold, which it has been shown originates on the ventral right side (fig. 42*b*). The two mesoderm bands unite ventrally under the rectum and between the rectum and the larval stomach at the posterior end of the mantle fold, as in *Patella* (Smith 1935). These bands are well developed in veligers 27 hr. old. In the middle region of these larvae they are still solid bands, placed symmetrically on either side of the foregut, but their anterior ends are broken up into irregular spindle-shaped mesenchyme cells, which will develop into muscle cells and vascular tissue of the head and foot (figs. 29, 30 and 31, Plate 26).

The velum retractor muscle cells develop from the dorsal region of the right mesoderm band, which is larger than the left (fig. 42*a*). In *Patella* they arise from the anterior ends of both mesoderm bands (Patten 1886; Smith 1935).

In *Haliotis* elongated cells can be first recognized in larvae 19 hr. old (fig. 41). Three or four of these large spindle-shaped cells are seen in sections on the right-hand side of the digestive system, posterior to the mantle cavity, and are attached posteriorly to the part of the integument which is fixed to the shell (fig. 24, Plate 25). They do not appear to be efficient contractile cells until some hours later, when the shell has become large enough to accommodate the body of the larva. In the oldest pre-torsional veligers there are six muscle cells extending the whole length of the body posterior to the velum (fig. 27, Plate 25 and fig. 43). These cells are extremely long, and are inserted anteriorly round the foregut and stomach and to the posterior part of the velum in bilaterally symmetrical fashion. They curve round the left dorsal digestive gland enlargement and pass along its right side into the integument of the right ventral part of the visceral hump, which is attached near the central part of the shell. The arrangement of these muscles is shown in figs. 15 and 15*a*, Plate 23; fig. 25, Plate 25. These muscle cells have very large nuclei and minute vacuoles. By the time larval torsion takes place, beginning at an age varying from 27 to 35 hr. old, this right retractor muscle is well developed, but the larvae cannot be withdrawn into the shell completely until about 40 hr. after fertilization.

Early in the second day there are invariably two spindle-shaped cells derived from the left mesoderm band. They are about one-third the length of the muscle cells of the right side and have no shell attachment. The two ectoderm cells, which make a second posterior attachment of the visceral hump with the shell, have no muscular connexion (fig. 3, Plate 21). The two elongated mesenchyme cells are shown in transverse section in fig. 25, Plate 25. They are always in a cramped position because the bulky primitive digestive gland leans to the left side. This may be the reason why they are arrested in development for about 5 days, after which they develop into the columellar muscle of the plantigrade larva (figs. 44*a* and 46; fig. 11, Plate 22). It is, therefore, probable that the ancestors of *Haliotis* possessed paired larval retractor muscles. Although the right side retractor muscle of *Haliotis* appears to correspond remarkably closely with that of *Patella vulgata* (compare Smith 1935, fig. 11 with *Haliotis*, fig. 1, Plate 21 and fig. 15, Plate 23), it is not possible to agree with Smith's deductions. He assumes that this muscle was originally a median one "which has become diverted to one side by the pressure of the large yolky endoderm mass". Because an incipient representative of a left muscle is always present in *Haliotis*, it is unsuitable to adopt Smith's term "dorsal shell retractor muscle" for the right velum retractor muscle of *Haliotis*.

The nervous system originates immediately before torsion begins, at an age varying from 27 to 30 hr. after fertilization, with the rudiments of the cerebral ganglia. They develop similarly to those of *Patella* (Smith 1935); but, as in *Acanthochiton* (Hammersten and Runnström 1925), the rudiments are not sunken in pits of the embryo cap. Lateral thickenings of the ectoderm of the pre-velar area are readily seen in sections (fig. 31, Plate 26). The nuclei of many of these cells are undergoing mitosis; the cells gradually become rounded nerve cells. These are sunken although not completely delaminated from the ectoderm until after the first half of torsion is completed, when they form the strap-shaped cerebral ganglion band (fig. 32, Plate 26). Slightly later, paired antero-lateral thickenings of the pedal ectoderm sink into the foot and constitute the rudiments of the fused pedal ganglia. The remainder of the nervous system develops after the first torsion phase (p. 248).

Topography of the Veliger immediately before Torsion

The operculum rudiment is secreted just before torsion begins. It arises on the posterior pedal ectoderm, the future metapodium, to the left of the mid-ventral line (fig. 2, Plate 21). Its appearance, when first recognized in serial sections, is shown in fig. 31, Plate 26. It is secreted by the simple glandular ectoderm. Boutan, Patten and others do not appear to have observed the operculum in gastropod larvae until a much later stage than this, but Robert and Smith saw the operculum rudiment in *Trochus and Patella* respectively, during torsion.

The mantle fold has extended so that it almost envelops the pedal rudiment. It has reached slightly more dorsally on the right side of the body than on the left, but otherwise the anterior end of the veliger is bilaterally symmetrical at this stage (fig. 31, Plate 26; fig. 46A). A very shallow groove, continuous with the mid-ventral mantle cavity, has developed by rapid multiplication of cells on both lateral extremities of the mantle fold. As the pedal mass becomes more swollen, the pallial cavity separating it from the mantle fold gradually deepens (fig. 43). At the same time there is a marked dorsal constriction between the velum and the enlarging dorsal mass of digestive gland, where the umbo of the shell is commencing. The veliger has, therefore, a constricted "neck" region which is hidden ventrally by the pouch-like mantle fold (fig. 43).

Short apical cilia can be found in sections at this time. They are on two or three small cells in the centre of the apical plate (figs. 29 and 30, Plate 26). An hour or two afterwards they have disappeared. These were not discovered by MURAYAMA for *Haliotis gigantea*, and BOUTAN (1899) saw no apical cilia at any stage of *Haliotis* development. ROBERT found none in *Trochus*, but PATTEN (1886), WILSON (1904) and SMITH (1935) figure *Patella* veligers and trochophores with long cilia on the apical cells. If, as SMITH supposes, the telotroch serves as a rudder in *Patella*, its absence in *Haliotis* may be explained by the brevity of pelagic life.

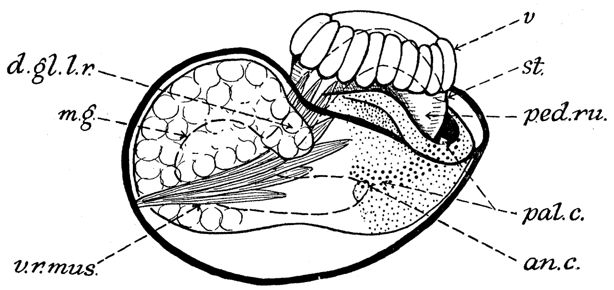

FIG. 43—Right side of veliger about 30 hr. old, immediately before torsion begins. From reconstructions made from serial sections, one of which is seen in fig. 25, Plate 25. The asymmetrical velum retractor muscle of the right side is shown. ×200.

The visceral hump, which is posterior to the constricted "neck" region described above, is superficially bilaterally symmetrical, and in the works on other gastropod veligers, with the one exception of *Patella vulgata* (SMITH 1935), it has been assumed that this symmetry extends to the organogeny, but the serial sections of many veligers of *Haliotis* at this stage show that it is asymmetrical, as in *Patella*. The primitive digestive gland forms the whole of the left and most of the dorsal part of the visceral dome, and it has a conical anterior diverticulum on the dorsal left side. Immediately before pelagic torsion a second small conical process of the digestive gland grows towards the dorsal right side. It lies dorsally to the velum retractor muscle which passes to the right side of the body in this region (fig. 25, Plate 25; fig. 15, Plate 23). The asymmetrical position of the velum retractor muscle on the right side has already been described (p. 230); it is also shown in these two figures.

Pre-torsionally, the primitive mesoderm bands unite beneath the primitive rectum and, during the early part of torsion, the solid rudiments, which later form the coelomic walls of the kidneys and pericardium, develop in the region of the union of the mesoderm bands (fig. 42*b*). The renal rudiments remain solid until the late veliger stage is reached, as in *Acanthochiton* (HAMMERSTEN and RUNNSTRÖM 1925) and in *Patella* (SMITH 1935).

In *Haliotis*, therefore, the two solid renal rudiments and the proctodaeum are the only representatives of the pallial complex when the early phase of torsion takes place. It may be gathered from SMITH's account that this is also true for *Patella*. It is important to note that in this respect *Haliotis* and *Patella*, which are undoubtedly primitive, depart from the theories of the mode of evolution of gastropod torsion, which are based on the assumption that the anus, the renal apertures, the ctenidia and the visceral loop were all established pre-torsionally. The full complement of these structures is not present in *Haliotis* until many weeks after torsion is complete.

FIRST 90° PHASE OF TORSION IN THE PELAGIC LARVA

This process was watched in the larvae resulting from fertilizations made on six different dates in July, August and September. It began while the veligers were swimming actively at a time varying from 29 to 35 hr. after fertilization. The torsion is a rotation in counter-clockwise direction, when the larva is regarded from its posterior aspect, and is a movement at right angles to the ano-pedal flexure.

Rapid rotation of 90° takes from 3 to 6 hr., after which the axis of the foot is situated at right angles to the median plane of the shell, so that only part of the margin of the shell is now ventral and the pallial cavity lies on the right side of the larva. The twist is made possible by, and localized to, the narrow neck-like region between the cephalo-pedal mass and the visceral organs enclosed in the shell (fig. 43 and fig. 16, Plate 23). Torsion begins as soon as the larval muscle cells have developed their retractile power. When these cells are contracted they become straight instead of curved (compare figs. 15 and 16, Plate 23). This would obviously force the newly formed "liver" diverticulum overlying the muscle towards the left side of the body. The contraction of the muscle pre-torsionally would also pull the enlarging pedal mass towards the exogastric shell. It is notable that the minute operculum rudiment has always appeared before torsion begins and is slightly to the left side of the foot (p. 231). Although it cannot be a very rigid cuticular plate at this time, it appears to collide with the left margin of the mantle and to act like a wedge pushing the mantle fold and shell margin away from the foot (fig. 2, Plate 21; fig. 31, Plate 26). It is therefore probable that the operculum is a contributory mechanical cause of the beginning of the rotation, although the contraction of the asymmetrical velum retractor muscle is the primary cause.

The attachment of the integument of the visceral mass to the shell on the pre-torsional left ventral side holds the visceral mass in position during torsion.

Resulting from this pelagic torsion the pallial cavity, containing the proctodaeum, is on the right side of the cephalo-pedal mass, which no longer hinders free entrance of water into the pallial cavity. The deepest part of the shell aperture is also to the right and the umbo to the left, thus giving sufficient freedom for the foot and operculum until they are larger. The velum retractor muscle is now straight (fig. 16, Plate 23) and can retract the cephalo-pedal mass into the shell (fig. 3, Plate 21). The muscle is dorsal to the visceral mass, although its attachments are the same as before torsion begins. As a result of this first phase of torsion the weight on the two sides of the muscle is more symmetrically distributed. Prior to this 90° torsion the weight of the yolky digestive gland is nearly all on the left side of the body, giving an unstable equilibrium (compare fig. 25, Plate 25 with fig. 16, Plate 23 and fig. 27, Plate 25).

There is never more than 90° rotation of the pallial cavity at this stage in *Haliotis*, and it remains on the right side of the body for many days (figs. 46 and 48). The remaining 90° of torsion is a slow process of unequal growth spread over 8–10 days of ontogeny (figs. 46 and 48), and during most of this time the larva is benthic.

It is important to compare these observations of torsion in *Haliotis* with those of other authors. Boutan (1899) states that torsion begins when the shell is sufficiently developed to impede the spreading of the foot. This may be compared with Smith's observation for *Patella vulgata* (1935) that growth of the foot produces an unstable condition. The possible influence of the development of the operculum is not mentioned by these authors. It is of particular interest to note that Smith also holds the opinion that the action of the asymmetrical retractor muscle "plays a major part in bringing about torsion". His investigation of the torsion of *P. vulgata*, however, differs notably from the observations described above for *Haliotis* in that the pelagic torsion in *Patella* involves 180°, but in *Haliotis* 90° only. The diagram of the post-torsional larva of *Patella* shown in fig. 22*b* (Smith 1935), however, scarcely appears to have undergone the complete 180° rotation of the pallial cavity, for the anal cell and visceral ganglia are to the right side. In *Patella* the first half of torsion takes about 40 hr., but the final stages are passed through quickly. In *Haliotis* the slow and rapid phases are reversed; the first half of torsion is accomplished in 3 or 4 hr., and the second half takes many days to complete. Boutan (1899) states that 180° torsion is completed in 2 or 3 min. in *Haliotis* and almost as rapidly as in *Acmaea*. He did not examine the succeeding stages in sections, and he was unable to determine the length of larval life. Without transverse sections and models of such minute larvae it is impossible to get an exact idea of the amount of torsion accomplished.

Transition from Pelagic to Benthic Life

Bionomics of Young Plantigrade

This period begins when the veliger is 2 days old and ends when it is from 10 to 14 days old. As in lamellibranchs, the pelagic life is brief and, when 40 hr. old, the larvae rest at the bottom between intervals of swimming. These intervals shorten and life is entirely benthic after the 3rd day, but the dorsal part of the velum is not completely thrown off until nearly 2 weeks after fertilization. The changes in appearance of living larvae during this transitional period are shown in figs. 7–14, Plate 22.

Feeding does not begin until the larvae cease to be entirely pelagic. Veligers from 40 hr. old can make use of a mixed culture containing *Pleurococcus* and other organisms smaller than *Nitzschia*. At this time there are long mouth cilia which aid the long velum cilia in wafting food into the mouth. Feeding continues in this manner during creeping so long as the velum persists. From 8 to 14 days old the larvae can make use of *N. closterium*, which is frequently found in transverse sections passing through the larval stomach.

The teeth of the radular ribbon and the two first formed supporting cartilages are only sufficiently developed for use by the time the velum disappears at the end of 2 weeks of development (fig. 33, Plate 27). At first the radula scrapes up loose fragments, such as diatoms and foraminifera, from the surface of the stones on which the larvae creep. The shell is tinged with pink and the soft parts of the body are faintly green, so that the young creeping animals resemble their food in colour.

The pedal sole is first seen at the end of the 3rd day of development as an invagination on the antero-left surface of the foot. The area of the pedal sole rapidly increases and a carpet of short and very active cilia clothes the epithelium (figs. 7 and 9, Plate 22). When the veliger retracts the foot is folded so that the pedal sole is completely hidden.

The first attempts at creeping were watched at the close of the 3rd day of development. The early efforts of these veligers met with little success. Larvae which were lying on their sides in a resting contracted state inside the shell suddenly began to open the shell aperture by rotating the operculum towards the shell umbo (figs. 7, 8, 9 and 10, Plate 22). During this rotation the mobile foot spread its pedal sole gradually, first concave and then flat and the larva attempted to cling by the plantar surface. The posterior part of the pedal sole seemed to touch and obtain a hold first (figs. 8 and 12, Plate 22). The anterior part then moved in a stretching and searching manner (fig. 11, Plate 22). In larvae 3 days old, however, the foot seemed unable to get a suitable hold for creeping. This was apparently because of difficulty in getting into equilibrium the weighty visceral hump over the foot. Obviously the relation of the visceral hump to the force of gravity had changed when creeping was attempted. The larvae fell sideways and retracted into resting position, usually lying on the left side because the shell margin is shorter on this side (figs. 8 and 9, Plate 22).

Further attempts at creeping were made after a considerable period of rest, but they were not successful until the larvae were between 4 and 5 days old, when the pedal sole was considerably larger and, as sections show, had well developed muscle strands. An attempt has been made, in figs. 7–14, Plate 22, to show the appearance of the larvae during these creeping efforts but, as Boutan noticed, the larvae are difficult to observe because they are very sensitive and rest for prolonged periods. A larva $4\frac{1}{2}$ days old struggled for 10 min. after lifting its operculum and clinging with its foot. There was much elongating, stretching and swinging in the "neck-like" region between the cephalo-pedal mass and the visceral hump enclosed in the shell and in the now constricted region above the foot (fig. 9, Plate 22). As the shell with its contents was swung from side to side, apparently in an attempt to get it into equilibrium, the operculum appeared to collide with the shell (figs. 9 and 10, Plate 22). Finally, with the operculum and metapodium directed to the right side and the visceral hump leaning a little to the left, as shown in fig. 13, Plate 22, creeping was successful for about 40 min. The larvae progressed in a gliding manner, by the aid of the very active cilia of the pedal sole, the latter presumably being lubricated by the mucus of the pedal epithelium. During the 6th and 7th days, the larvae were visible to the naked eye creeping on the surface of flat stones. They were also seen to make use of the surface film. The habit of creeping beneath stones was not acquired until after the first fortnight of development.

Larvae of *Patella vulgata* (Smith 1935) began to crawl on the 9th day, but they were not entirely sedentary until about 15 days old.

Pedal Glands

From the 3rd day of development there are large unicellular mucous gland cells scattered in the pedal epithelium (fig. 34, Plate 27). In the metapodial region, where the operculum is secreted, these gland cells are more spherical than those of the pedal sole. The operculum appears to be secreted by these simple gland cells, for no special foot organ, such as is found in *Patella* (Smith 1935) in relation to secretion of the operculum, is present in *Haliotis*. In the 7-day-old plantigrade there is, however, a large anterior pedal gland. It is an aggregation of very large cells of mesodermal origin, which stain deeply with aniline-blue as do the epidermal mucous cells. This gland lies close to the pleuro-pedal ganglia and appears to discharge into a small depression of the anterior end of the foot beneath the mouth (fig. 33, Plate 27). It is a simpler gland than the pedal glands of *Patella*.

In the oldest veligers there are also pedal mesoderm cells of very large size and vacuolated appearance, which resemble the cells of unknown fate in *Patella* (Smith 1935); they cannot be distinguished from the lymphoid cells of the adult *Haliotis* (Crofts 1929, p. 100).

Changes in the Velum

During the 3rd day a vertical groove forms in the prevelar area. This extends ventrally to make a cleft in the velum in the region of the mouth (fig. 6, Plate 21). Boutan (1899) states that in *Haliotis* he is unable to determine whether the velum remains entire or indents, as in the later stages of *Fissurella*.

The age at which the velum begins to diminish varies from 7 to 10 days in different individuals. The velum cells decrease in size and are gradually nipped off, as in *Patella* (Smith 1935), by the tegumentary cells of the head growing beneath them (fig. 35, *integ.v.c.*, Plate 27). In *Haliotis* the velum disappears from the right side before the left (fig. 33, *v.v.*, Plate 27). This may be due to development of the large mantle fold on this side. In some larvae at 14 days there are still velar cells although the velum has entirely disappeared in other larvae at 10 days old.

Sense Organs

The sense organs of *Haliotis* begin to develop at about the same stage as in *Trochus* (Robert 1902). In *Paludina*, according to Erlanger (1891) and Drummond (1902), the rudiments of the sense organs arise when development in other respects is much less advanced than in *Haliotis*. This may be due to abbreviation of the developmental stages in *Paludina*, as a result of viviparity.

The single pair of cephalic tentacles develops from small prominences on the lateral region of the enlarged part of the pre-velar area. These rudiments are first recognizable in veligers about 2½ days old (fig. 6, Plate 21). At first they point dorsally, but when the larvae are 4 days old they point ventrally, having elongated and become mobile (fig. 9, Plate 22).

During the 4th day there is pale green pigment in the epithelium of the tentacles. At this time they develop papillae, the larger of which bear terminal tufts of cells with rigid sensory threads (figs. 7–14, Plate 22), the taste-buds or "Pinselzellen" of Flemming (1883). The papillae do not increase in size but their number is gradually increased until, in the post-larval stages, they are finally arranged close together and give the appearance of velvet pile covering the whole surface of the tentacles. Innervation of the cephalic tentacle by an outgrowth of the cerebral ganglion is shown in fig. 35, *ceph.t.n.*, Plate 27.

The rudiments of the eyes are first seen early in the 3rd day as a group of several epithelial cells, which have acquired pigment granules, situated near the velum on the outer sides of the cephalic tentacle rudiments (figs. 5 and 6, Plate 21). Before the close of the 3rd day these eye rudiments are raised on small projections of the base of the tentacles, which are the rudiments of the optic tubercles (fig. 17, Plate 23). Owing to thickening of the epithelium, the pigmented cells begin to sink in and form a shallow retinal invagination. In the sections of larvae a week old, the retinal epithelium is in the form of a cup and is innervated by a process from the cerebral ganglion, which, like that innervating the tentacle, is ganglionated (fig. 35, Plate 27).

The retinal cells have begun to secrete cuticular outgrowths to initiate the retinidian layer and the crystalline lens (fig. 35, Plate 27). This refractive body grows large enough by the end of the 2nd week to block the opening of the cup and to project at the tip of the optic tubercle. The ocular cup never becomes closed, so that the eye does not acquire a cornea and in this respect the eye is more primitive than that of many members of the Archaeogastropoda. It was not found possible to trace the development of different types of retinal cells, which are described for the adult (Crofts 1929, fig. 24, Plate VI).

The statocyst rudiments are first seen in veligers about 30 hr. old, which have undergone 90° torsion. They arise as a pair of shallow invaginations of the ectoderm near the junction of the latero-dorsal part of the foot with the head (fig. 30, Plate 26 and fig. 5, Plate 21). They are farther from the mouth than Patten (1886) describes them for *Patella*, but Smith (1935) shows that Patten had mistaken the precocious mantle cavities for statocysts. In *Haliotis* during the latter half of the 2nd day these invaginations sink into the foot and by the 3rd day the statocysts are cut off from the pedal ectoderm (fig. 44*b*). The spherical statocysts are now embedded in the foot and are situated close to the rudiments of the pleuro-pedal ganglia (fig. 32, Plate 26). They remain adherent to these nerve centres although they have no physiological connexion with them. They become innervated during the 3rd day by nerve cells connected with the cerebral ganglia, which are but a short distance from the statocyst in these minute veligers (fig. 44*b*). The branched sensory processes of the statocyst epithelium, which are seen only with an oil immersion lens, are present in older veligers. One statolith only is secreted in each statocyst, but in the post-veliger there are additional statoliths.

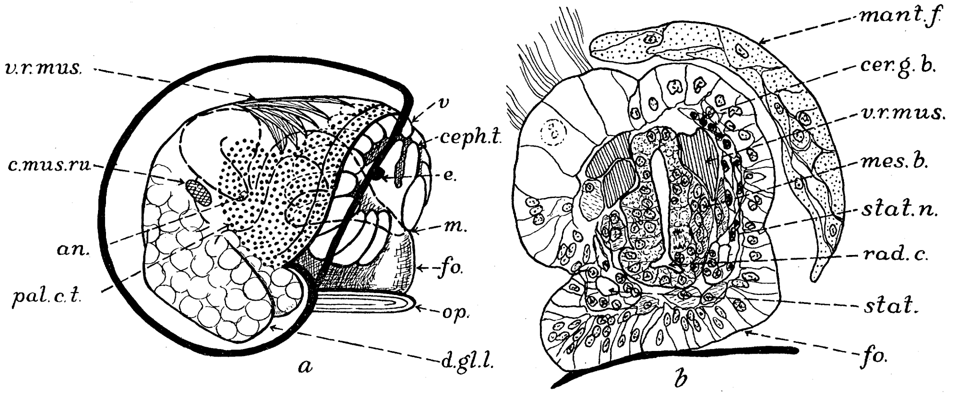

Fig. 44—*a*, veliger 61 hr. old, seen from right side, drawn from reconstruction; pallial cavity and anus show 90° torsion. Rudiment of columellar muscle also on right; velum retractor muscle partially migrated to left. *b*, transverse section at same age, passing through rudiment of radula and showing innervation of statocyst from cerebral ganglion. ×450.

According to Drummond (1902) *Paludina* has its statocysts already enclosed in the foot some time before torsion begins. In *Patella* they are formed later and, although not quite so early as Patten (1886) imagined, just before torsion begins (Smith 1935). It has been shown above that the statocyst invaginations of *Haliotis* do not develop until the pelagic half of torsion is accomplished.

Muscles

The development of the muscles, which has been followed in serial sections and reconstructions, is of particular interest since it differs from the generally accepted hypothesis of the mode of origin of gastropod musculature.

The velum retractor muscle develops pre-torsionally and its significance in relation to the first half of torsion has been described (pp. 233 and 234; figs. 15 and 16, Plate 23; fig. 27, Plate 25). At the end of this pelagic phase of rotation this muscle is dorsally situated and during the 2nd day of development it can withdraw the cephalo-pedal mass completely into the shell. In the contracted state shown in fig. 17, Plate 23, the velum retractor muscle is a stout short pillar inserted under the velum and passing postero-dorsally to its shell attachment. The position of the attachment is now displaced slightly to the left because of the enlargement of the primitive digestive system and of the pallial region on the posterior right side. In 3-day-old larvae the velum retractor muscle occupies most of the dorsal left side of the visceral hump and is bordered on the right side by the pallial cavity anteriorly and the primitive gut posteriorly (fig. 45*a* and fig. 17, Plate 23).

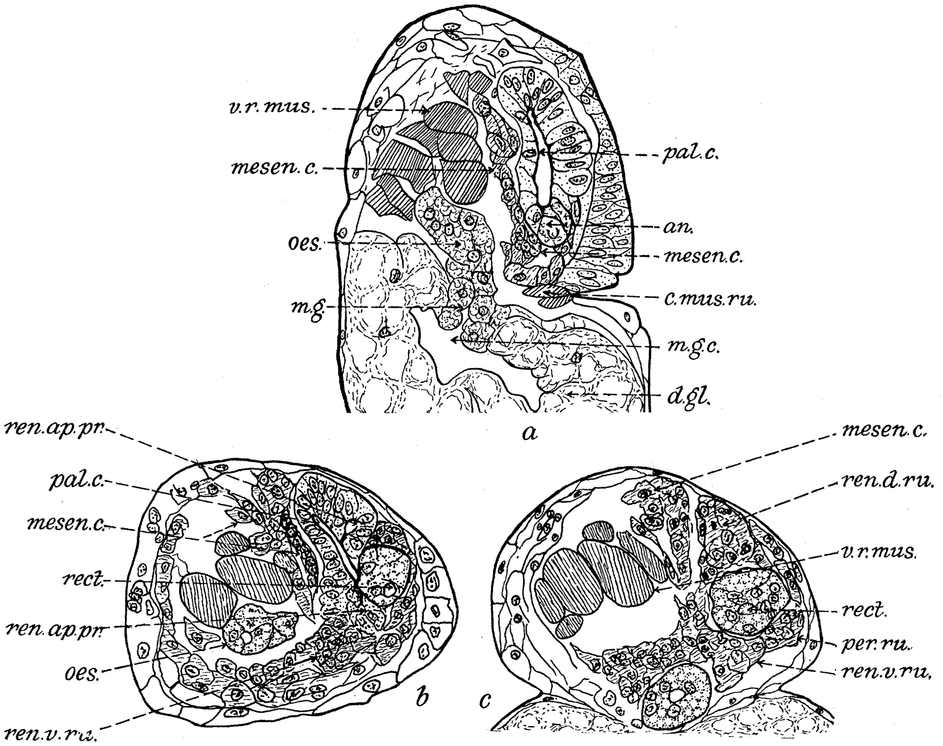

FIG. 45—Transverse sections of veligers 61 hr. old, passing through posterior end of pallial cavity. ×450. *a*, shows rudiment of columellar muscle on right, ventral to pallial cavity and mesoderm band. *b*, from another series, showing diverticula of posterior end of pallial cavity (precocious renal apertures); solid mesoderm rudiments of renal walls dorsal and ventral to anus. *c*, from same series as *b*, shows renal rudiments united by solid mesenchyme rudiments of pericardial wall.

Further change in position of the muscle attachment to the shell takes place in veligers from 4 days old and is brought about both by migration and by addition of new muscle cells from the mesoderm of the left side. As the shell grows, the muscle attachment moves in an antero-left direction so that it becomes progressively nearer the left shell margin (figs. 7, 9 and 12, Plate 22; figs. 17 and 18, Plate 23). In these creeping veligers the velum retractor muscle develops spindle-like muscle cells extending into the left side of the foot (fig. 35, Plate 27). Thus it serves as an initial, if somewhat inadequate, pedal retractor.

When the velum is in process of disintegration, at an age varying from 9 to 14 days, the velum retractor muscle ceases to grow. It is now inserted on the left half of the developing buccal apparatus and its shell attachment is close to the small mantle fold, which has now extended round the left side. The topographical relations are shown in transverse sections and in the figure drawn from a reconstruction of a larva 14 days old (figs. 33 and 34, Plate 27; fig. 18, Plate 23). Muscle cells in the dorsal part of the foot connect the velum retractor muscle with the enlarging columellar muscle (fig. 34, Plate 27).

The columellar muscle develops from two mesoderm cells of the pre-torsional left side (fig. 25, Plate 25 and p. 230), which are retarded in development until the creeping habit begins. These two cells are recognizable in sections of a number of larvae after the first phase of torsion and they are shown in the transverse sections of a veliger at 61 hr., lying under the groove between the pallial cavity and the digestive gland on the right side of the visceral dome (figs. 44*a* and 45*a*). At this time these mesoderm cells are insignificant in comparison with the velum retractor muscle cells, but they elongate and multiply and in larvae 6 days old have formed muscle cells running into the metapodium and its opercular process, which has developed on the right side. The columellar muscle and its shell attachment, near the right side of the shell umbo, are shown in a 6-day larva in fig. 8, Plate 22.

When the velum begins to disintegrate, at an age varying from 9 to 14 days, the columellar muscle is still much smaller than the velum retractor muscle. The columellar muscle lies to the posterior right side of the foot, and has only a small attachment to the shell (fig. 18, Plate 23). In addition to the opercular muscle strands, which are derived from mesenchyme and are inserted under the opercular epithelium, muscle processes are also added to the columellar muscle in the centre part of the foot. Some of these processes are attached under the epithelium of the pedal sole (fig. 34, Plate 27).

In larvae, which have lost almost all the velum, the two muscles are approximately equal in size, for the velum retractor muscle has now ceased to grow. The latter muscle is situated on the antero-left side and the columellar muscle is on the postero-right side (fig. 19, Plate 24; fig. 46E). They function in directions approximately at right angles to one another, the velum muscle contracts in an antero-posterior direction, thus retracting the head, and the columellar muscle contracts in a dorso-ventral direction withdrawing the foot into the shell. With the change in topographical relations when benthic life begins, it seems probable that the columellar muscle is more effective in helping to preserve the balance of the visceral hump over the foot during creeping than is the velum retractor muscle on the left side. From this time the columellar muscle becomes the important muscle, the velum retractor muscle becoming less and less significant.

It has already been shown (p. 231) that the velum retractor muscle of *Haliotis* closely resembles the dorsal retractor muscle of *Patella vulgata* (Smith 1935). From the evidence of *Haliotis* pre-torsional and post-torsional stages, however, it appears probable that originally the veliger retractors were paired and that the columellar muscle develops from one member of the pair, which is arrested in development until creeping is attempted. Although Smith states that the larval retractor muscle cells disappear after pelagic life ceases and that the adult shell retractors have an entirely different origin, the rudiment of the adult shell muscle of *Patella vulgata* (fig. 22*a*, Smith 1935) closely resembles the rudiment of the columellar muscle of *Haliotis* in position and in

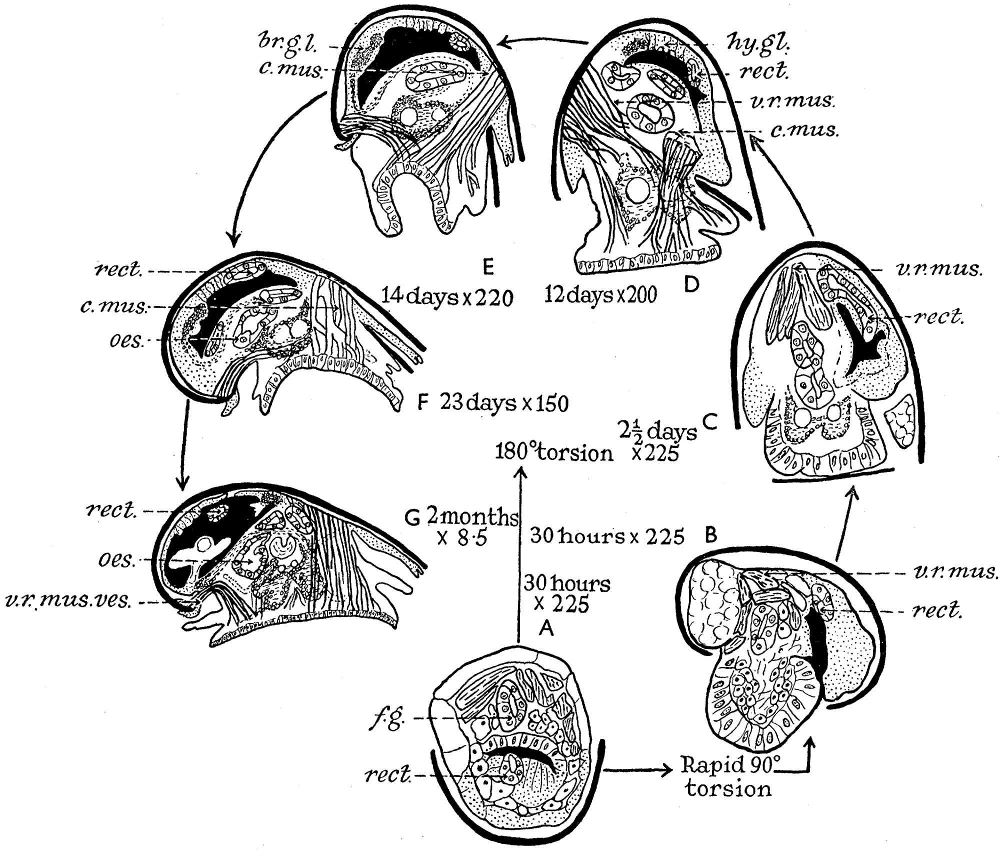

Fig. 46—Diagrammatic transverse sections of veligers and post-veligers to show development of muscles, pallial complex, and migration of the pallial cavity. Right side of animal towards right side of page, pallial cavity shown in black, mantle fold stippled, shell in heavy outline, muscles striated. A, immediately prior to torsion, through posterior part of pallial cavity. B, after rapid 90° torsion. C, at 2½ days with pallial cavity still on right side. D, oldest with velum, pallial cavity almost dorsal with hypobranchial gland and branchial ganglion rudiments; two muscles equal in size. E, early post-veliger with rectum still on right side of pallial cavity; supra-oesophageal pleuro-visceral cord dotted. F, post-veliger (23 days old); first ctenidium, final left, now developing lamellae; velum retractor muscle inconspicuous. G, at close of metamorphosis (2 months old) well-developed final left ctenidium and rudimentary final right ctenidium.

its function (figs. 8 and 11, Plate 22). For *Haliotis* it is impossible to agree with SMITH's theory, which is also the generally stated one, that the functional retractor muscle of the pelagic larva is homologous with the columellar muscle of spirally twisted gastropods. Although the veliger retractor muscle of *Haliotis* is retained, unlike that of *Patella* (SMITH 1935), it becomes an insignificant shell muscle and is not the columellar muscle. Its fate in the post-veliger is described on p. 252 and its final position is shown in fig. 22, Plate 24 and fig. 38, Plate 27.

In *Haliotis* there is no corresponding muscle to the ventral retractor which appears after torsion in *Patella*, although pre-torsionally there is a simple tegumentary attachment of the visceral hump to the shell in postero-left position (fig. 3, Plate 21).

Mantle and Shell

The mantle and its derivatives change much during the transition to benthic life. As a result of the first torsion phase, the shell is half endogastric (figs. 3 and 4, Plate 21; fig. 16, Plate 23). The deepest part of the shell, which coincides with the deepest part of the mantle fold, is on the right side of the body with a slight tilt dorsally because, pre-torsionally, it was a little to the right side (p. 231). The umbo is therefore on the left ventral side of the body (fig. 16*a*, Plate 23). There is now room for growth of the mantle and shell on the right and right-ventral side. The foot and operculum have freedom for movement which is adequate for a few hours.

During the late part of the 2nd and the early part of the 3rd day, semblance of an endogastric shell is brought about gradually by retardation of shell growth due to the movement of the enlarging foot and operculum over the ventral shell margin as the larva moves in and out of the shell. The umbo, therefore, spreads from the left towards the right side (figs. 3 and 4, Plate 21). The asymmetrical increase to the shell margin is shown in fig. 47. Examination of the shell alone gives the misleading appearance of 180° torsion with a completely endogastric shell (figs. 5 and 6, Plate 21). Figs. 44 and 45*a* show that the mantle cavity, containing the anus, is still on the right side of the larva. A very shallow mantle fold extends dorsally to the left side (fig. 17, Plate 23).

Rapid growth of the margin of the shell gives a more rolled character, so that, at about 60 hr., the shell can accommodate the retracted veliger completely (fig. 17, Plate 23). The operculum is now large enough to close the shell aperture.

During the 3rd day the shell shows curved lines radiating from the umbo to the margin and on these are glistening specks, which are probably carbonate of lime deposited to strengthen the original shell of conchiolin.

The foundation of the dextral coil of the shell can be detected from the 3rd day, in a more rapid addition to the shell margin on the right side than on the left (figs. 8 and 9, Plate 22). This appears to be due to extensive proliferation of the cells of the deep mantle fold overlying the pallial cavity, which remains entirely on the right side of the body until after the 6th day of development, when creeping has become established (figs. 44, 45 and 46). This results, during these 4 days, in additions to the shell mainly on the right side so that the shell leans towards the left side during creeping. An additional cause of this tilt of the shell and its contents may be that the left half, containing the velum retractor muscle and the digestive system, is heavier than the right half, which is largely occupied by the pallial cavity (fig. 18, Plate 23).

During late veliger development the right mantle fold gradually surrounds the posterior part of the columellar muscle and joins the smaller left mantle fold beneath the visceral hump, so that the original umbo is lifted above the new peristome (figs. 11 and 14, Plate 22).

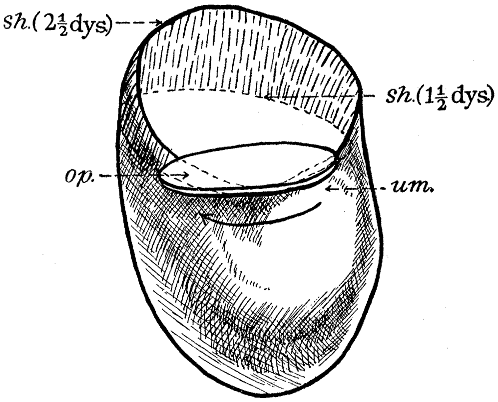

Fig. 47—Diagram of ventral view of reconstruction of shell to show its asymmetrical growth after 90° torsion. ×200 approx. Shell margin immediately after 90° torsion, when shell is half endogastric, is indicated. Outer shell margin is at $2\frac{1}{2}$ days old, when shell is completely endogastric, although pallial cavity has not yet undergone 180° torsion. *op.*, position of operculum; *um.*, umbo.

Gradual Completion of Torsion of the Pallial Cavity

At the time the creeping habit is established in larvae about 6 days old, the second 90° of torsion of the pallial cavity has begun. This is accomplished mainly by a gradual migration, due to differential growth, but conceivably the leaning of the shell and its contents to the left side, which is mentioned in the preceding section, contributes to the rotation. The process is not completed until about a week later, when the early post-veliger stage is reached.

It has been shown in the account of the muscles (p. 239) that the larval retractor muscle gradually migrates to the left side during late veliger development. At the same time, the columellar muscle migrates from the right side towards the centre of the shell and, in contrast to the velum retractor muscle, it gains in size and functional significance (compare fig. 18, Plate 23 with fig. 19, Plate 24 and fig. 46, D and E). Thus it is clear that more and more room is left for the pallial cavity to expand dorsally from the right side of the body, but that the development of the columellar muscle prevents spreading from the right border of the cavity. Therefore, in the late veligers and early post-veligers, the gradual expansion of the pallial cavity concerns only that part which is to the left side of the rectum (fig. 36, Plate 27).

By the time the velum is lost, at not earlier than 12 days old, the pallial cavity is dorsal and has undergone 180° torsion from its original position, but the anus is still on the right side of the pallial cavity (fig. 19, Plate 24; fig. 48E).

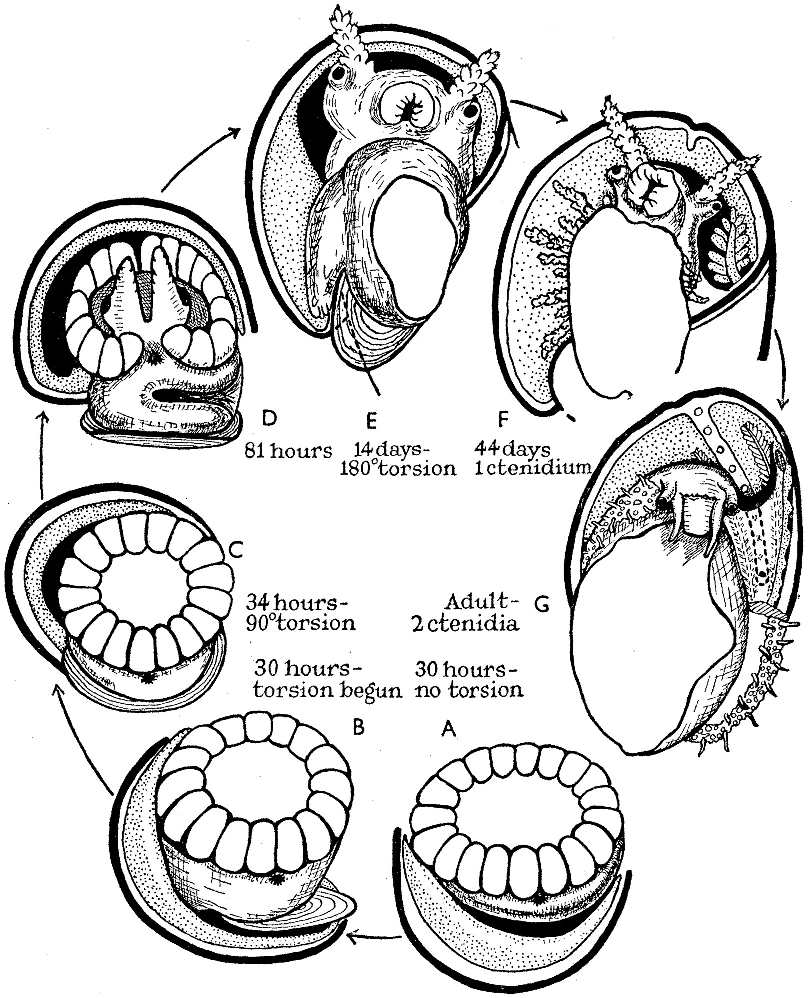

FIG. 48—Anterior views to show phases of torsion and later displacement of the pallial cavity. Pallial cavity shown in black, mantle fold stippled, velum unshaded, foot cross-hatched, operculum with concentric curves. A, B and C show sudden migration of pallial cavity through 90°, from ventral position to right side. 180° torsion is completed slowly after about 14 days. E shows dorsal pallial cavity. F and G show displacement of pallial cavity to the left side by hypertrophy of columellar muscle. G shows adult with pallial cleft, bilateral symmetry of pallial complex and shell holes placed dorsally to anus.

The Pallial Complex

The pallial complex, which in the adult is constituted by two ctenidia with their osphradia and hypobranchial glands, the median anus and renal openings on either side of it, is not complete until the end of nearly 2 months of development (figs. 21

and 22, Plate 24). The relations existing between these structures and the mantle and shell are of the highest importance in Mollusca, therefore the order of development of these organs has been investigated. It has already been shown on p. 233 that, at the time of the first half of torsion, the proctodaeum and the solid mesodermal rudiments of the kidneys are the only representatives of the complex. The following account will show that, by the time 180° rotation of the pallial cavity is complete, the rudiment of one ctenidium only is present. The corresponding osphradium and hypobranchial gland have appeared in addition to the anus and two kidneys which have acquired cavities and apertures.

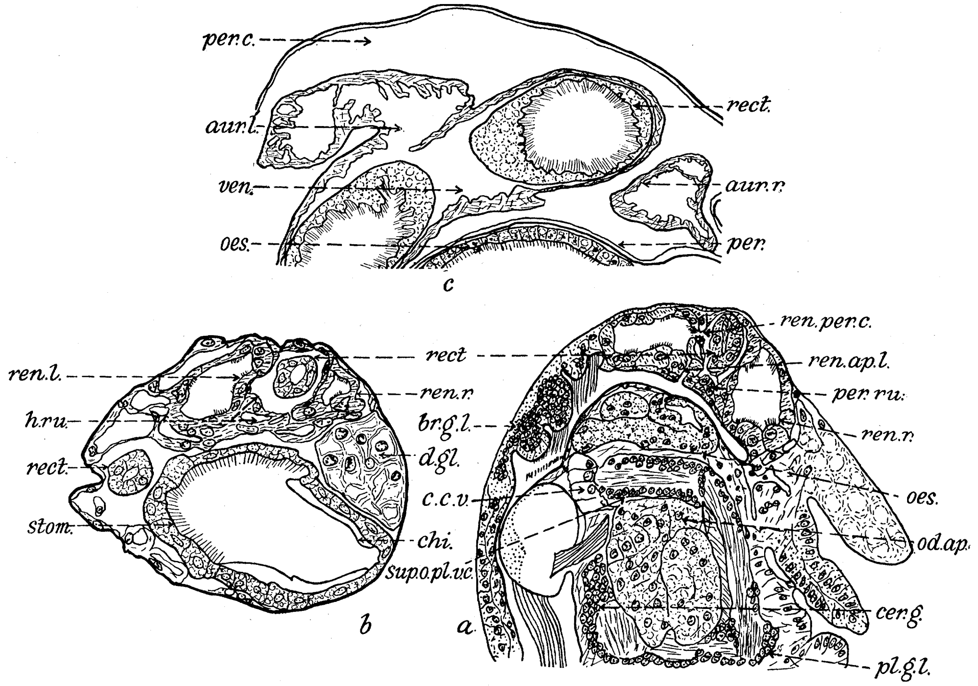

FIG. 49—*a*, parasagittal section of late veliger viewed from right; definitive left kidney now mid-dorsal and definitive left one on right side; mesenchyme cells migrating to form pericardial wall, which envelopes rectum. Epithelial cells about to cut off velum cell. ×450. *b*, transverse section of youngest post-veliger, immediately posterior to pallial cavity, two adjacent sections combined; shows two kidneys in post-torsional position and rectum surrounded by pericardial coelom and heart rudiments. ×450. *c*, transverse section of metamorphosed *Haliotis* at 2 months showing heart, with two auricles, enveloping rectum and surrounded by pericardium. ×100.

Renal organ rudiments. The kidney rudiments, as seen in sections of various 3rd-day veligers, are still solid masses of mesenchyme cells, such as were described for the pre-torsional veliger (p. 232), but situated dorsally and ventrally to the rectum and attached by the solid pericardial wall rudiment close to the rectum (fig. 45*c*).

At the time reduction of the velum has begun, the rudiments of the renal cavities develop as spaces in the renal rudiments, which are now on either side of the rectum. Fig. 49*a* shows the renal organs in a transverse section of a larva whose velum has almost gone. The two kidneys are almost equal in size and are lined by ciliated cubical cells. In the earliest post-veliger they are in post-torsional position (fig. 49*b*). The mesenchyme cells nearest the rectum are now arranged to make a delicate coelomic wall of small irregularly disposed cells surrounding the rectum and enclosing the pericardial cavity next to the rectum (fig. 49*a* and *b*). In having the pericardium traversed by the rectum *Haliotis* resembles the lamellibranchs and differs from *Patella*. When first the pericardial rudiment forms, the reno-pericardial canals are obvious and the left one is shown in fig. 49*a*. They were not found in *Patella* (Smith 1935).

The renal apertures appear to arise as precocious rudiments, which are seen late in the 3rd day after fertilization as simple ectoderm invaginations in the deepest part of the pallial cavity. They can be recognized only in sections; the post-torsional left one lies dorsally to the anus and the post-torsional right one is ventral to it (fig. 45*b*). These invaginations do not communicate with the renal organs until about 9 days later, when the velum has disappeared. Although the cells lining the renal cavities possess short cilia (fig. 49*a*), the renal apertures are not ciliated like those of *Patella* (Smith 1935).

In the early post-veliger, torsion is complete and the renal organs are now to the right and left of the anus, as in the adult (fig. 19, Plate 24; fig. 49*b*).

The classic account of Erlanger (1891, 1894) and that of Drummond (1902), which are mainly concerned with the coelom and its derivatives, show that in *Paludina* the kidneys and their pallial apertures take part in 180° of torsion. Pre-torsionally, however, organogenesis is more advanced in *Paludina* than in *Haliotis*, since in the latter the rudiments of the renal cavities and of their apertures are obvious only after the first half of torsion, although the mesoderm from which the kidneys are formed undergoes 180° torsion. It may be noted that Drummond repeats Haller's erroneous statement that there is only one renal organ in *Haliotis*.

First ctenidial rudiment. The ctenidial and osphradial rudiment of the final left side alone is developed in the veliger. At the 7th day it is a thickened epithelial ridge in the roof of the pallial cavity to the left side of the anus but posterior dorsal to the right eye. In sections the branchial ridge is seen thickly clothed with long cilia, which, even in the oldest veliger, is a simple small ciliated band in the roof of the pallial cavity (fig. 35, Plate 27 and fig. 18, Plate 23). This ctenidial rudiment remains a simple ciliated band for about a week.

A small part of the mantle prominence, which bears the ctenidial rudiment, has shorter cilia and is the osphradial rudiment of the definitive left side. The position of this rudiment relative to the branchial ganglion is shown in the transverse section of an early post-veliger in fig. 36, Plate 27.

First hypobranchial gland. The final left hypobranchial gland develops in the roof of the respiratory chamber of the late veliger. It is very small in sections of 12-day-old larvae with reduced velum, and is situated dorsally between the rectum and the first ctenidial rudiment (fig. 46D; fig. 36, Plate 27). Already this gland has large mucous cells and small ciliated cells.

Digestive System

The description of the pre-torsional veliger includes an account of the development of the primitive gut and its flexure (figs. 41, 42 and 43; figs. 15 and 15*a*, Plate 23).

After the first half of torsion, in veligers 2 days old, the stomodaeal invagination is elongated into the foregut, which now communicates with the short oesophagus. The latter, like the primitive stomach, the digestive gland rudiment and the primitive intestine, has indistinct limits. The digestive gland lies mainly on the left side of the visceral dome, with a dorsal conical process pointing anteriorly (figs. 26 and 27, Plate 25; figs. 28 and 29, Plate 26). At this stage it has only one stomach orifice, which is to the left side of the primitive stomach (fig. 16, Plate 23). In the late veligers, which can retract completely into the shell, the digestive gland is able to change its shape considerably to fit in with the other organs when they are contracted. At 60 hr. the two anteriorly directed digestive gland processes are in ventral position, so that there is room in the dorsal part of the shell for accommodation of the velum and developing sense organs (figs. 44 and 45*a*). In contracted specimens at this stage there is a groove between the right ventral part of the digestive gland and right dorsal pallial cavity.

In veligers a week old the intestine has elongated, the intestinal cells are now smaller and have acquired cilia. The anus opens into the most posterior part of the pallial cavity (fig. 17, Plate 23). During the 2nd week the intestine is further elongated and is thrown into two short loops so that it can be accommodated in the dorsal part of the visceral hump. The anus still opens on the right side of the body as it did immediately after the first half of torsion, but the pallial cavity is now extended considerably on the dorsal side of the anus (fig. 18, Plate 23 and fig. 33, Plate 27).

In the oldest veligers the larval stomach has enlarged so that it reaches the extreme posterior end of the body (fig. 18, Plate 23).

The rudiment of the radular caecum is first seen after the first phase of torsion, in veligers about 40 hr. old. In this respect *Haliotis* differs from *Paludina* (Drummond 1902) and *Patella* (Smith 1935), in which it is already obvious pre-torsionally. This caecum arises as a simple ventral diverticulum of the foregut (fig. 44*b*). During the succeeding days it enlarges until, in 5-day veligers, it has become the radular sheath in which the radular ribbon is secreted by the epithelium at the extremity of this sheath. At 7 days the epithelium has secreted several rows of teeth and, as in *Patella* before the end of metamorphosis (Smith 1935), there is a central tooth in each row. In the early stages of metamorphosis in *Haliotis*, however, there are three lateral teeth on either side of it (fig. 33, Plate 27) instead of one as in *Patella*. Before the velum has disappeared the radular ribbon begins to function. It appears to catch up loose diatoms, etc., since these are found in sections through the stomach. There is no evidence of fragmentation of seaweed at this stage.

Nervous System

The development of the nervous system was followed from transverse sections and from six reconstructions of the nervous system and related digestive system, which were removed from the wooden reconstructions of whole larvae of different ages.

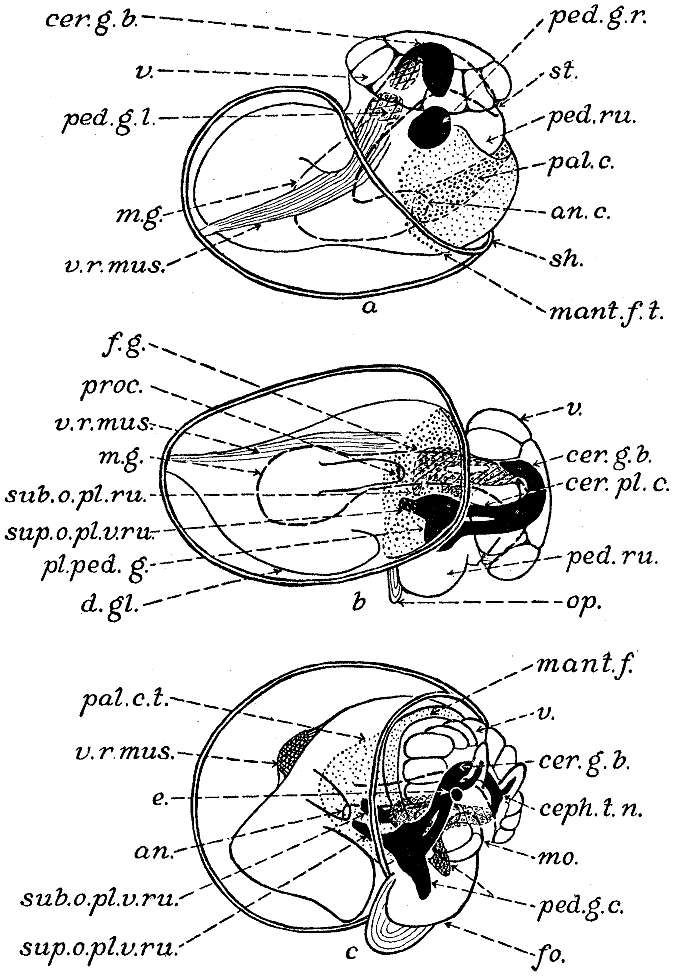

FIG. 50—Diagrams to show the development of the nervous system. Right side views from whole mounts and reconstructions. Nervous system indicated in black for right side and cross-hatched with circles for left side. Size of nervous system somewhat exaggerated in *a* and *b*. Pallial cavity stippled. *a*, Pre-torsional veliger; cerebropedal nerve ring almost delaminated. *b*, Veliger immediately after 90° torsion. Rudiments of cerebral, pedal and pleural ganglia are shown and pleuro-visceral processes are very rudimentary. *c*, Veliger 3 days old. Optic and tentacular nerves; pedal ganglia have begun elongation to pedal cords; fusion of pleural and pedal ganglia; right pleuro-visceral process short, left one already sub-oesophageal.

It has already been shown that, in the pre-torsional stage, the cerebral ganglia alone are delaminated and the pedal ganglia are in process of delamination (p. 231). The rudiments of the pleural ganglia are first noticed before the pelagic half of torsion is completed. They form a collection of sinking ectoderm nuclei situated dorsally to the pedal ganglion rudiments, but on either side of the head near the most lateral parts of the mantle fold (fig. 31, Plate 26). Before the end of the 2nd day after fertiliza-

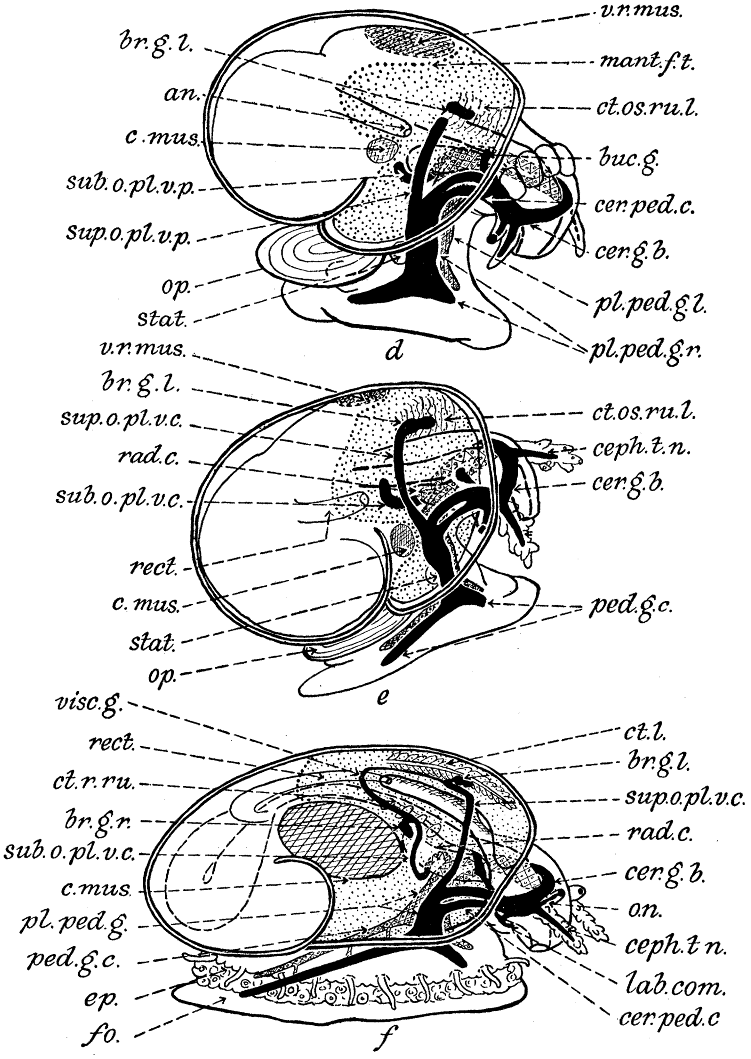

FIG. 51—Continuation of diagrams to show development of the nervous system. (For simplification the labial commissure is omitted.) *d*, Oldest stage with vestiges of velum (12 days); one branchial ganglion, definitive left, in dorsal part of pallial roof but not yet united to supra-oesophageal pleuro-visceral cord. Rudiment of definitive left osphradium and ctenidium indicated near branchial ganglion. *e*, Post-veliger soon after loss of velum (14 days); supra-oesophageal pleuro-visceral cord now united with its branchial ganglion. *f*, Post-veliger at 2 months old; metamorphosis complete; definitive right ctenidium developing and giving bilateral symmetry of pallial complex; sub-oesophageal pleuro-visceral cord has acquired a branchial ganglion; visceral part of the pleuro-visceral loop has developed.

tion the pleural ganglia are delaminated. They lie close to the pedal ganglia and from this early period they are fused to form the pleuro-pedal nerve mass. The cerebro-pedal and cerebro-pleural connectives are formed at the same time by the migration of the nerve cells and fibres to make the anterior nerve ring (fig. 50*b*; fig. 32, Plate 26).

In *Haliotis*, unlike *Patella* (Smith 1935) and *Paludina* (Drummond 1902), it is impossible to distinguish precisely the limits of the ganglia because the nerve cells spread on to the nerve cords in primitive fashion, as in the Amphineura.

Towards the end of the second day of development the rudiments of the pleuro-visceral cords are brief outgrowths from the pleural ganglia delaminated from the ectoderm of the deepest part of the pallial cavity (figs. 28 and 29, Plate 26; fig. 50*c*). The process of the right ganglion, the definitive supra-oesophageal, is short, and is at the right side of the oesophagus. The process of the left pleural ganglion, the final infra-oesophageal, is slightly longer and is already ventral to the oesophagus, and its extremity points to the right, towards the ventral part of the pallial cavity, which is on the right side of the body after pelagic 90° torsion. Thus there is already an indication of the influence of the 90° torsion on the nervous system, but it is so far obvious only in the infra-oesophageal visceral process. The ectoderm overlying this process of the left pleural ganglion was on the left side of the body before torsion began, but at the time of delamination it is ventral in position (fig. 50*b*).

In older veligers the visceral processes consist of nerve cells surrounding nerve fibres (fig. 34, Plate 27). During the 7th and 8th day of development one branchial ganglion, the supra-oesophageal, which in the adult belongs to the topographical left side, is initiated by a collection of nerve cells in the roof of the pallial cavity on the dorsal side of the body (fig. 51*d*; fig. 35, Plate 27). It innervates the first ctenidial rudiment, which is merely a ciliated mantle ridge at this stage. This branchial ganglion connects with the supra-oesophageal visceral nerve cord when the velum has almost disintegrated, at an age varying from 9 to 14 days (fig. 51*e*). At this latter time the supra-oesophageal cord is anterior to the sub-oesophageal cord and passes round the right side of the oesophagus to unite with the dorsal branchial ganglion. There is an enlargement of this ganglion to innervate the osphradial rudiment nearby (fig. 36, Plate 27). The supra-oesophageal pleuro-visceral cord now ends at the branchial ganglion (fig. 51*e*). At its origin from the left pleural ganglion the sub-oesophageal visceral cord is approximated to the posterior end of the larval retractor muscle. It passes, anteriorly to the developing columellar muscle, beneath the oesophagus and terminates on the right side of the pallial cavity (fig. 34, Plate 27). This pleuro-visceral process has now almost post-torsional streptoneury, but there is yet no trace of the rudiment of the final right ctenidium with its branchial ganglion. This, together with the remainder of the pleuro-visceral loop, develops with the post-veliger expansion of the pallial cavity on the right side of the anus and posteriorly (p. 258).

The labial commissure is derived, during the late veliger stage, from ventral processes which grow out from the cerebral ganglia. The buccal ganglia, which also develop before the velum disappears, appear to arise as outgrowths of the labial processes of the cerebral ganglia. They can be seen in the angle between the oesophagus and the radular diverticulum (fig. 33, Plate 27; fig. 51*d* and *f*). The nucleated sheath of the buccal ganglia is continuous with that of the cerebral ganglia. They stain more readily with cotton red or with borax carmine than do the cells of the neighbouring foregut wall.

In this respect *Haliotis* exhibits another primitive feature, for the buccal ganglia of *Acanthochiton* (Hammersten and Runnström 1925) develop in this manner. In *Patella vulgata*, however, they arise from local thickenings of the foregut wall (Smith 1935). In *Paludina* (Drummond 1902) all the ganglia arise separately from the ectoderm and are connected secondarily by the growing out of nerve fibres. In *Haliotis*, even in the adult, the ganglia are scarcely distinguishable from the commissures and connectives because all are clothed with nerve cells.

The cephalic tentacles, eyes and statocysts (fig. 44*b*) are innervated by nerves which develop from the cerebral ganglia during the veliger stage (fig. 35, Plate 27; fig. 51). These nerves are described with the sense organs.

Beginning during the 3rd day, the pedal ganglia are gradually prolonged into long posterior and shorter anterior paired processes (fig. 50*c*). The posterior ones lie side by side and finally elongate into cord-like pedal ganglia (fig. 51). The elongation of the pedal nerve ganglia is a primitive condition, which is found in other members of the Archaeogastropoda.

Post-Veliger Development

The final phase of metamorphosis begins at the age of about 12 days and is completed at about 2 months. In *Patella vulgata*, however, metamorphosis appears to be completed earlier, during the 3rd week of development (Smith 1935).

At the beginning of this phase in *Haliotis* the velum has gone and the creeping habit has already been established for some days. The shell is still dome-shaped but, during creeping, it has a list towards the left side and dextral coiling has begun. The larva is now similar to *Trochus* and one might imagine it developing into an adult with a tall spiral shell and a *Helix* method of retraction. Instead, during post-veliger development, it acquires a limpet-like clinging habit and the shell spiral becomes flattened into an ear-shape.

Foot and Operculum

During early post-veliger life the foot becomes extensive and the plantar surface is relatively larger. By the end of the 3rd week after fertilization the larva loses the early plantigrade method of retraction which begins by folding the posterior part of the pedal sole against the anterior part preparatory to withdrawing into the shell and closing its aperture by the operculum, as in *Helix*. At this time retraction is accomplished by the foot clinging to the rock, using the pedal muscles, together with the related columellar muscle, so that the shell aperture is approximated as closely as possible to the rock surface. This function of the columellar muscle probably helps in producing the flattening of the shell, which is a characteristic feature of the late metamorphosis of *Haliotis* (figs. 46E, F and G).

Although the operculum ceases to grow and to function after the velum is thrown off, it was present in the post-larva 44 days old, when it was still uncalcified. Its disappearance was not observed, but it is probably lost when the shell is pulled closely to the rock by the columellar muscle. In the metamorphosed specimen at 2 months old it was missing.

Sense Organs

The epipodial tentacles arise considerably later than the cephalic tentacles and the development of the characteristic epipodial fringe of sensory structures is confined to the post-veliger stage.

The dorso-lateral protuberance, which is first seen at the time the velum is disintegrating on the right side of the foot, is then the opercular support. Figs. 11 and 14 on Plate 22 show that, in early post-veligers, the first epipodial tentacle arises on this opercular process. It is, therefore, impossible to agree with the statement of Boutan (1899) that in *Haliotis* epipodial tentacles are present immediately the larva begins to creep as in *Fissurella*, and that the epipodium has a pallial origin.

During the 3rd week additional tentacles develop on the dorsal enlargements, which are now on both sides of the foot (fig. 20, Plate 24). According to Robert (1902) they develop from the anterior end backwards in *Trochus*, but the reverse is true for *Haliotis*.

The epipodial tentacles develop papillae, some of which bear cells with stiff threads similar to those of the cephalic tentacles and, like the latter, these tentacles are pale green in living larvae. In the 44-day-old specimen there were ten tentacles on each side of the epipodium (fig. 48F).

In the larva 23 days old and in that 44 days old there is a large epipodial tubercle posterior to the right eye (fig. 20, Plate 24; fig. 48F). This possesses cilia, which are very active in the living state. A similar process was also seen in *Trochus* by Robert, who called it a sensory structure. It is possible that it may produce an outgoing current from the pallial cavity to the right side of the head for the removal of used respiratory water. Water enters under the left side of the shell, owing to a current produced by the single ctenidium of the left side. In the 2 months old larva, in which the pallial cleft and one shell perforation have developed for the exit of water, this organ has merged into the epipodial fringe and the eye peduncle has outgrown it.

Muscles

At the beginning of post-veliger life the veliger head retractor muscle and the columellar muscle are situated on the antero-left and postero-right sides of the visceral hump respectively, and are approximately equal in size (p. 240; fig. 19, Plate 24; fig. 34, Plate 27). The functional significance of the velum retractor muscle as a head retractor is now lost and it acquires the new function of attaching the developing left margin of the mantle fold to the shell (fig. 46E). As the pallial cavity is gradually displaced to the left side during hypertrophy of the columellar muscle, the velum retractor muscle migrates from the dorsal position shown in fig. 17 on Plate 23 to the extreme left side of the shell (fig. 19, Plate 24; fig. 46E). In the 2 months old larva, as shown in transverse section in fig. 38, Plate 27, it is insignificant in comparison with the columellar muscle.

The columellar muscle gradually increases in size and importance during metamorphosis. In the late veliger it has the same arrangement as the columellar muscle of gastropods with typical dextrally coiled shells, like *Helix*, for it is attached to the shell in the same position as the rudiment of a columella and runs from the right side of the visceral dome under the right margin of the mantle cavity into the foot (fig. 34, Plate 27). After the 2nd week, however, it ceases to retract the cephalo-pedal mass and operculum into the shell and functions during adhesion and creeping. In post-veligers the columella does not develop, but the shell attachment of the columellar muscle migrates anteriorly, so that it approaches the centre of the last whorl of the shell. It occupies an increasingly larger area on the shell (fig. 52). After the 2nd week of development muscle fibres are added rapidly to the columellar muscle so that it becomes a stout central pillar adhering to the pedal musculature. The gradual change in size and position of the columellar muscle is shown in figs. 19 to 22, Plate 24 and fig. 46). Smith's statement that, in *Patella*, the ability to retract into the shell is lost during metamorphosis because the larval retractor muscle disappears obviously does not apply to *Haliotis*. In this case it is lost because the columellar muscle, which functions in the early veliger as a foot retractor, hypertrophies and its function is highly modified.

The elaborate buccal musculature develops during late metamorphosis from the mesenchyme cells surrounding the foregut (fig. 33, *mus.c.ru.*, Plate 27). In the larva 23 days old the buccal muscles are beginning to link up with the pedal musculature. This connexion is well seen in sections of the 2 months old specimen, in which the most powerful retractor of the odontophore has its origin in the junction of the columellar and foot muscles and its insertion on the posterior end of the odontophore.

Mantle and Shell

At the beginning of the post-veliger metamorphosis the right mantle fold has grown so considerably that, in living specimens, it extends some distance in advance of the shell and it is reflected posteriorly on the right side of the shell umbo (figs. 11 and 13, Plate 22). It has already been shown on p. 242 that this fold is responsible for the foundation of dextral coiling and the tilt of the shell to the left side. During the end of the 2nd week and throughout the 3rd week this fold proliferates shell so rapidly on the right side that it is far in advance of shell growth on the left side, which is now rolled inwards (fig. 14, Plate 22; fig. 46F and G). The posterior right side of this asymmetrical peristome is attached to the right side of the umbo (figs. 19 and 20, Plate 24). Fig. 52 shows diagrammatically the progressive shell increments, which are seen in the larvae from the beginning of metamorphosis. Boutan (1899) described the protrusion of the mantle on the right side of the shell of post-veligers, but he was unaware that the mantle fold is much larger on the right side from an early veliger stage. This is a consequence of the pelagic half of torsion, which leaves the pallial cavity on the right side. The newly added shell is tinged with pink and has radial ridges and a marked growth ridge beyond the smooth veliger shell (fig. 13, Plate 22).

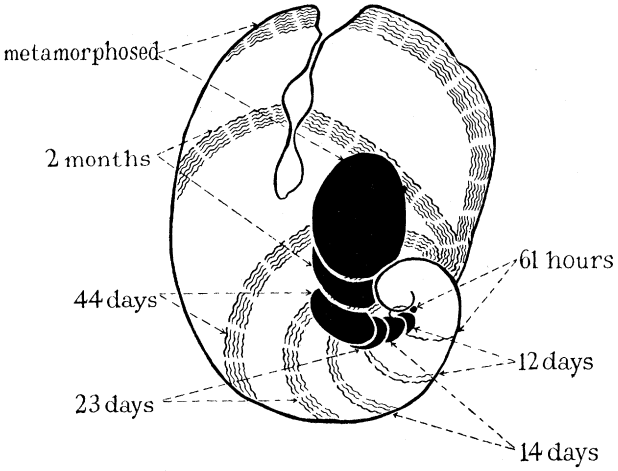

Fig. 52—Diagram to show changes in the shell during metamorphosis. Each pair of converging lines indicates margin of shell and corresponding position of columellar muscle for each stage. Margin of shell is shown by addition of a waved line for increment of shell for each stage. Owing to rapid shell increase on right side, larval shell of 61 hr. lies on its left side in older stages.

In the two larvae which attained 44 days the margin of the shell was still entire, but a small cleft in the mantle on right side of the head had appeared. One of these specimens was fixed, but the other had formed a shell slit corresponding with the mantle cleft, and later, by approximation of the mantle margins, the slit was transformed into the first shell hole, which is shown in the figure of the metamorphosed specimen at 2 months old (fig. 21, Plate 24). At this time the mantle cleft was deeper and had three pallial tentacles.

In the last phase of metamorphosis a mantle pocket develops to cover over the rudiment of the small visceral diverticulum, which borders the right side of the columellar muscle and is shown in fig. 21 on Plate 24. In the adult this is an enlarged conical process accommodating part of the digestive gland and gonad and compensating for the reduced visceral spire (fig. 22, Plate 24).

Post-torsional Displacement of the Pallial Cavity

The rotation of the pallial cavity through 180° is complete by the time the velum is lost and an account of this is given on pp. 243 and 244. From the mid-dorsal position in the earliest post-veligers (fig. 19, Plate 24; fig. 36, Plate 27), the pallial cavity undergoes a further gradual movement to the left side. Stages in this post-torsional migration are shown in figs. 46 and 48. This displacement is produced by a continuation of differential growth, which appears to be due to hypertrophy of the columellar muscle and its migration towards a central position. Gradual flattening of the shell, which occurs at the same time, may be a contributory cause of the displacement of the pallial cavity (fig. 46). In the metamorphosed specimen 2 months old this cavity is on the extreme left side of the body, which is the position characteristic of the adult (fig. 38, Plate 27; figs. 21 and 22, Plate 24).

Completion of the Pallial Complex

At the close of veliger development the pallial complex comprises the renal organs, the rudiments of one ctenidium, osphradium and hypobranchial gland and the anus, which is situated on the extreme left side of the mid-dorsal pallial cavity (fig. 36, Plate 27).

At the beginning of post-veliger development the pallial cavity has deepened posteriorly and expanded considerably to the left of the anus. In this region is situated the first ctenidial rudiment, which is still a simple ciliated ridge containing the branchial ganglion, overlying a blood space (fig. 19, Plate 24; fig. 36, Plate 27). Immediately ventral to the ctenidial rudiment, on the floor of the mantle cavity, is a corresponding ciliated tegumentary track, which is not, however, a raised band (fig. 36, Plate 27). This may help in maintaining the respiratory current of the deepening pallial cavity. Although the first ctenidial rudiment and its ganglion are now on the left side of the oesophagus (fig. 19, Plate 24), they have taken part only in the last quarter of the 180° torsion of the pallial cavity. In the specimen 23 days old tegumentary ridges have become prominent and form two folds covered with long cilia, which are the rudiments of the ctenidial lamellae. At this time this first formed ctenidium is already on the left side of the body, the displacement of the pallial cavity to the left side having begun. In the specimen 44 days old it has six ctenidial lamellae on either side of the ridge, which now forms the rachis of the ctenidium (fig. 20, Plate 24; fig. 48F). The terminal part bears the osphradium on its proximal border. The topographical left hypobranchial gland lies between the posterior end of the ctenidium and the rectum.

Until the post-veligers are about a month old there is room in the pallial cavity on the right side of the rectum only for the aperture of the right renal organ (fig. 19, Plate 24). In the specimen 44 days old the ciliated band rudiment of the final right ctenidium is present in the now expanding region between the rectum and the columellar muscle (fig. 20, Plate 24). The 2 months old specimen shows much greater expansion of the pallial cavity on the right side of the rectum so that the latter is placed centrally in the cavity. The ctenidium of this side has begun to form lamellae (fig. 46G; fig. 21, Plate 24; fig. 38, Plate 27).

The final right hypobranchial gland also develops when the posterior right side of the pallial cavity has expanded and at this time the final left one is considerably enlarged. The two glands differ much in size in the adult, but Haller (1886) denies the existence of the right hypobranchial gland. The ctenidium of this side is also somewhat smaller in the adult than the first formed ctenidium, but both ctenidia are bipectinate, unlike those of *Scissurella*.

The pallial complex in *Haliotis* is shown by this investigation to be complete only at the end of 2 months of development.

In the earliest post-veligers the two renal organs are equal in size and their cavities have enlarged. In the specimen 23 days old the one on the right of the rectum is slightly larger than the one on the left (fig. 20, Plate 24), as in the post-larval *Patella* (Smith 1935). The left one, which has a simple cavity, is a little anterior to the right one. The latter now has its epithelium thrown into a few folds, which become very complicated tubules in the adult (fig. 37, Plate 27). In the adult, the two renal organs are of very unequal size (figs. 21 and 22, Plate 24). The large one on the right is excretory and serves also for passage of the genital products through its cavity and orifice to the pallial cavity.

The heart is first noticed in living early post-veligers by its pulsation in the neighbourhood of the rectum, slightly posterior to the renal organs (fig. 14, Plate 22). It develops during early metamorphosis by ingrowth of the cells of the pericardial rudiment, which it has been shown arises from the solid pericardial rudiment attaching the two renal rudiments (pp. 232 and 246). The ingrowing cells of the pericardial wall become arranged to envelop the rectum and form the ventricle, as in lamellibranchs.

Some of the cells of the heart rudiment connect with the efferent ctenidial vessel of the final left ctenidium and form the definitive left auricle. Fig. 49*c*, which is part of a transverse section of the 2 months old metamorphosed specimen, shows the left auricle in the region of its ventricular aperture and the anterior part of the right auricle. It is clear from an examination of other sections in this series that the right auricle is about one-quarter the size of the left auricle.

Digestive System

In the early post-veligers the short cylindrical snout, with its vertical mouth, is developed (fig. 48E; fig. 14, Plate 22). The laterally placed chitinous jaws are already forming from the aggregation of perpendicular rods, which are secreted by the specialized columnar cells internal to the buccal opening. The jaws and lips move laterally and the buccal cavity has acquired dorso-lateral ciliated pockets. The spherical rudiment of the odontophore apparatus, which is shown in fig. 19, Plate 24, can be seen, in the transparent living specimens, to move rhythmically in antero-posterior direction. It has already been shown on p. 253 that the main retractor muscle of this apparatus has its origin in the anterior part of the columellar and pedal muscular mass. The rhythmic movements of the odontophore may help the circulation, even at this early stage.

The two dorsal supporting cartilages and the controlling muscles of the odontophore apparatus begin to develop, during the late veliger, as derivatives of the mesoderm in the region ventral to the buccal cavity (fig. 33, *mus.c.ru.*, Plate 27). The odontophore cartilages enlarge as the radula is used more and more, but even in the 2 months old post-larva the extra cartilages, found in the adult, are not developed.

At the end of the first fortnight of development the radula can be protracted and retracted by the movements of the muscular odontophore apparatus. In post-veligers 3 weeks old the distal end of the radula can be used for rasping off fragments of seaweed. Evidence of this is provided by fragments of the more delicate red seaweeds which were found in sections passing through the stomach. At this time there are nine large teeth and five minute marginals on either side of them for every row. The teeth increase in size and, after 2 months of development, there are five lateral teeth on each side of the central tooth and the marginals have increased in number, so that the typical radula of the adult is fully developed (fig. 38, Plate 27). In *Patella* the radula of the adult becomes more specialized than in that of *Haliotis* and the median tooth is lost (Smith 1935).

In the earliest post-veligers the stomach is larger and has expanded to the left side, so that it now occupies a considerable part of the posterior end of the visceral hump. The ventral digestive gland is pushed somewhat anteriorly by the enlarged stomach and it is still bilobed as in the veliger (fig. 19, Plate 24).

During the 3rd week the digestive gland enlarges. This plastic gland is pushed considerably to the right by development of the stomach and enlargement of the oesophagus near it to form the crop. It is now obvious, from a comparison of figs. 19–22 on Plate 24, that the region of the digestive gland, which lies posterior to the columellar muscle in the earliest post-veliger, forms the reduced visceral coil of the adult. A new diverticulum of the digestive gland, with a separate orifice from the stomach, develops towards the close of metamorphosis, on the dorsal side of the visceral hump. It lies to the right side of the stomach and developing crop and is that lobe of the digestive gland which surrounds the left side of the columellar muscle of the adult (fig. 22, *d.gl.l.l.*, Plate 24).

During the 3rd week there is considerable elongation of the intestine so that another loop forms (fig. 20, Plate 24). An elongated portion of the rectum is suspended from the dorsal wall of the pallial cavity, which has now deepened a great deal posteriorly (figs. 19 and 20, Plate 24; fig. 46). The cilia of the rectum are now very long. While the columellar muscle is developing and the pallial cavity is migrating in the late veligers, the anus gradually travels from the right side of the body to a dorsal position. In the early post-veligers it is mid-dorsal in position (fig. 19, Plate 24) but in the 23-day post-veliger it is already displaced to the dorsal left side by the commencement of hypertrophy of the columellar muscle (fig. 46F). At this time the intestine becomes still more elongated and a loop of it is accommodated near the left margin of the columellar muscle (figs. 20–22, Plate 24).

The small stomach caecum of the adult develops very late and is first seen in a specimen 2·5 mm. long. It is contained in the reduced visceral spire.

Nervous System

Development of the nervous system in the veliger is described on p. 248. Early in post-veliger life the supra-oesophageal pleuro-visceral cord is displaced somewhat to the left side by the enlarging columellar muscle. This cord now passes dorsally to the gut and terminates in the single branchial ganglion, which is now on the left side of the pallial cavity (fig. 51*e*). At this time the pallial cavity has completed 180° torsion and the proximal halves of the pleuro-visceral cords show the streptoneurous condition, but the typical figure of eight made by these cords in the adult is not yet complete.

In the 23-day post-veliger there is still only one branchial ganglion, but the pleural ganglia have processes, which are the rudiments of the external pallial nerves. These were clearly seen in the reconstruction. Since they develop after 180° torsion is accomplished, the external pallial nerves are uncrossed. Dialyneury must be established later, but it was not discovered in the sections of the 2 months old specimen.

At 44 days after fertilization the rudiment of the second ctenidium, that of the post-torsional right side, is obvious and the branchial ganglion, which innervates it, is initiated from the integument on the extreme right margin of the pallial cavity (fig. 38, Plate 27). Like the left one, it is a branchial and osphradial centre. In the sections of a specimen 2 months old there is now a slender union of the final right branchial ganglion with the infra-oesophageal visceral cord (fig. 51*f*). The pleuro-visceral cords no longer terminate at the branchial ganglion region, for there are short posterior prolongations immediately beneath the epithelium of the floor of the pallial cavity which unite to form the short visceral ganglion portion of the loop. The lateral branchial ganglia are now unlike typical parietal ganglia, because they are placed on brief off-shoots of the visceral cords. As in the adult, there is little enlargement of the single visceral ganglion. This posterior part of the visceral loop is situated dorsally to most of the digestive system, although that part of the rectum which is attached to the roof of the pallial cavity is bent over dorsally to the visceral ganglion region (fig. 37, Plate 27).

The pedal ganglion cords steadily increase in length as the foot elongates and, in the metamorphosed post-larva, the two posterior cords are connected by a few nerve cells making fine irregular transverse commissures (fig. 51*f*). In addition to minute branches in the foot there are dorsal strands which innervate the developing epipodium.

The investigation shows that parts of the nervous system of the adult are added gradually throughout the whole period of metamorphosis and the nervous system is completely established only after a developmental period of about 2 months.

DISCUSSION

Asymmetrical Coiling of the Visceral Hump

With the one exception of ANDERSEN (1924), all the more recent views concerning the evolution of the asymmetry of gastropods are concordant in the following hypotheses: symmetrical exogastric coiling of the shell began before the onset of torsion and was independent of it; the pallial cavity was transferred, during torsion, from a posterior into an anterior position, before shell growth began to be asymmetrical; because of the loss of equilibrium when creeping began, the heavy visceral hump fell to one side and pressed upon the foot so that shell growth was retarded on that side and sinistral or dextral rolling resulted. It is presumed by BOUTAN (1899–1919) and by NAEF (1913 and 1926) that in dextral forms the left side of the visceral hump is the heavier and in sinistral forms the lighter, but this remains to be proved.

The conclusions arrived at from the investigations of the development of *Haliotis* appear to throw new light on these suppositions.

In *Haliotis* the pre-torsional shell is symmetrical and has a rudiment of nautiloid coiling before torsion begins; since 90°, only, of rotation occurs in the pelagic period, the shell is then only half endogastric and the pallial cavity is transferred only as far as the right side. With regard to the initiation of dextral coiling in *Haliotis* two factors appear to be responsible.

First, as a consequence of the incompleteness of the early torsional process, the pallial fold remains on the right side of the body for some days and therefore the new part of the shell, which is proliferated from it on this side of the body, is always in advance of that on the left side. The shell thus becomes asymmetrical and such a shell must inevitably lean towards the left side during creeping.

Secondly, it has been shown that, at the time the first phase of torsion has occurred, the main bulk of the visceral mass, comprising the velum retractor muscle and the digestive gland, lies on the left side, whereas the pallial cavity is on the right side. Thus it appears evident that the left side must be heavier.

Consequently the side to which the visceral mass falls during early creeping is determined in *Haliotis* by these two mechanical factors and dextral coiling is the result.

During late metamorphosis the pallial cavity is displaced to the left side by hypertrophy of the columellar muscle, but the addition of new shell is still greater on the right than on the left side, owing to the activity of the extensive right mantle fold.

Theories of Gastropod Torsion

The hypotheses which have been formulated to explain the evolution of the torsion process are numerous. SIMROTH (1896–1907), BOUTAN (1899, 1902, 1919), ROBERT (1902) and DRUMMOND (1902) have summarized the older theories, therefore only the salient points concerned in the recent theories will be mentioned.

Since ANDERSEN (1924) stands alone among the modern theorists, his view may be stated separately. From his work on the development of *Paludina* he concludes that larval torsion does not bring about streptoneury. He states that the larva develops an untwisted visceral loop, which is gradually twisted into a figure of eight, due entirely to the dextral spiral twist of the visceral hump during late metamorphosis. To accomplish the streptoneury, two and a half spiral windings must be completed. In ANDERSEN's view there is stretching and overgrowth on the right side, and the left side is not inverted, as has been represented by other writers. His description of the nervous system does not, however, agree with that of DRUMMOND (1902). The evidence from the development of *Haliotis* does not help to substantiate his conclusions.

The larvae of *Haliotis*, as of *Patella* (SMITH 1935), do not develop a complete untwisted visceral loop. In this connexion SMITH (p. 116) says of *Patella*, "It is of particular importance to note that, though the pedal and pleural ganglia begin to develop before the torsion process is complete, it is not until afterwards that the visceral and pleural ganglia are formed (delaminated), so that the twist in the visceral loop is not produced during the torsional rotation. It may be that although the visceral ganglia are not formed at this time, yet the ectoderm to which they owe their origin has already become differentiated physiologically." In *Haliotis* the pleuro-visceral loop originates as processes of the pleural ganglia, which are delaminated from the ectoderm of the twisted "neck" region soon after it has been involved in the first half of torsion. The visceral portion of the loop is formed from the ectoderm of the floor of the pallial cavity only at the final phase of metamorphosis. The stretching and overgrowth of the right side of the pallial cavity and its organs, to which ANDERSEN refers, appears to take place in *Haliotis*, not after the formation of the complete pleuro-visceral loop, but during its development.

Other theorists have been greatly influenced by the work of BOUTAN (1886–1919). In his view, the varying degrees to which streptoneury or euthyneury are exhibited depends on the relative amount of foot and shell development in the early veliger. If both organs are well developed at the same time, they interfere with one another and the conflict of pressure brings about torsion and complete streptoneury. Little development of one of these organs results in euthyneurous types, brought about by a process which he calls "larval deviation" rather than by a process of detorsion. Considerable importance has been attached by theorists to his claim to have observed 180° torsion to take place in 2 or 3 min. in *Acmaea* and almost as rapidly in *Haliotis*. MURAYAMA (1935) assumes that 180° is likewise involved in the rapid pelagic rotation of *H. gigantea*. In *Trochus* and in *Patella vulgata*, ROBERT (1902) and SMITH (1935), respectively, state that torsion is completed in the early pelagic rotation.

From the preceding account of the development of *Haliotis tuberculata* it is obvious that BOUTAN's statement is not fully justified for this species. In *Haliotis* a rapid torsion does actually take place in early pelagic life, but it involves only 90° rotation and the further 90° of revolution are completed gradually after many days have elapsed.

From the work of BOUTAN on *Acmaea* (1899) and DRUMMOND (1902) and ERLANGER

(1891) on *Paludina*, Naef (1913) concluded that slow achievement of torsion by growth processes is a secondary modification found only in less primitive gastropods. There is obvious discrepancy between Naef's conclusion and the ontogenetic facts for *Haliotis*, for in this undoubtedly primitive member of the Prosobranchia, the accomplishment of complete torsion takes about 2 weeks.

In the light of the existing knowledge of gastropods, the theories of torsion which have been favourably received have sought for the cause of the twist during the adult life of a hypothetical primitive mollusc (Bütschli 1887, Lang 1891, Plate 1896, Fleure 1902 and Naef 1913). Others are of opinion that torsion was not primarily developed in the interest of the adult, but is a larval adaptation; those who seek for ontogenetic evidence are Boutan (1899), Robert (1902), Pelseneer (1911), Garstang (1928). How far ontogenetic facts can be used in relation to phylogenetic theory is problematical. If only from the point of view of their possible bearing on the existing theoretical views, such facts may be enlightening, for as Drummond (1902) remarked, knowledge of the organogenesis of gastropods is so meagre, that a study of the development of even a single type is helpful.

From the embryological point of view it has been shown by Crampton (1894) that asymmetry is foreshadowed in the cleavage of the ovum, since in sinistral forms there is a complete reversal of the cleavage planes as compared with dextral gastropods. Moreover, it has been shown by Conklin for *Crepidula* (1897) and by Robert for *Trochus* (1902) that there is asymmetry at the time of gastrulation, after which process the right side is slightly larger than the left.

Thiele (1902), in his criticism of Boutan's view that torsion results from the conflict of growth of the developing foot and shell, supports the hypothesis that there must be asymmetry in some form before these organs are formed and therefore they can be only a secondary cause of torsion. Drummond (1902) states that unfortunately in *Paludina* torsion begins very early and is taking place at the same time as ano-pedal flexure, so that she can demonstrate only that the liver and the rudiment of the mantle cavity are never completely symmetrical.

The description of *Haliotis* development shows that the two mesoderm bands develop unequally, the rudiment of the shell develops somewhat to the right of the dorsal position and only later extends ventrally and to the left to make an almost bilaterally symmetrical cup. The velum retractor muscle develops on the right side, as in *Patella vulgata* (Smith 1935) and the "liver" rudiment occupies the left side of the visceral hump. In *Haliotis*, therefore, even more than in *Patella*, there is ample evidence that the veliger is already asymmetrical pre-torsionally.

Boutan (1899), Naef (1913, 1926) and Garstang (1928) find it difficult to conceive that a rotation of 180° is accomplished by a growth process alone and imagine that a certain amount of true twisting by muscular contractions must occur. Garstang suggests that the only mutation required to start torsion in a hypothetical larval ancestor is the development of asymmetrical retractor muscles. Torsion could be accomplished by a right-sided cephalic retractor, with a posterior attachment and a left-sided pedal retractor, with a more anterior attachment. It remains, in GARSTANG'S view, for further investigation to show if two such muscles, functioning more or less at right angles to one another, do actually exist when torsion begins.

In *Haliotis* (fig. 43; figs. 15 and 15*a*, Plate 23) as in *Patella* (SMITH 1935, figs. 11*a* and 11*b*) the velum retractor muscle develops on the right side. In *Haliotis* there is, moreover, an indication that ancestrally there may have been a pair of retractor muscles, but because of the asymmetrical development of the primitive gut on the pre-torsional left side, the retractor muscle of that side is arrested in development until creeping begins (fig. 25, Plate 25; fig. 44). Then it develops into the columellar muscle. The supposition of SMITH (1935), NAEF (1913, 1926), PELSENEER (1911) and others that the columellar muscle is homologous with the velum retractor muscle is therefore erroneous.

Although the developmental evidence in *Haliotis* lends support to SMITH'S view that the right side retractor muscle provides the main mechanical cause for the beginning of torsion, it neither supports his suggestion that this muscle was originally an unpaired dorsal one nor his statement that the complete 180° is involved in the pelagic rotation. It has been shown that 90°, only, is involved in this rapid rotation. The remainder of torsion appears to be caused mainly by the development of the columellar muscle, which is situated on the right side of the pallial cavity. By its gradual enlargement it suppresses the development of the pallial region on that side. With the antero-left migration of the columellar muscle and the velum retractor muscle the pallial region gradually expands and moves dorsally, so that the second phase of torsion is completed. The second half of torsion is, therefore, brought about by differential growth, which is an inevitable result of the first phase of torsion, after which the pallial cavity was situated on the right side of the body.

In addition to the 180° torsion, which is brought about during the first 2 weeks of development, continued migration of the pallial cavity to the left side takes place during the late development of *Haliotis*. This is due to hypertrophy and further migration of the columellar muscle and thus the spatial relations peculiar to the adult are produced.

It might be suggested with caution that, in opisthobranchs with a very reduced columellar muscle, the cause for completion of torsion is removed, but it is irrelevant here to discuss the probability of deviation or of detorsion in these forms.

Order of Formation of the Pallial Organs

The interpretations of the phenomenon of gastropod torsion have been based on the assumption that the pallial complex of the hypothetical ancestor is already constituted before torsion begins and that it is simply inverted during the process. In *Haliotis* and in *Patella* (SMITH 1935) this is not the case. In both genera the protodaeum and the solid mesoderm rudiments of the kidneys are the only representatives of the pallial complex when torsion begins. Even in *Paludina*, in which the developmental stages are abbreviated owing to viviparity, the single ctenidium and the visceral part of the pleuro-visceral loop do not develop until the late larval stage, after torsion is complete (DRUMMOND 1902).

During the second phase of torsion in *Haliotis* the first ctenidial rudiment, the definitive left, together with its branchial ganglion migrates with the antero-left migration of the pallial roof. The major portion of the pallial cavity, on the definitive left side of the rectum, grows and expands in a dorsal direction, but the topographical right region of the cavity does not begin to develop until after torsion is complete. Until this part of the pallial cavity enlarges there is no room for the topographical right ctenidium, which therefore arises in the last stage of development.

The zygobranchiate members of the Archaeogastropoda have the ctenidia placed on either side of the anal complex. These forms have in common a characteristic system of currents maintained by cilia. Fresh supplies of water pass to the ctenidia from around the shell margin; deoxygenated water and products of excretion invariably escape from the middle of the pallial cavity through a slit, a hole or series of holes, placed dorsally to the anal complex. GARSTANG (1928) explained that the palaeontological evidence in *Bellerophon* and the shell evidence in the recent forms *Pleurotomaria* and *Fissurella* show that the slit or hole never develops until the end of metamorphosis; thus *Fissurella* has added the metamorphosing young adult stage of *Emarginula* to its ontogeny. GARSTANG points out that this theory differs slightly from the Haeckelian hypothesis, according to which *Fissurella* and *Haliotis* would inherit all that the adult *Emarginula* had developed. In GARSTANG's view the time of divergence is different for different organs.

GARSTANG further suggests that since the shell outlet corresponds in position with the anus and renal openings, it is probably made by inhibition of mantle and consequently of shell growth, due to the stream of poisoned water. The mantle can only grow together again when out of the range of this current. In *Haliotis* the outgoing current is vertical and there is alternate splitting and closing of the mantle margin as the pallial cavity grows forwards. The description of the development of *Haliotis* shows that the first shell hole actually does appear at the close of metamorphosis and, moreover, the final right ctenidium develops only at about the same time. The "sanitary" arrangements during the intervening period after the formation of the first ctenidium may be presumed to resemble those of the members of the Archaeogastropoda, which have a single ctenidium supplied by fresh water from under the left shell margin. After use, the water passes away above the anus on the right side of the pallial cavity.

The fact that the topographical right ctenidium and the hypobranchial gland of that side, which secretes mucus to clean the respiratory chamber, do not appear until a month later than those organs of the definitive left side appears to be significant. Both ctenidia in *Haliotis* are bipectinate, whereas in *Scissurella* the definitive left one is monopectinate; in the adult *Haliotis*, as in *Pleurotomaria* and *Scissurella*, the definitive right ctenidium is invariably somewhat smaller than the left one, and this difference in size also applies to the hypobranchial glands.

Two equal-sized ctenidia are never present in prosobranchs with asymmetrically coiled shells. Since the gills are the latest organs to form in gastropods, it would be anticipated that the asymmetry would affect their development more than that of other organs. It is a generally accepted hypothesis that asymmetrical coiling of the shell and enclosed visceral mass produces pressure on one side of the pallial cavity, as a result of which the organs of this side are reduced or atrophied. This is substantiated by the order of development of the pallial organs of *Haliotis*. It is important to note that the situation of the pallial cavity, on the right side of the body for some days after the first phase of torsion, is the cause both of dextral coiling and of compression of the right side of the cavity.

The delayed development of the pallial organs of the right side in *Haliotis* foreshadows the complete disappearance of the organs of that side in forms like *Acmaea* and *Trochus* of the Archaeogastropoda and in the Mesogastropoda.

Summary

1. The development of *Haliotis*, which takes about 2 months, is described from living specimens, serial sections and reconstructions. Comparison is drawn with the development of *Patella*, *Trochus* and *Paludina*.

2. The trochophore has neither apical cilia nor a telotroch, but the veliger has transitory apical cilia. The larvae are mainly benthic after 2 days, although the velum persists for 2 weeks.

3. The formation of mesoderm resembles that process in *Patella*, but the mesoderm band of the right side is larger than that of the left side. Pre-torsionally the velum retractor muscle arises from this mesoderm band and is asymmetrically placed.

4. Asymmetry is also shown in the rudiments of the molluscan organs.

5. The asymmetrical velum retractor muscle is mainly responsible for the rapid first 90° of torsion. The rudiment of the operculum develops immediately before torsion begins and is probably a contributory cause of the beginning of rotation. Boutan and Murayama are shown to be mistaken in the hypothesis that 180° is involved in this pelagic rotation.

6. The second half of torsion of the pallial region is brought about slowly, by differential growth. The development and migration of the columellar muscle is mainly responsible for it.

7. Contrary to the general supposition concerning gastropod veligers, the velum retractor muscle does not become the columellar muscle. The latter develops from mesoderm cells of the pre-torsional left side, which are arrested in development until the early plantigrade stage. At the time the velum is lost, the two muscles are equal in size and bilaterally situated. During late metamorphosis the columellar muscle

hypertrophies and migrates to a central shell attachment, but the vestige of the velum retractor is an insignificant muscle on the left side.

8. After the first half of torsion, the pallial cavity remains on the right side for some days. Consequently the visceral mass is heavier on the left side and the pallial fold is responsible for rapid addition to the shell on the right side. The shell, therefore, leans to the left and dextral coiling begins.

9. Pre-torsionally the proctodaeum is the only representative of the pallial complex. The solid rudiments of the renal organs acquire cavities, reno-pericardial canals and renal apertures during the second phase of torsion. They become asymmetrical only during late metamorphosis.

10. The two ctenidia and the two hypobranchial glands develop at widely separated periods and, at the end of development, those of the topographical right side are smaller than those of the left side.

11. The definitive left branchial ganglion connects with the supra-oesophageal process of the right pleural ganglion in the veliger. The definitive right branchial ganglion connects with the infra-oesophageal process of the left pleural ganglion during late metamorphosis. The visceral ganglion region of the pleuro-visceral loop then develops. Its late development may account for its position in relation to the rectum differing from that of the Amphineura.

12. The external pallial nerves arise after the streptoneurous condition is established and are therefore untwisted.

13. Development of the sense organs is traced.

14. The digestive organs arise similarly to those of *Patella*, but the radula retains a more primitive character after metamorphosis.

15. The characters peculiar to *Haliotis* develop in the late plantigrade larva. Hypertrophy of the columellar muscle is accompanied by displacement of the pallial cavity to the left side and shell flattening. The ability to retract into the shell ceases, but the operculum does not fall off for some time after its function is lost. The cleft in the roof of the pallial fold is responsible for the formation of one shell perforation, at the close of metamorphosis. It provides for the increased respiration made possible by the addition of the second ctenidium.

16. The possible bearing of the ontogenetic facts upon phylogenetic theories is discussed.

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KEY TO LETTERING ON FIGURES

a.ao.	anterior aorta.	*br.g.r.*	post-torsional right branchial ganglion.
an.	anus.	*buc.cav.d.f.*	dorsal fold of buccal cavity.
an.c.	anal cell; position of anus.	*buc.g.*	buccal ganglion.
ap.c.	apical cell.	*c.c.v.*	cells cutting off velum.
ap.cil.	apical cilia.	*c.mus.*	columella muscle.
arch.	archenteron.	*c.mus.ru.*	rudiment of columellar muscle.
aur.l.	left auricle.	*ceph.t.*	cephalic tentacle.
aur.r.	right auricle.	*ceph.t.n.*	cephalic tentacle nerve.
bl.	blastopore region.	*ceph.t.p.*	cephalic tentacle papilla.
br.g.l.	post-torsional left branchial ganglion.	*cer.g.*	cerebral ganglion.

cer.g.b.	cerebral ganglion band.
cer.g.ru.	cerebral ganglion rudiment.
cer.ped.c.	cerebro-pedal connective.
cer.pl.c.	cerebro-pleural connective.
chi.	chitinous lining of stomach.
ct.l.	ctenidium of post-torsional left side.
ct.l.p.	posterior end of left ctenidium.
ct.l.ru.	rudiment of post-torsional left ctenidium.
ct.os.ru.l.	ctenidial and osphradial rudiment of post-torsional left side.
ct.r.	ctenidium of post-torsional right side.
ct.r.ru.	rudiment of post-torsional right ctenidium.
d.gl.	digestive gland.
d.gl.l.	digestive gland lobe.
d.gl.l.l.	left digestive gland lobe.
d.gl.l.r.	right digestive gland lobe.
d.gl.stom.	opening of digestive gland from larval stomach.
e	eye.
e.l.	left eye.
end.	endoderm.
ep.	epipodium.
ep.la.p.	larval process of epipodium.
ep.t.	epipodial tentacle.
f.g.	foregut.
fo.	foot.
h.ru.	heart rudiment.
hy.gl.	hypobranchial gland.
in.	intestine.
integ.v.c.	integument cutting off velar cell.
lab.com.	labial commissure.
m.	mouth.
m.g.	midgut.
m.g.c.	cavity of midgut.
mant.f.	mantle fold.
mant.f.t.	posterior border of mantle fold.
mant.m.	margin of mantle.
mant.ru.	mantle rudiment.
mesen.c.	mesenchyme cell.
mes.b.	mesoderm band.
mes.b.u.	ventral union of mesoderm bands.
mes.ru.	rudiments of mesoderm.
mi.f.	mitotic figure.
mo.	mouth.
mus.c.	muscle cell.
mus.c.ru.	rudiment of muscle cell.
o.n.	optic nerve.
od.ap.	odontophore apparatus.
od.cart.	odontophore cartilages.
oes.	oesophagus.
op.	operculum.
op.ru.	rudiment of operculum.
os.	osphradium.
pal.c.	pallial cavity.
pal.c.r.p.	right posterior horn of pallial cavity.
pal.c.t.	termination of pallial cavity.
pal.cl.	pallial cleft.
pal.n.r.e.	right external pallial nerve.
pal.t.	pallial tentacle.
ped.ci.	pedal cilia.
ped.ep.m.c.	mucous cell of pedal epithelium.
ped.g.	pedal ganglion.
ped.g.c.	pedal ganglion cord.
ped.g.l.	left pedal ganglion.
ped.g.r.	right pedal ganglion.
ped.gl.	pedal gland.
ped.ru.	pedal rudiment.
ped.s.	pedal sole.
per.	pericardium.
per.c.	pericardial cavity.
per.ru.	rudiment of pericardium.
pl.g.l.	left pleural ganglion.
pl.g.r.	right pleural ganglion.
pl.ped.g.	pleuro-pedal ganglion mass.
pl.ped.g.l.	left pleuro-pedal ganglion mass.
pl.ped.g.r.	right pleuro-pedal ganglion mass.
pr.mes.	primitive mesoderm cells.
pr.vel.a.	pre-velar area.
pr.vel.c.	pre-velar cell.
pr.vel.gr.	groove in pre-velar area.
proc.	proctodaeum.
prot.	prototroch.
rad.	radula.
rad.c.	radular caecum.
rad.t.	tooth of radula.
rect.	rectum.
rect.pr.	primitive rectum.
ren.ap.l.	post-torsional left renal aperture.
ren.ap.pr.	precocious renal aperture.

ren.d.ru.	dorsal rudiment of renal organ.
ren.l.	post-torsional left renal organ.
ren.per.c.	reno-pericardial canal.
ren.r.	post-torsional right renal organ.
ren.v.	ventral renal organ.
ren.v.ru.	ventral rudiment of renal organ.
sh.	shell.
sh.at.integ.	shell attachment of integument.
sh.gl.	shell gland.
sh.m.	margin of shell.
sh.p.	shell perforation.
sh.ru.	shell rudiment.
sn.	snout.
st.	stomodaeum.
stat.	statocyst.
stat.in.	statocyst invagination.
stat.n.	statocyst nerve.
stom.	stomach.
sub.o.pl.v.c.	sub-oesophageal pleuro-visceral cord.
sub.o.pl.v.p.	sub-oesophageal pleuro-visceral process.
sub.o.pl.ru.	rudiment of sub-oesophageal pleuro-visceral process.
sup.o.pl.v.c.	supra-oesophageal pleuro-visceral cord.
sup.o.pl.v.ru.	rudiment of supra-oesophageal pleuro-visceral cord.
um.	umbo.
v.	velum.
v.c.	velar cell.
v.c.n.	nucleus of velar cell.
v.r.mus.	velum retractor muscle.
v.r.mus.ped.	pedal addition to velum retractor muscle.
v.r.mus.ves.	vestige of velum retractor muscle.
v.v.	vestige of velum.
ven.	ventricle.
visc.	reduced visceral coil.
visc.g.	visceral ganglion.

Description of Plates

Plate 21

Drawings of living veligers up to the time when pelagic life ceases. The details of the muscles were added after determination of their arrangement from reconstructions based on serial sections. The orientation of the larva is indicated by letters. ×170 linear approx.

Fig. 1—Right side of veliger at 27 hr. after fertilization, a short time before torsion begins. The ventral pallial cavity and the velum retractor muscle can be seen on the right side.

Fig. 2—Left side of veliger $31\frac{1}{2}$ hr. after fertilization. The rudiment of the operculum is present, although inconspicuous.

Fig. 3—Ventral view of veliger 33 hr. old. Torsion has begun and the visceral hump has rotated, so that the pallial cavity is displaced somewhat to the right side of the foot. The cephalo-pedal mass is partially retracted into the shell, but the operculum does not completely close the shell until several hours later.

Fig. 4—Left side view of veliger 35 hr. old. 90° of torsion have taken place, so that the shell is half endogastric. This view shows the "neck" region, which is involved in the twisting.

Fig. 5—Veliger 54 hr. old seen from the left side. At this time the larvae swim for short periods only. The rudiments of the sense organs are obvious.

Fig. 6—View of left side of veliger at 79 hr. after fertilization. The larvae are now entirely benthic, although creeping is not successfully accomplished until about 24 hr. later. The velum retractor muscle has migrated to the left side. The shell is endogastric, although the pallial cavity is still on the right side of the body.

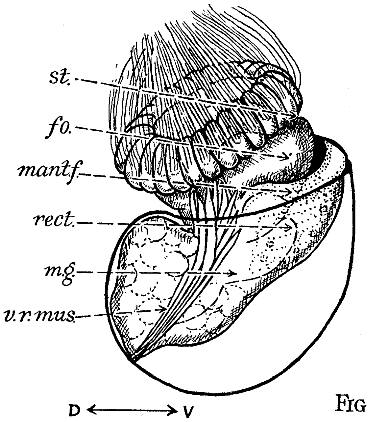


Fig. 1.

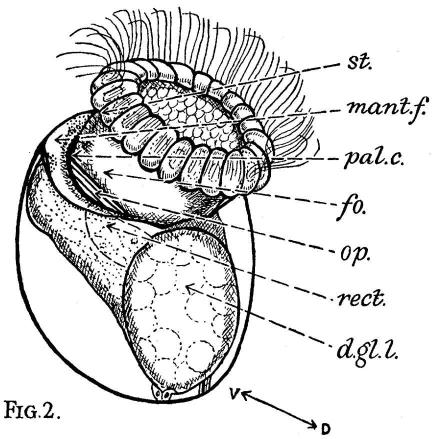
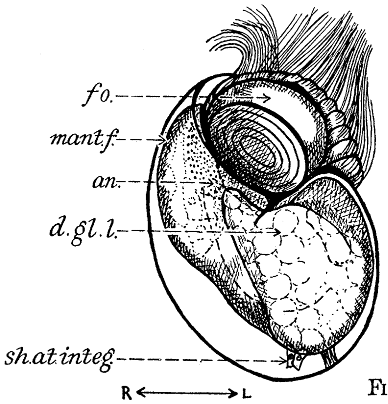


Fig. 2.



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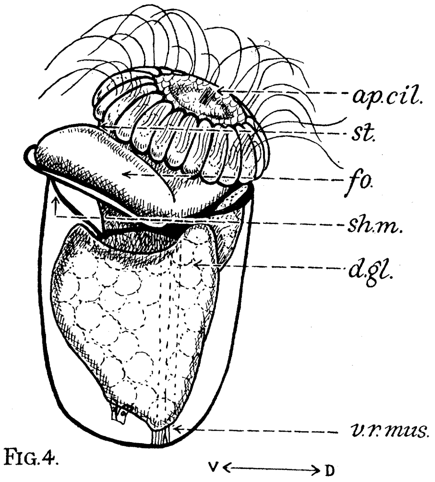


Fig. 4.

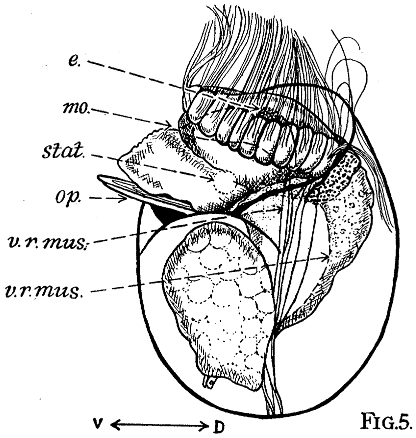


Fig. 5.

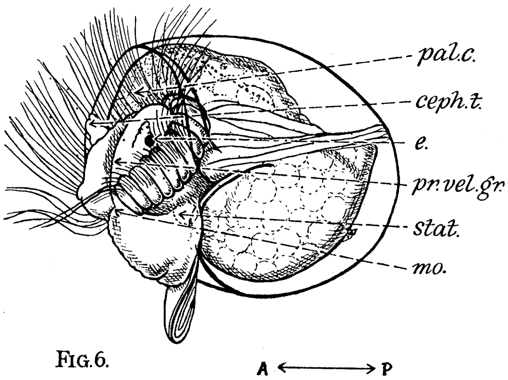


Fig. 6.

PLATE 22

Drawings of living larvae from the beginning of benthic life. The figures of the younger stages show the larvae making attempts at creeping. In the later stages the gradual loss of velum is shown. The areas of attachment of muscles are labelled as the muscles themselves. ×160 linear approx.

FIG. 7—Larva 5 days old, seen from the left side. The operculum is in process of releasing the head and ciliated pedal sole from the shell.

FIG. 8—Larva 6 days old, seen from the right side. The specimen was about to cling by means of the pedal sole. Note the opercular process of the metapodium and the beginnings of asymmetrical growth of the shell on the right side. The renal organ rudiments and the developing columellar muscle on the right side are shown. The eyes are now pedunculated.

FIG. 9—Left side view of larva 4½ days old, which was clinging with the pedal sole and appeared to make contortions of the "neck" region in order to lift the shell and its contents into a comfortable position.

FIG. 10—Dorsal view of larva 10 days old, a few hours after the velum was thrown off. The pallial cavity is still somewhat to the right side of the body. The area of attachment of the velum retractor muscle is now near the left side of the shell.

FIG. 11—Right side view of post-veliger 11 days after fertilization. A few hours previously the remainder of the velum was thrown off. The mantle fold projects beyond the shell margin and the beginning of asymmetrical growth of the shell is obvious on this side. The pallial cavity has reached an almost dorsal position, but the anus is still at the extreme right side of it.

FIG. 12—Left side view of post-veliger 11 days old. This was drawn from the same specimen as the above, at a time when it was emerging from the shell. The area of fixation of the velum retractor muscle is now near the left margin of the shell.

FIG. 13—Post-veliger 12 days old, seen from the anterior right side. The pallial cavity is now dorsal. The shell is markedly asymmetrical and leaning towards the left side. The first ctenidial and osphradial rudiment, the definitive left, is seen in dorsal position. Ciliary movement made this obvious from about the 7th day of development. The radular apparatus moved up and down rhythmically and the jaws were seen to move.

FIG. 14—Ventral view of post-veliger 12 days old, drawn when it was creeping upside down and suspended from the water surface. Asymmetry of the shell and mantle are obvious. As the post-veliger no longer retracts into the shell, the operculum has now lost its function. The first epipodial tentacle, which originates from the opercular process, is seen on the right side.

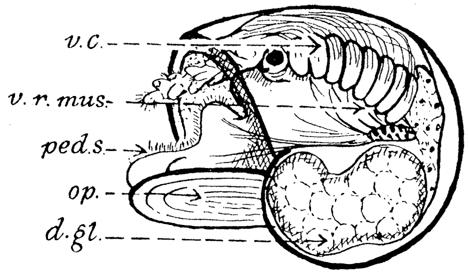


FIG. 7.

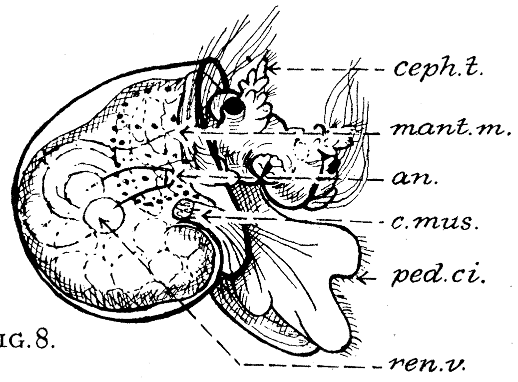


FIG. 8.

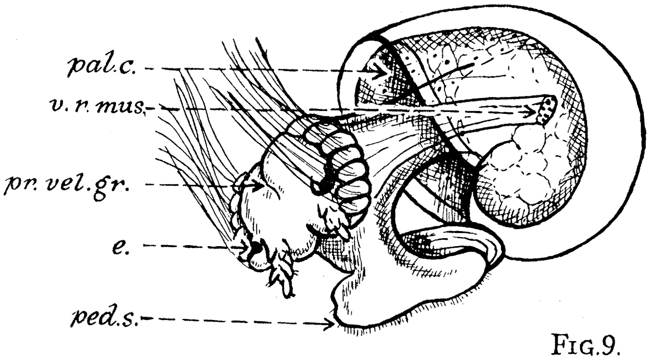


FIG. 9.

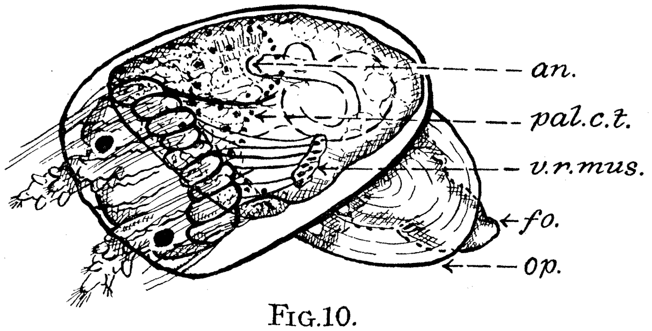
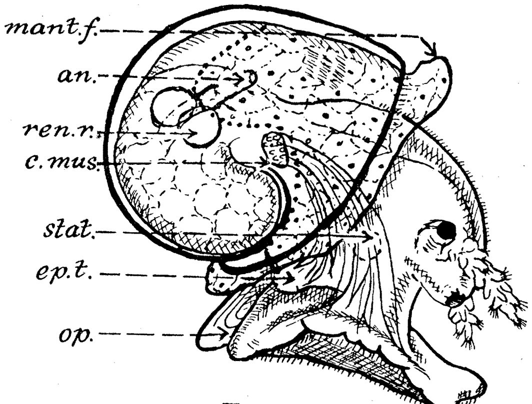


FIG. 10.



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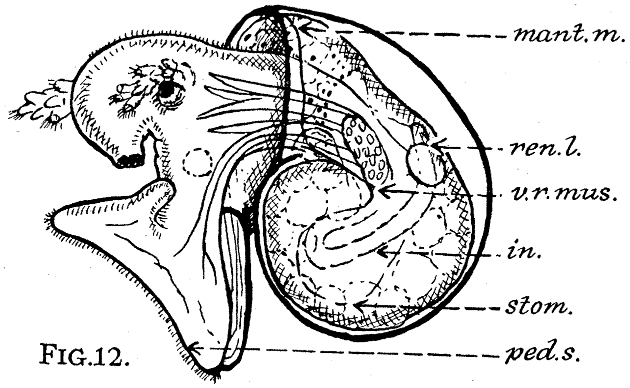
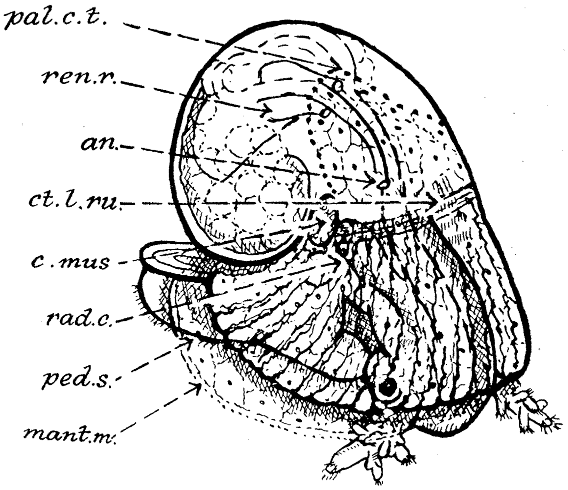


FIG. 12.



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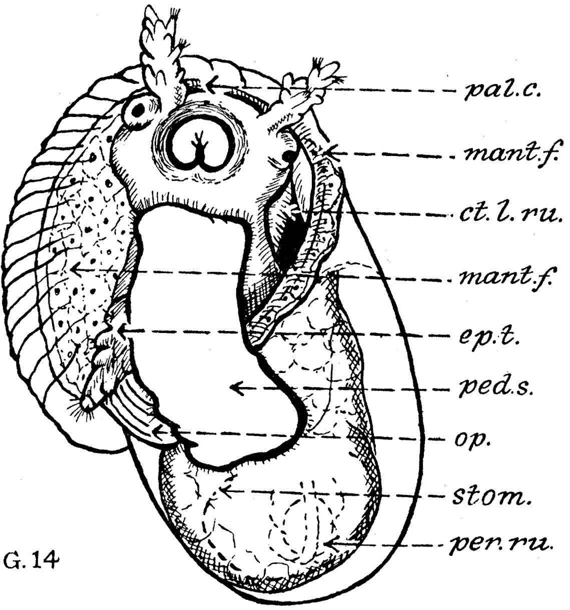

FIG. 14

Plates 23 and 24

A series of diagrams based on reconstructions from serial sections and on observation of living specimens. The migration of the pallial cavity, the changes in the spatial relations of the velum retractor muscle and columellar muscle and in the digestive system are shown. The shell is indicated by a heavy outline. In Plate 23 the magnification is approximately 200, but in Plate 24 it is indicated for each figure.

Plate 23

Fig. 15—Dorsal view of veliger immediately before torsion, about 30 hr. old. The pallial cavity is ventral and the retractor muscle curves round the right side.

Fig. 15*a*—Ventral view of the same stage.

Fig. 16—Dorsal view of veliger at about 34 hr. old, soon after rapid torsion of 90° has occurred. The velum retractor muscle is now straight and in dorsal position; the pallial cavity and the rectum are on the right side.

Fig. 16*a*—Ventral view of the same stage.

Fig. 17—Dorsal view of retracted veliger 61 hr. old. The pallial cavity and the anus remain on the right side and the renal rudiments are dorsal and ventral to the rectum. The rudiment of the columellar muscle is seen on the right side.

Fig. 18—Dorsal view of larva 14 days old. This was the oldest specimen which retained vestiges of the velum. The shell is asymmetrical, the pallial cavity has migrated almost into dorsal position and the mantle fold has extended round the left side. The first ctenidial rudiment, the definitive left, is dorsal and the velum retractor muscle has migrated to the left side.

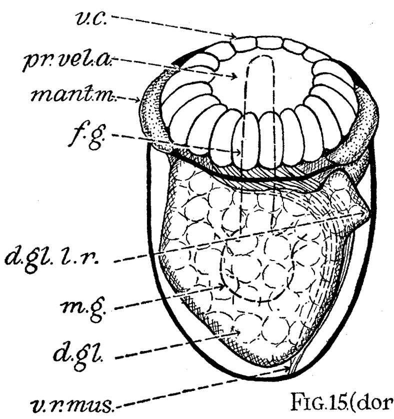

FIG. 15 (dorsal)

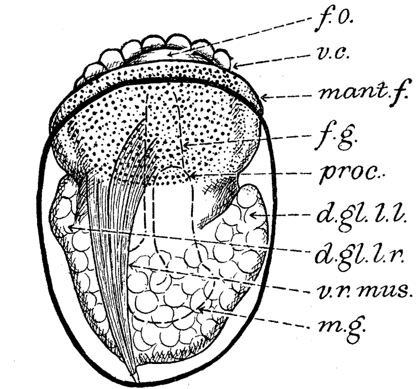

FIG. 15a (ventral)

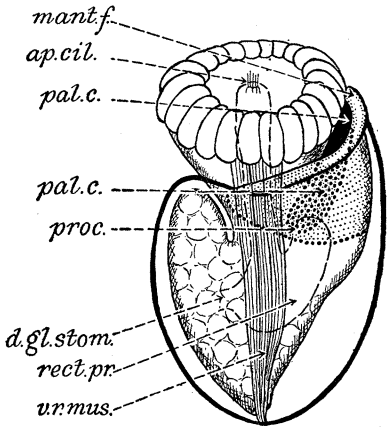

FIG. 16 (dorsal)

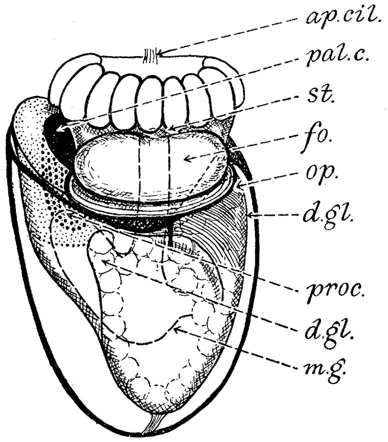

FIG. 16a (ventral)

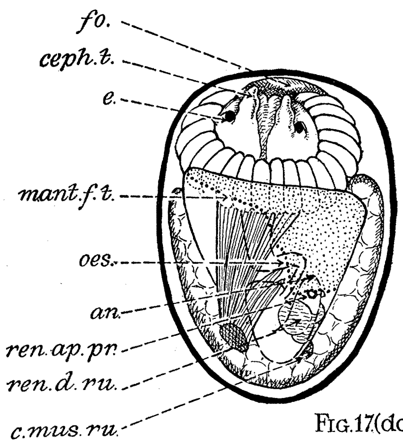

FIG. 17 (dorsal)

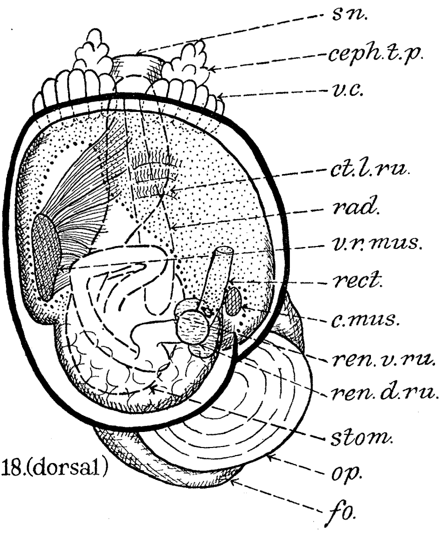

FIG. 18 (dorsal)

Plate 24

Fig. 19—Post-veliger 12 days old. This was a specimen which had recently lost the velum. Note the extensive mantle fold of the right side and the dextral coiling of the shell. The pallial cavity has now completed 180° migration from its position before torsion began. The anus still occupies the extreme right side of the pallial cavity and the one ctenidial rudiment, the definitive left, is already slightly to the left side. The two muscles are now about equal in size. ×200 approx.

Fig. 20—Post-veliger 44 days after fertilization. There is one well-developed ctenidium, the final left, and the anus is still placed at the right side of the pallial cavity. The latter is already displaced somewhat to the left side by hypertrophy of the columellar muscle. The pallial cleft has begun to form and the renal organs are now unequal in size. ×38.

Fig. 21—Metamorphosed *Haliotis* 2 months old. There are two ctenidia but the definitive right one is yet very immature. It has begun to form ctenidial lamellae, but is very small in comparison with the definitive right ctenidium, which has its free tip bent over in the diagram. The anus is now in the centre of the pallial cavity, with ctenidia and renal apertures placed in bilaterally symmetrical fashion. Pallial tentacles and one shell hole are shown. ×28 approx.

Fig. 22—Dorsal view of adult *Haliotis* without the shell. The topographical right ctenidium is now only slightly smaller than the topographical left one. The visceral coil is vestigial in comparison with that at 2 months old. The conical process of the digestive gland and gonad, which curves round the columellar muscle into a pocket of the mantle on the right side, has developed from the rudiment seen under the visceral coil in fig. 21. $\times\frac{2}{3}$ approx.

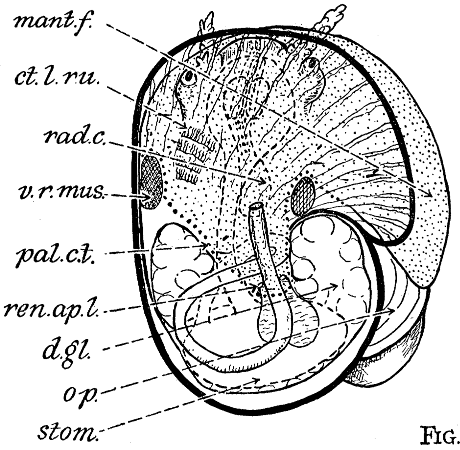

FIG. 19.

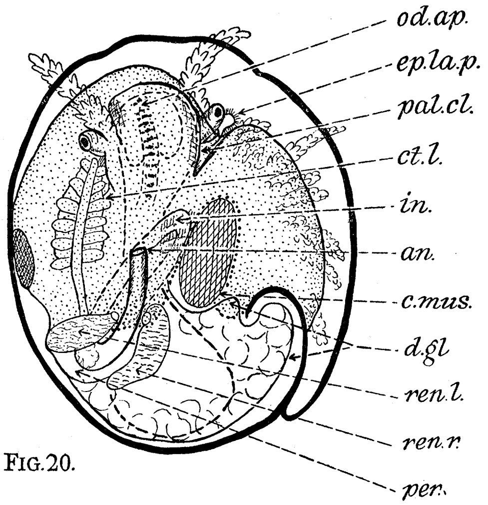

FIG. 20.

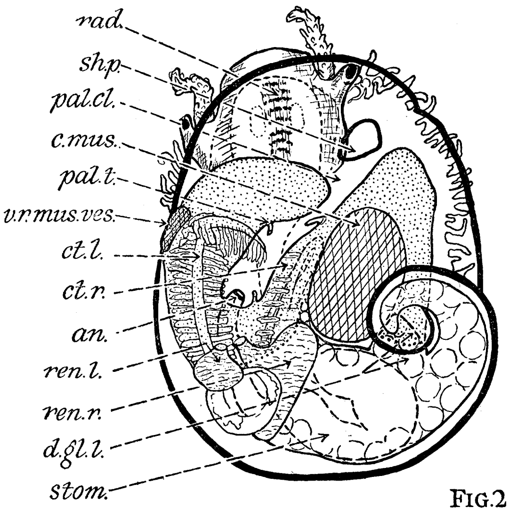

FIG. 21.

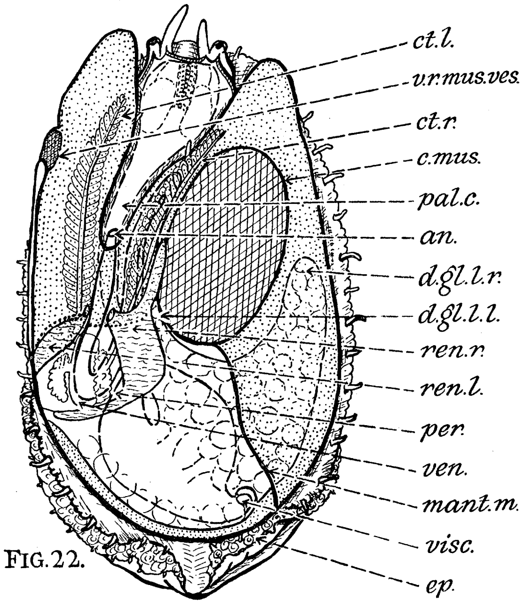

FIG. 22.

PLATE 25

Sections showing the development of the velum retractor muscle, etc. ×450 approx.

FIG. 23—Transverse section of veliger 19 hr. old, passing through the foot and posterior end of the velum in the neighbourhood of the stomodaeum. The mesoderm bands and the right anterior extremity of the mantle rudiment are seen.

FIG. 24—Parasagittal section of veliger 21 hr. old. The section passes through the developing muscle cells of the right side which, a few hours later, constitute the velum retractor muscle. The mantle fold and foot rudiments are seen.

FIG. 25—Transverse section through the posterior part of the visceral hump of veliger 33 hr. old. In this specimen torsion has not begun. The section shows the cells of the velum retractor muscle situated on the right side of the visceral hump. The two cells on the left side later give rise to the columellar muscle, which is delayed in development until creeping begins.

FIG. 26—Transverse section of veliger 30 hr. old, which is more advanced in development than the specimen shown in fig. 25 and already shows 90° torsion. The section passes through the posterior end of the foot and shows the dorsal position of the velum retractor muscle.

FIG. 27—Frontal section through a veliger of the same age as in fig. 26 with 90° torsion. The section is dorsal to the larval stomach and shows the full length of the cells of the velum retractor muscle, which is now in dorsal position.

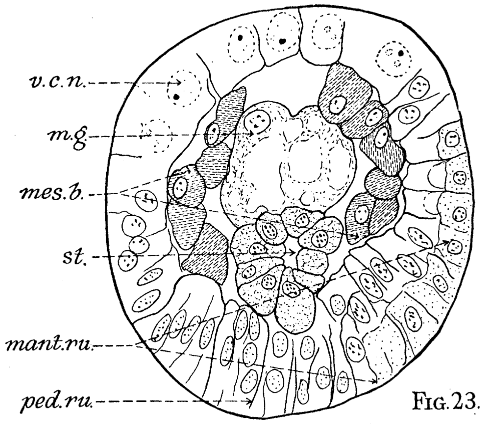

FIG. 23.

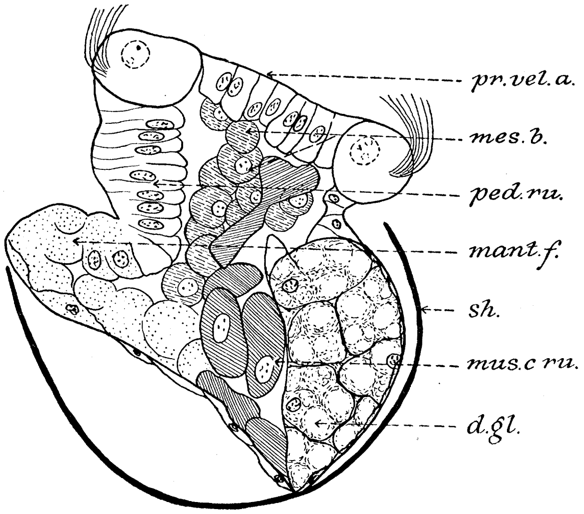

FIG. 24.

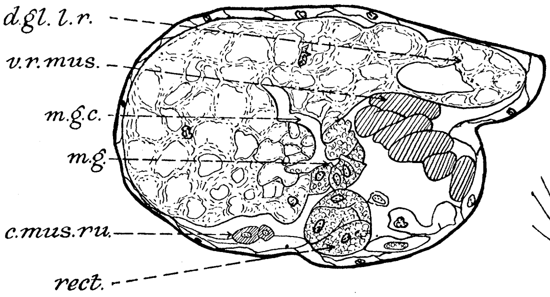

FIG. 25.

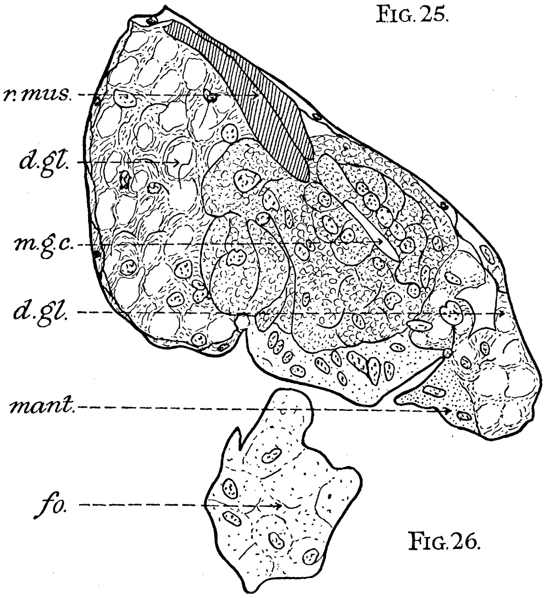

FIG. 26.

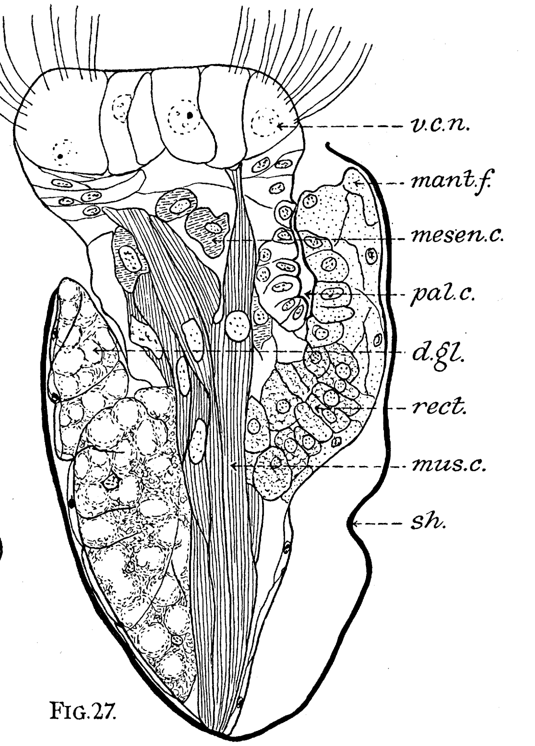

FIG. 27.

PLATE 26

Sections showing the early stages in development of the nervous system. ×450 approx.

FIGS. 28, 29 and 30—Frontal sections of the same series as in fig. 27 of Plate 25.

FIG. 28—Section next ventrally to that of fig. 27. It passes through the short rudiment of the supra-oesophageal pleuro-visceral process, which is seen on the right side. The pallial cavity, with the rectum, is also on the right side.

FIG. 29—Section ventral to the oesophagus and anal cell, passing through the rudiment of the sub-oesophageal pleuro-visceral process.

FIG. 30—Section passing through the foot, showing the anterior end of the statocyst invagination, rudiments of the cerebral ganglia and cerebro-pedal connective. The insignificant ciliated apical cells are shown.

FIG. 31—Transverse section of veliger 33 hr. old immediately before torsion begins. The section passes through the cephalo-pedal mass and shows the first rudiments of the operculum above the ventral mantle fold. The cerebral and pleural ganglia are almost completely delaminated from the epithelium.

FIG. 32—Transverse section of veliger 61 hr. old, passing through the foot and velum close to the pre-velar plate. On the right side the apical plate cells neighbouring the eye are seen. Note the cerebral ganglion band, pleuro-pedal mass, cerebro-pleural connective, statocysts and operculum.

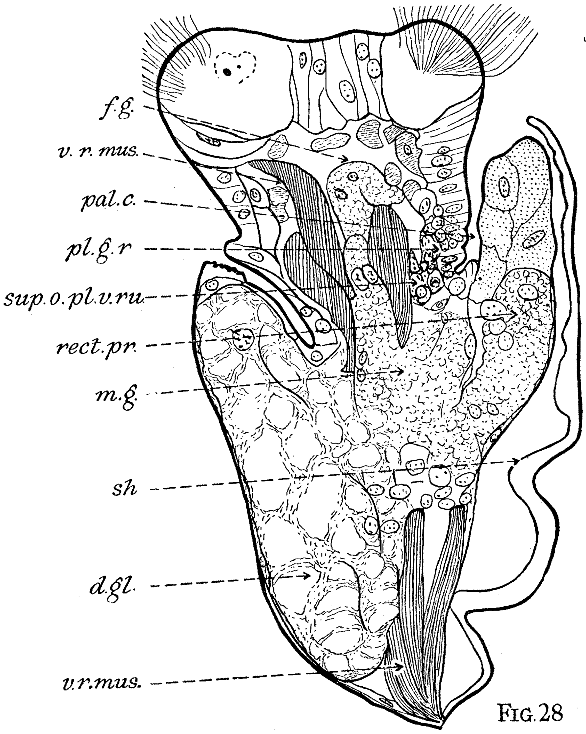

FIG. 28

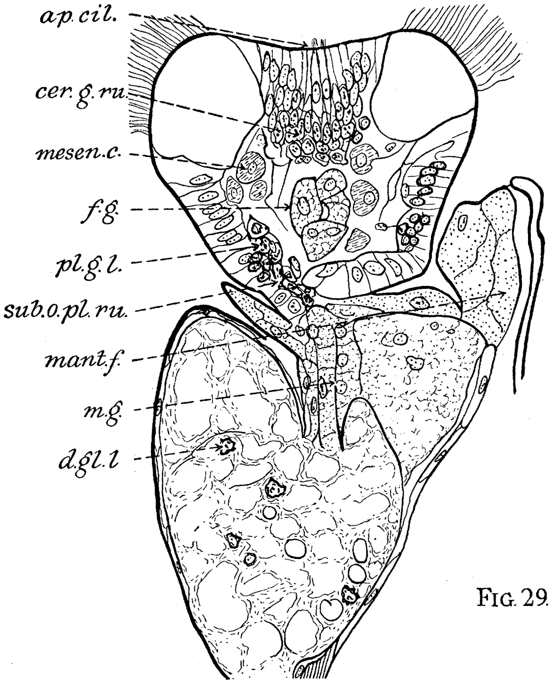

FIG. 29

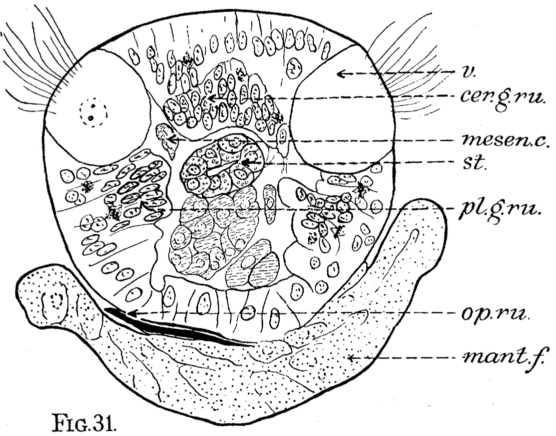

FIG. 31.

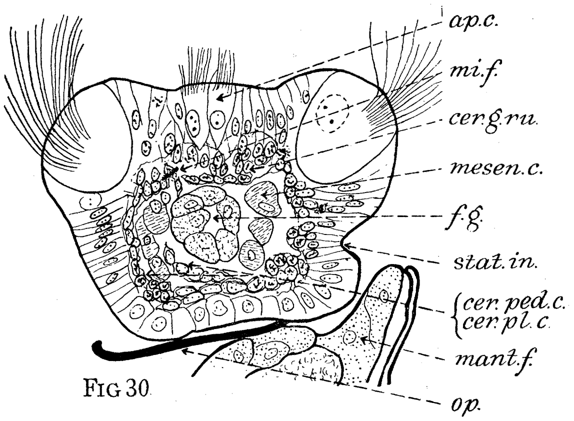

FIG 30

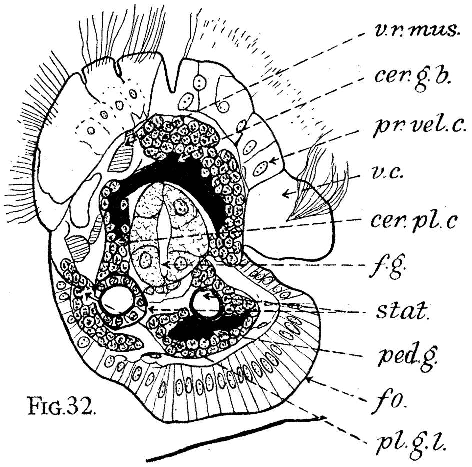

FIG. 32.

Plate 27

A series of sections to show the later development of the nervous system, the muscles and the pallial complex. The areas of insertion of the muscles are labelled as the muscles themselves.

Figs. 33 and 34—Slightly oblique transverse sections passing through the middle region of larva 14 days old. This was the oldest specimen possessing vestiges of the velum; it was somewhat contracted. The section of fig. 33 passes through the anus and the extreme anterior end of the operculum. The pallial cavity is still somewhat to the right of the dorsal position. The supra-oesophageal pleuro-visceral process is seen. In fig. 34 the section passes through the velum retractor and the columellar muscle, which are now almost equal in size. The sub-oesophageal pleuro-visceral process terminates on the right side. ×450 approx.

Fig. 35—Parasagittal section, passing about 15μ to the left side of the median plane and radular caecum, of veliger 7 days old. It passes through the extreme left side of the first ctenidial rudiment (final left). ×450 approx.

Fig. 36—Transverse section through post-veliger 12 days old, the youngest specimen without the velum. The section is slightly anterior to the middle region and passes through the pallial cavity, which is now dorsal, after completing 180° torsion. The rectum is still to the extreme right side of the pallial cavity and there is only one ctenidial rudiment, the topographical left. Parts of the supra- and sub-oesophageal pleuro-visceral processes are seen. ×450 approx.

Fig. 37—Transverse section of metamorphosed *Haliotis* 2 mm. long, passing through the viscera ganglion and the posterior end of the pallial cavity, which has two diverticulae in this region. The two renal organs now differ much in size and appearance as in the adult. ×20 approx.

Fig. 38—Transverse section through the same specimen as in fig. 37, passing through the well-developed definitive left ctenidium and the rudimentary right ctenidium. Note the supra- and sub-oesophageal pleuro-visceral cords, the uncrossed external pallial nerves and the vestige of the velum retractor muscle. ×20 approx.

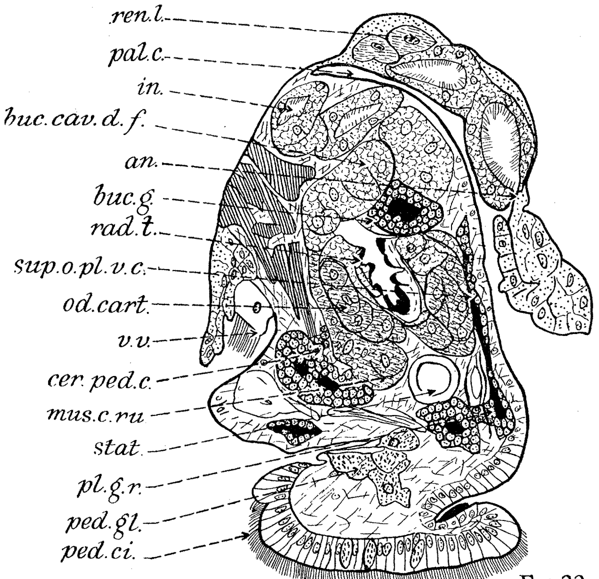

Fig. 33.

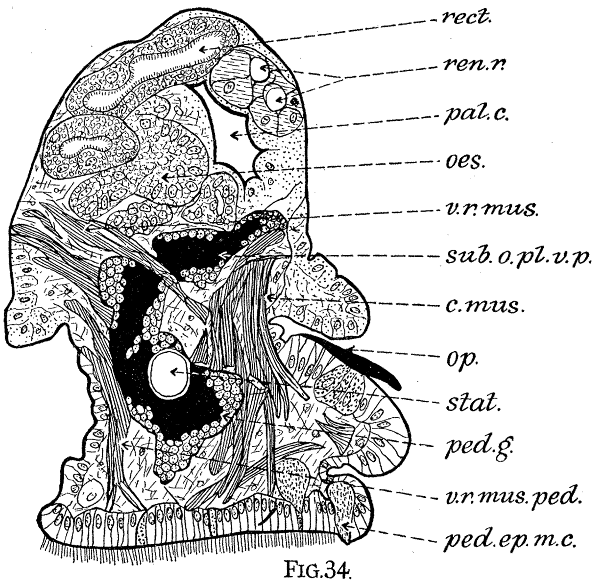

Fig. 34.

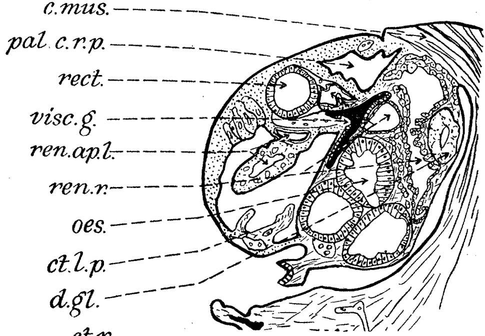

Fig. 37.

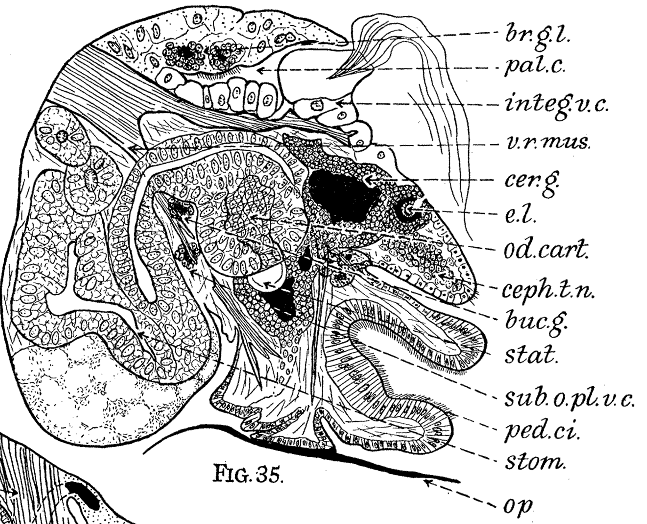

Fig. 35.

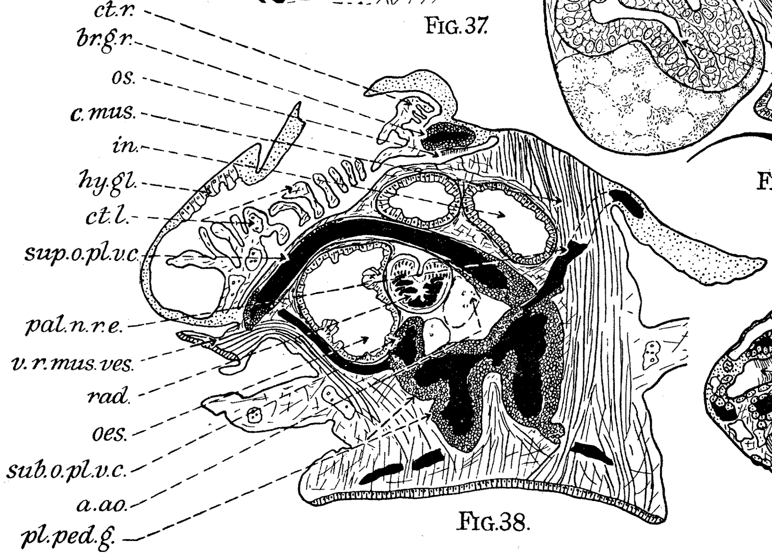

Fig. 38.

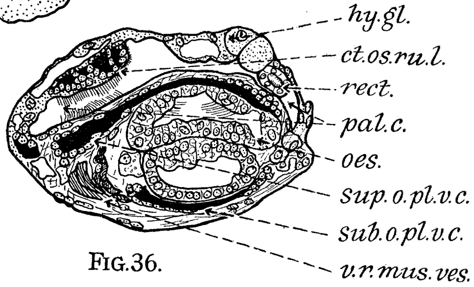

Fig. 36.