On the Embryology of the Isopod *Irona*[1]

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INTRODUCTION

ALTHOUGH Rathke (1834), Dohrn (1867), van Beneden (1869), and Roule (1889, 1890, 1891, 1894, 1896) have studied the embryology of Isopoda, the first detailed account and the one that is ordinarily quoted in text-books is that of Bobretzsky (1874) on *Oniscus murarius*. This work is informative in a general way, though the details of segmentation and germ layer formation are not accurate. Bullar's (1878) work on the parasitic isopods was largely influenced by the generalizations of Bobretzsky. Nusbaum (1891*a*, 1898) and McMurrich (1892, 1895) have contributed considerably to our knowledge of segmentation and post-mandibular growth in isopods but their accounts of the different fates of the germ layers left several problems of embryology unsolved. Goodrich's (1939) studies on *Porcellio* and *Armadillidium* were confined mainly to the origin and fate of the endoderm elements. Manton's (1928) paper on the development of *Hemimysis* serves as a landmark in the history of Crustacean embryology. A study of isopod literature reveals that the earlier workers did not take into account details regarding the structure and distinguishing features of mesoderm and endoderm. It is therefore possible, as Manton (1928) suggests with regard to germ layer formation of Malacostraca in general, that improved technique may yield different results.

The significance of the origin, differentiation, and fate of the mesoderm in the pre-antennulary segment was first described for *Hemimysis* and *Nebalia* by Manton (1928, 1934). Later Nair (1949) and Aiyer (1949) described it in the decapods, *Caridina* and *Palaemon*. The occurrence of the pre-antennulary mesoderm in isopods has not been recorded, though Bullar (1878) and Goodrich (1939) have sketched it without describing it as such.

It was therefore felt that a study of one of the parasitic isopods in the light of the recent work of Manton (1928, 1934) and Nair (1939, 1949) would add to our knowledge of Malacostracan embryology, especially if the process of gastrulation, the formation of the liver, the development of the pre-antennulary, thoracic and abdominal mesoderm, the formation of the heart, and the fate of the endoderm cells were investigated in detail.

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MATERIAL AND METHODS

The following account of the embryology of *Irona* is based mainly on the eggs of *Irona robusta* and supplemented from a study of the eggs of *Irona far*. These forms, parasitic on *Hemirhamphus* and *Ptylosurus*, were collected when the host fishes were netted along the Madras coast, mainly during the months of October

and February (1949–52). The eggs in each brood were at the same stage of development, and numbered 275–350.

Eggs were removed from the brood pouch and fixed and embedded according to the procedure of Manton (1928). As the large quantity of yolk present at early stages interfered with sectioning, it was found necessary to remove as much of it as possible. Sections were cut at 8 μ and stained with iron haematoxylin and counterstained in eosin. The earlier stages of cleavage, after the appearance of the blastomeres on the surface of the egg, were followed by staining the egg in bulk with Delafield's haematoxylin and differentiating with acid alcohol, whereby the yolk alone appeared deep blue leaving the cytoplasm as whitish stellate patches with central dark nuclei.

For preparing whole mounts of the blastodiscs, eggs in which a blastoderm could be seen under the binocular were selected and the chorion removed. The bulk of the yolk was then removed from the blastoderm with a scalpel, and the yolk granules adhering to the lower surface were scraped off carefully with needles under a binocular microscope. The blastodiscs were then stained with iron haematoxylin and mounted in glycerine.

THE EGG

The egg of *Irona*, Fig. 1, when fresh is white in colour and oval in shape, measuring about 1·02 mm. in length and 0·90 mm. in breadth with a central nucleus, surrounded by a stellate mass of protoplasm, embedded in a semi-fluid yolk, and covered by a thin layer of peripheral protoplasm. It thus resembles the eggs of *Jaera*, *Asellus*, *Porcellio*, and *Armadillidium* (McMurrich, 1895), and *Hemimysis* and *Nebalia* (Manton, 1928, 1934). The extruded egg has only one enveloping membrane, the chorion, which is elastic and sticky. A definite vitelline membrane is not evident in the single-celled stage, but a thickening of the peripheral protoplasm noted after the third division probably represents this membrane.

SEGMENTATION OF THE EGG AND FORMATION OF THE GERMINAL DISK

The earliest stage examined shows eight blastomeres within the yolk just internal to the peripheral protoplasm, of which two are seen in Fig. 2. Since no blastomeres could be detected on the periphery of the egg prior to the eight-celled stage, it has to be inferred that the first three divisions were internal. These eight blastomeres emerge out of the yolk as stellate masses of protoplasm with deeply staining nuclei at one pole of the egg and arrange themselves in the form of a circle (Fig. 3).

In 16-, 32-, and 64-celled stages (Figs. 4, 5, and 6) the blastomeres were seen to migrate to the opposite pole. A group of 10–11 cells always moved ahead of the rest in the form of a circle, while the others were scattered in the region where

they first appeared. The 10–11 cells moving in a ring, after reaching the opposite pole, arrange themselves in a compact manner to form the rudiment of the blastoderm. Migration of the other cells follows subsequently (Fig. 7), and they all become incorporated into the blastoderm.

The cells of the early blastodisc are polygonal in shape, with prominent central nuclei, and rest directly on the yolk. Immediately below the blastoderm the superficial yolk is granular and contrasts with the compact globules seen in the bulk of the yolk inside. This change in the composition of yolk may be the first indication of the 'utilization of the yolk by the embryo by a hydrolysis of the complex lipoprotein' (Brachet, 1950). As development proceeds this granular yolk increases in quantity. When the blastoderm grows to about 479 μ in diameter there are no loose blastomeres, as all have taken part in the formation of the disk.

When fully formed the blastoderm exhibits three regions where the cells proliferate more rapidly than elsewhere, as can be seen by the greater number of mitotic figures (Fig. 8). Of these three regions the anterior two give rise to the future cephalic rudiments while the posterior one forms the blastoporal area which is demarcated from the rest of the blastoderm by a crescentic row of cells (Figs. 7 and 8 *c.r.*). Goodrich (1939) found a similar crescentic arrangement of cells delimiting the blastoporal area in *Porcellio*. This crescentic arrangement of cells leads to the horseshoe of ectodermal teloblasts which may be the direct successors of these blastoderm cells.

GASTRULATION

The studies of McMurrich (1895), Manton (1928), Goodrich (1939), and Nair (1939) show that gastrulation in Peracarida is by the immigration of cells from the blastoporal area towards the yolk. In *Irona* the blastoporal cells, delimited from the rest of the blastoderm by the crescentic row (Figs. 7 and 8), show a greater affinity for stains than the rest of the blastoderm. Cells migrate inwards from the posterior part of the embryo (Figs. 9–12) and leave gaps or small pits on the surface of the blastodisc, as seen by Manton (1928). A shallow depression, which is caused by the migration of cells into the interior, is the blastoporal homologue (Fig. 12, *bl.a.*). In slightly older embryos the depression fills up, probably by the multiplication of the adjacent cells. The internal cells arrange themselves below the blastopore as a plug (Fig. 13) projecting into the yolk, which can be compared to the 'bouchon blastoporique' of Sollaud (1923). Later stages show that this plug gives rise to the mesodermal head bands, the mesodermal teloblasts, the liver, and a portion of the endoderm. As the derivatives are both mesodermal and endodermal in character, this plug may be called the mesendodermal plug. The pre-antennulary mesoderm arises independently from the blastoporal mesendodermal mass (see p. 10).

In the embryos where the mesendodermal plug has become a few layers thick, two small groups of cells are formed at the anterolateral margins of the plug,

which grow so that the plug becomes V-shaped. This V-shaped mesoderm is characteristic of malacostracan development. In the initial stages the arms of the V are not conspicuous and are seen to be made up of a single row of cells. The arms appear more marked when rudiments of the naupliar appendages become distinguishable (Fig. 19).

When the V-shaped mesodermal band is being formed, a few isolated cells from the mesendodermal plug at the apex of the V degenerate (Figs. 14 and 15). These cells show certain cytological changes prior to degeneration. Their nucleoli become enlarged and globular, though no change is at first evident in the nuclear reticulum. When the nucleolar globules reach a certain size other small globules appear in the nuclei and the chromatin becomes scanty. Later the nucleolar globules as well as the others unite to form a large globule altering the shape of the nuclear membrane. This is followed by the rupturing of the nuclear membrane and the breaking up of the cells. The globules, the fragments of the nuclear matter as well as the cytoplasm of the cells, are left on the surface of the yolk and are stained deeply.

When the headbands are differentiated some of the cells at the antero-lateral margins of the mesendodermal plug become transformed into the mesodermal teloblasts (Fig. 17). The nuclei in these cells appear slightly larger than those of the surrounding cells and occupy a central position within the cytoplasm. The chromatin granules become arranged in the peripheral region of the nucleus. These features of the nucleus distinguish the mesodermal teloblasts from the rest of the mesendoderm cells. The mesodermal teloblasts are arranged in the form of two arcs with a space between, below the crescentic row of ectodermal cells (Fig. 16). Each group is made up of four cells placed close to each other. Since all of them appear together in the same stage and since no sign of their differentiation is noticeable in slightly earlier stages it is fair to presume that they all arise independently by the transformation of existing mesodermal cells and not as products of division of one cell as stated by Nusbaum (1891*a*) for *Ligia*.

When the mesodermal teloblasts are well differentiated, a few cells from the posterior apex of the V immigrate towards the yolk. These cells absorb yolk into vacuoles. Such a transformation is characteristic of endoderm cells, as described by Manton (1928, 1934) and Nair (1949). Immigration of large numbers of endoderm cells from an area behind the ectodermal teloblasts follows (Figs. 18 and 19). The endoderm cells formed from these two places are scattered over the yolk below the other tissues. A few cells in the mesendodermal plug do not join in the formation of either the naupliar appendages or the endoderm. They are found to give rise to the future liver rudiment (see p. 12).

Just after the mesodermal teloblasts are fully formed the ectodermal teloblasts appear by the transformation of blastoderm cells. Whole-mounts of blastoderms show practically no differentiation in the ectoderm cells till the rudiments of the headband of mesoderm are laid down and the mesodermal teloblasts are formed. In the earliest stage nineteen ectodermal teloblasts are differentiated simul-

taneously (Fig. 16). The ectodermal teloblasts closely resemble the mesodermal ones in cytological details. In Fig. 16, where all the nineteen ectodermal teloblasts are present, no more immigration of cells from the blastoporal area is seen. But when the teloblasts commence proliferation immigrations of ectodermal cells take place from two places on the blastodisc: (1) in front of the antennulary rudiments (Fig. 43), and (2) posterior to the teloblasts, to give rise to endoderm (Figs. 18 and 19).

The differentiation of the three primary germ layers which give rise to the various internal organs is complete once the teloblasts are fully differentiated, though the immigration of the endoderm cells is continued even up to a stage in which the rudiments of all the thoracic and abdominal segments are established. The history of blastoderm cells can be summarized as follows:

A. The ectoderm is formed from three primordia:
   1. The ectoderm of the naupliar region directly from the blastoderm cells anterior to the crescentic row.
   2. The ectoderm of the post-mandibular region from the ectodermal teloblasts.
   3. The telson ectoderm from the blastoderm cells lying behind the teloblasts.

B. The mesoderm is formed from two sources:
   1. The pre-antennulary mesoderm is formed independently by the migration of blastoderm cells anterior to the antennules.
   2. The mesendodermal plug gives rise to (*a*) the mesoderm of the naupliar appendages, (*b*) the mesoderm of the liver, and (*c*) the mesodermal teloblasts supplying the post-mandibular segments, and the telson mesoderm.

C. The endoderm is formed from two places:
   1. From the mesendodermal plug.
   2. From the blastoderm cells lying behind the ectodermal teloblasts.

THE NAUPLIUS

Korschelt & Heider (1899) state that 'in those cases in which the young animal is hatched at a later stage of development (Cladocera, Arthrostraca and most Decapoda), the nauplius stage is thrown back among the series of embryonic changes'. In *Irona* the nauplius is only a passing stage when the differentiation of the headbands of mesoderm and the formation of the rudiments of the appendages first become evident.

The headband after its differentiation shows three groups of cells (Fig. 19) along each arm of the V which on further growth form the mesoderm of the naupliar appendages. That of the antenna appears first, then that of the mandible, and lastly that of the antennule. The ectodermal cells overlying the naupliar mesodermal somites do not show any differentiation at this stage (Fig. 16), and the nauplius stage can only be recognized from sections.

POST-NAUPLIAR DEVELOPMENTAL STAGES

The two species of *Irona* show only minor variations from the nauplius to the newly hatched larva, such as the intensity of pigmentation of the body wall. The salient features of the post-naupliar stages of *Irona robusta* are shown in Figs. 20–32.

Two rounded cephalic lobes, two pairs of antennae, and a pair of mandibles are seen externally in Fig. 20. The teloblasts have divided in such a way that their products are arranged in transverse rows which are destined to give rise to the first five post-mandibular appendages. Two pairs of maxillae and the maxillipeds have made their appearance as small protuberances in Fig. 21. The teloblasts continue to be active. Four of the anterior thoracic legs are differentiated in Fig. 22. The teloblasts here have ceased activity and are not recognizable.

The stomodoeum forms on the ventral side as a small depression at the junction of the two pairs of antennae in Fig. 23. The dorsal organ appears on the dorsal side of the head as a whitish crescentic disk. The thoracic region shows all the seven segments but there are only six pairs of appendages; the last pair appears only after hatching.

The cephalic lobes migrate laterally (Fig. 24). The oral appendages appear as buds while the maxilliped and the thoracic appendages appear as finger-shaped outgrowths. Slight bulgings appear in the middle of the posterior margin of each thoracic leg. These were considered to be the embryonic rudiment of the exopodite of the leg by Nusbaum (1891*b*). The telson grows towards the ventral side concealing the proctodaeum from view.

The antennae, the maxilliped, and all the thoracic appendages show constrictions into joints in Figs. 25 and 29. The rudimentary exopodites disappear. The pleopods become bilobed, the outer lobes arising as buds. The uropods and telson are seen only in lateral views.

Ommatidia of the developing eyes are seen on the posterior margins of the cephalic lobes in Figs. 26 and 30. The antennae move towards the ventral side. The mandible develops a three-jointed palp which projects laterally. Distally the mandibles turn anteriorly like the cephalic appendages. The seventh thoracic segment is seen only in lateral view. The rami of the pleopods have become foliaceous.

The cephalic lobes grow together and fuse on the dorsal side forming a compact head (Figs. 27 and 31). The first and second antennae show the full number of joints, viz. eight and nine respectively as in the adult.

In Figs. 28 and 32 the embryo is ready to hatch. Hatching takes place inside the brood pouch, when the mother is attached to the host. The straightening of the appendages and the telson appears to be responsible for rupturing the chorion and liberating the larva.

The larva measures 2·45 mm. in length with a distinct rounded head, a large thorax, and a narrow abdomen (Fig. 33). All the body segments are now clearly

seen, but while metamorphosing into the adult the first two abdominal segments become tucked under the last thoracic segment when its appendages develop, thereby reducing the length of the abdomen. The appendages of the larva resemble those of the adult (Nair, 1950).

ORGANOGENY

Growth of the post-naupliar region

The development of the post-mandibular region in all Malacostraca so far investigated takes place by the activity of the teloblasts. In the Leptostraca, Mysidacea, most of the Decapoda and Stomatopoda, the formation of the caudal papilla during teloblastic growth appears to be a common feature, whereas in Peracarida, excepting the Mysidacea, no caudal furrow is formed and the products of the teloblasts grow over the yolk posteriorly and are responsible for the growth of the post-naupliar region of the embryo.

The formation of the teloblasts has already been described. The blastoderm of Fig. 18 has twenty-five ectodermal teloblasts more or less in a line. It would appear that the nineteen ectoteloblasts of the earlier stage (Fig. 16), which were arranged in a horseshoe, have been reinforced in number from the ectoderm cells. In all mitoses of the teloblasts the axes of the spindles lay parallel to the longitudinal axis of the embryo, and their products were in a line with them anteriorly. Therefore the new teloblasts could not have originated by the division of existing teloblasts. Cytological changes in the ectodermal cells lateral to the teloblasts have often been noticed in surface views of blastoderms, thereby strengthening the view that these additional teloblasts arise by a transformation of already existing ectoderm cells. Anterior to the row of twenty-five ectodermal teloblasts lie rows of narrow elongated cells, arranged so that each of the cells of one row is in front of a cell of the row behind. This linear arrangement suggests that these cells are the descendants of the ectodermal teloblasts, as in other Malacostraca. The characteristic arrangement in rows makes it easy to distinguish the teloblastic from the original naupliar area. The straightening of the horseshoe of ectodermal teloblasts is due to the increased growth in size of the cells in the median region as suggested by McMurrich (1895). The mesodermal cells continue to be eight in number as they were in Fig. 16.

A longitudinal section through the embryo (Fig. 19) shows that while the ectodermal teloblasts have given rise to ten rows of descendants the mesodermal teloblasts have produced only seven. Computing the number of divisions which have yielded these seven rows, it is probable that only seven divisions of the original teloblasts in both rows have taken place, but that the first three rows of ectodermal descendants have divided again, so that for each mesodermal row there are two rows of ectoderm. Manton (1928) and McMurrich (1895) found this relation to be a constant feature in the formation of each post-naupliar segment.

Longitudinal sections of the differentiating telson of this stage (Fig. 34) show mesoderm cells arranged in three to four rows just behind the middle four mesodermal teloblasts. These cells go to the formation of the telson mesoderm while the blastoderm cells lying behind the teloblasts give rise to the ectoderm of the telson (Fig. 34).

The identity of the ectodermal and mesodermal teloblasts disappears when the sixth abdominal segment is formed. In the present study the author has not seen any evidence of the formation of a seventh abdominal segment.

Gut

Unlike the mysids, amphipods, and decapods, where the endoderm contributes towards the formation of the mid-gut, the entire gut in *Irona* is formed from ectodermal cells without the endoderm contributing towards its development, as in the other isopods *Porcellio* and *Armadillidium* (Goodrich, 1939).

The first part of the digestive tract to be formed is the stomodoeum, followed immediately by a proctodoeum. A small invagination of ectoderm cells between the two pairs of antennae in the mid-ventral region is seen in Fig. 35. This stomodoeal invagination becomes deeper, enlarging ventrally and posteriorly into a flask-shaped sac (Fig. 36). The proctodoeum is formed as an invagination from the blastoderm cells, which have been moving backwards *pari passu* with the growth in length of the embryo. This invagination begins from the region where the telson meets the last abdominal segment (Figs. 38 and 39). As growth proceeds the mouth becomes narrower, the long constricted part of the stomodoeum is destined to become the oesophagus while the rest forms the stomach. The walls of the stomodoeum are thicker on the dorsal and ventral sides but thinner at the posterior basal aspect. In Fig. 30 the proctodoeum has pushed forwards as far as the third abdominal segment.

The stomach assumes a triangular shape in Fig. 37, with a thicker ventral wall. The inner surface of this wall gives rise to three prominences, the rudiments of the gastric mill. At the angle opposite to this side of the triangle the cells increase in number and this part of the stomach appears to be pulled dorsally. Sections of later embryos suggest that this is due to the insertion of the pre-antennulary mesodermal muscle strands. It is also probable that owing to this pull the side of the stomach with the rudiments of the gastric mill becomes erected as in Fig. 32. At this stage the proctodoeum has extended forwards as far as the third thoracic segment. The wall of the proctodoeum, which had 1–2 rows of narrow elongated darkly staining cells near the opening, now becomes 2–3 cells thick. It has a distinct mesodermal investment over it. When the proctodoeal invagination enters the thorax it acquires a small cavity and broadens slightly, the wall being made of only one row of rounded cells.

In Figs. 32 and 37 the three rudiments of the gastric mill have become more pronounced, the middle one being the largest. The oesophagus has elongated, shifting the stomach backwards into the second thoracic segment. By the time

the larva (Fig. 33) is formed, the proctodoeum has pushed its way into the second thoracic segment and makes contact with the stomach dorsal to the gastric mill rudiments where the stomach is one cell thick. Continuity is established by the absorption of the two-cell thick septum. The three lobes of the liver (see p. 13) reach the ventro-lateral part of the stomach close to the gastric mill rudiments (Fig. 33). Therefore the forward extension of the proctodoeum has to pass between the liver lobes and the yolk before it can reach the stomach wall. Thus the gut is formed entirely by the stomodoeal and proctodoeal invaginations and the endoderm does not enter into its formation.

Dorsal organ

By the time the embryo reaches the stage shown in Fig. 22 a group of free ectoderm cells dorsal to the cephalic lobe on the median side of the head appears as a whitish circular patch and forms the rudiment of the dorsal organ. The cells of this group are elongated radially with prominent rounded nuclei. A slight invagination at the posterior end (Fig. 40) transforms this group of cells into a bag-like structure.

When the invagination is complete the cuticular covering of the cells within the sac becomes thicker and corrugated as in Fig. 41. This corrugated cuticle is at first seen very close to the cells of the sac or almost touching them. The pre-antennulary mesodermal strands become attached below the dorsal organ at this stage. Later, the cavity of the sac enlarges and the cuticular lining appears roughly in the centre of the cavity with a space separating it from the cell layer. A narrow ridge originating from the posterior end of the opening of the sac runs towards the postero-ventral floor of the sac, dividing the cavity into two at the extreme posterior end (Fig. 42). The nuclei of the cells then become elongated and their cytoplasm drawn out. The yolk immediately below the dorsal organ is made up of smaller globules which stand out in contrast to the solid bulk of yolk mass seen in the centre of the embryo. Very often globules of yolk lie between and at times inside the cells. This relation and distribution of the yolk suggests that the dorsal organ plays a part in the absorption of the yolk.

Before the larva hatches the ectoderm cells grow towards the dorsal side and form a layer, separating the dorsal organ from the yolk in which it was immersed. In the larva, the dorsal organ is raised and during the subsequent moult it is cast off.

Pre-antennulary mesoderm

When the teloblasts have commenced active proliferation (Fig. 18) a group of 6–8 cells of the blastoderm lying between the optic rudiment and the antennule in a line with the rest of the naupliar appendages sinks into the yolk to form the rudiments of the pre-antennulary mesoderm (Fig. 43). The migrating cells have narrow attenuated ends towards the outside and swollen basal portions towards the yolk, and are strikingly unlike the surrounding ectoderm and mesodermal

cells in their prominent nuclei and darkly staining granular protoplasm. No difficulty was experienced in recognizing these cells in *Irona*, in contrast to *Hemimysis* and *Nebalia* (Manton, 1928, 1934), because of their slightly larger number and their contrasting staining reactions.

The group of pre-antennulary mesoderm cells has multiplied to form a solid mass of cells with ectodermal connexions in Fig. 44 and Diagram A, 1. A coelomic cavity is formed in the pre-antennulary mesoderm by the time the stomodoeum invaginates between the antennules and the antenna in the midventral

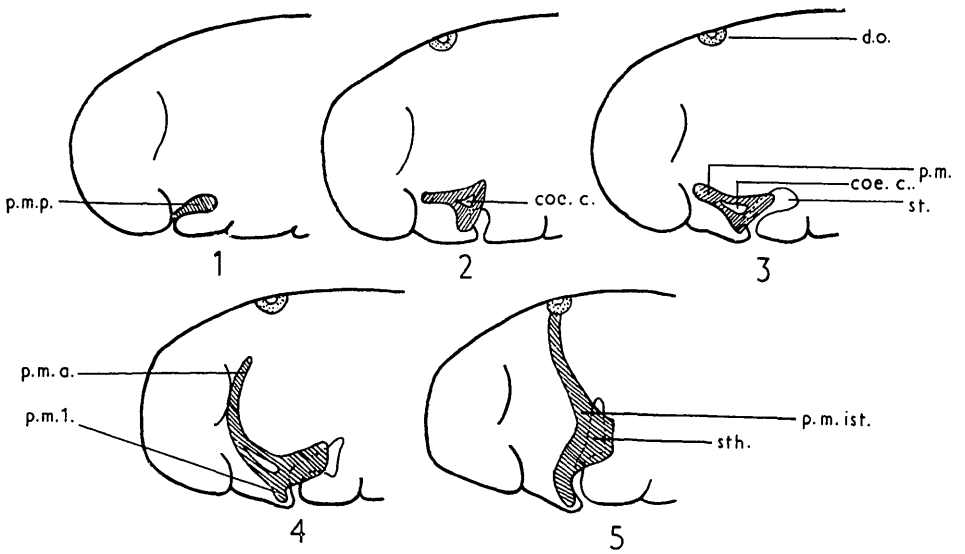

DIAGRAM A. Development of the pre-antennulary mesoderm. Key on p. 22.

region. Prominent changes in the pre-antennulary somite are noticed after the formation of the stomodoeum. The cells loose their ectodermal connexion and the two mesodermal blocks shift into the interior and come to lie obliquely, one on either side of the stomodoeum, their cavities enlarging. Later (Fig. 27), the cells of the posterior sac-like parts of the somite multiply in such a way that they give rise to two solid strands (Diagram A, 2). The ventral one grows towards the labrum, and from either side contributes towards the labral musculature. The other strand applies itself to the lateral walls of the stomodoeum (Diagram A, 3 and 4). The cavity of the somite develops only towards the stomodoeal branch and not towards the labrum.

The stomodoeal branch from each somite grows towards the dorsal side, the pair forming narrow solid divergent strands, the mesodermal cavity being confined to the region of the stomodoeum (Fig. 45). The broad ventral portion of the mesodermal mass, which first became attached to the stomodoeum, grows and meets its counterpart on the opposite side and forms an investment round the foregut. The divergent free ends of the blocks grow upwards along the inner side of the cephalic lobe and become attached dorsally to the tergum of the first

thoracic segment and then extend to the lateral margins of the dorsal organ (Diagram A, 4 and 5). Later still they grow under the anterior region of the dorsal organ, meet medially, and between them give rise to the lumen of the dorsal aorta (Fig. 46). The coelomic cavity becomes obliterated when the strands reach the dorsal organ and are converted into muscles.

As the dorsal organ grows and shifts above the surface of the embryo the pre-antennulary strands also become pulled upwards and with them the stomodoeum (see p. 9). During this process the curved mesodermal strands are straightened. The stomodoeal part of the pre-antennulary mesoderm gives rise to the circular muscles of the oesophagus and the muscles of the gastric mill, while the dorsal strands which suspend the stomodoeum at this stage later give rise to the dorsal mucles of the stomach. Thus from the pre-antennulary mesoderm are derived the labral muscles, the anterior end of the dorsal aorta, and the muscles of the gastric mill as well as the dorsal muscles of the stomach.

Naupliar mesoderm

The formation of the headband of mesoderm in the form of a V and its division into three pairs of somites at the nauplius stage has already been described. When the naupliar appendages become prominent, their mesoderm is derived from these solid somites which ultimately form the core of muscles. Sections of the naupliar region at different stages show that the headband is practically all used up in the formation of the naupliar appendages.

Liver

The liver has an undoubted endodermal origin in *Nebalia* and some other Malacostraca (Manton, 1934), but it was Manton (1928) who first described the development of the liver in *Hemimysis* from the mesoderm, unlike Bobretzsky (1874), Nusbaum (1886), Reinhard (1887), Roule (1895), McMurrich (1895), and Goodrich (1939), who believed that the liver had an endodermal origin. Nair (1939) described the liver in *Mesopodopsis* as originating from the naupliar mesoderm. In the development of the liver from the mesoderm, *Irona* resembles *Hemimysis* and *Mesopodopsis.*

In a median longitudinal section of a stage slightly earlier than Fig. 20, a group of about 7–10 mesoderm cells is noticeable in the maxillulary segment. These cells are characterized by their compactness and length as well as their darkly staining protoplasm. This is particularly clear when stained with haematoxylin. Sections of later stages (Figs. 21 and 22) show that this group of cells is the liver primordium. Since the products of the mesodermal teloblasts are arranged in rows one behind the other, and since this liver primordium occurs as a group of mesoderm cells distinct from the teloblastic products in the maxillulary segment, it is inferred that this group has originated from the apex of the V-shaped head mesoderm band formed at the naupliar stage.

As growth proceeds (Fig. 22) the development of the nerve ganglia of this

segment causes the division of the original central liver rudiments into two groups, one on either side (Fig. 47). In the next stage (Fig. 23) each group moves towards the lateral margins of the embryo and comes to lie as a plate between the yolk and the ectoderm. While so shifting the edges curl dorsally (Fig. 48), the rudiments becoming saccular. The isolated mesoderm cells often seen in the vicinity of the liver give rise to the connective tissue of the liver. Sections of the liver at this stage show that each rudiment grows in length and extends posteriorly to the maxillary segment.

In Fig. 24 each liver rudiment has its open end directed towards the dorsal side as before. The opening contracts slightly, and in Fig. 25 the primordium shows indications of three lobes (Fig. 49). These primordial lobes (Fig. 50) become differentiated into the three liver lobes of the adult. The growth of the liver in relation to other organs can be seen in Figs. 29–33. The sac-like primordium on either side, with its small opening dorsally facing the yolk, grows posteriorly in such a manner that, while the opening remains anterior, the three lobes extend backwards as far as the last thoracic segment. In this backward growth the three lobes become elongated into three hollow tubes, the anterior undivided part being still open towards the yolk (Fig. 32). Later the paired anterior openings of the liver primordium meet the wall of the stomodoeum as it grows backwards, and then open into its lumen (Fig. 33).

Histological changes in the liver cells during development. In Figs. 47–49 the walls of the liver sac are made up of compact uniform cells with no vacuoles, arranged in 3–6 rows. When the differentiation of the liver lobes starts minute vacuoles of about 1 μ diameter appear scattered in the protoplasm, and cell limits are not here discernible (Fig. 50). These vacuoles gradually enlarge and unite with each other to give larger vacuoles (Fig. 51) which are formed towards the interior of the lobes, the nuclei thus becoming displaced towards the periphery.

Sections taken along the length of the liver lobes show that in the most posterior region the vacuoles are large and are surrounded by a ring of nuclei while in the more anterior region where the cells are younger the vacuoles are small and not definitely arranged in relation to the nuclei.

Histological studies of later embryos show that these tubes help in the absorption of yolk, which in the absence of an endodermal mid-gut has to be utilized by different organs. Sections (Fig. 53) of the larva (Fig. 33) wherein the peripheral arrangement of the nuclei of the liver lobes is complete, show that the yolk surrounding the outer side of the lobes is broken up into small fragments. Figs. 52 and 53 show fragments (*y.b.*) of yolk very closely contiguous with the protoplasm of the liver lobes in which the nuclei are embedded. Here and there in the more posterior region of the tubes finer yolk particles (*y.p.*) are seen to lie between the nuclei, penetrating into the interior. Several such lines of small particles lead towards the lumen of the tube, where they lose their identity and appear to be absorbed. If this close association of the yolk outside the liver

lobes with the protoplasm of the liver cells is not interpreted as a process in the absorption of the yolk, it may suggest that the liver functions in the same way as the endodermal cells which surround the yolk during the formation of the mid-gut of decapods and mysids. Previous workers such as Bobretzsky (1874), Roule (1889), Bullar (1878), and Goodrich (1939) who studied the embryology of isopods may have been led to such an incorrect interpretation, in their search for uniformity with the rest of the Crustacea (see pp. 19–20).

When the larva hatches from the egg membrane, the protoplasm of the liver is highly granular, doubtless due to the absorption of yolk. The granules now do not stain with haematoxylin or eosin as did the yolk particles. It may be inferred that as the yolk fragments split and move towards the lumen of the tube they become chemically changed or absorbed.

Bullar (1878) in his sketches of sections of liver of *Cymothoa* indicates liver cells with vacuoles arranged in a similar manner. Unfortunately he has not interpreted the arrangement. It is very likely that in other cymothoans also the digestion of yolk by the liver cells may occur as in *Irona*.

Trunk mesoderm

When the rudiments of the naupliar appendages are differentiated from the arms of the V-shaped mesoderm band, and the liver rudiments are differentiated from the apex of the V, the eight mesodermal teloblasts lying below the ectodermal teloblasts give rise to sets of eight daughter cells in rapid succession. The eight cells of each set form the foundation cells of the mesoderm of each of the sixteen segments of the entire post-naupliar region (Fig. 54). Each segment at first possesses two rows of ectodermal cells. These as well as the foundation cells of the mesoderm divide rapidly. The mesodermal descendants arrange themselves in definite patterns as can be seen in Figs. 55 and 56, which are transverse sections through the metanaupliar region. When the eight foundation cells divide they give rise to an anterior row of eight cells, four of which after moving laterally to either side of the nerve-cord divide again and form a narrow band of eight cells (Fig. 56). The posterior eight cells also shift to either side of the nerve-cord. These cells also divide a second time, and their products shift so that four cells are crowded into a central group with a pair on either side, as seen in Fig. 55. Thus in each segment on either side of the nerve-cord there is an anterior strip of four cells closely set, and behind them eight cells arranged in three groups.

In Fig. 23 the number of cells forming the three posterior groups of cells within every segment has increased considerably although their arrangement is not altered. On each side of the nerve-cord three blocks of cells, the ventral, middle, and dorsal mesodermal blocks, can be seen (Fig. 57). In Fig. 24 the limb rudiment makes its appearance in each segment, and a block of cells enters the ectodermal dilatation to form the limb mesoderm which ultimately supplies the limb muscles. The dorsal block of mesoderm in each segment develops a cavity

(Fig. 57) and by further development gives rise to the heart, the pericardium, and the dorsal muscles in the posterior trunk segments, and to the dorsal aorta and muscles in the anterior eight post-mandibular segments. The ventral mesodermal block undergoes comparatively slower growth and gives rise to the ventral longitudinal muscles.

Meanwhile the closely set cells of the narrow band lying in the anterior part of each segment divide and increase in size. The inner end of this strip now shows a clear ectodermal connexion. Since there are no limb buds in this region, this strip divides into two, a ventral and a dorsal block. The former gives rise to the ventral muscles and the latter to the dorsal muscles, the heart, and the pericardium, in close relation with the posterior sets of mesoderm cells in the same

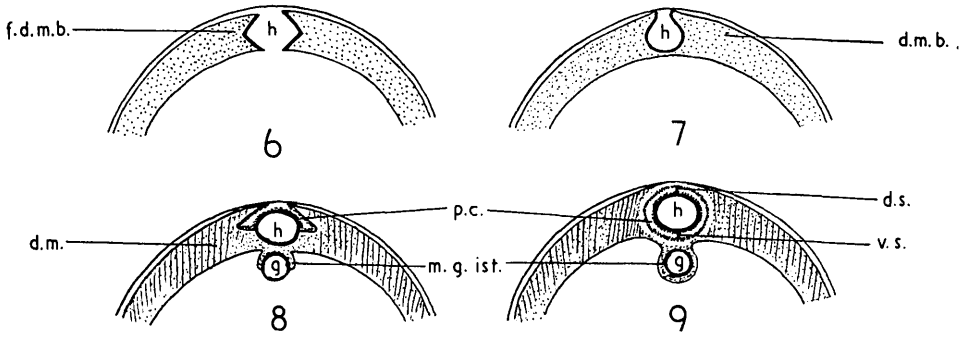

DIAGRAM B. Development of the heart. Key on p. 22.

segment. The cells of each segment multiply and differentiate in close relation to the cells of the segment in front and behind. As the heart is formed only in the abdominal and last two thoracic segments, the course of development of the dorsal blocks of cells in the maxillulary to sixth thoracic segment differs from that in the hinder region.

(A) *Development of the heart and pericardium.* Development of the heart first begins in the last abdominal segment and proceeds anteriorly to the sixth thoracic segment. All details of development of the heart can be seen in the same embryo (Fig. 31). The stages in the formation of the heart and pericardium are shown in Figs. 58 and 59 and Diagram B. The dorsal mesodermal blocks, which have the beginnings of the coelomic cavities, rapidly grow upwards as solid strips, the cavities being confined to the lower part of the mesodermal blocks. When the somites approach the mid-dorsal region from opposite sides each bifurcates into two branches (Diagram B, 6). The ventral branches unite with their fellows from the opposite side, while the dorsal branches attach to the dorsal body wall so that a haemocoelic space (*h*) is enclosed between the forks of the mesodermal blocks on either side, the dorsal ectoderm forming the roof (Fig. 58 and Diagram B, 7). This space so enclosed develops into the lumen of the heart.

Meanwhile the coelomic cavity within each mesodermal block attains its maximum size and extends upwards to about half the length of the block as a narrow elongated cavity with a thin inner wall made up of 1–2 rows of cells and a slightly thicker outer wall of 3–4 rows of cells. This cavity becomes obliterated by the multiplication of the cells on either side by the time the lumen of the heart is well established.

The rudimentary heart now develops a mesodermal roof by the multiplication of the cells from its sides (Diagram B, 8). By the time the roof of the heart is complete the bulk of the mesodermal strands differentiate into muscles dorso-laterally and two spaces appear on either side of the heart (Diagram B, 8). Each cavity is roughly triangular in cross-section and is roofed by the ectoderm above and flanked by the heart on one side and the differentiating dorsal muscles on the other side. These are the beginnings of the pericardium. The proctodoeum now lies below the heart. During further growth the pericardial cavity extends towards the ventral side encircling the heart laterally and ventrally. Cells from the ventral wall of the heart multiply and spread round the dorsal, lateral, and later the ventral surface of the gut (Fig. 59 and Diagram B, 8 and 9). Thus the ectodermal alimentary canal acquires a mesodermal investment. During the formation of this investment the pericardial cavities from opposite sides meet medially below the heart, leaving a thin septum dorsal to the proctodoeum. The pericardial wall extends more slowly towards the dorsal side of the heart, and then the heart sinks away (Fig. 59 and Diagram B, 9) from the ectoderm with which it retains its connexions by thin strands of mesoderm cells at irregular intervals along the mid-dorsal line. A compact pericardial wall is defined by the time the dorsal longitudinal muscles are fully formed.

(B) *Development of the dorsal aorta.* As the dorsal aorta represents the continuation of the heart anterior to the sixth thoracic segment, its development is essentially similar to that of the heart. The forks of the dorsal mesodermal blocks are smaller, the lumen of the aorta being formed by their union. Thus a median dorsal aorta is established from the sixth thoracic segment up to the cephalic region. The anterior tip of the aorta is formed from the pre-antennulary mesodermal strands (see p. 12).

Sections through the sixth thoracic segment of the stage in Fig. 28 show two constrictions dividing the lumen of the dorsal aorta in this region into three inter-communicating spaces at the junction of the aorta and the heart. The median space forms the dorsal aorta and the others form the beginnings of the lateral aortae which are completed after hatching.

Endoderm

The role of the endoderm cells in the formation of the liver in isopods has been emphasized by various investigators (Bobretzsky, 1874; Roule, 1891, 1894; Nusbaum, 1891*a*; and Goodrich, 1939). Since the results of the present investiga-

tion show that the liver is mesodermal in origin, the formation and fate of the endoderm cells were traced with special care in *Irona*.

Endoderm cells are seen to originate from two places: (1) the earliest endoderm cells from the mesendodermal plug (see p. 5), and (2) the later endoderm from the blastodermal cells posterior to the ectodermal teloblasts after the latter become arranged in a straight line (Fig. 23). Since the majority of the cells in the mesendodermal plug are used up in the formation of the headband of mesoderm, the mesodermal teloblasts, and the liver, only a few cells remain to contribute to the endoderm.

Isolated cells of the blastoderm posterior to the teloblasts migrate inwards and absorb yolk. These cells as well as the earliest endoderm cells form a thin endodermal sheet which extends forwards over the yolk below the mesoderm. This process continues to the stage of Fig. 22, where the endoderm forms a lining separating the yolk from the germinal disk which lies ventral to it. In Fig. 23 the endoderm cells grow towards the lateral and dorsal sides of the yolk forming an endodermal covering, namely, the yolk membrane. Sections of the yolk membrane (Fig. 34, *y.m.*) show the presence of many thin elongated cells which have cast off their yolk as well as many others which retain yolk to varying degrees. This suggests that some of the cells, after having absorbed the maximum quantity of yolk into their vacuoles, separate from it, as in other Malacostraca.

In Fig. 29 the yolk membrane is fully formed around the yolk and a number of cells are seen scattered in the yolk at varying distances from the yolk membrane. Their appearance and distribution show that they have separated and wandered into the yolk from the yolk membrane. These are undoubtedly vitellophags. Their protoplasm is spread round the nucleus in the form of radiating strands which penetrate into the yolk. This migration of the vitellophags into the yolk occurs from all sides of the yolk membrane, and while wandering the vitellophags are seen to divide and increase in number. These vitellophags help in the 'splitting of the yolk balls' (Bobretzsky, 1874) before they disintegrate. The presence of a large number of these vitellophags below the differentiating liver lobes suggests that they may be playing an important part in the transformation of the yolk in this area and thus facilitate the growth of the liver through the yolk.

As growth proceeds (Figs. 31 and 32) some of the vitellophags disintegrate in the interior of the yolk. The process of disintegration conforms to the usual course except for certain features. The nucleus shows 3 or 4 lobes (Fig. 60). Later the nuclear reticulum appears loose and the chromatin scanty as found in disintegrating vitellophags described by previous workers. The number of vitellophags decreases after the stage shown in Fig. 32. Only a few are seen scattered in the yolk of the larva and even these show a tendency to degenerate. Thus the endoderm cells do not contribute to the formation of any permanent organ in *Irona* (see p. 19).

DISCUSSION

The eggs of isopods were considered telolecithal by Dohrn (1867), Bobretzsky (1874), Roule (1889, 1890, 1891), and Nusbaum (1886), who did not study the egg in the unsegmented and early stages of cleavage. Reinhard (1887) first described the centrolecithal nature of the isopod egg in *Porcellio* and it was confirmed by McMurrich (1892, 1895). The protoplasmic connexions between the central and peripheral cytoplasm described by McMurrich for *Jaera* are not seen in the oocytes and the extruded eggs of *Irona*.

In the isopods, *Jaera*, *Asellus*, *Porcellio*, *Armadillidium* (McMurrich, 1895), *Porcellio*, *Armadillidium* (Goodrich, 1939), and *Cymothoa* (Bullar, 1878), the only membrane described is the chorion. In *Irona* also there is only one membrane, the chorion, which is secreted by the follicular cells. But during later stages a second membrane is secreted by the peripheral protoplasm of the embryo, making its appearance at the eight-celled stage. The late appearance of a vitelline membrane has been observed by van Beneden (1869) for *Asellus* and Terao (1929) for *Panulirus*.

The early cleavages of *Irona* resemble those of *Porcellio* and *Armadillidium* (McMurrich, 1895), the mysids (Manton, 1928; Nair, 1939), and *Nebalia* (Manton, 1934) in that these divisions take place within the yolk but do not affect it. The blastomeres appear on the surface of the egg in *Irona* at the eight-celled stage, but in *Porcellio* not till the thirty-two-celled stage, and in mysids a completed layer within the yolk is formed before the blastomeres appear on the surface. In the early appearance of the blastomeres at the periphery *Irona* shows more resemblance to *Nebalia*, in which the cells reach the surface of the egg at the four-celled stage.

A tendency for a group of 10–11 cells to move ahead of the others in a circle from their pole of origin to the opposite pole is an unusual feature. The present study of *Irona* shows that the egg and embryos are less determinate than are those of *Jaera* (McMurrich, 1895); the blastoderm cells in *Irona* are so alike that the cells which are destined to become the mesoderm and endoderm cannot be recognized in the early stages.

The type of germinal disk formation in *Irona* is more like that of *Leander* (Sollaud, 1923) than that of a mysid (Manton, 1928; Nair, 1939). In *Hemimysis* the germinal disk starts as a transverse band which later becomes V-shaped. In *Nebalia* (Manton, 1934) the germinal disk is at first pear-shaped, then it divides anteriorly, becoming V-shaped and later U-shaped as in Decapoda. Though the germinal disk of *Irona* is pear-shaped to begin with as in *Nebalia*, it does not become either a V or a U. In *Irona* the mesendodermal plug gives rise to mesoderm from the anterior and endoderm from the posterior regions, a spatial relationship characteristic of Malacostraca (Manton, 1928).

The entire post-mandibular region in *Irona* is formed by the activity of the teloblasts as in other Malacostraca (Manton, Nair, and others). The absence of

a caudal furrow may be due to the fact that the growth of the post-mandibular region is relatively slow and the elongated egg gives the embryo ample room for developing its entire length on the surface without folding inwards.

Irona resembles *Hemimysis* (Manton, 1928) in the prolonged endoderm formation from the blastoderm cells situated behind the teloblasts. Differentiation of the vetellophags occurs rather late and, unlike a mysid, all the endoderm cells or vitellophags disintegrate without contributing towards the formation of any permanent tissue of the isopod. In *Porcellio* and *Armadillidium* Goodrich (1939) has described a 'clumping' of 4–6 cells of the serosal nuclei which he marks clearly inside the yolk in his figures. These, from their position, must be considered to be vitellophags. A casual study of *Irona* may also suggest such a condition, but careful examination will show that there is no real grouping of cells. The nucleus of each vitellophag becomes lobed prior to its breaking up, and in this condition the nucleus gives the appearance of 4–6 nuclei coming together.

The discovery of the pre-antennulary mesodermal somite, first reported by Manton (1928) in *Hemimysis* and then in *Nebalia* (1934) has since been recorded in *Mesopodopsis*, *Squilla*, and *Caridina* (Nair, 1939, 1941, 1949) and *Palaemon* (Aiyer, 1949). The two species of *Irona* investigated here conform to the general features outlined by Manton (1928). In *Irona* a coelomic cavity is formed as in *Hemimysis* but is obliterated before the mesoderm strands reach the dorsal organ. The second cavity described for *Hemimysis* does not appear in *Irona*. The pre-antennulary mesodermal somites move between the cephalic lobes to reach the dorsal side of the animal as in *Nebalia*. This course of the somites between the cephalic lobes may be due to the lesser quantity of yolk present in the head at this stage.

The liver is mesodermal in origin in *Irona* as well as in the mysids (*Hemimysis*, Manton, 1928, and *Mesopodopsis*, Nair, 1939). Manton (1928) has defined the features which distinguish endoderm cells from those of the other two germ layers in *Hemimysis*, and these features can only be seen with good fixation. Not being able to distinguish the endoderm from other tissues, the older writers, Dohrn (1867), Roule (1891, 1894), Reinhard (1887), and Nusbaum (1891*a*, 1898) considered the liver to be endodermal. Even Goodrich (1939) has not recognized these cytological differences, and has described the liver in *Porcellio* and *Armadillidium* as endodermal. He failed to note both the origin of the liver from the naupliar blastoporal mesoderm, and its mesodermal character.

Diagnosis of the endoderm is essential in following the origin and formation of the gut. In *Irona* the yolk membrane is the homologue of the endodermal mid-gut of mysids and decapods, but it does not contribute to the formation of the gut as in mysids (Manton, 1928; Nair, 1939), decapods (Sollaud, 1923; Nair, 1949; Aiyer, 1949), and the Leptostraca (Manton, 1934). Manton (1928) suggested that if the proctodoeum were to become longer in a form like *Hemimysis*, then many of the yolk cells would not be included in the formation of an endo-

dermal mid-gut and would degenerate. As shown above, the ectodermal proctodoeum of *Irona* extends forward so completely that the endoderm cells are all excluded.

Since the gut of *Irona* is ectodermal, and the endodermal yolk membrane is broken up and functionless in the later embryonic stages, some device for yolk absorption appears to be necessary. Evidence has been given to show that the liver performs this function. Manton (1928) found alterations in the yolk taking place opposite the future lumen surface of the liver lobes, and this presumably occurs as a result of their presence. In *Nebalia* also yolk is absorbed from the lumen surface of the liver lobes (Manton, 1934). *Irona* is remarkable in the yolk absorption taking place from the future external surface of the liver lobes. Yolk particles are found also in the dorsal organ which therefore may assist in absorption of yolk. The capacity of the adult liver cells to absorb fat and other food substances has been observed by McMurrich (1898), Murlin (1902), Nusbaum (1917), Nicholls (1931), and Chandy (1938). McMurrich (1898) even suggests that in parasitic isopods 'the intestine, not being absorptive but merely serving as a passage for the extrusion of undigested material, is, in *Bopyrina*, exceedingly reduced, while the digestive and absorptive liver pouches are enlarged'. From the present study it appears that the absorptive capacity of the liver cells is a marked feature of *Irona* in the embryonic stages.

As in other Crustacea the heart and dorsal aorta are formed from a fork of the dorsal mesodermal blocks. The pericardial floor is differentiated at a late stage from the dorsal mesoderm after the formation of the heart in *Irona*, unlike *Hemimysis* (Manton, 1928) wherein it is differentiated at a very early stage.

SUMMARY

1. The structure of the egg is described.

2. Segmentation of the egg is followed from the eight-celled stage up to the formation of the blastoderm. A migration of blastomeres from one pole of the egg towards the opposite has been observed and in the course of this migration a circle of 10–11 cells moves in front of the others.

3. Gastrulation takes place by immigration. A V-shaped mesodermal headband is differentiated which gives rise to the rudiments of the naupliar appendages after gastrulation is completed.

4. The entire post-naupliar region of the body is formed by the activity of ectodermal and mesodermal teloblasts. No caudal furrow is formed.

5. The gut is ectodermal, formed by the union of the stomodoeum and a long proctodoeum.

6. An ectodermal dorsal organ forms in early development and persists throughout embryonic life. The pre-antennulary mesodermal strands become attached to this organ.

7. The origin, development, and derivatives of the pre-antennulary mesodermal somites are described.

8. The origin of the liver is traced from the naupliar mesoderm. The probability that the liver plays an important part in yolk absorption is discussed.

9. The development of the trunk mesoderm and an early grouping of cells into segmental and intersegmental regions are described.

10. The formation of the heart, pericardium, and dorsal aorta is described.

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EXPLANATION OF FIGURES

ABBREVIATIONS

a.a., anterior aorta. *a.1*, antennule. *a.2*, antenna. *bl.*, blastomeres below the peripheral protoplasm. *bl.a.*, blastoporal area. *bl.d.*, blastodisc. *bls.*, blastomeres on the surface of the egg. *c.*, circle of ten blastomeres. *c.c.*, corrugated cuticle. *c.d.*, cavity inside the dorsal organ. *ch.*, chorion. *c.l.*, cephalic lobe. *cl.r.*, cephalic rudiment. *c.l.r.*, cephalic lobe rudiment. *c.m.b.*, central mesodermal block. *c.n.*, central nucleus. *c.p.*, central protoplasm. *coe.c.*, coelomic cavity. *c.r.*, crescentic row of blastoderm cells. *d.a.*, dorsal aorta. *d.c.*, degenerating cells. *d.m.*, dorsal muscles. *d.m.b.*, dorsal mesodermal block. *d.o.*, dorsal organ. *d.s.*, dorsal septa in the pericardial cavity. *e.*, eye. *end.*, endoderm. *end.a.*, area of endoderm formation. *e.t.*, ectodermal teloblast. *f.d.m.b.*, fork of the dorsal mesodermal block. *g.*, gut. *g.m.r.*, gastric mill rudiments. *h.*, heart. *i.g.*, inner group of segmental mesoderm cells. *l.m.*, limb mesoderm. *li.ce.*, liver lobe. *li.ru.*, liver rudiments. *lu.li.*, lumen of the liver tubes. *man.*, mandible. *man.p.*, mandibular palp. *max.1*, maxilla 1. *max.2*, maxilla 2. *max.p.*, maxilliped. *m.en.*, mesendodermal cells. *m.en.p.*, mesendodermal plug. *m.g.*, middle group of segmental mesoderm cells. *m.g.ist.*, mesodermal investment of the gut. *m.m.b.*, middle mesodermal block. *m.t.*, mesodermal teloblast. *n.g.*, nerve ganglion. *o.g.*, outer group of segmental mesoderm cells. *oes.*, oesophagus. *op.r.*, optic rudiment. *p.c.*, pericardial cavity. *pl.1–5*, pleopods 1–5. *p.m.*, pre-antennulary mesoderm. *p.m.a.*, anterior strand of the pre-antennulary mesoderm. *p.m.c.*, coelomic cavity of the pre-antennulary mesoderm. *p.m.ist.*, investment of the pre-antennulary mesoderm over stomach. *p.m.l.*, labral branch of the pre-antennulary mesoderm. *p.m.r.*, rudiment of the pre-antennulary mesoderm. *p.p.*, peripheral protoplasm. *pr.*, proctodoeum. *p.rid.*, posterior ridge of the dorsal organ. *p.w.*, pericardial wall. *st.*, stomodoeum. *st.f.*, flask-shaped stomodoeal sac. *sth.*, stomach. *tel.*, telson. *th.l.1–6*, thoracic legs 1–6. *t.m.*, telson mesoderm. *ur.*, uropod. *v.*, vacuole. *v.m.b.*, ventral mesodermal block. *vi.*, vitellophag cell. *v.s.*, ventral septa in the pericardial cavity. *y.*, yolk. *y.b.*, yolk fragment. *y.g.*, yolk globule. *y.m.*, yolk membrane. *y.p.*, yolk particle.

DESCRIPTIONS OF FIGURES

1. Section of the extruded egg.
2. Section of the egg at the eight-celled stage, before the blastomeres have emerged from the yolk. Two blastomeres are seen.
3. Lateral view of the egg at the eight-celled stage.
4. Lateral view of the egg at the sixteen-celled stage showing the ring of ten cells.
5. Lateral view of the egg at the thirty-two-celled stage, slightly tilted to show the ring of ten cells.
6. Lateral view of the egg showing migration of cells to form the blastodisc.
7. Blastodiscs, being completed, on surface of the egg. (Blastomeres on the opposite side are dark.)
8. Surface view of the blastodisc before gastrulation showing the crescentic row of cells and three proliferating areas.
9. L.S. of germinal disk of the same age as Fig. 8, before gastrulation.
10. L.S. of a blastodisc showing immigration of a single cell.
11. L.S. of a blastodisc showing a few cells immigrated.

12. L.S. of a blastodisc showing the shallow depression (the blastoporal homologue).
13. L.S. of the blastodisc showing the mesendodermal plug.
14. L.S. of the mesendodermal plug showing degenerating cells.
15. Nuclei of cells at different stages of degeneration:
    (*a*) nucleolus globular; two other globules have also appeared inside the nuclear reticulum;
    (*b*) globules increased in size;
    (*c*) two of the globules have fused;
    (*d*) nucleus before rupturing; a large globule has almost filled the entire nucleus.
16. Surface view of the blastodisc showing the ectodermal and mesodermal teloblasts.
17. Slightly sagittal section of the embryo of the same age as Fig. 16, showing ectodermal and mesodermal teloblasts.
18. Surface view of the blastodisc showing the teloblastic row straightened.
19. L.S. of the embryo of the same age as Fig. 18.
20–28. Post-naupliar stages as described on pp. 7–8.
29–33. Diagrammatic representation of the development of heart, liver, and gut at various stages of growth.
29–32. Lateral view of the embryos represented in Figs. 25–28.
33. Lateral view of the newly hatched larva.
34. L.S. of the embryo of the same age as in Fig. 21; the rudiments of all body segments are established.
35–37. Three stages in the formation of the stomodoeum.
38–39. Two stages in the development of the proctodoeum.
40. L.S. of the embryo of the same age as in Fig. 23, showing the cuticular lining receding from the invaginated sac (dorsal organ).
41. L.S. of an embryo of the same age as in Fig. 26, showing the cuticle becoming corrugated.
42. T.S. of an embryo of the same age as in Fig. 27, passing through the posterior ridge of the dorsal organ showing the two cavities; yolk particles seen inside are dark.
43. Parasagittal section of an embryo of the same stage as in Fig. 20, showing the immigration of the pre-antennulary mesodermal cells.
44. Parasagittal section of an embryo of the same age as in Fig. 21. Pre-antennulary mesoderm is growing backwards as a solid strand, from its ectodermal connexion.
45. T.S. of an embryo older than in Fig. 31, showing the course of the pre-antennulary mesodermal strands and the coelomic cavity fully developed.
46. T.S. of an embryo older than in Fig. 32, showing the formation of the dorsal aorta from the pre-antennulary mesoderm.
47–53. Sections showing the development of the liver.
47. T.S. through the maxillulary segment of an embryo of the same age as in Fig. 22, showing the liver rudiment lateral to the nerve ganglion.
48. Embryo as in Fig. 23. T.S. showing the curling of the liver rudiment dorsally.
49. Embryo as in Fig. 25. T.S. showing the liver rudiment forming a sac.
50. Embryo as in Fig. 26. T.S. showing the lobing of the liver sac.
51. T.S. through the second thoracic segment of an embryo showing the three liver lobes cut in a transverse plane; vacuoles are being formed in the liver cells.
52–53. T.S. and L.S. respectively of the liver lobes of the larva showing the absorption of the yolk by the liver cells. Yolk particles of varying sizes are represented as black dots.
54. T.S. through the posterior region of an embryo as in Fig. 21 showing the eight mesodermal teloblasts.
55. T.S. of the same embryo as in Fig. 54 passing through the second thoracic segment showing the three groups of mesoderm cells in the segmental region.
56. T.S. through the inter-segmental region between the second and third thoracic segments of a slightly older embryo than the last showing the single mesodermal strand.
57. Same embryo as in Fig. 23. Transverse section through the fourth abdominal segment showing the formation of the coelomic cavity in the dorsal mesodermal block.
58. Transverse section through the third abdominal segment of an embryo of the same age as in Fig. 26, showing the dorsal block of mesoderm forking to form the heart.

59. T.S. through the fourth abdominal segment of the larva showing the heart and the pericardium.

60. Lobing of the vitellophag nuclei before disintegration.

Approximate Magnifications

Figs. 1–7, ×32; 8–14, ×160; 15, ×360; 16–19, ×160; 20–33, ×32; 34–59, ×160; 60, ×360.

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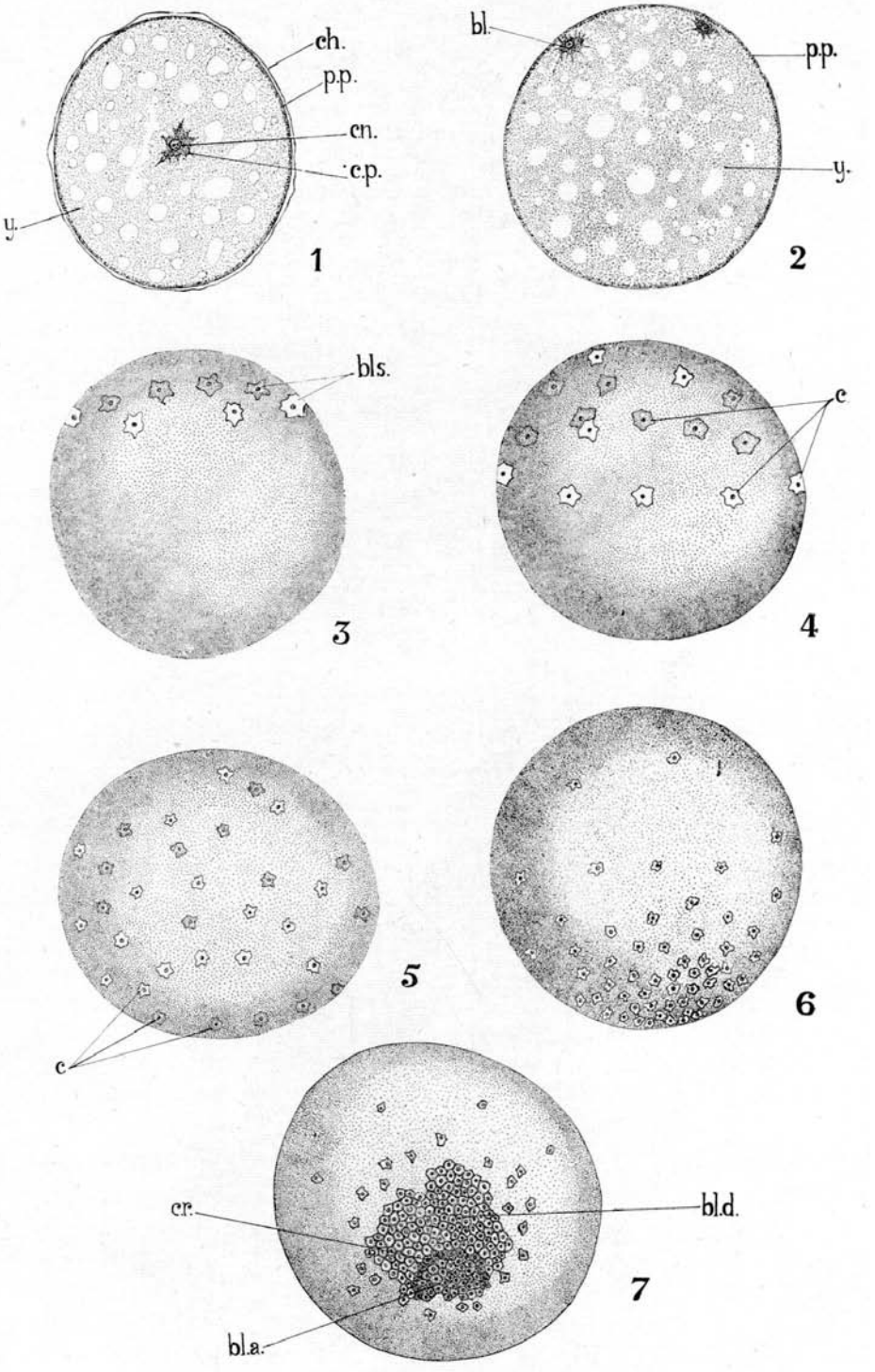
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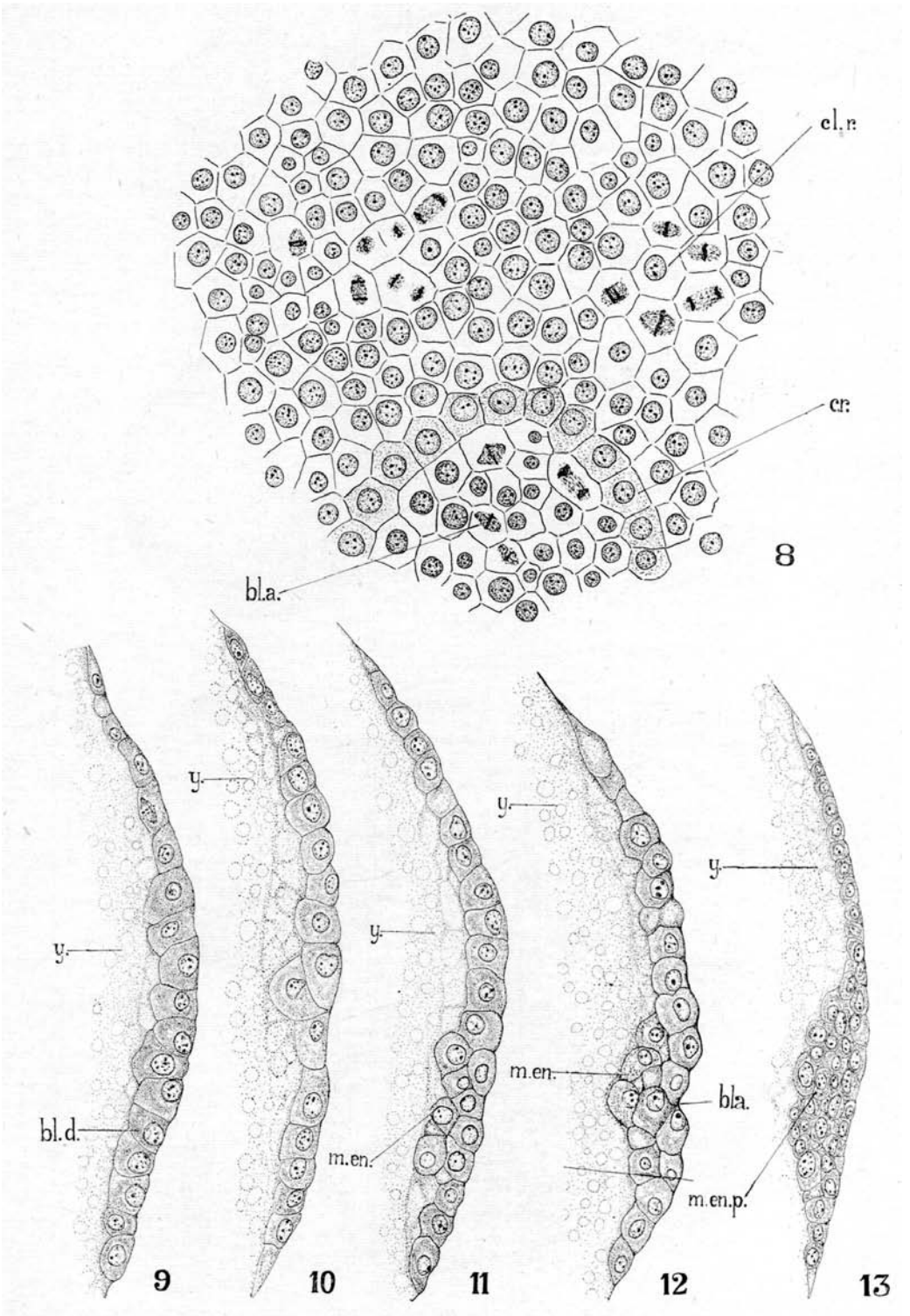
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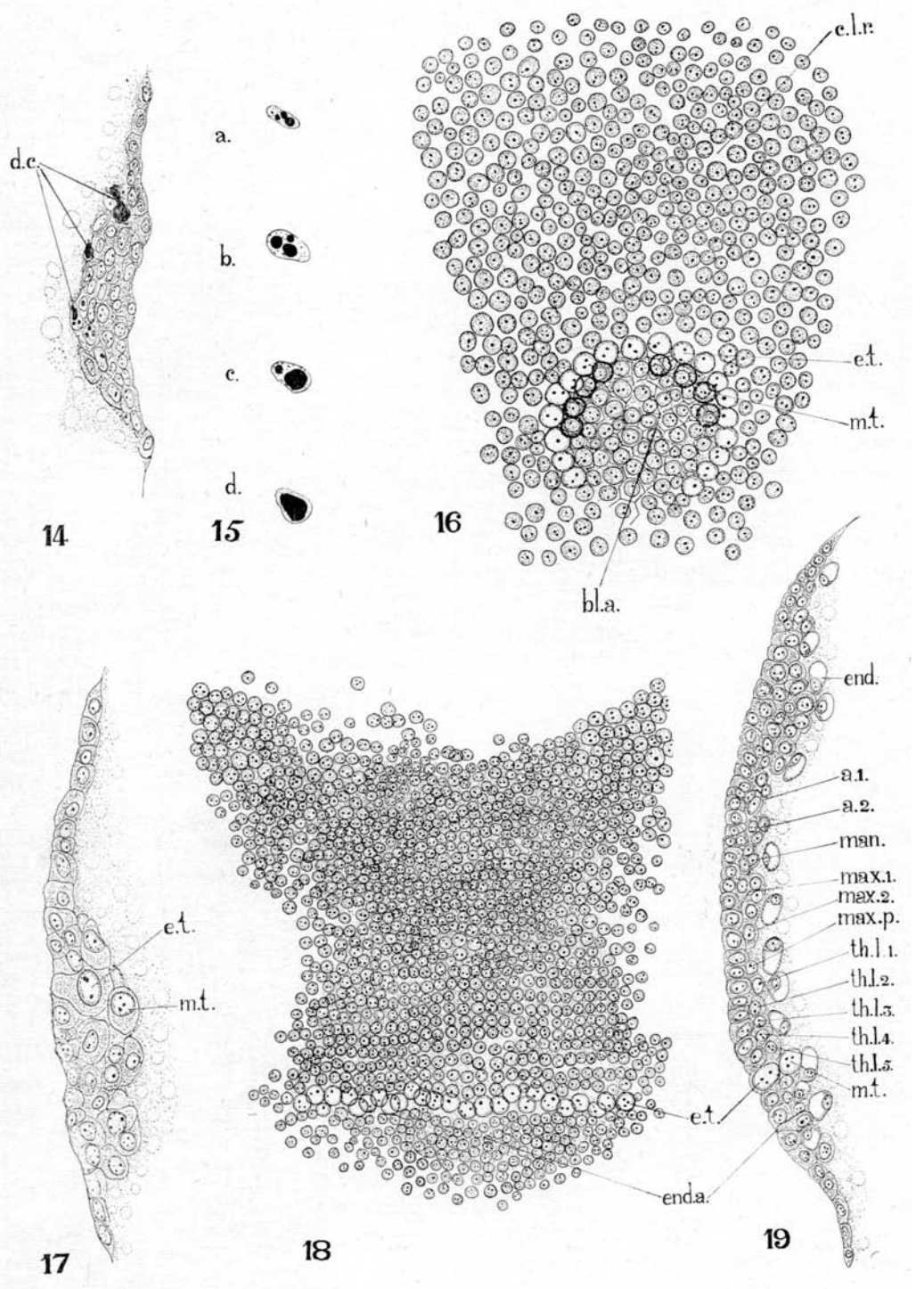

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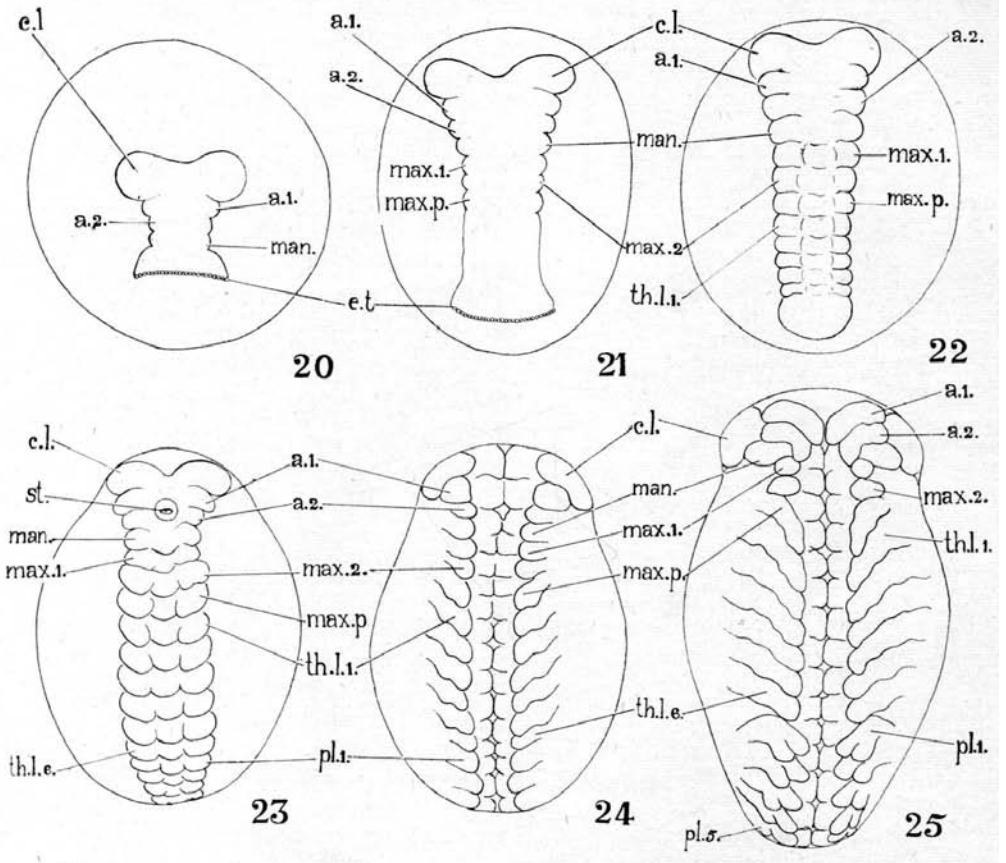
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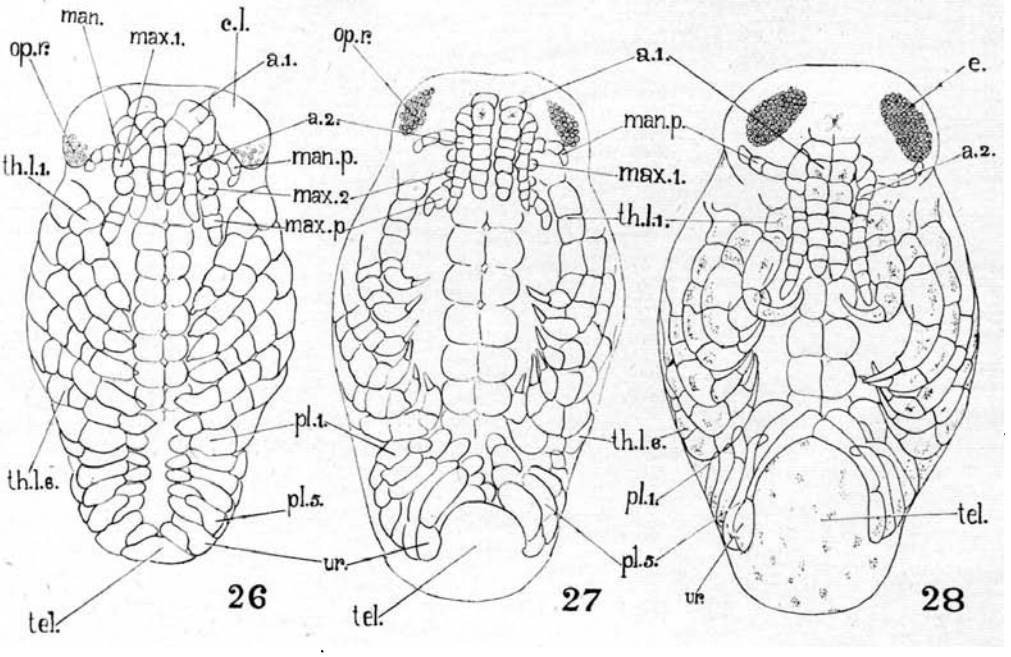
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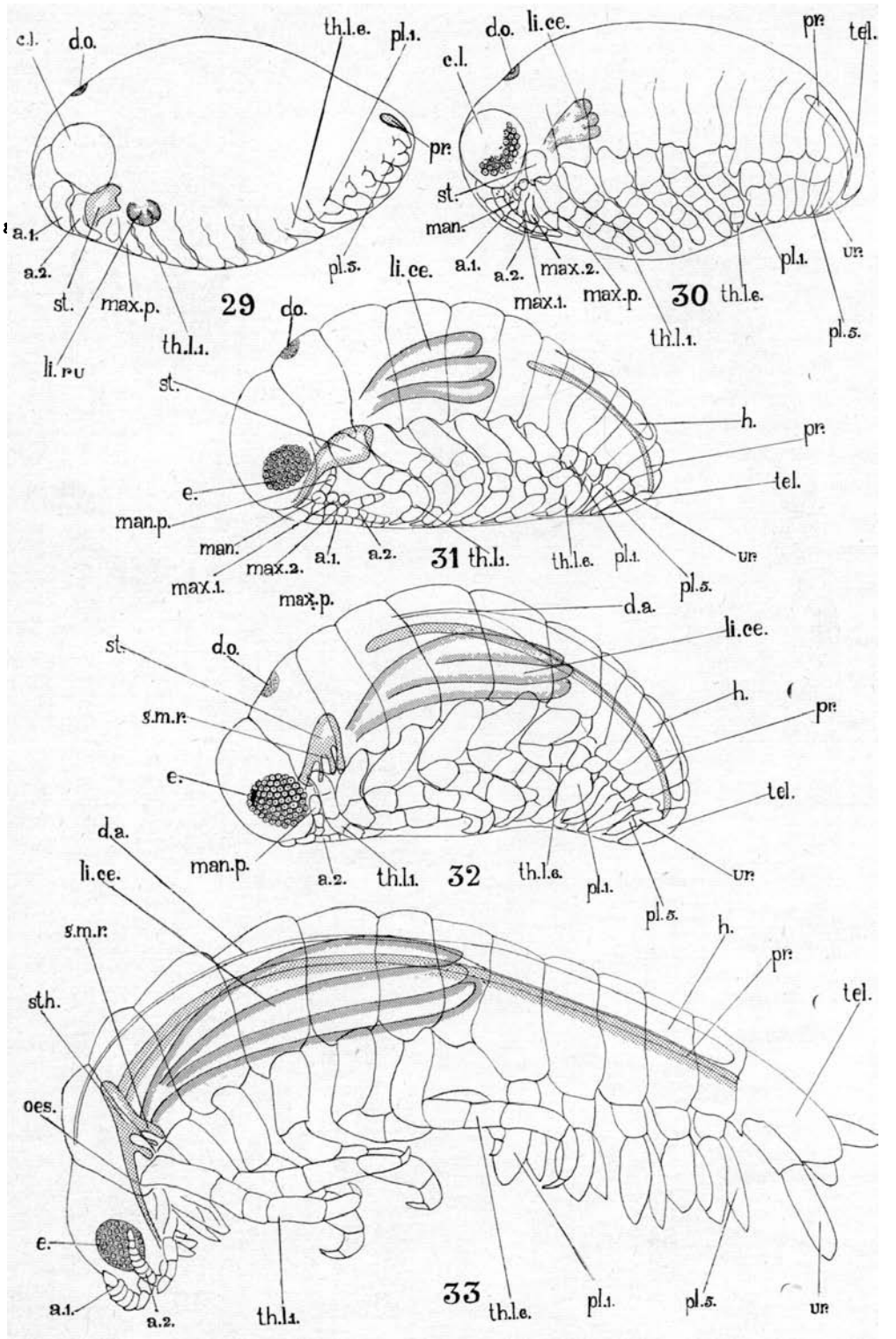
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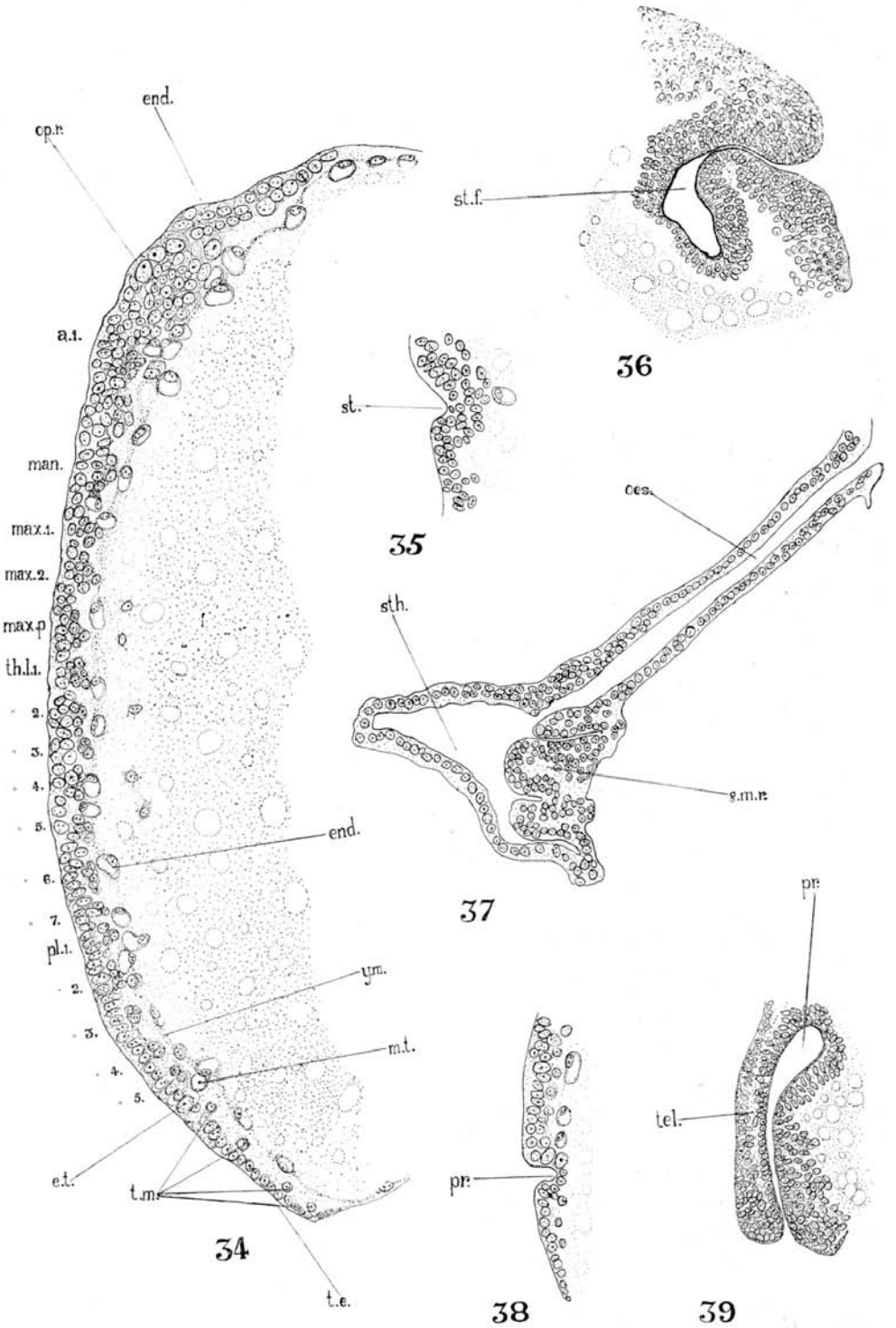
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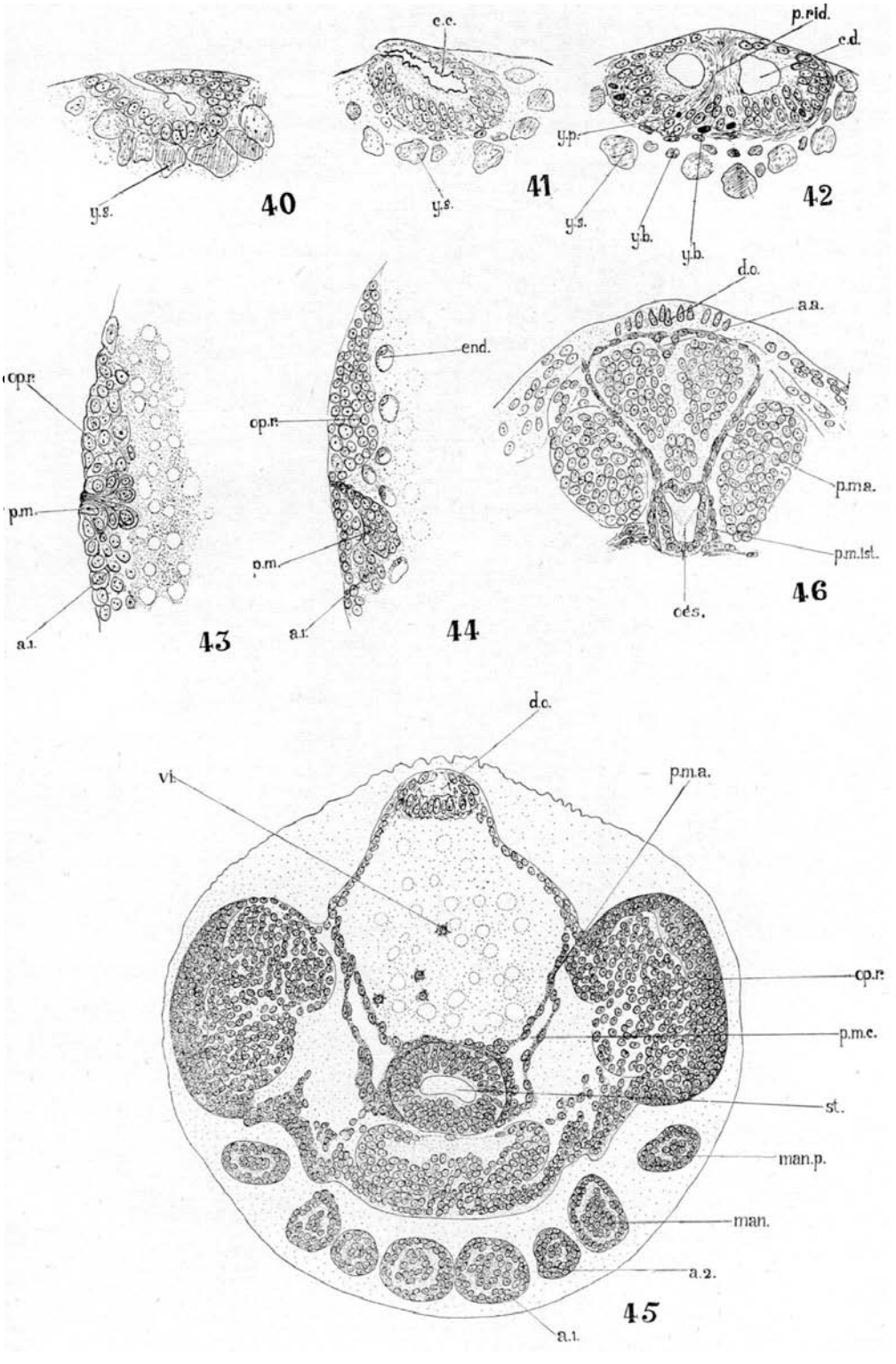
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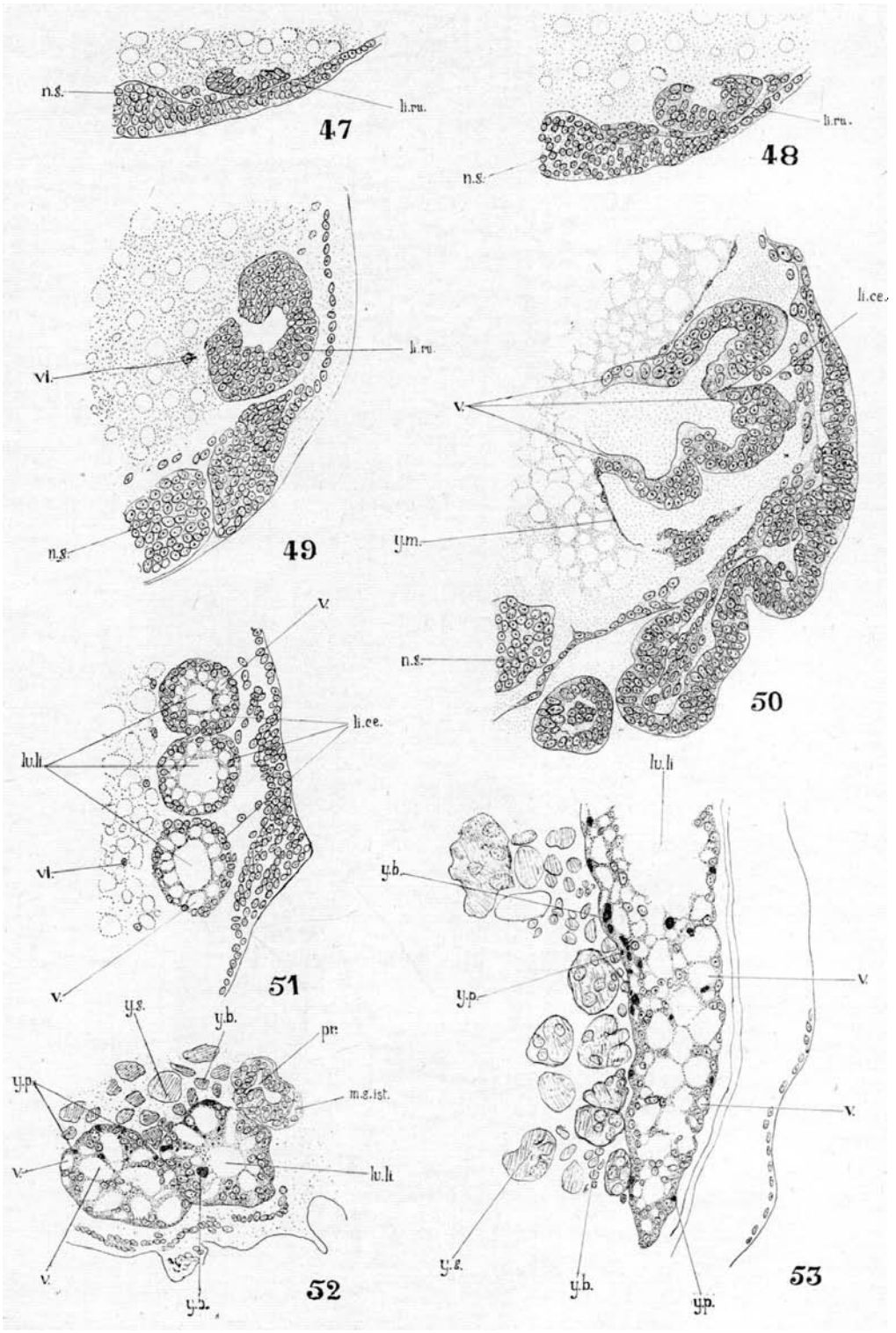
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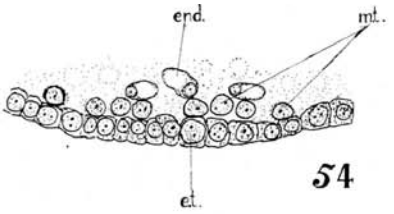

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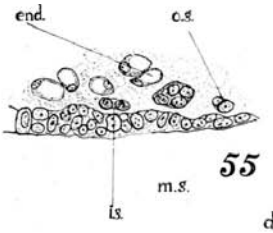

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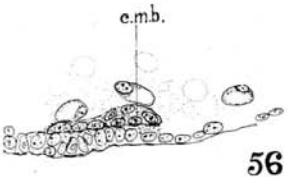

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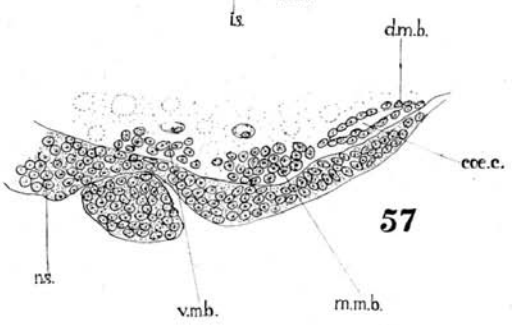

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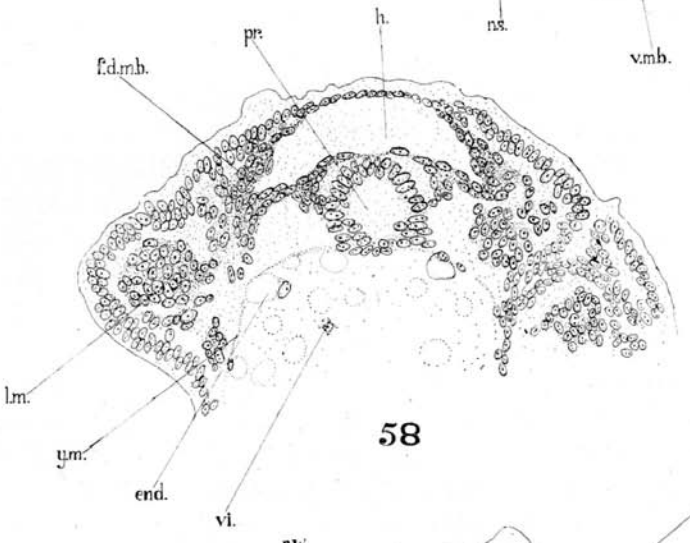

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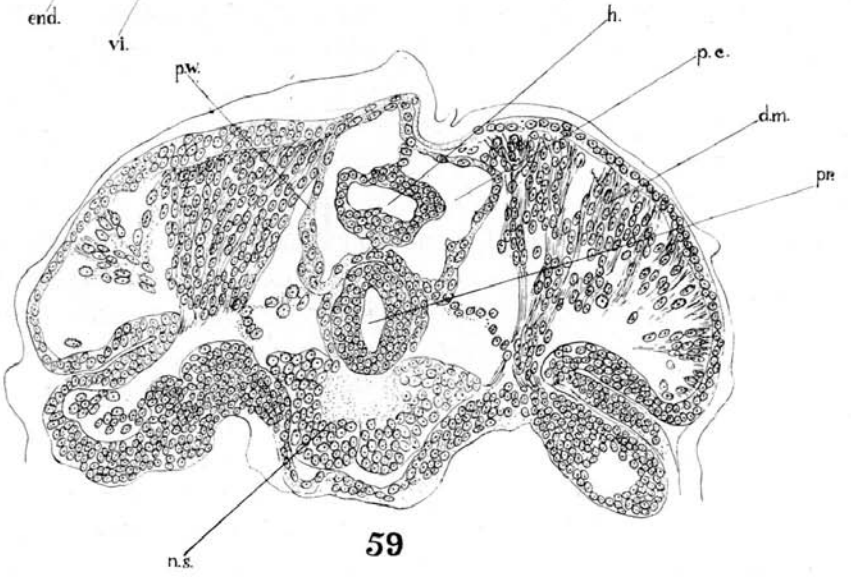

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