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Studies on the Embryology of *Squilla oratoria* de Haan

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Introduction

Although many works have been published on the embryology of the Crustacea during the last hundred years, little has been contributed to that

of Stomatopoda. BROOKS (1892), who succeeded in collecting a good number of eggs of *Gonodactylus chiragra*, was not interested in its embryonic development and confined his studies to the larva after hatching. GIESBRECHT (1910), having made an observation about the egg laying in *Squilla mantis*, reported the constitution of the egg clusters in that species, but he again did not go into embryology. The subject was first studied by KOMAI (1924) with *Squilla oratoria* as material. The principal features in the development of this species as specified by KOMAI are: 1) the flatness of the embryo in its early stages; 2) the presence of the egg-nauplius stage, 3) and of a stage in which there appear 7 pairs of limbs; 4) the maintenance of the ventral curvature of the embryo, and 5) the absence of the dorsal organ. He emphasized the similarities in the development of *Squilla* to that of Decapoda, Mysidacea as well as Nebaliacea. His studies, however, were limited to the external change of the embryo and the internal development has remained untouched up to the present.

The present study was undertaken primarily for the purpose of elucidating the internal changes which take place in the course of the entire embryonic life. The second object of the investigation was to contribute something to our knowledge on the phylogeny of this abberant crustacean from the standpoint of ontogeny. Although the results of my observations extend much beyond those described in the following pages, the present circumstance does not permit me to give a full account. I shall therefore confine myself to a description of the essential parts of the results for the present, but it is hoped that I shall have an opportunity in the future to report the rest of the work.

This investigation was carried out under the supervision of Prof. T. KOMAI. It gives me much pleasure to take this chance to express my hearty thanks for his courteous directions and valuable criticisms.

Material and Technique

The ova of *Squilla oratoria* DE HAAN, used as material, were collected at Oyehama, Kasaoka, Okayama Prefecture, in June of 1937 and 1938. There the mantis shrimps inhabit burrows in the muddy beach which are bare or nearly bare at low tide. It was very easy to attack the dwelling and fish the mother shrimp with her brood; in this way I obtained about 300 egg-clusters. As Oyehama is a small village lacking facilities for the use of biological instruments, I was obliged to give up the observation of living ova and my rearing experiments.

Various fixatives were tried, such as: picro-nitric acid, BOUIN's fluid, PETRUNKEWITSCH's, ZENKER's, FLEMMING's, CARNOY's, REICHENBACH's method and acetic-sublimate solution. Of these the last named, i. e. saturated solution of sublimate in 5% acetic acid heated to a temperature of 70°—75°C, gave the most satisfactory results. The material was fixed for 3-12 hours and washed with iodinized 70% alcohol. After removing the

chorion with a fine needle the egg was stained with either borax-carmine or DELAFIELD's haematoxylin modified by CONKLIN (DELAFIELD's haematoxylin 10 cc., water 40 cc. and KLEINENBERG's picro-sulphuric acid 10 drops) in order to facilitate the orientation. Ceder-wood oil or oil of bergamot was used as clearing agent from 96% alcohol. When the yolk was so brittle that the material crumbled in front of the knife because of long preservation, the following precaution was employed. That is, the exposed surface of the material in the paraffine block was wiped with a brush moistened with a very weak solution of celloidin and gum masticum (with caster-oil added) just before cutting each section. Sections were cut 6-10 μ thick and stained with DELAFIELD's haematoxylin and eosin or iron haematoxylin counter-stained by orange G. MALLORY's triple stain gave good differential staining for examining fibrous tissues and chitinous structures in the older embryos. For the toto-preparation CONKLIN's solution named above proved very useful for preventing the yolk from staining. The surface study of the embryo was made with ceder-wood oil, the viscosity of which facilitated the rotation of the egg under the cover-glass in observing it from all sides.

General Remarks

As KOMAI (1924) has given a precise account of the brood-caring of the mother shrimp and the constitution of the egg-cluster, it may be unnecessary to repeat it again.

Egg Membrane. The ova are enclosed in two tough membranes, the internal being chorion and the external exo-chorion (after ZEHNDER's terminology, 1934). The exo-chorion is provided with an indefinite number (5-10) of filamentous elongations extending to the same membrane of neighbouring eggs. Connected by these filamentous parts all the eggs aggregate to form a disk-like compact egg-cluster.

In the youngest brood collected (8-cell), the exo-chorion had not yet taken a definitive form and all eggs, enclosed only by the chorion, were closely agglomerated in an irregular mass by a viscous gelatinous substance. In the fixed condition this substance forms a thick membrane around the whole egg mass, sending out many folds or lobes between the egg-spherules. These lobes gradually penetrate into all interstices between the eggs and separate them. This substance solidifies with the effect of water and becomes the membraneous covering of the egg; the part of the membrane in contact with that of the neighbouring egg develops into long filament. By the blastula stage the exo-chorion has completed its definitive constitution. GIESBRECHT (1910), who made an observation of the brood of *Squilla mantis* two days after oviposition, states: "Laich nunmehr zwar die Form eines flachen runden Fladens angennomen hatte, das der Kitt aber nicht von normaler Beschaffenheit war, denn er hatte sich nicht zu den die Eier verbindenden Bälkchen umgeformt, sondern bildete zwischen den Eier eine noch ziemlich klebrige homogenes nur stellenweise etwas

faserige, elastische Mass, aus der eine Menge Eier während Kretens herausfielen". He considers this condition an abnormal state due to the confinement of the mother in an aquarium for two weeks. However, the same cluster was found in the 32-cell stage on the third morning according to his report; thus such a state seems to have been a natural one, representing, in my opinion, nothing but a stage in the normal course of development of the exo-chorion.

The same author further observed that the white markings on the sternum of the thoracic segments of the gravid female had disappeared with oviposition. ZEHNDER (1934) reports similar patches on the female abdomen of *Astacus* which he found represented the tegumentary glands that furnish the source of the exo-chorion. It is highly probable, therefore, that in *Squilla* also the exo-chorion is produced by these white glands.

In a later developmental stage a third membrane is secreted from the egg body to lie inside the chorion. This membrane which represents the embryonic exuviae will be described later.

A Brief Sketch of the Developmental Course. KOMAI (1924) gives a precise description of the external changes which occur during the embryonic development, dividing the whole course into 11 stages. As for the division of stages, I largely followed him except in a few case which were altered merely for convenience in describing the internal development. The main changes taking place in each developmental stage may be tabulated as follows:

Table 1: The stages in the embryonic development of *Squilla oratoria*, with brief descriptions of the changes occurring in each of them.

Stage	Changes in each stage
0	Segmentation (figs. 11–13).
1	Blastula, last segmentation stage (fig. 15).
2	Gastrula, appearance of blastopore, and immigration of mesendoderm cells.
3	Establishment of optic lobes and ventral plate followed by closure of blastopore; beginning of extra-blastoporic cell-sinking, differentiation of mesoderm layer from mesendoderm, and of mesoteloblasts (fig. 1).
4	Appearance of proctodaeum, differentiation of endoderm plate from mesendoderm, and first development of naupliar appendages (figs. 2 & 3).
5	Appearance of stomodaeum, protrusion of posterior endoderm plate as the intestine, differentiation of ectoteloblasts, and upheaval of appendages and thoracico-abdominal process (fig. 4).
	Appearance of 3 pairs of cerebral and mandibular ganglia, constriction

6	of appendages from egg surface and beginning of the forward growth of thoracico-abdominal process (fig. 5).
7	Differentiation of retina cells and optic ganglion, formation of nerve fibres, external development of maxillular and maxillar segments, and appearance of serum space (fig. 6).
8	External development of maxilliped 1 and 2 segments and succeeding several segments, completion of ectoteloblastic ring, dislocation of anus to the end of telson accompanied by the development of caudal furca, appearance of dorsal organ, and formation of anterior endoderm plate (fig. 7).
9	Branching of antennules, forward elongation of maxillipeds 1 and 2, disappearance of dorsal organ followed by embryonic ecdysis, completion of retina and ganglionic layers, formation of heart and blood corpuscles, and ventral displacement of anus.
10	Differentiation of visual elements associated with pigment formation both in compound and median eyes, completion of all body-segments, development of pleopoda, segmentation of all limbs, formation of rostrum and carapace, disappearance of caudal furca, appearance of muscle fibres, and protrusion of posterior liver lobes (figs. 8 & 9).
11	Last embryonic stage just prior to hatching: erection of eye stalk,liberation of maxilliped 1 and 2 segments from the cephalic region, attainment of the posterior liver lobe as far as telson, and formation of anterior and lateral mid-gut cœca (fig. 10).

Since all the organs of the body undergo conspicuous differentiation from stage 8 on, it is desirable to divide the stages more minutely than has KOMAI. For this the number of segments which are externally differentiated serves as the criterion. I shall use such expressions as "stage Th 5" and "stage Abd 3" in the following description to indicate the stages in which the external differentiation of segments reaches the 5 th thoracic and the 3rd abdominal segments. Simultaneously with the completion of the last abdominal segment, the posterior liver lobe begins to protrude from the mid-gut and, after entering the thoracico-abdominal process, it gradually extends to the posterior end of the process. The degree of elongation of the liver lobe therefore furnishes a criterion for discriminating the developmental stages subsequent to the formation of the last segment. Thus, "stage L, Th 5" and "stage L, Abd 3" denote the stages in which the posterior liver lobe reaches the 5 th thoracic and the 3 rd abdominal segments respectively. When the lobe enters the telson (abbreviated "stage L, T"), hatching takes place.

PART I EARLY DEVELOPMENT

1 Segmentation

The 8-cell ova (fig. 11), the youngest stage collected, are nearly spherical

and measure 0.51-61 mm (averaging 0.53 mm) in diameter. The filamentous part of the exo-chorion are not yet developed, and all the ova are closely aggregated; when fixed, they become more or less irregular in shape due to mutual pressure. In these ova no segmentation furrow is observed on the surface. All the nuclei which have submerged in the yolk are found slightly above the center of the egg, being distributed uniformly around it. They are oval and composed of granular nucleoplasm containing an irregular mass of chromatin substance. Each of them is surrounded by a small quantity of cytoplasm with fine pseudopodia-like processes radiating in all directions like an amœba. These processes, however, neither join with those of other blastomeres, nor do they reach the egg surface. The blastomeres are quite isolated from one another without forming any cytoplasmic reticulum crisscrossing the entire yolk. There is apparently no peripheral protoplasmic layer around the egg surface. The superficial layer of the egg plasm stuffed with very small yolk spherules. These spherules gradually become larger toward the center of the egg and merge into the undivided homogeneous yolk mass which, however, shows little difference in its chemical constitution from the peripheral yolk.

The nuclear division from the 8-cell to 16-cell stage takes place almost simultaneously and in the tangential direction in all blastomeres. The division figure belongs to the type reported by ZEHNDER (1934) as peculiar to the crustacean ova with abundant yolks; that is, the cytoplasm assumes a dumbbell-shape in the metaphase stage, while the chromosomes are still on the equatorial plate, so that cytoplasmic division precedes chromosomal division (fig. 12). In the earlier 16-cell stage the daughter nuclei derived from the same blastomeres of the previous stage lie close to each other in pairs. Later they part and all the nuclei become scattered about uniformly in the egg plasm. The positions of the nuclei within the plasm become somewhat more raised than before, with their distance from the center 3, 5-4/5 of the radius.

All nuclei of the 16-cell stage divide tangentially and more or less synchronously as before, and continue to shift toward the surface of the egg. At the close of the stage the blastomeres are situated close to the egg surface, but separated from it by a thin layer of yolk spherules. The division of the 32-cell stage is also simultaneous. In the next division (64 to 128), however, notable differences in the stage of nuclear division become apparent among blastomeres. In fig. 12 the nuclei are in the metaphase on the right side of the egg, while on the left side the anaphase is the predominant stage; in the central part the blastomeres are in an intermediate state between the two. In the 128-cell stage all the nuclei with their surrounding cytoplasm completely break through the yolk to the surface none remaining within. They are arranged evenly on the egg surface without showing any regional difference in their distribution. The granular cytoplasm containing the nuclei spreads all over the egg surface

and sends very fine processes into yolk crevices. In the later period of this stage the segmentation furrows in all the blastomeres simultaneously become perceptible for the first time, and the egg surface is sectioned into small polygonal areas. These furrows, however, are only superficial in this stage.

The synchronism is lost in the division of the 128-cell nuclei. While in one region of the egg the nuclei are in the midst of division, the division is over and the daughter nuclei remain close to each other in pairs in another; in still another region they have already parted. Such different stages however never mingle, and the nuclei in a region are in more or less the same stage. The nuclear division first begins in the region which probably corresponds to the future germinal region and proceeds centrifugally toward the periphery, almost to the other side of the egg. Thus a zonal distribution of nuclei in the same phase of division is observed. The division wave, however, does not appear actually to reach the antipole, since the number of nuclei in the ova of this stage, which ranges between 200 and 230 (fig. 13), never reaches 256. In the mean time the segmentation furrows become deeper and extend into the yolk, diving it into many primary yolk pyramids (fig. 14). The interpyramidal boundaries remain very short attaining a distance of only about 1/10 of the egg radius from the surface, leaving the greater part of the yolk undivided. The external surface of the pyramid is covered with a thin coat of protoplasm showing a slight convexity. I was unable to determine whether the peripheral protoplasm extends internally to the lateral side of the pyramid or not.

When the number of nuclei attains 450-500, the hemisphere of the egg where the germinal disk is to develop becomes denser in nuclei than in the other half (fig. 15, *g. r*). This is principally due to the acceleration of karyokineses in the denser region; more precisely, it is due to the fact that before a karyokinetic wave reaches the animal pole, another wave is started in the vegetal area; these succession of waves are repeated. In this stage, the last stage of blastula, the ovum is entirely surrounded by a cell-layer which is the blastoderm. The cytoplasm of these cells is lentiform in section and sends out fine precesses into the deutoplasm which anastomose with the processes from the neighbouring cells. The vertical borders of the yolk pyramids are almost completely obliterated, yet the cell boundaries are clearly seen in surface view. The central part of the yolk, remaining quite homogeneous, has no "Centralkörper" which was found in *Astacus* (REICHENBACH, 1886); in the peripheral layer a decomposed yolk substance of more or less granular appearance is found here and there mixed with ordinary yolk spherules. No nucleus remains in the yolk.

In short, the *Squilla* egg is centrolecithal and undergoes partial cleavage; the primary yolk pyramids are rather rudimentary and of short duration.

2 Gastrulation

The blastula, which has more than 500 nuclei, exhibits a prominent regional difference in the distribution of cells, as the whole surface is divided into two hemispheres, one crowded and the other sparse with nuclei. The former hemisphere represents the first rudiment of the germinal disk and the future ventral side of the embryo (fig. 15, *g. r*). An eccentric small area particularly dense in nuclei becomes apparent in this hemisphere (fig. 15, *bp'*). This area, characterized by somewhat deeper staining reaction of its nuclei than elsewhere, is triangular, crescent or oval. This is the region where the blastoporic invagination takes place shortly afterwards, and it marks the posterior end of the germinal disk. At the periphery of the denser hemisphere many mitotic figures which contribute to the formation of the germinal disk are seen (fig. 15). Nuclear divisions occur in the blastoporic area, also indicating that they are the principal cause of the formation of the area. In the other hemisphere, on the other hand, no nuclear division can be observed. Judging from the fact that in this stage the density of nuclei in the animal hemisphere is much smaller than that of the previous stage, the formation of the germinal disk on the vegetal pole may be partly due to the condensation of the nuclei. The diversity in the shape of the blastoporic area in different eggs, even of the same batch, is apparently due to individual variation rather than to the difference in the developmental stages.

In the area corresponding to the future blastopore (fig. 16, *bp'*), the surface of the blastoderm is more or less flattened and composed of cells arranged in a pavement-like manner, showing clear cellular borders on the surface. The cytoplasm is thicker than in the other region and contains somewhat deeper staining nucleus. Outside this area the blastoderm becomes gradually thinner toward the antipodal region where the cytoplasm is reduced to a mere membrane with very flattened nuclei.

With further development the blastoporic region becomes smaller, with component cells closely aggregated. The cells become taller and cylindrical, and show nuclei in the innermost part. Soon afterwards the distal ends of these cylindrical cells incline toward the center of the blastoporic area, presenting a bouquet-like arrangement. Throughout the whole course of these changes the cell borders remain distinct. The underlying yolk mass is divided into cylinders composed of numerous yolk spherules, corresponding to the protoplasmic cylinders. The yolk cylinders are distinct for some distance below the surface and merge inwardly into the undivided central mass. The overlying cells send fine protoplasmic processes, which may be made out with some difficulty, into the crevices between the yolk spherules. The processes also cover the lateral sides of the yolk cylinder. This state which bears some resemblance to the condition of the primary yolk pyramids lasts only for a short time.

The condensation of the blastoderm toward the blastoporic area gives a lateral pressure to the superficial layer which becomes depressed at this point. The depression of the surface, gradually growing deeper, develops into a conical blastoporic invagination. In consequence, the cells are forced to sink into the yolk one after another, forming a temporary sub-blastoporic cell complex (fig. 22). The sunken cells, showing very clear boundaries, do not form a syncytium as in *Panulirus* (TERAO, 1929) etc., but soon become liberated from the complex one by one to migrate in all directions, like so many amœbae, through the crevices of yolk spherules. The yolk cylinders, which have been observed beneath the blastopore, have completely disappeared by the commencement of the cell immigration.

All nuclear divisions take place tangentially and never radially from the beginning of segmentation to the last blastula stage. As soon as the gastrulation sets in, radial nuclear divisions first become apparent in the peripheral region of the blastopore, though divisions in other regions are all tangential. Thus wandering cells are produced not only by the sinking of the cells from blastoporic region but also by the radial division at the periphery. They multiply actively by mitosis, both while in the sub-blastoporic cell complex and in the course of migration. KOMAI (1924) did not observe the blastopore, but this is apparently due to the lack of the stage which shows distinct invagination among his material; in fact the stage appears to be of very short duration.

3 Formation of Germ Layers

Germinal Disk. As stated in the preceding chapter the first rudiment of the germinal disk is indicated by the greater density of nuclei. The germinal disk occupies an extensive area extending over nearly a whole hemisphere of the egg by the time the nuclear migration begins at the blastoporic region. The blastopore situated at the margin of this hemisphere marks the posterior end of the longitudinal axis of the germinal disk. Close to the anterior margin of the disk and on both sides of its longitudinal axis, the blastoderm cells accumulate to form a pair of more or less oval areas. These areas represent the optic lobes whose longer axes are trasverse to the germinal disk (fig. 1, *o. l*). The lobes, situated nearly a quarter of the egg's circumference away from the blastoporic region, form an isosceles triangle with the latter.

Shortly after the establishment of the optic lobes, further accumulation of cells takes place on each side of the germinal disk and gives rise to a pair of bands crowded with nuclei. These bands (fig. 1, *ect. b*), extending from the blastopore to the posterior margin of the optic lobes on either side, transform the germinal disk into a U-shape. As the result of the condensation of the formative cells of the blastoderm toward these bands, the central portion of the germinal disk grows much more scarce in nuclei than before. A similar, more pronounced condition is observed in the extra-

germinal region, especially in the part antipodal to the disk. Further development of these rudiments is carried out principally by active cell multiplication.

The optic lobes and lateral ectoderm thickenings are composed of a layer of cubic epitherial cells containing round or oval nuclei (figs. 20-21, *ect. b*). The cells gradually become shorter toward the periphery of the rudiments, continuing without any distinct demarcation to the extra-germinal region in which the cells are flattened and more or less lentiform, and their nuclei appear to be spindle-shaped in section (fig. 19). The cells composing the mid-ventral region (fig. 18) are also flattened and very similar to those of the extra-germinal region.

Yolk Cells. Although the cells which sank from the margin of the blastopore develop into a temporary cell complex, they do not form any conspicuous "plug of mesendoderm" as in Decapoda (TERAO, 1929, etc.). The submerged cells soon become liberated from the complex to migrate in all directions through the yolk (fig. 22, *y. c*). They make their way only through the superficial layer of the yolk not far from the egg surface to disperse, not beneath the germinal disk alone, but also toward the extra-germinal region and sometimes, though rarely, to the deeper part of the yolk. A surface study of an egg in an earlier stage of migration clearly indicates that the wandering cells are scattered within a circle described with the blastopore at its center. Later, however, these cells move to all parts of the superficial yolk.

The wandering cells, namely the yolk cells (figs. 17-24, *y. c*), possess nuclei with denser chromatin than those of ectoderm cells. They actively multiply by mitosis while migrating, but never by amitosis which has been occasionally reported in decapod yolk cells. These yolk cells are variable in shape, for in most cases they are amœboid, being more or less polygonal, stellate or lunar. They are situated in the crevices of yolk masses. Some of them enclose in their cytoplasm small, apparently decomposed yolk particles (fig. 17, *y. c*). In others the cytoplasm presents a crescentic form tapering at both ends into very thin processes which appear to meet each other on the opposite side, thereby encircling a large block of yolk. These cytoplasmic processes, however, are generally difficult to make out except in short bits (fig. 28, *y. c*). The yolk cells sometimes have rather indistinct contours and are surrounded by a swarm of small yolk particles, some of which enter the cytoplasm. The yolk cells may also occupy the peripheral part of a large yolk mass and encroach upon a portion of the mass itself. There are even cases where they are situated in the center of a large yolk block with their cytoplasm distinct from, or confluent with, the deutoplasm (fig. 31, *deg'*).

As the cell emigration from the blastopore proceeds, the degeneration of yolk cells becomes apparent. Disintegration figures may be found everywhere under the blastoderm and even directly beneath the blastopore.

The process of cell degeneration consists in the decomposition (fig. 17, *deg*) and diffusion of the chromatin substance in the nucleus, followed by a dissolution of the nuclear membrane (fig. 31, *deg'*). The chromatin thus liberated at first forms an irregular mass of a deeply and uniformly staining substance, which breaks down subsequently into numerous small particles of chromidia (figs. 31, etc.). The chromidia eventually lose their staining capacities to become, together with the cytoplasm, indistinguishable from the deutoplasm.

As stated above, the yolk cells rarely reach the deeper part of the yolk. Most of them are found within the undivided block of yolk and not in the yolk crevices (fig. 31). Perinuclear protoplasm can be made out in some cases, but in others it cannot be distinguished from the yolk, presenting the appearance of nuclei directly surrounded by deutoplasm. In all circumstances the nuclei, having diffused chromatin, show signs of disintegration; liberated chromatin balls may occasionally be found in place of the nucleus. All the yolk cells that migrate in the central part of yolk therefore degenerate sooner or later and never reach the blastoderm on the other side of the blastopore to form the primordium of the mid-gut, contrary to cases reported as found in Decapoda by CANO (1893 a, b), HERRICK (1892), and others. At about the time of the closure of the blastopore, all the cells rise to the inner face of the blastoderm, except a few which lie at some distance beneath the surface.

Although the yolk cells are supplied chiefly by the immigration from the blastopore, they also originate in other sources. Before the blastoporic invagination takes place, one or a group of several cells are at times found below the blastoderm in a region somewhat apart from the future blastopore which is defined by an accumulation or a thickening of cells. As an example of such a case, an inner cell found under the blastoderm of the extra-blastoporic region is shown in fig. 16 (*im'*). The egg from which this figure was drawn was in the last blastula stage, being composed of about 500 blastomeres and having none of the inner cells except the one in the figure. In another case this inner cell was found in mitotic division. In the egg drawn in fig. 25 (*im'*), the inner cells are represented by a (probably syncytial) mass of six cells (one of them being found in the next section). They still retain protoplasmic connection with the surface, indicating their derivation from the blastoderm just above them. Since all the segmentation nuclei rise to the surface in the stages up to the 128-cell, it is evident that the inner cells illustrated in these examples do not come from their remaining in the yolk without taking part in the blastoderm formation. Further, the fact that they are found under the extra-blastoporic region prior to gastrulation, tells their origin to be from the blastoderm and not from the blastopore. These facts remind us of the "primary yolk cells" of Decapoda (HERRICK, 1892; SOLLAUD, 1923) which similarly come from the blastoderm before gastrulation. Such a derivation of yolk cell

apparently occur very commonly in that order though rather exceptionally in *Squilla.*

The immigration of yolk cells from the extra-blastoporic region also occurs in the course of gastrulation. Fig. 26 (*im'*) shows a yolk cell lying below the blastoderm and nearly antipodal to the blastopore. In this egg all the yolk cells derived from the blastopore were confined within a circle described with the blastopore at its center and passing the posterior margin of the optic lobes. No yolk cell was found beyond this circle except the one mentioned just above. Since the cell lies thus apart and isolated from other cells, it is believed to have been derived from the overlying blastoderm. In fig. 18, showing the mid-ventral region of an egg of a slightly more advanced stage, one of the blastoderm cells is now going to submerge into the yolk to become a yolk cell. In fig. 19, which was drawn from another egg of the same stage showing the extra-germinal region behind the blastopore, the blastoderm cells are also in various stages of sinking. Moreover, radial division of the blastoderm cells were sometimes observed on the lateral margin of the U-shaped ectoderm band. The internal daughter-cell produced by such a division may develop into yolk cell. It must be concluded, from the fact enumerated above, that the yolk cells originate from the extra-blastoporic region as well as from the blastopore. Some consideration will be made later for the question of the germinal layer to which these cells ought to be assigned.

Naupliar Mesoderm. In an earlier period of gastrulation in which the yolk cells do not extend beyond the optic lobes, a pair of mesoderm plates closely attached to the ectoderm (fig. 20, *mes*) appear on either side of the blastopore. The plate is one-cell thick and composed of cells probably derived from the anterior and lateral edges of the blastopore. Each of the plates makes its way forward along the lateral thickening of the ectoderm, and becomes inserted between this and the yolk surface. At the time of the closure of the blastopore, the plate extends as far as the posterior margin of the optic lobe (fig. 21, *mes*). The posterior end of the plate is directly continuous to the sub-blastoporic cell complex. Thus the plates on both sides together form a U-shape much like the ectoderm band, though somewhat narrower. The mesoderm bands, composed of loosely connected spindle-shaped cells containing slightly flattened nuclei, are in close contact with the lower side of the ectoderm (fig. 20, *mes*). These bands give rise to the mesoderm elements of the naupliar region, i. e. the region in front of the maxillular segment. The mid-ventral region of the germinal disk as well as the extra-germinal region is devoid of mesoderm cells.

At the beginning of their proliferation the mesoderm cells are morphologically indistinguishable from the yolk cells. The discrimination can be made only after the establishment of the mesoderm layer. Therefore, the inner cells constituting the sub-blastoporic cell complex can only be said to be termed "mesendodermal" (fig. 22). The later differentiation of the

mesendoderm reminds us of the Decapoda and presents a striking contrast to the morphological distinction of the two elements in the Mysidacea which are clearly differentiated from the beginning, even before gastrulation. MANTON (1928), who has demonstrated the spacial relations between the germ-layers in the blastosphere of *Hemimysis* paid special attention to the fact that the sinking of the mesoderm takes place in the region anterior to that which produces the endoderm. Quoting many investigations on this subject, she has suggested that this may be considered a universal scheme in the germ-layer formation of this sub-class in general. In *Squilla* the proliferation or the sinking of the mesoderm cells are actually observed in the anterior lip of the blastopore. It seems probable, therefore, that the mesoderm is formed from the more anterior region than the endoderm which immigrates from the base of the blastoporic invagination. There is no sound evidence, however, to prove that none of the immigrants from the blastoporic invagination takes part in the formation of the mesoderm bands. On the contrary, it can not be maintained that all the cells derived from the anterior margin of the blastopore develop into the mesoderm. At any rate, any distinct spacial relations such as that found in Mysidacea are not observed in *Squilla*.

As stated before, the yolk cells make an ascent to the surface at the close of gastrulation. These cells are attached to the lower surface of the ectoderm or the mesoderm. They are sometimes found to be about to touch the ectoderm on the immediate lateral side of the mesoderm band. It is not improbable that they join the mesoderm band, losing their primary characteristics as the "vitellophags"; as a matter of fact, this has been actually observed by HERRICK (1892) in *Alpheus*. Cases in which some of the mesoderm cells show division in radial direction may also be found. Since the mesoderm band remains one-cell thick for a long time up to the earlier egg-nauplius stage, the division seems to show the proliferation of yolk cell from the mesoderm rather than the multiplication of the mesoderm cell itself.

The mesoderm cells are also derived from the ectoderm cells constituting the lateral thickening. Fig. 21 (*im*), an example of such a case, shows the sinking of an ectoderm cell near the posterior end of this thickening. Although a decisive observation to show whether these sinking cells represent the mesoderm or yolk cells is lacking, it is very unlikely that they submerge into the yolk by penetrating the underlying mesoderm layer and become the yolk cells. New cells are supplied to the mesoderm also by the radial division of the ectoderm cells of the lateral band.

Preantennulary Mesoderm. The component cells of the optic lobes are somewhat larger than those of the lateral ectoderm thickenings from the beginning. The cells grow much taller and cylindrical with development. Apparently indicating a sign of sinking from the surface, the cytoplasm of some of these cells is attenuated toward the outer end, having a nucleus

at the inner end (fig. 29, *o. l*). Actual cell sinking takes place first at two points far apart from each other, namely in the inner and outer parts of the optic lobe, and then can be seen along the whole length of the posterior margin of the lobe. The immigrated cells come together and form a loose layer under each optic lobe (fig. 23, *pa. mes*). The layers of both sides then extend internally to meet each other, as well as posteriorly to join with the naupliar mesoderm. Thus a complete ring of a layer of inner cells is produced beneath the germinal disk. These immigrants from the optic lobes are, without doubt, homologous with the preantennulary mesoderm of Mysidacea (MANTON, 1928) and Nebaliacea (MANTON, 1934), and may well deserve the same term. This is the only mesoderm derived from the extra-blastoporic region among these orders. In view of the facts observed in *Squilla*, however, the formation of the preantennulary mesoderm appears to represent nothing but a specialized and more concentrated state of the sinking of mesoderm cells which takes place in the lateral ectoderm bands.

Mesoteloblasts. Before the differentiation of the naupliar mesoderm from the sub-blastoporic mesendoderm cell complex, several large inner cells different in their constitution from others are proliferated from the anterior lip of the blastopore (fig. 22, *mes. tel*). When the paired naupliar mesoderm bands are laid down, these cells are aggregated in an irregular mass anterior to the blastopore at some distance from it, and inserted between the posterior part of both mesoderm bands (figs. 20 & 34, *mes. tel*). They are eight in number, rich in cytoplasm and possess round vesicular nuclei containing large nucleoli. These cells represent the mesoteloblasts which provide the meta-naupliar region with mesoderm elements.

Further Change in the Germinal Disk. The blastopore is of rather short duration, and is soon closed. The closure is brought about by the backward growth of the anterior lip over the blastopore to meet the posterior lip. After the closure, the blastoporic region and its immediate vicinities, composed of tall cylindrical cells rich in cytoplasm and containing large nuclei, are slightly depressed for some time (fig. 21, *bp. a*). This region is the ventral plate or the thoracico-abdominal rudiment. It imperceptibly merges both anteriorly and laterally into the thickening of the germinal disk; posteriorly, however, it is distinctly demarcated from the flattened cells of the extra-germinal region. A small group of flask-shaped cells is found in the middle of this plate (fig. 24, *pr.*). They are enlarged at the inner ends, each of which encloses a small nucleus, and remain in direct contact with the depressed surface of the egg by their filiform outer ends. These cells represent the earliest rudiment of the proctodaeum the position of which is in accord with that of the former blastopore indicated by the slight depression on the surface. The sinking of the mesendoderm cells from the ventral plate lasts for a while even after the closure of the

blastopore (fig. 24, *im*).

Immediately after the closure of the blastopore, the ectoderm cells between the optic lobes accumulate to form a transverse band connecting the inner margin of the lobes (fig. 1, *tr. b*). By the formation of this band from the several rows of cubic epithelial cells, the germinal disk is more or less transformed in an O-shape from its original U-shape. In other words the ventral plate and optic lobes are connected by the lateral ectoderm thickenings, and the optic lobes in turn are united by the transverse band (fig. 1). A similar condition is observed in the mesoderm layer as stated before. Each of the mesoderm bands, originated on either side of the ventral plate, runs forward along the lateral thickening of the ectoderm as far as the optic lobe to join with the preantennulary mesoderm which, on its part, extends internally and meets its partner on the other side under the transverse ectoderm band. Thus a circle is formed by the whole mesoderm.

Endoderm Plate. The differentiation of the endoderm occurs somewhat later than that of the mesoderm. The mesendoderm cells immigrating from the ventral plate after the closure of the blastopore comprise two kinds of cells which have different fates, though they are indistinguishable in their cellular constitutions (fig. 24, *im*). The majority of them become the mesoderm cells joining the posterior end of the mesoderm band; a few, however, do not participate in the formation of the mesoderm and remain as the components of a loose cell mass situated behind the band and beneath the ventral plate. These cells are amœboid with more or less indistinct cell boundaries and remain completely outside the yolk. Although these cells send out fine protoplasmic processes into the yolk, they do not include the yolk spherules in the plasm. In stage 4, in which the first rudiment of the naupliar appendages becomes apparent, the cell mass gradually condenses and develops into a disk-shaped plate composed of one or two layers of compact cells (fig. 23, *end*). The component cells come to show clear boundaries, and their granular cytoplasm encloses deeply staining nuclei which have rather diffuse chromatin. These are the endoderm cells. Already in the first stage of the appearance of the endoderm cell mass, the adjoining yolk cells begin to gather together and join with the mass. It is believed, therefore, that the endoderm cells are nothing but yolk cells which, without sinking into the yolk and behaving like "vitellophags", remain aggregated in a mass.

4 Egg-Nauplius

The developmental changes in stages 4-6 will be described under this heading.

Changes in External Form. Shortly after the formation of the ventral plate which is recognized superficially by a deeply staining oval region, three pairs of similar regions become apparent in the lateral ectoderm

thickenings between the ventral plate and the optic lobes (fig. 2). These are the first rudiments of the naupliar appendages. Of these the mandibles are the first to be defined and the antennae last. In this stage they are all mere transverse ectoderm bands formed by the agglomeration of nuclei and disposed radially toward the center of the germinal disk. The development of the appendage consists in the elevation of the band followed by the constriction from the egg surface along the margin. Although the mandibles are the first to develop, they remain in the state of small protuberances until later stage, but the other two pairs of limbs greatly develop and grow into dactyliform processes by the end of the egg-nauplius stage.

The ventral plate, which has been a mere thickening of the germinal disk, is gradually raised along the anterior margin and develops into the more or less oval thoracico-abdominal papilla (figs. 3-5, *v. p.* & *th. ab.*). With the development of the appendages the transverse band between the optic lobes becomes disconnected in the middle into two halves which become confluent with the basal portion of the lobes (fig. 2). At the same time the optic rudiments, the lateral portions of which shift slightly to the anterior, are transformed into a pair of foliaceous lobes (figs. 3-5, *o. l.*). They are stained more faintly than the appendage rudiments and their outlines are rather indistinct. The oral aperture makes its appearance at about this time as a crescentic transverse slit on the middle line at a level with the anterior margin of the antennae (figs. 4 & 5, *st*). The anus develops, as stated before, in the center of the ventral plate prior to the latter's elevation and immediately after the closure of the blastopore. It is at first defined as a clear spot, but later it becomes hard to see from without by low power magnification. In stage 6, four pairs of ganglionic masses are differentiated in the ventral region close to the bases of the optic lobes and appendages (fig. 5). Like in the decapod egg (TERAO, 1929), the germinal disk continues to contract from the stage in which the appendages are formed to the end of egg-nauplius (figs. 2-5); this may be clarified by the measurements shown below:

Stage	Diagnoses of stages	Length of germinal disk in mm	Width of germinal disk in mm
3	Formation of optic lobes and ventral plate (fig. 1)	0.32	0.44
4	First appearance of naupliar appendages (fig. 2)	0.36	0.42
5	Beginning of the constriction of naupliar appendages at the lateral end (fig. 4)	0.32	0.30
6	Appearance of ganglia (fig. 5)	0.28	0.24

Naupliar Appendages. As soon as the first rudiments of the naupliar appendages become faintly visible, active multiplication of the ectoderm cells of the germinal disk causes the crowding of cells, which results in the thickening and slight elevation of the disk from the surface (fig. 29). In the antennular region, for example (fig. 30), the elevation of the disk is divided into five parts separated from each other by slight depressions. Of these parts the lateral ones are the appendage rudiments (*an. 1*), and on the inner side of these are a pair of ganglionic parts (*dc*) with a mid-ventral region (*mv*) inserted between them. The egg surface slopes abruptly toward the extra-embryonic region at the lateral end of the appendage. Along the anterior and posterior margins the borders of the appendages are not so marked, being indicated only by a slight waving of the surface.

Owing to the rapid multiplication of the component cells, the appendage rudiments are gradually raised over the surface of the germinal disk to form transverse linear elevations. They are now dome-like in cross section and separated from one another by deep furrows (fig. 35). At the lateral end the appendages are demarked from the egg surface by short longitudinal grooves. The grooves subsequently develop into the ingrowths of ectoderm directed toward the median. Together with the further development of these ingrowths, the appendages elongate outward and their distal portions constrict away from the egg surface (figs. 36 & 39). The mandibles, however, remain in mammiform protuberances without developing lateral constrictions (fig. 6). At the inner end, all appendages are limited by slight depressions caused by the sinking of cells which mark the outer margin of the ganglia (figs. 30 & 36).

During the course of the uplifting of the limbs the cell boundaries are not clearly defined. The ectodermal parts of the rudiments, however, are crowded with cells, the condition being indicated by the nuclei which are found at various depths below the surface (fig. 30). Such an arrangement of the ectoderm nuclei suggests that the sinking of cells is going on. This is especially the case with the mandible rudiment. The nuclei are situated at the top of this mammiform appendage at a lower level than those surrounding them, and the general arrangement of the nuclei appears to show the presence of invagination though the surface of the appendage remains smooth. As will be discussed later, this state apparently indicates the actual sinking of the cells. The "growth stripes", which were found between the appendages on the surface of *Panulirus* egg by TERAO (1921, '29), who explained their presence as an aid to uplift the limbs, are not observed in the *Squilla* egg.

The antennule in stage 5 is completely uplifted on the distal part which has a slightly bilobed tip (fig. 4). The bilobed nature of this limb, however, is only transitory. Growth takes place chiefly at the posterior angle of the tip in the postero-lateral direction, but the anterior angle remains quiescent. The antennule in stage 7 is consequently represented

by an undivided rod which is curved somewhat angularly in the middle and whose distal part is directed postero-laterally (fig. 6). In stage Th 5 a small anteriorly directed process, protruding from the curved middle part, becomes apparent. The process corresponds to the undeveloped anterior angle of the earlier biramous tip, and develops into a branch which runs parallel to the other branch represented by the distal part of the main stem. At the time of hatching the antennule is a biramous appendage composed of a non-articulated short protopodite and two rami similar in constitution and setose at the tip (figs. 8-10).

The antenna, which is uniramous from the beginning, is a more or less straight appendage extending in the same direction as the antennule in stage 5 (fig. 4). At the time of hatching it is composed of two joints of subequal length and bears setae at its tip (fig. 10). The mandible remains in a mammiform process in stage 5, but its outlines become somewhat more inconspicuous in the following stages, as the growth simply concerns the enlargement of the base. The appendage does not show much change in the course of further development, and finally becomes a round naked protuberance situated on each side of the oral aperture (fig. 10).

Naupliar Mesoderm. Hand in hand with the development of the appendages above the germinal disk, marked changes are undergone below. Shortly after the establishment of the O-shaped band, the mesoderm layer moves toward the median to meet each other in the mid-ventral region and extends laterally also to the external margin of the germinal disk (fig. 30, *mes*). At the time when the naupliar limbs become faintly defined (stage 4), the mesoderm forms a continuous sheet lining the greater part of the under surface of the embryonic rudiment except the ventral plate and the optic lobes. As stated before, the interior of the ventral plate is occupied by the endoderm elements; the distal part of the optic lobe has no mesoderm lining from the beginning. In the mid-ventral region as well as in the regions between the limbs, the mesoderm remains rather thin and sparse in nuclei. In this stage active nuclear decompositions may be observed under the proximal part of the optic lobes, especially under the border between these and the antennular segment (fig. 29). Fig. 31 shows that these changes take place at various depths: the disintegration products may be found immediately beneath the ectoderm layer of the optic lobe, and also at the level of the mesoderm which is indicated by the residual flattened mesoderm nuclei found on the right side of the figure. Thus some of the degenerating cells found in this region apparently come from the superficial mesoderm cells, though there are some of the other cells originated in the deeper yolk cells. These degenerative changes of the mesoderm and yolk cells go on hand in hand, since the latter cells undergo decomposition everywhere in the yolk (figs. 29 & 30). It has been stated that the anterior end of the mesoderm band is completed by the

addition of the preantennulary mesoderm. Accordingly, the degenerating cells found just beneath the ectoderm are nothing but the decomposing preantennulary mesoderm cells. In later stages the under surface of the optic lobes becomes scattered only with a few residual cells.

With the elevation of the appendages the underlying mesoderm cells multiply actively and form the lumps which invade the cavities formed by the elevation (fig. 35). With the constriction and uplifting of the appendages on the egg surface, these cell lumps become included by them and develop into muscles. The mesoderm cells invading the appendage cavities form three pairs of masses, though these, being continuous, do not separate completely into mesoderm segments. Stomodaeal invagination goes on during the appendage formation (stage 5, fig. 32, *st*). Cell multiplication occurs in this stage in the thin central part of the mesoderm of the antennular segment, producing a small cellular mass in front of the stomodaeum (fig. 36, *pst. mes*). When the labrum develops into the fold of the anterior stomodaeal wall, this mass greatly enlarges and intrudes into its cavity, sending a pair of cellular strands anteriorly to the base of the antennule (figs. 41 & 50, *mes*). Except for these, the mesoderm layer of the mid-ventral region is represented by nothing but a thin protoplasmic membrane scanty in nuclei. The greater parts of the mesoderm which remain are caught within the limbs.

Here we must stop to mention the serum space. When stage 7 is attained, the germinal disk which has been in close contact with the yolk surface becomes detached from the latter, thereby forming a narrow space. This space (figs. 40, etc., *s. s*), the primary body cavity, is probably produced by the contraction of the yolk sac and filled with a plasmic substance, "serum" (REICHENBACH's terminology, 1886), which is the dissolved deutoplasm exuded from the sac. Such serum spaces are already developed in previous stages, in front of the brain, behind the stomodaeum, and also in the base of the thoracico-abdominal papilla. Since the egg body enlarges and the yolk sac contracts, the primary body cavity enlarges, extending toward the dorsal side, finally to surround completely the yolk sac.

With the appearance of the serum space and at the same time as the segmental condensation of the cells, the naupliar mesoderm, which has been confined within the ventral region, extends laterally in varying degrees beyond the base of each limb. Further, the mesoderm is indefinitely divided into several more or less continuous parts. In the mandibular segment, which is most typical in constitution, the mesoderm is divided on both sides into lateral, limb, and internal parts. The lateral mesoderm is a thin cellular plate extending laterally through a narrow serum space for some distance from the base of the mandible. The limb mesoderm, which has already been referred to, is a large mass enclosed within the limb cavity. On account of the broadness of the base of the mandible, the limb mesoderm, is rather indistinctly separated from the other two parts. The

internal mesoderm, after departing from the inner margin of the limb mesoderm, runs toward the median as a rather thick cellular band which is connected with its partner on the opposite side by a membraneous plate under the ganglionic pair. In the antennal segment also these three parts of the mesoderm are well distinguished. The internal mesoderm extends to the stomodaeum and surrounds it as a rather thick coat which may be termed the peristomodaeal mesoderm (figs. 36 & 40, *pst. mes*). A part of this coat invades the labral cavity (fig. 40). The mesoderm of the antennular segment is undivided and the aggregation of cells takes a form somewhat different from those in other segments. The internal mesoderm gives place to a pair of longitudinal bands which originate in the anterior side of the peristomodaeal mass and extend forward beneath the halves of the brain as far as its anterior end (fig. 50, *mes*). These paired bands have been observed in the previous stage.

As a consequence of the above described aggregation of cells, the continuous mesoderm layer ruptures at the thinner parts between the thicker parts which later grow into muscles and other mesodermal tissues. Unlike the Mysidacea (MANTON, 1928) but like the majority of Malacostraca, the naupliar mesoderm of *Squilla* never, in any stage, forms a distinct somite or a cœlom in any segment. The division of the mesoderm in each of the segments mentioned above strongly reminds us of the condition in the mysid, reported by VOGT (1935 a), in which the mesoderm is similarly divided on both sides into three parts.

Cell Degeneration. In the egg nauplius a remarkable phenomenon may be observed; namely, from the stage of the establishment of the germinal disk to that of the uplifting of the naupliar appendages, active degeneration of the cells goes on not noly in the yolk but also within the mesoderm layer. The disintegration products scattered in the yolk mass are evidently the result of the degeneration of the yolk cells. The disintegration products found within the mesoderm layer, however, need some description.

During the development of the appendages, the chromidia liberated by nuclear disintegration are frequently found in the mesoderm layer or between it and the ectoderm, in the appendage cavities and even in the developing ganglia (figs. 30, 32, 35 & 36). The following facts are very suggestive as to the origin of these chromidia. As pointed out before, in an earlier stage of the uplifting of the limb, the arrangement of nuclei in its ectoderm becomes very irregular presumably due to cell sinking (fig. 30). In later stages the limb cavity includes a number of chromidial particles (fig. 35). The chromidia are usually found intermingled with the mesoderm nuclei or immediately above them. In this case, however, they are often observed at the same level with the ectoderm nuclei. They are also seen in the ganglion amidst the ectodermal ganglionic cells (fig. 36). The most noteworthy is their presence in the labral region.

As will be described later, the stomodaeum which is originally an

invagination directed posteriorly rotates in stage 5 to become anteriorly directed. Prior to this rotation, the epistomal ectoderm is composed of tall cylindrical cells which show more or less distinct cellular borders and contain nuclei at various levels. When the stomodaeum makes its definitive orientation, the epistomal part of the ectoderm is protruded backward as the labral rudiment, and its cells grow shorter and thicker with most of the nuclei at the same level. The chromidial particles make their appearance in the labral cavity at the same time as this change in the arrangement of the ectoderm nuclei. All these facts apparently indicate that the sinking of the ectoderm cells actually takes place, and that the disintegration products originate from these sunken cells.

The above mentioned sinking of the ectoderm cells is practically of the same nature as that which takes place in the extra-blastoporic region before and after the closure of the blastopore. In fact the cell immigration continues more or less without interruption, except in the extra-embryonic region where the immigration stops much earlier, till the appendages are constricted from the egg surface. The nuclear disintegration in the region outside the yolk sac has already been noticed in the nauplius of *Panulirus* by TERAO (1921, '29), who explains it as due to the degeneration of yolk cells which sank from the ectoderm in the areas "which are either depressed or composed of more compactly set cells" (p. 443). In HERRICK's (1892) figures of the nauplius of *Alpheus* and also in BUMPUS' (1891) drawings of the same in *Homarus*, the decomposition products are found in exactly the same place as in *Squilla*, though they are not specially mentioned by either of the authors. Thus, the extra-blastoporic sinking of the ectoderm cell appears to be of a universal occurrence in Decapoda.

Remarks on Extra-blastoporic Immigration of Cells. In connection with the cell degeneration mentioned above, let us consider the significance of the immigration of the extra-blastoporic cells. The cells include the mesoderm cells sunken from the U-shaped ectoderm band, the preantennulary mesoderm cells derived from the optic lobes, and the yolk cells from the mid-ventral as well as the extra-embryonic regions. Of these, the preantennulary mesoderm will be taken up first. In an earlier phase of the formation of this mesoderm, many chromatin particles were found intermingled with the cells which are loosely attached to the lower surface of the optic lobes and about to aggregate to form a continuous sheet. Such particles are also found within the cell complex of the optic lobe which is in the course of cell sinking, showing a very irregular nuclear arrangement. Immediately after the formation of the preantennulary mesoderm, the yolk cells mixed with disintegration products are found beneath the optic lobe in much greater numbers than in any other part except the ventral plate (fig. 29). These facts appear to indicate that the optic lobe produces yolk cells besides the named mesoderm cells. This explains

the greater abundance of yolk cells in this region than in other regions. The chromidia found in the ectoderm and immediately beneath it are apparently the products of a premature degeneration of the yolk cells in the course of submergence. Most of these cells degenerate almost at the same time as the destruction of the preantennulary mesoderm. The degeneration of the latter after the formation of a temporary layer is very significant. Since the nuclear decomposition seems to have a connection with the liquefaction of the deutoplasm, these two kinds of cells are materially identical in their fates and functions. That one forms a layer whereas the other does not, is an unimportant difference mainly due to the former's remaining attached to the ectoderm while the latter sinks more or less into the yolk.

As said before, the U-shaped ectodem band produces the mesoderm and the extra-embryonic region the yolk cell. This distinction, however, does not necessarily suggest the fact that these two regions produce the elements belonging to different germ layers. In the region of the U-shaped band the mesoderm layer is already formed beneath it. The immigrants from this region therefore join with the mesoderm without penetrating it. On the other hand, in the extra-embryonic region, as well as in the mid-ventral region where the inner layer is not found, the immigrants immediately submerge into the yolk and become yolk cells. The yolk cells may also originate in the mesoderm and, on the contrary, may unite with the latter by passing through the yolk (cf. p. 89). These facts clearly show the identity of the fundamental nature of the two elements. The immigrants from the extra-blastoporic region do not comprise the elements belonging to different germ layers, but the cells from the same origin may behave differently according to circumstances.

TERAO (1921, '29) holds the view that the yolk cells coming from the extra-blastoporic region are endodermal, because "their function as vitellophags seems to point to their endodermal origin, since such a function is one of the essential attributes of the cells of the endodermal mid-gut" (p. 440). In that the immigrants degenerate eventually, there is no objection to considering them as yolk cells. But the vitellophagous function, in my opinion, does not necessarily suggest their endodermal origin. If they were all endodermal, then it must be admitted that the lateral ectoderm band in *Squilla* produces the mesoderm first and the endoderm later. Further, since the mesoderm layer is already laid in the nauplius, the endodermal cells should invade the space between the ectoderm and the mesoderm. These inconsistencies disappear when these yolk cells are considered as mesodermal. In fact there is no sound evidence that all of the immigrants disintegrate without joining with the preexisting mesoderm. Furthermore, there is apparently no reason for attributing the vitellophagous function to the endoderm only. Yolk spherules which have probably been caught by the invading mesoderm are frequently observed in the limb cavity of

the *Squilla*. HERRICK's (1892) figure depicts similar bodies in the appendage of *Alpheus*. As these yolk spherules disappear later, even true mesoderm cells also seem to retain an ability to dissolve the deutoplasm. Further evidence may be found in the degeneration of the preantennulary mesoderm. Thus it is certain that the extra-blastoporic immigrants consist of only mesodermal elements which may develop either into true mesoderm cells or into yolk cells. The latter degenerate completely sooner or later. They may be derived also from the blastoporic region as stated before, but should not be confused with endodermal yolk cells which participate in the formation of the mid-gut. The endodermal yolk cells will be mentioned later.

The formation of a part of the mesoderm by the immigrants from the extra-blastoporic region seems to be a rather universal occurrence in Decapoda. TERAO (1929) acknowledges a similar origin of the yolk cells (mesodermal in my opinion) in *Panulirus* and suggests that this might be the case in *Alpheus* (HERRICK, 1893) and *Homarus* (BUMPUS, 1891). HERRICK's primary yolk cells really appear to me to be nothing but the forerunners of extra-blastoporic immigrants. Such cells are also recorded of *Panulirus* (TERAO, 1929) and *Leander* (SOLLAUD, 1923). Moreover, LEBEDINSKY (1890, in *Eriphya*) and BUTSCHINSKY (1894, in *Gebia*) clearly state that the proliferation of mesoderm cells as well as yolk cells start from the lateral thickenings of the ectoderm. This mode of mesoderm formation has never been observed in Malacostraca other than Decapoda, except for the preantennulary mesoderm of Mysidacea and Nebaliacea.

In these two orders, according to MANTON (1928, '34), the optic lobe produces inner elements which form a pair of preantennulary mesoderm somites enclosing the cœlom. As stated above, such a mesoderm in *Squilla* forms a transient sheet of which the larger part later degenerates. In no other malacostracan order has the presence of this type of somite ever been noticed. TERAO (1921, '29) reports active sinking of yolk cells in the optic lobe of *Panulirus*. These cells are considered mesodermal, and it is highly probable that the cell sinking represents a rudimentary state of the formation of the preantennulary segment. Evidently the cell immigration from the optic lobe was taken by most of the previous authors for a process in the formation of the optic ganglion. If this is the case, a notable series of gradual reductions of the preantennulary mesoderm somite can be traced from the Nebaliacea and Mysidacea, through the Stomatopoda, to the Decapoda. Namely, in the first two orders a cœlom is formed in the somite, in the second the somite is represented by a transitional cell layer, while in the third only scattered yolk cells are found. On the other hand, with the reduction of the somite, the extra-blastoporic immigration of the mesoderm becomes more conspicuous. In Nebaliacea and Mysidacea this immigration is limited to the above-named somite, whereas in Stomatopoda it extends over the blastosphere, and finally in Decapoda immigra-

tion takes place even prior to gastrulation. From these facts, it may be emphasized that the preantennulary mesoderm formation is a specialized case of extra-blastoporic immigration, or, more appropriately, the former represents the first step to the latter.

5 Meta-naupliar Region

Changes in External Form. As soon as the naupliar appendages rise from the egg surface, the oval ventral plate also emerges on its anterior margin (stage 5, fig. 4). With gradual development (figs. 4-6), it grows into a more or less quadrangular thoracico-abdominal papilla, folded over the egg surface and directed towards the anterior (stage 7, fig. 6.). The tip of the papilla, however, does not go beyond the level of the posterior margin of the mandible in stages 6 and 7 (figs. 5 & 6). This is due to the displacement of the papilla towards the posterior brought about by the elongation of the embryonic disk in the region between the mandible and the base of the papilla. A pair of deeply staining areas then appear on the embryonic disk close to the thoracico-abdominal rudiment on either side; subsequently, another pair appear behind them. These areas represent the rudiments of the maxillulae and maxillae, which grow into mammiform processes arranged antero-posteriorly (fig. 6, *mx 1*, *mx 2*). After these appendages are formed, the thoracico-abdominal papilla continues to move backwards and produces two more pairs of small processes behind the maxillae and close to its base. Unlike the foregoing appendages these pairs lie side by side. The external one, situated on the germinal disk, represents the first maxilliped, and the internal one, located at the junction of the thoracico-abdominal rudiment and the germinal disk, is the second maxilliped (fig. 7, *mxp 1*, *mxp 2*). Both pairs of maxillae are directed somewhat antero-internally and do not develop much until hatching, but the maxillipeds are directed anteriorly and undergo great development.

Thoracico-abdominal Rudiment. The ventral plate immediately after the closure of the blastopore is repesented by a layer of tall cylindrical cells abundant in cytoplasm and with round or oval large nuclei containing few chromatin (fig. 21, *bp. a.*). The cells gradually become shorter toward the anterior and are continuous to those of the germinal disk, but posteriorly and laterally they are sharply demarcated by extremely flattened cells of the extra-germinal region. In this stage, the proctodaeum is a small group of flask-shaped cells occupying the central part of the plate (fig. 24, *pr*). When stage 4 is attained, the anterior margin of the plate is limited by a very shallow groove on the surface (fig. 29, *fx*). On the lateral and posterior sides the cells become shorter and continue imperceptibly into the extra-germinal blastoderm. A small part of the ectoderm surrounding the anus has much smaller nuclei than other regions. On both sides of these cells are three or four cells containing abundant cyto-

plasm and round, voluminous nuclei with a few large nucleoli. They are arranged in a pair of longitudinal rows. In surface view these cell rows are not so distinctly defined as in section, but it is very likely that they represent the ectoteloblasts which soon become more clearly defined. As stated before, eight mesoteloblasts proliferated from the blastopore form an irregular mass in front of this in the preceding stage (fig. 34, *mes. tel*). They migrate somewhat posteriorly and to a position beneath the proctodaeum in stag 4 (fig. 29, *mes. tel*). Besides these cells, the inner space below the ventral plate is occupied by undifferentiated mesendoderm cells sunk from the region just above, and also by the disintegration products of these cells.

In stage 5, the ventral plate develops into a process pyramidal in section (figs. 32 & 33). The anterior side of the process slopes very steeply, as it is separated from the egg surface by a semicircular groove laid in the preceding stage, while on the lateral and posterior sides the slope is much more gentle and there is no distinct line of demarcation. The anterior slope repeseents the future ventral side of the process. The nuclei of the other side of the process are of various sizes, smaller in the perianal or anterior region, larger in the posterior (fig. 76). The ectoteloblasts can clearly be seen from the exterior for the first time in this stage. They are seven in number and arranged in a semicircular row along the anterior margin of the process (fig. 76, *ect. tel*). The row is composed of a central cell (*c. ect. tel*) which is furthest toward the anterior (morphologically posterior) and three lateral cells which gradually range backward from it. The whole row lies on a plane parallel to the egg surface but slightly oblique to the dorsal surface of the thoracico-abdominal process (figs. 32, 33 & 44). Eight mesoteloblasts, also regularly arranged, are disposed symmetrically and form an incomplete ring surrounding the proctodaeum (fig. 76). They lie on a plane below and nearly parallel to the plane of the ectoteloblasts (fig. 32). More ectoteloblasts are added with further development probably by the modification of ordinary ectoderm cells. Their increase may also be due to the division of preexisting teloblasts. The division figures shown in fig. 76 represent this mode of increase, since the spindle fibres are oriented transversely to the body axis instead of in the longitudinal direction which would indicate a proliferation of descendants. The number of mesoteloblasts remains unchanged till the end of the teloblastic division.

The thoracico-abdominal process continues to grow forward. It protrudes anteriorly over the egg surface in stage 6 to become a quadrangle with a notch on its margin (fig. 6). Ectoteloblasts increase in number to 13 and form a horse-shoe-shaped row encircling the process ventrally and laterally but not in the mid-dorsal region. The plane on which the row lies makes a sharp angle with the egg surface and cuts the thoracico-abdominal process obliquely (fig. 37). The central teloblast situated mid-

ventrally is well defined. The mesoteloblasts have moved somewhat (morphologically) more posteriorly than in the previous stage and lie on the same plane as the ectoteloblasts (fig. 37). Two of them separate from the rest to lie close each other on both sides of the mid-ventral line. The others form two groups of three cells and become attached to the dorsal wall of the process in pairs (fig. 77).

Before going further it is necessary to describe the development of the segments from the maxillula to the second maxilliped in stages 6 and 7.

Segments of Maxillula and Maxilla. The development of the maxillula precedes that of the maxilla. As stated before, the interspace between the mandible and the base of the thoracico-abdominal process is enlarged by the backward movement of the latter. The maxillulae make their appearance in this region laterally to the process as mound-like elevations. They are in such close contact with the lateral side of the process that they are rather difficult to make out in surface view. In sections, however, the rudiments are clearly separated from the process by deep furrows. With further displacement of the thoracico-abdominal process, the maxillae develop behind the maxillulae in a rather similar manner (fig. 43, *mx 2*).

Both pairs of rudiments are composed of a rather thick but one-layered ectoderm enclosing a mesoderm mass. In the mid-ventral region between the limb rudiments, the ectoderm is much thinner and sparser in nuclei (fig. 40) but shows active nuclear division. The mesoderm mass confined within the limb cavity does not extend beyond the limb base either externally or internally. This is not the case at the antero-postorior. Although the mesoderm of the maxillula is separated anteriorly from that of the mandible, it is connected posteriorly by a thin cellular band to the maxilla mesoderm, which in turn continues to that of the thoracico-abdominal process. In the mid-ventral region, a few scattered mesoderm cells are found attached to the ectoderm. The limb rudiments of these segments do not show any sign of ectoderm cell immigration such as those observed in the naupliar limbs.

It is somewhat difficult to determine whether the ectoderm of these segments is derived from the teloblasts. In Peracarida there is a coincidence or a certain correlation between the number of segments and that of the teloblastic descendants. The origin of the named segment may be surmised from the number of the latter. It is difficult to make out such a correlation in *Squilla*, however, since the multiplication of the teloblastic descendants begins before the end of the division of teloblast. Further, the fact that the thoracico-abdominal process is folded over the egg surface makes the matter more difficult. Were the row of teloblasts situated close behind the mandible when the former becomes externally differentiated for the first time, the origin of the segments in question may be apparent. But this is not the case in *Squilla*. The teloblasts are differentiated only after

the thoracico-abdominal rudiment is elevated; and in this stage a narrow area is formed between the base of this rudiment and the mandible. It is therefore not altogether impossible to ascribe the origin of the segments to this narrow area. On the other hand, if internal differentiation of the teloblasts have already taken place, though not discernible on the exterior, the segments can be assigned to these teloblasts. In all probability at any rate, the following facts appear to indicate a teloblastic origin of the maxillular and maxillar segments.

1) Although the teloblasts can not be distinguished in the surface view of the early ventral plate (stage 4), three or four comparatively large linearly arranged cells are found on both sides of the peri-anal region in the section (cf. p. 100f). These cells possess all the teloblastic characteristics, such as the abundance of a more or less granular cytoplasm and the presence of a voluminous nucleus scanty in chromatin but having a few large nucleoli. The anterior extremity of these cell rows is found immediately behind the groove which borders the posterior margin of the mandibular segment. 2) In the sections, the teloblasts are first seen on the anterior margin of the slightly elevated thoracico-abdominal process before the maxillulae are laid down. 3) In the same stage (figs. 32 & 33), the anterior (ventral) side of the process is composed of regularly arranged cells rather suggestive of their teloblastic origin. 4) In a slightly later stage, but before the appearance of the maxillar segment, one finds two or three very regularly placed nuclear rows in the mid-ventral region of the germinal disk facing the thoracico-abdominal process. Such an arrangement of the nuclei clearly indicates that they originated from the teloblasts and that they have been displaced to the germinal disk. 5) At the point of ventral flexure of the thoracico-abdominal process, the descendants of the teloblasts appear to rotate toward the germinal disk. Similar displacement of cells has also been observed by BERGH (1893) in *Mysis*. 6) The lateral members of the teloblastic row are situated, in this stage, on the border between the process and the germinal disk. These teloblasts send their descendants out toward the germinal disk (fig. 44, *etc. tel*).

From these facts, the origin of the maxillular and maxillar segments may be surmised as follows: The teloblasts are already functionally diffferentiated before their superficial specialization. Their descendants multiply by division and spread over the germinal disk, passing around the thoracicoabdominal flexure toward the anterior, or going immediately laterally. By the spreading of these cells the thoracico-abdominal rudiment is forced to move backward, and the two maxillar segments develop in the space thus formed.

The mesoderm of these segments is evidently derived from the teloblasts, because, in the stage during which the ventral plate begins to elevate, the inner cavity is occupied only by endodermal cells and scattered yolk cells (figs. 32 & 33). In fact the mesoderm of the maxillar segment is

completely cut off from the mandibular mesoderm as stated before. In fig. 43, drawn from an egg which has the maxillular segment alone, the mesoderm within the limb cavity is continuous with that of the thoracico-abdominal process, clearly indicating that the former came from the latter, or namely, that it evolved from the teloblasts.

As far as can be concluded from careful studies carried out on the embryonic development of Malacostraca, the authors are in complete agreement on the view of the teloblastic origin of these segments in the whole of the sub-class except in Decapoda. In regard to the Decapoda also, REICHENBACH (1886, in *Astacus*) and FULINSKI (1908, in *Astacus*) hold a similar view, but TERAO (1929, in *Panulirus*) and SOLLAUD (1923, in *Leander*) are of the opinion that the two maxilliped segments have no relation to the teloblast. TERAO traces the orgin of these segments to his "anterior budding zone". As will be discussed later, this zone is, in my opinion, nothing but the ganglia of these segments. To my regret, I have been unable to have access to SOLLAUD's work. There are some ambiguities and inaccuracies as regards the origin of the mesoderm in Decapoda. REICHENBACH (1886), KINGSLEY (1887 b, in *Palaemon*), HERRICK (1892, in *Alpheus*), WELDON (1892, in *Crangon*), TERAO (1929) and others do not make any distinction between the naupliar and meta-naupliar mesoderm, and they therefore do not express any definite opinion concerning the origin of the mesoderm of the two maxillar segments. FULINSKI (1908), who was the first to apply the modern conception of the crustacean teloblast to Decapoda, however, firmly adheres to the teloblastic origin theory of the mesoderm of the post-mandibular segments.

Both pairs of maxillae first develop as antero-internally directed small protuberances. They afterwards become directed antero-externally but do not show much advance in their development (fig. 59). At the time of hatching the maxilla is represented by a small foliaceous lobe on the side of the hypostome, and the maxilla, taking a position close behind the former, is somewhat narrower and dactyliform (fig. 10). Both pairs are non-articulated and devoid of distal setae.

Segments of the First and the Second Maxillipeds. After the establishment of the maxillar segment, the thoracico-abdominal process moves further backward, sending the teloblastic prducts to the germinal disk. The first maxillipeds make their appearance somewhat apart from and behind the maxillae, close to the base of the thoracico-abdominal process. They are pushed away from the base of the process by short and shallow grooves, thereby becoming mound-like protuberances. The second maxillipeds are then formed in a similar manner to lie inside the first maxillipeds (figs. 7 & 92). These rudiments subsequently develop into anteriorly directed processes (fig. 59). The mid-ventral region of these segments is very thin as in the maxillar segment; the mesoderm also is mostly confined

within the limb cavities.

After the rudiments of these limbs are laid, the translocation of the cells from the thoracico-abdominal process to the germinal disk ceases, and the succeeding segments are differentiated in this process. Although the thoracico-abdominal process moves further backward, this is entirely due to the growth of the segments from the maxillula to the second maxilliped.

Unlike the cephalic limbs, both pairs of maxillipeds undergo great developments. In the stage when all abdominal segments are differentiated, the maxillipeds are represented by long anteriorly directed rods (fig. 59). The development of the first maxilliped, however, is somewhat retarded both in length and in thickness, as compared with that of the second which grows as far as the mandible. Each limb is divided almost simultaneouly into six joints, by the appearance of transverse grooves on the limb surface in this stage. As the development proceeds, the maxillipeds are forced to bend in various directions on both sides of the thoracico-abdominal process because of the lack of space (fig. 9). The first maxilliped is articulated with six subequal joints at the time of hatching (fig. 10, *mxp 1*). The second is also six-jointed but much stouter and longer; its basal joint is provided with an oval epipodite which is a hypodermal expansion of the joint (fig. 10, *mxp 2*).

External Development of Thoracic and Abdominal Segments. The thoracico-abdominal process is about a third of the length of the embryonic disk (cephalic region) at the time the maxilliped segment are laid. Although the process has greatly lengthened, it does not extend anteriorly beyond the level of the mandible because of the backward translocation of its base (fig. 7). Later, however, the tip of the process gradually grows forward, finally reaching the rostral region (fig. 8). The free thoracic and abdominal segments become twice as long as the cephalic region at about the time of hatching.

Shortly after the formation of the second maxilliped segment, the third thoracic segment is constricted away from the basal part of the thoracico-abdominal process by the formation of shallow lateral grooves. The succeeding segments are differentiated in the space between the pre-existing segment and the undifferentiated terminal part by similar constrictions which appear on the lateral side of the process (fig. 9). Thus the develepment of segments proceeds from the front toward the back. Eventually six thoracic and six abdominal segments become marked out by lateral grooves. These grooves later extend toward the median on both dorsal and ventral surfaces and develop into articulation furrows. The distal margin of the process, *i. e.* the tip of the telson, is at first round (fig. 4) but becomes slightly notched when the maxillae are laid (fig. 6). The telson is bilobated by the gradual deepening of the notch, by the time the thoracic segments are all differentiated (fig. 77). The notch grows

shallower again after this, and the telson finally takes a more or less quadrangular form (fig. 10). The two maxilliped segments, which have been laid down on the germinal disk at the beginning, are later constricted away from the cephalic region to become the most anterior of the free body-segments (fig. 10). Besides these two segments, only the first four abdominal segments develop appendages; the rest remain without appendages until hatching. The limb buds of the abdominal segents appear as lateral projections of the segments; each of them splits in two and becomes biramous pleopod (fig. 10).

Additional Remarks on the Teloblasts. When the maxillar segment is laid down, the number of ectoteloblasts is raised to 21 (fig. 77). This number is maintained to the end of the teloblastic division. The posterior ends of the horse-shoe-shaped row meet each other on the median line and the teloblasts form a complete ring around the thoracico-abdminal process. The angle between the surface of the process and the row of teloblasts is enlarged to about 45°. The angle increases still more with development, but the teloblasts disappear before it reaches 90°. The number of mesoteloblasts remains unchanged, and the relative positions between themselves as well as between them and the ectoteloblastic row also stay the same as that observed in the preceding stage. The teloblasts disappear, or maybe it is more appropriate to say, they cease to divide at about the time the eighth thoracic segment is externally differentiated.

Before the proliferation of the teloblasts comes to an end, the multiplication of their descendants begins in the anterior segments. This is the case both in the ectoderm and in the mesoderm. It is therefore hardly possible to find out how many times the teloblasts undergo division in order to produce one segment, or how many direct offsprings of the teloblasts constitute a segment. However, so far as the mesoderm is concerned, it appears certain that one offspring gives rise to one segment. The final division of the teloblasts is easily distinguished from the foregoing ones by the fact that it is an equal division instead of an unequal one. As stated above, the final division takes place when the eighth thoracic segment is externally differentiated. A careful examination of an egg in this stage revealed that: the dorsal mesoderm in the part included within the undifferentiated region of the thoracico-abdominal process (from the posterior member of the products of the last teloblastic division to the posterior end of the eighth thoracic segment) forms a regular linear row of seven sells arranged antero-posteriorly, whereas the eighth cell divides transversely to the axis of the thoracico-abdominal process; and that from this cell forward, the regular arrangement of cells is disturbed. The division of the eighth cell, therefore, is believed to represent the first multiplication of the direct descendant of the teloblast, taking place simultaneously with the external differentiation of the segment. The number of cells arranged in a regular row from the eighth cell backward is in strict accord with

that of the segments to be differentiated later (seven abdominal segments being counted from the ganglionic pairs). From this fact it is evident that an offspring corresponds to a mesodermal segment. Namely, after undergoing 15 unequal divisions, the mesoteloblast divides equally, and each of the products of this division gives rise to the mesoderm of the sixth and the seventh abdominal segment respectively. This mode of formation of the mesoderm of the last two segments is in complete agreement with that in Mysidacea.

As aforesaid, two of the mesoteloblasts are situated on either side of the median line on the ventral wall of the thoracio-abdominal process, and the remainders are attached to the dorsal wall, three on each side (fig. 77). The descendants of the teloblasts on the ventral side form a pair of distinct longitudinal bands. These bands run to the anterior along the ventro-lateral corners of the process, gradually diverging (fig. 81, *v. mes*). Similarly, the groups of teloblasts on the dorsal side construct, on either side of the median line, a pair of broad bands attached to the dorsal wall (fig. 81, *d. mes*). These mesoderm bands show rather distinct locations and have different fates. Because of these remarkable features, I shall name these teloblasts "ventral and dorsal mesotelobalsts", and their offsprings "ventral and dorsal mesoderm bands" (figs. 77-81). When the segments are differentiated externally, these mesoderm bands become divided more or less distinctly into segmental masses, the mesodermal somites (fig. 78). The cœlom, however, never develops in any segment.

The ectoderm constituting the dorsal and lateral walls of the thoracico-abdominal segments remains one-layered until the time of hatching. But, on the ventral side, the composing cells multiply in all directions to construct the ventral nerve cord (fig. 78). Since the ectoteloblasts form a ring, it is evident that the whole surface of the body wall is derived from the teloblasts in most of the segments. However, since the ring is open on the dorsal side in an earlier developmental stage, it is evident that the ordinary blstoderm cells also participate in the formation of dorsal wall of a few anterior segments.

The *Telson and Its Mesoderm.* As the teloblasts send out their offspring in the anterior direction only, the ectoderm of the telson must be derived from some other source. This ectoderm is originated from a few cells situated distally to the toloblastic ring (fig. 40), namely, from the small cells of the peri-anal region of the earlier nauplius stage (fig. 37; cf. p. 24) or, tracing it back further, from the peri-blastoporic ectoderm cells, as the position of the blastopore corresponds to the anus (cf. p. 14).

The development of the median notch at the tip of the telson and its subsequent disappearance are associated with the translocation of the anus. In the beginning stage of the elevation of the thoracio-abdominal process, the anus is found in the mid-dorsal region of the process (figs. 29, 33, 40 & 76). The space between the anus and the teloblastic row is subsequently

slightly enlarged, and the anus is displaced to a position near the distal margin of the telson. On the other hand, the more active cell multiplication in the region lateral to the anus and the stoppage of the development of the post-anal area, mould the telson into a pair of caudal furcae with a deep median furrow (fig. 77). The anus reaches the furrow and becomes terminal in about stage Th 4 (fig. 78). The ventral lip of the anus is formed by the central ectoteloblast; that is, the ventral lip represents the posterior margin of the undifferentiated abdominal segment. It is extended farther than the dorsal lip. The median groove is deepest, in stage Th 7, almost attaining the anterior end of the telson. After that the growth of the dorsal lip gradually fills up the median groove and at the same time brings the anus to the ventral side. As the ventral lip remains quiescent, the translocated anus becomes bordered anteriorly by the posterior margin of the last abdominal segment (figs. 79 & 105). With the complete disappearance of the provisional caudal furcae, the telson appears more or less quadrangular at the time of hatching (fig. 10). Thus the translocation of the anus is a passive process brought about by the appearance and disappearance of the caudal furcae.

The mesoderm of the telson is independent of the mesoteloblast in its origin. Just after the thoracico-abdominal process begins to elevate, a few cells immigrate into the inner cavity from the peri-anal ectoderms on both sides of the anus. The immigration is continued up to the time of the formation of the second maxilliped segment (figs. 40 & 86). The sunken cells represent the telson mesoderm, the formation of which is nothing but a continuation of the blastoporic cell immigration, in so far as the anus corresponds to the blastopore.

6 Early Development of the Digestive System

Stomodaeum. Although the stomodaeal invagination is not clearly visible from the exterior in stage 4, it is represented in section by a slight depression on the mid-ventral line between the levels of the antennule and antennae. The oral aperture can be seen from the surface for the first time in the same region as a narrow transverse and crescentic aperture in stage 5 (fig. 4). The stomodaeum is a sac-like invagination of the surface, located between the post-oral ectoderm and the mesodem and posteriorly directed, but not penetrating the mesoderm (fig. 32, *st*). It is lined with a layer of ectoderm cells, and contains a slit-like cavity which is wide transversely, but so narrow antero-posteriorly, that practically no lumen is found in it. In the later stage 5 the posterior wall of the stomodaeum, which has been in close contact with the lower surface of the hypostomal ectoderm, becomes detached from the latter. The stomodaeum then rotates anteriorly at its inner end, and in stage 6 it shows an inclination opposite to that of the preceding stage (fig. 40, *st*). At the same time, the stomo-

daeal cavity enlarges and becomes shaped like a flask with a narrow entrance and a rather spacious lumen, oval in horizontal section. With this change in form, the stomodaeum comes into direct contact with the yolk surface at the inner end, penetrating the mesoderm sheet. The ectoderm of the pre-oral region gradually rises above the surface, shortly afterwards, and grows posteriorly into a linguiform process covering the oral aperture. This is the rudiment of the labrum (fig. 40, *lb*). By the backward growth of this labrum, the oral aperture is gradually translocated toward the posterior to extend beyond the antenna (fig. 7).

Proctodaeum. It has been stated before that immediately after the closure of the blastopore, the central part of the ventral plate becomes occupied by a group of elongated flask-shaped cells (figs. 24 & 33, *pr*). These cells, which represent the first rudiment of the proctodaeum, are the remnants of the cells which constituted the wall of the blastoporic pit. These cells gradually grow inward and, together with the new cells coming from the surface, develop into a short tubular structure. As the ventral plate rises above the egg surface as the thoracico-abdominal process, this structure becomes included within its cavity. In stage 4 this proctodaeal rudiment is packed with cells and the anus is merely a longitudinal slit. The lumen of the proctodaeum first appears in stage 6 (fig. 42, *pr*) as a funnel-shaped space lined with an epithelial layer and clearly outlined only in the distal part of the proctodaeum. The proctodaeum, however, does not come in contact yet with the mid-gut.

Endoderm. The immigration of yolk cells from the extra-germinal ectoderm ceases before stage 4 is attained. The majority of yolk cells, which have previously been found in large numbers immediately beneath the surface of the extra-germinal region, submerge deeper into the yolk and sooner or later disintegrate (figs. 29, 30, etc.). Consequently, they completely disappear from this region in stage 4 and, being attached either to the mesoderm or to the ectoderm, remain only in the germinal region and its circumference (fig. 101, *e. y. c*). These cells are characterized by their more or less triangular nuclei, flattened on the external side and either cuspidate or round on the internal side, containing little chromatin reticulum besides a large central mass. In addition to these cells, disintegration products are found in abundance especially under the optic lobe and thoracico-abdominal rudiment. The deeper part of the yolk is usually devoid of nuclei except degenerating ones. The yolk cells, confined within the germinal region in this stage, gradually make their way along the most superficial part of the yolk to extend as far as the mid-dorsal region. In stage 6 the whole surface of the yolk is scattered with these yolk cells (fig. 102, *e. y. c*).

The constitution of these yolk cells could not be made out distinctly. The cytoplasm is recognizable only in the immediate vicinity of the nucleus, and is hardly distinguishable from the deutoplasm in the peripheral part,

lacking any distinct outline. It was impossible to find out whether cytoplasm of the yolk cells forms a membrane all around the whole yolk mass, although the presence of a plasmic membrane around the yolk surface is clearly recognizable at least in the immediate neighbourhood of the endoderm plate (figs. 40-43). Nevertheless the term "yolk sac" will hereafter be used for the sake of convenience, irrespective of the presence or the absence of the membrane. The yolk cells are very similar to those of Mysidacea (MANTON, 1928) and Nebaliacea (MANTON, 1934) in that they are found only in the superficial layer of the yolk. This mode of migration makes a striking contrast to that observed in Decapoda, the yolk cells of which pass through a deeper part of the yolk. The cells of *Squilla*, however, are quite different in constitution from those in the former two orders, which have voluminous yolk-laden cells, but closely resemble those in the latter order, especially *Alpheus* (HERRICK, 1892).

As stated before, the endoderm plate is differentiated from the posterior end of the mesendodermal mass. In stage 5 this plate is situated beneath the thoracico-abdominal process and is composed of rather flattened cells, quite different from the yolk cells, with granular cytoplasm and more deeply staining nucleus containing a granular chromatin substance (figs. 32, 33, 37 & 38). The endoderm plate grows by the multiplication of its component cells as well as by the addition of yolk cells. The yolk cells, which are about to unite with the periphery of the plate, undergo some changes in their constitutions. Their cytoplasm become more compact, have no processes, and the nuclei appear rather similar to those of the endoderm plate. In stage 6 the plate forms a protuberance in its central part. Subsequently a tubular process develops from the protuberance, and enters into the cavity of the thoracico-abdominal rudiment. In the next stage the process comes in contact with the proximal end of the proctodaeum (fig. 42, *int*). Although the process of the endoderm plate is solid and packed with cells at this time, it is soon pierced by a narrow intercellular lumen which represents the first rudiment of the intestinal cavity. As shown in figs. 40 & 43, the lumen in this stage is pervaded by protoplasmic strings developed from the cells lining the intestinal wall. At the funnel-shaped proximal end of the intestine, with which it continues to the yolk sac, the intestinal lumen is screened by a thin cellular membrane from the yolk sac lumen (fig. 43). These facts apparently point to the fact that the intestine does not develop as a hollow outgrowth of the endoderm plate, but that its lumen is produced secondarily by intercellular splitting. With the development of the thoracico-abdominal process, the intestine gradually elongates, whereas the endoderm plate spreads over the yolk sac as a layer of cubic epithelial cells. This is the first rudiment of the midgut epithelium (fig. 43).

Endodermal Yolk Cells. It has been stated that in *Squilla*, as well as in Decapoda, the term "yolk cells" signifies two different elements, namely

mesodermal and endodermal. Although the yolk cells which immigrate from the extra-blastoporic region are largely, if not entirely, mesodermal, those from the blastopore seem to comprise both endodermal and mesodermal elements. Since the immigrants from the blastopore consist of the so-called "yolk cells" and mesoderm cells, it is practically certain that the solitary mesoderm cells are included in the term "yolk cells". These two kinds of yolk cells belonging to different germ layers, however, are at first indistinguishable in their constitution. The endodermal elements are clearly differentiated for the first time in stage 4 when they become characterized by their peculiar nuclear structures (figs. 71 & 101). As mentioned above, active degeneration of the mesodermal yolk cells are observed beneath the germinal disk in this stage. After that, the yolk sac is occupied only by endodermal cells. As these cells later take part in the mid-gut formation, there is no room for doubting their endodermal nature.

It is not sufficiently clear whether all of these endodermal yolk cells have come from the blastoporic region or whether some of them have migrated from the extra-blastoporic region. The obscurity of their origin is due to the fact that they migrate separately without maintaining any connection with one another, as reported of Decapoda. It has definitely been shown that in *Panulirus* (TERAO, 1929) the yolk cells from the extra-blastoporic region degenerate without participating in the formation of the mid-gut, and that the latter is due to the expansion of the protoplasmic reticulum of the yolk cells invaginated en masse from the blastopore. It is therefore quite possible that in *Squilla* also the mid-gut is constructed from the yolk cells originated in the blastoporic region alone, though the precise mode of formation might not be quite identical to that in Decapoda. In Mysidacea (MANTON, 1929) and Nebaliacea (MANTON, 1934), which show superficial migration of yolk cells as in *Squilla*, the yolk cells are derived from the blastoporic region and its immediate vicinity. The mesodermal yolk cells of the members of these orders have not been found. In this connection, however, I am rather interested to the fact that some of the vitellophagous nuclei of Isopoda are said to be mesodermal (ROULE, 1895; MCMURRICH, 1895 b; GOODRICH, 1937).

It seems futile to regard all of the degenerating yolk cells as mesodermal. Inasmuch as the degeneration of the endodermal yolk cells is definitely known to take place in Mysidacea and in *Panulirus*, those cells in *Squilla* are likely to have the same fate. As a matter of fact, they are seen degenerating beneath the dorsal organ as will be described later. It is highly probable, therefore, that the degenerating cells found in abundance prior to the differentiation of the endodermal yolk cells partly owe their origin to the disintegration of these cells as well as to that of the mesodermal ones. In later stages, however, the endodermal cells do not degenerate, except under the dorsal organ, but take part in the mid-gut formation.

PART II ORGANOGENESES

7 Nervous System

A) *Early Development of the Optic Lobe and the Ganglia*

The initial step in the formation of the ganglia in stage 4 is marked by the sinking of the ectoderm cells on either side of the mid-ventral surface (figs. 30 & 32). In surface view, however, the ganglionic rudiments can not de clearly distinguished from other tissues before the end of the next stage. They are found for the first time in stage 6 at the base of each of the naupliar appendages and the optic lobes as four pairs of deeply staining small areas with indistinct outlines (fig. 5). Pairing of the ganglia in each segment is clearly shown in section because of the absence of sinking cells on the median line (fig. 36). Although the segmentation is distinct externally, the individual ganglia are not very distinct in longitudinal section (fig. 41). Cell sinking takes place throughout the length of the nervous system with no interruption in the intersegmental areas. In these areas, however, the cell sinking is less active and the nuclei are more sparse than in the segments. This difference appears externally as segmentation.

Before going further it is necessary to relate the profound change the optic lobes undergo, as this has a close connection with the development of the ganglia. In stage 4, in which the appendage rudiments are laid, the optic lobe is separated from the antennule by a shallow groove. The middle and the distal parts of the lobe are greatly thickened and composed of tall cylindrical cells, each of which has, near its inner end, a large oval nucleus scanty in chromatin except for large nucleoli; in the proximal part, on the other hand, the cells are shorter and contain ordinary small nuclei (figs. 29 & 35). Since the cells forming the entire margin of the lobe gradually continue to the ordinary blastoderm cells without demarcation, the growth of the lobe appears to be brought about also by the modification and addition of the blastoderm cells as well as by the multiplication of the component cells. Accordingly, the outline of the lobe is rather inconspicuous when viewed from the surface (figs. 4-6). In this stage, energetic disintegration of the preantennulary mesoderm is observed beneath the optic lobe.

Cell sinking begins in the basal part of the optic lobe immediately afterwards and produces the primordium of the protocerebrum. The optic lobe is differentiated, in stage 5, into a many-layered proximal and a single-layered distal part. The superficial layer of the proximal part, the protocerebral region, is composed of large nuclei scanty in chromatin, whereas the nuclei in the deeper layer are smaller and have more chromatin material. The constituent cells in the distal part are rich in cytoplasm and contain round vesicular nuclei even larger than the superficial nuclei of the proximal part.

In stage 6 the optic lobe is somewhat more compact than in the preceding stage and is divided into three portions (fig. 5). The proximal portion, the protocerebrum, stains most deeply, the middle, the ganglion opticum, is more extensive and somewhat lighter staining; while the distal part, or the retina, is narrow, crescentic and stains the lightest. In a section sagittal to the optic lobe, the ganglionic masses of the protocerebrum and the ganglion opticum are quite distinct from each other (fig. 45). The ganglion opticum is not an outgrowth of the protocerebrum as MOROFF (1912 a) states, but is derived from the ectoderm of the region lateral to the protocerebrum and independent of it. As in the preceding stage the ganglionic parts are composed of superficial and deeper layers containing large and small nuclei respectively. The large nuclei lie in various depths below the surface, clearly indicating the dislocation of some of them, and cells dividing perpendicularly to the surface may also be found. Thus, in addition to their own multiplication, the inner nuclei are increased in number by the immigration and the radial division of the superficial nuclei. The retina part remains unchanged and is composed of a layer of large vesicular nuclei. The two halves of the protocerebrum, developed in both optic lobes, are clearly separated from the beginning.

The other pairs of ganglia are the same in constitution as those of the optic lobe in this stage. In the mid-ventral region of the antennal segment (fig. 36), the nuclei of the most external layer are sunk more or less deep as in the lateral ganglionic regions. These nuclei later form the median connective part of the antennular ganglia. Both members of the antennal ganglia are situated laterally to the stomodaeal depression. The ganglia of the mandibular segment are rather compact and lentiform in section. They slightly bulge and are separated by a longitudinal median furrow which extends from the oral aperture to the base of the thoracico-abdominal process and is shallower toward the posterior end. The three pairs of ganglia belonging to the optic lobe, antennular and antennal segments respectively, fuse to form the brain in a later stage, and they are then called protocerebrum, deuterocerebrum and tritocerebrum.

By the time stage 7 is attained, the three portions of the optic lobe named above are more distinctly differentiated. The halves of the protocerebrum, which are roughly a square, approach each other along the median line, although they are distinctly separated from each other, as well as from the ganglion opticum, by a protoplasmic membrane. In transverse section, they are round masses crowded with small ganglionic cells, and covered on the anterior side by a layer of large cells which are the direct continuation of the layer covering the whole surface of the optic lobe. The small cells of the inner part of the ganglion opticum have increased considerably and spread out distally under the retina part. They are divided into proximal and distal masses, concealed from above by the layers of large cells in the ganglionic and retina parts respectively (fig.

53, *g. op. 3; g. op. 4*). In the retina part, which is indistinctly separated from the ganglionic part, the sinking of superficial cells is apparent (fig. 53, *r. l.*).

The deuterocerebrum is clearly demarcated from other parts by the protoplasmic membrane developed on the outside (fig. 39, *dc*). The superficial layer of large cells (*nb*) and the inner mass of small ganglionic cells are more clearly distinguished than in the preceding stage. The median connective part, occupying the space between the protocerebrum and the stomodaeum, is a transverse, tubular group of large cells which have already been separated from the hypodermal ectoderm (figs. 39-40, *dc. c.*). These cells are very rich in cytoplasm, have rather distinct boundaries, and their staining reactions are somewhat different from that of the smaller ganglionic cell. The tritocerebrum and the ganglion mandibulare become more compact than in the previous stage (fig. 41).

As mentioned above, each ganglion is made up of the superficial layer of larger cells and the inner mass of smaller ganglionic cells in these stages. Although the sinking of the ectoderm cells takes a leading rôle in the earliest stage of the formation of the ganglion, in the stages after the differentiation of the superficial cells, the enlargement of the ganglion is mainly due to the proliferation of these cells by unequal nuclear division, which produces smaller cells, as well as to the multiplication of the pre-existing smaller sized cells. The larger cells strongly remind us of the "Neuroblasten" recorded by BERGH (1893) as found in the ventral nerve cord of *Mysis*. Several of the offspring of the ectoteloblasts located on the mid-ventral surface are, according to him, differentiated into "Neuroblasten", which occupy the most superficial part of the body wall and proliferate internally to form regular vertical rows of small ganglionic cells. Although such regularity in cellular arrangement is not observed in *Squilla*, there is no doubt that the superficial layer of large cells is homologous to BERGH's neuroblast layer. These cells therefore will hereafter be called neuroblasts (figs. 39, 50-52, *nb*).

B) *Cerebrum*

In a surface view of the cerebrum in stage Th 3, the three pairs of component ganglia are rather compact and more or less clearly distinguished from one another (fig. 46). Both members of the protocerebra are rod-shaped and arranged in a V-shape diverging anteriorly. The deuterocerebra, which are on either side of the protocerebra, are oval masses connected by a median bridge not shown in the figure. The tritocerebra are nearly quadrangular in shape and also far apart from each othor on either side of the stomodaeum. The neuroblasts occupy the anterior and median surfaces in the first ganglia, while in the next and last pairs they cover the external surface. Paired bundles of the nerve fibrils make their first appearance in this stage, but they are too thin to be distinctly recognized

unless MALLORY's stain is used. Each bundle, after departing from the ganglion opticum, enters the protocerebrum at its antero-lateral corner and runs posteriorly along the middle of the ganglia as far as the maxillar segment. The fibril-bundle, situated in the innermost part of the ganglion, is not covered with ganglionic cells on the side facing the yolk sac. In the protocerebrum, however, the bundle is surrounded by the cells for some distance from the entrance. The paired longitudinal bundles connecting the consecutive ganglia are united by a transverse bundle in each segment except in the protocerebrum. In the deuterocerebrum (fig. 51, *n. f*) the transverse bundle develops in the lowest part of the median, transverse connective cell-group; in the tritocerebrum (figs. 64-65, *n. f*) it is found close behind the posterior wall of the stomodaeum. As the nerve fibrils are already continuous throughout these ganglia when they first can be made out, it is not certain whether they develop by the union of the fibre centers in each ganglion, or as continuous bundles from the beginning.

With the increase of cellular elements and the thickening of the fibre bundle, the three cerebral ganglion pairs, which have been more or less clearly demarked by narrow spaces scanty in nuclei, gradually become indistinguishable from one another. By stage Abd 2, the spaces between the consecutive ganglia have completely disappeared (fig. 47). The right and left halves of the brain are almost in contact with each other on the median line, but are distinctly separated by a protoplasmic membrane developed on the surface of each half (figs. 50 & 52). Although the inter-ganglionic spaces indicated by the scantiness of the nuclei in the earlier stages (fig. 41) are completely effaced, the demarcations between the fused ganglia are represented in another way. As fusion continues, deep transverse furrows develop on the external surface of the brain along the border lines between cosecutive ganglia. Thus the brain in this stage is divided, in its superficial part, into three swellings arranged antero-posteriorly and corresponding to the component ganglia. The protocerebra are closer to each other than before. Furthermore the transverse connection between the deuterocerebra contains more cells than in the preceding stage. The cells are reduced to the size of the ordinary ganglionic cells, but may be distinguished from them by containing fewer chromatin substance (fig. 51, *dc. c*). They are grouped into two masses which join the inner face of the deuterocerebrum. By this means, the deuterocerebra grow inward and approach each other along the middle line.

In the small area lateral to the deuterocerebrum and internal to the antennular base, a few neuroblasts are differentiated from the hypodermis. These neuroblasts proliferate inward to produce a number of smaller ganglionic cells. These cells multiply and spread over the lateral surface of the brain as a rather thick layer reaching the inner end of the lateral side of the brain (fig. 52, *x*). This layer then begins to cover the inner surface

from both sides toward the median, in the regions of the proto- and deuterocerebrum. The nerve fibre bundle which has been exposed to the serum space gradually becomes surrounded by ganglionic cells. The new layer thus takes part not only in the increase of the width and height of the brain, but also in its reconstruction. The nerve fibres have grown into a rather thick bundle by this stage. The transverse connective bundle between the deuterocerebra is much thicker than that in other parts, forming a rather conspicuous fibrous bundle occupying the central part of the brain (fig. 47). On the other hand, the post-stomodaeal bundle, namely that of the tritocerebral region, remains thin and is surmounted with a narrow cellular band. This cellular band, which seems to provide the underlying bundle with more fibrous substance, is connected on both sides to the cellular part of the tritocerebra and is clearly differentiated from other tissues for the first time in this stage. The fibres innervating the limbs are now apparent: the antennular nerve leaves the longitudinal bundle just behind its juncture to the deuterocerebral connective bundle; and the antennal nerve departs from the bundle in front of the stomodaeum (74, *n. f*). Each nerve can be traced to its respective limb base.

The brain has undergone a remarkable change in its shape as well as in its constitution by stage Abd 6 (fig. 48). The lateral side of the deuterocerebrum is provided with a triangular outgrowth which has been produced by the development of the new layer mentioned above. Of the three swellings of the cerebral surface corresponding to the component ganglia, the anterior two are almost confluent; the border line is indicated only by a shallow groove in the lateral part. The third, the tritocerebral swelling, expands anteriorly over the posterior part of the deuterocerebrum, from which it is clearly demarked by the slit-like groove made deeper than before by the intrusion of the mesoderm strand (a part of stomodaeal muscles, fig. 103). The back of the tritocerebrum is completely separated from the mandibular ganglion. The connection between the two, however, is retained only by naked nerve fibres. The greater part of the neuroblasts have disappeared, but two or three of them still remain in a very small area of the surface of each component ganglion. In the deuterocerebrum, the constitution of the cells derived from the transverse connective part are now indistinguishable from the other ganglionic cells. In the deeper part of the brain a few large cells somewhat resembling the neuroblasts are found mixed among small ganglionic cells. As the submergence of the neuroblasts have never been observed in the foregoing stages, these large inner cells are probably differentiated from ordinary small cells. On the level of the lateral outgrowth of the deuterocerebrum, namely just behind the central fibre mass and at the departing point of the antennular nerve, the longitudinal fibre bundles have a pair of small processes on the lateral side (fig. 48). These nerve fibres are nearly completely covered from below by the median growth of the inner end of the cellular part (fig. 52).

The brain is separated from the hypodermis and invested with a protoplasmic membrane in about stage L, Th 5. The membrane develops even on the median side of the cerebral hemisphere and completely separates the cellular part of the hemispheres which, however, are connected by the transverse nerve fibre bundles (fig. 106). The membrane is scattered with very flattened nuclei on the inner surface. It probably develops by the specialization of the ganglionic cells in the peripheral layer of the brain.

At the time of hatching the brain is roughly V-shaped with the arms of the V pointed backward and having the stomodaeal complex inserted between them (fig. 49). In the proto- and deuterocerebral regions the cerebral halves are in contact with each other, though distinctly demarcated by the membrane named above. The lateral process of the deuterocerebrum is turned forward. The surface of the brain is quite smooth, as the inter-ganglionic grooves have completely disappeared without the slightest indication of the suture. The brain is most raised in its anterior end closely attached to the hypodermis; it grows gradually lower toward the posterior and more separated from the body wall. As the neuroblasts have completely disappeared, the cellular constituents of the brain are all small ganglionic cells mixed with a few giant cells (fig. 71, *g. g. c*) which are differentiated from the latter. The giant ganglionic cell is characterized by its abundant cytoplasm with a clear border, as well as by its large, faintly staining nucleus. Although the brain is separated from the ganglion opticum as well as from the ganglion mandibulare in the cellular parts, the three are connected by a pair of longitudinal nerve fibre bundles which run through the whole length of the central nervous system. Thus the bundles are naked for short distances in the interspaces between the named ganglia. They are relatively very thick, their diameters being nearly half the width of the brain. The central fibre mass, occupying the proto- and deuterocerebral regions, is almost completely enclosed by the cellular part. In transverse section (fig. 106), the cellular part of each cerebral half, in this region, appears as a U-shape, with the arms of the U directed medially and enclosing a cavity containing the central fibre mass (*n. f*). The anterior part of the central fibre mass is bilobed, being cut along the median line by a thin membrane which is continuous to that which envelops the outside of the brain. The bilobed ends continue anteriorly to the V-shaped, longitudinal protocerebral bundles. These observations apparently indicate that the anterior part of the central fibre mass is formed by the mutual approach of the thickened longitudinal bundles. In the posterior part of the central mass which represents the connective bundle of the deuterocerebrum, the median intercepting membrane is naturally missing. A pair of longitudinal bundles depart from the posterior margin of the central mass and skirt the inner side of the tritocerebra; they are connected just behind the stomodaeum by the thin, transverse

tritocerebral bundle which has become completely naked by this time (fig. 65, *n. f*). The circum-œsophageal commissures are constructed with these bundles. The central fibre mass is provided, on each side, with a small fibre mass derived from the lateral process described in the preceding stage (fig. 49). The antennular nerve is sent out from the anterior side of this fibre mass, while the antennal nerve departs from the longitudinal bundle behind the former. The brain is not invested with the mesodermal neurilemma till the time of hatching.

C) *The Ventral Nerve Cord*

The differentiation of the ventral nerve cord formed by all the ganglia posterior to the mandibular ganglion, proceeds from the front toward the back. The early development of the mandibular ganglion has already been described. When the segments between the maxillula and the second maxilliped are first laid down, the ventral region internal to the limb base is composed of a single layer of ectoderm cells. Active cell division in this region causes the surface to bulge out on both sides in a short time. Thus the rudiments of the ganglia are represented in each segment by a pair of lentiform cell groups arranged side by side on each side of a median longitudinal furrow. When viewed from the surface (fig. 59), the ganglia of all these segments present a ladder-like chain, with more or less extensive intersegmental areas, entirely devoid of nucleus, on the mid-ventral line. The ganglia of the first and the second maxillipeds are first laid in the cephalic part, leaving a narrow intersegmental area in between. The ganglia posterior to these develop in the thoracico-abdominal process from the beginning. They are separated from one another only by very slightly staining transverse lines. The cellular parts of the ganglia composing the ventral nerve cord, except for those between the mandibular and maxillar segments which are somewhat intimately associated to form a sub-œsophageal ganglion, do not fuse as in the cerebrum until the time of hatching.

Sub-œsophageal Ganglion. As in the cerebrum, the ganglia between the mandibular and maxillar segments are also composed of a neuroblast-layer and an inner mass of small ganglionic cell mass derived from the former. In a longitudinal section cutting the lateral part, one ganglion can scarcely be distinguished from another in any stage, because of the cellular constituents are continuous and uniformly distributed throughout. In the middle part, however, the successive ganglia are clearly separated by the aforementioned intersegmental spaces devoid of nuclei (fig. 59). Although these spaces are gradually reduced with the increase of ganglionic cells, they remain even when the ganglia attain a considerable thickness. In about stage Th 8, the neuroblasts completely disappear and the nerve fibrils become apparent. The longitudinal bundles which are continued from the brain are connected by the transverse bundle at the middle of

each ganglion and form a chain similar to a ladder-like cellular part. The transverse bundle, extending laterally slightly beyond the external margin of the longitudinal bundle, forms a pair of small lateral fibril masses from which the limb nerve departs (fig. 103). In the middle part limited by the longitudinal bundles, the transverse bundle is composed of two parallel strands separated by a narrow cellular sheet (fig. 104). The bundle is not divided in the mandibular ganglion. The nerve fibres largely develop close to the inner surface of the ganglia without being covered by a cell layer.

These ganglia have coalesced to form a more or less compact sub-œsophageal ganglion by the time of hatching (fig. 105). The demarcation of the component ganglia, however, are shallow superficial grooves in the lateral region and the funnel-shaped pits on both upper and lower surfaces in the middle. The pits of both surfaces which communicate with each other through a very narrow channel, represent the remnants of the inter-segmental spaces mentioned above. Thus, in a section cut through the middle line, the three ganglia appear as if independent of one another, though a section through the lateral part proves this not to be the case. The lateral halves of the sub-œsophageal ganglion are also completely fused and not separated by a median protoplasmic membrane, as in the cerebrum. The border is represented only by a shallow longitudinal groove on the surface. The cellular part of the sub-œsophageal ganglion is completely separated not only from the cerebrum in front, but also from the ganglion of the first maxilliped behind it, the only connection being maintained by the paired nerve fibres. Each segment of the nerve in the ladder-like chain has a pair of large fibre masses developed at the junctures of the longitudinal and transverse bundles. The two strands of the latter bundles are completely fused by the withdrawal of the intercepting cellular part, and the lateral fibril masses are nearly consumed by the central pair of fibre masses.

Thoracic and Abdominal Ganglia. The ganglia of the thoracic and abdominal segments, except those of the first and second maxillipeds the primordia of which are laid down in the cephalic region, develop in the thoracio-abdominal process. The development of the ganglia is initiated, in an early stage of the external differentiation of the segments with the appearance of lateral constrictions, by the active multiplication of the cells composing the ventral wall (fig. 78). As the multiplication is more energetic in the middle of the segments than in the part between them, the ventral wall develops segmental swellings separated from one another by shallow transverse surface grooves (fig. 78). These swellings, which correspond to ganglion rudiments, are very conspicuous in the anterior segments but gradually become less so toward the posterior segments. The transverse grooves between the consecutive segments are deepest in the middle; they gradually grow shallower laterally, and completely disappeared in the marginal part. The grooves which appear shortly after the differen-

tiation of the third thoracic segments attain their highest development in stage Th 7, thence retrogressing to disappear completely in stage Abd 2. Accordingly, they remain rudimentary or missing in the posterior segments from the beginning.

At about the time when all the body segments are differentiated, the ganglia, except those of the first maxilliped segment, bulge a great deal in the dorso-lateral portion to form two swellings, one in front and one in the rear (fig. 103). These swellings are first and best developed in the second maxilliped segment but become more and more obsolete toward the back, remaining almost rudimentary in the few segments of the posterior. The ganglion of the first maxilliped segment is undivided, though bulged in the lateral portion. Secretion of the nerve fibrils is clearly seen for the first time in the anterior segments in stage Abd 4. Studies of serial sections of the egg in this stage show that, though the fibril centres of the third and fourth thoracic ganglia are united laterally by transverse commissures, they have scarcely any antero-posterior connection. It seems therefore certain that the nerve cord is formed by the union of the segmentally differentiating fibre centres, and that the transverse union precedes the longitudinal one. As in the two maxillar segments, the transverse fibre bundles of the thoracic and abdominal ganglia are first composed of two strands which later fuse to form one (fig. 104). In the completed condition, each ganglion is provided with a pair of large central fibre masses, each of which projects a limb nerve from the lateral margin. As in the cephalic region, the nerve fibres take a position dorsal to the cellular part and are exposed to the serum space.

The Inter-ganglionic Cell Group and the 7th Abdominal Ganglion. In the early stages of the development of the ventral nerve cord, the successive ganglia viewed from the surface are distinctly separated by very lightly staining transverse lines. Each ganglion is also divided into right and left halves by a similar longitudinal line passing through the whole length of the cord. These lines are nothing but the vertical inter-ganglionic spaces filled only with cytoplasm. In stage Th 7, in which the inter-segmental grooves of the ventral wall are in the height of their development, one or two special nuclei differentiate from those of the ordinary ganglionic cells to occupy the columnar part formed by the intersection of the longitudinal and tranverse inter-ganglionic spaces fig. 60, *i. g. c*). These nuclei are distinguished from others by being comparatively elongated. As development proceeds, more of these nuclei are added by further specialization of the ganglionic cells. They become spindle-shaped and more deeply and uniformly dyed (fig. 61, *i. g. c*). In about stage Abd 4, the inter-ganglionic cell groups expand laterally along the border surface of consecutive ganglia as thin cellular plates, although their development in the posterior segments is retarded. The cellular plates reach the lateral intersegmental folds of the body wall on both sides, and develop into double sheets pressed tightly

together, each sheet being connected with the wall of the lateral fold. By the gradual delamination of these double sheets, which proceeds from the lateral side toward the median, the ventral half of the successive ganglia become separated. Parallel to this delamination, on the ventral surface of the ganglia, the cytoplasm of several very flattened nuclei, differentiated from the ganglionic cell nuclei, constitute the epithelium which becomes continuous with the lateral body wall as well as with the lining of the intersegmental furrows. Thus the successive ganglia are connected only by the paired longitudinal fibre cords at the time of hatching, the cellular part being separated by these deep furrows (figs. 62-63).

The inter-ganglionic cell groups also develop in the cephalic region—between each of the ganglia from the mandible to the second maxilliped, in front of the mandibular ganglion, behind the deuterocerebrum as well as between this and the protocerebrum (figs. 65, 104 & 105, *ect. ing*). As stated before, the ganglia of the first and second maxilliped segments are first formed on the germinal disk, but they gradually move backwards with the advance of the stage. At the same time, the external part of the posterior member of these ganglia becomes shorter (fig. 61, *g. mxp 2*) and, by passing the thoracico-abdominal flexure, it is translocated from the cephalic region to the most basal part of the thoracico-abdominal process (figs. 103-105). Hand in hand with this change, the inter-ganglionic cell group between the two maxilliped segments develops into a cellular plate, which later constitutes an intersegmental furrow in a manner similar to that described above. The furrow gradually extends dorsally and, making a complete ring, it circumscribes the whole segment thus constricting the second maxilliped segment from the cephalon. The first maxilliped segment also becomes separated from the cephalon before the time of hatching. This, however, is principally accomplished by the development of the carapace fold and not by the dorsal extension of the intersegmental fold which here remains rather rudimentary. The inter-ganglionic cell groups anterior to these segments constitute the rudiment of the endophragmal system.

As stated before, six of the abdominal segments are formed externally. The ganglion of the ultimate segment, however, is composed of two masses arranged one in front of the other, marked by a lightly staining transverse line and by marginal notches on the surface. In section, an inter-ganglionic cell group is found inserted between these masses, but it remains rudimentary and never develops into an epithelial furrow as in the foregoing intersegments (fig. 62). Each ganglionic mass is provided with a pair of fibril centers and a transverse commissure composed of two strands (figs. 62-63). Thus it is evident that the ganglion of this segment consists of the sixth and the seventh abdominal ganglia. These ganglia, which presumably unite during the post-embryonic development, remain distinct till the time of hatching. This fact is in complete agreement with the

presence of the mesoteloblastic descendants corresponding to the seventh abdominal segment (cf. p. 106 f). These findings are very instructive from the phylogenical point of view. The presence of the seventh abdominal segment in the rudimentary state appears to be a more primitive character than that in the Decapoda and others, where no such ganglion is formed, and reminds us of what is found in Mysidacea and Nebaliacea. The formation of the seventh abdominal ganglion in these last two orders, followed by its subsequent fusion with the foregoing one, has been confirmed by MANTON (1928, '34).

The inter-ganglionic cell group is, without doubt, homologous with MANTON's (1928, '34) median "ectoderm intucking", which was described as taking part in the formation of the endophragmal system in *Hemimysis* and *Nebalia*. KINGSLEY (1889, in *Crangon*) and HERRICK (1892, in *Alpheus*) also draw a figure of exactly the same structure in the inter-ganglionic spaces of the abdomen, labelling it "mesoderm" or "muscle".

Some Remarks on the Neuroblast Layer. It has been repeatedly stated that in the earlier stages of development the central nervous system consists of a superficial neuroblast layer and an inner mass of smaller ganglionic cells derived from the former (figs. 50-52). The neuroblasts are most conspicuous in the cephalic region, though they are found in the thoracic and abdominal ganglia also (fig. 82, *nb*). REICHENBACH (1886, in *Astacus*) and HERRICK (1892, in *Alpheus*) believe this neuroblast layer to be a group of giant ganglionic cells already differentiated in the superficial part of the ganglion, instead of being a proliferating layer. The former author first found the layer in the brain of an *Astacus* in the stage with maxillipeds, and holds that the giant ganglionic cells, first seen in the most peripheral part, later submerge into the deeper part to take up their final positions. His figs. 114 and 115 drawn to support this statement are, in my opinion, only sketches of the neuroblast layer lining the anterior side of the protocerebrum. As stated before, the layer in question covering the anterior and median faces of each protocerebrum slightly extends to its ventral surface, so that a transverse section through a region near the anterior end of the brain shows the inward bend, in exactly the same manner as in REICHENBACH's figure, of the layer along the median line. The giant ganglionic cells are much fewer in number than the neuroblasts in *Squilla*. They make their appearance, from the start, in the deeper part of the brain, and there is no conclusive evidence of the downward migration of the neuroblasts. On the other hand, successive stages of the transformation of the small ganglionic cells into tho giant cells may be found —namely, the nuclei losing their former staining ability, the increase of the quantity of their karyoplasm as well as cytoplasm, and the cells finally taking the definitive character of the giant cells. A remarkable difference between the constitution of the neuroblasts and the giant cells is usually observed. The former elements, having a rather homogeneous cytoplasm,

do not seem to have distinct boundaries either between themselves or between them and the inner smaller ganglionic cells, while the granular cytoplasm of the giant cells are very clearly separated from the syncytial protoplasm of the smaller cells (fig. 71). Further, although the neuroblasts are present in the earlier developmental stages of the thoracic and abdominal ganglia, the giant cells never develop in these two regions of the central nervous system. REICHENBACH speaks of the superficial cell layer in the following manner: "Es ist gewiss von hohem Interesse, dass in diesen frühen Stadien, wo die Organsystem kaum deutlich zu erkennen sind, eine so hochgradige histologische Differenzierung ausgebildet, dass . . . die eigentlichen Ganglienzellen von den übrigen Nervenelementen schon durch solche Eigentümlichkeiten sich unterschieden, die sich in den reifen Tier beibehalten" (p. 65). According to the findings of my research, however, the superficial large cells are never highly differentiated, but they are merely undifferentiated ganglionic mother-cells.

TERAO (1929) describes, in his report of the development of the *Panulirus*, that the maxillulae and the maxillae are derived from a proliferating zone situated on the surface of the germinal disk between the labrum and the base of the thoracico-abdominal process. He calls this zone "the anterior budding zone" in contrast to "the posterior budding zone" which encircles the thoracico-abdominal process near its distal end and gives rise to the maxillipeds and thoracic legs. (Needless to say, the "posterior budding zone" is synonymous with the "teloblastic row" of most authors.) According to his statement, the "anterior budding zone" is represented by 7 or 8 transverse cell rows each composed of 4-6 large nuclei; "beneath this area numerous small nuclei are found close to each other and to the rows just mentioned, and sometimes partly inserted between the large nuclei" (p. 412). The superficial large nuclei are said to proliferate the inner smaller cells which later constitute the maxillula and maxilla (TERAO's fig. 20). It seems rather extraordinary that the two named appendages are different in their origin from those of the succeeding segments, since all of the postmandibular segments in all Malacostraca, except *Leander* reported by SOLLAUD (1923), are generally believed to originate from the teloblasts. In my opinion, it is highly probable that TERAO's "anterior budding zone" represents the neuroblast layer of the ganglia of the two maxillar sements, and the inner smaller cells which he takes for mesendoderm cells are ganglionic cells. In *Panulirus* also, the segments in question seem to be produced by the teloblasts as in other animals. To my regret, I have not had access to SOLLAUD's paper.

8 Ganglion Opticum, Compound and Median Eyes

Ganglion Opticum and the Compound Eye. The early development up to stage 7 of the optic lobe has been described in the foregoing chapter. The ganglion opticum of stage 7 is sharply differentiated from the proto-

cerebrum and provided with a well-developed neuroblast layer. The inner true ganglionic cells are divided into two groups, of which the proximal one is a large mass situated in the immediate neighbourhood of the protocerebrum, while the distal linguiform one extends laterally and is covered by the part which forms the retina (fig. 53). These ganglionic cell masses represent the third and fourth segments of the ganglion opticum. In the retina part the large, oval and lightly staining nuclei are in the course of sinking.

The cells sunk from the retina part form another layer of large nuclei beneath this (fig. 54, *nb 1-2*). Differentiation of this layer of large nuclei proceeds from the lateral margin toward the median, but the two layers remain in union with each other in the most proximal part for a considerable length of time. With this delamination of the retina part, the primordia of all parts of the compound eye are completed for the first time, the upper layer being the true retina layer and the lower one the neuroblast layer of the first and second segments of the ganglion opticum. The neuroblast layer greatly enlarges with the active multiplication of the component cells and, growing somewhat concave upward, becomes separated from the retina layer by a narrow space (fig. 55). In the mean time the cells of this layer more or less diminish in size and become differentiated into true neuroblasts. They then begin to proliferate a number of small ganglionic cells internally; these cells are shifted either to the lateral or to the median side, owing to the lack of space, to form two masses (fig. 56). Thus the ganglion opticum is gradually enlarged by the addition of elements from the new neuroblast layer, besides the multiplication of the preexisting cells.

The nerve fibrils are first made out in stage Th 6. Unlike the fibrils of the central nerve cord, these are surrounded by ganglionic cells and extend lengthwise, occupying the central part of the ganglion. The fibres are already continuous proximally with the longitudinal bundle of the brain, but distally, they curve downward and end on the inner surface of the ganglion opticum. There are two somewhat dilated parts or nodules, in the nerve fibres, corresponding to the third and fourth segments of the cellular parts which can no longer be discriminated from each other, being completely coalesced. The terminal part of the fibre bundle is also dilated to form the second nodule. As this nodule is close to the neuroblast layer mentioned above, there is no doubt that the former has been secreted by the cells proliferated by the latter.

At about stage Th 7, the cells of the future retina begin to differentiate into retina cells, growing smaller in size and richer in chromatin net-work. The differentiation proceeds from the lateral margin towards the median; the retina part becomes many-layered at the same time. In stage Abd 4 this part is completely separated from the neuroblast layer, even in the most proximal part, and the whole retina is crowded with

numerous cells arranged in several layers (fig. 56). The retina cells are now characterized by elongated nuclei which stand vertical to the surface and contain darkly staining granular karyoplasm. The neuroblast layer beneath the retina layer becomes more concave than before and its distal part bends upwards.

With this bending of the distal part and its subsequent contact with the proximal part, the neuroblast layer is transformed in stage Abd 5 into a U-shaped fold which stands almost vertical to the surface of the optic lobe (fig. 57). The outer wall of the U-shaped fold produces the elements of the first segment of the ganglion opticum distally (*g. op. 1*), and the inner wall proliferates proximally those of the second segment (*g. op. 2*). In this stage the first segment forms a rather compact mass shaped like an arrow-head, while the second is inseparably united with the third. The nerve fibres are greatly thickened in three nodules, the first being not yet secreted. Near the proximal portion of the retina layer there is a small area where the nuclei are situated somewhat more deeply than in other portions and show active mitoses (fig. 57). In the distal portion, however, several retina cells are already aggregated into a pillar-like group, thus foreshadowing their differentiation into ommatidial components. At about the time when all body segments are formed, the pillar-like group begins to secrete pigment in its most internal part (fig. 66). Like in the earlier developmental stage, the differentiation of the visual elements as well as the pigment secretion proceeds from the lateral side toward the median.

Immediately after the stage described above, a part of the internal surface of the ganglion opticum, which is just heneath the U-shaped neuroblast layer, begins to rise and becomes separated from the yolk surface by a narrow hollow lumen. With this change, the first and cecond segments of the ganglion rotate in such a manner that their surfaces, which were formerly internal, come in direct contact with each other (fig. 68). The nerve fibres, having curved downward in the second segment, are consequently straightened in stage L, Th 7, and the second, third and fourth nodules are arranged in a straight line. The nodule of the first segment is disk-shaped and composed of very short fibrils; it is not yet connected with the second nodule. The U-shaped neuroblast layer, which is now placed between the two distal segments of the ganglion, still remains though rather reduced. A large part of the same layer of the third and fourth segments has also disappeared, remaining only in a very small area. Prior to this and at about stage L, Th 1, the ectoderm cells begin to submerge along the line just outside the lateral margin of the retina layer as a wedge-shaped ingrowth (fig. 66, *ect. ing*). This ingrowth develops into an ectoderm fold thrust into the space between the ganglion opticum and the yolk surface. Next a similar ectoderm fold is formed along the anterior and posterior margins of the optic lobe. With the gradual extension of the fold circumscribing the optic lobe and with the subsequent meeting of

the inner edges of the fold on the middle line, the base of the optic lobe is screened from the yolk sac by a double sheet of ectoderm. The upper layer of this sheet is the epithelium covering the lower surface of the optic lobe, and its distal end is connected with the retina layer. The lower layer is the continuation of the body epithelium. With the development of the ectoderm fold, the marginal part of the retina layer curves downward and extends as far as the lower surface of the first segment of the ganglion opticum, completely covering its lateral side (fig. 68).

Just before hatching, the optic lobe is liberated from the cephalic region as an eye-stalk by the delamination of the double sheet of the ectoderm (fig. 68). A greater part of the ganglion opticum is differentiated from a thin hypodermis which continues distally to the retina layer. The first and second nodules of the nerve fibres are connected. The neuroblasts have completely disappeared, and giant ganglionic cells are present as in the cerebrum. At the time of hatching the eye-stalk stands erect on the cephalon and is surmounted by a corona of the ommatidia layer in which all components are thoroughly differentiated (fig. 10). It is provided with muscle fibres and blood vessels in the basal part. The former is derived from a part of the cephalic mesoderm included within the eye-stalk. The origin of the blood vessels was not studied.

There are two different views as regards the mode of development of the crustacean eyes. REICHENBACH (1886, in *Astacus*) and KINGSLEY (1887a, in *Crangon*) state that the early development of the eye is due to the formation of a vesicle from an ectoderm invagination. The outer wall of the vesicle with the overlying hypodermis is differentiated into ommatidia and the inner wall joins the ganglion opticum. On the other hand, PARKER (1880, in *Homarus*), HERRICK (1892, in *Alpheus*), MOROFF (1912a, in *Palaemon* and *Artemia*) and others, maintain that the ommatidia are formed by a mere thickening of the hypodermis. As pointed out by these authors, the notion that the eye vesicle takes part in the formation of the visual elements is evidently erroneous. In fact KINGSLEY (1889) discarded his former opinion in his third paper and took the view that the invagination concerns only the ganglion formation.

It is rather problematical whether the ectoderm of the optic lebe is actually invaginated. HERRICK (1892) emphasizes the absence of any invagination in the early developmental stages of the eye of *Crangon*, in spite of KINGSLEY's assertion of its presence. REICHENBACH (1886) gives figures (figs. 5, 6, etc.) showing the first stage of the alleged "optic invagination," but he does not give any clear figure of the stages to demonstrate satisfactorily the transformation of the invagination into the optic vesicle. His fig. 173, etc. show that the optic vesicle is composed of a U-shaped layer of large nuclei and two masses of much smaller unclei situated respectively outside and inside the former. There is no doubt that his "optic vesicle" is nothing but the first and second segments of the ganglion opticum, and

the U-shaped layer is the neuroblast layer of these segments. As mentioned above, in *Squilla* this neuroblast layer arises from the fold of the layer which first stretches horizontally. The horizontal layer, in turn, is derived from the sinking of the cells from the retina layer and not from invagination. It is rather probable that REICHENBACH's "optic invagination" is due to an artefact and that the optic vesicle is formed in a way similar to that in *Squilla*. The present study verifies the views of PARKER and others by showing that the visual elements develop from a simple thickening of the hypodermis.

As for the origin of the ganglion opticum, BULLAR (1879, in *Cymothoa*) NUSSBAUM (1887, in *Mysis*), PARKER (1891, in *Homarus*) and HERRICK (1892, in *Alpheus*) agree that it develops from the hypodermis lateral to the brain and independent of the latter. MOROFF (1912a), on the other hand, in his report of the development of the eye of *Artemia* and *Palaemon*, states that the ganglion originates from the lateral outgrowth of the brain. Reviewing various previous investigations on this subject, he further comes to the conclusion that the optic ganglion of all crustanceans is derived from the brain. His fig. 1 (pl. 29), intended to demonstrate the invasion of the outgrowth from the brain into the space beneath the retina layer, however, does not appear to substantiate his view. His figure does not seem to represent the first step of the formation of the ganglion but the state after its differentiation from the retina layer. This may be obvious if one compares his figure with my fig. 54. The rudiment of the ganglion opticum and that of the protocerebrum in *Squilla* are independent from the beginning, as the former is differentiated from the ectoderm lateral to the latter. Therefore, as far as *Palaemon* is concerned, MOROFF's belief appears to be founded on his observation of the state of the ganglion already differentiated from the retina part and not of any earlier stages.

As stated before, the first and second segments of the ganglion opticum of *Squilla* are derived from the retina part, while the third and fourth are formed from the region between this and the protocerebrum. At first sight this fact brings to mind the two-fold origin of the ganglion in Phyllopoda as recorded by CLAUS (1886). In this case, however, the ganglion is said to be derived partly from the brain and partly from the retina layer. The two-fold origin in *Squilla* is merely superficial. When the neuroblast layer of the first and second segments is formed, the retina layer external to that is composed of undifferentiated cells instead of differentiated ones. The process of the formation therefore consists simply in a premature separation of the ganglion from the hypodermis; it does not necessarily show a derivation from the retina part, because this part is a thickening of the hypodermis, and the specialization of retina cells belongs to a future event. The first and second segments do not differ from the third and fourth in their origin. The seeming difference is entirely due to the fact that the retina part develops from the hypodermis in the same part as that which

produces the first two segments of the ganglion opticum.

BERNARD (1937) appears to have recently expressed his belief in the hypodermal origin of the nervous centre of the compound eye. Unfortunately I have been unable to see a copy of his paper. On the other hand, SCHATZ (1929, in *Gammarus*) and PEABODY (1939, in *Idothea*) maintain the cerebral origin of the compound eye in the Edriophthalma. It is highly probable that the ganglion opticum develops independently of the cerebrum at least in the Podophthalma.

Ommatidium Components. At about the time when all the body-segments are differentiated, the retina cells get together to form a number of columnar groups, the process beginning from the lateral margin of the retina layer (fig. 68). All the cells composing each of the columnar groups become all the components of one ommatidium. Although the histogeneses of the ommatidium was not studied thoroughly, the following statements may not be amiss (fig. 69).

The secretion of pigments bofore the formation of the rhabdome occurs at the sacrifice of the chromatin substance in the nuclei found in the basal part of the cellular column. The rhabdome is formed by seven cells, the crystalline cone (*c. c*) by four cells (*cc. c*), while the corneagen cells are two (*cg*). The number of the proximal retina cells (*p. r. c*), which surround the basal portion of the crystalline cone at the time of hatching, is unknown. A few retina cells are also found in the most peripheral part of the compound eye. The chitinous membrane (*ed*) covering the surface of the ommatidial layer and continuous to the epidermis of the eye stalk is not yet sectioned into lens thickenings. At the level of the border between the crystalline cone and the rhabdome, the ommatidial layer is crossed by a protoplasmic membrane which, however, does not interrupt the direct connection of the two structures (fig. 70). A similar membrane also lines the lower surface of the ommatidial layer and the upper surface of the first segment of the ganglion opticum (fig. 70). The narrow space enclosed by these two surfaces is scattered with numerous flattened nuclei derived from either retina cells or ganglionic cells (figs. 68-70). The central part of this lumen is somewhat enlarged and packed with a few large accessory pigment cells (*a. pg. c*). The abundant cytoplasm of these cells have many pigment stripes which are continuous from the retinal pigment to the surface of the ganglion. The nuclei are large and scanty in chromatin except for the central small chromatin spherule. These cells are derived from the retina layer. At the time when the ectoderm ingrowth begins to develop on the margin of the optic lobe, the retina cell complex liberates a few cells from the basal part of its lateral margin (fig. 66, *a. pg. c*). These cells, attached to the lower surface of the ommatidial layer, grow rich in cytoplasm and secrete pigment granules. With the involution of the ommatidial layer, they become enclosed within the space named above and are differentiated into accessory pigment cells.

Median Eye. In stage Abd 5 the protocerebrum is already separated from the hypodermis. At the anterior end of this portion of the cerebrum, several cells liberated from the hypodermis are thrust more or less deeply into the narrow space between the right and left protocerebra. Of these cells two are situated most deeply and in close juxtaposition to form a flask-shaped group which has a distinct cytoplasmic boundary (fig. 58, *pg. c*). They are the pigment cells of the median eye. Shortly afterwards and simultaneously with the pigment formation in the compound eye, pigment granules begin to appear in the cytoplasm of these cells. The retina cells derived from other sunken cells form a thick one-celled layer which encircles the pigment cell group (fig. 58, *r. c*). The retina cells have distinct borders and are more or less quadrangular in shape. The median eye which is now vesicular is situated below the hypodermis somewhat apart from it. Until the end of embryonic life, the eye does not make much progress in its development except for a small increase in the number of retina cells and its slight approach to the hypodermis. Neither lens formation nor nervous connection with the brain takes place. The division of the retina cells into three groups, reported by HANSTRÖM (1931) and others, is not clearly indicated. At the time of hatching, the median eye is seen from the surface as a pair of rectangular pigment spots placed side by side.

9 Other Ectoderm Derivatives

Dorsal Organ, Epidermis and Embryonic Exuviae. The dorsal organ makes its appearance first in the mid-dorsal region antipodal to the stomodaeum in stage Th 5 or 6 (figs. 95-97, *d. o*), and attains the height of its activity in about stage Th 8. It is a circular area of ectoderm crowded with nuclei. In this area the ectoderm cells submerge below the surface, disclosing vigorous degenerative changes with the liberation of chromidia (fig. 73). Apparently in close relation to these changes, the surface of the yolk beneath this region is very depressed and shows many yolk spherules being discharged to the outside, probably indicating a dissolution of the yolk. The endodermal yolk cells come together, some of them apparently disintegrating. The dorsal organ degenerates by stage Abd 4 and the depression of the yolk surface disappears.

By the time the dorsal organ is formed, the ectoderm covering the body has secreted a very delicate chitinous epidermis on its external surface. The epidermis of this region becomes detached from the surface of the body as soon as the dorsal organ commences its activity. The detachment of the epidermis extends throughout the whole surface of the cephalon in a short time and finally to the thoracico-sbdominal process. The whole process, representing the embryonic moulting, ends by stage Th 8. The exuviae surround the cephalic region as a round sac lying slightly apart

from the surface, and show a projection which is folded over the main sac in conformity to the shape of the thoracico-abdominal process. The exuviae are also cast off from the inner surfaces of the stomodaeum and the proctodaeum. After the moult, the ectoderm resumes the secretion of the chitinous epidermis which becomes so thick by the time of hatching that the embryo can not be stained in toto. The second moult does not occur during the embryonic life.

Rostrum. At about stage Abd 1, the ectoderm cells constituting the roof of the wide serum space in front of the protocerebrum, get together to form a transverse band. This band is composed of several rows of rather thick cells and connects the antero-lateral margin of the optic lobes, enclosing a triangular area devoid of nuclei. By stage Abd 4, the ectoderm band greatly increases in cell number, thereby extending posteriorly to the anterior margin of the protocerebrum. The central part of the band is now crowded with extremely elongated cells. In section, these cells are attenuated distally so as to converge into a point, and form a more or less conical group of cells inclined anteriorly. These cells, having nuclei in their basal parts, are traversed by many fibrous striations concentrated toward the tip of the cell group. This cell group represents the first rudiment of the rostral spine. When it enlarges, the ectoderm behind it becomes depressed, thus reducing the underlying serum space (fig. 67). The posterior wall of the depression is closely applied to the nearly vertical frontal surface of the protocerebrum, while the anterior wall slopes gently continuing gradually to the general body surface. The rostral spine (*r. s*) is now laid nearly flat over the latter wall, its distal end being directed anteriorly. The spine then greatly bulges in its basal part, but elongates at the same time, its fibrous distal part turning posteriorly. Since the cavity is covered by the embryonic exuviae from above, the growing spine is forced to bend to some degree. The spine, posteriorly directed at first, is forced to curve downward due to the presence of the posterior wall of the cavity, then it again turns anteriorly along the bottom of the cavity (fig. 105, *r. s*). In the stage just before hatching, the curved filiform part of the rostrum is entirely constructed of a chitinous substance converted from the aforesaid fibrous structures, without having either nuclei or a protoplasmic matrix. The very thick basal part of the rostrum, however, is provided with an abundance of protoplasm which is crowded with nuclei and has numerous fibrils continuing to the distal chitinous part. With hatching, the curved spine extends anteriorly in the same manner as in the larva.

Carapace. The carapace is merely a fold of the ectoderm. At about stage Th 7, a semicircular transverse band composed of three or four rows of cells makes its appearance at the proximal end of the dorsal surface of the thoracico-abdominal process. In this band the epithelium is much thicker than in the neighbouring region and has large oval nuclei. With the displacement of the nuclei of (morphologically) the posterior rows to positions

beneath those of the anterior rows, the ectoderm band develops into an epithelial fold. This fold grows more prominent with development and becomes composed of two layers attached close together. At about stage Abd 6, a hollow cavity appears between the two layers by their delamination (fig. 100, *c. f.*). The cavity is traversed by a number of plasmic fibres connecting the inner surfaces of both layers, thus generating a complicated lacunae system. The above is the state of the posterior part of the carapace fold in this stage.

The anterior part of the carapace fold, which extends from the lateral end of the posterior carapace fold to nearly the level of the stomodaeum, is formed by a somewhat different process. At about stage Abd 6, the serum space lateral to the ventral nerve cord is traversed by a number of parallel fibres running in the vertical direction which terminate on the inner surface of ectoderm cells at both ends. Gradual contraction of these fibres causes the ventral surface of the cephalon to form a pair of ridges which run antero-posteriorly on both sides of the nerve cord.

Further development of the carapace fold consists in the expansion of its posterior part in the form of a pair of large lateral lobes, while the anterior part, remaining as a ridge of the body wall, does not make much progress. With the forward displacement of the line of attachment of the posterior part, the first maxilliped segment becomes independent from the cephalic region, at least on the dorsal and lateral sides, by the close of embryonic life (cf. p. 45). At the time of hatching the carapace fold is separated into two more or less triangular, acuminate, lateral lobes, by a deep, median, posterior incision (fig. 10, *c. f*). The lacunae of the fold communicate with the general body cavity and are invaded by blood corpuscles.

10 Digestive System

Stomodaeum and the Visceral Ganglion. The stomodaeum of stage 6 has its wall composed of tall cylindrical cells arranged around an oval lumen. The hypostome is depressed in a median longitudinal groove owing to the protrusion of the labrum. The labrum attains, in the next stage, the level of the posterior margin of the antenna. With the posterior elongation of the labrum, the external portion of the stomodaeum bends backward nearly horizontally, while the internal portion stands erect over the yolk sac; the whole organ is L-shaped (figs. 40 & 64). The cavity of the vertical portion remains oval, while that of the horizontal portion is now reduced to a slit-like lumen.

The labrum reaches midway between the antenna and the mandible in stage Th 7. The stomodaeum is further converted into a V-shape by the turning back of the internal portion. The anterior wall of the stomodaeum is somewhat thickened at the inflexed point of the V, where the nuclei are irregularly arranged. In stage Abd 3 the wall of the stomodaeum is composed of a layer of very tall cells with elongated nuclei, except in

the part mentioned just above. In this thickened part there are a number of small round unclei outside the layer of elongated nuclei. These small nuclei subsequently form the visceral ganglion which belongs to the sympathetic nerve. While the ganglion is still united to the wall of the stomodaeum in the form of a protuberance of the latter in the following stage, a small mass of neuroglia fibrils makes its appearance in the midst of the group of round nuclei (fig. 64, *g. vis*). The ganglion becomes entirely independent of the stomodaeum as a round cell mass enclosed by a peri-stomodaeal mesoderm, at about stage L, Th 1 (figs. 65 & 104).

With the separation of the visceral ganglion from the stomodaeum, the anterior wall of the latter regains its original state of one-celled layer with elongated filiform nuclei. The posterior wall, on the other hand, grows many-layered by the multiplication of the component cells, and bulges out towards the anterior into the stomodaeal cavity (fig. 65). In sections, the cavity of the internal portion of the stomodaeum is U-shaped with the arms of the U directed backward, while that of the external portion remains a horizontal slit, although it is much wider than before.

At about this time, the paired mesodermal bands, connecting the peri-stomodaeal mesoderm with the rostral base, become fibrous. The fibres are divergent in their posterior ends end attached to the anterior wall of the stomodaeum at various points (figs. 65 & 105, *m*). The gradual contraction of the fibres drags the stomodaeum forward, so that the latter changes its external form as well as the shape of its cavity considerably. The external portion of the stomodaeum now extends straight in the antero-internal direction and its wall has become rather thin. The internal portion on the other hand, almost comes in contact with the yolk sac throughout its whole length. It remains very thick and is curved into an S-shape with subsequent development (fig. 104). The two portions thus differentiated become the œsophagus and the cradiac portion of the stomach respectively. The latter gets its communication with the mid-gut or the pyloric portion at about stage L, Th 5.

These portions of the digestive system are constructed in the following manner at the time of hatching (figs. 56 & 107). The oral aperture, which is bounded in front by a semicircular labrum and in behind by a bilobed hypostome, leads to the short, straight and antero-internally extending œsophagus (fig. 65, *oe*). The latter is composed of one layer of flattened cells and contains a horizontal slit-like lumen which grows gradually narrower toward the internal end. The lumen of the stomach is compressed laterally, opening to the œsophagus by a vertical slit extending practically throughout its length. Accordingly, the lumen of the œsophagus and that of the cardiac stomach together form a T. The main part of the cardiac stomach is curved in an S-form (fig. 65, *card*) and has a very thick wall crowded with filiform nuclei; the cross section of the internal cavity is Y-shaped.

The visceral ganglion does not develop much from the state described above. It is attached as a round body to the ventral (formerly anterior) wall of the œsophagus near its internal end (fig. 65, *g. vis*). The ganglion remains completely isolated from the ventral nerve cord, though very similar in cellular constitution. The nerve fibre mass is surrounded by ganglionic cells and does not send any strand to any structure. The ganglion is now invested with a protoplasmic membrane which it secretes; the peristomodaeal mesoderm has been withdrawn from the surface.

The development of the sympathetic ganglion in Crustacea has never been studied. Its development in *Squilla* is in exact accord with what was observed by HEYMONS (1901) in *Scolopendra*. As in the "ganglion frontale" of *Scolopendra*, the ganglion of *Squilla* develops from the wall of the stomodaeum. But, whereas this ganglion fuses with the posterior end of the cerebrum after it is separated from the stomodaeum in *Scolopendra*, in *Squilla* it remains distinct from the cerebrum even in the larval stage and develops into a somewhat complicated system. It is said that in *Scutigera* the "ganglion frontale" remains independent of the cerebrum.

Proctodaeum. The early development of the proctodaeum as well as the displacement of the anus to the ventral side have already been mentioned.

At the time of the formation of the maxillar segment, the proctodaeum comes in contact with the endodermal mid-intestine (fig. 42). The former is merely a blind sac rounded at its end and contains no cavity except in the part close to the anus which is a longitudinal slit-like aperture. Although the round end of the proctodaeum is set close to the posterior end of the mid-intestine, the two portions are clearly distinguishable from each other by the absence of a cavity in the former (fig. 40). Besides, they are entirely different in cellular constitution. The constituent cells of the ectodermal portion possess very clear cytoplasm enclosing a nucleus scanty in chromatin, while those of the endodermal portion are characterized by granular cytoplasm and darkly staining nuclei.

At about stage Th 4, a cavity appears throughout whole length of the proctodaeum, but it does not communicate with the mid-intestinal lumen yet, being screened by a protoplasmic membrane. The anus is displaced to the base of the median furrow between the caudal furca, and opens as a wide aperture. Communication between the proctodaeal and intestinal cavities opens at about stage Th 7 with the confluence of the walls of the two portions, though the differences in their cellular constitutions remain unchanged. In contrast to the remarkable elongation of the endodermal part, the proctodaeum does not make much development and is limited to a small terminal portion of the intestine, the rectum, which is slightly dilated in this stage (fig. 78). As the wall grows thicker the rectum curves downward in a right angle. This displaces the anus to the ventral side which narrows in the meantime. The boundary between the rectum and

the endodermal intestine becomes inapparent with development (figs. 88, 89 & 105). From this stage on until the time of hatching, the rectum does not undergo much change.

Mid-gut, Intestine and Liver Lobes. The early development of the endoderm plate and that of the intestine have been described. In spite of the active multiplication of component cells the growth of the mid-intestine does not match the rapid elongation of the thoracico-abdominal process. This inconformity in the relative growth stretches the mid-intestine making it thin. The inner cavity is reduced and the cells composing the wall are elongated (fig. 61). Thus, in stage 8, the intestinal cavity becomes so narrow that it is practically obliterated except in the proximal portion (figs. 79-84). The wall, however, is rather thick and composed of one-layered cells, fan-shaped in section. The cytoplasm of these cells is somewhat clearer than before, while the nuclei, retaining their former condition, possess darkly staining karyoplasm with granular chromatin substances.

The endoderm plate lying over the yolk surface is gradually enlarged by the division of the constituent cells as well as by the addition of yolk cells to the periphery of the plate. As the enlargement occurs principally in the transverse direction and not much in the longitudinal, the width of the plate becomes four or five times the length at about the time when all the body segments are formed. Even then the plate only covers a small part of the postero-ventral side of the yolk sac. The plate represents the posterior rudiment of the mid-gut epithelium, and may be termed the "posterior endoderm plate" (figs. 92-94 & 100) to distinguish it from the "anterior endoderm plate" which develops beneath the stomodaeum to be described below.

Beneath the posterior endoderm plate, there is a rather wide space in the yolk sac deprived of yolk blocks and filled with a fluid substance. This fluid is nothing but the liquefied yolk and dyes blue with MALLORY's stain; it appears finely granular, a striking contrast to the yellow and rather homogeneous yolk blocks of the circumferences (fig. 100, *y. g*). The blue granules are also found within the intestinal lumen. The nuclei of the endoderm plate are very irregular in shape, often with pseudopodia-like processes. This observation seems to indicate that the mid-gut epithelium actively dissolves the yolk substance. Moreover, the blue substance is found in the intra-cellular vacuole of the epithelial cells and even in the cells of the intestinal wall. This again appears to point to the assimilation of the yolk substance actuated by the endoderm plate.

As soon as all body segments are differentiated externally, the mid-gut epithelium is somewat thickened in two small areas forming a pair, with one on either side of, and very slightly dorsal to, the base of the intestine. In these areas the cells are more crowded than in other parts and much taller, having elongated nuclei. These thickenings which represent the rudiments of the posterior liver lobes are raised from the mid-gut

surface, developing, in a little while, into a pair of hollow blind tubes inclined somewhat internally towards the intestine. These tubes enter the cavity of thoracico-abdominal process, where they gradually make their way backward along either side of the intestine. They reach in the middle of the telson in the stage just before hatching (figs. 100 & 105). The liver lobes, which end blindly, show much longer and wider cavities than the intestine. They have rather thick wall composed of a layer of cubic epithelial cells (figs. 85 & 91, *pos. liv*). Closely associated with the intestine, the lobes occupy greater part of the cavities of the trunk segments. Since the intestine starts from the mid-gut slightly more ventrally than the liver lobes, it is inserted between the ventro-internal sides of the lobes in the anterior segments. In the posterior segments, however, the intestine gradually comes higher in position and comes to lie between the dorso-internal sides of the liver lobes. The liver lobes develop no branch or outgrowth and remain as a simple elongated blind tube until the time of hatching. Their cavities contain a large amount of liquefied yolk which is also found within the intra-cellular lumen of the cells constituting the wall (fig. 85, *y. g*). These liver lobes may be called the "posterior liver lobes" in contrast to the "anterior liver lobes" which develop from the anterior endoderm plate.

At about stage Th 8, the yolk cells scattered over the yolk surface gradually concentrate around the base of the stomodaeum. They are rearranged and transformed into the epithelium which is the rudiment of the anterior endoderm plate (figs. 64, 103 & 104, *ant. end*). At first the plate occupies only a small area extending laterally for a short distance from the stomodaeal base. The plate is soon enlarged in the antero-lateral direction to become V-shaped at about stage Abd 4 (fig. 52). It is very broadened and bilobed in front, extending from the stomodaeal base to the posterior margin of the optic lobe. By stage L, Abd 6, the bilobed plate is transformed into a triangle which reaches as far as the anterior end of the rostral base (figs. 65 & 105). In breadth, however, it goes only beyond the lateral margin of the brain even in the widest anterior region (figs. 71 & 106). The anterior endoderm plate is thus a definite contrast to the posterior plate which is much wider than it is long. Like the latter plate, the former develops by the constant addition of yolk cells as well as by the multiplication of the already differentiated cells (fig. 71). There is a difference, however, between the two in that the anterior plate is entirely constructed by the concentration of yolk cells, and lacks the compact kernel of endoderm cells.

Just before the time of hatching—namely, when the posterior liver lobes reach the telson cavity—the anterior endoderm plate becomes grooved along the median longitudinal line throughout its whole length (fig. 72). The groove is deepest at about the anterior end of the cerebrum; it grows gradually shallower towards both ends, and divides the antero-ventral

side of the yolk sac rather incompletely into a right and a left lobe. These lobes are the rudiments of the anterior liver lobes or, more precisely, the mid-gut diverticula (fig. 72, *ant. end*). The endoderm plate, which is now γ-shaped in transverse section, covers a small area of the liver lobes, and forms the epithelial lining of the latter. The liver lobes do not undergo much change until hatching.

The mid-gut proper, derived from the yolk sac, remains incomplete till the close of embryonic life. The whole yolk is broken up into small blocks without any regularity in size or arrangement in earlier stages (figs. 101 & 102). At about the stage in which the dorsal organ is formed, the yolk is divided into more or less pyramidal blocks arranged nearly radially. Owing to the brittleness of the yolk, the development of these pyramids was not sufficiently clear. Nevertheless, there is no doubt that they represent the secondary yolk pyramids present in many other crustaceans. The yolk pyramids (fig. 105, *s. y. p*) can be most distinctively observed in the stage shortly before hatching. Although each pyramid is provided with a nucleus close to the external surface, the cytoplasm is seen only in the immediate circumference of the nucleus. I did not succeed in ascertaining whether the cytoplasm covers the external and lateral sides of the pyramid or whether it is limited to the periphery of the nucleus. Toward the internal end, the yolk pyramid becomes gradually indistinguishable from the liquefied yolk substance occupying the central part of the yolk sac.

At the close of the embryonic life, only the antero-ventral and posterior sides of the yolk sac are covered by the endoderm epithelium; the other sides remain uncovered and scattered with a rather few residual yolk cells (fig. 105). The two endoderm plates are close to each other on the middle line, though they remain distinct. The yolk cells are much fewer than when they are first dispersed over the yolk surface. This is due to the fact that some of the yolk cells join the endoderm plate and some degenerate under the dorsal organ, when no multiplication takes place after their first dispersion. Owing to the conversion of the yolk into a body fluid, the yolk sac shrinks to a certain extent by the time of hatching. The yolk sac is nothing but the pyloric part of the adult stomach.

The mid-gut develops a pair of shallow vertical grooves at the level of the mandible at about the time the anterior liver lobes become distinguishable. These grooves constrict the mid-gut and produce inconspicuos round swellings toward the posterior direction which seem to represent the lateral pair of mid-gut cœca. The mid-gut muscles which have been developed from the mandibular mesoderm are attached to the surface of the yolk sac along those grooves. Thus, the grooves apparently owe their origin to the tension of these muscles. The lateral pair of cœca are covered only by the endoderm plate on their posterior side.

It is rather interesting from the standpoint of comparative embryology that three pairs of mid-gut cœca are formed in *Squilla* as in Decapoda,

though two of them remain in a very rudimentary condition until hatching. The completion of these cœca seems to be delayed to the larval stage. GIESBRECHT's figures of his "propelagisches Stadium" in *Squilla mantis* (1910, Taf. 9, Fig. 1, 2 u. 6) as well as BROOKS' drawings of the same in *Gonodactylus chiragra* (1892, pl. 14, fig. 16; pl. 15, fig. 9) show the bilobed anterior part of the yolk sac and a pair of short postero-lateral processes. According to these figures, it is clear that these two pairs of annexes of the yolk sac develop more with the advance of the larval stage. There is no doubt that they represent the anterior and lateral mid-gut cœca. These cœca seem to be absorbed again in a later stage by the mid-gut, as found in Decapoda, since the adult mid-gut is not provided with such structures. Unlike this order in which the posterior liver lobe is divided into several lobules, it remains as a simple elongated tube extending as far back as the telson. The constitution of the lobe is in exact accord with that found in *Nebalia* (MANTON, 1934). There are differences such as the subsequent disappearance of the anterior liver lobes and the absence of the posterior mid-gut cœca in *Squilla*, however, as both of the structures persist in the adult *Nebalia*. GIESBRECHT (1913) classifies the crustacean mid-gut cœca into several categories and states that Stomatopoda have cœca anteriora dorsalia instead of the ventralia of Nebaliacea. As may be evident from the description given above, the cœca dorsalia of *Squilla* are entirely identical in formation to the cœca ventralia of *Nebalia* (cf. MANTON, 1934). These two differently termed cœca are, without doubt, homologous to each other, however divergent they may be in the adult state.

Earlier authors (J. MÜLLER, 1830; DUVERNOY, 1836; MILNE-EDWARDS, 1859, etc.) have alleged that the liver lobes of the adult *Squilla* are derived from the segmentally arranged diverticula of the intestine, which are connected to it by a series of apertures along its whole length. ORLANDI (1901) corrected this erroneous idea to a large extent, arguing that the liver lobes open into a pair of longitudinal ducts which are united before entering the dorsal part of the pyloric stomach. WOODLAND (1913), however, believes that the lobes open directly to the pylorus by separate apertures. The present study substantiates WOODLAND's view in so far as it has demonstrated that the posterior liver lobes develop separately forming a pair.

11 Mesoderm Derivatives of Trunk Segments

As for the development of the mesoderm in the trunk segments, only the first four abdominal segments will be mentioned herein. The other segments appear much the same, except for the absence of the limb mesoderm only. The differentiation of the mesoderm proceeds backward from the front. It has been stated before that the mesoderm of the trunk consists of dorsal and ventral bands, each forming a pair (fig. 81), and also that each band is divided into segmental masses or mesodermal somites (fig. 78). These conditions are merely transitory, as more or less closer

relations are soon formed both between mesoderm bands and between consecutive somites.

Early in the proliferation of cells from the teloblast which follows the establishment of the maxilla segment, the ventro-internal corner of the dorsal mesoderm in the basal part of the thoracico-abdominal process thrusts out a few cells on to the intestinal wall (fig. 79). A similar phenomenon is also presented by the ventral mesoderm at about the time when the third thoracic segment is formed (fig. 80). The thrusting of cells, however, is more pronounced in the dorsal mesoderm than in the ventral one, the former sending out many cells one after another. With the expansion of the cavity of the thoracico-abdominal process, these cells are greatly drawn out and grow into cellular strands connecting the intestinal wall with the ventro-internal corner of the dorsal mesoderm on both sides (fig. 82). These strands then, extending all over it, completely encircle the intestine. The cellular strands and intestinal coverings are formed segmentally from the front backwards. The segmental arrangement is clearly noticeable especially in the first and second maxilliped segments. Since in these segments the bands of the dorsal mesoderm are widely separated from each other and extend nearly laterally, two independent cellular strands which are much thicker than in other segments may be distinguished in a favourable section cut in a somewhat obliquely transverse direction. Before the formation of the segmental strands is completed in the ultimate segment, they fuse successively into a continuous membrane beginning from the most anterior segment backward. Thus, at the time when all body segments are differentiated, the trunk is traversed throughout its whole length by a pair of thin cellular membranes connecting the dorsal mesoderm and the intestinal wall. The intestinal covering is also continuous in this stage. For convenience' sake, the former membrane will be termed "suspending mesoderm" (fig. 82 *s. mes*) and the latter "periintestinal mesoderm" (figs. 61 & 82, *pi. mes*). The cavity surrounded by the ectoderm on the dorsal side, by the inner margin of the dorsal mesoderm on the lateral side, and by the suspending mesoderm on the ventral side, represents the space to be occupied by the dorsal blood vessel (fig. 82, *ves*).

The cells thrust from the ventral mesoderm are soon liberated from the band and join the periintestinal mesoderm. Even in a later stage subsequent to the expansion of the segmental cavity, the ventral mesoderm is occasionally found sending cells here and there to the intestine in the form of a thin protoplasmic strand containing nuclei (fig. 82, *x*). This, however, is merely a temporary condition for there is no real connection between the ventral and the periintestinal mesoderms in the older embryo.

Posterior Dorsal Blood Vessel or the Elongated Part of the Heart. By the constant addition of cells from the dorsal band, the suspending mesoderm gradually grows thicker and shorter until it becomes three or four cells thick (fig. 83, *s. mes*). With the development of muscle fibers in the central

part of the dorsal mesoderm band, a thin peripheral layer becomes differentiated from the lower and inner surfaces of the band, by a rather distinct protoplasmic boundary which appears between the two (fig. 83, *x*). This layer is confluent with the muscular part near the lateral margin, and is attached to the body wall on the inner margin. Further, it is connected with the periintestinal mesoderm by a thickened suspending membrane. Thus a system of more or less membraneous connective tissues is formed.

The blood vessel is now constructed by the ectoderm on the dorsal side, by the peripheral layer of the dorsal mesoderm on the lateral side, and by the suspending mesoderm on the ventral side (fig. 83, *ves*). Both of the lateral walls of the vessel then come together with their dorsal margins meeting on the median line, thereby making a roof over the vessel cavity. The subsequent development of the vessel consists in the detachment of the dorsal wall from the ectoderm and in the narrowing of its cavity (fig. 84, *h*). The vessel thus completed is closely attached to the dorsal side of the intestine with certain modifications of its connective tissue, by which it becomes suspended on both sides by a membrane adhering to the lower surface of the dorsal muscle sheath. The delamination of the membrane from the muscle sheath takes place soon after (fig. 84, *x*). The vessel (fig. 85, *h*) represents the elongated part of the heart which corresponds to the dorsal aorta of other crustaceans. This part of the heart has no ostium until hatching.

Limb Mesoderm and Trunk Musculature. Prior to the formation of the blood vessel, the mesodermal inclusions of the pleopoda originate in the dorsal band. When the limb bud develops as the lateral outgrowth of the segment (fig. 82, *lm. b*), the dorsal mesoderm expands by active cell multiplication to invade the limb cavity. As the ramification of the apex of the limb bud takes place shortly afterwards, the lateral expansion of the mesoderm is divided into two masses corresponding to each branch (fig. 82, *l. mes*). In accordance with the elongation of the limb, these masses are completely separated from the mesoderm band and grow into the muscular elements filling up the limb cavity.

In stage Abd 4, the suspending mesoderm is continuous throughout the length of the trunk segments. The somites of the dorsal mesoderm, however, remain to a certain degree, being indicated by the segmental aggregations of nuclei, though not by the separation of protoplasm. In this mesoderm band the cellular constitution remains in a rather undifferentiated condition. In the ventral mesoderm (fig. 82, *v. mes*), on the other hand, the segmental arrangement is already missing; cells which compose it are strikingly elongated antero-posteriorly and show spindle-shaped nuclei (fig. 90, *v. mes*). Being completely isolated from other tissues, this mesoderm forms a compact tubular band which is oval in section.

After the union of successive somites, the dorsal mesoderm sends out a series of cellular strands from its lateral margin towards the ventral meso-

derm (fig. 90, *ob. m*). These cellular strands are formed in the articulating part between consecutive segments, and are united with the surface of the ventral mesoderm at the lower end. These intersegmental vertical strands of cells are the rudiments of the oblique muscle fibre groups.

At about stage L Th 5, namely subsequent to the separation of the limb mesoderm, the dorsal mesoderm band again expands laterally along the dorsal body wall of the first four abdominal segments (fig. 83, *lm. m*). Careful examination shows that the mesoderm is distinguished into internal and external parts by the difference in cellular constitutions. The internal part is characterized by having antero-posteriorly elongated spindle-shaped nuclei and by being traversed by several muscle fibres, while the external part is composed of undifferentiated round nuclei. The former part (fig. 83, *d. mes*), continuing both anteriorly and posteriorly to its corresponding part in the neighbouring segments, represents the rudiment of the extensor. The external part (fig. 83, *lm. m*), however, is separated not only segmentally, but also each of its segments is divided into two masses arranged in front and in back. These two masses, growing into conical cell group, later develop into the anterior and posterior limb muscles (figs. 84-85, *lm. m*).

At about this stage myofibrils make their appearance in the remaining parts of the dorsal and ventral mesoderms as well as in the intersegmental strands (figs. 83-85). The dorsal and the ventral mesoderms may now be called the extensor and the flexor of the trunk segments respectively (figs. 84-85, *ex* & *fl*). The fibres of these muscles are extended longitudinally, being continuous at least through two or three segments. The oblique muscle fibre groups derived from the intersegmental strands are rather short. They converge to a point in each intersegment, radiating both dorsally and ventrally to join with extensor and flexor fibre groups.

With the delamination of the above named connective tissue from the ventral surface, the extensor attains its final state (figs. 84-85). At the time of hatching, all muscles of the trunk contain numerous myofibrils and are enclosed by a protoplasmic sheath, the myolemma, which is differentiated from the peripheral layer (fig. 85). The extensors running lengthwise along the dorsal body wall on both sides are elongated oval in section. The flexors, which are just above the ganglion and lateral to the liver lobes, are much smaller than the extensors, having a round cut surface. Conforming with the diversity in the direction of the fibres, the myolemma of the oblique muscle is narrow in the middle, but greatly widened above and below, to coalesce with that of the extensor and the flexor. The anterior and posterior limb muscles (*lm. m*), which are attached to the dorsal body wall, lateral to the extensors, by their circular bases, terminate in the basal part of the appendage by their pointed ends. They are traversed by muscle fibres cenverging downward dorso-ventrally.

In concluding the description of the development of the trunk muscu-

lature, an account of the anterior and posterior attachments of the extensor and the flexor remains to be given. The anterior end of the extensor is found within the pericardial cavity, being attached to the dorsal body wall of the cephalic region. It terminates posteriorly in the intersegmental region between the telson and the last abdominal segment. The flexor is separated in its anterior termial part into several fibre groups diverging and ending on the yolk sac. The anterior end of the ventral mesoderm is at the flexure point of the thoracico-abdominal process during the course of the formation of segments. In stage Abd 5, the mesoderm enters the cephalic region turning the flexure around, and extends along the ventral surface of the yolk sac as far forward as the level of the maxillula. At the same time, the mesoderm sends out several branches to the ventro-lateral side of the yolk sac, thus forming diverging ends. The posterior end of the flexor is divided into two branches respectively attached to the dorsal and the ventral wall (fig. 90). This is due to the fact that the end of the flexor becomes bifurcated as the result of its development along the lateral body wall to the dorsal wall (fig. 88, *fl*). The dorsal branch attaches to the body wall at a point slightly lateral and posterior to the extensor attachment, and the ventral one ends on either side of the anus.

Prior to the development of the myofibrils, active formation of the chromidia is observed. This appears to substantiate MOROFF's (1913b) view that the myofibrils are formed at the sacrifice of chromatin substances.

Connective Tissue. At the time of the delamination of the connective tissue layer from the extensor (cf. p. 64), it is occasionally found that the two structures, mostly separated, remain united with each other in the lateral and internal parts, thus enclosing a cavity between them (fig. 84). The cavity appears to represent a cœlom at first glance, but this is not the case. Despite the presence of both the lateral and internal unions in the middle of the segment, the internal union is lacking in the intersegmental region and the cavities of both sides are fused into one above the blood vessel. Further, there is no segmental separation of the cavites, for these are longitudinally continuous throughout, from the beginning. These cavities are therefore only temporary formations in the course of the delamination of the connective tissue from the extensor muscle sheath. No cœlom is formed in any stage of development.

The tip of the posterior liver lobe is provided with a mesoderm mass (fig. 100, *l. t. mes*) derived from the mesoderm of the second maxilliped segment. By the elongation of the lobe this mesoderm is carried as far as the telson. The mesoderm, in the form of a thin membrane, also covers the entire length of the lateral wall of the lobe. As the liver lobe elongates close along the side of the intestine, the covering mesoderm membrane of the lobe fuses with the preexisting connective tissue complex. Thus at the time of hatching, the intestine, the liver lobes and the blood vessel are closely associated, being enclosed by a complicated system of connective

tissues (figs. 85 & 91, *c. t*). The tissues are attached by a pair of horizontal membranes either to the lateral body wall or to the lower surface of the extensor muscle sheath. The germ cells which supposedly develop from the connective tissue are not differentiated by the time of hatching.

12 Circulatory System

The development of the posterior dorsal artery or the elongated part of the heart has been mentioned. The present chapter will be devoted to the developments of the dilated part of the heart, the anterior dorsal artery, and the lateral vessels.

It is not sufficiently clear whether the mesoderm invading the limb cavity of the maxillula, maxilla and two maxillipeds comes from the dorsal mesoderm band or the ventral one. In an early stage in the development of these limbs, the two mesoderm bands are inseparable from each other as the narrow lumen of the thoracico-abdominal process is closely packed with cells. The participation of both of them in the formation of the limb mesoderm is, however, rather improbable, since the mesoderm of the pleopoda is derived from the dorsal mesoderm alone. The mesoderms of the two maxilliped segments extend for a little distance posteriorly, beyond the limb bases. The suspending mesoderm strands given before are produced from the (topographically) posterior ends of the limb mesoderms. On account of the side-by-side position of the maxillipeds, the strands are arranged almost laterally. In the second segment they are attached to the intestine at its juncture with the mid-gut epithelium, whereas in the first segment they are attached directly to the yolk sac. Accordingly, when the fusion of the consecutive strands takes place, the suspending mesoderm membranes of both sides are widely separated from each other in these segments which constitute the posterior end of the cephalic region.

The Heart and the Pericardium. Meanwhile, the anterior end of the suspending mesoderm becomes very thickened by the addition of new cellular elements from the mesoderm in the maxillipeds. In stage 7, this thickened part of the suspending mesoderm develeps a posteriorly (or morphologically dorsally) extending membraneous outgrowth on each side invading the narrow serum space between the dorsal body wall and the yolk sac. Although the paired outgrowths are free when projected into the serum space, they soon become attached to the body wall and the yolk sac. It is found in the transverse section (fig. 93) that each of the membranes, which is attached to the dorsal body wall, extends down to the yolk sac nearly vertically, then laterally along the yolk surface, touching it. Thus the serum space is divided into three portions by the vertical part of the membrane of either side, the central portion representing the heart cavity (figs. 93-94, *h. c*), and those lateral to this the paired rudiments of the pericardial cavity (*per*). The vertical and horizontal parts of the membrane respectively indicate the heart wall (*h. w*) and the pericardial floor

(*per. f*). Since the (morphologically) posterior margin of the floor is connected to the mesoderm mass in the maxillipeds, the pericardial cavity is closed posteriorly, unlike the heart cavity which continues to the aortic space of the trunk region. Anteriorly, these cavities are still wide open. These conditions are attained before stage Abd 1.

Subsequently, the dorsal and the ventral attachments of the heart wall move gradually along the body wall and the yolk surface respectively toward the median. The heart cavity is completely enclosed by the union of these vertical walls in their upper and lower margins, and the paired rudiments of the pericardial floor fuse into a continuous sheet. The anterior side of the heart is completed by the forward extension of the free margin of the wall which accompanies the narrowing of the lumen (figs. 96-97, *h*). The pericardial floor extends laterally and anteriorly over the yolk sac until it touches the body wall to enclose an extensive cavity (fig. 100, *per*). The pericardial cavity is roofed by the ectoderm and not by the mesoderm. In about stage Abd 6, the heart wall becomes detached from the dorsal body wall as well as from the pericardial floor (fig. 100, *h. w*). Near the anterior and posterior ends of the heart, however, its lower wall remains in contact with the pericardial floor up to the time of hatching. The heart is connected also with the body wall by several fibrous structures which have developed from the wall of the heart in an early stage of its development (fig. 94, *x*). The completion of the dilated part of the heart is immediately followed by the consummation of the elongated part.

The anterior margin of the heart wall grows forward still farther as a narrow tube which represents the posterior half of the anterior dorsal artery (fig. 97, *x*). The heart valve is formed at the junction of the heart and the artery by the paired ingrowths of the wall. The ingrowths meet on the median line, except for a longitudinal slit. One pair of ostia are present on the dorsal surface of the heart as a round hole encircled by a few nuclei (fig. 100, *os*). The heart wall remains very thin and single-layered until hatching.

As stated before, a narrow lumen is formed between the connective tissue layer and the ectoderm in the trunk segments, by the delamination of the layer from the extensor rudiment. The pericardial floor, which is attached anteriorly and laterally to the body wall, continues posteriorly to this connective tissue. The delamination therefore brings the pericardial cavity into communication with the lumen of the trunk at the same time. As this lumen contains the principal part of the extensor, so the cavity includes its anterior terminal part within itself. This is due to the following process. After the pericardial floor and the heart wall are formed, the mesoderm of the maxilliped segments expands beneath the body wall and above the rudiment of the pericardial floor farther antero-laterally (fig. 94, *ex*). With the completion of the pericardial cavity, the expanded part

detached from the limb mesoderm, becomes included within the cavity, and constitutes the anterior end of the extensor.

Although there is a great difference between the develepment of the dilated part of the heart and that of the elongated part at first sight, conformity is found as regards the fact that both parts are derived from the suspending mesoderm. The seeming difference is due merely to the wide separation of the mesoderms of both sides from each other in the maxilliped segments. REICHENBACH (1886) describes in his paper on the *Astacus* that a pair of cell sheets derived from the rearrangement of the mesenchymatous loose mass fuse to form the ventral wall of the heart. The heart is enclosed in the cavity formed by the upward extensions of the margins of the ventral wall which come together on the dorso-median line. FULINSKI (1908) states, also of *Astacus*, that instead of a mesenchymatous mass, the splanchnic layer of the mesoderm produces the heart wall; he emphasizes his idea that this and the pericardial floor are morphologically one unit. Thus the development of the heart appears to follow a similar course in *Astacus* and in *Squilla*. Both TERAO (1929, in *Panulirus*) and MANTON (1928, in *Hemimysis*; 1934, in *Nebalia*) mention the heart as being formed by the cœlomic walls of both sides. The absence of the cœlom in *Squilla* somewhat modifies this mode of development, but this does not make any essential difference.

Anterior Dorsal Artery. This artery has a two-fold origin. At about stage Th 3, a number of mesenchymatous cells, released from the anterior end of the naupliar mesoderm complex, migrate toward the rostral region by passing through a narrow space between the lower face of the optic lobe and the yolk sac. These migrating cells apparently comprise at least a remnant of the preantennulary mesoderm. They proceed farther, along the yolk surface and across the rostral base. At about stage Abd 4, they are rearranged in a pair of longitudinal linear rows extending from the rostral base to the lateral side of the dorsal organ in the shape of a V (fig. 95, *mes*). These rows form a narrow vertical membrane connecting the dorsal body wall with the yolk sac surface and, with the collapse of the dorsal organ, gradually approach each other (fig. 97). The rows represent the paired rudiments of the vessel wall. On the other hand, the anterior end of the heart wall elongates anteriorly as a narrow tube, at about this time, reaching a point near the posterior margin of the dorsal organ (fig. 97, *x*). Immediately after the disappearance of this organ, each rudiment of the anterior vessel wall is united with the posterior tube extending from the heart, thus forming a continuous vessel cavity (fig. 98, *a. d. a*). The walls on both sides, however, still remain apart for a certain distance; the upper and lower walls are represented by the ectoderm and the yolk surface respectively. The vessel wall is completed by the coming together of the vertical membranes as well as by their union on both dorsal and ventral sides. The anterior dorsal artery or the cephalic aorta of KOMAI and TUNG

(1931), which departs from the anterior end of the heart, terminates in the sub-rostral connective tissue complex in front (fig. 99, *a. d. a*).

FULINSKI (1908) holds that this artery in *Astacus* has a two-fold development. *Squilla* is in exact accord with this decapod in this respect, though a difference may be found in that a pair of lateral cephalic arteries are produced in addition to this artery, by a similar process in the latter animal. In *Squilla*, this pair of arteries do not have a two-fold origin as will be described below. According to MANTON (1928, '34), the anterior dorsal artery in *Hemimysis* and *Nebalia* is formed by the backward elongation of the preantennulary mesoderm along the dorso-median line and by its subsequent fusion to the anterior end of the heart. She speaks of the forward movement of the heart, but does not recognize its formation of a tubular process.

Lateral vessels. Two pairs of lateral vessels are formed by the thickenings of the pericardial floor by the time of hatching. As stated before, the pericardial floor remains in contact with both the anterior and posterior parts of the heart wall. In the anterior point of contact, namely just behind the heart valve, the pericardial floor thickens into a pair of linear ridges departing from either side of the heart and extending laterally for some distance (fig. 100, *x*). These ridges become hollow and separated from the pericardial floor in stage L, Abd 6 (fig. 99, *l. v. 1*). They do not communicate with the heart until hatching and their lateral ends terminate on the yolk surface without reaching any tissue. The posterior lateral vessels, which develop much earlier than the anterior pair, are similarly derived from the transverse thickenings of the pericardial floor close to the posterior end of the heart. The thickenings are made hollow in stage L., Th 2 (fig. 100, *l. v. 2*). With the perforation of the heart wall, the vessels soon communicate with the heart cavity at its posterior end. The posterior vessel has a larger lumen than the anterior one and runs laterally in a straight line as far as the base of the second maxilliped, terminating in its mesoderm complex. A pair of valves are produced by the ingrowths of the wall at the place where the vessel and the heart meet. Unlike the anterior pair, the posterior pair keep in touch with the pericardial floor until hatching. Except for these vessels, the hatching embryo is not provided with any additional pair of lateral vessels or with a sternal artery.

The sternal artery first appears as paired rudiments in *Astacus* (FULINSKI, 1908) and *Hemimysis* (MANTON, 1928), but only one of them undergoes development. This artery therefore is evidently equivalent to one of the segmental lateral vessels of *Squilla* which develop in larval stages. MANTON describes the sternal artery of *Hemimysis* as originating from the outgrowth of the heart wall. In *Squilla*, however, the lateral vessel develops from the pericardial floor. Its origin closely resembles that of the segmental vessel of *Nebalia* which arises from a lacunae-system within the connective tissue complex. The heart wall does not take part in the formation

of the vessel in both cases.

Although the *Squilla* embryo develops only two pairs of lateral vessels before hatching, the *Erichthus*-larva is provided with more pairs of vessels arranged more or less segmentally and possess an elongated heart which extends nearly to the end of body, exhibiting a distinct cardiomere (following MANTON's terminology in *Nebalia*, 1934). According to CLAUS (1880, '84), the lateral vessels of this larva consist of "Schalenarterie" originated from the frontal margin of the dilated part of the heart and fourteen pairs of vessels departing from the elongated part posterior to the dilated part. KOMAI and TUNG (1931) show the same distribution of vessels in the adult. The anterior pair of lateral vessels in the embryo, therefore, correspond to the "Schalenarterie" or KOMAI and TUNG's "arteria lateralis cephalica," and the posterior pair extending to the base of the first maxilliped represent the first of the fourteen posterior pairs in the larva and adult.

Blood Corpuscle. The blood corpuscle is a round cell having darkly and rather uniformly staining karyoplasm (fig. 100, *b. c*). It makes its appearance first in stage Abd 4, in the cavity of the thoracico-abdominal process, as a proliferation product of the lower surface of the dorsal mesoderm. Accordingly, the rudiment of the vessel lumen does not contain any blood cells in this stage. Soon afterward, the blood cells appear in the pericardial cavity by proliferation from the anterior end of the extensor included within this cavity. Many intermediate stages of the developing corpuscles are found among the constituent cells of this muscular bundle, and the immediate circumferences of the extensor are crowded with liberated blood cells. The production of the blood cell is also carried out later in the mandibular and maxillar adductors as well as in the sub-rostral connective tissue. The pericardial floor seems to produce the blood cells in the anterior and posterior thickenings which develop into lateral blood vessels. However, there is no evidence to indicate that the dorsal artery and the heart wall produce the corpuscles. At the time of hatching there is a great quantity of blood corpuscles throughout the whole body. The corpuscles enter the heart through the ostia.

13 Telson Mesoderm

The origin of the telson mesoderm has already been described. The mesoderm forms a pair of masses each of which is enclosed within the cavity of the caudal furca. In stage Th 3, the mesoderm is clearly discriminated from the ectoderm layer with the complete cessation of cell immigration. At about the time when the anus becomes terminal, this mesoderm extends anteriorly to cover the proctodaeum as a rather thick membrane (fig. 87, *pp. mes*). When the telson cavity begins to appear, the membrane develops, on each side, a protoplasmic process connecting the proctodaeum with the dorsal body wall (figs. 88–89, *s. mes*). At this time, the posterior part of the mid-intestine is not yet covered by the periintestinal mesoderm derived

from the teloblasts. The intestinal investment is completed by the mutual approach of this periintestinal mesoderm and the periproctodaeal part of the telson mesoderm. The protoplasmic processes of the latter also fuse with the suspending membranes of the former, making the vessel cavity continuous. When the anus is transferred to the ventral side, the principal mass of the telson mesoderm occupying the lower part of the telson cavity forms a number of protoplasmic fibres connecting the dorsal and ventral body walls. Thus the telson cavity, crossed by these fibres, froms a complicated lacunae system (fig. 105) into which the posterior end of the dorsal blood vessel opens. Most of the mesoderm, except for a small cell mass left at the tip of the telson, is used for the formation of these fibres. These residual mesoderm cells secrete several chitinous rods which grow into the terminal setae of the telson after penetrating the ectoderm.

Anal Gland. In stage Abd 6, the telson mesoderm investing the proctodaeum gradually thickens on either side, at the point where the latter curves downward, and grows into a pair of round cell masses (fig. 88, *pp. mes*). These masses are then differentiated into peripheral and central parts. The former (fig. 89, *c. t*) is a thin layer composed of very flattened nuclei which completely surrounds the latter and continues to the principal mass of the telson mesoderm. The central part (fig. 89, *a. gl*), occupying the greater part of the cell mass, has large round nuclei; it is separated from the peripheral part by a distinct protoplasmic border. At about stage L, Th 8, a small intercellular lumen is formed in the central part by the rearrangement of the component cells. The lumen is encircled by a layer of tall cylindrical cells with rather conspicuous boundaries (fig. 89, *a. gl*). The central part containing the lumen represents the anal gland and the peripheral layer is its connective tissue investment. With the advance of the stage, the lumen gradually enlarges, while the surrounding wall grows thinner. At the time of hatching, the anal gland, an oval body with a very large cavity and a very thin wall, is attached to either side of the rectum by the connective tissue covering (fig. 91, *a. gl*). It has no communication with the rectum.

KOMAI and TUNG (1931), in their study of the adult and larval anal gland, state that it consists of two pairs of glandular sacs each of which opens into the digestive tract by a short duct. The development of another pair of sacs as well as that of the duct is believed to be undergone in the larval stages. The gland can not be homologized with the posterior mid-gut cœcum of *Nebalia*, since the former is derived from the mesoderm, whereas the latter develops as an evagination of the mid-intestine.

14 Cephalic Mesoderm

The fate of the cephalic mesoderm as well as that of the ectoderm closely associated with it will be described as briefly as possible.

It has been stated that in the meta-naupliar stages the cephalic meso-

derm consists of the peristomodaeal mass, a pair of the longitudinal bands extending forward from the former and the mandibular mesoderm. The anterior end of the longitudinal band becomes included in the eye-stalk (fig. 68, *mes*) and develops into its musculature. The paired bands then extend farther forward to the rostral base where they constitute a connective tissue (fig. 105, *c. t*). The remaining parts of the bands approach each other to form a longitudinal, median muscle-fibre bundle which is attached posteriorly to the œsophageal and stomachal wall and terminates in the above named connective tissue anteriorly (figs. 65, 71, 72, 105 & 106, *m* or *mes*). In front of the stomodaeum, the muscle is in contact with a plate-like, median ectoderm ingrowth which apparently gives support to the muscle (figs. 65 & 105, ect. ing). A part of the muscle is inserted into the median groove between the anterior liver lobes. The peristomodaeal mesoderm gives rise to four pairs of outgrowths which, on reaching the body wall lateral to the labrum, develop into stomodaeal muscles. Of these four pairs, two pass over the ventral nerve cord and the other two under it. Each of the supra- and subneural muscles is arranged antero-posteriorly (fig. 65). The circum-œsophageal musculatures are also derived from the same source. The mandibular mesoderm, as stated before, is divided into lateral, limb and median parts on either side. The first develops into the mid-gut muscle extending laterally along the yolk surface. The other two parts come in close association with each other to form a thick cellular bundle; the bundle of both sides are connected by a thin protoplasmic membrane on the dorsal side of the nerve cord. With gradual chitinization, the membraneous part develops into the mandibular tendon (fig. 65, *x 1*). The cellular bundle lateral to the tendon becomes separated dorso-ventrally into two bundles. The ventral bundle grows into a very thick mandibular adductor departing from the mandibular cavity and ending on the surface of the tendon. The dorsal bundle, which is thinner, is attached to the yolk sac by its lateral and the tendon by its inner end; this is the mandibular levator. The maxillular mesoderm is very similar to the mandibular, consisting of a tendonous (fig. 65, *x 2*) and an adductor part. But no levator is formed.

The tendonous plates of the mandibular and maxillular segments are closely united with the tip of the median ectoderm ingrowths developed in front of the ganglia of the respective segments. On both sides of the stomodaeum, the ventral body wall produces a pair of ingrowths which, elongating postero-internally, develop into rods with cores of chitinous fibres. These rods provide a support for the mandibular and maxillular tendons by the close union of their inner ends with the lateral margins of the latter. The posterior pair of subneural muscles of the stomodaeum are attached to these lateral rods along nearly their whole length. The ectoderm ingrowths, both median and lateral, seem to be homologous with the inter-ganglionic cell groups of the trunk region. The antennae and maxillae

have no appreciable muscular bundles, though, several fine fibres connect them with either yolk surface or other structures.

Antennal Gland. In stage Th 8, the two or three mesoderm cells occupying the basal part of the antennal cavity become specialized by growing rich in cytoplasm. These cells enter the body cavity and aggregate closely into an oval mass suspended from the body wall by a protoplasmic membrane (fig. 74, *an. gl*). With the advance of stages, the cells composing this mass greatly enlarge and produce a rather spacious intracellular lumen. The lumen contains a fluid which is dyed blue by MALLORY's stain and has a finely granular appearance. This body, with all possibilities, represents the rudimentary antennal gland, the intracellular inclusion being a waste product (fig. 75, *an. gl*). The antennal gland does not make much progress until hatching. It develops no leading duct or any intercellular cavity. This gland has never been recorded either in the adult or in the larva of the Stomatopoda. Therefore, it seems the gland degenerates during the larval development without making any further development.

Maxillar Gland. The maxillar gland does not develop until hatching. At first sight it appears rather strange that the *Squilla* embryo has an antennal gland instead of a maxillar gland. However, inasmuch as the co-existence of these two glands during the embryonic life is reported in many other crustaceans (CANNON, 1924; MANTON, 1928, '34; TERAO, 1929; etc.), this state in *Squilla* seems to be due merely to the chronological difference in the appearance of these glands. WOODLAND (1913) describes the maxillar gland as being derived from the ectoderm invagination during the larval development. In the other crustaceans, however, the gland is generally regarded mesodermal. Further confirmation on this point is desirable.

Labral Gland. As stated before, the labral cavity contains cells derived from the peristomodaeal mesoderm coat. In about the stage when the abdominal segments are formed, a few of these cells grow rich in cytoplasm and coalesce into a syncytial mass. The cytoplasm of this mass is characterized by a large amount of granules deeply stained by eosin (fig. 64, *lb. gl*). Since the nuclei gradually become scanty in chromatin in an inverse proportion to the increase of the granules, the latter seem to be produced at the sacrifice of the former. Until the time of hatching, the syncytial mass does not show much development except the increase in the quantity of granules (fig. 65, *lb. gl*). The mass is covered with a connective tissue and attached directly to the ectoderm, but it is not provided with any duct leading to the exterior. This is the labral gland.

A glandular tissue in the *Furcilia*-stage of the *Euphausia* closely resembling this gland is described by TAUBE (1915) as forming two pairs of masses present in the labrum and hypognath respectively. These masses

presumably represent the elongation of the antennal and the maxillar glands transformed into supporting tissues according to him. CLAUS (1884), in his study of the *Squilla* larva, states that the labral gland is an assemblage of unicellular glands each opening to the exterior by a fine duct. He also records the presence of a similar structure in maxillae. No glandular tissue, however, is found in the maxilla during embryonic life.

Liver Tip Mesoderm. Just before the anterior endoderm plate is formed, several cells separated from the paired longitudinal bands of the mesoderm, given above, become attached to the yolk surface on both sides in the region beneath the cerebrum, forming a pair of small masses. At about stage Abd 3, each of these masses is arranged in a single-layered cell plate spreading over the anterior endoderm plate (fig. 106, *lt. mes*). By forward expansion of the endoderm plate, the mesoderm plate is carried to the rostral region. In the stage when the former develops into anterior liver lobes with the appearance of a median groove, the latter becomes situated on the anterior surface of each lobe. The component cells of each mesoderm plate again aggregate, making an irregular mass between the ectoderm and the endoderm. This is the tip mesoderm of the anterior liver lobe which apparently constitutes the connective tissue of the lobe.

The mesoderm of the posterior liver lobe is derived from that of the second maxilliped segment. Just before the development of the lobe, the suspending mesoderm of this segment becomes greatly thickened on both sides by active cell multiplication. With the protrusion of the underlying endoderm as a pair of liver lobes, these thickenings are detached from the rest of the mesoderm and are transported by the liver tip as far as the telson (fig. 100, *lt. mes*). As stated before, the tip mesoderms contain a layer of filiform nuclei elongted in a direction parallel to the axis of the liver. The mesoderm also covers the lateral side of the elongated liver as a thin membrane. The principal mass of the mesoderm, however, remains in its original constitution and bulk, even in the stage when the liver reaches the telson. It is thus independent of other tissues.

Discussion

As the adult *Squilla* preserves many primitive structures, so its embryonic development retains many primitive features. The ontogeny of this crustacean closely resembles, in some points, the development of Decapoda, but it shows undeniable similarities to that of Nebaliacea in many other respects. At the same time, it has its own peculiarities. It is thus rather interesting and important from the phylogenical point of view to compare the development of *Squilla* with that of other Malacostraca. It is inevitable, however, that comparison with some of the imperfectly known orders can not be perfect.

In the fact that the egg is typically centrolecithal and shows partial segmentation, *Squilla* is in accord with Decapoda but differs from other orders which are either deprived of primary yolk pyramids (e. g. Mysidacea, Nebaliacea) or total in cleavage (Euphausiacea, Amphipoda). Like the embryos of Decapoda, the *Squilla* embryo leaves its mother as a free-living larva and undergoes a rather extensive series of metamorphosis. In Peracarida as well as in Leptostraca, the hatched larva remains for a considerable time within the brood-pouch of the mother animal, the first free-living larva more or less resembling the adult. The embryos of the Isopoda and Cumacea retain a dorsal curvature throughout, while the Amphipodan embryo changes it into a ventral curvature in a later embryonic stage. KOMAI (1924) stresses the resemblance of Stomatopoda to Decapoda, Mysidacea and Nebaliacea in that "the thoracico-abdominal region of the body is kept turned over on the ventral side throughout the embryonic stages" (p. 276). In the last two orders the ventral curvature is changed simultaneously with the hatching into the dorsal. The hatching in these, however, takes place before or after the naupliar stage and much earlier than in Decapoda and Stomatopoda. The Stomatopoda are therefore in complete agreement with the Decapoda in maintaining the ventral curvature even in the stage corresponding to the later embryonic or, more appropriately, non-free-living larval stage of Mysidacea and Nebaliacea. All of these characters, however, are due only to the difference in the amount of yolk contained in the ova or to the difference in the mode of life of the animals.

The formation of the segments in *Squilla* proceeds backward from the front as in Peracarida. But the development of the limbs is retarded in the third to seventh thoracic segments. The consititution of the two pairs of antennae are rather noteworthy. In Decapoda the antennule remains uniramous while the antenna becomes biramous. A reverse relation is observed in Stomatopoda and Nebaliacea (MANTON, 1934), the first pair being divided instead of the second. Contrary to the lifelong preservation of this relation in the latter, however, it merely represents the embryonic and earlier larval condition in the former, the second pair also developing later into biramous limbs. In Mysidacea, both pairs grow biramous nearly simultaneously and immediately after hatching.

As regards the formation of the germinal disk. Malacostraca can be divided into two groups. In Eucarida and Leptostraca a V-shaped germinal disk is transformed into an O by the appearance of a transverse band between the optic lobes. The disk of Peracarida, on the other hand, retains the V-shape without acquiring its transverse band. In this point *Squilla* belongs to the former group.

As for the differentiation of germ layers, Stomatopoda are rather indeterminate unlike Mysidacea and Euphausiacea but like the other orders. Especially in contrast to the above two orders as well as to Isopoda which produce the genital rudiment at a time early in the differentiation of the

germ layers, in Stomatopoda and other orders of Malacostraca the germ cells make their appearance for the first time just before or after hatching.

MANTON (1928), in her study of the development of *Hemimysis*, discusses the spacial relation of the primitive rudiments over the blastoderm at some length. After reviewing many investigations on other crustaceans, she comes to the conclusion that the mesoderm in Malacostraca is formed anteriorly to the endoderm, but that the relation is reversed in Entomostraca. Her view regarding the former group is based on the facts previously reported of *Leander*, *Jaera*, and *Euphausia* in addition to her own conclusions concerning *Hemimysis*. The same author, in her subsequent work on *Nebalia* (1934), mentions that in this animal the endoderm is derived from the posterior end of the mesendodermal mass after the immigration of the latter into the blastocœl. She emphasizes this fact to provide a further support for her belief. However, so far as *Nebalia* is concerned, her view appears to be far-fetched. The spacial relation resulting from the internal differention does not necessarily coincide with what is found on the blastosphere. At any rate, *Squilla* is in accord with *Nebalia* in showing similar differentiations of the endoderm.

In Leptostraca as well as in those orders of Peracarida studied carefully, namely Isopoda and Mysidacea, the immigration of cells from the extra-blastoporic region is not known, except for the preantennulary mesoderm formation. Although ROBINSON (1906) derives the yolk cells in *Nebalia* from the whole surface of the germinal disk, MANTON (1934) restricts the extra-blastoporic immigrants only to the named mesoderm. As discussed before, this mode of formation is found in the mesodermal yolk cells of Decapoda and Stomatopoda. The presence of this kind of yolk cell appears to be a common characteristic of those orders and a rather striking contrast to what is known in Peracarida and Nebaliacea. A relation between these yolk cells and the preantennulary mesoderm has also been stated. Stomatopoda lie between Nebaliacea and Decapoda in the degree of development of this mesoderm.

All the previous studies carried out from the viewpoint of modern embryology confirm the presence of teloblasts in Malacostraca. This subclass is divided into two groups as regards the constitution of the ectoteloblasts. In one group the teloblasts are arranged in a complete ring and constitute the whole surface of the trunk segments, while in the other group they give rise to the ventral side of the segments only, without forming a ring, the rest being derived from the non-teloblastic blastoderm cells. The former group includes Nebaliacea (MANTON, 1934), Decapoda (FULINSKI, 1908) and Stomatopoda and the latter Isopoda (MCMURRICH, 1895; NUSSBAUM, 1904), Amphipoda (BERGH, 1894) and Mysidacea (BERGH, 1893; MANTON, 1928).

The ectoteloblasts are found in odd numbers in a majority of cases. For example *Nebalia* (MANTON, 1934) has 19 of them, *Hemimysis* (MANTON, 1928) 15, *Mesopodopsis* (NAIR, 1939) 14-16, and *Mysis* (BERGH, 1893) has 17

or 19. In all of these cases a "central teloblast" is always distinguishable from other cells in that it lies somewhat out of the row and is more or less larger in size. Sometimes the number of teloblasts is variable within a narrow limit (McMURRICH, 1895 in Isopoda; BERGH, 1893 in Amphipoda). Yet the central cell is present whether the number of composing cells is odd or even. Judging from the figures given by REICHENBACH (1886, fig. 106, Pl. IVb) and FULINSKI (1908, figs, 1-2) the ectoteloblasts are much more numerous in Decapoda than in other orders. Furthermore, MANTON (1934) assumes the absence of the central teloblast. In *Squilla* the teloblastic ring is composed of 21 cells including a distinctly specialized central cell. On this point *Squilla* is in harmony with other orders exclusive of Decapoda.

The row of ectoteloblasts is formed by the union of paired cell rows which first appear on both sides in *Hemimysis* (MANTON, 1928), *Nebalia* (MANTON, 1934) and in *Squilla.* In *Leander* (SOLLAUD, 1923) and in Isopoda (McMURRICH, 1895) it is differentiated as a single row of cells from the beginning. The whole number is present in *Hemimysis* and Isopoda before the teloblasts commence their first division; while in *Nebalia* and *Squilla,* the number is increased after the first differentiated teloblasts begin to produce their descendants. In Decapoda the time of the completion of the number is not known.

It is noteworthy that the mesoteloblasts are always 8 in number except in Decapoda; for example, that number is given for *Hemimysis* (MANTON, 1928), *Nebalia* (MANTON, 1934), *Ligia, Porcellio, Cymothoa* (McMURRICH, 1895) and so on. BERGH (1894) says *Gammarus* has 3 or 4 cells on either side of the middle line, though this needs further confirmation. Among Decapoda, *Astacus* (FULINSKI, 1908) has 8 mesoteloblasts, while *Leander* (SOLLAUD, 1923) has 14-16. NUSSBAUM (1908) states that 8 teloblasts are produced in *Cymothoa* by the division of the 2 cells differentiated first. McMURRICH (1895) and MANTON (1928) agree that the whole number is not derived from the preexisting teloblasts but come directly from the blastoderm cells. In *Squilla* all teloblasts are present from the beginning.

Some differences among the orders may be noticed concerning the spacial relation between the ecto- and mesoteloblasts at the time of their first appearances. In the more or less determinate forms such as Isopoda (McMURRICH, 1895) and Mysidacea (MANTON, 1928) the mesoteloblasts originate by the immigration of cells which are situated just behind the ectoteloblastic row on the blastosphere. In *Panulirus* (TERAO, 1929) the "posterior budding zone" is said to be composed of two rings arranged antero-posteriorly around the thoracio-abdominal process, and the mesoderm budding zone is derived from the distal ring by its sinking into the cavity of the process. If so, the condition is the same as that found in the determinate forms. In *Nebalia* (MANTON, 1934) the mesoteloblasts develop from the mesendoderm cells situated beneath the ectoteloblastic row after its differentiation. Unlike these cases, the mesoteloblasts of *Squilla* are

produced first from the blastopore, then they are displaced towards the back; the ectoteloblasts arise from the cells lying above the mesoteloblasts in their new loci. Therefore in the last named two forms there are no intimate relations between the two teloblastic rows as regards their original positions on the surface of the germinal disk.

It has been stated that the mesoteloblasts of *Squilla* are separated into two ventral teloblasts and two groups of dorsal teloblasts each composed of three cells. Such a condition emphatically reminds us of what is recorded of *Ligia* by McMURRICH (1895), who states that the mesoteloblastic row is divided into a central group of two cells and a pair of lateral groups each composed of three cells. The former is alleged to become the connective tissue, and the latter the limb mesoderm and the lateral mesoderm mass. These central and lateral groups seem to be equivalent to the ventral and dorsal teloblasts of *Squilla*. The derivation of limb mesoderm from the corresponding teloblasts in both animals may be especially worth noting. In *Nebalia*, judging from MANTON's (1934) figures, the teloblasts seem to be separated in their positions and different, to a certain extent, in their fates as in *Ligia* and *Squilla*. The limb mesoderm in *Nebalia* also originates from the dorsal mesoderm. In the other orders of Malacostraca, such differentiation among the mesoteloblasts is not decisively known.

The telson mesoderm of *Neomysis* (NEEDHAM, 1937) is derived from that of the seventh abdominal segment. In *Ligia* (McMURRICH, 1895), the posterior member of the products of the 16th division of the teloblast appears to become the telson mesoderm directly without constituting the seventh abdominal somite. In *Leander* (SOLLAUD, 1923) and *Nebalia* (MANTON, 1934) the mesoderm is represented by a loose post-segmental tissue derived from the posterior margin of the blastopore. In *Squilla* the mesoderm is formed by the immigration of cells from the telson ectoderm. Since this ectoderm is the offspring of the periblastoporic blastoderm, this origin of the telson mesoderm is essentially identical to that in *Leander* and *Nebalia*.

Setting aside the mesodermal yolk cells, two kinds of yolk cells are distinguished among those participating in the mid-gut formation in Malacostraca. The one is represented by stellate or amœboid cells containing little or no yolk substance; this kind is found in Eucarida and in the Peracarida except Mysidacea. The other which occurs in Nebaliacea (MANTON, 1934) and Mysidacea (NUSSBAUM, 1887; MANTON, 1934) includes a large amount of yolk by developing a fine protoplasmic membrane surrounding it. It is not very clear which kind of cells *Squilla* has. However, since even the fixing method successfully used by REICHENBACH for demonstrating the fine membrane of the *Astacus* endoderm did not prove the presence of such a membrane around the yolk cells of *Squilla*, these probably belong to the former type. The yolk cells show amœboid shapes at least during migration, even when they contain some yolk.

As regards the mode of formation of the mid-gut and its annexes, KORSCHELT and HEIDER (1902) distinguish three types, namely: the formation 1) "unter Filtration des Nahrungsdotters" (*Astacus, Panulirus* etc.), 2) "unter Durchwandrung des Nahrungsdotters" (*Maja, Palaemon,* etc.) and 3) "unter Umwachsung des Nahrungsdotters" (Peracarida, Nebaliacea). DAWYDOFF (1928) distinguishes two categories: 1) the intra-vitelline differentiation in which a compact group of endoderm cells containing all the yolk is developed, and 2) the perivitelline differentiation in which there is a gradual investment of the deutoplasm by an epithelium. Needless to say, *Squilla* belongs in the category of the "Umwachsung" and the perivitelline differentiation, and it is in this respect fundamentally different from Decapoda.

There are controversies concerning the origin of the liver in Malacostraca among previous authors. MANTON (1928) states that the liver lobe of *Hemimysis* is constituted of the mesoderm separated from the mandibular somite. She concludes, after reviewing many of the investigations on this subject, that in all probability the liver of all crustaceans is derived from the mesoderm. However, in her studies on *Nebalia,* the same author (1934) finds the liver of this animal originating from a pair of processes of the endoderm plate. She therefore discarded her former opinion and has accepted the view that the liver in Eucarida and Leptostraca at least are endodermal, thus restricting the mesodermal origin to Peracarida. NEEDHAM (1937), in a research on *Neomysis,* insists upon the endodermal origin of the liver, though his view is refuted by NAIR (1939) who reports on *Mesopodopsis.*

GOODRICH's recent study (1939) on the liver of *Porcellio* and *Armadillidium* appears to give further support to MANTON's view, despite his interpretation of the endodermal origin. The mode of formation of the liver in these isopods is said to be as follows: There are two types of potential endoderms, one being the vitellophags immigrated from the blastopore and the other epithelioid sheets differentiated from the mesendodermal cell mass in a pair. The former produces a transitory mid-intestine which is later lost and replaced by the stomodaeum and proctodaeum. A definitive intestine is formed by the fusion of the latter, not to persist as a median portion of the alimentary canal, but as a pair of tubes or ventro-lateral mid-intestinal lobes, according to him, from each of which grows a ventral hepatic diverticulum. Evidently his mid-intestinal lobes and hepatic diverticula are nothing but two pairs of adult liver lobes. Therefore, if we assume his mesendodermal cell mass to represent merely the mesoderm, confining the true endodermal elements to vitellophags, we arrive at the conclusion that his transitory mid-intestine is a true mid-intestine which is to be replaced by the ectodermal part (no endodermal part being present in the adult intestine) and that the two pairs of liver lobes (instead of mid-intestinal lobes and mid-gut diverticula) are derived from the paired rudiments, differentiated from the compact mesoderm mass as epithelioid sheets.

Thus the liver lobes of Isopoda may be interpreted exactly in the same way as in Mysidacea with the only reservation in the fact that the intestine is ectodermal throughout its whole length. At any rate, it is a remarkable characteristic of Peracarida that the liver lobes originate from paired epithelioid rudiments independent of the mid-gut, for such is also the case in Amphipoda and Cumacea. The mesodermal origin of the liver appears therefore to be rather probable in this Division as MANTON says.

Contrary to all authors' opinions on the endodermal origin of the liver in Decapoda, SOLLAUD (1923) maintains a mesodermal origin in *Leander*. MANTON (1934) refutes this view in her later treatise, pointing out his erroneous conception on this point. *Euphausia* (TAUBE, 1915), *Nebalia* (MANTON, 1934) and *Squilla* have also unquestionable endodermal liver lobes. Therefore in Malacostraca other than Peracarida, the development of the liver is inseparable from that of the mid-gut.

Among those orders which possess an endodermal liver lobe, two types may be distinguished in regard to whether only the yolk cells participate in the formation of the mid-gut and the liver or, in addition to them, an endoderm plate is present from the beginning. The former type includes the majority of Decapoda, and the latter *Nebalia* (MANTON, 1934) and *Squilla*. However, the difference does not necessarily imply a fundamental significance, inasmuch as the endoderm plate is nothing but a compact mass of yolk cells. In the former type, all yolk cells, after being scattered about, concentrate again to form the mid-gut epithelium, while in the latter type the formation of epithelium begins before all the cells are scattered. The presence of the endoderm plate from the beginning is therefore merely a result of the chronological overlapping of the two processes, namely, the dispersion and the re-condensation of yolk cells. Some differences may be found also in the method of condensation of the yolk cells: that is, by means of 1) a unipolar condensation of the cells at the base of proctodaeum (*Nebalia*, MANTON, 1934; *Alpheus*, HERRICK, 1892), 2) a bipolar condensation at the bases of proctodaeum and stomodaeum (*Mysis*, WAGNER, 1895; NUSSBAUM, 1887; *Hemimysis* MANTON, 1928; *Squilla*), and 3) a multipolar condensation (*Crangon*, KINGSLEY, 1889; *Palinurus*, DOHRN, 1870; *Gebia*, BUTSCHINSKY, 1894).

Although the development of the mid-gut cœca or liver lobes is not sufficiently clear in Eucarida, it is probable that several pairs of (posterior) liver lobes and a pair of anterior mid-gut cœca are developed. The anterior cœca in Decapoda are completely absorbed by the mid-gut during the larval development, according to MANTON (1934). These cœca, however, persist in the adult *Nebalia* (MANTON, 1934) as functional glands. In *Squilla* they are merely a larval organ like in Decapoda. With respect to the constitution and development of the posterior liver lobes, *Squilla* is in exact accord with *Nebalia*. In both cases the liver is formed as a pair of processes of mid-gut epithelium, extending as far as the posterior end of the body.

The greater part of the alimentary canal is derived from the ectoderm in Decapoda and Cumacea, the endoderm being confined to the pyloric stomach. The Isopoda are further advanced in this direction, and the whole canal is lined with the ectoderm epithelium. In the other orders of Malacostraca including Stomatopoda, however, the endodermal part occupies the greater part of the intestine, the ectoderm remaining only in a short rectum. As it may be clear from what has been stated, *Squilla* shows the greatest resemblance to Nebaliacea more than to any other order, so far as the development of the digestive system is concerned; it accordingly retains rather primitive character.

The cœlom is formed both in Mysidacea aud Nebaliacea. Among Decapoda, it is present in *Astacus* (REICHENBACH, 1886) and *Panulirus* (TERAO, 1929), but is absent in *Alpheus* (HERRICK, 1892). *Squilla* does not develop the cœlom in any segment. Even the antennal gland, the cavity of which is usually believed to represent a remnant of the cœlom, lacks an intercellular lumen. The anal gland may not be homologous to a cœlom, since it is derived from the post-segmental tissue. The development of this gland is without a parallel in other crustaceans.

The caudal furca of mysid (MANTON, 1928), being simply an ectodermal structure, is cast off with the embryonic ecdysis. The same in *Nebalia* (MANTON, 1934) is supplied with a mesoderm from the telson and persists in the adult. In *Squilla* the furca is merely a transitory structure, completely absorbed by the telson till the end of embryonic life, as in Decapoda though it has a mesoderm.

Similarly to Leptostraca and Eucarida, Stomatopoda are deprived of paired dorso-lateral organs, the presence of which constitutes one of the characteristics of Peracarida. The median dorsal organ is present as in all other malacostracans in spite of KOMAI's (1924) statement of its absence.

Nebaliacea, Mysidacea (MANTON, 1928, '34), as well as Stomatopoda develop the distinct seventh abdominal segment which is never formed in other malacostracans. Although this segment is not represented externally in these orders except in the first, its presence is clearly indicated by the ganglion and by the mesodermal somite. These structures later fuse with those of the sixth segment; no relic of the seventh segment remains in the older larvae, except for the presence of the lateral vessels belonging to this segment, which will be given below. In *Nebalia* the ultimate segment persists externally even in the adult, though the ganglion fuses with that of the penultimate segment. The formation of the seventh segment is without doubt a primitive character.

The constitution of the blood vessel of *Squilla* shows a remarkable difference from that of the other Crustacea. As stated before, till the time of hatching, the embryo develops only two pairs of lateral vessels departing from the anterior and posterior ends of the dilated part of the heart. The *Erichthus*-larva, however, is provided with a series of segmental vessels

issuing from a very elongated heart which shows a distinct cardiomere. This has been repeatedly pointed out by authors as representing a rather primitive character. The cardiomeres of the larva and the adult, indicated by the ostia, are rather indistinct in the posterior part of the heart, owing to the disappearance of the ostia in this part. But the segmental arrangement of lateral vessels is well retained throughout the whole length of the heart, in spite of the more or less anterior displacement of the posterior pairs of vessels. Since the first of the fourteen vessels, departing from the heart just behind its dilated part, bifurcates to form two branches which make their way respectively to the base of the first and the second maxilliped, it is regarded as representing the union of two segmental vessels (cf. CLAUS, 1884; KOMAI and TUNG, 1931). The second to the thirteenth vessels are respectively directed to the lateral margin of each segment from the third thoracic to the sixth abdominal. The posterior end of the heart is provided with a median caudal aorta extending to the telson and with the last pair of lateral vessels bathing the hepatic lobes found in this part of the body. Without regarding this pair as the last of the segmental vessels, CLAUS (1884) calls it "hintere Herzarterie" in contrast to the "Schalenarterie", departing from the anterior end of the heart. KOMAI and TUNG (1931), however, have correctly suggested that "they belong to the seventh somite which of course remains united with the telson and in an undifferentiated state" (p. 12). Thus in the larva and even in the adult, the presence of the seventh abdominal segment is indicated by this mesodermal structure in spite of its external absence.

It is an interesting and suggestive fact that such a system of segmental blood vessels has recently been discovered by MANTON (1934), also in the *Nebalia* larva. In this larva, the heart extends from the second thoracic to the fourth abdominal segment and sends off eleven pairs of lateral arteries corresponding to each segment.

In the last embryonic period of *Squilla*, the first thoracic segment is nearly completely separated from the cephalic region due to the displacement of the base of the carapace fold to as far forward a point as near the antero-dorsal margin of the segment. This strongly suggests that the same segment of *Nebalia* (MANTON, 1934) is similarly freed from the cephalic shield. The condition makes a striking contrast to that found in other orders of Malacostraca in which the anterior several segments of the thorax are fused in various degrees with the cephalon to form a cephalothorax.

As enumerated above, *Squilla*, in its embryonic development, exhibits rather marked and even fundamental differences from Peracarida, while it has a number of indubitable resemblances to Nebaliacea on one hand and to Decapoda on the other hand. The common characteristics in the embryonic development between each of these orders and Stomatopoda may be summed as follows:

Squilla agrees with Nebaliacea in 1) the constitution of the teloblasts, 2) the formation of the mid-gut and liver lobes, 3) the presence of the seventh abdominal segment, 4) the development of cardiomeres and segmental arteries, 5) the biramous antennule and uniramous antenna and in 6) the separation of the first thoracic segment from the cephalon.

It resembles Decapoda in 1) its early development up to the naupliar stage, 2) the formation of the mesodermal yolk cells, 3) the mode of formation of the anterior dorsal vessel and in 4) the maintenance of the dorsal curvature during embryonic life.

Yet *Squilla* has its own peculiarities such as, 1) the development of the anal gland, 2) the absence of the cœlom and 3) the rudimentary condition of the antennal gland.

Attention may be called, however, to the fact that although the resemblance of the embryonic development of Stomatopoda to that of Decapoda seems to be largely due to the richness in yolk substance, the affinity to the Nebaliacea is rather of a fundamental nature, as for example, the presence of the seventh abdominal segment and cardiomeres. KOMAI (1924) has pointed out the similarities of Stomatopoda to Decapoda, Schizopoda and Nebaliacea. He is essentially interested in its affinity to the last named order, for he says, " this affords another support for the opinion of GROBBEN, who gives special emphasis to the affinity of these two orders " (Nebaliacea and Stomatopoda, p. 276). The present study fully substantiates this view. But, as it may be clear from the comparison made above, *Squilla* has hardly any clear relationship to Schizopoda, the resemblance remaining only superficial.

The phylogeny of Stomatopoda has been repeatedly discussed from the standpoint of comparative anatomy by authors such as BOAS (1883), CLAUS (1885), GROBBEN (1892, 1919), HAECKEL (1896), CALMAN (1904) and GIESBRECHT (1910). Since a good résumé of these views is given by GROBBEN (1919), I shall not enter it here in detail. At any rate it is generally accepted that Stomatopoda must have branched early from the main stem of Malacostraca and have made development of their own. The embryological study of *Squilla* gives further support for this view. Inasmuch as *Nebalia* occupies the lowest position in the malacostracan sub-class, the similarities in the embryonic development of *Squilla* and *Nebalia* indicate that the former separated very early, or at least next after the latter from the main stem.

MANTON (1934) expressed her belief that *Nebalia* is most closely related to Decapoda, because it shares many features with this order. If so, it is natural that in its embryonic development *Squilla* has something in common with Decapoda. As stated before, however, apart from some common features among the three orders, the resemblances between Decapoda and Stomatopoda are apparently due merely to a parallelism brought about largely by the abundance of yolk; they are accordingly of a rather superficial nature. On the other hand, there is nothing to substantiate the affinities

of Stomatopoda to the orders of Peracarida. Moreover, the differences between them are undoubtedly more or less fundamental ones, as exemplified by the mesodermal derivation of the liver. Such a difference is, without doubt, due to a modification brought about in the phylogeny of the two groups, and indicates the fact that the Peracarida have no direct relationship to Stomatopoda.

A conclusion that Stomatopoda have the most intimate affinity to Nebaliacea therefore seems inevitable. Stomatopoda are apparently a group which has been separated only next to Nebaliacea from the main stem leading to Eucarida and has made its own development independent of other orders.

Résumé

1) The egg of *Squilla oratoria* DE HAAN is centrolecithal and undergoes partial cleavages resulting in rudimentary primary yolk pyramids.

2) The germinal disk is first represented by a pair of optic lobes and a ventral plate, which are afterward connected by paired, lateral ectoderm thickenings to form a U-shape. The U is then transformed into an O by the appearance of a transverse band between the optic lobes of both sides.

3) A small blastopore is formed. Of the mesendoderm cells derived from the blastopore by cell immigrations, those attached to the lower surface of the lateral ectoderm thickenings are differentiated into a U-shaped, naupliar mesoderm band. This mesoderm band joins the preantennulary mesoderm derived from the optic lobe, and grows into a complete ring conforming to the shape of the germinal disk.

4) The extra-blastoporic immigrants consist of a preantennulary mesoderm, mesodermal yolk cells and a part of the naupliar mesoderm. The greater part of the preantennulary mesoderm cells disintegrate sooner or later, without forming any distinct structure. The mesodermal yolk cells also degenerate after taking part in the dissolution of the deutoplasm. A discussion as regards the mutual relationship between these elements, with the conclusion that the formation of the preantennulary mesoderm represents the initial step of the extra-blastoporic cell sinking from the whole egg surface, is included.

5) The endodermal elements consist of a compact cell mass differentiated from the posterior part of the mesendoderm layer and the endodermal yolk cells immigrated from the blastopore. The yolk cells, after migrating through the most peripheral part of the yolk, scatter all over its surface. The endoderm plate is nothing but a mass of yolk cells which remain without scattering.

6) Eight mesoteloblasts derived from the blastoporic lip are attached to the inner surface of the thoracico-abdominal process, making four groups. The ectoteloblasts are differentiated from the ordinary blastoderm cells in

a later stage than the mesoteloblasts. In the final condition they consist of 21 cells forming a complete ring around the thoracico-abdominal process.

7) Both the ectoderm and the mesoderm are derived from the teloblasts in all of the post-naupliar segments. The dorsal ectoderm, however, is non-teloblastic in only a few anterior segments. Differentiation of segments proceeds from the front toward the back.

8) The telson mesoderm is formed by the cells sunk from the telson ectoderm which is derived from the peri-blastoporic ectoderm.

9) The anus is the remnant of the blastopore. In accordance with the change of the caudal furca, the anus is displaced from the dorsal side of the telson to the ventral border between this and the last abdominal segment.

10) There is a distinct nauplius stage. Of the meta-naupliar segments, those from the maxillula to the second maxilliped are laid on the germinal disk, the following segments together forming a thoracico-abdominal process. Two maxilliped segments, however, are later separated from the cephalon with the development of the carapace fold, and join the trunk segments. Externally, six abdominal segments are formed.

11) The ganglionic cells are proliferated from the neuroblasts occupying the most superficial part of the central nervous system. The giant ganglionic cells arise from the ordinary ganglionic cells and not directly from neuroblasts. The development of the cerebrum is described. The tritocerebra of both sides are connected by a transverse nerve-fibre bundle behind the stomodaeum. The ganglia of the segments from the mandible to the second maxilliped first exhibit a typical ladder-like shape. Of these ganglia, the anterior three constitute a sub-œsophageal ganglion by more or less complete fusion, while the posterior two are transferred from the cephalon to the thoracico-abdominal process with the constriction of the segments. The inter-ganglionic cell groups take part in the constriction of the consecutive segments. The seventh abdominal ganglion is clearly indicated by the presence of such a cell group as well as of a pair of nerve fibre masses.

12) The development of the compound eye is traced. The ganglion opticum is derived from the ectoderm of the optic lobe lateral to the protocerebrum; it is not an outgrowth of the cerebrum.

13) The ganglion visceralum is differentiated from the anterior wall of the stomodaeum.

14) A median dorsal organ is formed. In close connection with the activity of this organ, the embryo undergoes one ecdysis.

15) The mid-gut epithelium is formed by the gradual expansion of the anterior and posterior endoderm plates over the yolk sac. These plates, however, extend only on the ventral side of the yolk sac before hatching. The posterior plate is produced by the concentration of the scattered yolk

cells toward the periphery of the plate differentiated from the mesendoderm, while the anterior plate is formed by yolk cells alone.

16) The greater part of the intestine develops from the outgrowth of the posterior endoderm epithelium, the proctodaeum occupying only the rectum.

17) The posterior liver lobes are produced from the posterior endoderm plate as a pair of blind tubes and extend as far backward as the telson. The anterior liver lobes and the lateral mid-gut cœca are rather incompletely developed, being separated by shallow superficial grooves of the yolk sac. These two pairs of diverticula are only partially covered by the endoderm epithelium, and develop into more or less distinct cœca during larval life. They later seem to be completely absorbed again by the mid-gut.

18) The product of each division of the mesoteloblast is equivalent to one mesodermal segment. The mesoderm of the seventh abdominal segment is derived from the posteriorly situated daughter cell produced by the last division of the teloblast. In accordance with the grouping of teloblasts, the trunk mesoderm is separated into two ventral and two dorsal bands. Each band is further separated into segmentally arranged blocks, the somites. The cœlom develops in no stage and in no segment.

19) The dorsal mesoderm gives rise to the extensor and the oblique muscles of the trunk, the anterior and posterior limb muscles, as well as to the mesodermal inclusion of the limb. The ventral mesoderm grows into the flexor. The connective tissue investing the intestine and the liver lobes are principally constructed from the dorsal mesoderm. The germ cell does not appear until hatching. A brief account is also given of the fate of the naupliar mesoderm.

20) The heart wall and the pericardial floor are morphologically one unit. They arise from the dorsal mesoderm as a pair of membranes stretching between it and the intestine. The dilated and elongated parts of the heart are formed by the subsequent union of these paired rudiments.

21) The anterior dorsal vessel has a two-fold origin; it is formed by the fusion of an anterior rudiment extending backward from the rostrum and a posterior one developing as a tubular outgrowth of the heart. The former is derived from the rearrangement of mesenchymatous cells which migrated from the anterior end of the naupliar mesoderm.

22) By the time of hatching, two pairs of lateral vessels are formed as hollow linear thickenings of the pericardial floor in front and behind the dilated part of the heart.

23) The antennal gland remains rudimentary without acquiring any intercellular lumen. The maxillar gland is not laid until hatching. The labral and anal glands are derived from the peristomodaeal and the telson mesoderm respectively.

23) Comparisons are made bewteen *Squilla* and other orders of Malacostraca as regards the salient points of the embryonic development. These

have led to the conclusion that the Stomatopoda are most closely related in their embryonic development to Nebaliacea, and further that Stomatopoda represent a rather primitive group separated from the main stem of Malacostraca very early, only next in order to Nebaliacea.

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(The asterisks mark those to which I have not been able to gain access)

Explanation of figures

List of abbreviations :.....

a, anus; *a. d. a*, anterior dorsal artery; *a. gl*, anal gland; *a. pg. c*, accessory pigment cell; *ab*, abdominal segment; *an. gl*, antennal gland; *an 1* or *2*, antennule or antenna. *ant*, anterior; *ant. end*, anterior endoderm plate; *b. c*, blood corpuscle; *b. w*, body wall; *bp*, blastopore; *bp'*, future blastoporal area; *bp. a*, area of extinguished blastopore; *c. ect. tel*, central ectoteloblast; *c. f*, carapace fold; *c. t*, connective tissue; *card*, cardiac stomach; *cc*, crystalline cone; *cc. c*, crystalline cone cell; *cer*, cerebrum; *cg*, corneagen cell; *d. b. w*, dorsal body wall; *d. mes*, dorsal mesoderm; *d. mes. tel*, dorsal mesoteloblast; *d. o*, dorsal organ; *dc*, deuterocerebrum; *dc. c*, transverse connective cellular band of deuterocerebrum; *deg*, degenerating cell; *deg'*, degenerated cell or its disintegration product; *e. s*, eye stalk; *e. y. c*, endodermal yolk cell; *ect*, ectoderm or ectodermal cell; *ect. b*, lateral ectoderm band; *ect. ing*, ectoderm ingrowth; *ect. tel*, ectoteloblast; *ed*, epidermis; *el. h*. elongated part of heart; *end*, endoderm or endodermal cell; *ep*, epipodite; *ev*, exuviae; *ex*, extensor; *fl*, flexor; *fx*, thoracico-abdominal flexure; *g*, ganglion; *g. ab*, abdominal ganglion; *g. g. c*, giant ganglionic cell; *g. md*, mandibular ganglion; *g. mx 1* or *2*, maxillular or maxillar ganglion; *g. mxp 1* or *2*, maxilliped I or II ganglion; *g. op*, ganglion opticum; *g. op 1, 2, 3* or *4*, lst, 2nd, 3rd or 4th segment of ganglion opticum; *g. r*, germinal region; *g. s. oe*, sub-œsophgeal ganglion; *g. th*, thoracic ganglion, *g. vis*, ganglion visceralum; *h*. heart; *h. c*, heart cavity; *h. w*, heart wall; *i. g. c*, inter-ganglionic cell group; *im*, immigrating cell; *im'*, immigrated cell; *int*, intestine, *l. mes*. limb mesoderm; *l. t. mes*, liver tip mesoderm; *l. v. 1* or *2* 1st or 2nd lateral blood vessel (arteria leteralis cephalica and 1st segmental vessel); *lb*, labrum; *lb. gl*, labral gland; *lm. b*, limb bud; *lm. m*, limb muscle; *m*, muscle; *m. e*, median eye; *m. v*, mid-ventral region; *md*, mandible; *mes*, mesoderm or mesodermal cell; *mes. tel*, mesoteloblast; *mesen*, mesendoderm cells; *mx 1* or *2*, maxillula or maxilla; *mxp 1* or *2*, 1st or 2nd maxilliped; *n. f* neuroglia

fibrille; *nb*, neuroblast or neuroblast layer; *nb 1-2* or *3-4*, neuroblast layer of 1st-2nd or 3rd-4th segments of ganglion opticum; *o*, oral aperture; *o. l*, optic lobe; *ob. m*, oblique muscle fibre group; *oes.* œsophagus; *om. l*, ommatidia layer; *os*, ostium; *p. r. c*, proximal retina cell; *p. y. p.* primary yolk pyramid; *pa. mes*, preantennulary mesoderm or mesoderm cell; *pc* protocerebrum; *per*, pericardial cavity; *per. f*, pericardial floor; *pg*, pigment; *pg. c*, pigment cell; *pi. mes*, periintestinal mesoderm; *pl*; pleopoda; *pos. end*, posterior endoderm plate; *pos. liv*, posterior liver lobe; *pp. mes*, periproctodaeal mesoderm; *pr*, proctodaeum; *pst. mes.* peristomodaeal mesoderm; *r. c*, retina cell; *r. l*, retina layer; *r. s*, rostral spine; *rec*, rectum; *rh*, rhabdome; *s. mes*, suspending mesoderm; *s. s*, serum space; *s. y. p*, secondary yolk pyramid; *som*, mesoderm somite; *st*, stomodaeum; *t*, telson; *t. mes*, telson mesoderm; *tc*, tritocerebrum; *th*, thoracic segment; *th. ab*, thoracico-abdominal process; *tr. b*, transverse ectoderm band connecting optic lobes; *v. mes*, ventral mesoderm; *v. mes. tel*; ventral mesoteloblast; *v. p*, ventral plate; *ves*, vessel cavity; *x*, see text; *y. c*, yolk cell; *y. g*, altered yolk granule; *y. s*, yolk sac.

Fig. 1. Semidiagrammatic representation of entire egg; stage 3. ×80 ca.

Fig. 2. Same; earlier period of stage 4. ×80 ca.

Fig. 3. Same; later period of stage 4. ×80 ca.

Fig. 4. Same; stage 5. ×80 ca.

Fig. 5. Same; stage 6. ×80 ca.

Fig. 6. Same; stage 7. ×80 ca.

Fig. 7. Same; stage 8. ×80 ca.

Fig. 8. Antero-ventral view of entire egg; stage 10. ×60 ca.

Fig. 9. Postero-ventral view of same egg. ×60 ca.

Fig. 10. Ventral view of embryo just before hatching (extended). ×30.

Fig. 11. 8-celled stage, with all blastomeres in view. The blastomeres included in the upper hemisphere above the equator are shown by dotted cells and those in the lower hemisphere by clear ones. Numerals indicate the position of nuclei from the uppermost towards the lowest in due order. ×90.

Fig. 12. 64-128 cells in division, surface view. ×90.

Fig. 13. Stage of about 200 cells, surface view. ×90.

Fig. 14. The same in section, showing formation of primary yolk pyramid. ×90.

Fig. 15. Last blastura, showing the first rudiments of the germinal disk and blastopore, surface view. ×90.

Fig. 16. Section of last blastura, showing extra-blastoporic immigration prior to gastrulation. ×310.

Fig. 17. Longitudinal section through the lateral ectoderm band, showing yolk cells, including deutoplasm, and those disintegrating; stage 3. ×310.

Fig. 18. Longitudinal section through the mid-ventral region, showing the sinking of ectoderm cells; stage 3. ×310.

Fig. 19. Longitudinal section of the extra-germinal region just behind the blastopore, showing the derivation of yolk cells from this region; stage 3. ×310.

Fig. 20. Transverse section cutting the lateral ectoderm and mesoderm bands; stage 3. ×245.

Fig. 21. Longitudinal section passing through slightly lateral side of the mid-ventral line; stage 3. ×245.

Fig. 22. Longitudinal section through the blastopore, showing sub-blastoporic mesendoderm cell complex and mesoteloblasts; stage 2. ×245.

Fig. 23. Longitudinal section through the optic lobe, representing the formation of preantennulary mesoderm; stage 3. ×245.

Fig. 24. Longitudinal section through the ventral plate, showing the rudiment of proctodaeum and posterior migration of the mesoteloblast; stage 3. ×245.

Fig. 25. Section showing a group of cells immigrated from the extra-blastoporic blastoderm prior to gastrulation; stage 2. ×310.

Fig. 26. Longitudinal section of an entire egg through the blastopore, showing an immigrant from the extra-germinal region; stage 3. ×90.

Fig. 27. Higher magnification of the immigrant drawn in fig. 26. ×310.

Fig. 28. A yolk cell lying below the extra-germinal region; stage 3. ×310.

Fig. 29. Longitudinal section passing through the mid-ventral line of the embryo in stage 4. ×245.

Fig. 30. Transverse section through the antennular segment of the embryo in stage 4. ×245.

Fig. 31. Transverse section through the region of the optic lobe, showing the degeneration of the preantennulary mesoderm; stage 4. ×245.

Fig. 32. Longitudinal section passing through the mid-ventral line of the embryo in stage 5. ×245.

Fig. 33. Longitudinal section of the thoracico-abdominal process, through the proctodaeum; stage 5. ×245.

Fig. 34. Transverse section of the mid-ventral region in front of the ventral plate, showing the mesoteloblasts; stage 3. ×245.

Fig. 35. Longitudinal section through the naupliar appendages and optic lobe; stage 6. ×245.

Fig. 36. Transverse section through the antennular segment of the embryo in stage 6. ×245.

Fig. 37. Longitudinal section of the thoracico-abdominal process through a place somewhat lateral to the middle line; stage 6. ×245.

Fig. 38. Transverse section of the thoracico-abdominal process passing behind the anus and showing the teloblastic descendants; stage 6. ×245.

Fig. 39. Transverse section through the antennular segment of the embryo in stage 7. ×245.

Fig. 40. A median longitudinal section of the embryo in stage 7. ×245.

Fig. 41. Longitudinal section through the consecutive ganglia and the rudiments of maxillula and maxilla, stage 7. ×245.

Fig. 42. Median longitudinal section of the thoracico-abdominal process of an egg in a stage somewhat earlier than that shown in fig. 40; stage 7. ×245.

Fig. 43. Transverse section through the thoracico-abdominal process and the maxilla rudiment of the egg of the same stage as that shown in fig. 42; stage 7. ×245.

Fig. 44. Transverse section of the thoracico-abdominal process passing just behind the anus; stage 5. ×245.

Fig. 45. Section of the optic lobe cut somewhat obliquely to its longer axis, showing separate rudiments of the protocerebrum and ganglion opticum; stage 7. ×245.

Fig. 46. Surface view of the cerebrum of the stage Th 3. ×120.

Fig. 47. Same of stage Abd 2. ×120.

Fig. 48. Same of stage L, Th 2. ×120.

Fig. 49. Same of stage L, T. ×120.

Fig. 50. Transverse section through the protocerebrum, showing the neuroblast layer; stage Th 7. ×245.

Fig. 51. Transverse section through the deuterocerebrum, showing the joining of the connective part with the cerebrum; stage Abd 2. ×245.

Fig. 52. Transverse section of the protocerebra, showing the addition of the new ganglionic elements to the lateral and internal surfaces of the cerebrum; stage Abd 5. ×245.

Fig. 53. Sagittal section of the optic lobe, showing the cell sinking from the retina layer, and the formation of the 3rd and 4th segments of the ganglion opticum; stage 7. ×245.

Fig. 54. Sagittal section of the optic lobe in the stage after the differentiation of the retina layer and the neuroblast layer of the 1st and 2nd segments of the ganglion opticum; stage Th 2. ×245.

Fig. 55. Distal part of the sagittal section of the optic lobe, showing the formation of the 2nd segment of the ganglion opticum; stage Th 6. ×245.

Fig. 56. Same, showing the formation of the 1st segment of the ganglion opticum; stage Abd 4. ×245.

Fig. 57. Same, showing the folding of the neuroblast layer of the 1st and 2nd segments of the ganglion opticum; stage Abd 6. ×245.

Fig. 58. Paratangential section through the median eye in the early stage of pigment secretion; stage L, Th 2. ×245.

Fig. 59. Surface view of the anterior part of the ventral nerve cord; stage Abd 4. ×100.

Fig. 60. Median longitudinal section through the dorsal part of the thoracico-abdominal rudiment and the maxilliped region of the germinal disk, showing the first appearance of the inter-ganglionic cell groups; stage Th 8. ×245.

Fig. 61. Median longitudinal section through the thoracico-abdominal process and the post-stomodaeal region of the germinal disk, showing the ganglia and the inter-ganglionic cell groups; stage Abd 4. ×245.

Fig. 62. Median longitudinal section through the posterior abdominal ganglia, showing the presence of the 7th abdominal ganglion indicated by the inter-ganglionic cell group; stage L. Abd 6. ×245.

Fig. 63. Three sections lateral to that shown in the preceding figure. The 7th abdominal ganglion is indicated by the nerve fibre mass; stage L, Abd 6. ×245.

Fig. 64. Longitudinal section through the stomodaeum, showing the formation of the nerve fibre mass in the visceral ganglion which is not yet separated from the stomodaeal wall; stage Abd 5. ×245.

Fig. 65. Longitudinal section through the stomodaeum of the stage L, Abd 6. ×245.

Fig. 66. Section of the lateral margin of the optic lobe, showing the development of the ectoderm fold and the accessory pigment cells; stage L, Th 8. ×245.

Fig. 67. Longitudinal section in front of the protocerebrum, showing the formation of the rostral spine; stage L, Th 5. ×245.

Fig. 68. Sagittal section of the eye-stalk of stage L, Abd 6. ×245.

Fig. 69. Section of the ommatidia layer of the compound eye taken from the embryo ready to hatch. ×360.

Fig. 70. Section of the distal part of the eye-stalk of the embryo nearly ready to hatch, showing the accessory pigment cells. The specimen was depigmented with

MAYER's method; the visual elements and the ganglionic cells are not represented. ×245.

Fig. 71. Part of the transverse section through the protocerebral region showing the giant ganglionic cell and anterior endoderm plate; stage L, Th 1. ×245.

Fig. 72. Same taken from a more advanced embryo, showing the formation of the anterior liver lobes; stage L, T. ×245.

Fis. 73. Section showing the dorsal organ; stage Th 8. ×245.

Fig. 74. Part of the transverse section through the antennal segment, showing the first rudiment of the antennal gland; stage Th 8. ×245.

Fig. 75. Section of the antennal gland of the stage just before hatching (L, T). ×245.

Fig. 76. Surface view of the thoracico-abdominal process, showing the differentiation of the teloblastic rows; stage 5. ×310.

Fig. 77. Ventral view of the terminal part of the thoracico-abdominal process, showing the completion of the teloblastic rows; stage 7. ×310.

Fig. 78. Longitudinal section of the thoracico-abdominal process, representing the formation of the mesodermal somite; stage Th 4. ×245.

Fig. 79. Transverse section of a thoracic segment, showing the mode of formation of the periintestinal mesoderm; stage Th 6. ×245.

Fig. 80. Same, showing another source of the periintestinal mesoderm; stage Th 4. ×245.

Fig. 81. Transverese section of an undifferentiated segment, showing the mutual relation between the dorsal and ventral mesoderms; stage Th 6. ×245.

Fig. 82. Transverse section of the 1st abdominal segment, showing the formation of the limb mesoderm; stage Abd 4. ×245.

Fig. 83. Same, showing the separation of the rudiments of the extensor and flexor of the pleopod; stage L, Th, 5. ×245.

Fig. 84. Same, showing the formation of the limb muscle and the completion of the heart wall; stage L, Th 8. ×245.

Fig. 85. Transverse section of the 4th abdominal segment cutting through its anterior region; completed condition of the segment; stage L, T. ×245.

Fig. 86. Longitudinal section through the telson showing the immigration of the telson mesoderm; stage 7. ×245,

Fig. 87. Transverse section cut through a line near the anterior margin of the telson, showing the proctodaeum and its investment of the telson mesoderm; stage Th 6. ×245.

Fig. 88. Transverse section passing just in front of the anus, showing the commencement of the formation of the anal gland. Note the dorsal expansion of the posterior attachment of the flexor: stage Abd 6. ×245.

Fig. 89. Section showing the formation of the anal gland; stage L, Abd 1. ×245.

Fig. 90. Longitudinal section of the terminal part of the thoracico-abdominal process, representing the development of the rudiment of the oblique muscle group; stage Abd 5. ×245.

Fig. 91. Transverse section passing just in front of the anus; stage L, T. ×245.

Fig. 92. Transverse section passing through the 1st and 2nd maxilliped rudiments; stage 7. ×245.

Fig. 93. Transverse section of the region dorsal to the base of the maxillipeds, showing an earlier phase of heart formation; stage Th 8. ×245.

Fig. 94. Same, showing a somewhat advanced stage of the heart formation;

stage Abd 1. ×245.

Figs. 95–99. Semidiagrammatic representation of the consecutive stages in the formation of the anterior dorsal artery.

Fig. 95. Antero-dorsal view of an embryo in stage Abd 2. ×60.

Fig. 96. Postero-dorsal view of same embryo. ×60.

Fig 97. Dorsal view of an embryo of stage Abd 3. ×60.

Fig. 98. Same of stage Abd 6. ×60.

Fig. 99. Same of a stage just before hatching. ×60.

Fig. 100. Longitudinal section of the proximal part of the thoracico-abdominal process, showing the heart and the posterior liver lobe; stage L, Th 5. ×245.

Fig. 101. Longitudinal section of the entire egg of stage 4, showing the distribution of the endodermal yolk cells. The black spherules indicate the ectoderm nuclei and the white ones the mesoderm nuclei. ×90.

Figs. 102–106. The ectodermal part is shown in black (black spherules indicating the nuclei), mesodermal part is striated and the endodermal part is represented by stippled cytoplasm with white nuclei.

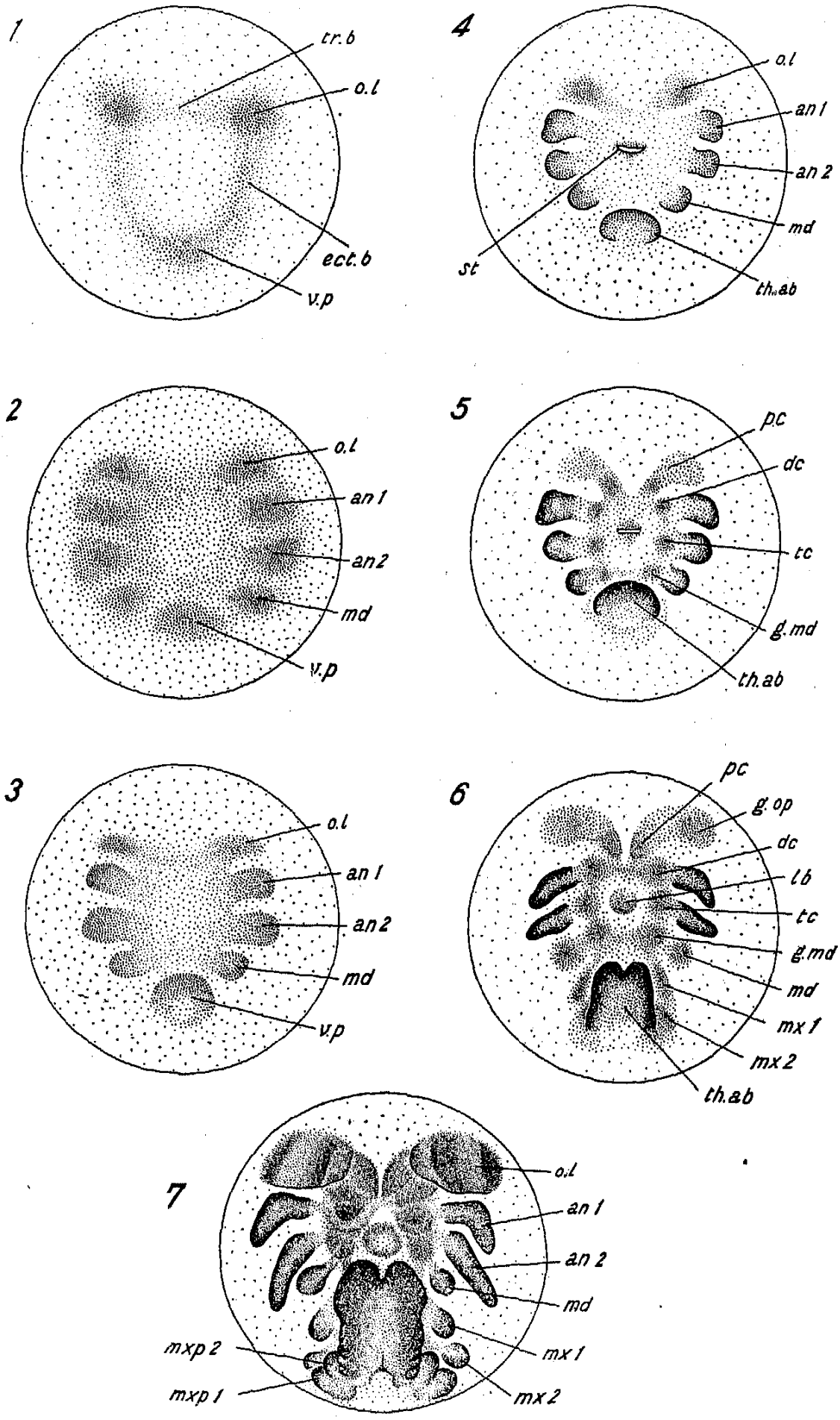
Fig. 102. Longitudinal section of the embryo of stage 6, showing distribution of the endodermal yolk cells. Black spherules indicate the nuclei of proctodaeum. ×90.

Fig. 103. Longitudinal section lateral to the middle line, showing the constitution of the nervous system; stage L, Th 2. ×120.

Fig. 104. Median longitudinal section of the same embryo. ×120.

Fig. 105. Median longitudinal section of the embryo in stage L, Th 6. ×120.

Fig. 106. Transverse section of the posterior part of the protocerebral region; stage L, Th 6. ×120.



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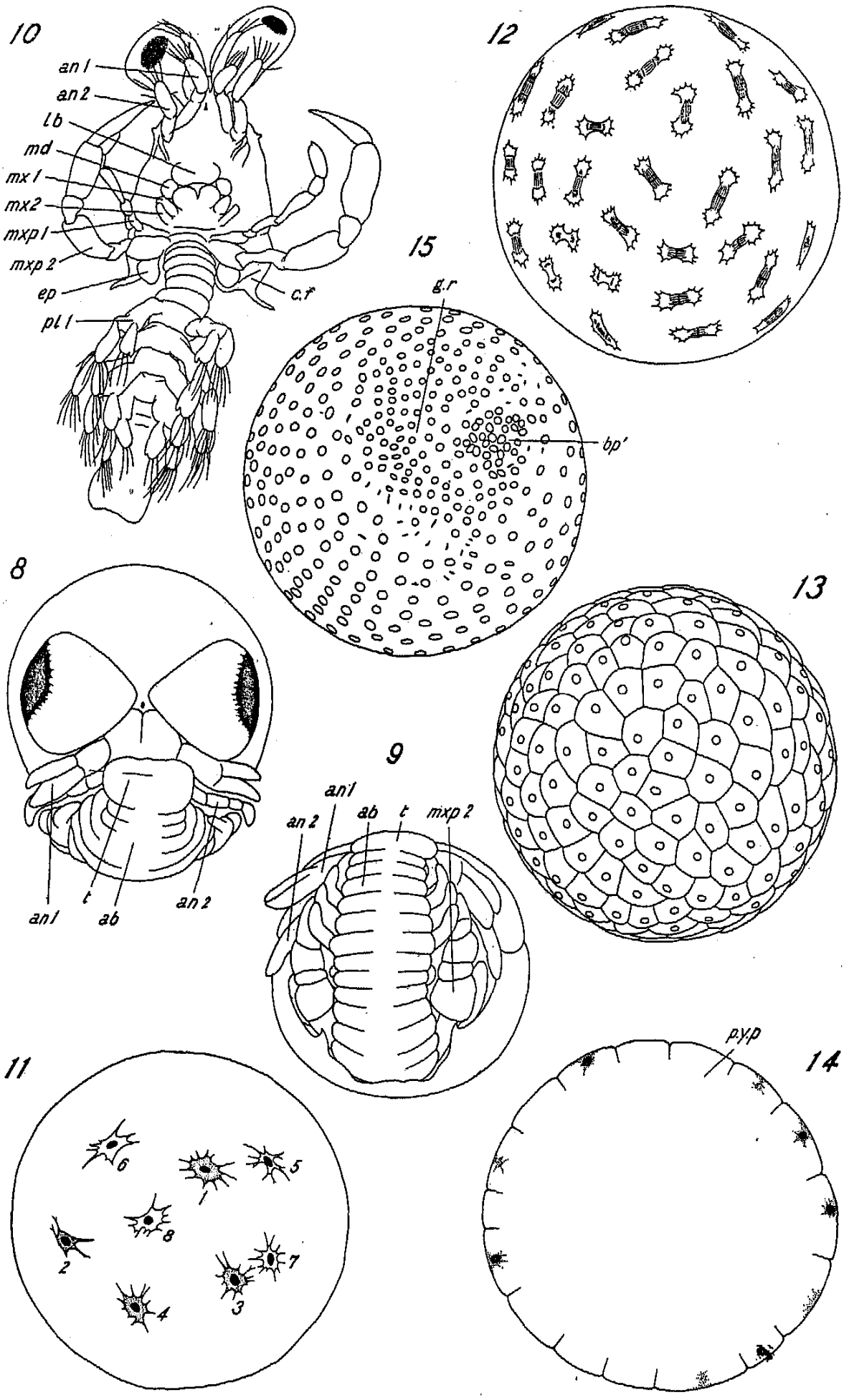

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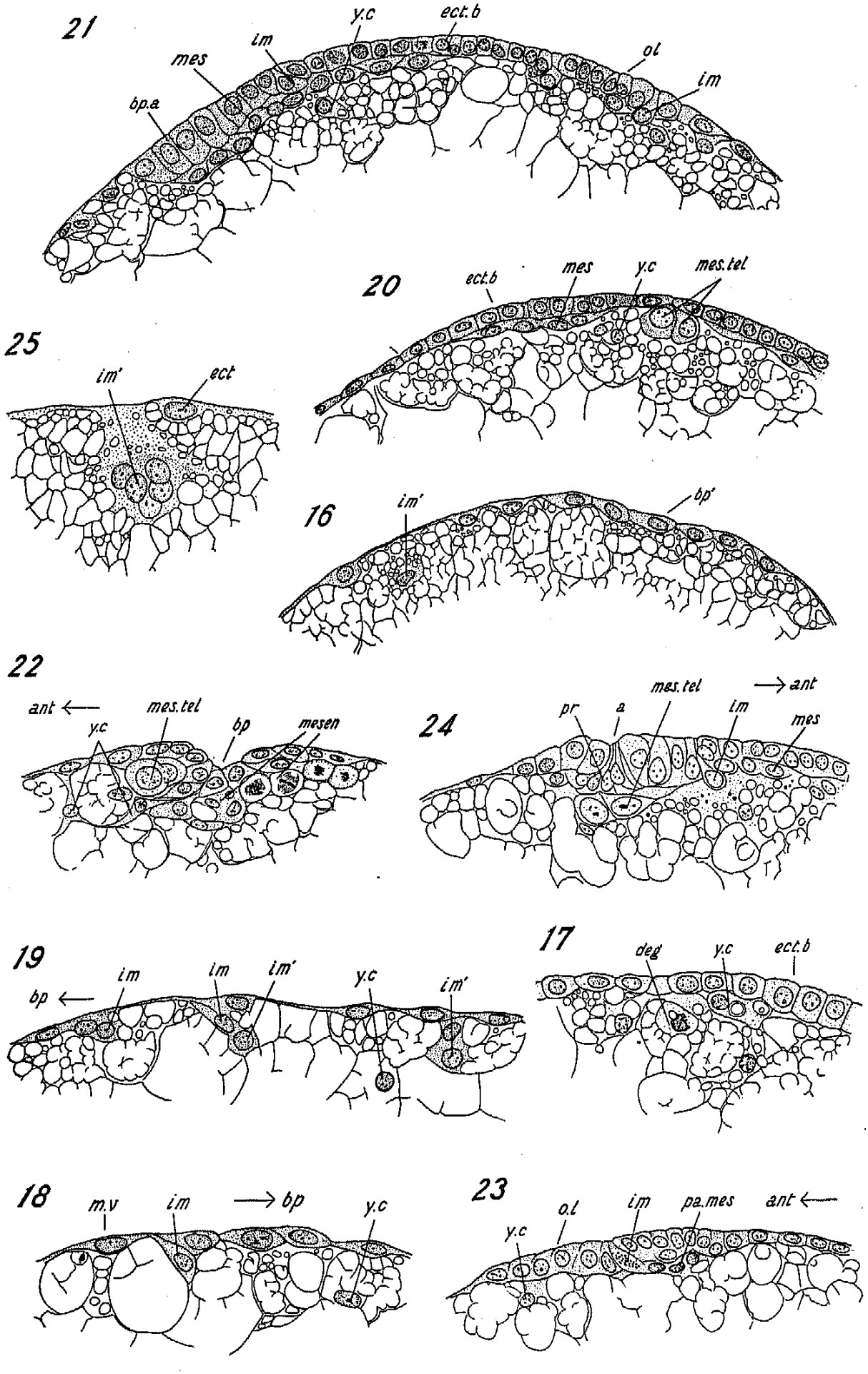

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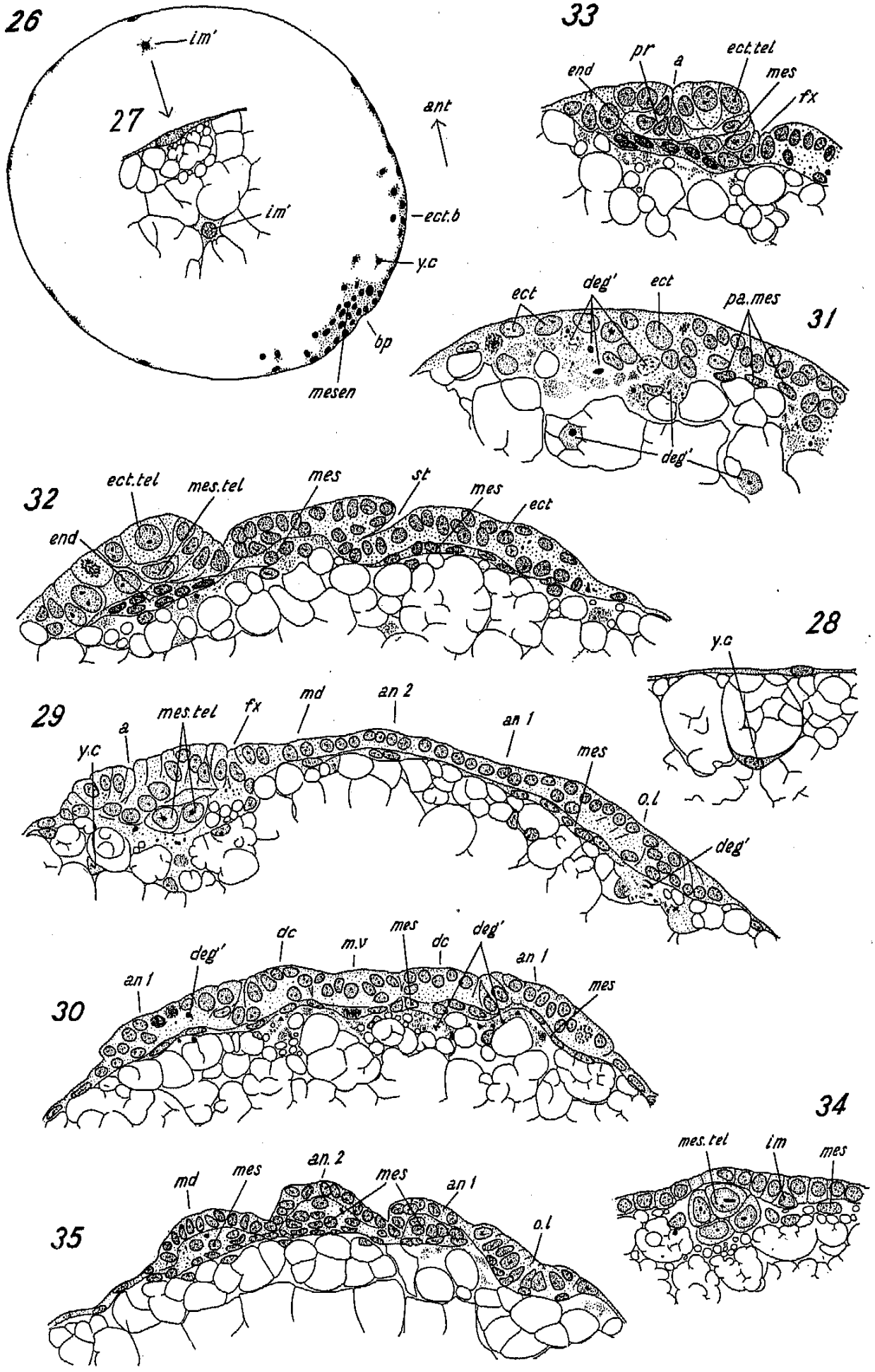

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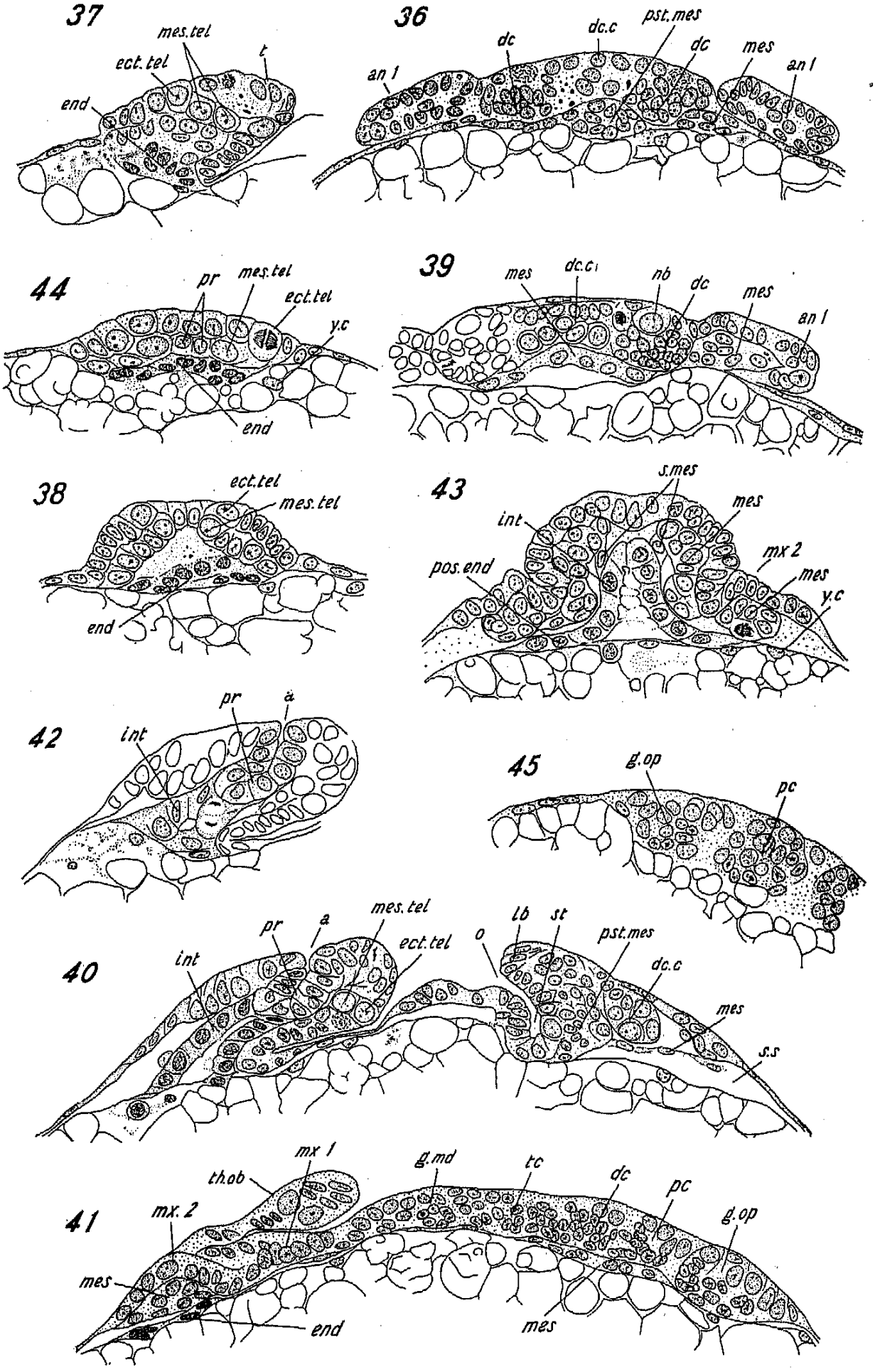

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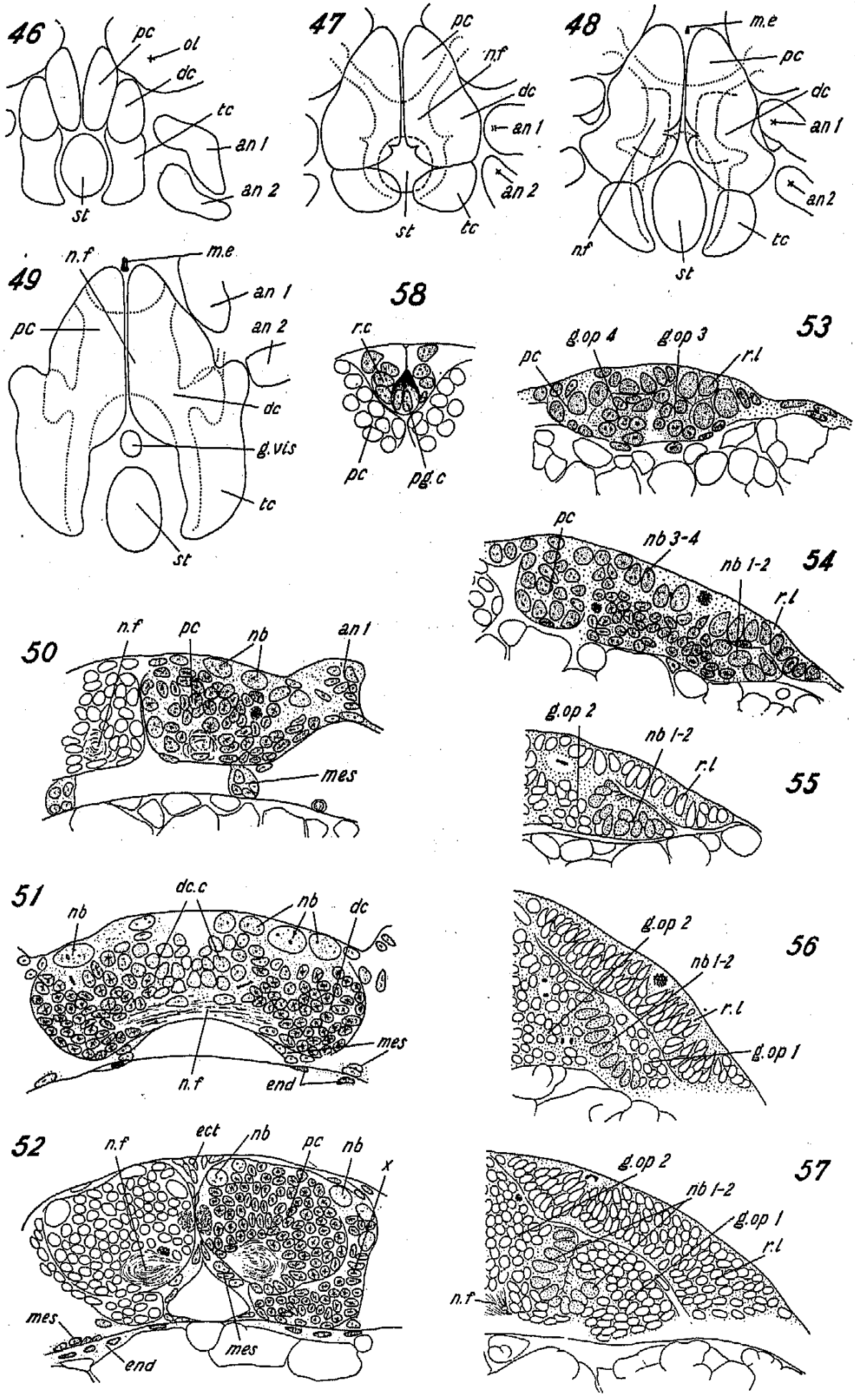

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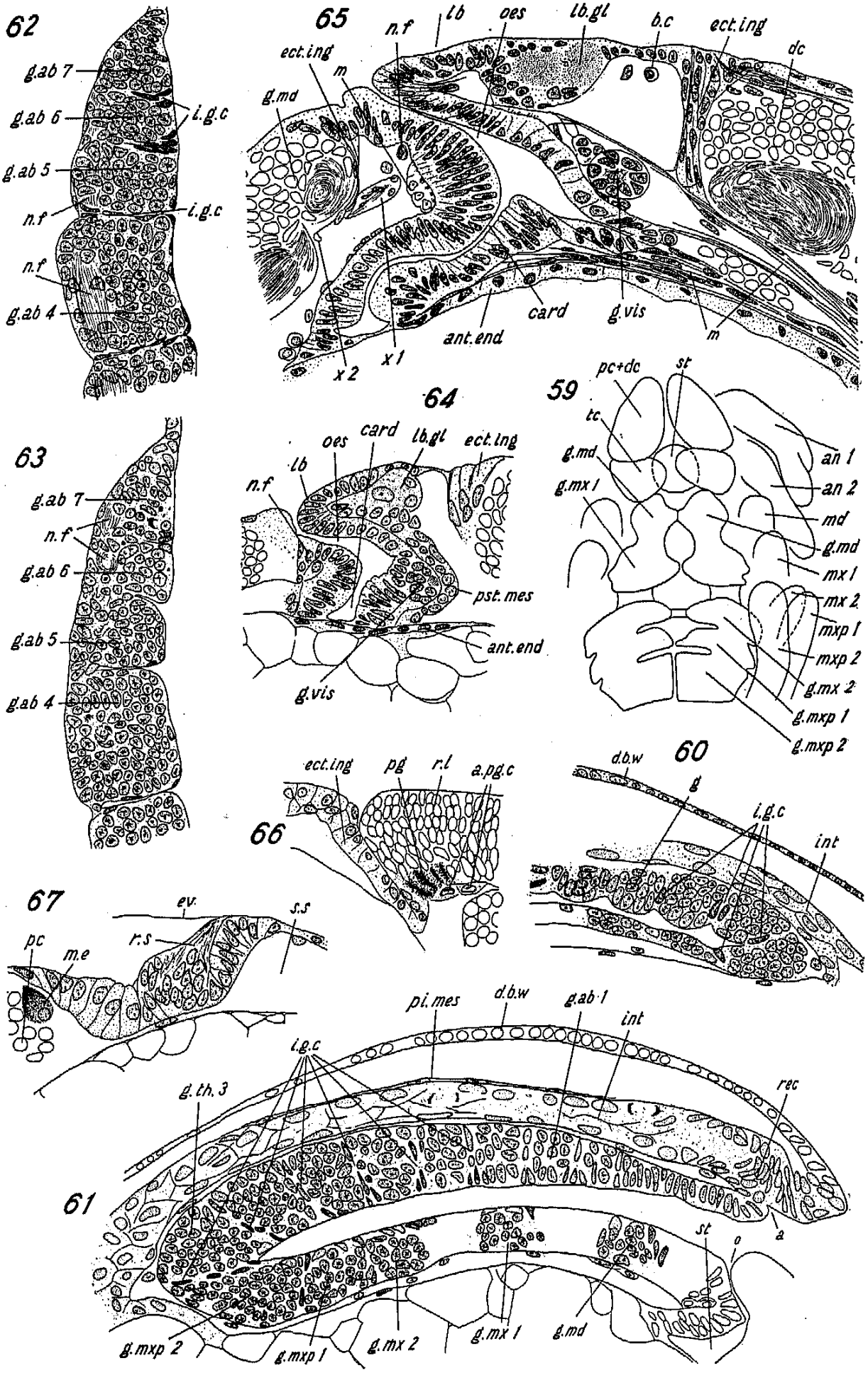

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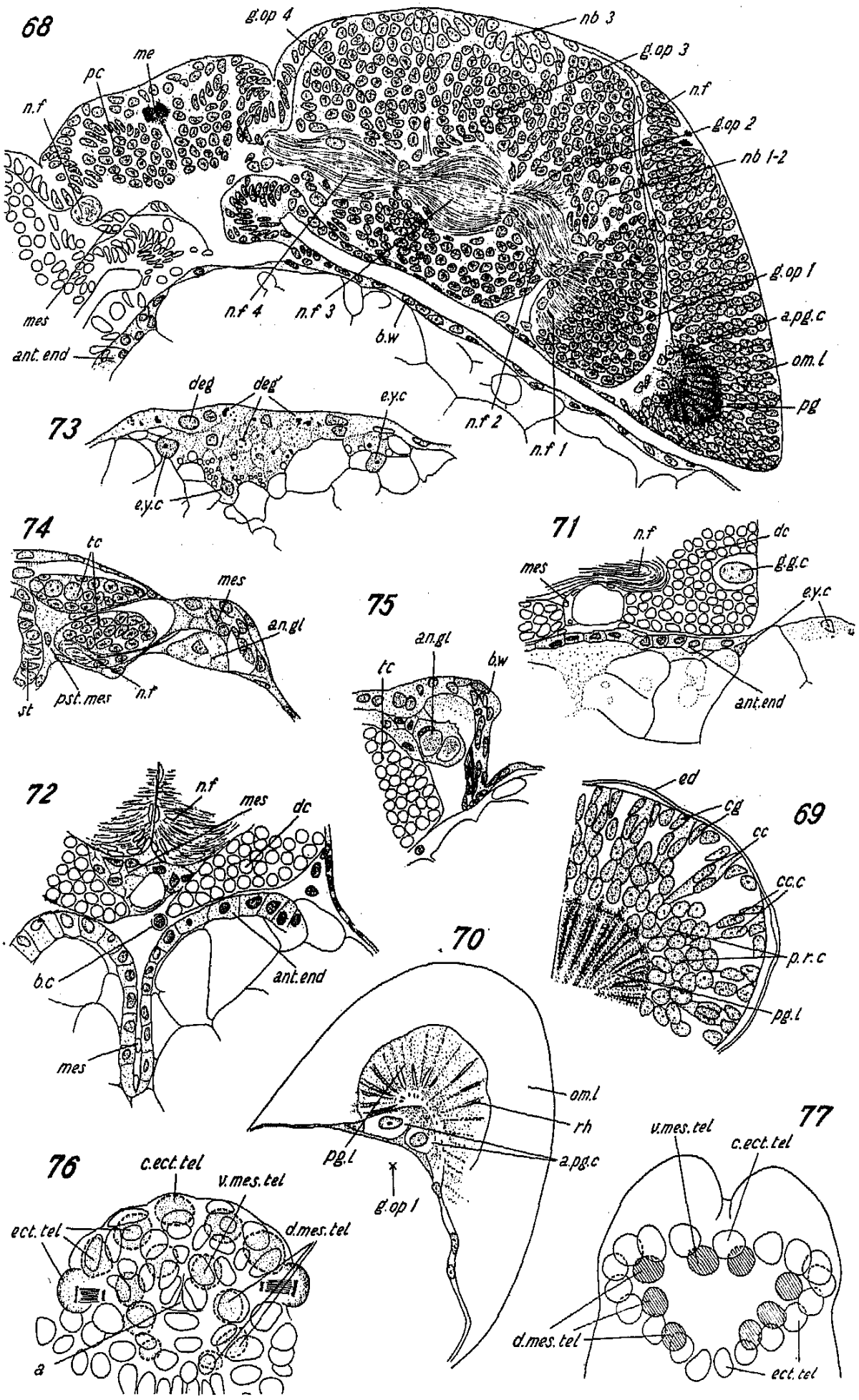

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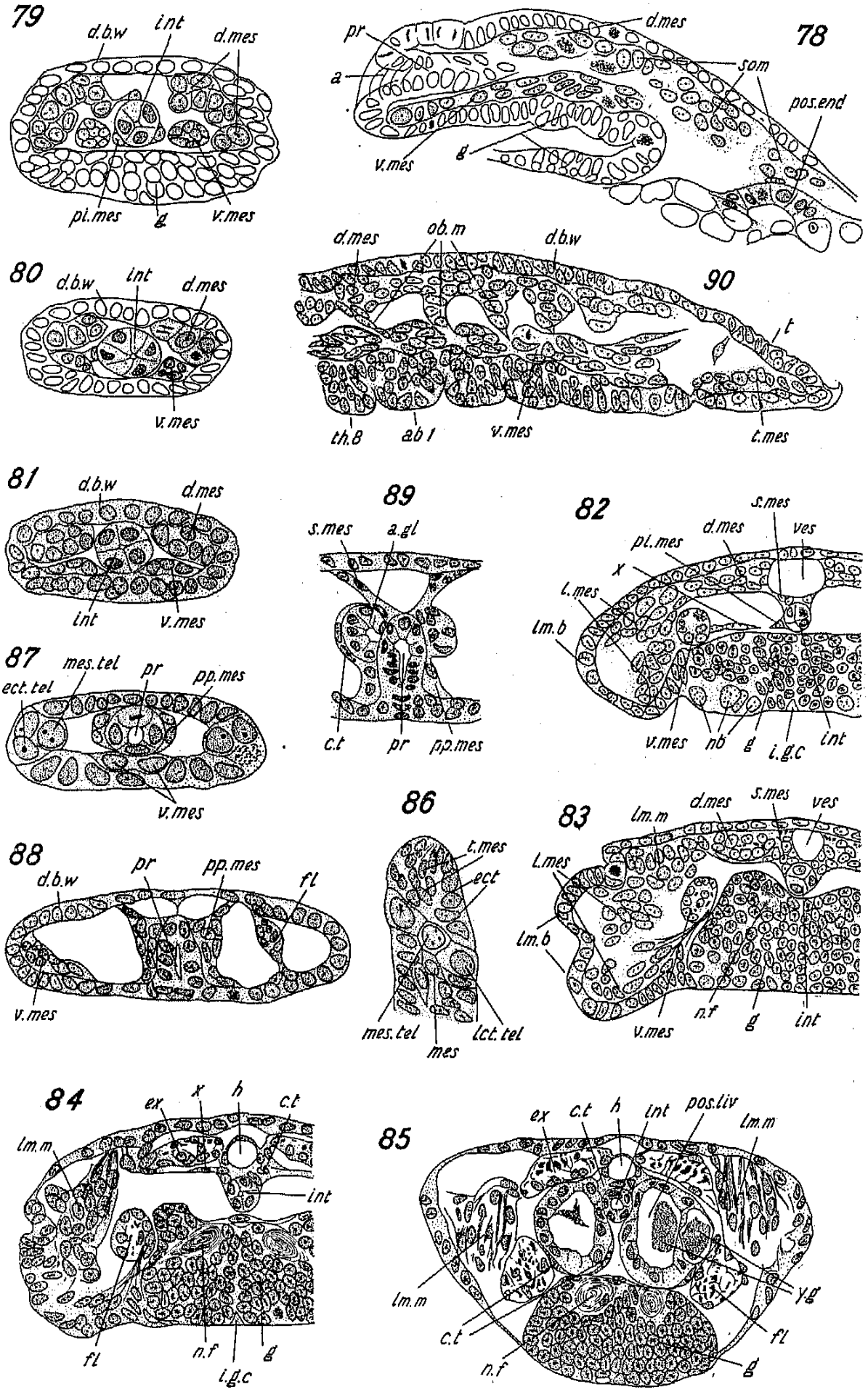

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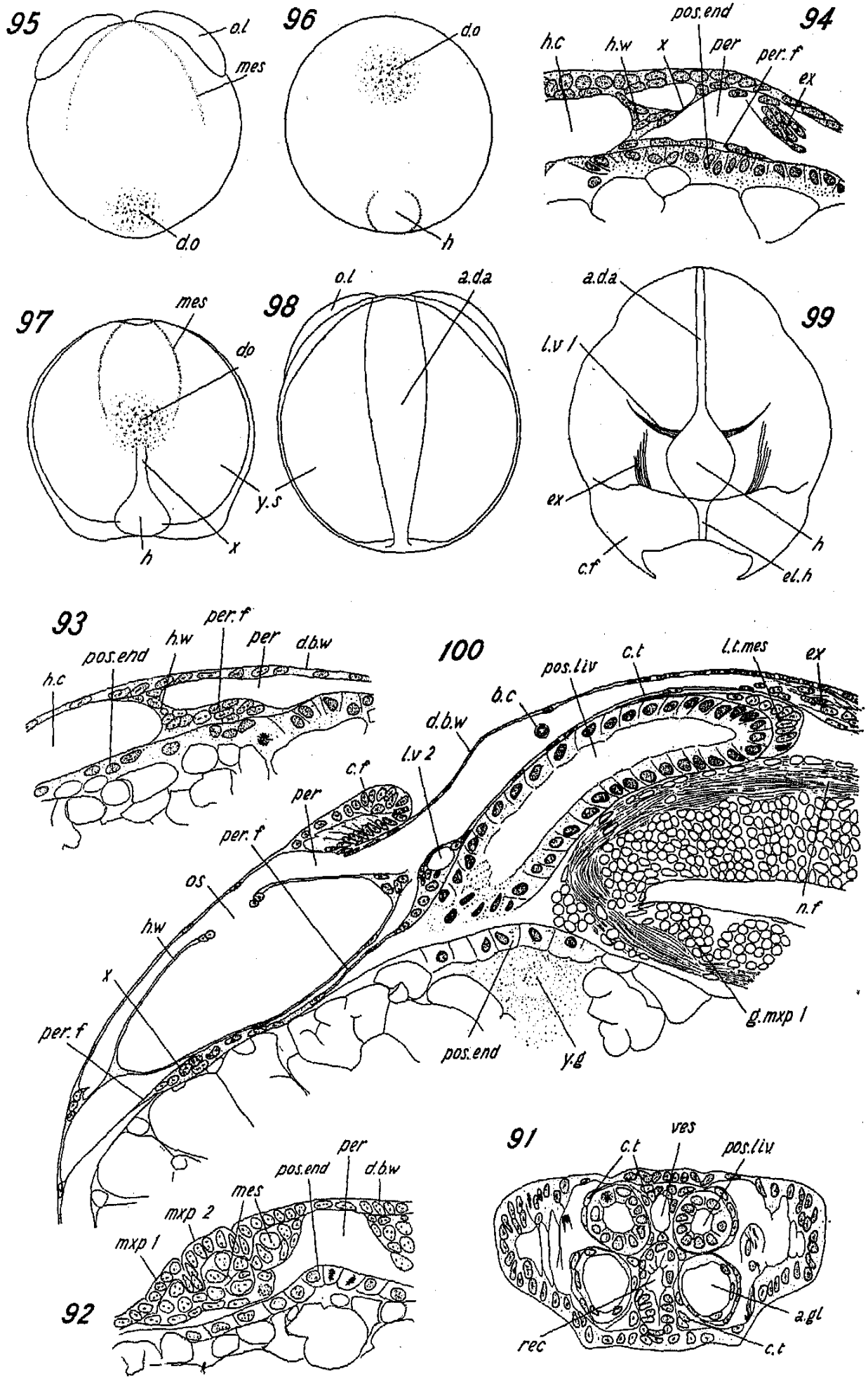

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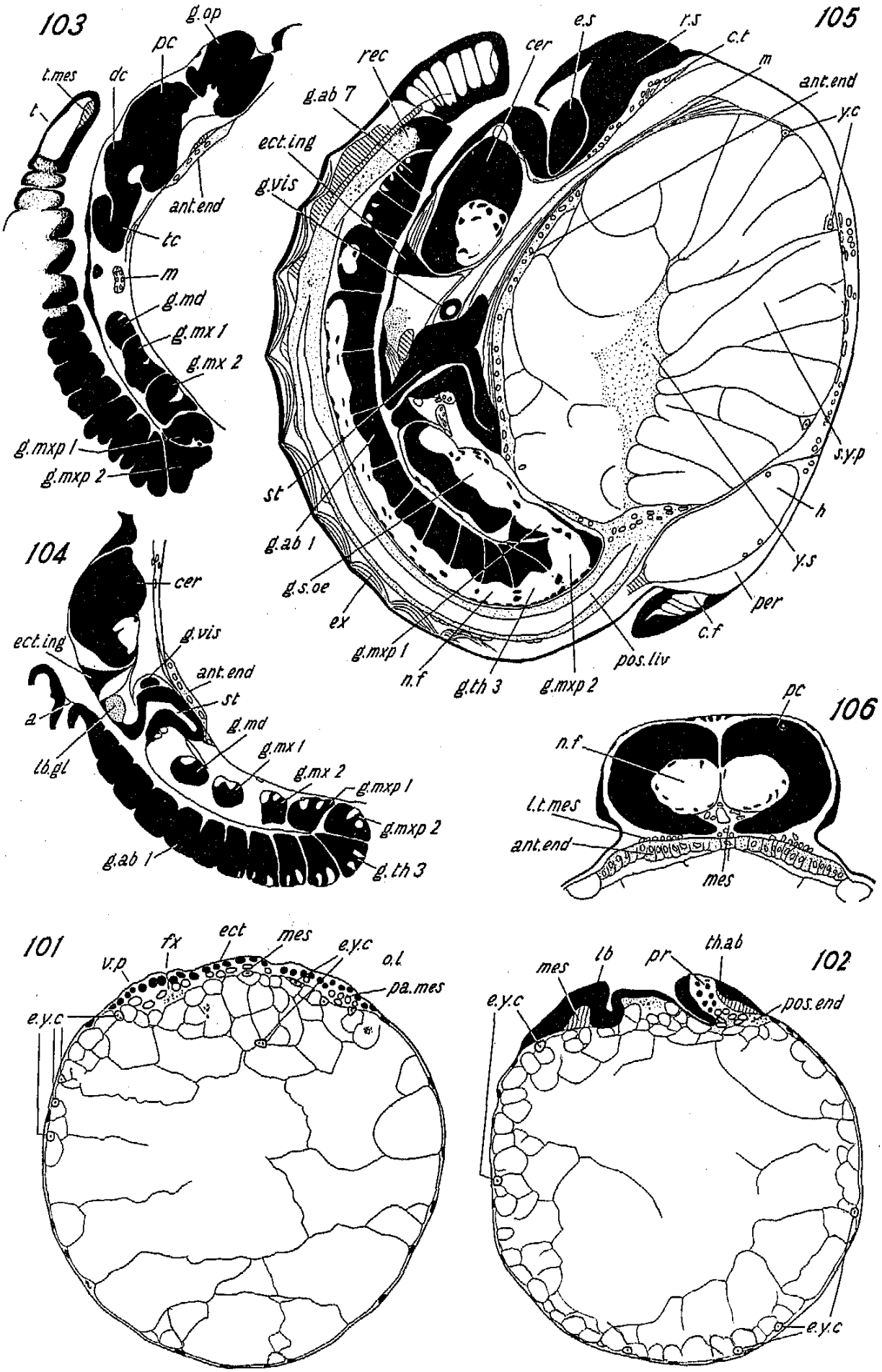

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