PAP. & PROC. ROY. SOC. TASMANIA, 1936 (31ST MAY, 1937)

I

The Embryology of the Syncarid Crustacean, Anaspides tasmaniae

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PLATES I-XIII

(Read 9th November, 1936)

INTRODUCTION

Within recent years our knowledge of crustacean embryology has been augmented by the work of Prof. H. G. Cannon on the Branchiopoda, and that of Dr. S. M. Manton on the Leptostraca and Mysidacea. Nothing, however, has been published on the embryology of the Syncarida.* An examination of the development of *Anaspides tasmaniae* Thomson was therefore undertaken. The investigation was carried out at the University of Tasmania during the years 1932-36. The following pages contain an account of the work accomplished up to the end of that period. It is hoped eventually to supplement this research by a further examination of the post-embryonic development.

I desire to express my thanks to the trustees of the John Ralston Bequest, under whose auspices the investigation was made; to Dr. S. M. Manton for copies of her publications; and to my former teacher, Prof. T. T. Flynn, for helpful advice and kindly interest in my work.

* As mentioned above, no previous work on the embryology of a Syncarid crustacean has been published. However, G. Smith (1909, p. 549) has given a brief description of the egg of *Anaspides tasmaniae*, and has stated that he was 'convinced that no complicated metamorphosis is passed through' during development, but that it was 'possible, however, that the young are batched out from the egg, not with the complete adult structure.'

Sayce (1907, p. 117) has described an immature form of *Koonunga cursor*, which differs but slightly from the adult, and Chappuis (1927, p. 602) states that there appears to be no metamorphosis in the development of the Bathynellidae.

Method of Obtaining the Eggs

The eggs of *Anaspides* measure about 1·0 mm. in diameter. They are laid singly, attached to pieces of wood or other débris in the streams and tarns where the shrimp occurs. Sediment and algal growths in the water soon cover the eggs, concealing them from view, and making it almost impossible to find them.

In March, 1932, a small laboratory aquarium was built and stocked with specimens of *Anaspides*. Little success, however, attended the experiment. It was soon realized that the conditions prevailing in the mountain streams could not be reproduced satisfactorily in the laboratory. Adult specimens of the shrimp rarely lived longer than six to eight weeks under artificial conditions, and no eggs were found in the aquarium. Half-grown specimens could be kept alive for a much longer period, but they died before reaching maturity.

In November, 1932, it was decided to keep a number of shrimps under more natural conditions in a stream on the slopes of Mount Wellington. For this purpose a tributary of the New Town Creek was selected. This stream flows down the north-eastern slopes of the mountain, and empties into the River Derwent at New Town Bay. The bed of the stream is composed of large basaltic rocks and boulders intermingled with coarse gravel and sand. Apart from algal slime there is very little aquatic vegetation in the creek.

During bright, sunny days the adult shrimps spend most of the time hiding in dark recesses among the rocks where the water is flowing rapidly, and it is in such places that they usually lay their eggs. In order to obtain the eggs two small wooden boxes, each measuring about 25 x 20 x 15 cm., were prepared. Through the ends of each box eight holes (15 mm. in diameter) were bored. These were covered on the inside with wire gauze to allow water to circulate freely through the boxes. Two or three stones, some vegetable débris from the bed of the creek, and some pieces of fibrous bark were placed in each box. Fifteen to twenty adult specimens of *Anaspides* were then introduced and the lid closed. The boxes were next completely submerged in a swiftly flowing part of the stream, a number of heavy stones being placed on top of them to keep them from being washed away.

The two boxes were prepared and stocked with shrimps in the above manner on the 9th November, 1932. The creek was not visited again until the 23rd January, 1933. The boxes had therefore been undisturbed for about ten weeks, but the specimens of *Anaspides* were still alive, and appeared to be quite healthy. The water circulating freely through the boxes had carried sufficient food for the shrimps, which had not only survived the ten weeks' confinement in almost complete darkness, but had also laid a number of eggs. Seven eggs were found in one box and thirty-five in the other. Most of the eggs had been deposited in cracks and crevices in the wood of the boxes,

some were on pieces of bark, but only a single egg was found attached to a stone. It was very difficult to remove the eggs without damaging them, since they adhered firmly to the surface on which they had been laid. The pieces of bark, with eggs attached, were therefore placed in water and taken to the laboratory for examination.

The boxes were restocked with *Anaspides* on the 23rd February, and examined periodically. It soon became evident, however, that two boxes were not sufficient. The necessity of leaving the boxes undisturbed over long periods in order to obtain eggs at advanced stages of development made it imperative to place a larger number of boxes in the stream. This procedure was also hastened by the fact that heavy rain fell on the 4th and 5th October, 1933; the creek was flooded and my two boxes washed away. On 10th October the floodwater had subsided sufficiently to allow a new box to be stocked and placed in the stream. Other boxes were added at intervals, and by 10th January, 1934, eleven boxes had been stocked with shrimps and placed in the stream at slightly different altitudes on the mountain. A record of the date, when each box was stocked with shrimps and when eggs were found in it, was kept.

If small strips of wood about the size of a microscope slide were lightly tacked on to the lid of the box, leaving a space of about 1·2 mm. between the wooden strip and the lid, the shrimps would often lay their eggs in this space. The eggs adhered to the wooden strip, which could then be removed with the eggs attached. Moss, rootlets, bark, and stones were also used as natural substances on which the shrimps might deposit their eggs. Of these materials fibrous bark proved to be the most satisfactory. Eggs were rarely laid on stones. (Fig. 1, Pl. I.)

Laying Period

In order to eliminate as far as possible any effect which long confinement might have on the laying period of *Anaspides*, some of the boxes were stocked with new shrimps each month, and the eggs were searched for shortly after the introduction of the shrimps. A fortnight usually elapsed before the shrimps became accustomed to the box and commenced to lay their eggs. Each month of the year eggs at the two-celled and four-celled stages of development were found in the boxes. Laying is therefore not restricted to any particular season, but goes on throughout the year. It appears, however, to be most active during October and November.

Time and Rate of Development

No difficulty was experienced in the laboratory in hatching embryos, which had been allowed to complete their gastrulation stage before being removed from the creek. Some were kept in running water; others were placed in water in petri dishes, and the water frequently

changed. Except for short intervals, when the eggs were being examined under the binocular microscope, they were kept in the dark. Some eggs were left to develop under natural conditions in the mountain stream, so that their time of development might be compared with that of eggs kept under laboratory conditions.

Owing to several of my boxes being washed away on four different occasions by floods in the creek, I am not able to give an unbroken series of results for any one particular year. However, observations carried out over a period of three years have made it possible to determine with reasonable accuracy both the time and the rate of development of the egg of *Anaspides*.

Some of the eggs found in the boxes on the 23rd January, 1933, had already reached the egg-nauplius stage. They were kept under observation in the laboratory until the 21st July, 1933, when one of the embryos hatched out. Eggs laid during the spring and summer months, October to March, take from eight to nine weeks to reach the egg-nauplius stage. Hence the total time of development in the case of the abovementioned embryo was about 35 weeks. Five eggs laid in one of the boxes on or about 28th November, 1933, were allowed to remain in the creek until 16th April, 1934. They were then removed to the laboratory. The embryos hatched out of three of the eggs during the second week of July, 1934, and out of the other two eggs in the following week, the total time of development being 32 to 33 weeks.

The time taken by the embryo to reach different stages in its development may be determined from the results shown in Table I. The transparent nature of the chorion and larval membranes makes it possible to recognize many of the stages of development without having recourse to dissection.

TABLE I.

Rate of Development of the Embryo of *Anaspides* in Eggs Laid during the Months October to March.

Approx. Date of Laying.	*Date of Examining.*	*Age of Embryo in Days.*	*Stage of Development.*	*Remarks.*
16 Nov., '32	23 Jan., '33	68	Early nauplius	fig. 23, Pl. III
16 Nov., '32	4 Mar., '33	108	Post nauplius	fig. 29, Pl. IV
16 Nov., '32	21 July., '33	247	Hatching	
31 Oct., '33	22 Dec., '33	52	Gastrulation	fig. 20, Pl. III
31 Oct., '33	4 Jan., '34	65	Early nauplius	fig. 23, Pl. III
16 Nov., '33	7 Feb., '34	83	Late nauplius	fig. 28, Pl. IV
21 Nov., '33	16 April, '34	146	Thoracic appendages	
28 Nov., '33	12 July, '34	226	Hatching	
5 Mar., '34	2 May, '34	58	Germinal disc	fig. 21, Pl. III
8 Mar., '34	2 June, '34	86	Late nauplius	fig. 28, Pl. IV
16 Jan., '35	18 Feb., '35	33	Beginning of gastrulation	fig. 17, Pl. III
28 Feb., '35	27 Mar., '35	27	Stage just previous to gastrulation	fig. 16, Pl. II.

Eggs laid during the autumn and winter months, April to September, develop to the gastrulation stage, and then remain dormant until the end of October, when development continues, and the embryos hatch out in the following June. An egg laid in April will therefore take about 60 weeks to hatch. The rate of development of eggs laid in the months April to September is indicated in Table II. The results given in this table and in Table I. are selected from observations made on eighty different eggs during the last three years.

TABLE II.

Rate of Development of the Embryo of *Anaspides* in Eggs Laid during the Months April to September.

Approx. Date of Laying.	*Date of Examining.*	*Age of Embryo in Days.*	*Stage of Development.*	*Remarks.*
1 April, '33	4 April, '33	3	Two cells	fig. 7, Pl. II
1 April, '33	8 April, '33	7	Thirty-two cells	
20 April, '33	17 Oct., '33	180	Gastrulation	fig. 18, Pl. III
31 May, '34	21 July, '34	51	Gastrulation	fig. 18, Pl. III
31 May, '34	8 Dec., '34	191	Post nauplius	fig. 29, Pl. IV
30 June, '34	4 July, '34	4	Eight cells	fig. 11, Pl. II
11 July, '34	8 Sept., '34	59	Gastrulation	fig. 18, Pl. III
11 July, '34	10 Oct., '34	91	Gastrulation	fig. 18, Pl. III
11 July, '34	20 Nov., '34	132	Late nauplius	fig. 28, Pl. IV
28 Aug., '34	12 Sept., '34	15	About 128 cells	
19 Sept., '34	20 Nov., '34	62	Gastrulation	fig. 18, Pl. III

The Hatching Period

It has already been mentioned that eggs laid in the creek during November, and kept for some time under laboratory conditions, hatched in the following July. In order to determine the limits of the hatching period under natural conditions a large number of shrimps were collected from the creek each month from March, 1934, to February, 1935. The length of each specimen from the anterior end of the rostrum to the posterior end of the telson was measured in millimetres. In the case of the small specimens in which the rostrum had not yet been formed, the length was taken from the front of the head to the end of the telson. The percentage number of shrimps of each size from 3·0 mm. to 20·0 mm., found in the catch for each month, was then determined. The results are shown in Table III.

The absence of small specimens of 3-4 mm. in length from the catches for the months November to May, and the presence of such specimens in the catches for the months June to October, make it quite clear that hatching takes place during the latter period. The results also indicate that most of the eggs hatch at the end of June or the beginning of July.

TABLE III.

Percentage Number of Specimens of *Anaspides* of Different Sizes taken in the New Town Creek each month from March, 1934, to February, 1935.

Length of Shrimps in mm.	*Percentage Number Taken on—*											
	7th Mar., 1934.	*16th Apr., 1934.*	*24th May, 1934.*	*16th June, 1934.*	*21st July, 1934.*	*21st Aug., 1934.*	*12th Sept., 1934.*	*19th Oct., 1934.*	*20th Nov., 1934.*	*20th Dec., 1934.*	*21st Jan., 1935.*	*18th Feb., 1935.*
3·0	....	....	....	3	12	2	1	....	....	....	....	....
4·0	....	....	....	....	40	3	37	15	....	....	....	....
5·0	....	....	....	....	12	17	6	18	8	1	....	....
6·0	....	....	....	....	2	17	7	16	14	1	1	....
7·0	....	....	....	....	....	6	....	7	28	14	1	....
8·0	9	....	....	....	....	....	....	2	8	23	8	1
9·0	31	6	....	2	....	....	1	6	3	24	14	8
10·0	19	6	12	4	6	....	1	2	3	6	18	11
11·0	15	38	4	7	4	6	4	....	....	6	14	18
12·0	16	21	14	15	6	2	1	....	....	2	9	23
13·0	4	4	23	13	....	5	7	....	....	....	3	16
14·0	1	10	6	17	4	20	8	....	....	....	2	5
15·0	....	4	17	9	2	12	5	....	....	....	1	3
16·0	1	2	12	7	....	5	8	3	4	1	....	....
17·0	....	....	2	3	2	2	3	7	11	....	....	....
18·0	1	2	....	3	....	....	....	15	3	1	2	....
19·0	....	....	....	....	2	....	....	6	4	2	2	....
20·0	....	....	....	2	....	....	7	....	2	11	2	....
Others	3	7	10	15	8	3	4	3	12	8	23	15

Technique, Fixation, and Staining

In eggs not covered with débris the chorion is so transparent that the embryo may be observed in the living state and certain phases of its development followed.

The fixation of the egg is most difficult. The chorion is not penetrated by Smith's formol-bichromate fluid, which Prof. Cannon (1921, p. 629) and Dr. Manton (1928, p. 364) used in their researches on crustacean embryology. Gilson's fluid and cold sublimate-acetic also fail to penetrate. Hot sublimate-acetic is far too drastic, and disorganizes the yolk. Bouin's picroformol penetrates the chorion very slowly, and will fix early stages. However, as soon as the vitelline membrane has been formed, Bouin's solution fails to give satisfactory results. The tendency of the chorion to curl inwards when broken, and the semi-fluid nature of the yolk, render removal of the chorion, without injury to the embryo, almost impossible. As development proceeds other membranes or larval integuments are formed, and these add to the difficulty of fixation.

The only fixative found to penetrate the chorion, vitelline membrane, and larval integuments is Carnoy's fluid (Glacial acetic acid 1 part, Absolute alcohol 6 parts, Chloroform 3 parts). This fluid

penetrates with considerable rapidity, and tends to cause invagination of the chorion, accompanied by distortion of the embryo. This may be avoided, however, by making a very small perforation in the chorion. Fixation is complete in from 40 to 50 seconds. The eggs are then transferred to 90 per cent. alcohol for 24 hours. The yolk is thus hardened sufficiently to allow removal of the chorion without injury to the embryo. It is not necessary to remove the vitelline membrane, but the thick chorion is an obstacle to accurate orientation. Moreover, it becomes hard and brittle during the process of infiltration, causing trouble later in section cutting. Its removal may be carried out under a binocular dissecting microscope with the aid of needles.

In the one-celled stage the zygote occupies the whole space enclosed by the chorion, and adheres to the latter on fixation. Sections of this stage, therefore, had to be cut with the chorion *in situ*. Many failures resulted, but several complete series of sections of the one-celled stage were thus obtained. In later stages this difficulty is not encountered, and the chorion may be removed in the manner described above.

To facilitate manipulation and orientation, the eggs were stuck on to small pieces of hardened sheep's brain by the celloidin method. They were then infiltrated with paraffin wax (M.P. 56° C.). Forty minutes in the wax bath gave satisfactory infiltration without rendering the yolk brittle. The wax was changed once before the definitive embedding.

Serial sections were cut at thicknesses of 8-12 μ, and stained with Ehrlich's acid haematoxylin, eosin being sometimes used as a counterstain.

In addition to serial sections, whole mounts of the young germinal disks were made. These were prepared in the following way: After fixation the embryo was stained for about 40 hours in alum-carmine, and then differentiated in acid alcohol for about the same length of time. It was then embedded in paraffin, placed on the microtome, and all the part, other than the germinal disk, cut away. The disk was then removed from the paraffin block by the aid of xylol, and mounted.

General Embryonic Development

The Unsegmented Egg

The newly laid egg of *Anaspides* has a faint purple tinge, and is surrounded by a thick transparent chorion. It is almost spherical in shape, and, including the chorion, measures about one millimetre

in diameter. Ten eggs, when measured under a micrometer eyepiece, gave the following results in millimetres:

(*a*)	1·03 x 1·07
(*b*)	1·01 x 1·05
(*c*)	1·03 x 1·03
(*d*)	1·05 x 1·07
(*e*)	0·98 x 1·04
(*f*)	0·97 x 1·05
(*g*)	0·98 x 1·03
(*h*)	0·96 x 1·08
(*i*)	1·03 x 1·08
(*j*)	0·92 x 1·08

The chorion measures about 14 μ in thickness, and is composed of two layers firmly united. The outer layer is 12 μ in thickness, and in transverse section is seen to be perforated by numerous minute radial tubules. The inner layer measures 2 μ in thickness, and is homogeneous. The outer surface of the chorion is slightly rough, and in the newly-laid egg it is sticky. Sand grains, algal filaments, and other débris in the water of the creek adhere to the egg, and soon hide it from view. The inner surface of the chorion is smooth and has a glazed appearance. When the egg is laid the chorion is quite colourless, but after a few days it takes on a brownish tinge, which is probably due to the absorption of tannins or other pigments derived from fallen leaves and other vegetable matter in the water.

In consistency the chorion resembles a layer of chitin of the same thickness, but it is more readily broken. When fractured it tends to curl inwards and crush the egg. This tendency is retained to some degree even in specimens which have been embedded in paraffin and sectioned.

The newly-laid egg fills the whole space enclosed by the chorion, and at this stage no vitelline membrane is present. The yolk granules are almost spherical in shape, and vary from 5 μ to 19 μ in diameter. The larger granules appear to be more numerous near the surface than near the centre of the egg.

The earliest cytological condition found among the unsegmented eggs examined shows the sperm-nucleus and the egg-nucleus approaching each other. Each nucleus is surrounded by an irregular mass of protoplasm, from which long protoplasmic filaments radiate out amongst the yolk granules. The sperm-nucleus has an irregular ovoid shape, and measures 42 x 48 μ. It is situated about half-way between the centre and outer surface of the egg. The egg-nucleus is also of an irregular ovoid shape, and measures 51 x 57 μ. It is near the centre of the egg.

The next stage shows the two nuclei in contact. The nuclear membranes, however, are still intact, and fusion has not yet taken place. (Figs. 3 and 4, Pl. I.) This stage was met with in a number of eggs,

and it is probable that the two germ-nuclei remain in contact for some time before actual fusion occurs. Eventually, however, the intervening nuclear membranes break down, and the two nuclei coalesce to form a zygote nucleus at the centre of the egg.

While these changes are in progress a marked decrease in the volume of the egg occurs. An egg which, excluding the chorion, measures 1·02 x 1·04 mm. when newly laid, may decrease in size to such a degree, that it measures only 0·65 x 0·71 mm. when the zygote nucleus is formed. As the volume of the egg decreases, the yolk granules, which are somewhat widely separated in the cytoplasm of the newly-laid egg, are brought closer together. The contraction also results in the formation of a wide space between the egg and the chorion.

Segmentation

The egg of *Anaspides* undergoes total segmentation, and, up to the eight-celled stage, the blastomeres are equal in size. The first cleavage furrow is meridional, and divides the egg into two cells, which, at first, are so loosely held together, that they readily fall apart (figs. 5 and 6, Pl. I). However, before the next division, the two cells appear partly to fuse again, and the cleavage furrow becomes shallow (figs. 7 and 8, Pl. II). Serial sections through embryos at the two-celled stage show the nucleus of each blastomere to be near the centre of its cell, and surrounded by an irregular mass of protoplasm, from which strands radiate out among the yolk-granules.

The second cleavage takes place in the usual manner, being meridional and at right angles to the first furrow (figs. 9 and 10, Pl. II). The third cleavage is equatorial, giving rise to eight cells. At first the four blastomeres at one pole are superposed on those at the other pole, but the cells soon move into a position in which the four blastomeres at one pole alternate with those at the other (fig. 11, Pl. II). These eight cells show no tendency to fuse, and after fixation they may be easily separated from one another. Yolk is distributed uniformly through the eight cells.

When segmentation commences, or shortly afterwards, a delicate vitelline membrane is formed around the embryo. At first this membrane is very thin, and fixatives penetrate it, but, when the eight-celled stage has been reached, the membrane is so thick, that it presents a serious obstacle to proper fixation.

The rate of cleavage is slow. An embryo examined at 8.30 p.m. on 4th April was at the two-celled stage. Twenty-four hours later it had reached the four-celled condition, and at 9 p.m. on the 8th April thirty-two blastomeres had been formed.

At the sixteen-celled stage (fig. 12, Pl. II) a small blastocoel has been formed in the centre of the embryo (fig. 13, Pl. II). As segmentation continues the size of the blastocoel becomes larger.

Mesoderm Formation

Segmentation has now become irregular, and appears to be more active at one than at the other pole of the embryo. When moved about, the living embryo usually rotates within the vitelline membrane so that the same pole is always uppermost. It is at this pole that segmentation appears to be more active and the cells smaller than at the other pole. Between the sixteen-celled stage and the thirty-two celled stage a blastomere at the uppermost pole slips into the blastocoel (figs. 13 and 14, Pl. II). As segmentation proceeds, further cells from this pole enter the segmentation cavity, with the result that the surface of the embryo at this pole presents a pitted appearance.

The embryo has now assumed the form of a blastula, the wall of which is composed of a single layer of wedge-shaped blastomeres, surrounding a cavity which is partly filled by an inner mass of cells not arranged in any definite manner (figs. 15 and 16, Pl. II). This inner cell-mass constitutes the primary mesoderm.

The total number of cells entering the blastocoel could not be determined. Serial sections showed that some cells, which had already entered the segmentation cavity, were undergoing mitosis, while others were passing inward.

As development proceeds the nuclei of the outer blastomeres gradually approach the surface. All the cells of the embryo are uniformly rich in yolk.

Gastrulation and Endoderm Formation

When the inward migration of cells into the blastocoel to form the primary mesoderm has ceased, the outer surface of the embryo presents a uniformly segmented appearance. There is very little difference between the blastomeres of the two poles. The pitted appearance of the surface is no longer visible.

The process of gastrulation is initiated by the formation of a crescent-shaped depression occupying a large area at the uppermost pole (figs. 17 and 19, Pl. III). The invagination gradually deepens, its opening becoming smaller and somewhat triangular (fig. 18, Pl. III). This opening is the blastopore. The invagination becomes so deep that it reaches the mass of mesoderm cells in the blastocoel (fig. 20, Pl. III). It constitutes the endodermal rudiment, and later gives rise to the yolk-sac, mid-gut, and liver lobes. The mesoderm cells are pushed to one side of the blastocoel by the invagination and become somewhat flattened. They eventually spread out under the ectoderm and below the future position of the germinal disk.

Invagination goes as far as possible, and at one stage there is a deep archenteric cavity (fig. 20, Pl. III). It is, however, not a permanent cavity, for cells continue to move inward, crowd together,

and obliterate its lumen. The blastopore grows smaller as gastrulation advances, and it finally closes when the cells around its margin come together. However, it never disappears entirely, its position being marked by a small depression in the surface of the embryo. This depression is later replaced by the opening of the proctodaeum.

The endoderm now forms a solid core of cells, which, together with the mesoderm, fills the whole of the blastocoel. All the cells of the embryo are laden with yolk-granules, and, apart from their position, there is little to distinguish the mesoderm cells from those of the endoderm.

In eggs laid in the spring and summer the close of gastrulation is marked by a short period of rest. In autumn and winter eggs it is followed by a long period of dormancy.

Formation of Germinal Disk and Egg-nauplius

After the quiescent period following gastrulation, cell division takes place actively over a wide area immediately in front of the blastopore. This active cell division gives rise to the germinal disk. Its narrow posterior end terminates at the blastopore, whilst its broader anterior end and its sides merge into the region surrounding them. In eggs laid during spring and summer the embryo takes about 60 days to reach the stage of development in which the germinal disk is fully differentiated.

The disk now becomes thickened laterally, while the cells composing its antero-median portion become thin. In this way the typical V-shaped form of the disk, seen in so many crustacean embryos, is attained (fig. 21, Pl. III).

This stage is soon followed by the appearance of the egg-nauplius. The first sign of its development is the formation of the stomodaeum. This appears as a deep crescent-shaped invagination between the arms of the V, and slightly in front of the middle of the disk. The invagination extends backwards below the disk towards the blastopore. At this stage the posterior margin of the stomodaeum is much higher than its anterior margin. The rudiments of the naupliar appendages appear simultaneously as three pairs of thickenings on the lateral arms of the disk. These thickenings soon stand out in high relief above the surface of the disk. The opening of the stomodaeum is now seen to lie between the rudiments of the antennae (fig. 23, Pl. III). Immediately in front of the blastopore is a pair of small lateral thickenings, which later give rise to the caudal papilla. The portion of the disk in front of the stomodaeum and between the antennules soon becomes thickened and elevated to form the labrum.

Up to this stage there has been very little indication of the development of the head-lobes, but now, on each side immediately in front of the bases of the antennules, active cell-proliferation occurs, and the paired rudiments of the head-lobes are established. The labrum

is gradually raised above the surface of the disk, and commences to project over the opening of the stomodaeum. The paired lateral elevations in front of the blastopore come together, forming the lobes of the caudal papilla. The extremities of the antennae and mandibles are now distinctly bilobed (fig. 24, Pl. III).

While these changes have been taking place, a marked contraction in the area of the germinal disk has occurred. When the rudiments of the naupliar appendages first appeared, they were widely removed from the median line, and projected beyond the sides of the embryo. Now they have been drawn towards the median line, and also closer together (fig. 27, Pl. IV).

Ectodermal Teloblasts

Soon after the establishment of the rudiments of the naupliar appendages the ectodermal teloblasts appear. These at first form an irregular transverse row on either side of the mid-ventral line and immediately in front of the blastopore. Each row consists of seven cells (fig. 25, Pl. IV). The inner ends of the two rows are united by a teloblast in the mid-ventral line. As the germinal disc contracts and the bases of the naupliar appendages are brought closer together, the teloblasts tend to form a curved row round the caudal papilla, which has now been formed (fig. 26, Pl. IV). Yolk-granules in the teloblastic cells are rapidly absorbed, and the cell-nuclei become greatly enlarged. This is soon followed by the division of the cells to form the usual tranverse rows of descendants. The teloblasts do not form a complete ring around the caudal papilla until about the fourteenth week. The complete ring consists of nineteen cells, there being one in the mid-ventral line and nine on each side (figs. 53-54, Pl. VIII).

During the development of the egg-nauplius a new investing membrane is formed. This is the *first larval integument* or *embryonic cuticle*. It eventually becomes very thick and elastic, and plays an important part in the process of hatching.

The embryo is now surrounded by three investments, namely, the chorion, the vitelline membrane, and the first larval integument.

Whenever the age of an embryo is mentioned in the following pages, it is to be regarded as having reference to an embryo developed in an egg laid in early summer.

Further Changes in the External Shape of the Embryo

In eggs laid during early summer the embryo takes about eleven weeks to reach the stage of development shown in fig. 27, Pl. IV. In the twelfth week the head-lobes develop rapidly and the labrum increases in length and breadth. Little change occurs in the shape of the antennules, but the bilobed nature of the antennae becomes still more pronounced, the exopodite being distinctly longer than the endopodite. The mandibles lose their bilobed appearance and become

pyriform, the narrow distal portion later giving rise to the mandibular palp. Meanwhile the caudal papilla has increased in size, and the opening of the proctodaeum has become established in the position formerly occupied by the blastopore. The first row of ectodermal teloblasts partly encircling the papilla appears at this stage (fig. 28, Pl. IV).

In fourteen weeks the head lobes are clearly defined, and curve outward in front of the base of the antennules. The central cell of each lobe is still visible. A rudimentary median eye in the form of a small pigment-spot has appeared in the apex of the V-shaped area between the head-lobes (fig. 29, Pl. IV). The tip of the labrum lies between the mandibles. The three basal segments of the antennules are established. In the antennae the two basal segments, coxopodite and basipodite, are first differentiated at this stage, and there is a marked increase in the length of the two rami, but the exopodite is still somewhat longer than the endopodite. The embryo has now become distinctly narrower and more elongate, but is wider anteriorly than posteriorly. Immediately behind and between the mandibles appear the rudiments of the maxillules. These are separated from the caudal papilla by the tranverse caudal furrow. This furrow and the maxillules are soon hidden by the bending forward of the papilla. The end of the papilla is divided into two blunt lobes, which subsequently give rise to the caudal fork. The proctodaeum opens in the notch between the caudal lobes.

The post-mandibular segments of the trunk are formed by growth from teloblasts in front of the blastopore, and arise in succession from before backwards. The limb rudiments also appear in succession from before backwards.

The first larval integument has now become relatively thick. It surrounds the embryo loosely, and is attached only at the ends of the antennules and antennae. A *second larval integument* has been formed, but is not shed until just before hatching.

In about sixteen weeks the central cell of the head-lobes has disappeared. The median eye-spot has become larger and more distinct. The antennules and antennae have commenced to curve upwards and backwards at the sides of the embryo. The two rami of the antennae are segmented, and the endopodite, which at first was shorter than the exopodite, is now equal to it in length. The rudiments of the maxillules are now followed by those of the maxillae and the first three pairs of thoracic appendages. The caudal papilla has curved forward, and the angle of flexure has shifted to the third thoracic segment (fig. 30, Pl. IV).

In eighteen weeks pigmentation of the paired eyes appears. The median eye-spot has become elongated and pear-shaped. The endopodite of the antennules is not yet formed. The antennary endopodite is now distinctly longer than the exopodite, and as development proceeds

the difference in length becomes more pronounced owing to retardation in the growth of the exopodite. The rudiments of the first seven pairs of thoracic appendages have been formed, and the biramous nature of the first six pairs soon becomes apparent. At first there is very little difference in length between endopodite and exopodite. Eventually, however, the growth of the endopodite exceeds that of the exopodite. The embryo has now completed a little more than half the period which it spends in the egg. Flexure of the body and the increase in length of the embryo have brought the caudal extremity into contact with the front of the labrum. The body tapers gradually from the anterior to the posterior end, there being no sudden diminution in size at any point.

From this stage onward the chief changes in form consist in the further development of the appendages. The eighth thoracic limbs soon appear, and are followed in succession by the abdominal limbs. The epipodial gills of the first seven thoracic appendages are developed shortly before hatching. The small leaf-like endopodite, which, in the adult, is present on the first four pairs of abdominal limbs, is not developed until after hatching. As they develop the thoracic limbs are directed downwards, the second, third, and fourth pairs being on the outer side of the others, which, owing to the flexure of the body, lie between them. The five pairs of abdominal appendages and the uropods at first curve upwards at the sides of the abdomen.

At the twenty-second week a large saddle-shaped median dorsal-organ has been formed. Anteriorly it is bounded by a transverse groove immediately behind the paired eyes, whilst its posterior margin is the junction between the first and second thoracic segments. Laterally it extends to the level of the paired eyes. In the living embryo the organ has a yellowish appearance. It seems to reach its maximum development about the twenty-fifth week, and then slowly degenerates, but does not disappear until after hatching. No dorso-lateral organs are present.

During the last few weeks before hatching the embryo becomes deeply pigmented on the front of the head between the eyes, and to a less extent on the back and sides of the trunk segments (fig. 31, Pl. V).

As stated above, the embryo hatches from eggs laid during early summer in from thirty-two to thirty-five weeks.

Post-Embryonic Development

The Process of Hatching

As mentioned previously, five eggs hatched in the laboratory during the second and third weeks of July, 1934. In the case of one of these eggs I was fortunate enough to observe the process of hatching. Shortly before 12 midnight on the 17th July a crack appeared in the chorion, and extended gradually round it in a meridional plane (fig. 32, Pl. V). At 12.10 a.m. on the 18th July the crack had opened

and the vitelline membrane had burst. The first larval integument, however, was still intact, but had commenced to bulge out through the opening in the chorion. It was becoming slowly distended by osmosis. The expanding of this membrane gradually forced apart the two portions of the chorion, thus preventing their curling inwards and crushing the embryo (fig. 33, Pl. V). The shrimp was now enclosed in a perfectly transparent ovoid sac formed by the first larval integument. This sac measured 2·0 x 1·8 mm. It still had the two portions of the chorion and fragments of the ruptured vitelline membrane attached to its outer surface. The increased space within allowed the shrimp to unflex its body, which up to the present had been strongly curved, with the ventral surface of the telson resting against the front of the head (fig. 34, Pl. V). The ovoid sac eventually became quite free from the chorion, and assumed a spherical form. At 1 a.m. it had expanded to a diameter of 2·5 mm.

The shrimp was now moving about actively, and endeavouring to throw off the second larval integument. This had already split on the dorsal side, and was being slowly pushed off the appendages. Ultimately the ecdysis was completed, and the second larval integument lay in a crumpled mass inside the balloon-like first larval integument. At 1.10 a.m. the latter burst, allowing the shrimp to escape.

In another specimen, in which the chorion cracked before 7.30 p.m. on 12th July, the first larval integument did not burst and liberate the shrimp until about 9 p.m. on 13th July.

From the above observations the first larval integument, which is very strong and elastic, seems to serve two important purposes. In the first place, it absorbs water by osmosis, expands, and forces apart the two portions of the fractured chorion. In the second place, it provides a roomy chamber where ecdysis of the second larval integument may take place in safety. (See also fig. 2, Pl. I).

External Characters of the Hatched Embryo

The newly-hatched shrimp (fig. 35, Pl. V) measures 2·70 mm. in length. It differs from the adult mainly in having sessile eyes, no rostrum, a notched telson, and no endopodites on any of the appendages of the first five abdominal segments.

The antennules measure about 1·2 mm. long. The peduncle consists of the three segments present in the adult. The inner flagellum has three, and the outer eleven, segments. Setae are distributed as shown in fig, 36, Pl. VI. The statocyst in the basal joint of the peduncle is well developed, and already contains five clavate rods.

The antennae are slightly shorter than the antennules. The protopodite consists of the usual two segments. The endopodite has nine segments, while the exopodite, which, during embryonic life, was relatively large, has now degenerated to a small scale (fig. 37, Pl. VI).

The head is rounded in front, and has a median longitudinal groove, which extends backward to meet a transverse groove close behind the paired eyes (fig. 40, Pl. VI). This transverse groove grows forward as a V-shaped structure, which subsequently gives rise to the rostrum (fig. 41, Pl. VI), and is therefore called the rostral groove. Immediately behind this groove is a second transverse furrow, which becomes the cervical groove of the adult. The gradual infolding of the ectoderm on each side of the rostral rudiment gives rise to the pedunculated condition later attained by the paired eyes (figs. 42 and 43, Pl. VI). The infolding takes place slowly, and movable articulation of the eyes is not established until eight weeks after hatching. The shrimp is then 4·6 mm. long, and, since escaping from the egg, has undergone at least two ecdyses.

A specimen which hatched in the laboratory on 18th July, 1934, and measured 2·70 mm. long, underwent an ecdysis on the 10th August, 1934, and then measured 3·25 mm. long. Its eyes were still sessile. The specimen was kept alive until 20th August, 1934, when it died, its length being 3·60 mm. All specimens under 4·6 mm. long collected from the mountain streams have sessile eyes.

The rudimentary median eye is still present, situated in front of the head, between and slightly above the basal joints of the antennules. It soon degenerates, and has almost disappeared in specimens 4·0 mm. long.

The four-celled sense-organ on the dorsal surface in front of the cervical groove does not appear until the animal is nearly 5·0 mm. long.

The number of trunk-somites is the same as in the adult, and on the dorsal side there is no indication of the anterior limit of the first thoracic somite. The distance of the cervical groove from the front edge of the second thoracic somite is relatively much greater than in the mature animal. The lateral extensions of the groove run vertically, instead of obliquely, down each side, and end just behind the mandibles. The horizontal groove running backward from the cervical groove on each side is present, but not very pronounced. There is little indication that the sixth abdominal segment is made up of two fused somites.

The telson (fig. 44, Pl. VII) is divided by a deep notch into two lobes, each of which ends in a fringe of six short setae. As the animal grows the notch becomes smaller, and disappears when the shrimp is about 5·3 mm. long.

The mandibles (fig. 39, Pl. VI), maxillules (fig. 47, Pl. VII), and maxillae (fig. 46, Pl. VII) differ very little from those of the adult. The thoracic limbs are also like those of the mature animal (fig. 38, Pl. VI). The first five pairs of abdominal appendages, however, consist only of the protopodite with a six-jointed exopodite (fig. 45,

Pl. VII). The small flabellate endopodite of the first four abdominal limbs does not appear until the animal is 7·0 mm. long. The uropods have the same form as in the adult.

External differences between the sexes do not become apparent until about twenty weeks after hatching. Indications of the development of the copulatory styles in the male are first visible in specimens 10·0 mm. long. In such specimens the endopodites of the first two pairs of abdominal limbs are distinctly elongated and narrow. The serrated spines on the basal part of the inner flagellum of the antennules in the male are not evident until the shrimp is 16·0 mm. long. The first spine to be developed is a long prolateral spine on the sixth segment of the flagellum.

In the female the first external sexual character to appear is the conical papilla situated between the last pair of thoracic limbs. This papilla makes its earliest appearance in specimens about 12 mm. long, but the opening of the spermatheca upon it is not developed until a later stage.

Development of Organs

Further Development of the Mesoderm

When differentiation of the germ-band is completed the mesodermal cells underly it. These cells now constitute the naupliar mesoderm, and are arranged in longitudinal strands below the rudiments of the naupliar appendages (fig. 49, Pl. VII). The posterior ends of the strands lie at the sides of the proctodaeum. A few mesoderm cells are also found in front of the stomodaeum, below the future position of the labrum. At this stage all the cells of the embryo are still laden with yolk-granules. As development proceeds some mesoderm cells and many endoderm cells undergo cytolysis, giving rise to numerous chromatin granules, which become scattered among the yolk-spherules.

Shortly before the appearance of the caudal papilla, the naupliar mesoderm cells at the sides of the proctodaeum grow larger, and their yolk disappears (fig. 50, Pl. VIII). As the stomodaeal invagination is drawn forward (see below) these cells move into position, forming a curved row in front of, and partly surrounding, the proctodaeum. These cells form the mesodermal teloblasts, and give rise to descendants from which the mesodermal somites of the post-mandibular trunk-region are derived (figs. 51 and 52, Pl. VIII).

Much of the naupliar mesoderm retains its yolk until after the embryo has hatched.

The mesodermal teloblasts form an incomplete ring of eight cells (fig. 54, Pl. VIII). Two of the cells are situated one on each side of the mid-ventral line and between the median ectodermal teloblast and the proctodaeum. The remaining six mesodermal teloblasts are situated three on each side of the proctodaeum and towards the

dorsal side. From these six teloblasts the dorsal mesoderm of the trunk somites is formed, while the two ventral teloblasts give rise to the ventral mesoderm (fig. 55, Pl. IX).

The descendants of the mesodermal teloblasts form paired blocks of mesoderm in each trunk segment from the maxillulary segment to the sixth abdominal segment inclusive. As the embryo lengthens, the pressure of the yolk-sac forces the mesodermal blocks to assume a more or less triangular shape in cross-section, and to occupy a position dorso-lateral to the nerve-cord. From its earliest formation each mesodermal somite is divisible into dorsal and ventral portions. The dorsal part of each mesodermal somite grows upward between the yolk-sac and the ectoderm. From this dorsal mesoderm are derived the dorsal vessel, pericardial floor, dorsal longitudinal muscles, and most of the mesodermal investment of the mid-gut.

The ventral part of the mesodermal somites gives rise to the ventral longitudinal muscles and the musculature of the trunk appendages.

The naupliar mesoderm extends beyond the head lobes and in front of the yolk-sac (fig. 64, Pl. XI). Here it constitutes the preantennulary mesoderm. As the embryo lengthens, some of the posterior cells of the naupliar mesoderm spread backwards (or are forced backwards by the elongating yolk-sac), and lie in the trunk segments below and at the sides of the yolk-sac (fig. 65, Pl. XI). In the posterior segments, where the yolk-sac does not press so closely against the dorsal ectoderm, some of these cells lie above it. In this position they become enclosed by the up-growing mesodermal somites, and later are found in both the cardiac and pericardial cavities (fig. 56, Pl. IX). Here and elsewhere many of them lose their yolk granules and become blood corpuscles. However, some of those lying below and at the sides of the yolk-sac become applied to it, and give rise to part of the muscular investment of the mid-gut.

The mesodermal investment of the stomodaeum is derived from the preantennulary mesoderm. Owing to the large quantity of yolk present in the embryonic tissues, I have not been able to recognize with certainty the early formation of a pair of preantennulary mesodermal somites. However, in transverse sections of a newly hatched embryo there is on each side of the stomodaeum a distinct cavity in the mesoderm. This cavity corresponds very closely with the preantennulary coelomic space of *Nebalia* (see Manton, 1934, Fig. 23, f. 1).

As mentioned above, part of the mesodermal investment of the mid-gut is formed from naupliar mesoderm that has spread backwards into the trunk. The larger portion, however, is derived from the dorsal mesoderm of the somites. As the trunk segments are formed, cells from the dorsal mesoderm grow inwards over the dorsal side of the yolk-sac, and then spread downwards to the ventral

side, forming a delicate circular band surrounding the gut. During embryonic life the yolk-sac is of such wide diameter, even in the abdominal region, that complete investment by the mesoderm is not effected until after hatching. Complete investment occurs first at the junction of the mid-gut and proctodaeum, then in the preceding abdominal segments in turn from behind forwards; but even in a newly hatched specimen it is not well defined further forward than the fourth abdominal segment.

Heart and Coelomic Cavities

The development of the dorsal vessel is most clearly observed in the posterior segments, where the yolk-sac does not press so closely against the dorsal ectoderm. As each segment is formed some of the cells in the dorsal part of the mesodermal somites become oriented lengthwise to form the dorsal longitudinal muscles, others creep upward between these muscles and the yolk-sac, finally reaching the dorsal ectoderm (fig. 55, Pl. IX). The mesoderm thus growing upward on either side encloses a space above the yolk-sac. This space becomes the cavity of the dorsal vessel, and the mesodermal upgrowths its lateral walls. Part of the dorsal mesoderm also grows inward over the yolk-sac, the portions from either side meeting near the mid-line to form the floor of the dorsal vessel. In all segments the lateral walls are formed before the floor. As the yolk-sac shrinks in size, the mesoderm between it and the dorsal longitudinal muscles is pulled inward, forming a space on each side between the lateral wall of the dorsal vessel and the ectoderm. This space is the pericardial cavity, and its floor the pericardial floor (fig. 56, Pl. IX). The roof of the dorsal vessel is formed by the upper parts of the lateral walls growing inwards and meeting in the mid-line below the dorsal ectoderm. In all segments the roof is formed after the walls and the floor. In front of the second thoracic segment in a newly hatched embryo the dorsal vessel expands to form a wide cavity, roofed over by the dorsal organ, and extending forward as far as the cervical groove (fig. 57, Pl. IX).

The mesodermal roof of this cavity is not formed until some time after the dorsal organ has disappeared and the shrimp is about 4·0 mm. long.

Coelomic cavities develop early in the ventral part of the pericardial floor (fig. 59, Pl. X). During embryonic life they are compressed in most of the segments by the yolk-sac. They persist, however, until the genital rudiments are formed, and in the newly-hatched embryo they are present in the six abdominal segments, and vestiges of them still appear in the posterior thoracic segments. The coelomic space in the preantennulary mesoderm at the sides of the stomodaeum has already been mentioned.

During the last few weeks of embryonic life the anterior aorta and lateral cephalic arteries develop *in situ* as haemocoelic spaces in the preantennulary mesoderm (fig. 60, Pl. X). The mesoderm, which was originally the anterior part of the naupliar mesoderm, now lies between the yolk-sac and the brain. It is still richly supplied with yolk granules. The haemocoelic spaces extend upwards and backwards, to unite and open into the wide anterior part of the dorsal vessel underlying the dorsal organ.

In the abdominal region behind the first abdominal segment, the wall of the dorsal vessel remains thin and its lumen narrow, but in the thoracic segments the vessel becomes wider and its walls thicker, thus forming the heart (fig. 58, Pl. IX).

The sternal artery, the ventral artery, and the subneural vessel are not formed during embryonic life, and their development after hatching has not been followed.

Alimentary Canal

(*a*) *Fore-gut.* As mentioned above, the crescent-shaped ectodermal invagination giving rise to the stomodaeum is formed shortly after the differentiation of the germinal disk and before the rudiments of the naupliar appendages appear. The posterior margin of the mouth is at first higher than the anterior margin, and the invagination extends backwards in the median line almost to the proctodaeum (fig. 61, Pl. X). As the labrum is formed and begins to project over the mouth, the stomodaeal invagination becomes bent, and its inner end is drawn forward until it lies between the antero-ventral portion of the yolk-sac and the brain (figs. 62-65, Pls. X and XI). Here it soon indents the yolk-sac. The yolk-globules in the ectodermal cells forming the stomodaeal wall are gradually absorbed. By the seventeenth week the cells toward the inner end of the stomodaeum begin to form a thick columnar epithelium, which gradually extends to the outer end. However, where the stomodaeum is in contact with the yolk-sac, the cells do not form a columnar epithelium, but remain thin and flat. The thickening of the wall is accompanied by an increase in the lumen of the stomodaeum at its inner end, to form the cavity of the future cardiac division of the stomach. At the twenty-fifth week the cavity is partly filled by four longitudinal ridge-like thickenings, which project inwards from its wall, one from the dorsal surface, one from the ventral surface, and one from each side. After hatching, and when the shrimp has reached a length of 3·4 mm., the dorsal ridge is differentiated to form the median setose prominence and the two dorso-lateral ridges of the adult. The two lateral ridges in the embryo give rise to the two ventro-lateral ridges in the adult, while the ventral ridge in the embryo forms the median ventral ridge in the mature animal.

(*b*) *Mid-gut.* At the close of gastrulation the blastocoel, as mentioned above, is filled with a mass of endodermal yolk-cells, together with the primary mesoderm (figs. 48 and 49, Pl. VII). The delicate membrane surrounding each yolk-cell is discernible only under the most favourable conditions of fixation. If Carnoy's fluid be allowed to act too long the membrane is destroyed.

With the formation of the germinal disk, many of the yolk-cells on the ventral side of the endodermal mass undergo cytolysis, their nuclei disintegrating into numerous deeply-staining granules, which are scattered among the yolk-globules and finally absorbed (fig. 49, Pl. VII). Cytolysis continues until about the eighteenth week, and then diminishes in activity. During the remaining part of embryonic life, however, isolated yolk-cells may be found in which the nuclei are in process of breaking up.

The outermost cells of the endodermal mass constitute the wall of the yolk-sac, their outer ends forming the yolk-sac membrane (figs. 64-66, Pl. XI). They surround an inner core of yolk-cells, which occupy the space destined to become the lumen of the mid-gut. These inner yolk-cells seem to fuse with each other and sometimes with the inner ends of the outer cells. They are gradually absorbed as development proceeds.

As the embryo lengthens the yolk-sac extends backwards into the caudal papilla (figs. 64-66, Pl. XI). It tapers gradually from the anterior to the posterior end, there being no sudden diminution in diameter marking off a cephalo-thoracic part from an abdominal part. The cells throughout its whole length have the nature of yolk-cells, and not until just before hatching do any of them become converted into epithelial cells. Even the cells opposite the stomodaeum and proctodaeum retain the nature of yolk-cells, and do not form epithelial plates at any stage.

As the yolk in the yolk-cells is absorbed the yolk-sac shrinks in diameter, and its cells become smaller. The conversion of the yolk-cells into the epithelial cells of the mid-gut commences during the last week of embryonic life. It first occurs in the cells forming the dorsal wall of the now elongated yolk-sac, immediately in front of the proctodaeum. It then spreads round to the ventral side, advancing forward at the same time (fig. 66, Pl. XI).

Immediately after hatching, the yolk-cells at the anterior end of the yolk-sac begin to assume an epithelial nature. The indenting of the yolk-sac by the stomodaeum has helped to form a median dorsal pouch overlying the future cardiac division of the stomach. The yolk-cells forming the wall of this pouch are the first anterior cells of the yolk-sac to be converted into epithelial cells. The pouch becomes the anterior diverticulum of the mid-gut.

When the embryo hatches, the lumen of the developing mid-gut behind the fifth thoracic somite is almost empty, but in front it still contains much unabsorbed yolk. This, however, rapidly disappears, and by the time the shrimp is 2·9 mm. long communication of the mid-gut with the stomodaeum and proctodaeum is established. This is brought about by the absorption of the yolk-cells and the breaking down of the thin ectodermal septa at the points of contact.

When *Anaspides* is 3·0 mm. long all the cells forming the wall of the lengthy yolk-sac have become converted into the epithelial cells of the mid-gut. The anterior diverticulum is now well developed, and resembles that of the adult.

The rudiment of the second diverticulum of the mid-gut appears as a dorsal thickening of the gut epithelium in the first abdominal segment when the shrimp is 3·5 mm. long. The diverticulum, however, does not attain its pouch-like form until the animal is about 5·5 mm. long.

The third diverticulum is first apparent as a dorsal thickening of the mid-gut epithelium in the fifth abdominal segment of specimens about 4·0 mm. long. It develops very slowly, and does not become pouch-like until *Anaspides* reaches a length of nearly 14·0 mm.

The endodermal yolk-cells give rise not only to the mid-gut and its three diverticula, but also to the lobes of the liver. The origin of these lobes is described below.

(*c*) *Hind-gut.* A second invagination of the ectoderm to form the hind-gut does not appear to take place. The cells immediately within the lip of the blastopore form the wall of the proctodaeum, and the blastopore becomes the anal aperture. At a later stage this opening is seen to occupy a postero-dorsal position in the notch between the lobes of the caudal papilla. At first the proctodaeum is very short, and the cells forming its wall are rich in yolk-granules. At the seventeenth week the yolk has been absorbed and the cells have become epithelial. The length of the proctodaeum now increases, and its aperture moves from its postero-dorsal position into the postero-ventral position occupied by the anal aperture of the adult. The hind-gut is well developed before hatching, but, as previously mentioned, it does not communicate with the mid-gut until some time after the embryo has escaped from the egg.

The Liver

The liver-lobes are developed from the endodermal yolk-sac. The posterior pair of lobes are the first to be formed. They appear about the nineteenth week as a pair of lateral outgrowths, one on each side of the yolk-sac in the maxillary segment. The outgrowths

soon grow backwards, becoming elongated and finger-like. The wall of each lobe consists of endodermal cells similar to those forming the wall of the yolk-sac. A cap of mesodermal cells covers the end of the lobes (fig. 69, Pl. XII). As the lobes lengthen their cells gradually become epithelial. The conversion takes place first at the posterior end, and then extends towards the front. The lumen of the lobes is filled with yolk-globules, which are slowly absorbed. On hatching, the posterior hepatic lobes have grown backward as far as the second thoracic segment.

Up to the twenty-second week of embryonic life the front of the yolk-sac is rounded. When, however, the dorso-ventral mandibular muscles are formed, they press against the front of the yolk-sac, forming a vertical groove or indentation on each side. The front of the sac is thus divided into a median lobe and two antero-lateral lobes. The median lobe eventually forms the anterior diverticulum of the mid-gut. The two antero-lateral lobes give rise to lobes of the liver. The apex of each antero-lateral lobe of the yolk-sac is attached to the dorsal ectoderm by a short ligament. Immediately behind the point of attachment of the ligament each lobe grows backwards as a finger-like outgrowth to form the anterior hepatic diverticula. These hepatic diverticula are anterior only in the sense that they arise from the antero-lateral lobes of the yolk-sac. They do not project towards the front, but grow towards the posterior end of the body (fig. 70, Pl. XII). They are soon followed by another pair of hepatic lobes, which arise in the same manner immediately behind the point of attachment of the dorsal ligament (fig. 71, Pl. XII). The animal usually hatches with two pairs of liver lobes, but in some cases the rudiments of a third pair are also well established. By the time the shrimp is 7·0 mm. long it has seven pairs of hepatic lobes, and when adult about fifteen pairs.

Genital Rudiment

The genital rudiment appears towards the end of embryonic life. Shortly before the embryo hatches germ-cells, having a large oval nucleus with finely granular chromatin and conspicuous nucleoli, are found on the floor of the coelomic pouches in the first and second thoracic somites. Similar germ-cells appear in succession in the coelomic pouches of the segments behind the second thoracic somite (figs. 72-73, Pl. XII). By the time the embryo hatches these segmental genital rudiments occur in the eight somites of the thorax. Soon after hatching they appear in succession in the six abdominal segments.

As each rudiment is established it grows in length by division of the germ-cells. When the animal is 6·0 mm. long the rudiments in the separate segments have united to form the long gonad of the

adult. Testes and ovary develop in a similar manner. The gonoducts do not appear until much later in the life of the shrimp, and no attempt was made to follow their development.

Whether the genital rudiments in the separate somites are derived from a primary germ-cell, formed in the early stages of the segmentation of the oösperm, could not be determined. They appear, however, to be derived from the mesodermal cells forming the walls of the coelomic pouches.

Nervous System and Sense Organs

Little need be said in regard to the nervous system, which arises in much the same way as in other Crustacea. The development of the protocerebrum, with its central cell surrounded by concentric rows of other cells (fig. 68, Pl. XI), may be compared with the corresponding structure in the egg-nauplius of *Astacus* (Reichenbach, 1886, p. 29).

The median eye at its earliest appearance seems to have a paired origin. It develops from a group of cells lying between the head-lobes (fig. 67, Pl. XI). Two cells in this group, one on each side of the mid-line, give rise to pigment granules. These granules eventually collect round yolk-spheres in the cells. As the yolk is used up the pigment granules form a dense pyriform black mass. The whole structure is very rudimentary, but, like the median eye of some of the lower Decapoda, it persists as a vestigial organ for some time after hatching. In having a paired origin, the median eye of *Anaspides* resembles that of *Artemia* (Moroff, 1912, p. 18). Yolk-granules are found in the plasma of the cells forming the eye in both species. In fact, Moroff (1912, p. 17) states in reference to *Artemia* that 'der ganze Embryo ist von grösseren und kleineren Dotterkugeln erfüllt, die gleichmässig um die Zellkerne verteilt sind.' This condition is not unlike that of the egg-nauplius of *Anaspides*.

The lateral eyes in their development resemble those of *Branchipus* (Claus, 1886, p. 60). During embryonic life, and for several weeks after hatching, they are sessile. The ectoderm gradually grows in under the eyes, both from the front and the back, but it is not until the shrimp is over 4 mm. long that the pedunculated condition is attained (fig. 43, Pl. VI). Hanström (1934, p. 36) has recently shown that the paired eyes resemble those of *Mysis* in their finer structure.

The statocyst in the basal segment of the antennulary peduncle develops as an invagination of the dorsal ectodermal. The club-shaped rods arise from the ectodermal cells forming the outer wall of the invagination. In a newly-hatched embryo five rods are usually present.

The four-celled sense organ, which develops in front of the cervical groove, and which has been compared with a similar organ in the Phyllopoda both by Calman (1896, p. 787) and by Hanström (1934, p. 52), does not appear until *Anaspides* is about 4 mm. long.

In the development of the nerve cord a very distinct ganglion is formed behind that of the sixth abdominal segment. This seventh abdominal ganglion is well defined about the twenty-sixth week of embryonic life (fig. 74, Pl. XIII). As the embryo lengthens the sixth abdominal ganglion is pulled away from the fifth, leaving an intervening space in which yolk-granules collect (fig. 75, Pl. XIII). At the same time the tension on the nerve cord appears to drag the seventh abdominal ganglion into a position partly overlying the sixth. After hatching the intersegmental bar between the sixth and seventh abdominal ganglia becomes very thin (fig. 76, Pl. XIII). It finally breaks down and disappears, and the two ganglia fuse.

Musculature and Endoskeleton

A detailed examination of the development of the musculature and endoskeleton has not been made. The origin and development of the trunk musculature and gut musculature have been briefly mentioned in other parts of this paper. The endoskeleton of *Anaspides*, like that of *Nebalia* (Manton, 1934, p. 202), is formed from intersegmental ectodermal bars which arise from lateral and ventral intuckings. These bars are strongly developed in the mandibular, maxillulary, and maxillary segments. The rudiment of the mandibular bar appears at about the fifteenth week. The other bars are developed in sequence. The greater part of the endoskeleton in the region of the mouth is formed from the first three post-oral bars. These bars are all nucleated, and remain nucleated even in the adult.

A critical study of the endoskeletons of *Anaspides*, *Paranaspides*, *Nebalia*, *Hemimysis*, and *Nyctiphanes* has already been made by Dr. Manton. As a result of this study the close similarity existing between the endophragmal structures of the Syncarida and Leptostraca has been demonstrated (Manton, 1934, p. 220). This similarity is further emphasized by the close agreement in the mode of development.

Maxillary Gland

The rudiment of the maxillary gland appears about the middle of embryonic life. Mesoderm cells begin to form a compact group on each side of the nerve cord in the maxillary somite (fig. 77, Pl. XIII). Yolk granules in the vicinity of these cells are rapidly

absorbed. At first no definite arrangement of the cells can be observed, but as development proceeds the nuclei of the cells become oriented to form more or less regular transverse rows, giving rise to the tubules of the gland (fig. 78, Pl. XIII). The end-sac of the gland soon appears as a large cavity in the group of mesoderm cells. From the gland a duct leads downward in front of the large transverse adductor muscle in the basal segment of the maxilla, curves under the muscle, and eventually opens near the centre of the posterior surface of the appendage (fig. 79, Pl. XIII). Smith (1909, p. 537), in describing the adult animal, states that the duct 'opens by a pore on the external border of the appendage'. This, however, is not the case. Sections through the maxilla of a mature specimen show quite clearly that the duct opens by a pore on the posterior surface. Just before hatching a small invagination of the ectoderm occurs at this spot, and communicates with the duct from the gland. With the exception of this ectodermal lining of the aperture, the whole of the gland and its duct are derived from mesoderm, and are fully developed on hatching (fig. 80, Pl. XIII).

Median Dorsal Organ

The median dorsal organ is not to be confused with the four-celled sense organ, which, in young adults, appears in a median position in front of the cervical groove, and which Calman (1909, p. 164) states 'may be comparable to an obscure "dorsal organ"'. The four-celled sense organ does not develop for some time after hatching, whereas the median dorsal organ appears at about the twenty-first week of embryonic life. It consists of a marked thickening of the dorsal ectoderm, extending from behind the eyes to the front of the second thoracic segment. The ectodermal cells composing it are long and columnar, but become smaller round the margin of the organ. At first the cells contain yolk-globules, and their boundaries are distinct. As development proceeds the cells degenerate, their walls break down, and in some cells the nuclei disintegrate. In the living embryo the organ has a yellowish colour, and is quite conspicuous. It persists for some time after hatching, but has disappeared by the time the animal is 3·5 mm. long.

Habits of Anaspides

The newly-hatched animal moves about actively, sometimes crawling over rocks and débris at the bottom of the water, at other times swimming up to the surface. If it is gently touched when swimming, it will often sink to the bottom, and, lying on its back with its body stretched out in a passive state, remain as if dead for several seconds. This death-feigning habit occurs only in the newly-hatched animal,

and is not exhibited by the adult. Herrick (1895, p. 184) has described a similar peculiarity in young specimens of *Homarus americanus*.

Smith (1909, p. 546) states that *Anaspides* 'will occasionally rise to the surface of the water and turn over on its back in the manner of a Phyllopod'. I am able definitely to confirm the accuracy of this observation. In quiet pools at the side of the mountain stream, where the water is not disturbed by ripples, *Anaspides* often comes to the surface, turns over on its back, and, moving about on the underside of the surface-film, searches for food among the small particles which are floating there. The habit is observed more frequently in young than in adult animals, since the weight of the latter is not so easily supported by the surface tension of the water. Small specimens (5·0 mm. long) not only move about on the under side of the surface-film, but also rest there in an inverted position. I have observed specimens resting in this way for over ten minutes.

The animal does not commence feeding until communication between fore-gut, mid-gut, and hind-gut is established. This occurs a few days after hatching. When the young shrimp begins feeding a long cylindrical tube, about equal in length to the mid-gut, is extruded from the anal aperture, and is carried about for some time before being expelled. This tube is probably composed of the inner ends of the yolk-cells forming the wall of the mid-gut, and is cast off when these cells become epithelial. It is certainly not the ectodermal lining of the hind-gut, which is comparatively short, and is cast off during ecdysis.

Mating has not been observed. However, male specimens in the creek are sometimes seen employing the armed basal joint of the inner antennulary flagellum in an attempt to seize hold of the base of one of the antennules in a female.

Discussion

Segmentation of the Egg

The egg of *Anaspides*, like that of *Lucifer* (Brooks, 1882, p. 64), exhibits complete and equal cleavage. In both a large segmentation cavity is formed, and into this cavity, shortly after the sixteen-celled stage has been reached, a blastomere moves. In *Lucifer* this blastomere divides as it passes inwards. In *Anaspides* it divides after it has entered, and at the same time other blastomeres appear to pass inwards. There is then formed in each case a deep invagination-gastrula with a primitive archenteric cavity. At first all the cells are equally provided with yolk, but at the commencement of invagination in *Lucifer* the yolk has largely disappeared from all

cells except those in the segmentation cavity. The cells of *Anaspides* are laden with yolk granules up to a late stage in development.

Brooks (1880, p. 563) originally regarded the cells lying in the segmentation cavity of *Lucifer* as mesoderm cells. In a later publication (Brooks, 1882, p. 70) he abandoned this opinion in favour of the view that they were yolk pyramids, because they were charged with yolk granules. Unfortunately the subsequent history of these cells was not followed. The corresponding cells in *Anaspides* constitute the primary mesoderm.

Ectodermal and Mesodermal Teloblasts

The trunk region of *Anaspides*, like that of the Leptostraca Peracarida, and Decapoda, is formed from rows of ectodermal and mesodermal teloblasts developed immediately in front of the blastopore. The teloblastic regions of *Hemimysis* and *Nebalia* have been described in detail by Dr. Manton (1928, p. 370; and 1934, p. 178). *Anaspides* agrees with both these forms in possessing an ectodermal teloblast in the mid-ventral line. It has been suggested by Dr. Manton (1934, p. 212) that 'possibly the Decapoda differ from the Peracarida in possessing no mid-ventral ectodermal teloblast'. Sollaud (1923, p. 93) gives a figure of the teloblastic region of *Leander* in which a mid-ventral teloblast is clearly indicated. It is highly probable that a mid-ventral teloblast will be found in all those Crustacea in which teloblastic development of the trunk occurs.

In *Anaspides*, *Nebalia*, and the *Decapoda* the ectodermal teloblasts form a complete ring around the caudal papilla. In both *Anaspides* and *Nebalia* the ring consists of 19 teloblasts.

Four pairs of mesodermal teloblasts are present in *Anaspides*, *Nebalia*, and *Hemimysis*. Patten (1890, p. 371) records a similar number in *Cymothoa*.

External Form

In the development of the external form of the body, and in the order in which the appendages appear, *Anaspides* resembles the Leptostraca and Mysidacea. Owing, however, to the much later rupture of the egg-envelopes, the ventral flexure of the body, like that in the Decapoda, is retained until the embryo is hatched. The strong development of both rami of the second antenna during early embryonic life, followed by the gradual degeneration of the exopodite, recalls the similar changes through which this appendage passes in the larval life of certain Decapoda. Thus in the protozooea of *Penaeus* the second antenna has a three-jointed endopodite and a four-jointed exopodite, but by the time the mysis stage is reached, the exopodite has degenerated into a scale (Müller, 1863, p. 8; and Claus, 1876, p. 11).

In the newly-hatched *Anaspides* the notched telson, with its six pairs of setae, bears some resemblance to that of a protozooea, and perhaps indicates that the ancestors of *Anaspides* passed through some such larval stage.

The Heart and Coelomic Sacs

In its main features the development of the heart resembles that of *Hemimysis* and *Nebalia*. In *Nebalia*, however, the ventral wall of the dorsal vessel appears first, and later the sides and roof, whereas in *Hemimysis* and *Anaspides* the lateral walls are first formed, and then the floor, followed by the roof. As in *Hemimysis*, the pericardial floor is formed from the dorsal mesoderm as it grows upward, and not, as in *Estheria*, by a later downward growth of the dorsal mesoderm.

Coelomic sacs have been demonstrated in *Estheria* (Cannon, 1924, p. 425), *Chirocephalus* (Cannon, 1926, p. 402), *Hemimysis* (Manton, 1928, p. 397), and *Nebalia* (Manton, 1934, p. 227). In *Anaspides*, as in *Hemimysis* and *Chirocephalus*, the coelomic sacs are early compressed between the yolk-sac and developing pericardium, but while in *Chirocephalus* they are soon obliterated, in *Anaspides* and *Hemimysis* they persist throughout embryonic life. In *Anaspides* they are large, and most clearly seen in the newly-hatched embryo, when the yolk-sac is somewhat shrunken, and the trunk, released from its flexed condition, has straightened out. The large size of these coelomic sacs is a primitive character comparable to that in *Estheria* (Cannon, 1924, p. 395).

Alimentary Canal

The position of the anus relative to the blastopore has been reported differently by different authors (see Korschelt and Heider, 1899, p. 173). As pointed out by Dr. Manton (1928, p. 431), it is not always possible to determine with accuracy the relative positions of these two structures, 'since the blastopore may be a vague area and is obliterated before the anus appears'. In *Anaspides*, however, the blastopore is a very definite aperture leading into an archenteric cavity. Although the lumen of this cavity is eventually rendered imperceptible by the crowding together of the endoderm cells, the blastopore is always well defined. It becomes the anal aperture, and the cells immediately within its lip give rise to the proctodaeum.

A critical account of the development of the mid-gut in Crustacea has recently been given (see Manton, 1928, pp. 433-436). A repetition of this account is not needed, but it may be said that generally in the centrolecithal eggs of Crustacea certain cells pass inward from the blastoporal area, absorb yolk, and form yolk-cells, which give rise partly or entirely to the mid-gut. In *Hemimysis* these yolk-cells

spread around the yolk, and form the yolk-sac. Later they are transformed into the epithelial cells of the mid-gut. In *Nebalia* the yolk-sac is at first composed of yolk-cells connected posteriorly with an epithelial endodermal plate. By proliferation of its own cells and transformation of the yolk-cells along its margin, this plate gradually extends forward until all the yolk is enclosed in an epithelial yolk-sac. A similar process probably takes place in *Leander* (see Sollaud, 1923, p. 162). In *Anaspides*, as in *Cetochilus* (Grobben, 1881, p. 243), the cells forming the archenteric invagination are heavily laden with yolk, and are virtually yolk-cells. They give rise directly to the yolk-sac, and later to the mid-gut. In *Cetochilus*, however, the lumen of the invagination persists, whereas in *Anaspides* it is obliterated by some of the yolk-cells crowding into its centre and forming a central core. This condition, although originating in a different way, is similar to that appearing in *Hemimysis* after the yolk-cells have formed the secondary yolk-pyramids. The outer cells of the endodermal mass in *Anaspides* form the yolk-sac, and correspond to the secondary yolk-pyramids of *Hemimysis*, while the inner core of cells in *Anaspides* corresponds to the central core of yolk in *Hemimysis*. In both, the cells forming the yolk-sac become transformed into the epithelium of the mid-gut, the transformation taking place first opposite the stomodaeum and proctodaeum, but somewhat earlier in *Hemimysis* than in *Anaspides*.

Cytolysis occurs only to a small extent in the yolk-cells of *Hemimysis*, but largely in those of *Anaspides*. Degeneration of the yolk-cells occurs extensively in many Decapoda, and has been recorded in *Alpheus* (see Brooks and Herrick, 1892, p. 425), *Homarus* (see Herrick, 1895, p. 211), and *Leander* (see Sollaud, 1923, p. 83).

The Liver

The liver, or hepatopancreas, of the Crustacea does not always develop in the same way. In *Hemimysis* the posterior liver-lobes 'arise independently of the yolk-sac from a pair of epithelial plates of mesoderm which grow round the yolk-sac' (see Manton, 1928, p. 433). In *Anaspides* these lobes are formed as out-pushings of the yolk-sac, which open latero-ventrally into the mid-gut immediately behind the stomodaeum. Sollaud (1923, p. 171) has described a somewhat similar origin for the liver-lobes of *Leander*. The hepatic diverticula of *Nebalia* also develop as outgrowths of the endodermal yolk-sac (see Manton, 1934, p. 183).

The anterior hepatic lobes of *Anaspides* arise in much the same way as those of *Nebalia*, except that the yolk-sac is indented not by a single median depression but by two vertical furrows, one on each side of the anterior mid-gut diverticulum. Moreover, the anterior lobes do not extend forward into the head, but curve over and grow

towards the tail, the primary pair of lobes being soon followed by a second pair, which develop at the point where the first pair bend over.

Maxillary Gland

The maxillary gland of *Anaspides*, like that of *Estheria* (Cannon, 1924, p. 424) and *Chirocephalus* (Cannon, 1926, p. 406), is of mesodermal origin. As in *Chirocephalus*, the end-sac and primordia of the coils appear early. The close similarity in the adult pattern of the maxillary glands of *Chirocephalus* and *Anaspides* has already been demonstrated (see Cannon and Manton, 1927, p. 445). It is not surprising, therefore, to find a similarity in their mode of development.

Genital Rudiment

In *Anaspides*, as in *Nebalia*, the gonads arise in the walls of the coelomic pouches at a late stage in embryonic life. Dr. Manton has already pointed out that, in this respect, *Nebalia* resembles the Annelids, *Peripatus* (Sedgwick, 1887, p. 467) and *Scolopendra* (Heymons, 1901, p. 1). A similar origin of the gonads is also found in spiders, *Limulus*, and other Arthropoda.

Hatching Process and Habits

There is a remarkable similarity in the hatching of *Anaspides* and that of certain Cladocera. The winter-egg of *Daphnia* has no chorion, but is surrounded by a primary yolk membrane or 'Dotterhaut', which corresponds to the vitelline membrane in the egg of *Anaspides*. Below this membrane, during the development of both *Daphnia* and *Anaspides*, two larval integuments are formed. The first appears at the egg-nauplius stage. It becomes strong, elastic, and semipermeable. The second appears somewhat later, and is consequently within the first. Now Volmer (1912, p. 646) has shown that the first larval integument is of the greatest importance in the hatching of *Daphnia*. By osmosis it absorbs water, and swells out like a balloon, bursting first the 'Dotterhaut,' and then the ephippium. In *Anaspides* it behaves in a similar manner, bursting first the vitelline membrane, then the chorion. In each case a long time elapses before the balloon-like structure breaks, liberating the embryo. During this time *Anaspides* throws off the second larval integument.

According to the observations of Spangenberg, quoted by Oehmichen (1921, p. 242), it appears that the larva of *Branchipus* is also surrounded by an expanded transparent investment during hatching.

Anaspides not only resembles the Cladocera in its method of hatching, but also in its habit, when young, of moving about in an inverted position on the under-side of the surface film in calm water. Wagler (1927, p. 353) gives a figure of *Scapholebris* in such a position.

The eggs of *Anaspides* laid during winter resemble the winter-eggs of the Cladocera in going through the early stages of segmentation soon after laying, and then entering upon a long period of dormancy.

Conclusions

From the above discussion it is clear that *Anaspides* shows in its development a close resemblance to the Leptostraca as exemplified by *Nebalia*, the main points of agreement being the following:

(1) The origin and number of ectodermal teloblasts.
(2) Presence of a mid-ventral ectodermal teloblast.
(3) Formation of a complete ring of nineteen ectodermal teloblasts around the caudal papilla.
(4) Presence of four pairs of mesodermal teloblasts.
(5) Irregular nature of the naupliar mesoderm.
(6) Development of the post-mandibular segments from before backwards.
(7) Origin of the liver lobes from the endodermal yolk-sac.
(8) Essential features of the development of the dorsal vessel.
(9) The late appearance of the genital rudiments in the coelomic pouches.
(10) Presence of a similar type of median dorsal organ, which eventually degenerates.
(11) Absence of a free-swimming larval stage.

In points (1), (2), (4), (5), (6), (8), (10), and (11), *Anaspides* and *Nebalia* both resemble the Peracarida.

Although in *Anaspides* the stages of development following differentiation of the germinal disk are mainly Malacostracan in character, the early stages, as in the case of *Lucifer*, bear some resemblance to those of certain Entomostraca. Thus the holoblastic segmentation, followed by the formation of a relatively large blastocoel, recalls the similar stages in the Copepod *Cetochilus*, and also in the Branchiopods *Branchipus* and *Bythotrephes*. The development of an invagination-gastrula, giving rise directly to the mid-gut, is a very primitive condition also seen in *Cetochilus*.

Anaspides also resembles the Branchiopoda in the following respects:

(1) Origin and development of the maxillary gland.
(2) Long persistence of yolk granules in the embryonic tissues.
(3) The prolonged dormancy of the embryo in winter eggs.
(4) The mode of hatching.
(5) The habit of moving about in an inverted position on the under-side of the surface-film in calm water.

SUMMARY

1. *Anaspides tasmaniae* Thomson lays its eggs singly on moss, bark, and other forest débris in the mountain tarns and streams of Tasmania.

2. Egg-laying goes on throughout the year, but is most active during October and November.

3. Eggs laid in the spring and summer hatch in about 32 to 35 weeks. Those laid in autumn and winter undergo the early stages of segmentation, and then become dormant until spring.

4. Hatching takes place in the winter months, June to October.

5. Segmentation is holoblastic, and a large blastocoel is developed.

6. The primary mesoderm is formed by migration of blastomeres into the blastocoel.

7. The formation of the primary mesoderm is followed by the development of a deep invagination-gastrula with a temporary archenteric cavity.

8. The invagination-gastrula gives rise directly to the endodermal yolk-sac, and later the mid-gut. Most of the endoderm cells do not become epithelial in nature until after hatching.

9. Marked cytolysis occurs in the endodermal cells, and also to some extent in the primary mesoderm.

10. A typical V-shaped germinal disk is formed, and gives rise to an egg-nauplius of the usual type. All the cells of the embryo at this stage are laden with yolk granules.

11. The caudal papilla is surrounded by a ring of nineteen ectodermal teloblasts, which give rise to all the post-mandibular segments of the trunk.

12. A mid-ventral ectodermal teloblast is present.

13. The naupliar mesoderm and four pairs of mesodermal teloblasts are derived from the primary mesoderm.

14. The mesodermal teloblasts form paired mesodermal somites, which give rise to the dorsal vessel, the pericardium, the longitudinal muscles of the trunk, the muscles of the post-mandibular appendages, and part of the gut musculature.

15. Coelomic cavities appear in the pericardial floor, and persist until after hatching.

16. The genital rudiments develop in the walls of the coelomic cavities towards the end of embryonic life.

17. The maxillary gland is of mesodermal origin, and appears at an early stage.

18. The liver lobes are formed as outpushings of the endodermal yolk-sac.

19. The presence of a rudimentary seventh abdominal segment, which becomes fused with the sixth, is indicated by the number of ganglia in the embryonic nerve cord.

20. A median dorsal organ is present, and persists for some time after hatching.

21. Yolk granules are found in the tissues of the embryo until a late stage of development.

22. The process of hatching resembles that of the Cladocera.

23. The newly-hatched *Anaspides* differs from the adult in having a rudimentary median eye, sessile paired eyes, no rostrum, a forked telson, no endopodites on any of the appendages of the first five abdominal segments, and no external sex organs.

24. The habits of the young *Anaspides* resemble those of certain Cladocera.

25. A comparison of the development of the Syncarid with that of the Leptostraca, Peracarida, Branchiopoda, and Copepoda is made.

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Plate 1

Fig. 1.—Eggs of *Anaspides tasmaniae* Thomson attached to a piece of bark from one of the boxes placed in the creek. × 10.

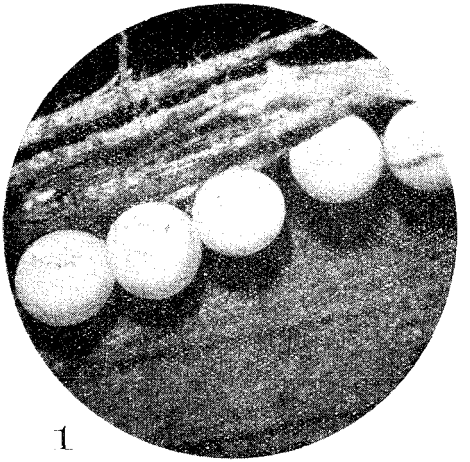
Fig. 2.—*Anaspides* surrounded by the distended first larval integument during the process of hatching. The broken chorion is seen at the left of the figure. The second larval integument is not yet cast off. × 10.

Fig. 3.—Male and female pronuclei in contact near the centre of the unsegmented egg. × 400.

Fig. 4.—Male and female pronuclei becoming rounded off preparatory to fusion. × 300.

Fig. 5.—Two-celled stage surrounded by the transparent chorion. × 40.

Fig. 6.—Two-celled stage surrounded by the chorion. The blastomeres almost separated by the first cleavage. × 40.



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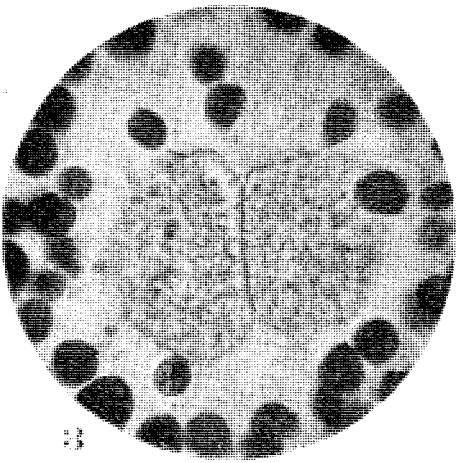

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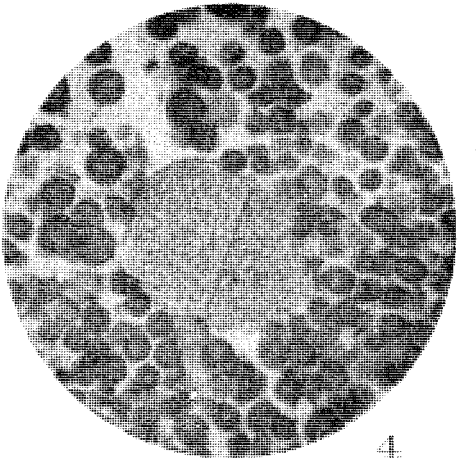

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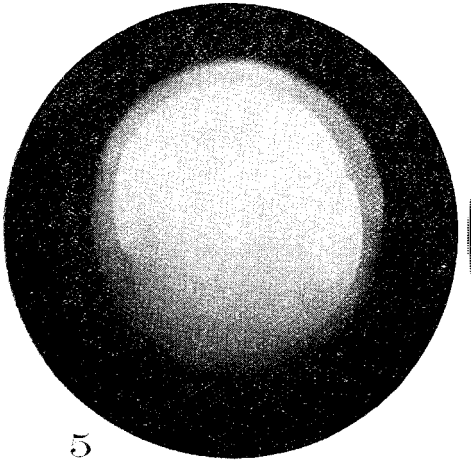

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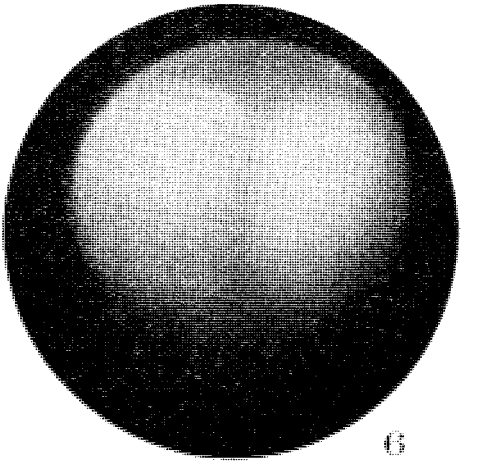

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PLATE II

Fig. 7.—Two-celled stage in which the two blastomeres have partially refused.

Fig. 8.—Section through the stage shown in fig. 7.

Fig. 9.—Four-celled stage.

Fig. 10.—Equatorial section through the four-celled stage.

Fig. 11.—Eight-celled stage.

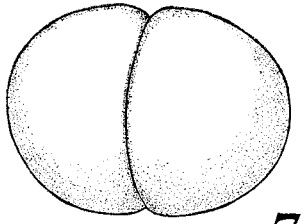
Fig. 12.—Sixteen-celled stage.

Fig. 13.—Section through an embryo immediately after the sixteen-celled stage, showing a blastomere entering the blastocoel.

Fig. 14.—Section through a slightly later stage than that shown in fig. 13. The blastomere is now in the blastocoel, and is undergoing mitosis to form the primary mesoderm.

Fig. 15.—Section through a stage more advanced than that shown in fig. 14. The blastocoel is much larger, and now contains a number of primary mesoderm cells.

Fig. 16.—Section through a stage just prior to gastrulation.



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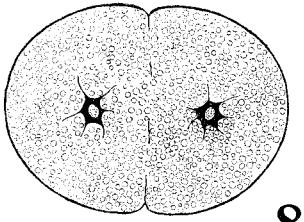

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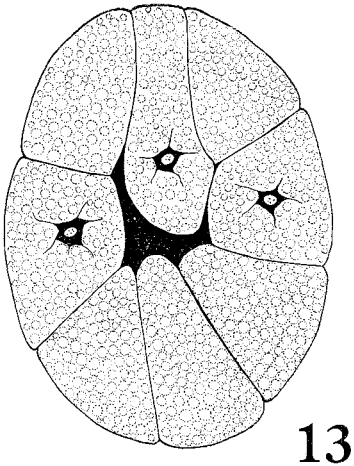

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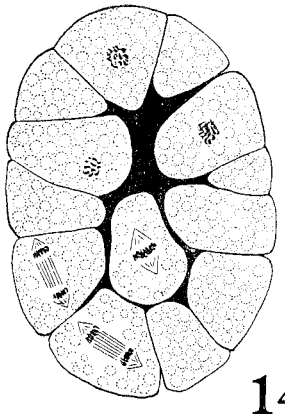

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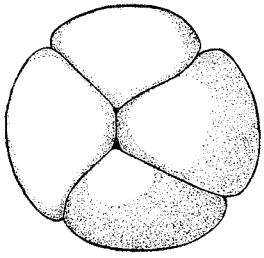

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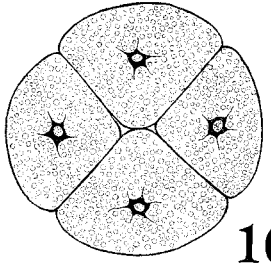

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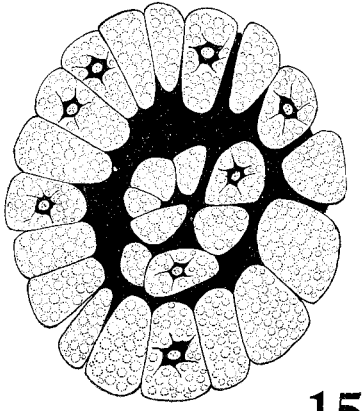

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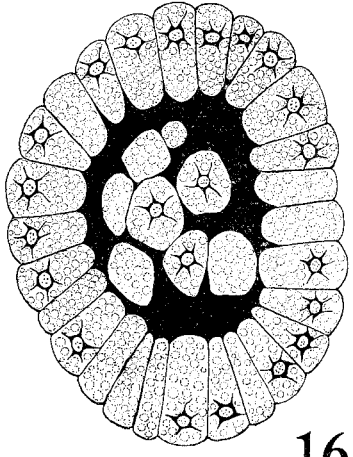

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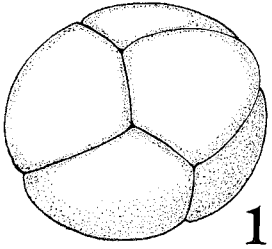

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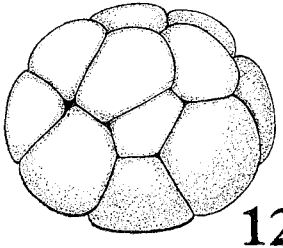

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PLATE III

Fig. 17.—Surface view of embryo shortly after the commencement of invagination.

Fig. 18.—Surface view of embryo towards the close of invagination.

Fig. 19.—Sagittal section through embryo at the commencement of invagination.

Fig. 20.—Sagittal section through an embryo during invagination, showing the formation of a temporary archenteric cavity.

Fig. 21.—Ventral view of an embryo stained with alum-carmine to show the V-shaped germinal disk.

Fig. 22.—Dorsal view of embryo at the same stage as that shown in fig. 21.

Fig. 23.—Ventral view of egg-nauplius at about the ninth week of summer-development. Drawn from a whole mount stained with alum-carmine.

Fig. 24.—Ventral view of egg-nauplius at about the tenth week, showing partial contraction of the disk and the formation of labrum and head-lobes.

a.1., antennule
a.1.g., antennulary ganglion
a.2., antenna
a.2.g., antennary ganglion
a.c., archenteric cavity
bl., blastopore
c.l., cephalic lobe or optic lobe
c.p., caudal papilla
en., endodermal cell
lb., labrum
m., primary mesoderm
md., mandible
md.g., mandibular ganglion
pr., proctodaeum
st., stomodaeum

18
17
19
m.
20
bl.
a.c.
en.
m.
21
st.
pr.
22
lb
23
st.
a1.
a2.
md.
pr.
cp
24
cl.
ant
ant
md
cp

PLATE IV

Fig. 25.—Surface view of region in the vicinity of the blastopore at the first appearance of the ectodermal teloblasts. Drawn with the aid of a camera lucida from a whole mount stained with alum-carmine.

Fig. 26.—Surface view of blastoporal region when, by the contraction of the disk, the naupliar appendages have come closer together and the row of ectodermal teloblasts has commenced to curve round the caudal papilla. (See also fig. 28.)

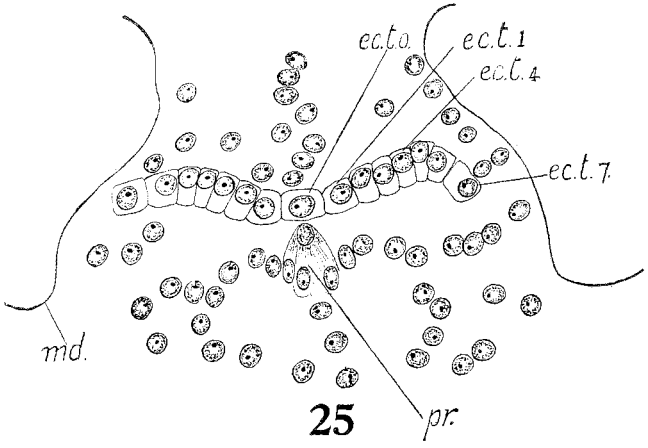
Fig. 27.—Ventral view of egg-nauplius at the eleventh week. The disk has now contracted to such an extent that the appendages no longer project beyond the sides of the embryo. The cells of the head-lobes now form concentric circles.

Fig. 28.—Ventral view of embryo at the thirteenth week. The caudal papilla is now well formed.

Fig. 29.—Ventral view of embryo at the fifteenth week. Median eye and the rudiments of the maxillules have now appeared.

Fig. 30.—Ventral view of embryo at the sixteenth week. Endopodite and exopodite of the antennae are now segmented and about equal in length.

a.1., antennule
a.2., antenna
c.c., central cell of head-lobe
c.l., head-lobe
c.p., caudal papilla
ec.t., ectodermal teloblast
ec.t.0., median ectodermal teleblast
ec.t.1.,-*ec.t*.7., lateral ectodermal teioblasts
lb., labrum
m.d., mandible
m.e., median eye
mx.1., maxillule
mx.2., maxilla
pr., proctodaeum
th.l.1., first thoracic appendage
th.l.3., third thoracic appendage



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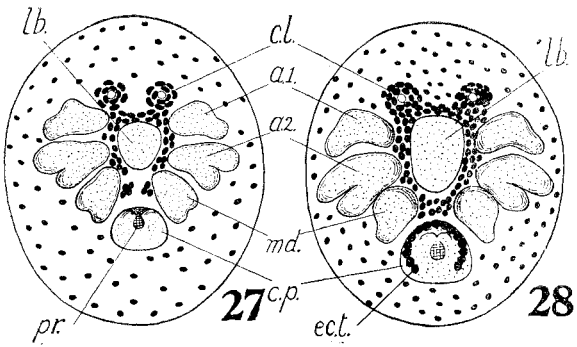

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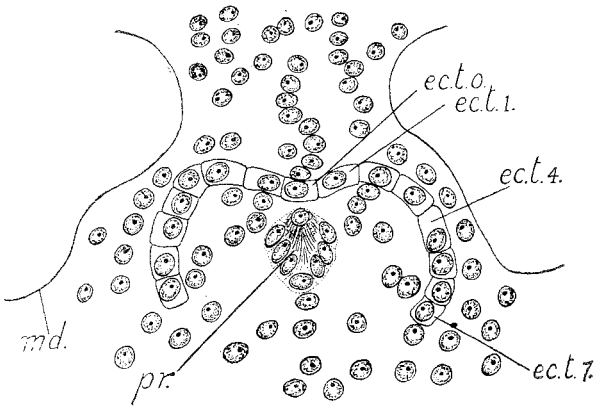

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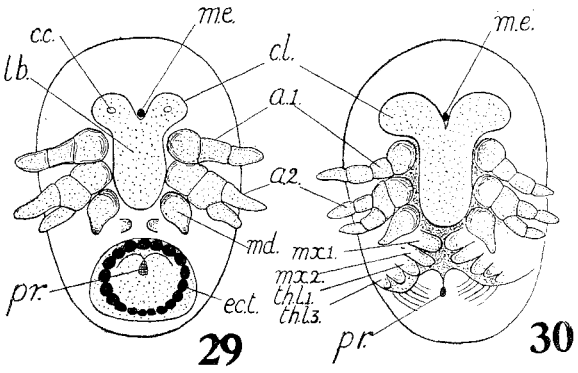

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PLATE V

Fig. 31.—Optical section of egg just before hatching, showing the embryo surrounded by the chorion, vitelline membrane, and first and second larval integuments.

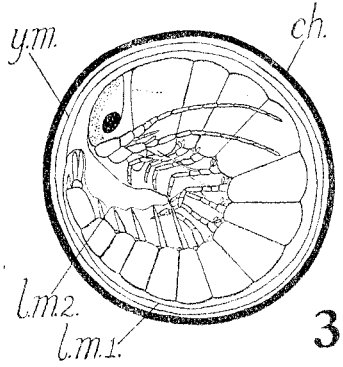
Fig. 32.—Egg at first stage of hatching, showing split in chorion.

Fig. 33.—Second stage in the hatching process. The first larval integument is bulging out through the split in the chorion, forcing it open.

Fig. 34.—Final stage in hatching. The chorion has burst, and the shrimp is now surrounded by the distended first larval integument, to the outer surface of which portions of the vitelline membrane still adhere. The second larval integument has been cast off, and lies within the first.

Fig. 35.—The newly hatched shrimp, showing the sessile eyes, the two pairs of hepatic lobes, and the elongated yolk-sac. The latter is clearly seen through the transparent ectoderm and muscles of the animal.

ch., chorion
*l.m.*1., first larval integument
*l.m.*2., second larval integument
v.m., vitelline membrane



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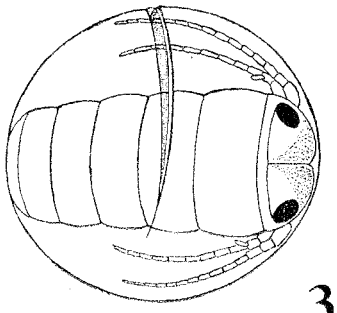

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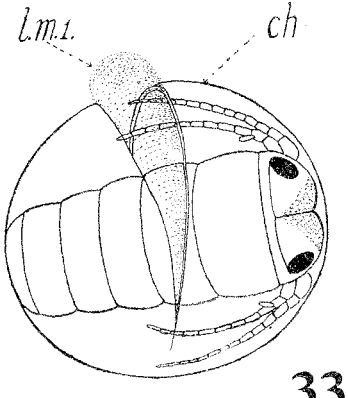

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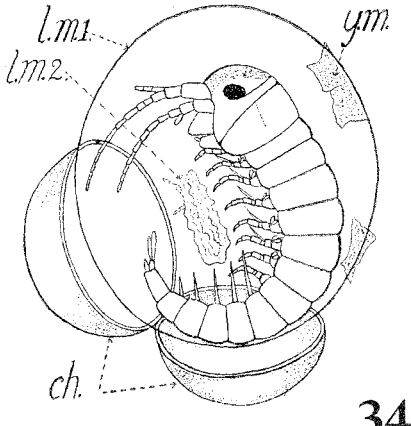

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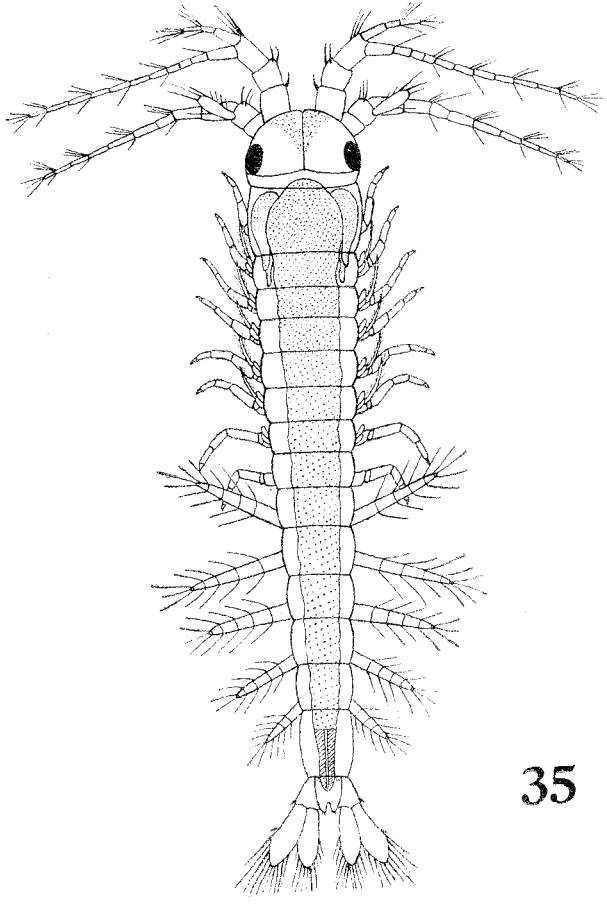

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PLATE VI

Figs. 36-39.—Appendages of the newly hatched *Anaspides:*

Fig. 36.—Antennule.
Fig. 37.—Antenna.
Fig. 38.—Third thoracic appendage.
Fig. 39.—Mandibles.

Figs. 40-43.—Dorsal views of the head region in young specimens of *Anaspides* to show the gradual development of the rostrum and of the pedunculated condition of the paired eyes:

Fig. 40.—Newly hatched specimen.
Fig. 41.—Specimen about 3·4 mm. long.
Fig. 42.—Specimen about 4·4 mm. long.
Fig. 43.—Specimen about 4·6 mm. long

c.gr., cervical groove
c.s.o., four-celled cervical sense organ
m.gr., median longitudinal groove of head
r., rostrum
r.gr., rostral groove
*th.*2., second thoracic segment

m.gr.
r.gr.
c.gr.
th.2.
41
40
m.gr.
r.
c.s.o.
c.gr.
th.2.
43
42
36
39
38
37

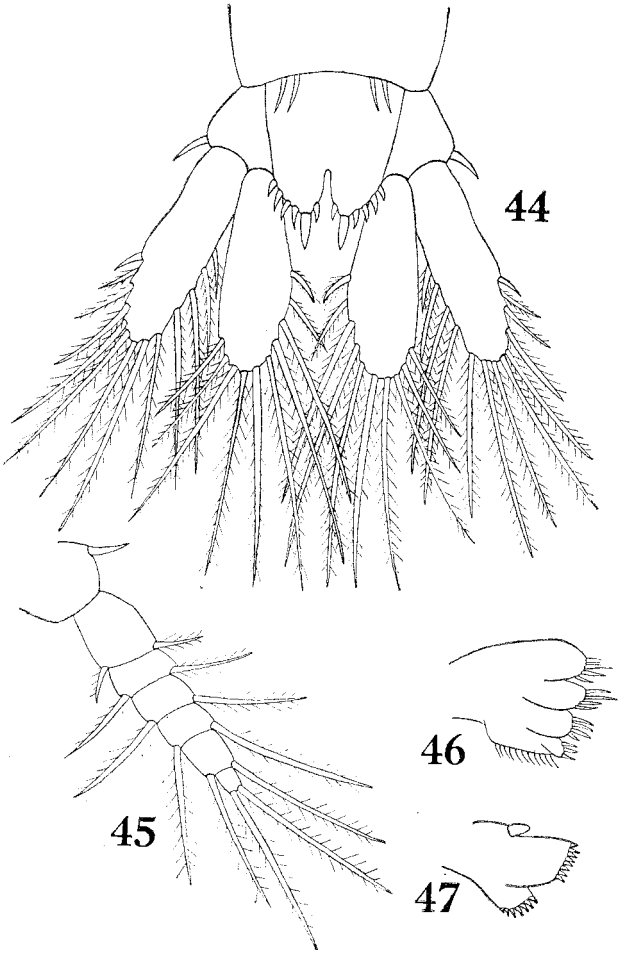
PLATE VII

Figs. 44-47.—Appendages and telson of the newly hatched *Anaspides:*
Fig. 44.—Uropods and the notched telson.
Fig. 45.—Third abdominal pleopod.
Fig. 46.—Maxilla.
Fig. 47.—Maxillule.

Fig. 48.—Sagittal section through an embryo at a stage immediately following gastrulation and just before that shown in fig. 21. The endodermal cells have crowded together, and now fill most of the blastocoel. The blastopore is closing, and the cells within its margin form the wall of the proctodaeum. The stomodaeal invagination is commencing. A few mesoderm cells appear below the future position of the labrum.

Fig. 49.—Transverse section of an embryo at the stage shown in fig. 23. The section passes through the opening of the stomodaeum. The strands of mesoderm on each side are seen in cross-section below the rudiments of the antennae. Cytolysis has occurred in some of the endodermal cells, giving rise to granules of chromatin.

a.2., antenna
en., endodermal cell
lb.m., labral mesoderm
n.m., naupliar mesoderm
pr., proctodaeum
st., stomodaeum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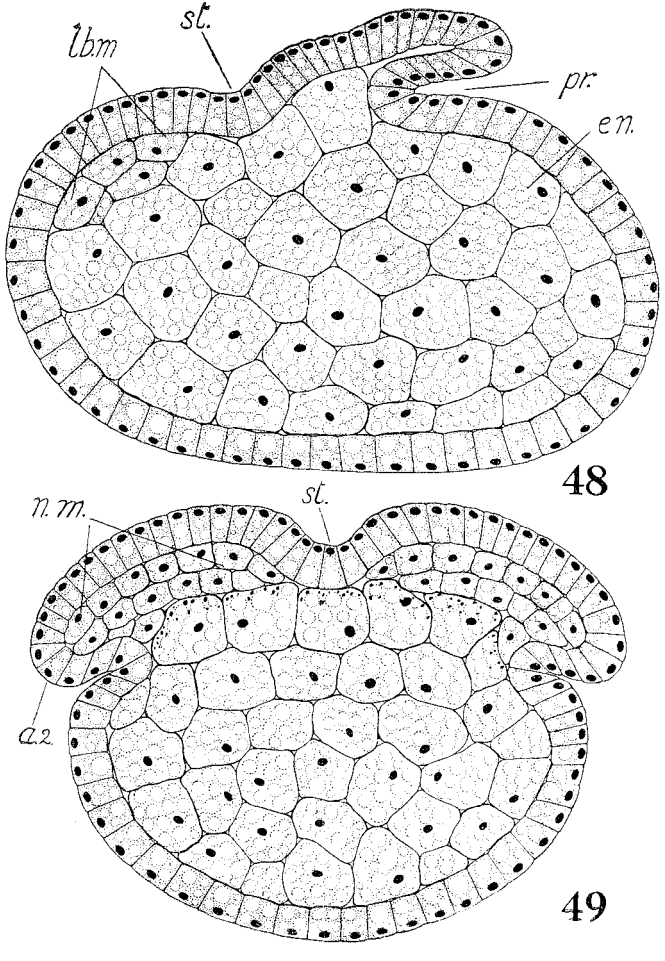

lbm
st.
pr.
en.
48
n.m.
st.
a.2
49

PLATE VIII

Fig. 50.—Transverse section of early egg-nauplius passing through the anterior lip of the blastopore. The cells of the posterior ends of the mesodermal strands lie on each side of the proctodaeum. These cells give rise to the mesodermal teloblasts.

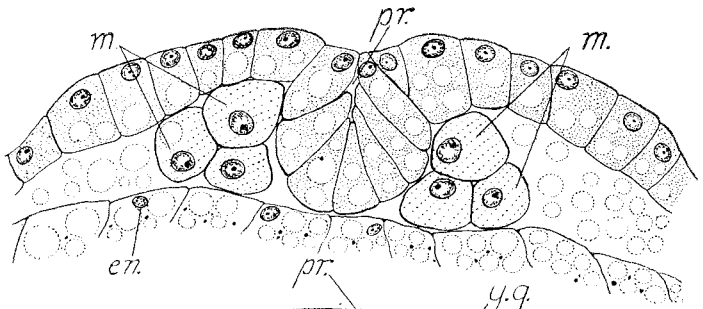
Fig. 51.—Transverse section through the stage shown in fig. 27. The section passes through the caudal papilla, and shows a mesodermal teloblast and its first descendant on each side of the proctodaeum.

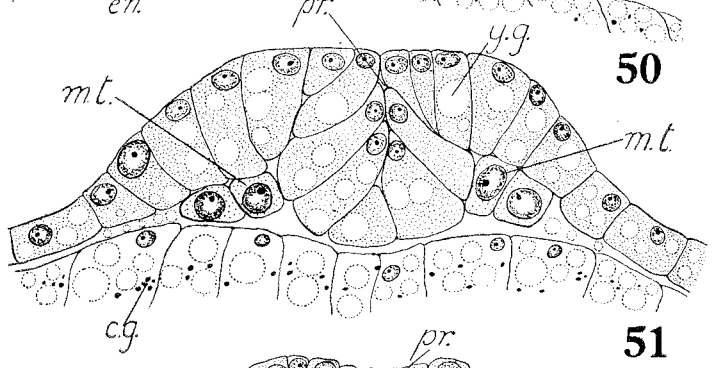
Fig. 52.—Transverse section of the nauplius stage shown in fig. 28. The section passes through the caudal papilla, and shows in cross-section on each side the ring of ectodermal teloblasts and two rows of descendants. The mesodermal teloblasts have also given rise to two rows of descendants.

Fig. 53.—Transverse section of the tip of the caudal papilla of an embryo at about the fifteenth week of development. At this stage the papilla cannot be removed from the embryo without injury, and hence had to be sectioned *in situ*. Orientation is not quite correct, and the section is somewhat oblique. It shows the median ectodermal teloblast and several of the lateral ones. The small cells forming the telson mesoderm also appear in the section.

Fig. 54.—Transverse section of the caudal papilla of another embryo of about the same age as that shown in fig. 53. The section is slightly more anterior than that of fig. 53, and shows the four pairs of mesodermal teloblasts and descendants of some of the ectodermal teloblasts.

c.g., chromatin granules
ec.t., ectodermal teloblast
ec.t.0., median ectodermal teloblast
ec.t.1.,-*ec.t.9.*, lateral ectodermal teloblasts
ec.t.d., descendant of ectodermal teloblast
ec.t.0.d.,-*ec.t.6.d.*, descendants of median and lateral ectodermal teloblasts
m., primary mesoderm
m.t., mesodermal teloblast
m.t.d., descendant of mesodermal teloblast
m.t.1.,-*m.t.4.*, the four mesodermal teloblasts of each side
pr., proctodaeum
t.m., telson mesoderm
y.g., yolk granule


m
pr.
m.
en.


pr.
y.g.
m.t.
m.t.
c.g.

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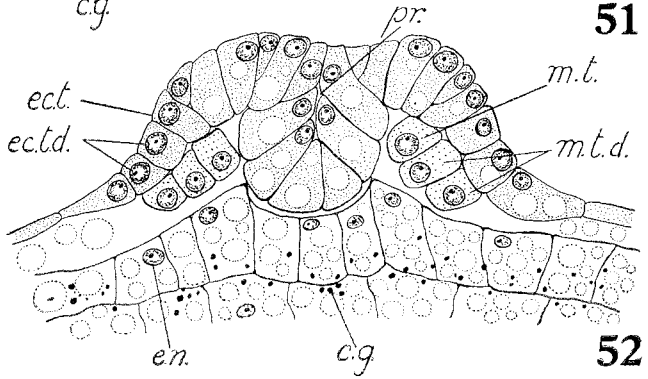
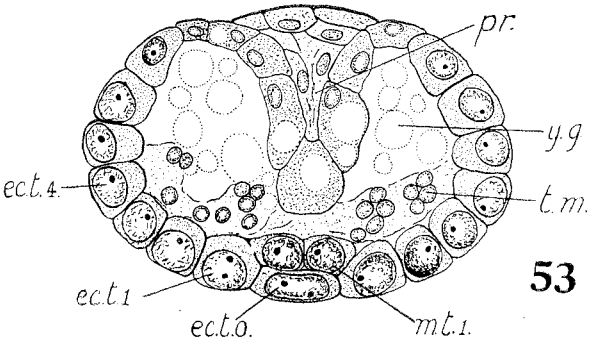

pr.
ect.
ec.t.d.
m.t.
m.t.d.
en.
c.g.

52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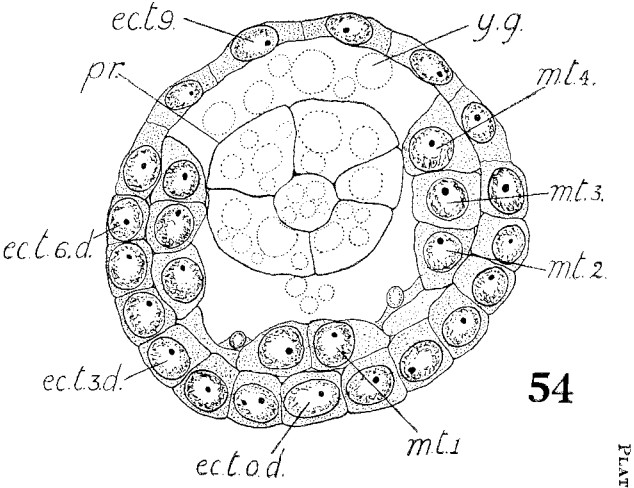
y.g.
ect.4.
t.m.
ect.1
ect.0.
mt.1.

53


ect.9.
y.g.
pr.
mt.4.
mt.3.
ect.6.d.
mt.2.
ect.3.d.
mt.1
ect.0.d.

54

PLATE IX

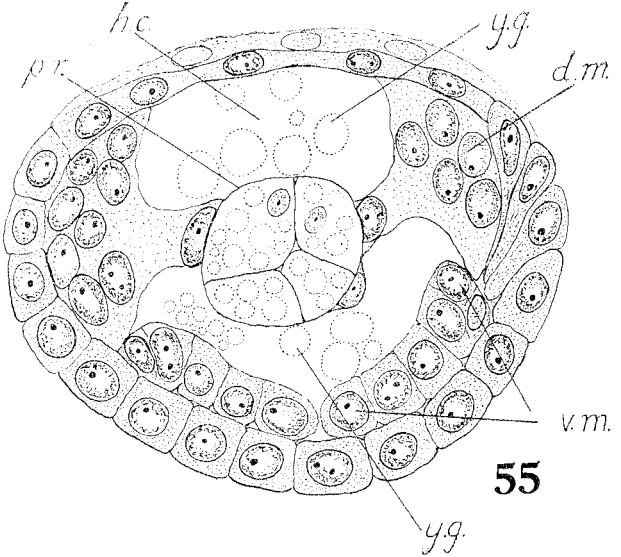
Fig. 55.—Transverse section of the caudal papilla of a 15-week embryo. The section is somewhat further forward than those in figs. 53 and 54. The dorsal and ventral mesoderm are differentiated, and the dorsal mesoderm has commenced its upward growth to form the lateral walls of the dorsal vessel.

Fig. 56.—Transverse section through the third abdominal segment of a 22-week embryo. The walls of the dorsal vessel are now formed, and the pericardial cavity is established by the shrinking away of the mesoderm from the dorso-lateral ectoderm. The floor of the dorsal vessel has been formed by the mesoderm growing over the yolk-sac. Yolk-granules and cells that have spread backward from the naupliar mesoderm are present in the cavity of the dorsal vessel and at the sides of the yolk-sac.

Fig. 57.—Transverse section through the maxillulary somite of a newly hatched specimen, showing the large anterior cavity of the heart roofed over by the dorsal organ.

Fig. 58.—Transverse section through the fourth thoracic somite of a newly hatched specimen, showing the thickened wall of the heart.

*a.l.*1., primary anterior lobe of liver
d.l.m., dorsal longitudinal muscles
d.m., dorsal mesoderm
d.o., dorsal organ
en., endodermal cell
g., genital rudiment
h.c., cardiac cavity or cavity of dorsal vessel
h.f., floor of cardiac cavity
*mx.*1.*c.*, coelomic cavity of maxillulary segment
n.m., naupliar mesoderm
pc.c., pericardial cavity
pc.f., pericardial floor
p.l., posterior lobe of liver
v.m., ventral mesoderm
v.l.m., ventral longitudinal muscles
y.g., yolk-granules


h.c.
y.g.
p.r.
d.m.
v.m.
y.g.

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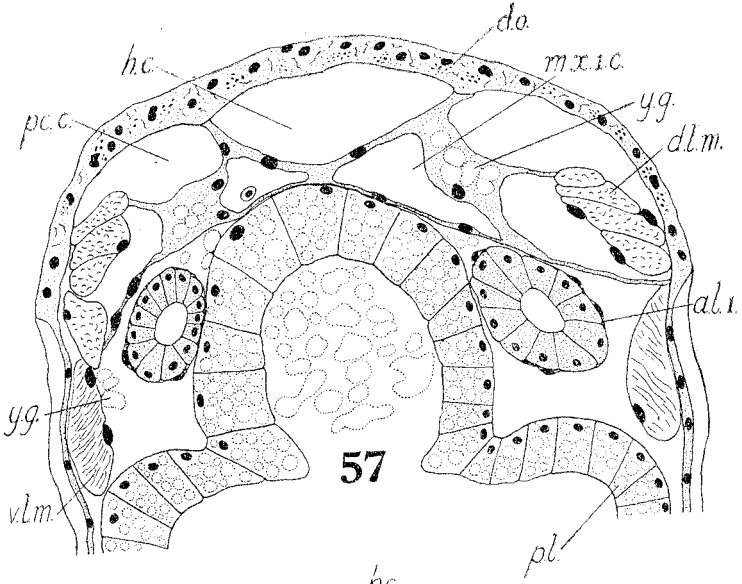
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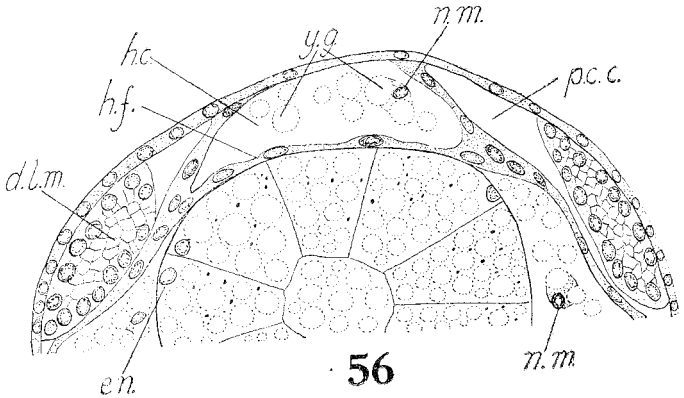
al.1.
y.g.
v.l.m.
pl.

57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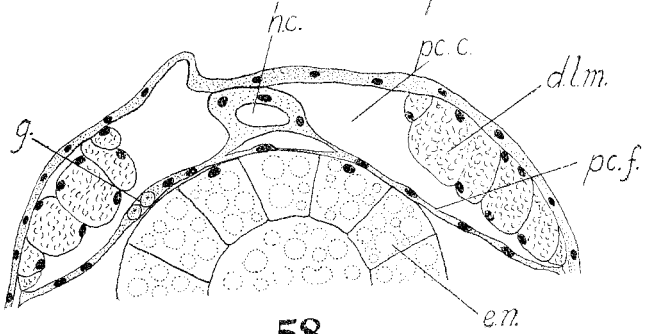
n.m.

56


h.c.
pc.c.
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e.n.

58

PLATE X

Fig. 59.—Transverse section through the fifth abdominal somite of a newly hatched specimen. The section passes immediately in front of the hind-gut, and shows the endodermal cells of the yolk-sac forming the epithelium of the mid-gut, which at this point is completely invested by mesoderm.

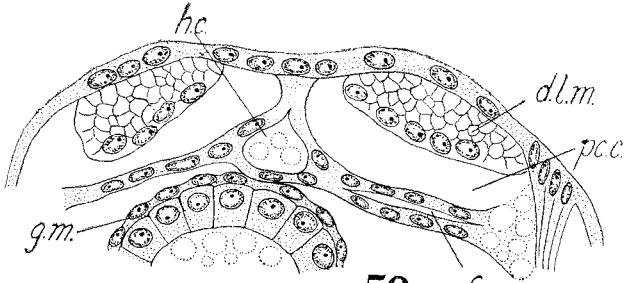
Fig. 60.—Transverse section in front of the stomodaeum of a newly hatched specimen. The anterior aorta and lateral cephalic arteries have appeared in the naupliar mesoderm between the yolk-sac and brain.

Fig. 61.—Sagittal section through an embryo at the stage shown in fig. 23. The stomodaeal invagination reaches almost to the proctodaeum.

Fig. 62.—Sagittal section through an embryo slightly older than that of fig. 61.

Fig. 63.—Sagittal section through an embryo about as old as that shown in fig. 27. The labrum is growing over the mouth and the posterior end of the stomodaeum is being pulled forward.

a.a., anterior aorta
b.c., blood corpuscle
br., brain
c., coelomic cavity
c.p., caudal papilla
cu., cuticle
d.l.m., dorsal longitudinal muscles
ec.t.d., descendant of ectodermal teloblast
en., endodermal cell
g.m., mesodermal investment of gut
h.c., cardiac cavity
lb., labrum
lb.m., labral mesoderm
l.c.a., lateral cephalic artery
m.t., mesodermal teloblast
n.m., naupliar mesoderm
pr., proctodaeum
st., stomodaeum


h.c.
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p.c.c.
g.m.
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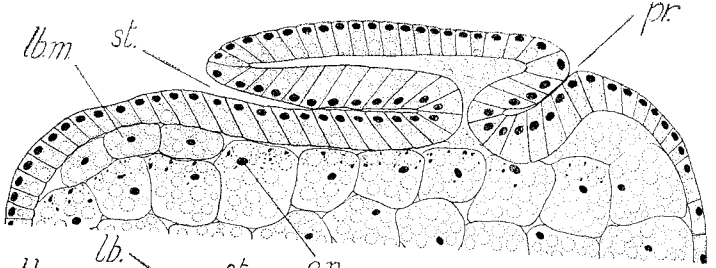
lb.m.
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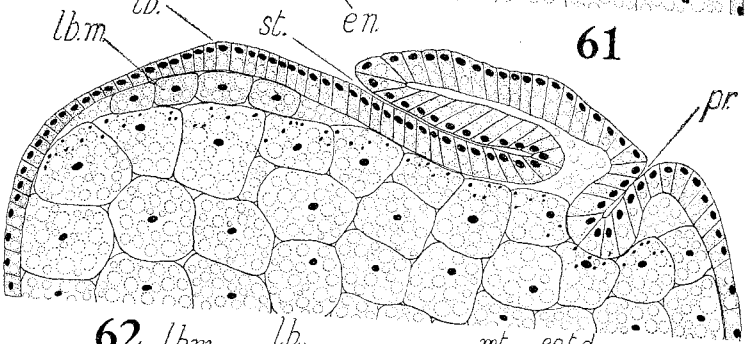
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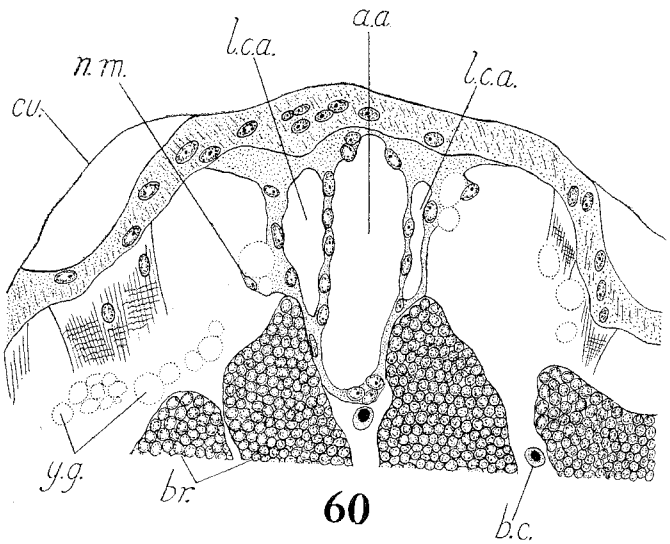
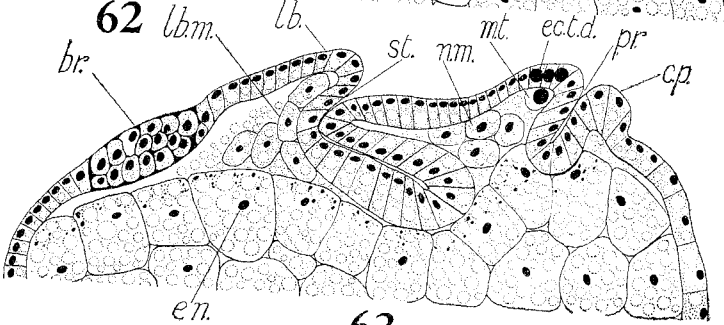
pr.

62


a.a.
l.c.a.
n.m.
l.c.a.
cu.
y.g.
br.
b.c.

60


lb.m.
lb.
st.
n.m.
mt.
ec.t.d.
pr.
cp.
br.
en.

63

PLATE XI

Fig. 64.—Sagittal section through a 15-week embryo. The caudal flexure occurs just behind the maxillulary somite. The caudal papilla is well developed, and the anal aperture occupies a postero-dorsal position. The end of the stomodaeal invagination now underlies the brain. The yolk-granules in the naupliar mesoderm are being slowly absorbed. The posterior end of the yolk-sac extends into the caudal papilla.

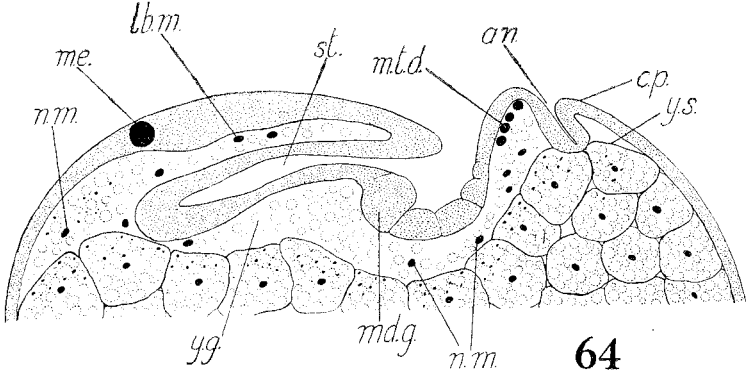
Fig. 65.—An older stage than that of fig. 64. The stomodaeum is now much shorter, the caudal flexure has shifted backwards to the first thoracic somite, and the yolk-sac has become longer. Cells from the naupliar mesoderm have moved backward into the post-mandibular region.

Fig. 66.—Sagittal section through an embryo about 25 weeks old. All somites are now formed. The nerve cord has a seventh abdominal ganglion. Cells which have shifted backward from the naupliar mesoderm are seen below the yolk-sac in the abdomen. Chromatin granules are still present among the yolk-globules of the endoderm.

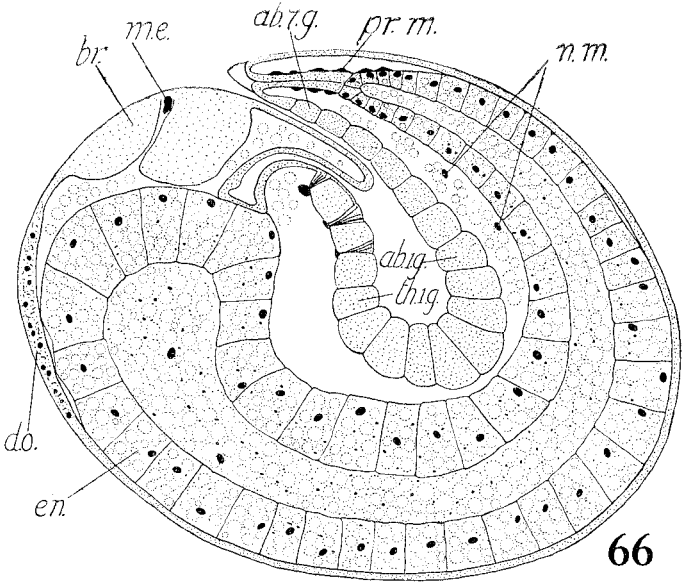
Fig. 67.—Transverse section through the median eye at its first appearance, showing its origin from paired rudiments. Pigment is being deposited in two cells, one on each side of the mid-line.

Fig. 68.—Surface view of the concentric rows of cells in the protocerebrum of an embryo at the stage shown in fig. 29.

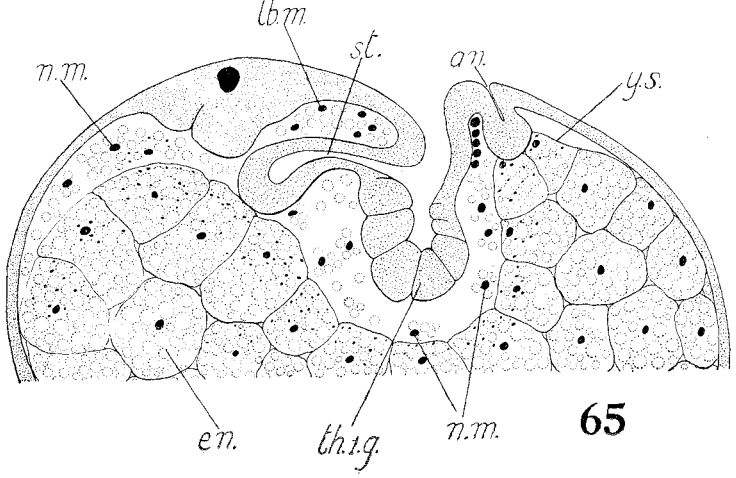
an., anus
ab.1.g., first abdominal ganglion
ab.7.g., seventh abdominal ganglion
br., brain
c.p., caudal papilla
d.o., dorsal organ
en., endodermal cell
lb., labrum
lb.m., labral mesoderm
md.g., mandibular ganglion
m.e., median eye
n.m., naupliar mesoderm
pr.m., mesodermal investment of proctodaeum
s.t., stomodaeum
th.1.g., first thoracic ganglion
y.g., yolk-granule
y.s., yolk-sac


lb.m.
me.
st.
m.t.d.
an
c.p.
y.s.
n.m.
yg.
md.g.
n.m.

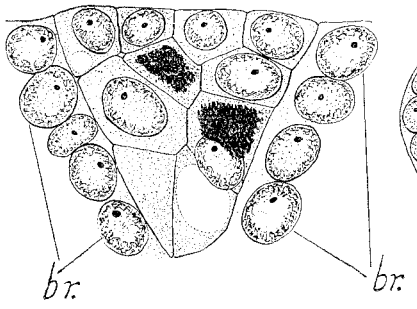
64


br.
m.e.
ab.t.g.
pr.m.
n.m.
ab.tg.
th.tg.
d.o.
en.

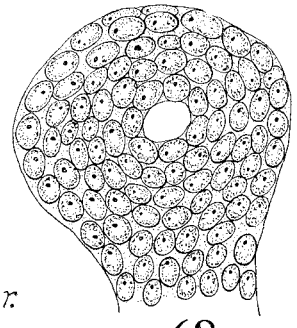
66


lb.m.
st.
an.
n.m.
y.s.
en.
th.t.g.
n.m.

65


br.
br.

67



68

PLATE XII

Fig. 69.—Frontal section through the anterior end of an embryo at a late stage of embryonic life. The posterior liver lobes appear as outgrowths of the yolk-sac. They already extend backwards for a short distance, and are capped with mesoderm.

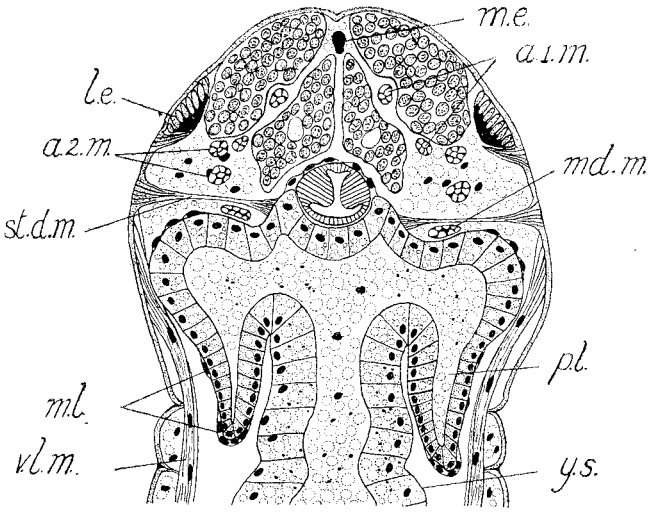
Fig. 70.—A reconstruction of the liver of an embryo about the same age as that shown in fig. 69. The posterior lobe is well developed. The primary anterior lobe has bent over, and is growing backward. The secondary anterior lobe is appearing at the bend in the primary lobe.

Fig. 71.—A reconstruction of the liver of a newly hatched specimen. The posterior lobe is now finger-like. The primary anterior lobe has increased in length, the secondary anterior lobe has bent over and is growing backward, and a third anterior lobe is forming at the bend in the secondary lobe.

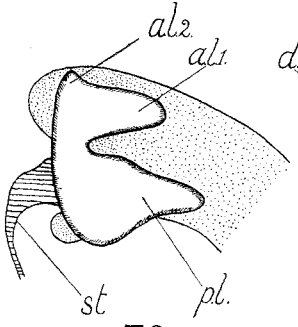
Fig. 72.—Transverse section through the sixth thoracic segment of a newly hatched specimen, showing the genital rudiment in the pericardial floor. The coelomic pouch has shrunken and disappeared.

Fig. 73.—Parasagittal section through the fifth thoracic segment of a newly hatched specimen, showing the length of the genital rudiment.

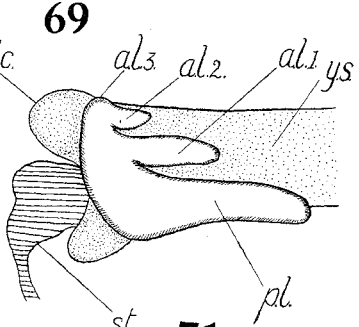
a.1.m., antennulary muscles
a.2.m., antennary muscles
a.l.1., primary anterior lobe of liver
a.l.2., secondary anterior lobe of liver
a.l.3., tertiary anterior lobe of liver
d.l.m., dorsal longitudinal muscles
en., endodermal cell
g., genital rudiment
h.c., cardiac cavity
l.e., lateral eye
m.e., median eye
md.m., dorso-ventral mandibular muscle
m.l., mesodermal investment of liver
pc.c., pericardial cavity
pc.f., pericardial floor
p.l., posterior liver-lobe
st., stomodaeum
st.d.m., dilator muscle of stomodaeum
v.l.m., ventral longitudinal muscles
y.s., yolk-sac


m.e.
a.1.m.
l.e.
a.2.m.
md.m.
st.d.m.
pl.
m.l.
v.l.m.
y.s.

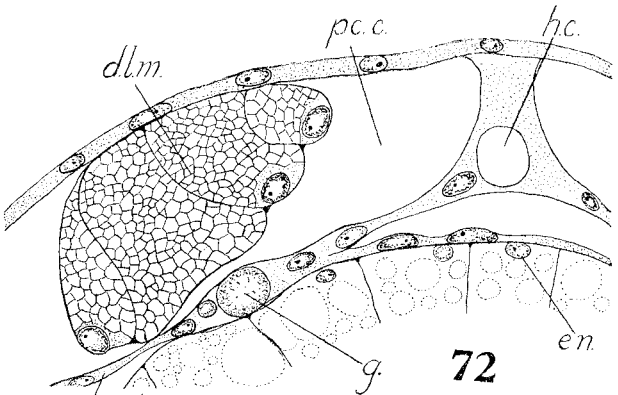
69


al.2.
al.1.
st
pl.

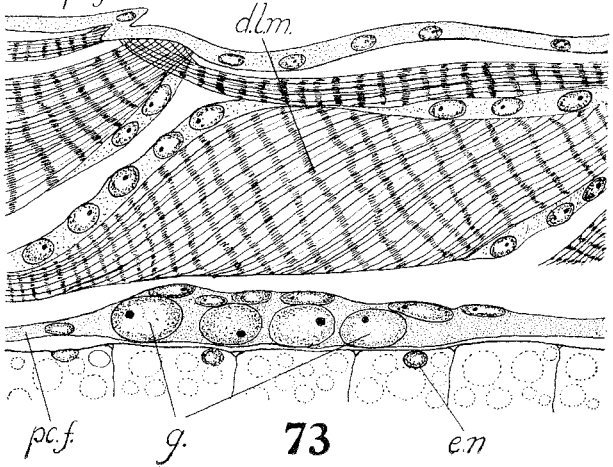
70


d.c.
al.3.
al.2.
al.1
y.s.
st.
pl.

71


p.c.c.
h.c.
d.l.m.
e.n.
g.
p.c.f.

72


d.l.m.
p.c.f.
g.
e.n

73

PLATE XIII

Fig. 74.—A sagittal section through the posterior end of the body of a 25-week embryo, showing the seventh abdominal ganglion below the junction of the yolk-sac with the proctodaeum.

Fig. 75.—A later stage than that of fig. 74, showing the sixth abdominal ganglion separated from the fifth. The seventh abdominal ganglion is being pulled into a position above the sixth.

Fig. 76.—An almost sagittal section through the end of the abdomen of a newly hatched specimen, showing the remnant of the seventh abdominal ganglion above the sixth, and separated from it by a slender intersegmental bar.

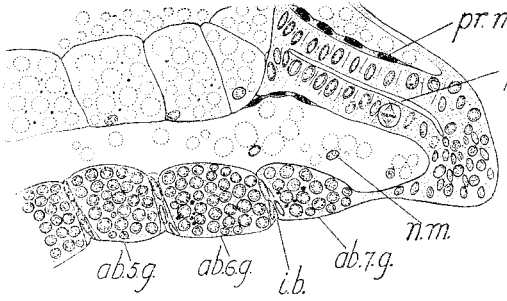
Fig. 77.—Transverse section through the base of the maxillary somite of a 17-week embryo, showing the mesodermal rudiment of the maxillary gland.

Fig. 78.—A slightly later stage than that of fig. 77. The mesodermal cells are becoming oriented transversely to form the tubule of the gland.

Fig. 79.—A sagittal section through the basal segment of the maxilla in a newly hatched specimen, showing the duct of the maxillary gland passing under the adductor muscle and opening by a pore on the posterior surface of the appendage.

Fig. 80.—Section through the lateral part of the maxillary gland of a newly hatched specimen, showing the well-developed tubule cut transversely in several places.

ab.5.g.-*ab.7.g.*, fifth-seventh abdominal ganglia
i.b., intersegmental ectodermal bar
n.m., cells from the nauplíar mesoderm, which have shifted backward into the abdominal region
mx.2., maxilla
mx.g., maxillary gland
mx.g.d., duct of maxillary gland
mx.g.p., external aperture of maxillary gland
mx.g.t., tubule of maxillary gland
mx.t.m., transverse adductor muscle in basal segment of maxilla
n.c., nerve cord
pr., proctodaeum
pr.m., mesodermal investment of proctodaeum
y.g., yolk-granules



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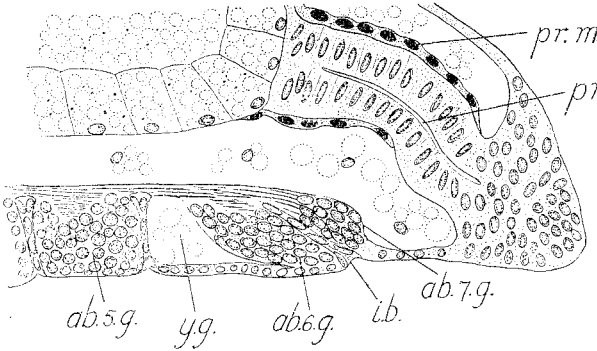

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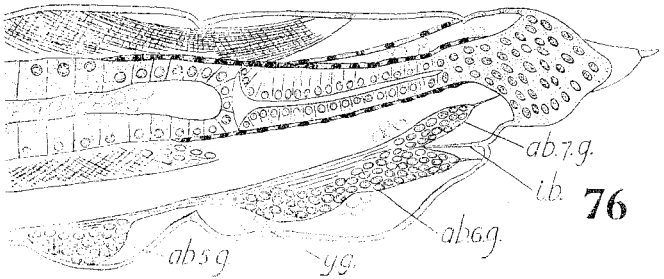

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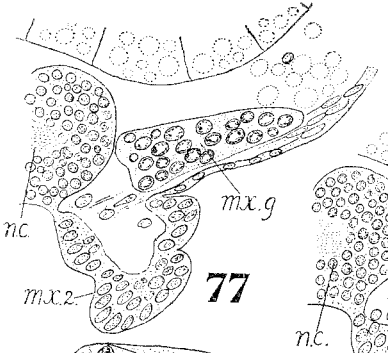

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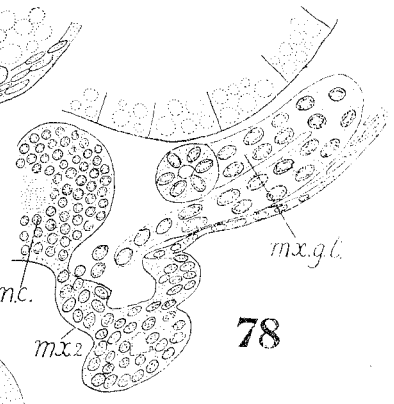

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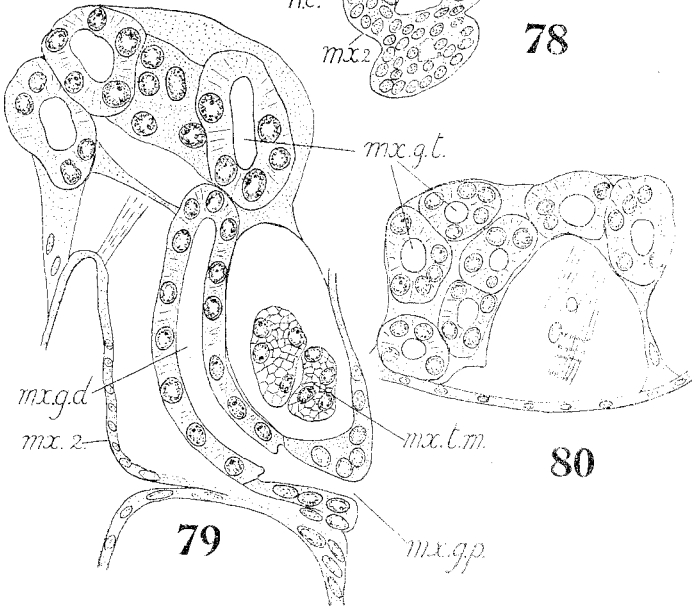

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