III—Studies on the Embryology of the African Migratory Locust, *Locusta migratoria migratorioides* Reiche and Frm. (Orthoptera, Acrididae)

II—Organogeny

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[Plates 1–7]

Contents

I—Introduction

This paper completes the account of the embryology of *Locusta migratoria migratorioides* R. and F., which is referred to for brevity as *Locusta migratoria*, and describes the development of the principal organs of the body. In Part I (Roonwal, 1936, *a*) of the present contribution, the early development up to the differentiation of the inner layer and the beginning of the definitive body segmentation was traced in detail. No special technique was employed beyond that already described in the earlier paper.

It is with great pleasure that I take this opportunity of expressing my sincere thanks to Professor J. Stanley Gardiner, F.R.S., for accommodating me in the Zoological Laboratory, Cambridge. To Dr. A. D. Imms, F.R.S., I owe a deep debt of gratitude for his kindly guidance and friendly counsel throughout the progress of this work. My thanks are due to Professor L. E. S. Eastham for suggesting some improvements in the text.

II—The Development of the Various Organs

1—*Time-table of Later Development*

In Table I an approximate time-table is given of the later development from about 75-hours stage onwards, the eggs being incubated at 33° C.

Table I

Age in days after egg-laying	State of development
4 days	Invaginations of tentorium and mandibular apodemes arise. Stomatogastric nervous system formed.
5 days	Cardioblasts and germ cells differentiated. Spiracular invaginations formed. Malpighian tubules arise. Anterior portion of cephalic aorta begins to be formed.
6 days	Rupture of embryonic membranes. Blastokinesis.
7 days (1 day after blastokinesis)	Heart formation begins and pericardial cells arise. Invaginations of salivary glands and corpora allata arise. Hypopharynx evagination begins. Amniotic dorsal closure formed. Circum-intestinal blood sinus arises. Embryonic cuticle secreted.
8 days (2 days after blastokinesis)	Heart formation complete. Serosal dorsal organ formed. The labial rudiments fuse together.
9 days (3 days after blastokinesis)	Definitive dorsal closure formed.
10 days (4 days after blastokinesis)	Serosal dorsal organ completely absorbed.
11 days (5 days after blastokinesis)	Mid-gut epithelium complete.
12 days (6 days after blastokinesis)	Anal portion of cephalic aorta complete.
13 days (7 days after blastokinesis)	Hatching.

2—*The Definitive Segmentation of the Inner Layer and the First Appearance of the Coelomic Cavities*

The primary segmentation of the inner layer into four macromeres has been already described. From it the definitive segmentation develops. The two processes are not sharply separated but, to some extent, merge into each other. The definitive segmentation of the inner layer as well as the subsequent process of the first appearance of the coelomic cavities differ markedly in the head, thorax, and first abdominal segment on the one hand and the rest of the abdomen on the other, as will be evident from the following account.

In about the 52-hours stage, the inner layer in the head and thorax is divided into segments corresponding to the three jaw and the three thoracic segments. The somites of the inner layer are not connected with one another by means of intersegmental cell-strands but are independent. Almost simultaneously with this process, each mesoderm segment is divided into two lateral halves (fig. 1, Plate 1). These paired, segmentally arranged mesoderm masses lie somewhat obliquely, so that the anterior and inner end of each meets with its fellow of the opposite side in the intersegmental region in front. The segmental mesoderm masses give rise to the coelomic cavities. The small, intersegmental median mesoderm masses (the " Blutzellenlamellae " of WIESMANN, 1926, and the median mesoderm of EASTHAM, 1930, *b*), on the other hand, give rise largely to the blood cells. A primary median mesoderm band, as has been described in some other insects, is not present in *Locusta*; here a median mesoderm strand is formed only secondarily by the extension of the blood cell-lamellae medially and by cells derived from the lower end of the median walls of the coelomic sacs (figs. 3 and 5, Plate 1).

The segmentation of the antennary and the pre-oral mesoderm is somewhat different from that described above. In the 52-hours stage it is seen that a pair of mesoderm bands extends upwards from the junction of the head-lobe with the trunk and meet over the stomodaeum (fig. 125). From this dorsal point the labral mesoderm is derived. The antennary mesoderm is derived from the postero-lateral edges of this mass and is already evident in the 50-hours-old embryo. Thus the antennary mesoderm is the first to be differentiated into a more or less discrete segment; the segmentation of the rest of the cephalic and the thoracic regions occurs slightly later.

The formation of the coelomic cavities in the head and thorax takes place in the following manner: The many-layered inner layer of each side in a segment spreads laterally over the ectoderm and becomes one-layered, although at some places it still retains a thickness of more than one layer. The ectoderm at the lateral edges of the germ band then curves dorso-medianally and the mesoderm in each segment follows suit. The free ends of the mesoderm layer in each lateral half of a segment then approach towards each other and unite to form a coelomic cavity (fig. 2, Plate 1). At the time of their first appearance these cavities lie *inside* the rudiments of the appendages belonging to their segment and may therefore be called appendicular

coelomic cavities. Like the original mesoderm masses from which they arise, these cavities, especially those in the thoracic region, are placed obliquely to the longitudinal axis of the embryo. They have a tapering dorso-median end which extends into the preceding intersegmental region (fig. 6, Plate 1). Later in life, each coelomic cavity exhibits a division into three lobes to be described in detail below. Thus, each pair of coelomic cavities is formed distinctly and separately.

Coelom formation in the first abdominal segment takes place in the same way as in the head and thorax. But in the following abdominal segments it is different and runs as follows : With the growth of the median portion of the ectoderm, the originally wedge-shaped mass of inner layer flattens out and spreads laterally in such

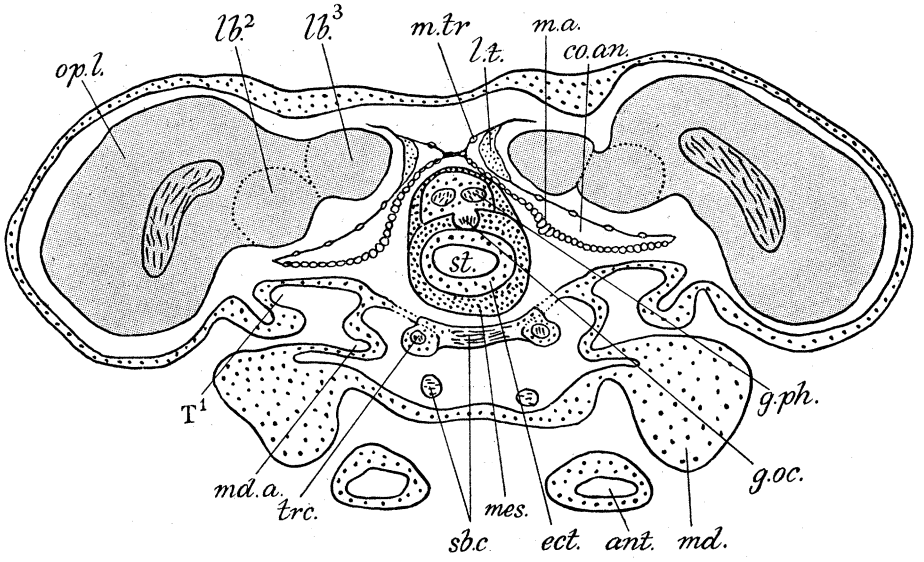

FIG. 124—Transverse section of embryo shortly before blastokinesis, passing across the intercalary segment. × 128.

a way as to lose its multi-layered condition and acquires instead a bilayered arrangement of its nuclei (fig. 7, Plate 1). Soon the dorsal of these two layers becomes extremely thin. So far, no sign of a cavity is seen between these two layers. Simultaneously with this process, the undivided mass of inner layer becomes constricted into segmental areas. Each segment, unlike what obtains in the head and thorax, remains connected for some time with its neighbours by means of a narrow intersegmental band of inner layer which does not show a regular bilayered arrangement of nuclei (fig. 8, Plate 1). The intersegmental bands soon disappear, but how this happens has not been followed. The two layers of the segmental mesoderm split apart in the middle and thus a single coelomic cavity arises in each segment (fig. 9, Plate 1). This cavity then divides into two separate lateral halves by the median portions of its walls coming together. All these three processes, viz., the segmentation of the inner layer, the first appearance of the unpaired coelomic cavities, and the

pairing of the latter, progress from in front backwards. At a later stage, the median-ventral walls of the coelomic cavities in each segment extend medially and thus secondarily form the so-called median mesoderm from which the blood cells arise (fig. 10, Plate 1). Like the coelomic cavities of the head and thorax, those of the abdomen become associated with the appendicular rudiments before they undergo further morphological differentiation.

3—*The Development of the Coelomic Cavities*

(a) The Coelomic Cavities of the Head

Labral Coelomic Cavities—In *Locusta* the labrum is provided with a distinct pair of coelomic cavities which are well seen in the 56- to 59-hours stage (figs. 12 and 13, Plate 1). There is no doubt regarding the coelomic nature of these structures, and I have seen them in both transverse and longitudinal sections.* In the above-mentioned stage, the mesoderm forming the two coelomic cavities is not joined medially, nor is it connected with the mesoderm surrounding the stomodaeum. Before the development of the labral coelomic cavities, the labral and stomodaeal mesoderm are seen to be connected together by means of loose strands of mesoderm (fig. 125). The labral coelomic cavities are pre-oral in position. By the 72-hours stage they have disappeared, leaving in their place a rather loose mass of mesoderm which still exhibits a paired arrangement. Shortly afterwards the labral mesoderm again becomes connected with the mesoderm investing the stomodaeum, and eventually gives rise to the labral musculature. The only other insect, besides *Locusta migratoria*, in which labral coelomic cavities have so far been recorded is *Carausius morosus* (WIESMANN, 1926), where also they are evanescent. A difference, however, lies in the fact that whereas in *Carausius* the walls of the labral coelomic cavities are connected medially, in *Locusta* they are not. Although in no other insects have labral coeloms been recorded, the existence in the labrum of paired mesodermal masses, which no doubt represent the vestiges of coelomic cavities, have been shown in some insects. Thus HEYMONS (1895, *a*) found them in *Forficula* and CARRIÈRE and BÜRGER (1897) and STRINDBERG (1915, *a*) in some Hymenoptera. EASTHAM (1930, *b*) describes two pairs of mesodermal masses in front of the antennae. These are the labral and the epipharyngeal, the latter being secondarily separated from the former and having no segmental significance. Irregular cavities may appear in both of these mesodermal masses, but are quite unlike true coelomic cavities, and are not regarded as such by this author. MANTON (1928, pp. 454–455) is inclined to question the validity of regarding the labral coelom sacs of *Carausius morosus* (WIESMANN, 1926) as being independent of those of the preantennary segment. She points out that, except in

* A special series of sections was cut in order to confirm the presence of the labral coelomic cavities described here.

insects, " there is no evidence of any other somite lying between the aeron and precheliceral, preantennulary or preantennary somite in any other form ". The preantennulary or precheliceral somites form the anterior aorta in most anthropods, although in insects this function is relegated to the antennary somites (intercalary in *Donacia*, HIRSCHLER, 1909, *a*). In the former case, two portions are distinguishable, viz., an upper anterior portion forming the aorta itself and a lower posterior portion giving rise to muscles at the sides of the stomadaeum. These two portions are united in *Scolopendra* and *Hemimysis*, but are separate in Spiders. On these grounds, MANTON concludes that the " preantennulary sacs in *Carausius*, lying at the sides of the stomadaeum and giving rise to stomadaeal musculature, clearly resemble the lower preantennulary sacs of *Hemimysis*, Spider, etc.", and, by inference, that the so-called labral coelomic sacs of *Carausius* correspond to the upper anterior portion of the preantennulary sacs. This view is not in accordance with WIESMANN's observations that in *Carausius* the labral and the preantennary somites are initially separate. MANTON's interpretation of this initial separation on grounds of degeneracy is unconvincing. The connexion between the two somites *via* the stomodaeal mesoderm is of no great significance because it occurs also in some of the posterior somites. A further strong objection to MANTON's view is furnished by the discovery of labral coelomic cavities in *Locusta* where there is no trace whatever of the preantennary coelom. (*Also see* discussion on p. 187.)

Antennary Coelomic Cavities—The antennary mesoderm is first differentiated, in the 52-hours stage, as a pair of mesoderm masses lying behind the stomadaeal invagination and at the angles formed by the junction of the head lobes with the trunk. These masses are connected with the stomadaeal mesoderm by cell strands. Coelomic cavities are first formed in them in the 56-hours stage and lie in the hollow of the antennae. They are sub-circular in shape but their inner ends taper dorso-medianally. With the growth of the antennae, the cavities are elongated (59-hours stage). At the same time their ventro-median walls thicken appreciably but remain un-layered, while their dorso-median walls become thinned. In the 75-hours stage, each antennary coelom has developed a long dorso-rostral pouch projecting far into the head and a much smaller dorso-anal pouch* (fig. 101, Plate 6). In other words, it undergoes a division into three parts, the significance of which will be discussed subsequently. As before, the ventral pouch—the original coelomic cavity—completely fills the hollow of the antenna. In the 112-hours stage both the rostral and anal dorsal pouches have become considerably extended. The former reaches as far forwards as the labrum and the latter as far back as the mandibular segment. The dorso-rostral portions of the two antennary coelomic cavities then approach each other over the stomodaeum and their median walls fuse together. This is seen in an embryo shortly before blastokinesis (fig. 124). By this means is formed the anterior portion of the cephalic aorta which functions as a blood-distributing

* The terms " dorso-rostral " and " dorso-anal " were introduced by WIESMANN (1926) to denote the coelomic pouches of *Carausius morosus*.

apparatus (*vide* p. 205). The median walls of the dorso-anal pouch form the proximal portion of the cephalic aorta (*vide* p. 206) ; its lateral walls form fatty tissue. The walls of the ventral pouch are converted into the antennary muscles. The antennary coelom is the largest in the body and forms a variety of structures, viz., the anterior and posterior portions of the cephalic aorta, the investment of the pharyngeal ganglia and of the corpora allata, the fatty tissue, and the antennary muscles.

Intercalary Coelomic Cavities—In *Locusta* the intercalary coelom is first seen during blastokinesis as a pair of very small cavities lying between the antennary and the mandibular mesoderm (fig. 14, Plate 1). Posteriorly its mesoderm is connected with the ectoderm of the mandibular segment by means of a cell strand. The intercalary coelom disappears soon afterwards. A distinct pair of intercalary coelomic cavities are found in the majority of the Apterygota (HOFFMANN, 1911). Among the Pterygota, however, only a few cases are known where these cavities are at all distinct ; these are *Xiphidium* (WHEELER, 1893) ; *Forficula* (HEYMONS, 1895, *a*) ; *Donacia* (HIRSCHLER, 1909, *a*). In the Phasmidae (WIESMANN, 1926), the Blattidae, the Gryllidae, and some other Pterygota they are represented only by a pair of mesodermal cell masses sometimes showing a bilayered condition, but with no distinct cavity. In others even these rudiments are not present. In a number of insects the suboesophageal body arises from the walls of the intercalary coelom. In *Locusta*, as described on p. 228, this body arises from the mandibular mesoderm.

Mandibular Coelomic Cavities—The mandibular coelom is first met with in the 56-hours-old embryo as a pair of small, round cavities lying in the hollow of the mandibular rudiments. Soon their dorsal walls give off cells which are at first indistinguishable from those which compose the rest of the coelomic wall, except that some of them are already bi-nucleate (figs. 18 and 19, Plate 2). These cells rapidly increase in size, become rounded, and meet medially to form a garland-like cluster of loose cells (fig. 23, Plate 2, and fig. 136). This cluster of cells is the suboesophageal body (*vide* p. 228). The walls of the mandibular coelom acquire a secondary connexion with the mesoderm of the first maxillary segment (fig. 101, Plate 6), as also in *Carausius morosus* (WIESMANN, 1926). The mandibular coelomic cavities do not show a division into three pouches. It is, however, possible to distinguish between a ventral portion, which fills the mandibular appendage, and a dorsal portion, which projects upwards beyond the appendage. This dorsal portion does not divide into rostral and anal pouches. In *Carausius* (WIESMANN, 1926) the mandibular coelom is the last one to develop and the first one to disappear in relation to the other coelomic cavities of the head and thorax ; in *Locusta* it is not so. The dorsal mandibular mesoderm gives rise to the suboesophageal body, while the rest of it forms the mandibular muscles. In *Carausius*, according to WIESMANN (1926), the mandibular coelom has a rostral pouch which forms an antennary muscle.

First Maxillary Coelomic Cavities (fig. 15, Plate 2, and fig. 101, Plate 6)—Excepting the labral and the intercalary coelomic cavities, those of the first maxillary segment are the smallest in the body. They first appear in the 56-hours stage as a pair of small, rounded cavities lying in the hollow of the first maxillae. In the 59-hours

stage their wall grows medially for a short distance but the cavities do not extend into them. HEYMONS (1895, *a*) mentions a similar median process in *Forficula*. According to this author and to WIESMANN (1926), the coelomic cavities of the first maxillary segment in several Orthoptera and in *Carausius* respectively first appear as an unpaired median cavity which afterwards becomes paired. This does not obtain in *Locusta*. In the 75-hours stage, the first maxillary mesoderm is seen to be connected with the mandibular mesoderm by means of a lateral strip. It is interesting to note that the first maxillary coelom never extends beyond the hollow of its appendage. Its walls eventually form the muscles of the first maxillae, as is already seen in the 112-hours stage. It does not show a division into three parts as obtains in the other coelomic cavities. In fact, it does not even develop a dorsal pouch. It therefore corresponds largely to the ventral portion of the other coelomic cavities.

Labial Coelomic Cavities (fig. 101, Plate 6)—The second maxillary or labial coelomic cavities first appear in the 56-hours stage when they lie in the hollow of their appendages. They grow very rapidly. Already in the 70-hours stage they show a long dorso-rostral and a short dorso-anal pouch. The former extends to the proximal ectoderm of the latter ; it is, however, not connected with the mesoderm of the first maxillary segment. The ventral pouch fills the hollow of the second maxillary appendage and forms the labial musculature ; this process is already evident in the 94-hours stage. The dorso-rostral and anal portions contribute to the formation of the splanchnic mesoderm, the lateral myoblast plate, and the fat-body in a manner similar to that obtaining in the thorax. The second maxillary coelom is the largest of those belonging to the jaw segments and is in size and appearance very similar to that of the thorax. Unlike the latter, however, its dorsal portion is not divided into upper and lower halves by means of a horizontal septum. The small mandibular and first maxillary coeloms correspond largely to the ventral portion of the fully developed second maxillary coelom. In *Carausius morosus*, WIESMANN (1926) finds a secondary connexion between the walls of the second maxillary coelom with those of the antennary coelom. This is not seen in *Locusta migratoria*.

(*b*) Coelomic Cavities of the Thorax (figs. 3–6, Plate 1)

The coelomic cavities of the three thoracic segments arise and develop in a similar manner and may therefore be treated together. Like the cephalic coelomic cavities, those of the thorax also first develop in the hollow of their appendages and lie obliquely. Their median, dorso-anterior end is pointed while the lateral, ventro-posterior end is rounded. In the 75-hours-old embryo, the coelomic cavities show three distinct pouches—the dorso-rostral, the dorso-anal, and the ventral. The first two reach dorsally far beyond the hollow of the appendage ; anteriorly and posteriorly they extend into the intersegmental areas in such a way that the distal tip of the rostral pouch of one segment lies beneath the proximal tip of the anal pouch of the preceding segment without, however, touching the latter. The rostral pouch is also connected with the ectoderm by means of a thick process. In this stage,

in the segmental region, the mesoderm does not extend very far medianally. In the intersegmental region, however, the rostro-lateral coelomic walls extend medially as a thin single-layered band over the ectoderm, and each fuses with its fellow of the opposite side. In this way is formed the so-called blood cell lamellae or median mesoderm (fig. 3, Plate 1). In a slightly later stage (80-hours) the segmental mesoderm also extends medially (fig. 5, Plate 1) ; this median extension eventually forms the ventral diaphragm whose topographical position is dorsal to the transverse intersegmental muscles formed by the blood cell lamellae. The ventral coelomic pouch lying in the hollow of the thoracic appendage elongates with the growth of the latter. In the 94-hours stage a deep furrow develops in the lateral coelomic walls at the junction of the dorso-rostral with the ventral pouch (fig. 5, Plate 1). This furrow deepens and eventually separates the dorsal from the ventral coelom. The ventral coelom gives rise to the leg musculature. It first divides, in each thoracic leg, into two, hollow, thick-walled mesodermal tubes lying along the length of the leg. These tubes are converted into muscles but they retain their hollow nature for a long time. This condition was also recorded by HEYMONS (1895, *a*) in several of the Orthoptera and by WIESMANN (1926) in *Carausius morosus*, and appears to be a peculiarity of the Orthoptera.

Also in the 94-hours stage, the dorsal coelomic portion (both rostral and anal) is divided by a horizontal partition into upper (dorsal) and lower (ventral) halves. This partition develops as a furrow similar to the lateral furrow mentioned above but lies a little dorsal to the latter. Soon the intersegmental partitions between the upper portions of the dorsal pouches of the coelomic cavities disappear. There are thus formed, extending from the first thoracic to the ninth abdominal segment, two continuous lateral tubes. The lower chambers, however, retain their segmental nature ; but their extensions into the intersegmental regions become solid. GRABER (1888, *a*) recorded in *Stenobothrus* a horizontal partition similar to that described above in *Locusta*. It has so far not been recorded in any other family of insects and appears to be a peculiarity of the Acrididae.

At this stage the dorso-lateral end of the median wall of the dorsal coelomic pouch separates from the provisional dorsal closure. A pair of lateral blood sinuses thus arises at the dorso-lateral edges of the embryo. They contain a few blood cells budded off from the mesoderm limiting the sinus ventrally.

The somatic mesoderm thickens considerably and forms the so-called myoblast plate whose dorsal end contains the cardioblasts. It has the following fate : its central portion becomes converted into fatty tissue except at the uppermost end. This latter forms, for a time, the wall of the mid-dorsal blood sinus ; after the completion of the heart it gives out cells which swell to form the pericardial cells. The outer layer of the upper portion of the myoblast plate forms the dorsal suspensory muscles of the heart, while its inner layer forms the pericardial septum.

The median walls of the upper portion of the dorsal pouch forms fatty tissue in the thorax and in the first, eighth, and ninth abdominal segments. In the abdominal segments 2 to 10, it forms the gonads as well.

Regarding the lower portion of the dorsal coelomic pouch, its lateral walls form the vertical muscles of the body-wall, while the median walls form fatty tissue.

This, in brief, is the fate of the thoracic coelomic cavities. Certain other small pouches also develop from these cavities but have not been studied in detail. WIESMANN (1926) describes four such pouches in *Carausius morosus*, and their position and number appear to be the same in *Locusta*.

(*c*) Coelomic Cavities of the Abdomen

The difference between the origin of the coelomic cavities of the first abdominal segment and those of the following ones has already been described. In the 75-hours stage (fig. 101, Plate 6) there are eleven coelomic cavities in the abdomen, and of which the first ten show a division into three portions, viz., into a dorso-rostral, a dorso-anal, and a ventral pouch.

The last or eleventh abdominal coelom (fig. 16, Plate 2, and fig. 101, Plate 6) does not show this triple division and is, in fact, very short-lived. It consists of a pair of long, narrow cavities running dorsally along the proctodaeum. Its walls, as seen both in transverse and longitudinal sections, are distinct from the proctodaeal mesoderm, so that there is no doubt of the independent existence of the eleventh abdominal coelom. It disappears before the 112-hours stage. Its mesoderm merges into that of the proctodaeum and takes part in the formation of the musculature of the cerci and also of the hind-gut ; a portion of it is converted into fatty tissue. Short-lived but nevertheless distinct coelomic cavities of the eleventh abdominal segment also occur in *Blatta** (*Phyllodromia*) *germanica* (WHEELER, 1889 ; CHOLODKOWSKY, 1891 ; HEYMONS, 1895, *a*), and in *Periplaneta* (HEYMONS, 1895, *a*) ; while in other Orthoptera the eleventh abdominal somite is represented only by solid, paired masses of mesoderm cells, as, for instance, in *Carausius morosus* (WIESMANN, 1926).

The further development of the abdominal somites differ from those of the thorax only in so far as the former are associated with the development of the gonads and the genital ducts. Thus the genital cells are differentiated in the median walls of the coelomic cavities from the second to the tenth abdominal segments, but subsequently undergo a concentration so as to become restricted to the abdominal segments 3 to 6. A greater part of the dorsal portions of the abdominal somites form the myoblast plates and the fat-body, precisely as in the thorax. The ventral portions of the abdominal segments 3 and 4 and 6 to 10 form coelomic ampullae which are comparable to the muscle-forming mesoderm of the thoracic legs. Their distribution and fate is discussed below on p. 233.

4—*Some Theoretical Considerations on Coelomic Cavities*

It will be seen from the account of coelom development given above that in *Locusta* each pair of coelmic cavities from the second maxillary to the tenth abdominal segments has three distinct pouches, viz., a ventral, a dorso-rostral, and a dorso-anal.

* NOTE—For "*Blatta*" read "*Blatella* (*Blatta, Phyllodromia*)" throughout.

This division is best seen in the 75-hours stage (fig. 101, Plate 6). (Other coelomic cavities, with the exception of the antennary pair, are very much reduced and do not show this typical division.) Afterwards, the ventral coelom in each of the segments referred to above is severed from the dorsal portion by means of a lateral furrow in the coelomic wall. The dorsal coelom is then divided into an upper and a lower chamber by means of a horizontal partition.

For the purpose of the following discussion, we shall regard the coelomic cavities as divided into two main parts—a ventral and a dorsal. A similar condition was observed by GRABER (1890) in *Stenobothrus* and *Mantis*. It also contains in *Blatta* (CHOLODKOWSKY, 1890), in several other Orthoptera (HEYMONS, 1895, *a*), and in *Carausius morosus* (WIESMANN, 1926), with this difference that here a median sac is also formed in many cases. The division of the coelom of *Blatta* into dorsal, ventral, and median pouches was homologized by CHOLODKOWSKY (1890) to the condition obtaining in *Peripatus* (KENNEL, 1885 and 1888). In both these animals the ventral and dorsal pouches form the leg musculature and the gonad rudiments respectively. The median pouch of *Blatta* CHOLODKOWSKY compared to the segmental funnel of *Peripatus* ; WIESMANN (1926), however, disagrees with this interpretation and regards the median pouch as an unimportant structure acquired afterwards. In this respect I agree with the latter author. The condition in *Locusta* where no median pouch is present is therefore a primary one. The septum separating the ventral and dorsal coelomic pouches of *Peripatus* (SEDGWICK, 1887) is comparable to the lateral (ventral) furrow in *Carausius* and *Locusta*. GRABER (1890) and HEYMONS (1895, *a*), while admitting the similarity between the coelomic structure of various Orthoptera on the one hand and *Peripatus* on the other, regard this merely as a case of analogy. GRABER, for instance, maintains that it is convergence. The similarity, however, not only in the structure but also in the fate of the coelomic cavities, is so great as to suggest an undoubted homology, and it is difficult to understand why these two authors could not concur with CHOLODKOWSKY's view-point. In conclusion, it may be pointed out that the division of the dorsal coelom of *Locusta* into upper and lower chambers appears to be a coenogenetic feature since it is found neither in *Peripatus* nor in *Scolopendra* (HEYMONS, 1901), whose coelom, in other respects, is so similar to that of *Locusta*. Moreover, among insects this feature is restricted to the Acrididae.

5—*The Appendages*

The Labrum (figs. 33–35, Plate 3)—In the 52-hours stage there appears at the mid-anterior edge of the embryo a pair of faint swellings (fig. 125) which are the paired rudiments of the labrum. Its paired nature very soon disappears and already in the 53-hours stage the labrum is an unpaired rounded body partly overlying the mouth. The way in which the labrum, originally in front of the mouth, comes to lie over (ventral to) the latter is interesting. This postero-ventral shifting of the labrum is brought about by a slight dipping-in of the mid-anterior edge of the embryo just

behind the labral rudiments dorsally. The labrum is thus pushed ventro-posteriorly. The anterior notch is soon filled up. In about the 70-hours stage, the labrum develops a cleft in its free edge and soon becomes heart-shaped with a truncated apex. This bifid nature of the labrum is secondary and is to be distinguished from its primary paired origin. In later stages, the labrum becomes sub-quadrate and develops hairy areas on its inner surface.

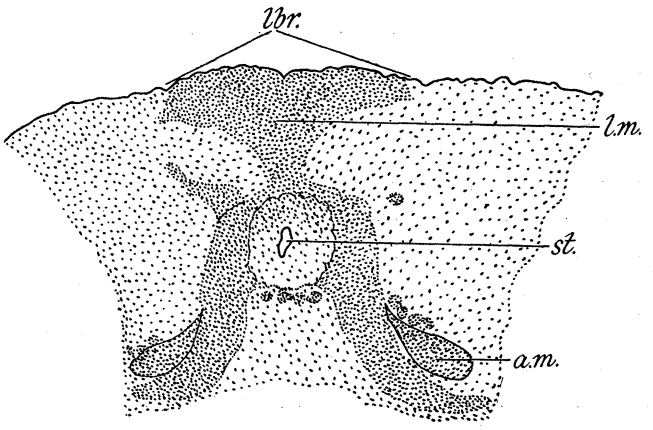

FIG. 125—A portion of the extreme anterior end of a 52-hours-old embryo, showing the paired labral rudiments. The ectoderm is sparsely dotted, while the mesoderm is thickly dotted. × 155.

The mode of origin of the labrum in the Orthoptera and the Dermaptera is given in Table II.

TABLE II

Paired rudiments	Unpaired rudiments
ACRIDIDAE *Stenobothrus variabilis* (GRABER, 1890) *Locusta migratoria* (ROONWAL, present paper)	MANTIDAE *Mantis religiosa* (VIALLANES, 1891)
TETTIGONIIDAE *Xiphidium* (WHEELER, 1893)	GRYLLIDAE *Gryllus* (HEYMONS, 1895, *a*)
PHASMIDAE *Carausius morosus* (WIESMANN, 1926)	BLATTIDAE *Blatta* (*Phyllodromia*) *germanica* (HEYMONS, 1895, *a*)
	DERMAPTERA *Forficula* (HEYMONS, 1895, *a*)

Among other Pterygota the labrum arises as a paired structure in several Lepidoptera (TICHOMIROFF, 1879 ; GRABER, 1890 ; EASTHAM, 1930, *b*), Coleoptera (KOWALEWSKY, 1871 ; NUSBAUM, 1889 ; GRABER, 1888, *a*, 1890 ; HEIDER, 1889 ; WHEELER, 1889 ; HIRSCHLER, 1909, *a* ; BLUNCK, 1914 ; and others), and Hymenoptera (GRABER, 1890 ; CARRIÈRE and BÜRGER, 1897). On the contrary, it is unpaired in origin in

some Hymenoptera (NELSON, 1915), Heteroptera (HEYMONS, 1899), and others. Among the Apterygota it is unpaired, viz., in *Lepisma* (HEYMONS, 1897, *a*), *Tomocerus* (HOFFMANN, 1911), and others. Its unpaired mode of origin among the Apterygota and some of the primitive Pterygota would suggest this to be the primary condition. However, the fact that the paired origin of the labrum is more widely distributed among insects, including the primitive Pterygota, suggests the contrary. On the whole, this difference in the origin of the labrum cannot be shown to have any phylogenetic significance.

The determination of the morphological significance of the labrum is not easy. The fact of its wide distribution (insects, Myriapoda and Crustacea) would seem to leave no doubt that morphologically the labrum is not an unimportant structure. It is also practically certain that the labrum of insects is homologous with that of *Scolopendra* and very probably also with the labrum of the Trilobites and the Crustacea. Whether the labrum is appendicular or not has been much discussed. The following points support its appendicular nature : (1) Its paired origin in several insects. (2) Occurrence of an independent *pair* of coelomic cavities (in *Carausius morosus* and *Locusta migratoria*) lying *in* the labrum. (3) The hollow nature of the labrum, exactly like the other body appendages. The objections to the above view are : (1) The labrum, in contrast to the other body appendages, arises medially to the neural swellings. (2) Its unpaired origin in the Apterygota and some of the Pterygota. On these grounds, HEYMONS (1895, *a*), HOLMGREN (1904), and HIRSCHLER (1909, *a*, 1924) regarded the labrum merely as an unpaired evagination of the primary head segment which does not bear any appendages. As pointed out by WIESMANN (1926), neither the absence of a segmentation in the labrum nor its pre-oral position would, by themselves, prove its non-appendicular nature, since the former character is shared also by the abdominal appendages and the latter by the antennae and the preantennae, at least developmentally. Although in the present state of our knowledge it would be extremely undesirable to dogmatize, it appears to me that the balance of evidence is in favour of regarding the labrum as of an appendicular nature. In arriving at this conclusion, I lay the greatest stress on the newly discovered labral pair of coelomic cavities. The latter bear precisely the same relation to the labrum as do the other coelomic cavities to their respective appendages. To minimize the importance of this point would involve the assumption of three independent postulates, all of which appear to me to be highly improbable. These are : (1) That the close association between the labral pair of coelomic cavities and the labrum is purely accidental and of no morphological significance. (2) That the labral coelom was originally unpaired in conformity with the unpaired labrum and that its paired nature, as seen in *Carausius* and *Locusta*, is secondary. (3) That the very existence of the labral coelom, whether paired or (theoretically) unpaired, is a secondary phenomenon.

A few words are necessary regarding HEYMONS's objection mentioned above, viz., that the labrum, unlike the other body appendages, arises medially to the neural swellings. It is well established that, during the course of embryonic development,

all the cephalic appendages secondarily undergo a more or less marked shifting towards the median line. Also, the preantennary appendages of *Carusius* (WIESMANN, 1926) occupy, in this respect, a position much closer to the median line than do the antennae. In fact, they can hardly be said to lie lateral to the neural swellings, and yet their appendicular nature is undisputed. From this a more median position, as occupied by the labrum, is only another step. Moreover, in those cases where the labrum is paired in origin, it is clearly to be seen that the two labral rudiments at first occupy a relatively large area of the head on either side of the median line, and subsequently undergo a concentration towards the median line. All these facts dispose of HEYMONS's objection quite satisfactorily.

The real objection, then, to regarding the labrum as representing a pair of appendages, is that it is difficult to fit in the existence of a labral segment side by side with the preantennary segment which seems to be well established both on morphological and embryological grounds. The homology of the insect antennae with the antennae of *Scolopendra* and the antennules of the Crustacea is generally accepted and no new evidence has accumulated to doubt its truth. (The view of CARRIÈRE and BÜRGER, 1897, homologizing the insect labrum with the crustacean antennules lacks evidence.) Consequently, while so far there has been shown to exist only one segment in front of the antennulary in the Crustacea and the antennary in *Scolopendra*, the insect head, as seen in *Carausius morosus* (WIESMANN, 1926), has two segments (preantennary and labral) in front of the antennary. In *Locusta migratoria* there is no trace of a preantennary coelom or appendages, while the labral coelom is distinct. If the preantennary and labral coelomic cavities are taken as representing true segments, then such a condition among insects is extremely difficult to fit in with the general scheme of the Arthropod head. The objection that the labral segment, if its existence were postulated, would lack a ganglion is not unsurmountable, since it has not yet been proved whether the protocerebrum is formed of one or more ganglia.

The Antennae (figs. 36–42, Plate 2)—The antennary rudiments arise in the 50-hours stage. Their position is at first behind the oral aperture but subsequently, owing to the backward shifting of the latter, they come to lie in front of the mouth. The antennae elongate rapidly. Already in the 100-hours stage their walls show undulations, and it is roughly possible to distinguish three divisions, viz., a short and broad basal one followed by a long middle portion and a narrower apical one. With further development, the apical division grows more rapidly in length than the others, and also swells up. By the stage one day after blastokinesis, the segmentation of the antennae is nearly established, but in the apical portion the number of segments is greater than the definitive number. In the stage 5 days after blastokinesis, the definitive segmentation is established in the entire antenna. The number of segments in the freshly hatched hopper is 13 in both the sexes ; this number increases during post-embryonic life.

The Intercalary Appendages—The intercalary appendage in *Locusta migratoria* is represented by a thickening of the ectoderm between the antennae and the mandibles

(fig. 101, Plate 6), but no definite evagination is formed. This thickening is first seen in the 75-hours stage and lasts a long time ; it disappears before hatching. The intercalary or premandibular segment was first described by VILLANES (1891) in the Orthoptera on the basis of his studies on the development of the brain. The ganglion belonging to this segment is the tritocerebral. Evanescent intercalary appendages have been recorded in several Apterygota and in some of the Pterygota. In *Campodea* (UZEL, 1898) and in the grasshopper *Dissosteira* (SNODGRASS, 1903) they persist in the adult. In this connexion it may be mentioned that in some Pterygota, viz., *Donacia* (HIRSCHLER, 1909, *a*) and *Carausius* (WIESMANN, 1926), a pair of appendage-like rudiments is seen lying immediately behind the antennae. These have been interpreted not as intercalary appendages (which are absent in these insects) but as the *paired* rudiments of the hypopharynx, the so-called " Hypopharynxhöcker ". In *Locusta* they are absent and the hypopharynx arises as an unpaired structure (p. 202).

The Mandibles (figs. 43–47, Plate 3)—They first arise in the 52-hours stage and lie behind the antennae. Subsequently, they come to lie at the sides of the mouth. In the 100-hours stage, the mandibles develop, on their inner border, a slight swelling which disappears after a short time. The mandibles then pass through a palp-like stage, but afterwards they become stout and their inner wall becomes thick. By the stage about three days after blastokinesis, teeth are formed on the inner border of the mandibles. Soon afterwards there are established a toothed, a molar, and a hairy area, and the condyles are also distinct.

The First Maxillae (figs. 48–54, Plate 3)—They make their appearance in the 52-hours stage. In the 100-hours stage, a lateral palp and a median galea is differentiated and a few hours afterwards the lacinia makes its appearance. Thence onwards the growth of the first maxillae consists largely in the formation of the usual sclerites (*vide* YUASA, 1920). The basal sclerites are formed from the base of the original maxillary rudiment and no portion of the sternum takes part in it.

The Labium (figs. 55–60, Plate 3)—The labium arises in the 52-hours stage as paired rudiments behind the first maxillae. In the 100- to 112-hours stage, a lateral palp and a median paraglossa are differentiated in each labial rudiment. After blastokinesis the two labial rudiments approach each other and about two days later they fuse together. A glossa is developed, soon after blastokinesis, on both the labial rudiments, but the left one subsequently becomes very reduced. In the freshly hatched hopper as well as in the adult insect both glossae are present, although the left one is extremely small and is visible only from the dorsal side.* Meanwhile a submentum is distinguished at the base of the labium. In the stage about five days after blastokinesis, the submentum is well marked and the labial palps are segmented. All the labial sclerites are differentiated before hatching ; the mentum is not present as a separate sclerite but is probably fused with the submentum. No portion of either the labial or the prothoracic sternum takes part in the formation of the labial

* I am indebted to Mr. K. A. RAHMAN for calling my attention to this.

base, and the posterior border of the submentum represents the true anterior boundary of the prosternum. As already mentioned, the sternum of the labial segment fuses with the two preceding sterna to form the hypopharynx.

HOLMGREN (1909) maintained, on developmental grounds, that the submentum of *Eutermes* is derived from the articulatory membrane between the second maxillary and the first thoracic segments and, ontogenetically, is not a part of the labium. My observations on *Locusta migratoria* do not support this view. According to HEYMONS (1899), in rhynchotan embryos the various portions of the jaw appendages such as the lacinia, galea, palpus, etc., arise independently and unite together secondarily to form the complete jaw appendage. No subsequent work has confirmed this view in any insect and it therefore seems probable that HEYMONS's observations are incorrect.

The Thoracic Legs (figs. 64–72, Plate 3)—The development of the three pairs of thoracic legs is so similar that they may be treated together. They first make their appearance in the 52-hours stage and lie on the outer edge of the primary latero-sternite (*vide infra*). In the 100-hours stage, each leg is seen to consist of five segments which are : (1) subcoxa + coxa + trochanter ; (2) femur ; (3) tibia ; (4) tarsus ; and (5) terminal joint. By the 120-hours stage, the basal joint divides into two segments, the proximal one of which represents the subcoxa ; the tarsal joint becomes 3-segmented. During blastokinesis the trochanter is differentiated from the coxo-trochanteral segment. In the stage about one day after blastokinesis the rudiments of the tarsal pads, the empodium, and the tarsal claws are formed. The first tarsal joint has three pads which is probably a secondary condition. The tarsus of *Locusta*, therefore, is 3- and not 5-segmented, even ontogenetically as shown above. At the time of hatching the thoracic legs consist of a coxa, a trochanter, a femur, a tibia, and three tarsal joints. The basal articular sclerites are not fully developed, this taking place during post-embryonic life. In the elongation of the legs during development, the hind thoracic legs lead the other two pairs from the very beginning.

In about the 120-hours stage, a minute invagination is formed on the ventral surface of the femora of the pro- and mesothorax but not of the metathorax. These invaginations disappear shortly after blastokinesis. Their significance is obscure.

The Abdominal Appendages—In *Locusta migratoria* a pair of appendages is formed on each of the eleven abdominal segments. Those on the first are the pleuropodia and are dealt with separately below. They attain a considerable size but eventually shrivel up and are shed during hatching. The appendages of the abdominal segments 2 to 7 are small and disappear during blastokinesis. The eighth pair of abdominal appendages are also small and disappear completely in the male. In the female they become reduced and probably eventually disappear. The ninth pair of abdominal appendages persist in the female as the upper (lateral) ovipositor valves, while the tenth pair, in the same sex, disappears during blastokinesis. In the male the ninth and tenth pairs of abdominal appendages fuse together to form the aedeagus

and associated parts. The appendages of the eleventh abdominal segment form the cerci in both sexes. (Also *vide* p. 232.)

Pleuropodia—The pleuropodia or the first abdominal appendages arise in the 53-hours stage as lateral evaginations of the body-wall in precisely the same way as the thoracic appendages with which they are homologous. With growth they become saddle-shaped and acquire a position on the pleura. They are joined to the body-wall by means of a short, narrow stalk (fig. 74, Plate 3). The mesoderm extends into the stalk of the pleuropodium, but in the cavity of the appendage itself only a few loose mesoderm cells are met with. The pleuropodia measure about 0·18 mm. in length in the 112-hours stage. They attain their maximum development during blastokinesis when they are about 0·35 mm. long. At this stage their wall consists of large, columnar cells with rounded nuclei and present the appearance of gland cells. After blastokinesis, the pleuropodia begin to shrivel up. Ultimately, in an embryo about to hatch, they are reduced to shrivelled, brownish bodies showing no distinct cellular structure, but filled with yellowish, highly refractile and yolk-like particles. During the process of hatching the stalk breaks and the pleuropodia are cast off, leaving a temporary scar on the skin of the hopper. The above account of the pleuropodia of *Locusta* agrees closely with that of GRABER (1888, *a*, 1889) in *Stenobothrus*. This author was, however, unable to determine the final fate of these structures.

Several authors, viz., GRABER (1888, *b*), WHEELER (1890), LONGCHAMPS (1904), etc., have given excellent reviews on the pleuropodia of insects, and among more recent works may be mentioned HUSSEY's (1926) bulky but uncritical review. I shall therefore give only a brief summary of our present knowledge regarding these interesting structures. Since RATHKE (1844) first discovered them in *Gryllotalpa*, they have been recorded in eleven different orders. Among the Apterygota, the ventral tube of the Collembola and the first abdominal appendages of the Protura are probably homologous with them. Pleuropodia are best developed in the more primitive Pterygotes like the Orthoptera, in all of which they are present. Among the more specialized insects (Hemiptera, Hymenoptera, Lepidoptera, Coleoptera) they are feebly developed, and their distribution is irregular. They are absent in the Diptera. Their mode of origin is always similar and they arise, like the other body appendages with which they are homologous, as evaginations of the body-wall. But, notwithstanding the fact that they are temporary embryonic structures, their development and final fate apparently varies considerably in different insects. Thus, in the Orthoptera, they shrivel up during late embryonic life and are probably (certainly in the Acrididae) mechanically cast off during hatching. A similar fate has been recorded in some of the Coleoptera (*Melolontha vulgaris*, GRABER, 1888, *b*) ; the Cicadidae (WHEELER, 1890 ; HEYMONS, 1899) ; *Blatta* (WHEELER, 1890) ; and some of the Hymenoptera (*Hylotoma*, GRABER, 1890 ; and ants, TANQUARAY, 1913). In others it becomes partly [(*Dytiscus*, KORCHELT, 1912 ; BLUNCK, 1914) ; and (*Tenebrio molitor*, CARRIÈRE, 1891)] or wholly [(*Coleoptera* (*Doncaia*, HIRSCHLER, 1909, *a*) ; Hemiptera-Heteroptera (*Naucoris*, HEYMONS, 1896 ; *Belostoma*, WHEELER,

1890, HUSSEY, 1926 ; *Ranatra*, HUSEEY, 1926) ; Lepidoptera (*Pieris rapae*, EASTHAM, 1930, *b* ; and in others] invaginated into the body and there resorbed before hatching.

It would, I believe, be convenient to distinguish between an " *evaginate* " and an " *invaginate* " type of pleuropodial development (fig. 126). In the former the pleuropodia never actually sink beneath the body surface, while in the latter they do so. Between these two extremes numerous intermediates are met with. The existence of the evaginate type of development, which occurs in the Orthoptera among others, appears to be the more primitive. Here, too, as for example in *Locusta*, the outer pleuropodial surface shows, in later developmental stages, a cup-like invagination which, however, does not sink into the body because of the long pleuropodial stalk. In the invaginate type the pleuropodia are sessible, so that the cupping-in of their outer wall makes them sink beneath the surface of the body. Apparently, the

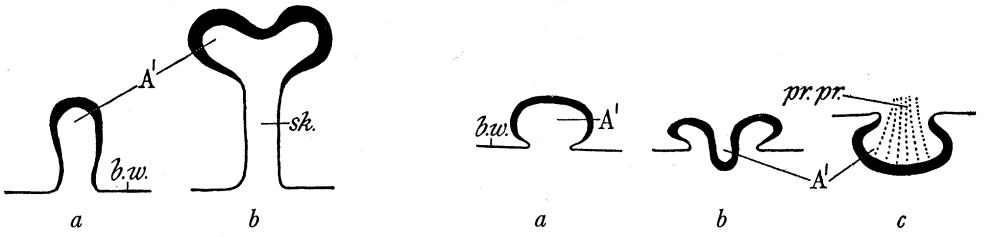

FIG. 126—Diagrammatic representation of the two main types of development of insect pleuropodia (A[1]). A, evaginate type ; B, invaginate type. (*a*), (*b*), (*c*), various stages of development.

invaginate type has been evolved from the evaginate one as a result of the reduction in the length of the pleuropodial stalk.

Little is known regarding their function, although much speculation exists. RATHKE (1844), AYERS (1884), and BAILLON (1920) regard them as respiratory organs, while PATTEN (1884) holds them as sensory. LONGCHAMPS (1904) believes that the pleuropodia assist the embryo in escaping from its membranes and the egg-shell. Some authors (WHEELER, 1890 ; and others) regard them as secretory, while others (HUSSEY, 1926, and others) regard them as excretory in function. It seems to be practically certain that in those cases where the pleuropodia are well-developed (Orthoptera, several Heteroptera, and Coleoptera) they are glandular in function, as is abundantly clear from their structure. But as to what function their secretion might perform is unknown. KORSCHELT (1912) and BLUNCK (1914) maintain that in *Dytiscus* their secretion renders the embryo flexible and keeps it moist so as to facilitate its movements within the egg-shell. The recent discovery of HAGEN (1931) that in the hemipteron *Hesperonectenes fumarius* the pleuropodia function as nutritive organs, analogous to the pseudo-placenta of *Hemimerus* (HEYMONS, 1909 and 1912), is of exceptional interest. In this insect, as in others, the pleuropodia arise as evaginations of the body-wall. Afterwards they sink into the body and send out long, protoplasmic processes which pass out through the open pleuropodial mouth and

enclose the embryo in a protoplasmic sheath. Externally this pleuropodial sheath is in contact with the ovarian walls—(The insect is viviparous and neither chorion nor vitelline membrane surround the egg ; the embryonic membranes have been dissolved at this state.)—Eventually both the pleuropodium and its extensions degenerate before hatching. In conclusion, it may be emphasized that the need is for a physiological determination of the function of the pleuropodia, instead of mere speculation based on histological structure.

6—*The Origin of the Tergum, the Sternum, and the Pleuron* (figs. 70–73, Plate 3)

The first division of each typical segment of the body is into a median sternum and two lateral primary tergal sclerites. The sternum is divisible into a median portion, which may be termed the primary medio-sternite, and two lateral portions, the primary latero-sternites.* The latter bear the appendages. The above description applies from the mandibular to the tenth abdominal segments. The following account of the further development of these sclerites is restricted to the thoracic segments which are typical in this respect. After blastokinesis the lateral edges of the embryo grow round and unite in the mid-dorsal line, thus forming a complete tergum. The legs move laterally and come to lie at the junction of the tergum with the sternum. At the same time, in each of the thoracic segments, the subcoxal joint (*vide supra*) grows and forms a large sclerite, the pleuron, between the tergum and the sternum. Each pleuron becomes divided into an anterior sclerite, the episternum, and a posterior sclerite, the epimeron. The episternum of the prothorax is prolonged into a short spine over the coxa.

It will thus be seen that the pleuron arises from the subcoxa. This was first shown by HEYMONS (1899), on embryological grounds, in some of the Rhynchota. Subsequently, SNODGRASS (1927 and 1929), EWING (1928), WEBER (1928 and 1933), and others have postulated this on morphological evidence. The above observations on *Locusta* confirm this subcoxal theory. WEBER (1933) maintains that in the Orthoptera the dorsal portion of the subcoxa forms the pleuron while the ventral portion disappears. The embryology of *Locusta*, however, shows that the entire subcoxa is converted into the pleuron and the basal articular sclerites of the thoracic legs. SNODGRASS (1929) has given reasons to hold that the subcoxa " has been produced by a secondary subdivision of the primitive limb-base or coxopodite ". I am in agreement with this view.

7—*The Number of Body Segments*

The problem of the number of segments entering into the head of insects has been recently reviewed *in extenso* by WIESMANN (1926) and EASTHAM (1930, *b*), and I need

* This is to be distinguished from the term latero-sternite employed by morphologists. Thus, SNODGRASS (1927) uses the term " latero-sternite " for the lateral portion of the *definitive* sternum with which the ventral portion of the subcoxa is supposed to have fused.

not therefore go into the details of it. The number of segments composing the head of *Locusta migratoria* is seven, as supported by the usual evidence from coelomic cavities, appendages, and nueormeres. This is in agreement with the findings of WIESMANN (1926) in *Carausius morosus* where, besides a labral coelom, a preantennary coelom as well as a preantennary pair of appendages are present. Neither of the last two structures is present in *Locusta migratoria*, but the existence of the preantennary segment here is indicated by a neuromere, viz., the protocerebrum. The labral coelom was first shown by WIESMANN (1926) in *Carausius*, and I have been able to confirm it in *Locusta*. Although evidence points to the existence of a labral segment in insects, it is difficult to fit in with the general scheme of the Arthropod head. This point has been fully discussed on p. 187.

Regarding the segmentation of the abdomen of *Locusta*, eleven segments take part in its formation. Of these, the last or eleventh one is, like those which precede it, provided with a pair of appendages, a pair of coelomic cavities, and a neuromere. The hypothetical twelvth segment or telson is not at all clear in *Locusta*.

Thus the total number of segments composing the body of *Locusta migratoria* is : cephalic 7 + thoracic 3 + abdominal 11 = 21—excluding the acron and the telson which are not developed in this insect.

8—*The Dorsal Closure of the Embryo and the Fate of the Embryonic Membranes*

In an embryo about 59 hours old, a thin membranous *provisional dorsal closure* is formed (fig. 15, Plate 2). It arises from the lateral edges of the embryo at a point slightly above the origin of the amnion and covers the entire dorsum. By its formation it cuts off the yolk from contact with the embryonic inner side and encloses, for the first time, an epineural sinus which contains a few blood cells but no yolk particles. Although resembling the amnion in structure, it is quite independent of this membrane in origin. The precise mode of spreading of the provisional dorsal closure is not clear. GRABER (1888, *a*) noticed a similar structure in *Stenobothrus variabilis*, but was not able to determine its fate. He, however, showed that it arises from the lateral edges of the germ band as two flaps which spread medianally towards each other and ultimately fuse into a single membrane. Most probably it arises in a similar way in *Locusta migratoria*. There is no doubt of the ectodermal nature of this structure. It is peculiar to the Acrididae and is not found in any other family of insects.

The fate of the provisional dorsal closure is remarkable. At first it serves as a gliding surface beneath which the splanchnic mesoderm progresses medially. For some time these two structures stand in very close association. Afterwards they separate from each other near the lateral edges of the germ band and thus the first pair of lateral blood sinuses arise (fig. 127*a*). (Also *vide* p. 207.) The blind ends of the stomodaeum and the proctodaeum are also closely associated with the provisional dorsal closure. During blastokinesis the portion of the provisional dorsal closure lying between the blind ends of the stomodaeum and the proctodaeum snaps

at the edges and grows round the yolk. Its pre-stomodaeal and post-proctodaeal portions remain unchanged until some time after blastokinesis when they probably degenerate, being replaced by the definitive hypodermis. Mid-dorsally it is fused with the amnion which now forms the second provisional dorsal closure of the embryo (fig. 127*b*). It will be seen that at this stage the first provisional dorsal closure forms a temporary mid-gut epithelium. Afterwards the splanchnic mesoderm grows round and separates the first provisional dorsal closure from the amnion. The former provisional dorsal closure then degenerates, leaving the inner layer of the splanchnic mesoderm as the second temporary mid-gut epithelium until the definitive mid-gut epithelium is formed from the ectoderm. Before degenerating, the nuclei of the provisional dorsal closure swell considerably (fig. 102, Plate 6).

The fate of the embryonic membranes and the definitive dorsal closure of the embryo may now be described. A short while before the beginning of blastokinesis, the amnion and the serosa become secondarily attached to each other in front of the cephalic end of the embryo and then rupture there (fig. 128*a*, *b*). As a result, the dorsal serosa becomes attached to the anterior end of the germ band near the point of attachment of the pre-stomodaeal portion of the provisional dorsal closure. The ventral serosa becomes attached to the amnion and both contract towards the hinder end of the embryo. A small portion of the serosa remains at the posterior (micropylar) pole of the egg and forms what may be called a posterior serosal patch (fig. 128). The cells in this rounded patch are at first irregularly arranged. Afterwards, in the stage about two days after blastokinesis, they show a definite bilayered arrangement (fig. 25, Plate 2), enclosing a rather indistinct space in between the two layers. The posterior serosal patch persists until hatching and is then cast off with the egg-wall. So far as I am aware, such a structure has not been described before among insects.* During blastokinesis the contraction and consequent thickening of the embryonic membranes continues and they become more and more restricted to the anterior end of the egg. At the completion of blastokinesis, the amnion forms the second provisional dorsal closure of the embryo (figs. 127*b* and 128, and fig. 102, Plate 6). The former provisional dorsal closure encloses the mid-gut yolk except at the cephalic end of the embryo where the mid-gut yolk is continuous with the yolk in the serosal sac (fig. 128*d*). The serosal sac then rapidly contracts and in so doing pushes its yolk contents into the mid-gut. At the same time (stage about two days after blastokinesis) the thickened serosal wall invaginates at the anterior end, forming a tubular structure, the "dorsal organ", which is composed of degenerating serosal cells (fig. 24, Plate 2, and fig. 128*e*). This organ becomes drawn into the distal end of the mid-gut, where it completely degenerates; no trace of the degenerating cells are visible in an embryo about four days after

* The persistence of the posterior serosal patch until hatching and the dissolution of the rest of the serosa long before hatching appears to me to be of considerable interest from the point of view of Entwicklingsmechanik. Is the degeneration of the serosa induced by its association with the yolk at the cephalic end of the embryo? It would be interesting to know whether these two portions of the serosa which behave so differently in the living egg would do the same in cultures *in vitro*.

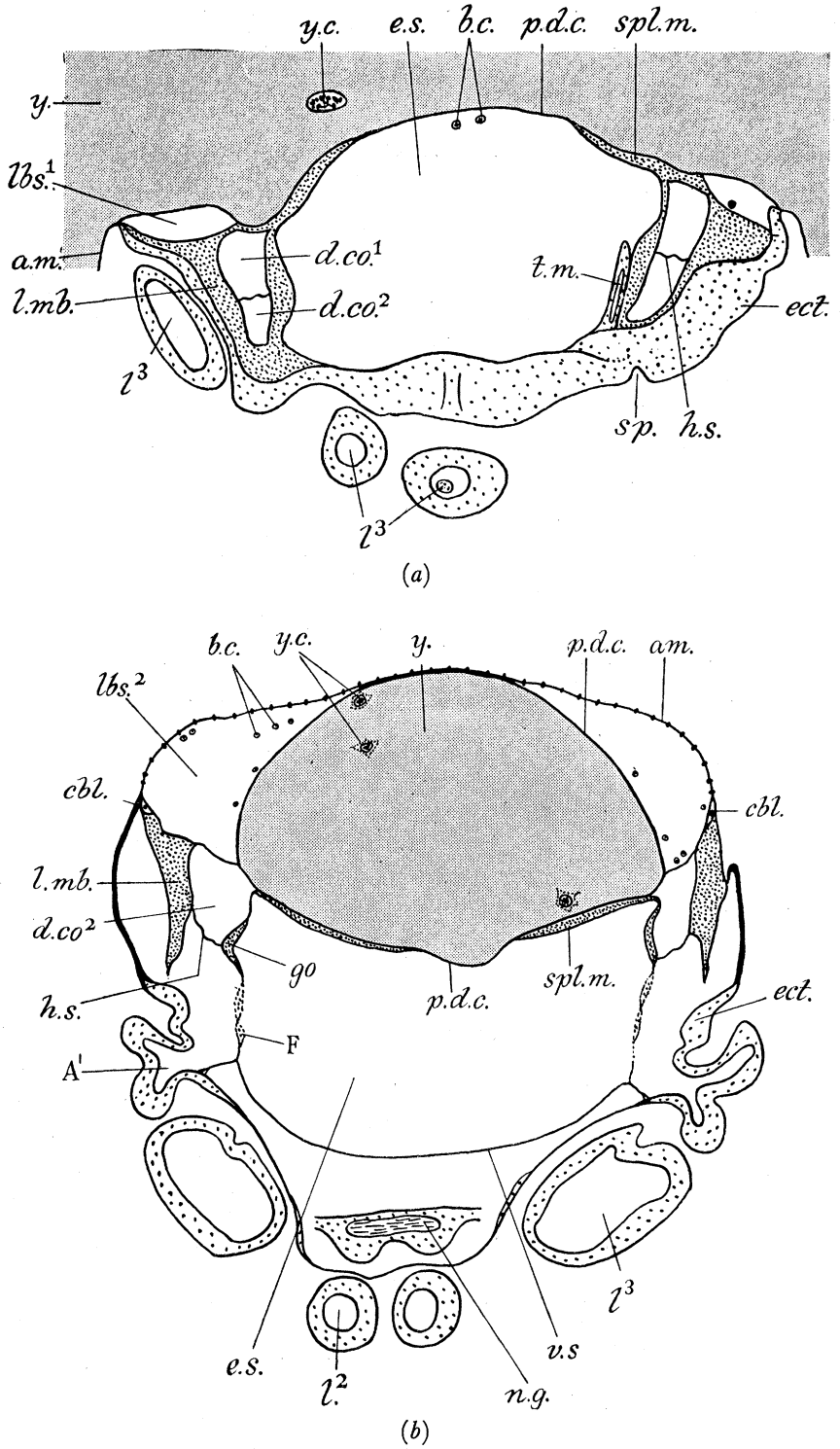

FIG. 127*a*, *b*—Semi-diagrammatic transverse sections of embryo. (*a*) Across the fifth abdominal segment of a 120-hours-old embryo, × about 128 ; (*b*) across the first abdominal segment of an embryo shortly after the completion of blastokinesis ; × about 91.

blastokinesis. In the meantime the amniotic dorsal closure is quickly replaced by the definitive dorsal closure formed by the growth of the edges of the germ band. The amnion becomes restricted to the mid-dorsal region (stage one day after blastokinesis) and there degenerates (fig. 26, Plate 2, and fig. 76, Plate 4). The degenerating amnion cells may extend into the mid-dorsal blood sinus but were not seen, being engulfed by blood cells ; unlike the serosa, they do not attain any structural organization much before degeneration. The definitive hypodermis quickly overgrows the degenerating amnion cells and thus the dorsum formation is complete. At the cephalic end the dorsum formation occurs last, and takes place by the overgrowth of the ectoderm.

It will be seen from the above account that, apart from the presence of the remarkable first provisional dorsal closure, the formation of the definitive dorsal closure and the fate of the embryonic membranes in *Locusta migratoria* is essentially similar to the condition obtaining in those Orthoptera where an internal serosal dorsal organ is formed. These are *Oecanthus* (AYERS, 1884) ; *Periplaneta* (HEYMONS, 1895, *a*) ; *Blatta* (*Phyllodromia*) *germanica* (WHEELER, 1889 ; HEYMONS, 1895, *a*) ; *Gryllotalpa* (HEYMONS, 1895, *a*) ; and *Carausius morosus* (STRINDBERG, 1914, *b*). In *Gryllus* (HEYMONS, 1895, *a*) the amnion forms the dorsal organ ; while the serosa forms the serosal sac in front of the cephalic end of the embryo and is then dissolved into the yolk without forming a dorsal organ. In the Tettigoniids *Xiphidium* and *Orchelimum* (WHEELER, 1893) and in the Mantid *Paratenodera sinensis* (HAGEN, 1917) a third membrane, the indusium, is found. In the first two cases the amnion and the serosa are dissolved into the yolk without forming a dorsal organ which arises from the indusium. In *Paratenodera*, on the other hand, two dorsal organs are formed, one from the serosa and the other from the indusium. It need hardly be pointed out that the serosal, the amniotic, and the indusial dorsal organs are not homologous structures. It will be seen that there is no uniformity in the fate of the embryonic membranes in the Orthoptera.

9—*Blastokinesis* (figs. 128 and 129)

Locusta migratoria shows a marked blastokinesis by means of which the embryo turns, along the posterior pole of the egg, through an angle of 180°. It thus shifts its position from the ventral to the dorsal surface of the egg ; and the embryonic head, which originally pointed towards the posterior pole of the egg, is now turned towards the anterior pole. The process was observed in living eggs from which the chorion had been peeled off, as has also recently been done by SLIFER (1932) in two other grasshoppers, viz., *Melanoplus femur-rubrum* and *M. differentialis*. It occurs about $5\frac{1}{2}$ to 6 days after the egg is laid. But the precise time of its occurrence, as well as the period of its duration, are subject to considerable variations dependent on the individual pecularities of the egg. The entire process is diagrammatically represented in fig. 129*a–g*. When it runs smoothly, it takes about 17 to 20 hours for its completion at 33° C. The rate of turning is not uniform throughout the process.

The first half-period (*a–d*) is accomplished comparatively quickly, lasting roughly for 6 to 7 hours. The period *d–f* is rather slow and takes about 8 hours. The last stages of blastokinesis (*f–g*) are very slow and may take about 4 to 5 hours or slightly more. A peculiarity noted during blastokinesis was that occasionally the process remained stationary for some time and then restarted. Thus, cases were noted in which stage *b* lasted for nearly 6 hours, *c* for 22 hours, and *f* for 13 to 24 hours. In short, blastokinesis in *Locusta* is not always a smoothly running process but sometimes proceeds in jerks.

Shortly before the beginning of blastokinesis, the abdomen of the embryo is slightly twisted and turned towards the dorsal surface of the egg (fig. 129*a*). However, this

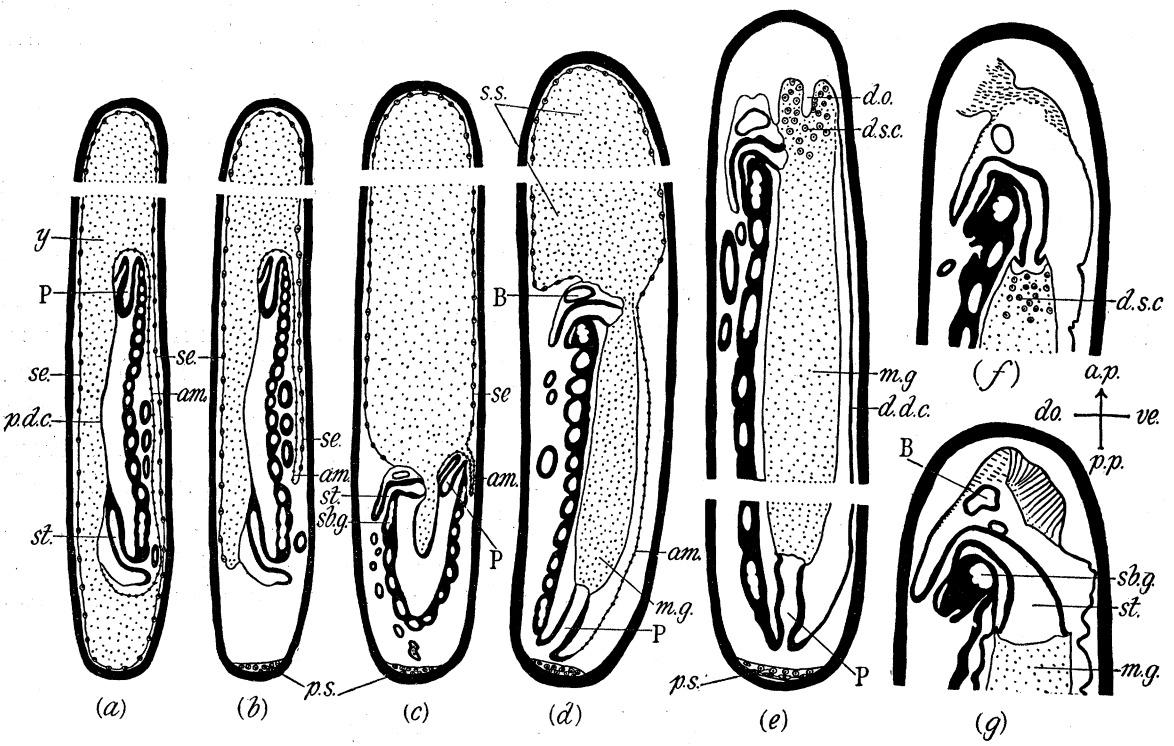

FIG. 128*a*, *b*—Diagrammatic representation of median longitudinal-vertical sections of eggs of various stages. (*a*) Just before blastokinesis and before the rupture of the embryonic membranes, × 30 ; (*b*) before blastokinesis but after the rupture of the embryonic membranes, × 30 ; (*c*) during blastokinesis, × 22 ; (*d*) one day after blastokinesis, × 22 ; (*e*) two days after blastokinesis, × 22 ; (*f*) anterior end of egg about two and a half days after blastokinesis, and shortly before the dorsal closure of the cephalic end, × 22 ; (*g*) anterior end of egg four days after blastokinesis ; the dorsal closure is complete, × 22.

twist is soon lost when the embryo begins to turn. About 2 to 3 hours before the starting of the process, peristaltic movements, originating at the caudal and going to the cephalic end of the embryo, are seen. At the same time the entire embryo pulsates in such a way that its dorsal surface abutting on the yolk expands and contracts. At 33° C., each pulsation lasts for about 1 to 2 seconds while the interval

between two pulsations is 3 to 6 seconds. The rate of pulsation increases with temperature, but critical experiments were not made. The peristaltic movements cause the head of the embryo to strike against the embryonic membranes and rupture them. The latter contract on rupturing, and the embryo now turns round the posterior pole of the egg and reaches its dorsal surface. During the later stages of blastokenisis, the embryonic abdomen contracts considerably and the whole embryo becomes short and stumpy. This account agrees with the findings of SLIFER (1932) in other grasshoppers. She also found that " after completing revolution the embryo turns slowly on its long axis until its ventral portions lie beneath the concave surface of the egg ". I could not find this movement in *Locusta migratoria*. The changes in the embryonic membranes and the enclosing of the yolk during blastokinesis has already been described (p. 194). Finally, it is interesting to note that among the Orthoptera some groups, viz., Acrididae, Tettigoniidae, and Gryllidae, show a full development of blastokinesis which occurs in about the same way as described above in *Locusta*. On the other hand, in the rest of the Orthoptera this

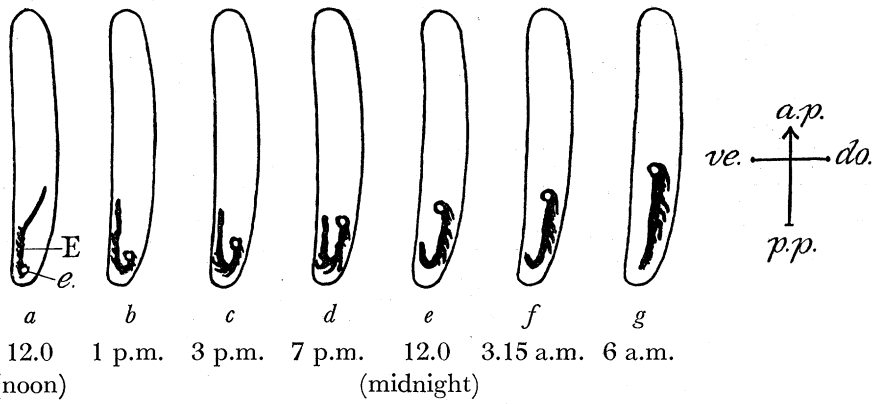

FIG. 129*a* to *g*—Diagrammatic representation of the various stages of blastokinesis, showing a typical example of a smoothly running case. Timings taken from an actual observation. (*a*) Just before the start ; (*d*) middle ; and (*g*) just after the completion of blastokinesis. Note the position of the abdomen in (*a*).

process is either faintly marked or is otherwise profoundly modified from the typical condition (*vide* also WHEELER, 1893). Thus in the Mantid *Paratenodera* (HAGEN, 1917) the embryo turns round along its long axis so as to transport itself from the central to the dorsal surface of the egg ; but there is no change in the direction towards which the cephalic end of the embryo points.

10—*The Corpora Allata* (figs. 27–29, Plate 2)

The corpora allata of *Locusta migratoria* arise, in the stage soon after blastokinesis, as a pair of invaginations of the lateral body wall of the embryo on either side of the intersegmental region between the mandibular and the first maxillary segments. The blind ends of these invaginations are directed medio-dorsally. They soon become

rounded and are eventually severed from the outer ectoderm. Thus they enclose a cavity which is retained for some time but finally becomes filled up, probably with secretory matter, and is then more or less obliterated. The corpora allata then move dorsally and posteriorly and come to lie on the stomodaeum. Their connexion with the stomatogastric nervous system is purely secondary and arises in an interesting way. The inner lateral walls of the antennary coelom grow round the corpora allata so as to invest them with a very thin mesodermal coat. In older stages it is difficult to distinguish this mesodermal covering from the ectodermal portion of the corpora allata. Anteriorly, this investment connects the corpora allata with the pharyngeal ganglia ; its posterior extension forms a nerve-like thread. HEYMONS (1897, *c*) in the Phasmid *Bacillus rosii* FABR. derives this investment from the walls of the mandibular coelom, while WIESMANN (1926) in *Carausius morosus* regards it as belonging to the antennary coelom.

Before HEYMONS (1895, *a*, 1897, *c*) first studied the development of the corpora allata in *Forficula* and in *Bacillus rossii*, they were regarded as true nerve ganglia belonging to the stomatogastric nervous system. HEYMONS attributed to them a glandular function, as was evident from their structure. The recent work of WIGGLESWORTH (1934) suggests that their secretion is probably of a hormonal nature and controls moulting.

The position of the invaginations forming the corpora allata apparently varies in different insects. Thus in *Forficula* (HEYMONS, 1895, *a*) they develop at the bases of the first maxillae. JANET (1899, *a*), in ants, and NELSON (1915), in the honey-bee, regard them as developing from the mandibular segment. In *Pieris* (EASTHAM, 1930, *b*) they belong to the mandibular apodeme. In *Carausius morosus* (WIESMANN, 1926) they arise, just as in *Locusta migratoria*, from the intersegmental region and are not associated with the mandibular apodeme. JANET (1899, *b*), TOYAMA (1902), and WIESMANN (1926), regard the invaginations which form the corpora allata as homologous with the tentorial invaginations. In *Locusta*, where the invaginations of both the corpora allata and the posterior tentorial arms arise from the intersegmental region between the mandibles and the first maxillae, this homology obviously cannot hold good.

11—*The Tentorial and Other Cephalic Invaginations*

Four pairs of cephalic invaginations will be considered here. Of these, the first (starting from the anterior end), second, and third respectively arise in front of, in the level of, and behind the mandibles, while the fourth pair arises behind the first maxillae. The first and third pairs form the tentorium, the second forms the mandibular apodeme, and the fourth gives rise to the salivary glands. Each of these structures is described below.

The Tentorium—In the 90-hours stage a pair of T-shaped invaginations arises between the mandibles and the rudiments of the intercalary appendages (fig. 124). They are small and directed backwards. In the same stage a pair of deep medianally

directed invaginations arises just behind the mandibles. They grow medianally and ultimately fuse together to form the posterior arms and the body of the tentorium. The anterior pair of invaginations proceed backwards and fuse with the body of the tentorium and thus form the anterior tentorial arms. The dorsal arms of the tentorium arise afterwards as outgrowths from the anterior tentorial arms. The mouths of the tentorial invaginations close down and cannot be detected in the late post-blastokinetic stages.

Mandibular Apodemes (fig. 124)—They arise in the 90-hours stage as a pair of epde invaginations near the middle of the inner side of the mandibular base. They reach almost up to the provisional dorsal closure. The lower flexor muscle of the mandibles becomes attached to them.

Salivary Glands (figs. 30–32, Plate 2)—In the stage soon after blastokinesis, a pair of invaginations appear on either side of the base of the ventral aspect of the newly formed hypopharynx. These invaginations proceed backwards and differentiate into the ducts and lobi of the salivary glands which, in the freshly hatched insect, extend as far back as the metathorax. They lie on the ventral septum. Already in the stage one day after blastokinesis, the two invaginations of the salivary glands approach each other and finally fuse together near their mouths to form the common salivary duct. The latter now opens to the outside through a single median aperture.

Discussion—It will be seen from the above account (also *vide* p. 199 under " corpora allata ") that, in all, five pairs of invaginations arise in the head region of *Locusta migratoria*. Their position and fate are summarized in Table III.

TABLE III—SHOWING THE POSITION AND FATE OF THE CEPHALIC INVAGINATIONS

No.	Position of invagination	Fate
1	Between intercalary and mandibular segments . .	Anterior and dorsal arms of tentorium.
2	Inner sides of mandibular bases	Mandibular apodemes.
3	Intersegmental region between mandibles and first maxillae. In front of No. (4).	Corpora allata.
4	Ditto. Behind No. (3)	Posterior arms and body of tentorium.
5	In front of labium. On hypopharynx	Salivary glands.

All these invaginations, except those of the salivary glands, arise early in embryonic development and indeed before blastokinesis. The invaginations of the salivary glands arise after blastokinesis. In other Orthoptera (*Periplaneta* and *Gryllus*) and in *Forficula*, the tentorium arises, according to HEYMONS (1895, *a*), from a pair of invaginations at the base of the antennae and a posterior pair lying in front of the base of the labium. In *Eutermes* (STRINDBERG, 1913) the first pair originates on the upper wall of the mandibles and the second pair at the hinder ends of the first maxillae. In *Pieris* (EASTHAM, 1930, *b*) the first pair arises close behind the antennae and the second pair behind the first maxillae. The last-named author also describes invaginations associated with the premandibular segment (forming the tendon of the

extensor mandibular muscles), the mandibular segment (forming the mandibular glands), and the labial segment (forming the silk glands). He further maintains that the cephalic invaginations " arise in perfect metameric fashion " which give support " to the orthodox conception of the head's six segmental constitution ". This view appears to be supported by good evidence so far as *Pieris* is concerned. But, in view of the diversity of positions from which the tentorial and other cephalic invaginations arise in different insects, it is difficult to accept this conclusion as final. *Locusta migratoria* does not easily fit into EASTHAM's scheme. Thus, the anterior tentorial arms here belong to the premandibular instead of the antennary segment, and the mandibular apodeme to the mandibular instead of the premandibular segment. Moreover, the corpora allata and the mandibular apodeme do not arise here from a common invagination as they do in *Pieris*, but have their own separate invaginations just behind the mandibles. The position of the posterior tentorial invaginations fall in with EASTHAM's scheme ; and so do the invaginations of the salivary glands which should be homologized with the maxillary glands (hypostigmal of TOYAMA, 1902 in the silk worm) of *Pieris*. In *Locusta* there are no glands corresponding to the mandibular and labial (silk) glands of *Pieris*.

12—*The Hypopharynx* (figs. 30 and 31, Plate 2, and figs. 61–63, Plate 3)

In the stage just after the completion of blastokinesis, the median area of the floor of the buccal cavity immediately in front of the labium becomes thickened and at the same time bulges out to form the hypopharynx. This area, it should be mentioned, arises by the fusion of the sternites of the three jaw segments. Two days before hatching it acquires its characteristic chitinous setae and spines. As the mandibles and the first maxillae move closer to the mouth, the hypopharynx becomes closely associated with them. Such an origin of the hypopharynx was also shown to occur in *Forficula* and several Rhynchota (HEYMONS, 1895, *a*, and 1899). In other insects this structure appears to be associated with the intercalary region, and HIRSCHLER (1924) suggests that this segment also shares in the formation of the hypopharynx. In a few insects the hypopharynx arises as a paired structure (" Hypopharynxhöcker " of the German authors)—as, for instance, in *Donacia* (HIRSCHLER, 1909, *a*) and in *Carausius morosus* (WIESMANN, 1926).

13—*The Splanchnic Mesoderm*

In the 112-hours-old embryo, the dorso-median walls of the coelomic cavities of all the segments posterior to the second maxillary one begin to grow medially beneath and along the provisional dorsal closure (fig. 75, Plate 4). This extension soon becomes solid, although a bilayered arrangement of the nuclei is discernible for a long time (figs. 103, 104, Plate 6). Two lateral bands of splanchnic mesoderm are thus formed. At the blind end of the stomodaeum and the proctodaeum these bands curve medially to meet each other through the stomodaeal and the proctodaeal

mesoderm respectively. The cells belonging to the dorsal layer grow more rapidly and finally meet medially. The nuclei in this layer are arranged irregularly. The ventral layer develops sluggishly. During blastokinesis the splanchnic mesoderm and the provisional dorsal closure exhibit the following arrangement (fig. 86, Plate 4). Lying next to the yolk is the thin, single-layered provisional dorsal closure with the nuclei elongated at right angles to the longitudinal axis of the embryo. Beneath it is a thick layer of splanchnic mesoderm with most of the nuclei elongated at right angles to those of the provisional dorsal closure ; in places it is 2–3 cell-layers thick. It represents the original dorsal layer of the splanchnic mesoderm and is the future rudiment of the circular and longitudinal muscles of the mid-gut. Beneath it again is a single layer of cells whose nuclei are elongated in the same direction as those of the provisional dorsal closure. This is the original ventral layer of the splanchnic mesoderm. Soon after blastokinesis it separates from the dorsal layer to form a thin, short-lived mesentery which bounds the circum-intestinal blood sinus (*vide* p. 207) from the outside. The provisional dorsal closure degenerates shortly after blastokinesis. As the splanchnic mesoderm grows round the yolk, the dorsal layer becomes thin and single-layered, so that in the stage one day after blastokinesis the mid-gut yolk is bounded by two thin mesenteries. In the distal region of the mesothorax the outer mesentery grows upwards to form a connecting sinus which opens into the heart (fig. 77, Plate 4)—this occurs in the stage two days after blastokinesis. This mesentery disappears soon afterwards. Then the inner layer thickens and ultimately differentiates into an inner layer of circular and an outer layer of longitudinal muscles. This process of thickening and subsequent differentiation first begins at the anterio-ventral end of the mid-gut and proceeds backwards and towards the dorsal side ; it is completed shortly before the embryo hatches out. In the meantime the definitive mid-gut epithelium is formed from the ectoderm. The growth of the splanchnic mesoderm is diagrammatically represented in fig. 127*a*, *b*.

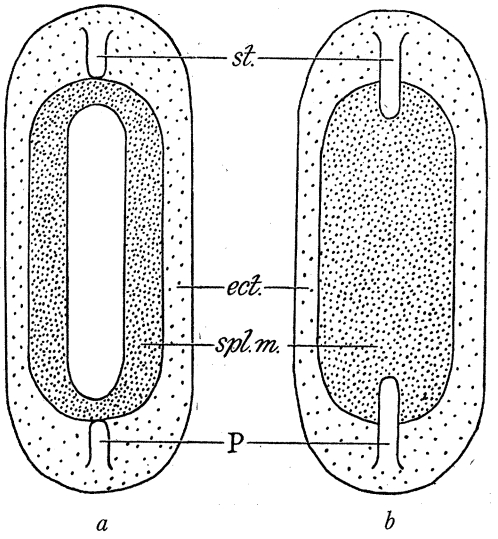

FIG. 130*a*, *b*—Diagrammatic representation of embryo, showing two stages in the development of the splanchnic mesoderm. (*a*) Before and (*b*) after blastokinesis.

It should be pointed out that the above account differs considerably from GRABER's (1888, *a*) interpretation of the development of the splanchnic mesoderm in *Stenobothrus*. According to him, the dorso-median walls of the coelomic cavities of either side rupture, grow medially, and eventually fuse together. Thus there arise two mesodermal membranes lying beneath the provisional dorsal closure. The outer (dorsal) one of these GRABER interprets as the " Hautfasserblatt " or somatic

mesoderm and the inner (ventral) lamella as the " Darmfasserblatt " or splanchnic mesoderm proper. Such a condition does not obtain in *Locusta migratoria* (also *vide* p. 194). It will be seen from the above account that the origin and early differentiation of the splanchnic mesoderm in *Locusta* agrees in essentials with what has been described in other insects. In the details of its later developments, however, it presents certain interesting peculiarities, such as its temporary serving as the mid-gut epithelium and the formation from it of the circum-intestinal mesentery.

14—*The Body-cavity*

The space which appears early in embryonic development between the germ band and the yolk and which contains blood cells, was termed epineural sinus by HEYMONS (1895, *a*). In all insects except the Acrididae it is at first not delimited dorsally, *i.e.*, on the side of the yolk, by a membrane. In the Acrididae, however, this sinus at the time of its first appearance is bound dorsally by the provisional dorsal closure (*Stenobothrus*, GRABER, 1888, *a* ; and *Locusta* (fig. 101, Plate 6). With the growth of the embryo the epineural sinus becomes enlarged, and forms the definitive body cavity which, it need hardly be pointed out, is a haemocoel. With the conversion of the walls of the dorsal coelomic pouches into fat, etc., the coelomic cavities also merge into the epineural sinus (fig. 76, Plate 4).

15—*The Heart, Blood Sinuses, and Associated Haemal Tissues*

(a) The Heart

The heart or dorsal vessel is formed by special cells, the cardioblasts. The latter are differentiated in the 112-hours stage (fig. 75, Plate 4) as two strings of single (in some places two), large, rounded cells extending from the second maxillary to the seventh or eighth abdominal segments. They are distinguishable from the rest of the inner layer cells by being larger and paler than the latter. They lie at the dorso-lateral border of the myoblast. The cardioblasts make their appearance almost simultaneously in all the body segments so that, soon after their first appearance in the more anterior abdominal segments, they can also be detected as far back as the tenth abdominal segment. As in most other insects, their differentiation occurs from in front backwards. With development the cardioblasts move towards the mid-dorsal line and come to lie beneath the first lateral blood sinus (*vide infra*) which they border from below. At the same time they become crescent-shaped with the concave surface facing upwards (fig. 80, Plate 4).

During blastokinesis the second pair of lateral blood sinuses is formed as described below. When they fuse together in the mid-dorsal line, the result is a single median sinus (fig. 76, Plate 4) which ultimately narrows down into the heart cavity. This process of narrowing down of the median sinus first begins at the posterior end of the embryo and proceeds forwards, as is clearly seen in an embyro one day after blastokinesis. At this stage, the mid-dorsal sinus in the posterior region of the abdomen

is bounded by the following parts : the lateral, ventro-lateral, and dorso-lateral walls are composed of the somatic mesoderm ; dorsally it is bounded by the hypodermis and ventrally by the provisional (mesodermal) mid-gut epithelium. The cardioblasts lie dorso-laterally close to the hypodermis. Inside the sinus a few blood cells can be seen. The dorsal portion of the somatic mesoderm mass (figs. 76, 78, 79, Plate 4), now completely separated from the ventral portion, becomes converted into fatty tissue. Its dorsal and ventral portions, however, do not share in this process but become membranous and acquire a connexion with the body-wall by means of fan-shaped processes. The dorsal membrane ultimately gives rise to the intersegmentally placed suspensory muscles of the heart and the ventral membrane to the pericardial diaphragm. The latter has segmental attachments with the body-wall ; while intersegmentally its lateral ends are in close association with the fat-body and eventually provide openings for the passage of blood.

With the fusion of the cardioblasts, which occurs from the hind to the front end, the heart can be said to have a wall of its own (fig. 79, Plate 4). Dorsally, the cardioblasts remain for a long time attached to the hypodermis. Ventrally, the pericardial diaphragm closes beneath the heart. These changes take place in the stage about two days after blastokinesis.

At this stage it is seen that in the distal region of the mesothorax the heart communicates with the circum-intestinal blood sinus (*vide infra*) by a long, slit-like passage (fig. 77, Plate 4). Elsewhere the heart has no communication with this sinus. Their relations are described fully while dealing with the circum-intestinal blood sinus.

(b) The Cephalic Aorta

The cephalic aorta develops from the internal walls of the dorso-rostral and dorso-anal pouches of the antennary coelomic cavities. It is convenient to divide its development into two parts, viz., that of (*a*) the anterior portion which forms the so-called blood-distributing apparatus or pulsatile vesicle, and (*b*) the posterior portion which forms the aorta proper.

(i) *The Anterior Portion of the Cephalic Aorta*—This develops from the dorso-rostral pouches of the antennary coelom. Its early development has already been described (p. 180). In the embryo just before blastokinesis (fig. 124), the internal walls of the coelomic pouches concerned meet medially over the stomodaeum, and eventually form the blood-distributing apparatus, as described forthwith. The dorsal portions of the external coelomic walls are converted into fat ; the rest of the wall degenerates. In forming the blood-distributing apparatus, the coelomic walls pass beneath the brain. Here they bend towards each other and finally fuse together to form a dorso-ventrally flattened sinus which becomes continuous with the posterior portion of the aorta (figs. 81–83, Plate 4). The frontal ganglion lies in this sinus. Later on it is converted into a non-muscular tube, the so-called supply tube (" Zufuhrungsrohr " of WIESMANN, 1926). The nuclei in the walls of this tube are elongated in the direction of the length of the tube. Farther anteriorly, the lateral walls of the supply tube bend outwards as thin strips and meet the body wall in the

clypeal region. Medial extensions of these walls later on give rise to a dorsal membrane or diaphragm (fig. 82, Plate 4). Like their dorso-lateral counterpart, the ventro-lateral portions of these coelomic walls also bend outwards without, however, reaching the body wall ; their terminal ends assume a fatty nature.

The anterior portion of the cephalic aorta forms, as already mentioned, the so-called blood-distributing apparatus or pulsatile vesicle described in many Orthoptera (PAWLOWA, 1895, SINÉTY, 1899, WIESMANN, 1926), by means of which the anterior end of the head is supplied with blood. Its development was first studied by WIESMANN (1926) in *Carausius*, with which the condition in *Locusta* agrees except in two respects. Firstly, the ventral lamellae in *Locusta* end in fat body and are not attached to the body-wall ; in *Carausius*, on the other hand, they are attached to the body-wall and do not end in fat. Secondly, muscles are not associated with this structure in *Locusta*, whereas in *Carausius* it is supplied by two pairs of muscles.

The exact mode of functioning of this apparatus is obscure. PAWLOWA (1895) attributed pulsatory movements to the supply tube and the dorsal diaphragm. WIESMANN (1926), however, could not observe any such movements in living embryos and in adults of *Carausius*, but suggests that the diaphragm is probably moved by the muscles associated with it. In *Locusta*, where no such muscles are present in the recently hatched hopper, WIESMANN's explanation obviously cannot hold. I was unable to detect any pulsatory movements in late embryos or in freshly hatched hoppers. PAWLOWA (1895) finds muscles associated with this structure in the adults of *Locusta* (*Pachytilus*) *migratoria* and other Arcididae. If this is so, then these muscles must be a post-embryonic development.

(ii) *The Anal Portion of the Cephalic Aorta* (figs. 81, 83, Plate 4, and fig. 124)—In the stage about one day after blastokinesis, the walls of the dorso-anal pouches of the antennary coelomic cavities are seen to be still diverging away from each other. A day later, their median portions become considerably thickened in the level of the pharyngeal ganglia, and the ventral ends become associated with the latter. The rest of the median walls curve inwards, on either side, in a trough-like manner and ultimately fuse together to form the cephalic aorta—this occurs shortly before hatching. By so doing, the coelomic walls enclose between them a portion of the epineural sinus. The lateral walls of the dorso-anal pouch of the antennary coelom forms the fat-body. The aorta formed in this manner becomes continuous with the heart in the second maxillary segment.

The development of the posterior portion of the cephalic aorta was first studied by HEYMONS (1895, *a*) in *Forficula* ; that of the anterior portion by WIESMANN (1926) in *Carausius*. The posterior portion has also been studied by CARRIÈRE and BÜRGER (1897) in *Chalicodoma*, HIRSCHLER (1909, *a*) in *Donacia*, STRINDBERG (1913) in *Eutermes*, NELSON (1915) in the honey-bee, WIESMANN (1926) in *Carausius*, EASTHAM (1930, *b*) in *Pieris*, and SMRECZYNSKI (1932) in the beetle *Silpha obscura*. All these authors, except HIRSCHLER, agree in the origin of the aorta from the median walls of the antennary coelom in the manner described above in *Locusta*. STRINDBERG, in *Eutermes*, and NELSON, in the honey-bee, however, maintain that in these insects

the walls of the antennary coelom grow round the stomodaeum and fuse together beneath it, so that a portion of the aorta encloses the oesophagus. HIRSCHLER differs from all others in maintaining that in *Donacia* the cephalic aorta arises not from the antennary but from the premandibular mesoderm.

(c) The Embryonic Blood Sinuses

Three kinds of temporary embryonic blood sinuses are formed in *Locusta migratoria*. These are (1) lateral blood sinuses ; (2) dorsal blood sinus ; and (3) circum-intestinal blood sinus.

1 *and* 2. *Lateral and Dorsal Blood Sinuses* (fig. 127*a*, *b*)—Two pairs of lateral blood sinuses are formed. The first pair arises after the formation of the provisional dorsal closure but before blastokinesis. The dorso-lateral ends of both the somatic and the splanchnic moieties of the coelomic walls throughout the length of the embryo meet the provisional dorsal closure from below and glide along it towards the mid-dorsal line. Later on, the outer dorso-lateral end of the somatic mesoderm separates from the provisional dorsal closure. In this way two more or less spindle-shaped, lateral sinuses arise. They are bounded dorsally by the provisional dorsal closure and ventrally by the somatic mesoderm (and sometimes also by the ectoderm forming the lateral edges of the germ band). Isolated cells, presumably blood cells, are present in these sinuses but are very rare. During blastokinesis, the provisional dorsal closure breaks away from the edges of the germ band and curls upwards to bound the yolk for some time. The first pair of lateral blood sinuses are thus destroyed. The amnion, which now forms the dorsal closure of the embryo, becomes joined to the provisional dorsal closure mid-dorsally. Thus a second pair of lateral blood sinuses arise in place of the first one. They are bounded dorsally by the amnion, ventrally by the provisional dorsal closure (afterwards by the splanchnic mesoderm), and laterally by the somatic mesoderm (myoblast plate, etc.). With the growth of the splanchnic mesoderm around the provisional dorsal closure, the latter degenerates. The amnion (afterwards replaced by the definitive dorsal closure formed by the growth of the edges of the germ band) separates from the splanchnic mesoderm (temporary mid-gut epithelium) dorsally, and thus unites the two lateral blood sinuses into a common dorsal blood sinus (fig. 76, Plate 4). Finally, from the latter the true heart cavity arises by the fusion of the cardioblasts of either side, as described above. Sinuses corresponding to the second lateral blood sinuses of *Locusta migratoria* have been recorded by GRABER (1891, *a*) in *Stenobothrus* and by HEYMONS (1895, *a*) in several Orthoptera and in *Forficula*. The first pair of lateral blood sinuses, however, are unique to the Acrididae, and are connected with the formation of the characteristic provisional dorsal closure from the edges of the germ band. GRABER (1889) does not record them in *Stenobothrus* (p. 194).

3. *Circum-intestinal Blood Sinus*—In an embryo about one day after blastokinesis it is seen that the provisional mid-gut epithelium (mesodermal) is invested externally by a thin mesentery (fig. 77, Plate 4, and fig. 112, Plate 7). The latter closely abuts

on the former, but is nevertheless separate from it except in the mid-dorsal region. The narrow space between the two is the circum-intestinal blood sinus. The sinus is often difficult to detect because during fixation its walls tend to collapse and fuse together in places. No blood cells were seen in the sinus, but since it is, in one place, connected with the heart cavity it is regarded as a true blood sinus. As already described above (p. 203), the outer mesentery of this sinus arises from the ventral portion of the splanchnic mesoderm. Except for a short distance in the distal region of the mesothoracic segment (fig. 77, Plate 4), this outer mesentery is intimately fused with the provisional mid-gut epithelium in the mid-dorsal line. This sinus, therefore, is not in communication with the heart* except in the said mesothoracic region, where a long, slit-like connecting sinus is present between the two structures. This condition is met with in an embryo about two days after blastokinesis. Soon

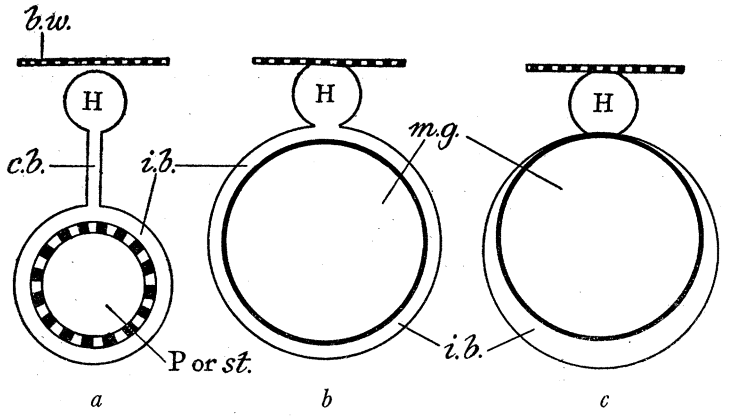

FIG. 131*a* to *c*—Diagrammatic representation of the relation of circum-intestinal blood sinus to heart. (*a*) Proctodaeal region of *Donacia* or the distal mesothoracic region of *Locusta migratoria*; (*b*) mid-gut region of *Carausius morosus*; (*c*) mid-gut region of *Locusta migratoria*.

afterwards the connecting sinus disappears; and so also does the mesentery of the circum-intestinal blood sinus throughout the length of the body.

A transient circum-intestinal blood sinus has also been described by HIRSCHLER (1909, *a*) in *Donacia* and by WIESMANN (1926) in *Carausius morosus*. In both these insects the sinus communicates with the heart.* The three insects in which this sinus has so far been described provide us with a series of stages by which we can visualize the process of reduction of the connecting sinus and, finally, the complete separation of the heart from the circum-intestinal blood sinus. These stages are as follows (fig. 131*a–c*):

(*a*) The heart opens into the circum-intestinal blood sinus by means of a long, slit-like connecting sinus. This obtains in the distal proctodaeal and the mid-gut regions in *Donacia* (HIRSCHLER, 1909, *a*), and in the distal mesothoracic region in *Locusta*.

* At this stage it is perhaps more correct to regard this cavity as a sinus ("medio-dorsalen Blutsinus" of LANG, 1903) rather than as a true cavity of the heart.

(*b*) The heart directly opens into the circum-intestinal blood sinus without the intervention of a connecting sinus—*Carausius morosus* (WIESMANN, 1926).

(*c*) The heart does not open into the circum-intestinal blood sinus but merely abuts on the mid-dorsal wall of the latter. This obtains in *Locusta migratoria* throughout the length of the heart, except in the distal mesothoracic region.

The short-lived occurrence of a circum-intestinal blood sinus in insects is of considerable phyletic importance. Since the heart never has any connexion with the secondary body cavity or coelom, the whole system (heart, circum-intestinal blood sinus, and the connecting sinus) is comparable to the schizocoel or primitive body cavity of the Annelids (*vide* also LANG, 1903 ; FUCHS, 1907).

(d) Pericardial cells (figs. 78, 79, Plate 4)

These cells first make their appearance in an embryo about one day after blastokinesis. They first arise in the thoracic and the first abdominal segment but very soon extend as far back as the eighth abdominal segment, forming an irregular string of large, rounded cells on either side of the heart. They arise from the somatic mesoderm abutting on the ventro-lateral aspect of the heart. These mesoderm cells swell up enormously and acquire the characteristic appearance of the pericardial cells. They persist in the freshly hatched hopper. In structure they remind one of the cells of the suboesophageal body with which they have been homologized by HEYMONS (1895, *a*). Their origin in *Locusta migratoria* agrees with the account of HEYMONS (1895, *a*) in several other Orthoptera and of WIESMANN (1926) in *Carausius*.

(e) Blood cells

Blood cells in insect embryos have been variously described as arising from yolk cells (DOHRN, 1876 ; WILL, 1888) ; from the cells of the serosa (AYERS, 1884) ; from the walls of the heart (WHEELER, 1889, and CHOLODKOWSKY, 1891) ; from undifferentiated mesoderm cells (WHEELER, 1892 ; CARRIÈRE and BÜRGER, 1897 ; and others) ; from mesoderm cells at the junction of the somatic and the splanchnic mesoderm (PATTEN, 1884) ; and, finally, from the median portions of the mesodermal somites just above the ventral nerve chain, *i.e.*, from the so-called " Blutzellenlamellae " of some authors (KOROTNEFF, 1883 and 1885 ; HEYMONS, 1895, *a* ; WIESMANN, 1926 ; EASTHAM, 1930, *b*). In *Locusta* the blood cells arise mainly from the median mesoderm or " Blutzellenlamelle " (*see* pp. 177 and 183), but partly also at the junction of the somatic and the splanchnic mesoderm, as PATTEN maintained for *Blatta*, and even from the splanchnic mesoderm in the pre-blastokinetic stages. It is not possible to assign the origin of blood cells to one single area since loose mesoderm cells (presumably blood cells) are met with in a variety of places. Recent workers, however, are generally agreed that the majority of the blood cells arise from the median mesoderm, and that there is no evidence for their origin from yolk cells or from the walls of the heart. Regarding the morphological nature of the blood cells or haemocytes, some authors (WILL, 1888 ; SCHWANGART, 1904 ; NUSBAUM and FULINSKI, 1906 ; HIRSCHLER, 1909, *a*) regard them as endodermal ; WIESMANN

(1926) in *Carausius morosus* considers them as indifferent or neutral between endoderm and mesoderm; while others regard them as mesodermal. I am inclined to subscribe to the last view.

In several insects, single mesodermal cells have been found to wander into the yolk and to degenerate there. Such cells have been named as paracytes. In *Locusta migratoria* I could not find any trace of them. Their absence is, I believe, related with the very early appearance of the provisional dorsal closure—a structure peculiar to the Acrididae only—as a consequence of which the yolk is cut off from any connexion with the mesoderm before the latter has started budding off many loose cells.

16—*The Fat-body*

The bulk of the median and lateral walls of the dorsal section of the coelomic cavities from the second maxillary to the tenth abdominal segments is converted in the fat-body. The lateral walls of the dorso-anal pouch of the antennary coelom also forms fat, but the labral, the mandibular, and the first maxillary mesoderm do not appear to share in this process. A small portion of the eleventh abdominal mesoderm is also converted into the fatty tissue. This mesodermal origin of the fat-body in *Locusta* is in agreement with the generally accepted opinion to-day regarding the origin of the fatty tissue of insects. HEYMONS (1891) was the first to show this in *Blatta* (*Phyllodromia*) *germanica*, and his conclusions have been confirmed by several authors. GRABER's (1891, *b*) view of the probable origin of the fat-body from oenocytes has found no support from other investigators.

17—*The Tracheal System*

The tracheal system of *Locusta migratoria* first makes its appearance in the 112-hours stage as ten pairs of ectodermal invaginations whose mouths form the spiracles. These invaginations belong to the meso- and methathorax and the first eight abdominal segments. They lie on the primary latero-sternite (*see* p. 193) at the distal end of the segment and laterally to the appendages. Ten pairs of spiracles, similar in position to that in *Locusta*, is the rule among the Orthoptera and the Dermaptera. The meso- and metathoracic spiracles subsequently migrate forwards so that the former comes to lie on the membrane between the prothorax and the metathorax, while the latter comes to lie on the posterior margin of the mesothoracic pleuron (figs. 70–72, Plate 3). The time of the first appearance of the spiracles varies in different insects. In the majority of the Orthoptera, including *Locusta*, they appear when all the body appendages are well developed. In *Forficula* (HEYMONS, 1895, *a*) they are formed soon after the segmentation of the inner layer and the first appearance of the appendages of the head and thorax.

Each spiracular invagination of *Locusta* is directed slightly backwards. Soon it develops, at its blind end, two diverticula—a short medio-dorsal one which is horizontal and a longer latero-dorsal one which is directed slightly backwards (fig. 84, Plate 4). With the growth of the embryo, the median diverticulum acquires

an intimate association with the mesoderm. This is brought about in two ways in the various regions of the body. In the meso- and metathorax and in the eighth abdominal segment its growth, like that of the lateral diverticulum, is limited. Both remain in association with the solid rostral end of the lower mesoderm of the dorsal coelomic pouch ; this rostral mesodermal end forms the fat-body. On the other hand, in the first to seventh abdominal segments, the median diverticulum becomes directed vertically, rapidly grows upwards along the median coelomic wall (posterior to the rostral mesodermal strand), and forms a characteristic structure. This is most marked in the abdominal segments 2 to 6 and less so in the first and seventh abdominal segments. Thus it will be seen that these abdominal spiracular diverticula are associated with that portion of the mesoderm which forms the gonads and the gonoducts. At the same time another median-horizontal diverticulum is formed from the spiracular invagination ; this is very short (fig. 132). Further development of the trachael system has not been followed.

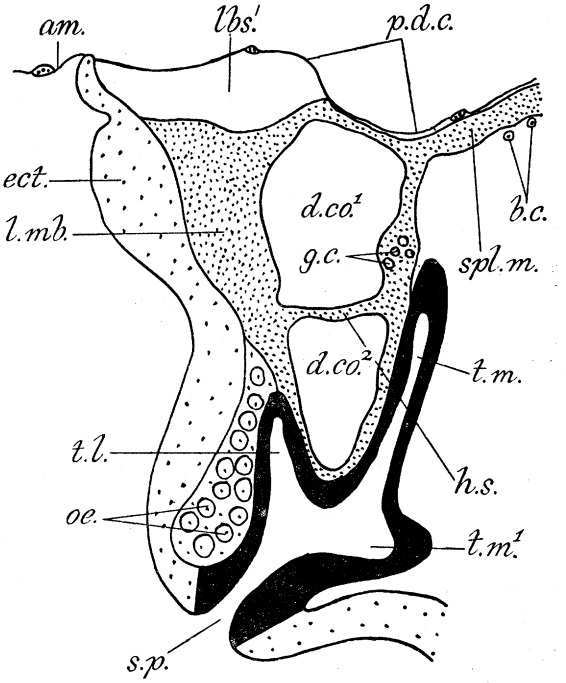

FIG. 132—Portion of a transverse section across the third abdominal segment of a 120-hours-old embryo, showing the spiracular invagination. Semi-diagrammatic. Combined from several serial selections. × 327.

The association thus obtaining between the spiracular diverticula and the mesoderm is so intimate that it is impossible to distinguish between the two in the earliest stages (112-hours stage). No trace of the lateral coelomic wall of the ventral section of the dorsal coelomic pouch can be seen in this stage. Whether it fuses with the ectodermal invagination it is impossible to assert as no intermediate stages could be seen. On the other hand, it is more likely that the lateral mesoderm in this region has simply disappeared. GRABER (1888, *a*) had observed the median diverticulum in *Stenobothrus* but wrongly interpreted it as belonging to the inner layer. A somewhat similar association between the mesoderm and the spiracular invagination, as described above in *Locusta*, also occurs in *Carausius morosus* (LEHMANN, 1925 ; WIESMANN, 1926), with this difference, that in the latter insect the condition obtaining in the first abdominal segment exactly resembles that in the thoracic ones. CARRIÈRE and BÜRGER (1897) also record this association in *Chalicodoma*. The theoretical significance of this intimate association of the spiracular diverticula with the gonadal mesoderm has been discussed by LEHMANN (1925) and RIPPER (1931). They homologize this condition with the development of the nephromixis (*vide* GOODRICH,

1895) in *Peripatus* (KENNEL, 1885 ; GLEN, 1919), the only difference being that in insects no actual connexion obtains between the cavity of the gonads and the ectodermal diverticulum. The condition obtaining in *Locusta* supports this view. However, it is important to point out here that the mere fact of the spiracular invagination touching the mesoderm is by itself of no importance since, by the very nature of its position, the ectodermal invagination is bound to come in contact with the mesoderm, as happens not only in the anterior abdominal but also in the thoracic segments. Therefore, the conclusions of LEHMANN (1925), based on the condition in *Carausius*, were perhaps premature and indeed unjustified. But when we now view them in the light of the condition in *Locusta*, where a truly intimate association obtains between the spiracular invagination and the mesoderm, they become significant.

18—*The Oenocytes*

In the 120-hours-old embryo, the ectoderm near each of the abdominal spiracles becomes thickened, and the nuclei of the cells lying immediately beneath the surface layer or future hypodermis become enlarged (fig. 103, Plate 6). These cells then gradually become segregated from the outlying hypodermis to form the oenocytes. The latter thus consist of segmentally arranged groups of cells which extend cephalad from the neighbourhood of the spiracle into the segment in front. In late embryos (post-blastokinetic stages) the oenocytes extend into the ninth and tenth abdominal segments as well, without, however, exhibiting a segmental arrangement there. Whether these posterior oenocytes arise from their respective segments or are extensions of the oenocytes of the eighth abdominal segment is not quite clear. Probably the latter condition obtains. In their fully differentiated condition the oenocytes, in each abdominal segment (they do not extend into the thorax), form a conspicuous and more or less rounded mass of closely packed cells with large nuclei (fig. 76, Plate 4). They persist in the larva.

It will be seen from this account that the development of oenocytes in *Locusta* is similar to that in other insects. GRABER (1891, *b*), who observed oenocyte formation in *Stenobothrus*, believed that some of them are directly transformed into the fat-body. In *Locusta* also the oenocytes stand in intimate association with the fat-body. Moreover, some of them are richly vacuolated and present an appearance identical with that figured by GRABER. But whether these are actually transformed into fat, it is difficult to say with certainty. In the majority of the Orthoptera, the oenocytes are restricted to the first eight abdominal segments. In *Forficula* (HEYMONS, 1895, *a*), they are present in the ninth, tenth, and eleventh abdominal segments as well.

19—*The Nervous System*

(a) The Ventral Nerve Chain

In the jaw segments, the thorax, and the abdomen the neuroblasts first become differentiated, in the 64-hours-old embryo, as a row of four, rarely five, large cells lying on either side of the median line of the ectoderm and facing the yolk (fig. 87, Plate 5). They are easily distinguishable from the rest of the ectodermal cells, the

dermatoblasts, by their large size and their massive, rounded nucleus. They first appear in the middle of the segment and then all around, including the intersegmental regions. With regard to the embryo as a whole, their differentiation occurs from in front to behind ; in the 70-hours stage, neuroblast differentiation in all the segments has occurred. In this way, two lateral bands of neuroblasts arise.

Simultaneously with the differentiation and multiplication of the neuroblasts, the germ band ectoderm swells up on either side of the mid-ventral line so as to form a pair of neural swellings which soon acquire a segmental arrangement (fig. 88, Plate 5). These swellings are less marked in the intersegmental regions. The wedge-shaped area in between the neural swellings forms the median cord. Beneath the median cord is a well-marked neural groove. The median cord is at first free from neuroblasts, but very soon one neuroblast differentiates in each intersegmental region (fig. 89, Plate 5). WHEELER (1893) records the same thing in *Xiphidium*, while in *Forficula* HEYMONS (1895, *a*) finds several neuroblasts in each intersegmental section of the median cord.

The neuroblasts divide mitotically and give rise to smaller and darker daughter cells. These arrange themselves in medially directed columns on the yolk or inner side of the neuroblasts and are the future ganglion cells (fig. 88, Plate 5). The neuroblasts themselves are pushed away from the yolk, until finally a single layer of nuclei remains between them and the periphery of the embryo. Whether the daughter cells also divide is not clear ; I have not seen any of them dividing. This neurogenic tissue then gradually becomes concentrated into ganglia which acquire a segmental nature corresponding to the external body segmentation. The cells of each segment form the ganglion. In about the 112-hours stage, the median cord neuroblasts, at first lying intersegmentally, shift forwards and become incorporated into the ganglion of the preceding segment. The ganglion cells send out long, thin processes, and thus there arise the nerve fibres and the neurospongium which constitute the intersegmental pair of connectives and the transverse commissures in each ganglion. These together form a characteristic ladder-like arrangement. The separation of the ganglionic mass from the dermatogenic tissue first occurs at the dorso-lateral and the ventral sides and afterwards at the lateral aspect of the ganglion. Each ganglion shows at first a mid-ventral furrow (fig. 90, Plate 5), which, with the growth of the nervous tissue, soon disappears. The ganglion cells then spread to the dorsal aspect of the ganglion as well.

In an embryo some time before blastokinesis a thin layer of elongated cells is seen to cover the neurogenic tissue dorsally (fig. 90, Plate 5). This is the neurilemma. Its origin is not clear, but it probably arises from the outlying ganglion cells themselves. The precise determination of its origin is rendered difficult by the presence of various loose cells, of different origins, which lie in a more or less close association with the neurogenic tissue. This undoubtedly is the cause of the difference of opinion regarding its origin in various other insects, although, like the rest of the nervous system, it is likely to be a strictly homologous structure throughout the insect world. It has been variously claimed as arising from wandering blood cells

(NUSBAUM, 1883, KOROTNEFF, 1885), from the intraganglionic regions of the median cord (WHEELER, 1893), from the dermatoblasts (HEYMONS, 1895, *a*), and from transformed ganglion cells themselves (NELSON, 1915 ; EASTHAM, 1930, *a*).

The neuroblasts degenerate rather suddenly. Between the first and second day after blastokinesis they begin to degenerate (fig. 96, Plate 5) ; after this stage no trace of them can be seen. Rarely, a few specially large ganglion cells are met with ; these, however, cannot be identified with neuroblasts.

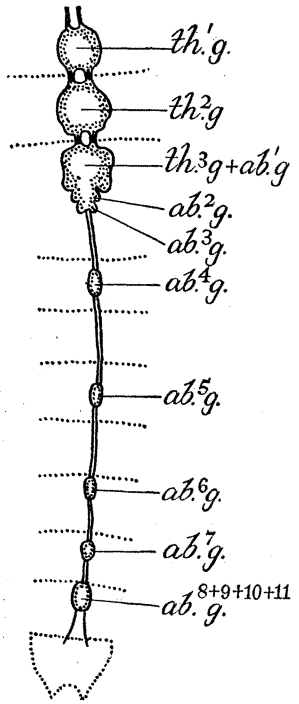

FIG. 133—Portion of the ventral nerve chain of a freshly hatched male nymph. × about 14.

The ganglia of the ventral chain at first closely follow one another, the connectives being hardly formed. However, in an embryo two days after blastokinesis there takes place a rapid elongation of the connectives all along the chain, except in certain regions where the reverse process occurs. Owing to the latter process, the abdominal ganglia lose their segmental character (*vide infra*).

In an embryo four days after blastokinesis, certain peculiar dark-staining bodies are seen in the nerve connectives (fig. 96, Plate 5). They have the appearance of degenerating nuclei and are very refractile. They do *not* extend into the neuro-spongium of the ganglia. So far as I am aware, they have not been described by any previous worker.

The total number of nerve ganglia belonging to the ventral chain is 17, one for each segment from the mandibular to the eleventh abdominal inclusive (fig. 102, Plate 6). The eleventh abdominal ganglion is very small and rudimentary. Of these 17 ganglia, the first three, viz., the mandibular, the maxillary, and the labial, fuse together to form the suboesophageal ganglion. The third thoracic ganglion fuses completely with the first abdominal ; and the second and third abdominal ganglia become closely applied to this centre (fig. 133). In this way a large metathoracic ganglionic centre arises, the so-called "Tetrakiganglion" of GRABER (1891, *a*) in *Stenobothrus*. The fourth, fifth, sixth, and seventh abdominal ganglia remain free. In the freshly hatched insect, the fourth ganglion lies in the middle of the first (ontogenetically the second) abdominal segment ; the fifth in the middle of the third abdominal segment ; the sixth in the distal portion of the fifth abdominal segment ; and the seventh in the middle of the sixth abdominal segment. The last abdominal ganglionic centre is a composite of four ganglia, viz., the eighth, ninth, tenth, and eleventh abdominal ; it lies in the middle of the seventh abdominal segment. Thus the original metamery of the abdominal ganglia is completely altered. GRABER (1891, *a*) could not find in *Stenobothrus* an eleventh abdominal ganglion, which in *Locusta* is small but distinct. The occurrence of a neuromere in the eleventh abdominal segment has also been recorded in *Leptinotarsa* (*Doryphora*) (WHEELER, 1889) ; *Hylotoma* (GRABER, 1890) ; *Gryllotalpa*, *Periplaneta*, and *Gryllus*

(HEYMONS, 1895, *a*) ; some Odonata and Ephemeroptera (HEYMONS, 1896) ; *Lepisma* (HEYMONS, 1897, *a*) ; *Chalicodoma* (CARRIÈRE and BÜRGER, 1897) ; *Donacia* (HIRSCHLER, 1909, *a*) ; and *Apis mellifica* (NELSON, 1915 and 1918).

(b) The Brain

As in all insects, the brain of *Locusta migratoria* consists, developmentally, of the proto-, deuto-, and tritocerebrum which correspond to the first three cephalic segments respectively, viz., to the oral,* the antennary, and the intercalary. The entire brain, with the exception of the optic ganglion, arises in a manner essentially similar to that described already for the ventral chain of ganglia. The neuroblasts are first differentiated in the 59-hours stage in the protocerebral and slightly later in the following two portions of the brain. Each of the three portions of the brain are dealt with separately below.

The protocerebral rudiments (figs. 91 and 94, Plate 5), which lie on either side of the labrum and the stomodaeal invagination, occupy the entire head lobes. They thus extend over a much more considerable area than the deuto- and the tritocerebrum. From the very beginning, the neuroblasts of each half of the protocerebrum are divided into two lobes which are separated from each other by a hypodermal invagination. A third lobe, the optic lobe, is then differentiated from the lateral ectoderm in a manner different from and independent of the other two lobes, but afterwards becomes connected with them (figs. 91, 93, and 94, Plate 5). It is separated from the middle protocerebral lobe by a hypodermal invagination which, like the one between the two median lobes, disappears later on. In this manner, three protocerebral lobes are formed which are generally known as the first (optic), second, and third lobes, counting from the outside. The exact number of neuroblasts in the protocerebral lobes is difficult to determine and appears to be inconstant. They are more numerous (about 4–6) in the median or third lobe and less (about 3–4) in the middle or second one. As in the ventral chain ganglia, the neuroblasts first appear on the inner periphery of the ectoderm and subsequently move towards the outer periphery. Their progeny is arranged in vertical columns over the mother neuroblast cell.

The Optic Lobe (figs. 91 and 93–95, Plate 5)—In the formation of the optic lobe of *Locusta*, neuroblasts do not take part (*see* discussion below). In about the 52-hours stage, the dorso-lateral edge of the head lobes is thickened into a more or less rounded mass, of which the peripheral nuclei are arranged in a single row, while in the rest of the mass they do not exhibit any regular arrangement. This mass is the common rudiment of the optic ganglion and the eye-plate. In a slightly older stage (59 hours) the inner mass (optic lobe) begins to cleft from the outer layer (the eye-plate). The nuclei of the former are somewhat larger and paler than those of the latter. In an 80-hours-old embryo, the separation of the optic lobe from the eye-plate is complete. In the meantime, the optic lobe becomes connected with the middle protocerebral lobe which ultimately forms the opticon or internal medullary mass of the optic lobe

* *See* discussion under labrum on p. 185.

and the optic nerve.* The optic lobe gradually becomes differentiated into its various elements. At first it is divisible into a relatively thin dorso-lateral area containing large nuclei and an inner, more extensive area containing small nuclei. The former is the "*bourrelet périleminaire*" of VIALLANES (1891) in *Mantis*. Later on it is converted into a V-shaped mass near the dorsal third of the lobe, where its position is marked by a peripheral notch. It disappears some time before hatching. The peri- and epiopticons and the external and internal chiasmas are also gradually differentiated. During blastokinesis, the optic lobe acquires a *secondary* connexion with the eye-plate. The nuclei of the optic ganglion near its dorsal edge elongate and send out nerve fibres which go to the retinulae, and form the post-retinular fibres. There is no evidence in my preparations of the retinulae themselves sending out nerve fibres to meet those proceeding from the optic ganglion.

The development of the optic lobe among insects occurs in two different ways, viz., by invagination (Hymenoptera and Coleoptera) and by delamination (Orthoptera and Dermaptera). As will be seen from the above account, the mode occurring in *Locusta* conforms to the latter type. It is generally agreed that no neuroblasts take part in the formation of the optic lobes of insects, and this is true of *Locusta* as well. However, a few doubtful cases of neuroblasts occurring in optic lobes have been reported. Thus VIALLANES (1891) in *Mantis* and HEYMONS (1895, *a*) in *Forficula* claim to have observed neuroblasts in the optic lobes. The connexion between the optic lobe and the eye-plate and the formation of the post-retinal fibres (the optic nerve of some authors—*vide* footnote below) need some comment. In *Mantis* (VIALLANES, 1891) and in *Xiphidium* (WHEELER, 1893), the optic lobe first becomes completely separated from the eye-plate and subsequently acquires a secondary connexion with the latter. On the other hand, in *Forficula* (HEYMONS, 1895, *a*) and in *Eutermes* (STRINDBERG, 1914, *b*) the connexion between the eye-plate and the optic ganglion is primary and the two structures never become separated.

The fate of the other two lobes of the protocerebrum may now be described. The middle or second lobe, as already mentioned, forms the internal medullary mass or opticon of the optic ganglion and the optic nerve or tract. The median or third lobe forms the future protocerebral lobes of the brain. Between the two protocerebral lobes runs the supra-oesophageal commissure which lies transversely in front of and above the stomodaeum. It arises from the protocerebral lobes themselves. The neurospongium in each lobe arises in precisely the same way as in the ventral chain ganglia.

The deuto- and the tritocerebrum, in their mode of origin and further development, are exactly comparable to the ganglia of the ventral chain. They are thus considerably simpler than the protocerebrum and, unlike the latter, are not sub-

* Several writers (WHEELER, 1893; HEYMONS, 1895, *a*; NELSON, 1925; and HIRSCHLER, 1924) regard the post-retinular fibres, lying between the optic ganglion and the retinulae, as the optic nerve. I have adopted the view generally accepted to-day that the optic nerve or tract consists of the fibres lying between the optic ganglion and the first or definitive protocerebral lobe (*vide* HICKSON, 1885; VIALLANES, 1891; WEBER, 1933; IMMS, 1934).

divided into lobes. Originally, they are post-oral in position but subsequently shift forwards in relation to the mouth, so that the deutocerebrum comes to occupy a position distinctly pre-oral, while the tritocerebrum lies beneath and behind the mouth. The two deutocerebral lobes, which at first lie close to each other on either side of the median line, gradually move apart and forwards and lose all evidence of their original connexion. There is no transverse commissure in the deutocerebrum, and VIALLANES (1891) is the only author who claims its existence in *Mantis*. The antennary nerve (fig. 92, Plate 5) arises from the deutocerebrum in a manner similar to that in *Mantis* (VIALLANES 1891), *Xiphidium* (WHEELER 1893), *Apis mellifica* (NELSON, 1915), etc. My preparations do not show the cells of the antennary wall growing inwards to meet the antennary nerve coming from the deutocerebral lobe. The two tritocerebral lobes lying beneath the oral aperture are joined to each other by a transverse commissure, the post- or suboesophageal commissure which, like the supra-oesophageal commissure, arises from the lobes to which it belongs, viz., the tritocerebral lobes. The tritocerebrum gives rise to the circum-oesophageal connectives which unite it to the suboesophageal ganglionic centre. It also innervates the labrum and is connected with the frontal ganglion.

Regarding the supra- and suboesophageal commissures, it will be seen that in *Locusta migratoria* they arise from the lobes to which they belong and the dermatogenic layer takes no share whatever in its formation. HEYMONS (1895, *a*) maintains that in *Forficula* both these commissures arise from a median ectodermal thickening. STRINDBERG (1913, *b*) holds that in *Eutermes* only the suboesphageal commissure arises from the medially lying ectoderm while the supra-oesosphageal commissure owes its origin to the protocerebral lobes. NELSON (1915), in the honey-bee, regards the anterior commissure as arising from the ectoderm, as in *Forficula*, but concerning the hinder commissure he is not definite. In *Locusta* there arises a median ectodermal ingrowth between the protocerebral lobes (fig. 97, Plate 5), but this has nothing to do with the formation of the supra-oesophageal commissure. The latter structure is already present before the formation of the ectodermal ingrowth.

(c) The Stomatogastric Nervous System*

The entire stomatogastric nervous system of *Locusta migratoria* arises in an embryo about 98-hours old, as three unpaired areas of cell-growth in the dorsal ectodermal

* A confusing terminology exists in the various ganglia of this system. I have employed the terminology of IMMS (1934) with the exception of the hypocerebral ganglion, which I have called the occipital. For the sake of clearness, I give below the corresponding names used by other authors :—

Frontal ganglion—Buccal ganglion of BORDAS, 1900.

Occipital ganglion—Oesophageal ganglion of SINÉTY, 1899 ; hypocerebral ganglion of BORDAS, 1900 ; " *ganglion di gozzo* " of PIERENTONI, 1901.

Pharyngeal ganglia—" *gangli pari anteriore* " of PIERENTONI, 1901 ; sometimes also called oesophageal ganglia.

Ventricular ganglia—Ganglion splanchnicum of HEYMONS, 1895, *a* ; " *ganglion du gésier* " of JANET, 1899, *b* ; " *gangli pari posteriore* " of PIERENTONI, 1901 ; sometimes also called stomachic ganglia.

wall of the stomodaeum. The buccal face of the wall usually shows slight wedge-shaped depressions beneath these areas (fig. 134). The mesodermal coat which surrounds the stomodaeum is wanting in these regions. Afterwards, when these masses are well differentiated into ganglia, and separate from the stomodaeal ectoderm, the mesoderm closes beneath them to form an unbroken ring round the stomodaeum. It also grows round to enclose the ganglia. The most anteriorly lying of these areas is situated nearly in the level of the proximal margin of the labrum and is the frontal ganglion (fig. 102, Plate 6, and fig. 134). The second mass arises behind the first and is the common rudiment of the unpaired occipital and the paired pharyngeal ganglia (fig. 100, Plate 5, and fig. 124). The hindmost mass is the common rudiment of the paired ventricular ganglia (fig. 99, Plate 5). These three ganglionic rudiments soon become connected with one another by the recurrens

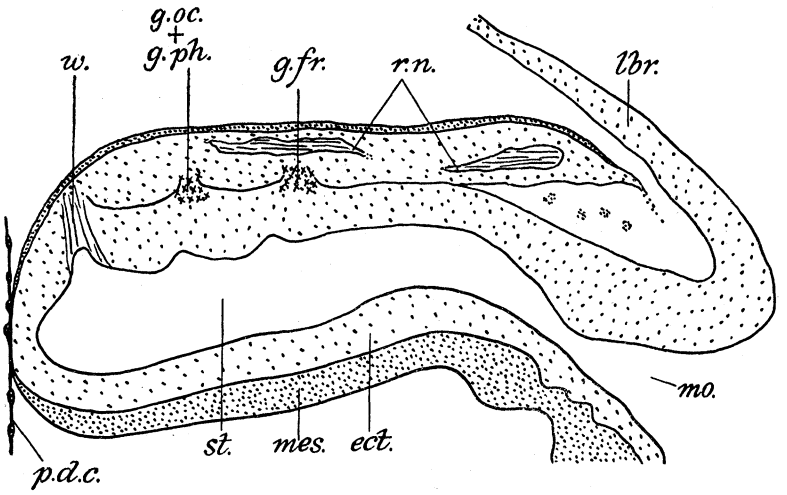

FIG. 134—Longitudinal-vertical section of the anterior end of a 112-hours-old embryo, showing the relation of the stomodaeum to the stomatogastric nervous system. Diagrammatic. In this stage the ventricular ganglion is already divided into two. × about 213.

nerve. The anterior portion of this nerve connecting the frontal ganglion with the occipital one is unpaired, while the posterior portion connecting the occipital ganglion with the two ventricular ones is paired. The two pharyngeal ganglia are differentiated from the median rudiment, mentioned above, at the posterior end of the latter. Later on they become intimately associated with the inner walls of the antennary coelom in the anterior region. Finally, when the latter form the cephalic aorta, the pharyngeal ganglia become *enclosed* in it (figs. 81 and 83, Plate 4). HEYMONS (1895, *a*), who first studied their development in *Forficula*, mentions their association with the antennary coelom ; but whether they become enclosed in the cephalic aorta, he does not say. WIESMANN (1926), in *Carausius*, finds a condition very similar to that in *Locusta*. The hindmost mass forms the ventricular ganglia. The mode in which it becomes paired is interesting. In the 112-hours stage it

divides into two masses, without as yet losing its connexion with the stomodaeal wall. A clear area devoid of nuclei, except at the dorsal periphery, separates the two masses. They are subsequently cut off from the stomodaeum. Each acquires a thin coat of mesoderm and thus forms a discrete ganglion lying at the hinder end of the stomodaeum. The above account of the development of the stomatogastric nervous system in *Locusta* agrees in all essential details with that in the other Orthoptera and Dermaptera (HEYMONS, 1895, *a*; WIESMANN, 1926). The only difference is that in all the forms whose development has been studied previously the ventricular ganglion is unpaired; in *Locusta*, as in all Saltatoria, it is paired.

20—*The Alimentary Canal*

(a) The Fore-gut, the Hind-gut, and the Malpighian Tubules

The Fore-gu (figs. 104, 105, and 106, Plate 6, and fig. 107, Plate 7)—This develops in the 52-hours stage as an invagination near the cephalic end of the embryo. In the early stages of its development it is directed postero-dorsally. At the time of its first appearance, its blind end is free from the cells of the inner layer but shows an outgrowth of cells which eventually form the mid-gut epithelium. The stomodaeal invagination rapidly deepens and its blind end secondarily acquires a covering of inner layer cells which form the stomodaeal musculature. This consists of an inner layer of longitudinal and an outer layer of circular muscles. This sheath of the inner layer also serves to connect the two lateral bands of splanchnic mesoderm. In the 120-hours stage, the blind end of the stomodaeum broadens out and becomes thin. A thin stomodaeal membrane is thus formed which temporarily separates the fore-gut from the mid-gut. Soon after the completion of the mid-gut epithelium, which occurs about five days after blastokinesis, this membrane ruptures. As development proceeds, the stomodaeum acquires a right-angled shape. Later on it becomes U-shaped, one arm (dorsal) of the U eventually becoming much longer than the other (ventral). At the same time, the various regions of the fore-gut are differentiated.

The Hind-gut—The proctodaeal invagination is formed in a manner similar to the stomodaeal invagination, but at the caudal extremity of the body behind the future eleventh (last) abdominal segment. At the time of its appearance, only in the first six abdominal segments is the inner layer segmented. The invagination is first seen in the 59-hours stage (fig. 108, Plate 7), *i.e.*, after the stomodaeum has been formed. This is the general rule among insects, although HASPER (1911), in *Chironomus*, and SEHL (1931), in *Ephestia*, record the reverse condition. The further development of the hind-gut is similar to that of the fore-gut except that, unlike the latter, it does not become U-shaped but remains a more or less straight tube. A proctodaeal membrane temporarily separates the hind- from the mid-gut; it ruptures about two days before the hatching out of the larva. Like the stomodaeum, the proctodaeum also elongates considerably during the last three days of embryonic life when the various regions of the hind-gut are differentiated.

The Malpighian Tubules (figs. 109, 110, and 112, Plate 7)—They first make their appearance in the 117-hours stage. In origin they are definitely ectodermal, arising as outgrowths of the proctodaeal wall near the junction of the latter with the mid-gut epithelium. Six Malpighian tubules thus arise (fig. 136). Of these, two pairs lie ventrally, and are the first to make their appearance (in the 117-hours stage). The other two are dorsal in position and lie a little (about 12 μ) anterior to the ventral tubules. They are formed in the 120-hours stage, thus a little later than the ventral tubules. GRABER (1891, *a*) mentions a similar number, viz., six, of Malpighian tubules in *Stenobothrus variabilis*, and so does WHEELER (1892, *b*) in *Melanoplus femurrubrum*. WHEELER also records the origin of the 6 Malpighian tubules in *Blatta* and *Xiphidium* in two groups of 4 and 2 each, the former developing slightly earlier than the latter, exactly as in *Locusta migratoria*. In works on insect embryology, the origin of the Malpighian tubules is, as a rule, summarily dealt with and they are merely described as evaginations of the proctodaeal wall. The exact

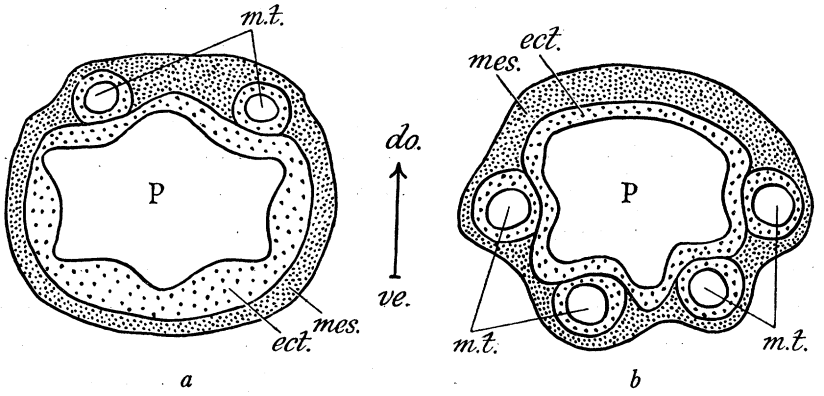

FIG. 135*a*, *b*—Diagrammatic transverse section of the proctodaeal end of a 120-hours-old embryo, showing the two groups of Malpighian tubules. Section (*a*) is about 12 anterior to section (*b*). ×327.

mode of their origin observed in *Locusta migratoria* is therefore of some interest. The area where the tubule is to arise becomes marked out from the rest of the proctodaeal wall by its paleness. The cells in this area then multiply and arrange themselves into a round mass which afterwards acquires a cavity opening into the proctodaeum. From the very beginning, the Malpighian tubules have a covering of mesoderm. All writers on insect embryology are agreed as to the ectodermal nature of the Malpighian tubules. Only HENSON (1932) has recently suggested that they are endodermal in origin. I am not in agreement with this author for reasons given in the foot-note below.* In some insects, the Malpighian tubules open

* HENSON (1932) has attempted to homologize the stomodaeal and proctodaeal invaginations of the *Pieris* embryo with the oral and anal remnants of the blastopore of *Peripatus*. This view is unacceptable. The blastopore of *Peripatus* is formed simultaneously with the differentiation of the endo-mesoderm. The stomodaeal and proctodaeal invaginations of *Pieris*, on the other hand, appear long after the differentiation of the endo-mesoderm (inner layer). Consequently, the stomodaeum, the proctodaeum, and the Malpighian tubules must be regarded as purely ectodermal.

directly to the outside as in *Leptinotarsa* (*Doryphora*) (WHEELER, 1889), *Microgaster* (KULAGNIN, 1892), *Chalicodoma* (CARRIÈRE and BÜRGER, 1897), *Gasteroidea* (HIRSCHLER, 1909, *b*), *Apis* (NELSON, 1915), and *Bruchus* (BRAUER, 1925). In *Chalicodoma* and in *Apis* they are formed before any trace of the proctodaeal invagination is seen. In most other insects, the Malpighian tubules open, from the very beginning, inside the body at the blind end of a more or less deep proctodaeal invagination. According to WHEELER (1889), this condition is secondary. That the Malpighian tubules may arise late in larval life is shown by the Ichneumon *Banchus fermoralis* (BLEDOWSKI and KRAINSKA, 1926) in which they are first seen in the larva about to pupate.

(b) The Mid-gut

In *Locusta* the definitive mid-gut epithelium arises from the ectoderm, as described below in detail.

From the very beginning of its formation, the stomodaeal invagination (fig. 104, Plate 6) shows at its postero-dorsal end a mass of cells which gradually extend backwards along the provisional dorsal closure. This cell-mass is a part of the stomodaeal wall, from which it is in no way separable ; it is thus ectodermal. A similar but smaller outgrowth is formed at the blind end of the proctodaeum and grows forwards. Soon, however, the progres of these outgrowths is considerably slowed down. In an embryo one day after blastokinesis, they extend only about 150 μ beyond the stomodaeal and the proctodaeal membranes ; while three days afterwards this figure has increased only to about 300 μ (fig. 136). Another change which occurs is that, during blastokinesis, the posterior outgrowth extends dorsally and becomes cup-shaped to enclose the end part of the mid-gut yolk. The anterior outgrowth undergoes this change two days later when the cephalic region of the embryo has closed dorsally.

In the meantime, the yolk becomes enclosed by the provisional dorsal closure, and the definitive dorsal closure is also formed, as already described above. At this stage (soon after blastokiness), the provisional dorsal closure forms the first provisional mid-gut epithelium (fig. 127*b*, and fig. 103, Plate 6). Very soon the splanchnic mesoderm grows round the yolk outside the provisional dorsal closure, and also at the open cephalic end of the mid-gut. It thus cuts off the mid-gut from the little that remains of the extra-embryonic yolk. The provisional dorsal closure then degenerates, leaving the thin layer of the splanchnic mesoderm (fig. 112, Plate 7) as the second provisional mid-gut epithelium until about four days after blastokinesis.

On the fifth day after blastokinesis, *i.e.*, two days before hatching, the ectodermal outgrowths at the blind end of the stomodaeum and the proctodaeum quickly spread over the entire yolk to form the definitive mid-gut epithelium (fig. 136*d*). At the same time, the stomodaeal and the proctodaeal membranes rupture, thus connecting the lumen of the mid-gut with those of the fore- and hind-guts.

It will be seen from the above account that in *Locusta* there are two different provisional mid-gut epithelia before the definitive one is formed. The first is formed by

the provisional dorsal closure and is ectodermal ; the second by the splanchnic mesoderm and is mesodermal. The definitive mid-gut epithelium is ectodermal.

When the definitive mid-gut epithelium is complete, many of its cells are seen to send out long, protoplasmic processes which go deep into the yolk (figs. 113 and 114, Plate 7). They give the impression of cells growing *in vitro*. In a freshly

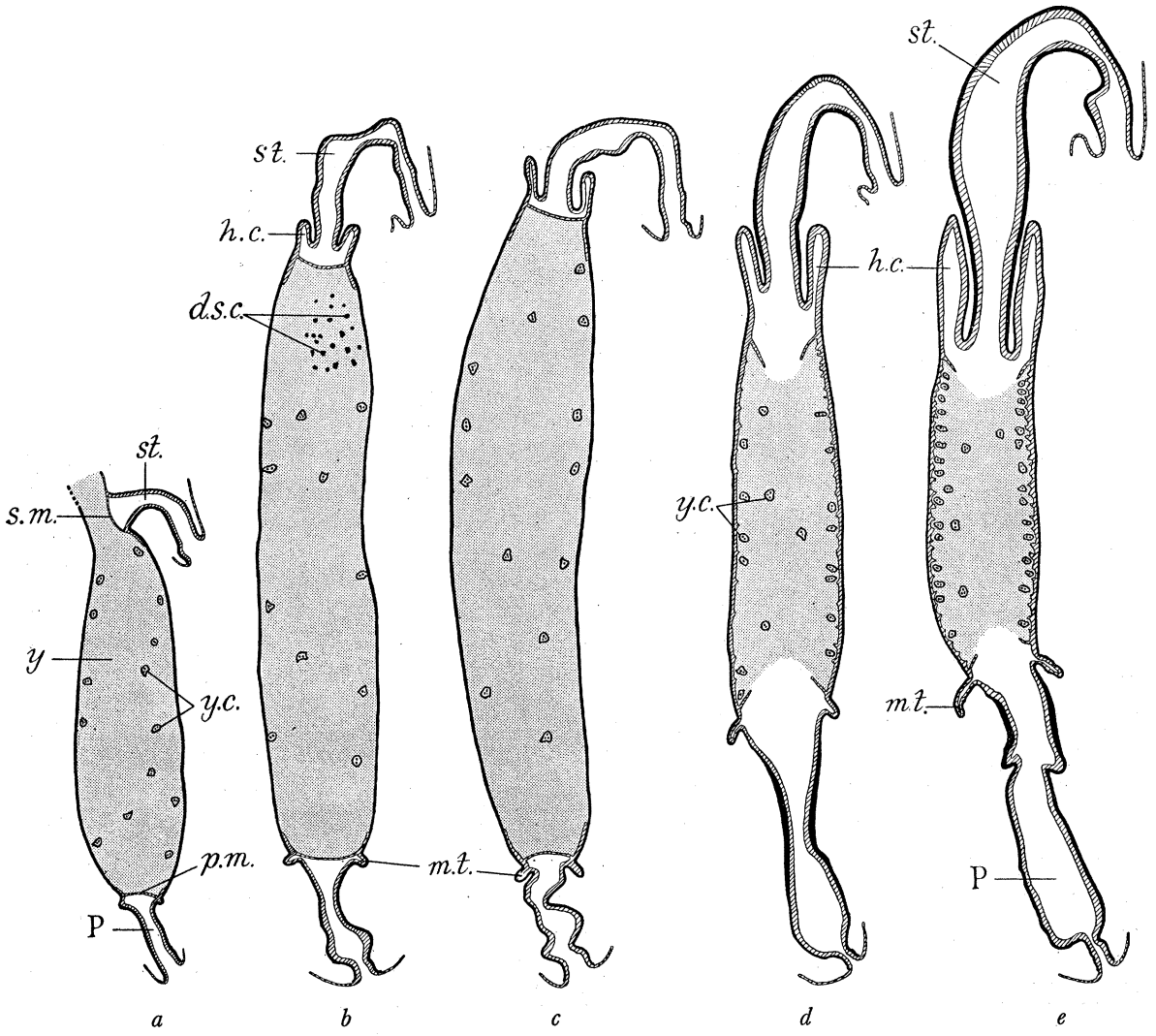

FIG. 136*a* to *e*—Semi-diagrammatic longitudinal-vertical section of the alimentary canal of various stages. Black outline represents mesoderm and red ectoderm. × about 18. (*a*) one day ; (*b*) two days ; (*c*) four days ; (*d*) five days ; and (*e*) six days after blastokinesis.

hatched hopper this condition is still more pronounced. The cells aggregate to form huge, syncitial pyramids which alternate with areas of a single-layered epithelium. This arrangement is by no means regular. GRABER (1891, *a*) describes a similar condition in *Stenobothrus*.

The length of the mid-gut, as measured from the stomodaeal to the proctodaeal membrane, shows interesting changes as shown by the measurements in Table IV.

TABLE IV

Stage.	Length of mid-gut.
1 day after blastokinesis	2·9 mm.
2 days after blastokinesis	4·4 mm.
4 days after blastokinesis	4·8 mm.
5 days after blastokinesis	2·6 mm.
6 days after blastokinesis (about to hatch)	2·0 mm.

It increases in length until four days after blastokinesis, and then undergoes a rapid contraction to less than half at the time of hatching. This suggests that the sudden spreading of the mid-gut epithelium all over the yolk on the fifth day after blastokinesis is probably due as much to the reduction in the length of the mid-gut as to the active extension of the epithelium itself.

Until four days after blastokinesis, the yolk cells are scattered irregularly throughout the mid-gut yolk. On the fifth day after turning, *i.e.*, simultaneously with the contraction of the mid-gut and the spread of its epithelium all round the yolk, the yolk cells migrate towards the periphery (fig. 136*d*). In a freshly hatched larva, the majority of the yolk cells are near the periphery, where they form a kind of pseudo-epithelium. They generally lie in between the pyramidal cell-clusters of the definitive mid-gut epithelium. GRABER (1891, *a*) had observed a similar condition in *Stenobothrus*, and named these yolk cells as " Krokocyten ". Also in other insects (Orthoptera and Hymenoptera) such a pseudo-epithelium of yolk cells and, in some cases, its persistence in larval life has been described. It is found among Orthoptera in *Oecanthus* (AYERS, 1884), *Gryllotalpa* (KOROTNEFF, 1885 ; GRABER, 1890), *Gryllus* and *Periplaneta* (HEYMONS, 1895, *a*), and *Mantis* (GRABER, 1891, *a*), and among the Hymenoptera in *Chalicodoma* (CARRIÈRE and BÜRGER, 1897) and *Vespa* (STRINDBERG, 1914, *a*). The theoretical significance, if any, of this phenomenon, is obvious. It might well represent a recapitulation of the condition obtaining in the insect forefathers when the mid-gut epithelium was of yolk cell origin. It should be emphasized here that there is nothing improbable in an origin of mid-gut epithelium from yolk cells. Unfortunately, the few cases of such an origin among insects (viz., *Lepisma*, *Anurida*, Libellulidae) were not too thoroughly investigated by the original authors, nor have subsequent workers confirmed their results. Consequently, these instances cannot be said to be quite convincing. Recently, however, GRANDORI (1932), while reinvestigating the embryology of the silk-worm, *Bombyx mori*, came to the conclusion that the mid-gut epithelium in this insect arises partly from the ectoderm and partly from the extra-embryonic yolk cells. In several other Arthropods, a yolk cell origin of the mid-gut epithelium has been demonstrated beyond doubt. To mention only one author, MANTON (1928 and 1934) has shown this in the Crustaceans *Hemimysis* and *Nebalia* respectively.

The mid-gut musculature, consisting of an inner layer of circular and an outer layer of longitudinal muscles (fig. 114, Plate 7), arises from the splanchnic mesoderm (*vide* p. 203). GRABER (1891, *a*, p. 55, and fig. 107, Plate 7) makes the curious mistake of describing an outer layer of circular and an inner layer of longitudinal muscles in *Stenobothrus*, which is the reverse of what obtains in *Locusta*. He says, " Von den übrigen Darmwandschichten unterscheidet man sehr deutlich die dem Drüsenblatt zunächst liegende Längsmuskel- (*lm*) sowie die nach aussen folgende Ringsmuskelschichte (*cm*). An die letztere schliessen sich einzelne lockere Zellen (*p*) an, die wohl als Anlage der Peritonealhülle zu betrachten sind ". It is clear from his figure that his inner layer of longitudinal muscles really represents a part of the mid-gut epithelium itself, while his " Anlage der Peritonealhülle " are the longitudinal muscles. Moreover, if GRABER's account were correct, which I am convinced it is not, the mid-gut musculature of *Stenobothrus* would be an exception to all the insects so far studied.

Discussion—In no aspect of insect embryology is there so much diversity of opinion as in the origin of the mid-gut epithelium. That this lack of unity is representative of the true condition regarding the origin of this structure it is difficult to believe. How, then, is it that the mid-gut epithelium has been derived in some insects from the ectoderm, in others from the inner layer (endo-mesoderm), or from early differentiated groups of cells interpreted as the true endoderm, and in still others from yolk cells? (For detailed reviews of the various methods of the origin of the mid-gut epithelium, *vide* KORSCHELT and HEIDER, 1895 ; NELSON, 1915 ; HIRSCHLER, 1924, and EASTHAM, 1930, *a*, *b*.) From time to time attempts have been made to reconcile these conflicting views and bring them into line with an idea which would be consistent with the provisions of the germ layer theory. The mid-gut epithelium in other Arthropods and, indeed, in all other Coelomates, is a derivative of the endoderm. Its ectodermal origin among many insects, therefore, appears anomalous at first sight. However, the fact that actual observations warrant no other conclusion, at least in some insects, is undisputed. To attempt to bring about a forced unity is perhaps not the best way of solving the question.

Below are given the various modes of the origin of the mid-gut epithelium among the Orthoptera and the Dermaptera :—

1—*Ectodermal*

ACRIDIDAE.—

Stenobothrus variabilis (GRABER, 1891, *a*).
Locusta (ROONWAL, present paper).

GRYLLIDAE.—

Gryllus (HEYMONS, 1895, *a*).
Gryllotalpa (HEYMONS, 1895, *a*. But *cf.* NUSBAUM and FULINSKI, 1909).

MANTIDAE.—

Mantis (GRABER, 1891, *a* ; RABITO, 1898).

PHASMIDAE.—

Bacillus rosii (HEYMONS, 1897, *c*. Account fragmentary).

BLATTIDAE.—

Blatta (*Phyllodromia*) *germanica* (HEYMONS, 1895, *a*. But *cf*. WHEELER, 1889, and NUSBAUM and FULNSKI, 1906).
Periplaneta (HEYMONS, 1895, *a*).
Ectobia (HEYMONS, 1895, *a*).

FORFICULIDAE.—

Forficula auricularia (HEYMONS, 1895, *a*. But *cf*. STRINDBERG, 1915, *a*).

2—*Endodermal*

GRYLLIDAE.—

Gryllotalpa (NUSBAUM and FULINSKI, 1909. But *cf*. HEYMONS, 1895, *a*).

BLATTIDAE.—

Blatta (*Phyllodromia*) *germanica* (WHEELER, 1889 ; NUSBAUM and FULINSKI, 1906. But *cf*. HEYMONS, 1895, *a*).

PHASMIDAE.—

Carausius (*Dixippus*) *morosus* (STRINDBERG, 1914, *b*. Account fragmentary. THOMAS, 1936. *Cf*. HAMMERSCHMIDT, 1910, and LEUZINGER and WIESMANN, 1925).

FORFICULIDAE.—

Forficula auricularia (STRINDBERG, 1915, *b*. But *cf*. HEYMONS, 1895, *a*).

3—*Mesodermal*

PHASMIDAE.—

Carausius (*Dixippus*) *morosus* (HAMMERSCHMIDT, 1910 ; LEUZINGER and WIESMANN, 1925. The latter authors derive it from blood cells and the mesoderm (intercalary) of the suboesophageal body ; they call it, nevertheless, " secondary endoderm ". *Cf*. STRINDBERG, 1914, *b*, and THOMAS, 1936).

BLATTIDAE.—

Blatta (*Phyllodromia*) *germanica* (CHOLODKOWSKY, 1888. But *cf*. HEYMONS and others).

It will be seen that in the majority of the Orthoptera, the mid-gut epithelium is regarded as of ectodermal origin. In some cases (*Gryllotalpa*, *Blatta*, *Carausius*) in the same insect different authors have given different interpretations. This shows how difficult it is to arrive at a true understanding of this problem. The interesting condition obtaining in *Carausius* needs some comment. LEUZINGER and WIESMANN (1925) maintain that it arises in this insect from the " secondary endoderm ". The latter is of a mesodermal origin and can be traced back partly to the suboesophageal

body (intercalary mesoderm in this case) and partly to the so-called blood cells (also mesodermal).

THOMAS (1936), on the other hand, regards it as arising from the anterior and posterior endodermal masses. He wrongly interprets these authors when he says that, according to them, the mid-gut epithelium arises " from the blind ends of the stomodaeum and proctodaeum " also, and further that in the post-embryonic stages . . . . the true endoderm is absent and that adult mid-gut is ectodermal. LEUZINGER and WIESMANN do not make these assertions at all.*

Regarding the Acrididae, GRABER (1891, *a*) showed its ectodermal origin in *Stenobothrus*. HEYMONS (1895, *a*), who afterwards had access to GRABER's original preparations, came to the same conclusion. Neither of them mentions the complicated formation of the two provisional mid-gut epithelia occurring in *Locusta*.

Among more recent authors on other insects, some have maintained the mid-gut epithelium as of an ectodermal origin (BRAUER, 1925 ; MANSOUR, 1927 ; SCHEINERT, 1933), and others of an endodermal origin (SHINJI 1924 ; SEIDEL, 1924 ; JOHANNSEN, 1929 ; EASTHAM, 1930, *b* ; SEHL, 1931 ; PATERSON, 1932 ; HENSON, 1932 ; RICHARDS, 1932 ; FERNANDO, 1934 ; THOMAS, 1936, and DRUMMOND, 1936). Still others maintain a mixed origin—from the ectoderm and yolk cells in *Bombyx mori* (GRANDORI, 1932) and in the Ichneumon *Banchus femoralis* (BLEDOWSKI and KRAINSKA, 1926). The last-named authors distinguish three sections of the mid-gut in *Banchus*. These consist of a middle yolk sac which forms the main portion of the mid-gut, and at either ends of it of a small " stomodaeal " and a small " proctodaeal " mid-gut.

HOFFMANN (1914) made an extremely interesting discovery which seems to have escaped the attention of most authors. He showed that while the definitive mid-gut (" sekundäre Mitteldarm ") in the Strepsipteron *Xenos bohlsi* arises from the ectoderm (outgrowth at the blind end of the stomodaeum alone), it is preceded by a " primary mid-gut " formed by the three yolk cells. The latter are comparable to the annelidan macromeres both in their mode of origin (by total cleavage) and their fate. Recently NOSKIEWICZ and POLUSZYNSKI (1928) have come to an almost identical conclusion for another Strepsipteron, *Stylops*, and maintain (p. 1221) that " Der Dotter des *Stylops*-Embryonen kann seinem ganzen Verhalten nach als eine primäres äusserst reduziertes Entoderm betrachtet werden ". Thus, Strepsiptera lend a very weighty support to the idea of a primary and a secondary endoderm and, consequently, furnish us with a key to the whole problem of endoderm formation

* This is clear in their paper. In a private communication (December, 1934), WIESMANN reiterates this. He says that " the entire mid-gut epithelium develops *without exception* from the secondary endoderm ". And further that " the ectodermal swellings at the stomodaeum and the proctodaeum have no developmental significance whatever. Later, when the essential portion of the mid-gut is complete, the ectodermal swellings degenerate ".

I might mention that HENSON (1932, p. 286) also wrongly attributes an ectodermal origin of the mid-gut epithelium of *Carausius* to these authors.

among insects. In them we see conclusively that the primary endoderm is represented by the yolk cells, and that the formation of the definitive mid-gut from the ectoderm is a secondary phenomenon. That there is nothing impossible in an ectodermal insect mid-gut has been discussed by MANSOUR (1934).

HENSON's (1932) view of regarding the stomodaeal and proctodaeal invaginations as endoderm need not engage our serious attention (*see* footnote, p. 220).

JOHANNSEN (1929), although finding that in the Lepidopteron *Diacrisia virginica* Fieb. the mid-gut arises from cell-masses proliferating from the blind ends of the stomodaeum and the proctodaeum, interprets these proliferations as endodermal. He thus reverts to the idea of a " latent endoderm " suggested long ago by HEIDER (1897). RICHARDS (1932) concurs, in the main, with JOHANNSEN but, further, brings in the idea of " prospective significances ". By this he means that " whatever cells in each particular case happen to be appropriately located at the time when the endodermal strands are due to be formed, those cells will be " determined " to form the mid-gut anlage, and subsequently differentiate into the structure typical of mid-gut epithelium ". Needless to say, these views, as well as those of NUSBAUM and FULINSKI (1906) and EASTHAM (1930, *a*), start with the assumption that the mid-gut epithelium cannot be anything but endodermal. Such an assumption is both misleading and not supported by facts.

From this mass of diverse evidence, the following conclusions emerge :

1. That the insect endoderm consists of primary and secondary portions which are made up as follows :

(*a*) *Primary endoderm.* Consists of the primary yolk cells (best seen in the Strepsiptera where they form a " primary mid-gut "), and the yolk cell membrane (found in *Locusta* and *Carausius*).

(*b*) *Secondary endoderm.* Consists of secondary yolk cells, and " cells " formed by secondary yolk cleavage. It may also consist (as, for instance, in *Carausius*) of the derivatives of the inner layer.

2. That the definitive insect mid-gut epithelium, no matter in what manner arising, is, in the majority of insects, a secondary phenomenon. It may arise from :—

(*a*) Pure ectoderm.

(*b*) Inner layer (*i.e.*, from secondary endoderm, as in *Carausius*).

(*c*) Ectoderm + secondary yolk cells (= secondary endoderm).

The only known instance where the *primary* yolk cells form a transient mid-gut (" primary mid-gut " of HOFFMANN, 1914) is in the Strepsipteron *Xenos bohlsi.* This insect is, therefore, of the utmost importance in understanding the fate of the primary endoderm, and the origin of the mid-gut epithelium among insects. (In this connexion the discussion under " gastrulation " in Part I of this paper (1936) should also be consulted.

21—*The Suboesophageal Body*

In *Locusta* the suboesophageal body arises as a paired structure from the mandibular mesoderm. In the 56-hours-old embryo, the dorsal walls of the mandibular coelom are seen to give out cells (figs. 18 and 19, Plate 2) which spread mediodorsally, and soon form an arched body. This is the suboesophageal body. It is composed of large rounded cells which are loosely arranged. In the 75-hours stage it has an extent and shape shown in fig. 137. It ultimately comes to lie beneath the stomodaeum (fig. 23, Plate 2)—hence the name suboesophageal body. Very soon it loses its connexion with the coelomic walls, and thus also the evidence of its paired origin. In the early stages of its development, the only difference between its cells and those of the rest of the coelomic mesoderm from which it arises is the slightly larger size of the former and their nuclei. Further, some of the cells of the suboesophageal body are already binucleate. The origin of this binuclearity is not

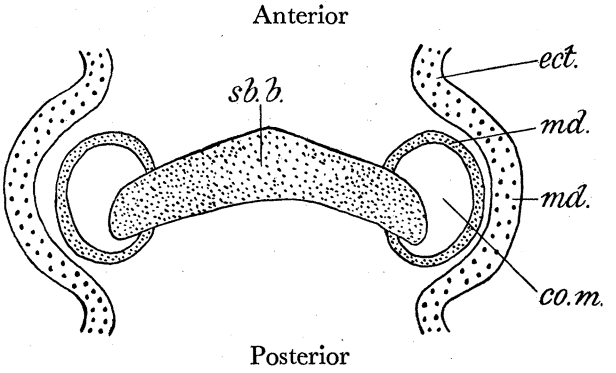

FIG .137—Diagrammatic representation of the mandibular region of a 75-hours-old embryo as seen from the dorsal side, showing the suboesophageal body. Reconstructed from several transverse sections. The suboesophageal body arises from the dorsal wall of the mandibular coelom.

clear since no dividing stages could be seen. The cells rapidly increase in size and their cytoplasm becomes more granular and vacuolated. In the 120-hours-old embryo they are seen to be extremely vacuolated (fig. 20, Plate 2). Shortly before blastokinesis the cells show a marked change in their contents. They become filled with small yellowish bodies which, in stained preparations, exactly resemble yolk particles (fig. 21, Plate 2). At the same time nearly all the vacuoles disappear. It seems that these yolk-like particles (" Dottereinschlusse " of SCHWANGART, 1904) represent secretory (excretory ?) matter which fills the former vacuoles. HEYMONS (1895, *a*), STRINDBERG (1915, *b*, 1916), and WIESMANN (1926) are of the same view. Soon after the appearance of the yolk-like particles, minute, rounded bodies of varying sizes are also seen (fig. 22, Plate 2). These bodies stain an intense black with iron-haematoxylin. Their significance is obscure but they are probably responsible for the disposal of the yolk-like particles mentioned above. The cells rapidly increase in size and reach a maximum during blastokinesis, after which they gradually become smaller. All these changes mentioned above might suggest a

relation to exist between the suboesophageal body and blastokinesis. However, the fact that this body is absent in some insects, which undergo a marked blastokinesis (*Forficula*), and present in others, where no blastokinesis occurs, is against any such hypothesis. The suboesophageal body is present even in the freshly hatched hopper, where it occupies a small area beneath the anterior end of the crop. Whether it persists in the latter instars has not been ascertained. In the late embryonic stages of *Xiphidium* (WHEELER, 1893) and of *Forficula* (HEYMONS, 1895, *a*) the cells of this body become attached to the salivary glands. No such association was observed in *Locusta*.

Discussion—The suboesophageal body has been shown to exist in the embryos of the Orthoptera, the Isoptera, the Rhynchota, and the Lepidoptera. It is usually of a temporary nature except in *Gryllus* and the Blattidae where it persists in the larva (HEYMONS, 1895, *a*), and in the Isoptera where it is present even in the sexually ripe individuals (HOLMGREN, 1909). It is generally unpaired in origin, but in the Orthoptera evidence of its paired origin has been produced (HEYMONS, 1895, *a* ; WIESMANN, 1926 ; ROONWAL, present paper). Notwithstanding the fact that the suboesophageal body shows a strikingly uniform structure and is, in all probability, homologous in all insects, its origin is remarkably varied. Below are briefly summarized the various modes of its origin in different insects. They fall into three main groups, viz. :

(*a*) *Endodermal Origin.*

It arises from the anterior endodermal mass—Lepidoptera (SCHWANGART, 1904 ; HIRSCHLER, 1907 ; JOHANNSEN, 1929) ; Orthoptera (NUSBAUM and FULINSKI, 1906).

(*b*) *Mesodermal Origin.*

(i). From the mesoderm of the intercalary segment—Lepidoptera (EASTHAM, 1930, *b*) ; Orthoptera (WHEELER, 1893 ; HEYMONS, 1895, *a* ; WIESMANN, 1926) ; Isoptera (STRINDBERG, 1913).

(ii). From the mesoderm of the mandibular segment—Acrididae, *Stenobothrus** (GRABER, 1880, 1891, *a*) ; *Locusta migratoria* (ROONWAL—present paper).

(*c*) *Mixed Origin.*

In *Bombyx mori*, according to the recent work of GRANDORI (1932), it arises partly from the mesoderm of the first body segment (*antennary* in this case) and partly from certain migratory cells of an endodermal nature.

The morphological nature of this body is obscure. WHEELER (1893) homologizes it with the green glands of the Crustacea ; in other words, he sees in it a modified nephridium. In support of this view he points out that the crustacean green glands develop from the segment which corresponds to the intercalary segments of insects. HIRSCHLER (1907) accepts this view, although he regards this body to be of endodermal origin. HEYMONS (1895, *a*), STRINDBERG (1913), and WIESMANN (1926), on the other hand, maintain that it represents the rudimentary coelomic remains

* GRABER observed this body in *Stenobothrus*, but interpreted it incorrectly as the " Pro-endoderm Anlage ". He maintained that it arises from the " prognathal ptychoblast " (mandibular mesoderm).

of the intercalary segment. According to LEUZINGER and WIESMANN (1925), a portion of the mid-gut epithelium arises from it. In view of the varied origin of this body among different insects, none of the above explanations can be completely satisfactory.

The function of this body is also problematical, but is assumed to be excretory. WHEELER compares it with the crustacean green glands. HEYMONS, STRINDBERG, and WIESMANN, on the other hand, regard it, functionally, as the equivalent of the paracardial cells present in certain insects (*Forficula*) where this body is absent. These paracardial cells are segmentally arranged all over the body, but are absent in the head. In structure they resemble the cells of the suboesophageal body and are most probably excretory in function. TOYAMA (1902) regards them as giving rise to the main mass of blood cells in *Bombyx mori*, a conclusion which EASTHAM (1930, *b*) could not confirm for *Pieris*. With HEYMONS, I am inclined to regard this body as excretory in function.

22—*The Gonads and the Genital Ducts*

(*a*) The Gonads

The genital cells are first distinguishable in the 112-hours stage (fig. 75, Plate 4), as cells which are larger and paler, and whose nuclei are poorer in chromatin, than those of the surrounding mesoderm cells. They lie in the median walls of the dorsal pouch of the coelomic cavities of the second to the fifth abdominal segments. They are at first segmental but afterwards extend into the intersegmental regions as well. Soon they can be traced as far back as the tenth abdominal segment. As seen in transverse sections of an embryo soon after blastokinesis, each gonad rudiment (figs. 116–118, Plate 7) is spindle-shaped and composed of five parts, viz., (*a*) a dorsally lying terminal filament consisting of a single row of cells ; (*b*) a large dorsal cell-mass lying beneath the terminal filament ; (*c*) a central cell-mass containing genital cells and other mesodermal cells ; (*d*) a small ventral cell-mass lying below the central mass ; and (*e*) follicle cells which limit the gonad rudiment from the outside. Interfollicular cells, as described by GRABER (1891, *a*) in *Stenobothrus*, appear only in later stages in *Locusta*. Towards the beginning of blastokinesis it is possible to distinguish the sexes by the disposition of the terminal abdominal appendages as shown below, and a little later by the gonads as well. Thus the testicular gonads (fig. 116, Plate 7) are smaller than the ovarian ones and tend to become rounded. Also their dorsal cell-mass is reduced and pushed ventrally beneath the central mass. The ovarian gonads (figs. 117, 118, Plate 7), on the other hand, are elongate. Their dorsal cell-mass is conspicuous, and retains its original position ; the nuclei in it are arranged in a single row. The fate of the various portions of the gonads is as follows :—*Male.* The terminal filament serves to connect the testes of the two sides. The dorsal cell-mass becomes incorporated into the central cell-mass which forms the testis proper. The ventral cell-mass gives rise to the gonadal portion of the vas deferens, which does not show any lumen at the time of hatching. The follicular cells form the outer covering of the testis

and of the gonadal portion of the vas deferens. *Female.* The terminal filament gives rise to the corresponding structure in the ovarioles and to a portion of the ovarian suspensorium. The dorsal cell-mass forms the germarium, while from the central cell-mass there arise the oogonia and the interfollicular cells. The ventral cell-mass forms the egg-calyx and the follicular cells give rise to the outer membrane

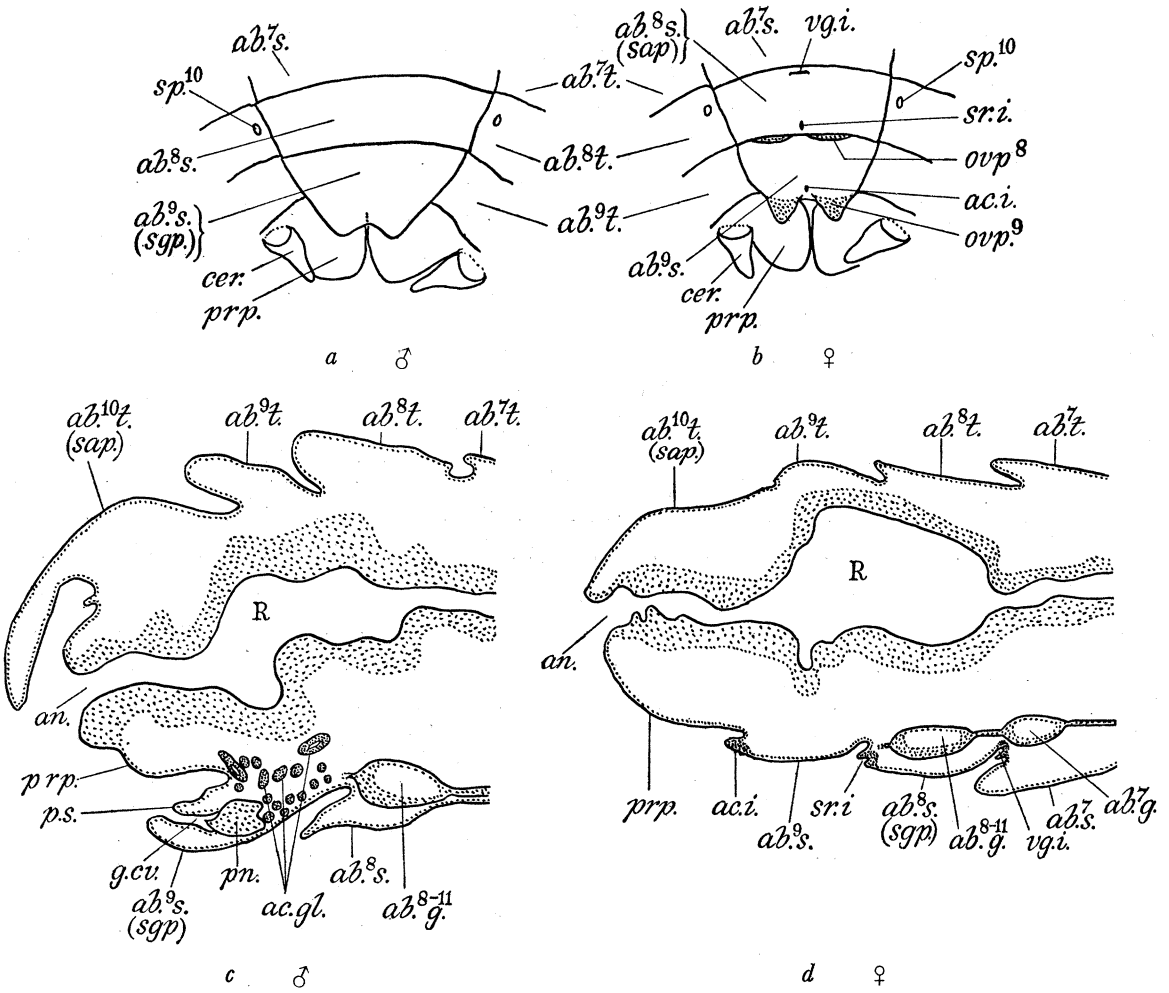

FIG. 138*a–d*—Terminal abdominal regions of male and female freshly hatched nymphs showing the accessory genital organs. (*a*) Ventral view of terminal abdominal sclerites of male (treated with KOH), × 31 ; (*b*) ditto, of female, × 31 ; (*c*) longitudinal-vertical section of the posterior abdominal end of male, × 413 ; (*d*) ditto, of female, × 493.

of the ovarioles and of the egg-calyces. The *boyau calicial* or female accessory glands are not present at the time of hatching but arise afterwards as forward extensions of the egg-calyces.

At the time of hatching, the testes extend from the middle of the third to the middle of the sixth abdominal segments and the ovaries from the posterior margin of the third to the anterior margin of the sixth abdominal segments. The ovaries

show three or four vertical folds which the testes do not. Further details of the testicular and ovarian development have not been studied. These changes have been described in great detail by GRABER (1891, *a*) in *Stenobothrus variabilis*, and by NELSEN (1931 and 1934, *a*) in *Melanoplus differentialis*—the latter author was apparently unaware of GRABER's work. It may be pointed out that the extent of the gonads in the abdomen varies in the different Acrididae so far studied. Thus the male gonad extends over the abdominal segments 4–5 in *Stenobothrus*, 3–6 in *Locusta*, and 3–7 in *Melanoplus differentialis*; the female gonads extend over the abdominal segments 2–3 in *Stenobothrus*, 3–6 in *Locusta migratoria*, and 2–7 in *Melanoplus differentialis*.

Among the Orthoptera an early differentiation of the germ cells, coinciding in time with the differentiation of the inner layer, has been found by HEYMONS (1895, *a*) in *Gryllus domesticus*, *G. compestris*, *Blatta* (*Phyllodromia*) *germanica*, and *Periplaneta orientalis*. GRABER (1891, *a*), in the Acridid *Stenobothrus variabilis*, and WHEELER (1893), in *Xiphidium ensiferum*, describe a latter segregation of the germ cells, viz., after the formation of the coelomic sacs, and I have found the same condition in *Locusta*. In these cases the germ cells arise from the inner walls of the coelomic sacs. Recently NELSEN (1934, *b*) claims that in *Melanoplus differentialis* the germ cells " are segregated from the lateral margins of the abdominal lobe ectoderm in the region of the amnion attachment ", and that " they ultimately become separated from the ectoderm cells of the lateral wall and from the amnion and migrate in a passive manner on to the coelomic sacs where they become associated with the inner walls of the sacs ". Although NELSEN gives good figures in support of his statement, I have the following criticism to make :—(i) The derivation of the genital cells from the ectoderm and the amnion is most unusual. In all insects in which the segregation of the genital cells occurs after the differentiation of the inner layer, it is this layer which gives rise to them. (ii) Neither GRABER (1891, *a*) nor I could detect such an origin of the genital cells in the Acrididae studied by us, viz., *Stenobothrus variabilis* and *Locusta*. In view of the close relationship between the three species studied, a fundamental difference in the origin of the germ cells is hardly to be expected. (iii) NELSEN has failed to observe the provisional dorsal closure described by GRABER (1888) in *Stenobothrus* and by myself in *Locusta*, and which, I am convinced, must be present in *Melanoplus differentialis* as well. Since this membrane arises from the lateral margins of the germ band near its junction with the amnion, a true understanding of the relationships of the various elements at this point is impossible without a study of this membrane. (iv) It appears to me that NELSEN's so-called early germ cells are, in all probability, cardioblasts.

(b) The Genital Ducts

As already pointed out above, the ventral cell-mass of the gonad rudiments forms the gonadal portion of the genital ducts both in the male and female. Just before the beginning of blastokinesis, it is possible to distinguish between the two sexes by the relative development of the tenth abdominal appendages—in the male they

are somewhat larger than in the female. After blastokinesis, in the female the tenth abdominal appendages disappear, the ninth ones are large and form the future upper (lateral) ovipositor valves, while the eighth ones are very reduced. In the male of the same stage one finds a pair of large appendages on the tenth abdominal segment, a pair of smaller ones on the ninth, and no trace of appendages on the eighth. A similar difference between the two sexes was also observed in *Melanoplus differentialis* by NELSEN (1931) and ELSE (1934).

In many of the abdominal segments in *Locusta* the ventral coelomic pouches form ampullae which usually remain connected for some time with the rest of the coelomic walls by means of solid strands. Since the fate of these ampullae is different in the two sexes, they may now be described separately.

In the female, the ampullae are formed in the third and the fourth and the sixth to the tenth abdominal segments. All of these, except the pair belonging to the ninth abdominal segment, have a distinct lumen until some time after blastokinesis. The strands which connect the ampullae of the fourth and ninth segments to their respective dorsal coelomic portions disappear early, while those of the other ampullae disappear much later. Portions of the latter in the seventh and eighth abdominal segments give rise to the paired (mesodermal) oviducts in the female ; in the male they form, together with the strands of the ninth abdominal segment, the paired vasa deferentia. The ampullae also eventually disappear in the female ; of these, the pair belonging to the eighth abdominal segment last the longest. During post-blastokinetic stages it shifts forwards and medially so as to occupy a position at the anterior border of the eighth sternum where the mesodermal oviducts of either side meet. It appears that the ampullae of the eighth segment do not take part in the formation of the end portion of the paired oviducts ; but this point cannot be said to have been cleared beyond doubt. It is, however, certain that the acquisition of a lumen in the entire mesodermal portion of the oviducts is a post-embryonic development. At the time of hatching, three median ectodermal invaginations are seen on the posterior abdominal sterna of the female (fig. 138*b* and *d*). The most anterior of these is placed at the distal border of the eighth sternum (female sub-genital plate), the second at the proximal border of the same and between the rudiments of the lower (anterior) ovipositor valves, and the last one is situated at the posterior border of the ninth sternum and between the upper (lateral) ovipositor valves. They are respectively the vaginal, the spermathecal, and the accessory genital invaginations—the last being very poorly developed. Their position is also marked by a thickening of the hypodermis. The vaginal invagination adjoins the common mesodermal portion of the oviducts but does not open into it at the time of hatching.

Coming now to the male (fig. 138*a* and *c*), it may be pointed out at once that here the definitive genital opening lies in the intersegmental region between the ninth and the tenth abdominal sterna, the former of these constituting the sub-genital plate. The tenth abdominal appendages shift forwards and fuse with the ninth, and together they form the aedeagus and its duct (ejaculatory duct) and

associated structures. The ampullae of the tenth abdominal segment are very large. With the development of the embryo they move medially, and eventually open into the ejaculatory duct. The male accessory glands arise as evaginations of the walls of these ampullae (fig. 119, Plate 7). ELSE (1934) describes a similar condition in *Melanoplus differentialis*. It is not certain whether the ampullae of the ninth segment fuse with those of the tenth, but probably they do not. The condition of the other ampullae has not been studied in detail. It is, however, clear that those of the eighth abdominal segment are less conspicuous in the male than in the female and disappear much earlier. The extra-gonadal portions of the vasa deferentia are formed in much the same way as the corresponding ducts in the female (*vide supra*).

An important point in regard to the development of the genital ducts of insects has been the formation of the so-called coelomic ampullae in the abdomen. They have been found in several Orthoptera (HEYMONS, 1891, 1895, *a* ; WHEELER, 1893 ; WIESMANN, 1926), in *Chalicodoma* (CARRIÈRE and BÜRGER, 1897), in *Eutermes* (STRINDBERG, 1913), and in *Pyrrhocoris apterus* (SEIDEL, 1924). In a number of these insects the gonad rudiments extend over almost the entire length of the abdomen, and subsequently a secondary contraction of this extent occurs. Also the coelomic ampullae are more or less segmentally arranged in the abdomen and one pair of them usually forms the termination of the mesodermal section of the genital ducts. These facts give support to the view, as pointed out by SEIDEL (1924) and WIESMANN (1926), that in the ancestors of insects the gonads stretched throughout the length of the abdomen and that they opened to the outside by means of segmentally-arranged ducts.

The development and homologies of the insect genitalia is a very vexed question. The various views regarding it have been dealt with by NEL (1929), and summarized and critically discussed by IMMS (1931). From a survey of the literature it becomes evident that our knowledge in this direction rests to-day almost entirely on the comparative morphology of the adults and in some cases on a study of the post-embryonic development. While such important questions as whether some of the abdominal appendages are directly converted into the genitalia, and if so which, can be solved satisfactorily only by a close study of the late embryos, such studies are confined to two cases only, viz., WHEELER (1893) on *Xiphidium* and ELSE (1934) on *Melanoplus*. NEL (1929) also claims to have studied late embryos ; but he gives no figures of them, and some of his conclusions need adequate confirmation before they can be accepted. These and other related questions, so far as they relate to *Locusta migratoria*, are now under investigation by me and will form the subject of a further communication which, it is hoped, will throw considerable light on this problem.

23—*The Embryonic Cuticle*

About a day after blastokinesis, the embryo secretes a cuticular membrane all round its body. This membrane is shed just after hatching, constituting the so-called " intermediate moult " of UVAROV (1928). In an embryo about to hatch,

the embryonic cuticle shows numerous close-set papillae on its surface (fig. 120, Plate 7). These papillae are rounded and weakly developed at the extreme anterior end of the embryo (fig. 121, Plate 7), but over the rest of the body, and more specially in the neighbourhood of the thorax, they are well developed and have pointed ends directed backwards (fig. 122, Plate 7). This significant difference strongly suggests that the papillae have an important function in the process of hatching. As pointed out below, the egg-wall, during the process of hatching, is first broken through in the thoracic region where the papillae of the embryonic cuticle are sharp and pointed and serve to tear the egg-wall during the wriggling movements of the embryo. CAROTHERS (1923) has demonstrated the chitinous nature of the embryonic cuticle in several Acrididae, and presumably the same obtains in *Locusta*, although I have not tested for it.

24—*Hatching*

The process of hatching in locusts has been described in detail by UVAROV (1928) and others, and I have only confirmed their observations in many respects. Besides the vermiform movements of the embryo described by these authors, I have also observed a peristalsis which starts at the hind end and stops at the prothorax. The head does not take part in it, but undertakes circular movements which are specially marked after it becomes free. All these movements, aided by the alternate swelling and sinking of the cervical ampullae and also by the spiny papillae of the embryonic cuticle (*vide supra*), serve to rupture the egg-wall in the thoracic region, and the embryo slowly emerges out of the egg. During hatching the embryo is often bent at right angles. Hatching has been said to depend on several external factors, viz., temperature, humidity, and light, but exact experimental evidence is wanting for all of these. I might mention here an interesting observation which throws some light on the influence of humidity on hatching. A partly hatched egg was exposed to the room atmosphere on a dry glass plate. Owing to the rather rapid drying up of the egg, the hatching movements soon stopped, but recommenced on moistening the egg. This was repeated five or six times until the nymph hatched out. KÜNKEL D'HERCULAIS (1893–1905) claimed that light was necessary for the hatching of the Moroccan Locust, and LA BAUME (1918) maintained that the intermediate moult does not occur in darkness. The fact that in *Locusta* and in *Schistocerca gregaria* I have observed both these processes to occur in complete darkness (in an incubator which had not been opened several hours before and after the occurrence of these processes) would appear to discount the observations of the above-mentioned authors. It seems certain that light is not one of the stimuli which initiate the process of hatching and intermediate moulting.

III—SUMMARY

The development of the coelomic cavities is described in detail. Transient *labral* and intercalary coelomic cavities are formed. The labial coelomic cavities resemble the three pairs of thoracic somites in their division into a dorso-rostral, a dorso-anal,

and a ventral pouch, but differ from them in the absence of a horizontal partition in the dorsal coelom. The fate of the labial and the thoracic mesoderm is fully described. The presence of a horizontal partition dividing the dorsal coelom into upper and lower chambers is a feature unique to the Acrididae. The ventral coelomic pouches in abdominal segments 3 and 4 and 6–10 form coelomic ampullae, while those of the fifth abdominal segment disappear early.

The division of the majority of the coelomic cavities into dorsal and ventral pouches is homologized to a similar condition in *Peripatus* and the Myriapods.

The labrum is paired in origin. The intercalary appendages are represented by a mere thickening of the ectoderm. The basal sclerites of the first maxillae and the submentum of the labium are formed from the base of the appendages themselves ; no portion of the sternum takes part in their formation.

The first abdominal appendages or pleuropodia are large and glandular in structure. They attain their maximum development during blastokinesis, after which they shrivel up and are finally cast off mechanically during hatching. A classification of insect pleuropodia into " evaginate " and " invaginate " types, based on their development, is proposed. The appendages of the abdominal segments 2–7 disappear during blastokinesis. The eighth pair of abdominal appendages disappear in the male ; in the female they become much reduced, but their final fate has not been followed. The ninth pair of abdominal appendages form the upper (lateral) ovipositor valves in the female. In the male, they fuse with the tenth pair to form the aedeagus and associated structures. The tenth pair in the female disappears soon after blastokinesis.

The pleuron, in the thorax, arises entirely from the subcoxa. This gives support to the subcoxal theory of the origin of the pleuron.

The number of body segments in *Locusta* is reckoned at 21 (7 cephalic, 3 thoracic, and 11 abdominal), excluding the acron and the telson which are not developed here.

A provisional ectodermal dorsal closure of the embryo is formed very early in embryonic life. It arises from the embryonic edges in close proximity to the origin of the amnion, and spreads dorsally, enclosing, for the first time, an epineural sinus. Such a provisional dorsal closure is peculiar to the Acrididae. During blastokinesis it ruptures at the edges and bends round dorsally to enclose the yolk. It eventually degenerates.

The amnion and the serosa degenerate, a serosal dorsal organ being formed. A small posterior serosal patch persists until hatching and is then cast off with the egg-wall.

Blastokinesis has been observed in living eggs and takes about 12–70 hours at 30° C. The embryo, during this process, turns round through an angle of 180°.

The development of the corpora allata, the tentorium, the mandibular apodeme, and the salivary glands is described.

The cephalic aorta arises from the walls of the antennary coelom. Its anterior portion forms the so-called pulsatile vesicle or blood-distributing apparatus. The

posterior portion of the cephalic aorta forms the aorta proper. Several embryonic blood sinuses are formed during development. These are the lateral and the dorsal blood sinuses and a circum-intestinal blood sinus. The last-named sinus is of phylogenetic significance. Pericardial cells arise from the somatic mesoderm. Blood cells arise mainly from the median mesoderm, but partly also at the junction of the splanchnic and the somatic mesoderm and from the splanchnic mesoderm.

Ten pairs of spiracles are formed belonging to the meso- and metathorax and the first eight abdominal segments. During further development, the invaginations on the abdominal segments 2–6 become intimately associated with the mesoderm, thus giving support to the nephromixis theory of the origin of insect tracheae.

The development of the nervous system is described. The ventral nerve chain consists developmentally of 17 pairs of ganglia, one for each segment from the mandibular to the eleventh abdominal. The optic lobes do not arise from neuroblasts, but as delaminations from the lateral ectoderm. The optic nerve or tract arises from the optic ganglion.

The fore-gut and the hind-gut are formed in the usual manner as ectodermal invaginations. The Malpighian tubules arise from the proctodaeum in two groups of 4 and 2 each.

The mid-gut epithelium is ectodermal in origin. Its rudiments are seen very early but its final extension occurs very late in embryonic life. Several other peculiar features associated with this condition are fully described.

The nature of the insect endoderm is discussed.

The suboesophageal body arises from the mandibular somites. It persists in the freshly hatched larva.

The genital cells are differentiated from the mesoderm after the formation of the coelomic cavities. Shortly before blastokinesis, the sexes can be distinguished by the relative development of the tenth pair of abdominal appendages—in the male they are somewhat larger than in the female. The further development of the genital organs is described.

An embryonic cuticle is secreted by the embryo. It is papillate and probably aids in the process of hatching.

Hatching and intermediate moulting are dependent on humidity but are not influenced by light.

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V—EXPLANATION OF PLATES

NOTE :—All figures, except where otherwise stated, are from camera-lucida drawings. The age of the stages referred to signify the period after egg-laying when kept at a constant temperature of 33° C. and on moist sand (humidity near saturation).

Lettering of Plates and Text-figures

a., area of distribution of cleavage cells.
A^1-A^{11}, 1st to 11th abdominal appendages.
ab., abdomen.
ab.^{1}-*ab.*^{11}, 1st to 11th abdominal segments.
ab.^{1}*g.*–*ab.*^{11}*g.*, 1st to 11th abdominal nerve ganglia.
ab.^{2}*s.*–*ab.*^{9}*s.*, 2nd to 9th abdominal sterna.
ab.^{7}*.t*–*ab.*^{10}*t.*, 7th to 10th abdominal terga.
ac.gl., male accessory glands.
ac.i., accessory genital invagination.
am., amnion.
a.m., antennary mesoderm.
ama., anterior extension of mesodermal investment of corpus allatum, going to the pharyngeal ganglia.
am.cv., amniotic cavity.
amh., posterior extension of mesodermal investment of corpus allatum.
amp.^{10}, coelomic ampulla of 10th abdominal segment.
an., anus.
ant., antenna.

ant.n., antennary nerve.
a.p., anterior pole of egg.
B., brain.
b.b., black bodies of suboesophageal body.
b.c., blood cells.
br.p., " bourrelet périlaminaire."
bs., base of 1st and 2nd maxillae.
b.w., body wall.
c.b., connecting sinus between heart and circum-intestinal blood sinus.
cbl., cardioblasts.
c.c.m., central cell mass.
cd., condyles.
cer., cercus.
cl., clypeus.
c.m., circular muscles.
cn., canal.
co., coelom.
co.ab.^{1}–*co.ab.*^{11}, 1st to 11th abdominal coelomic cavities.
co.an., antennary coelom.
co.i., intercalary coelom.
co.lb., labral coelom.
co.m., mandibular coelom.
co.mx.^{1}, 1st maxillary coelom.
co.mx.^{2}, 2nd maxillary coelom.
co.th.^{1}–*co.th.*^{3}, 1st to 3rd thoracic coelom.
cp., corpus allatum.
cph.a., cephalic aorta (posterior portion).
cp.i., invagination of corpus allatum.
cr., also *cr*^{1}, *cr*^{2}, cardo.
cu., cuticle.
cw., tarsal claws.
cx., coxa.
d.a.c., degenerating amnion cells.
da.co., dorso-anal pouch of coelom.
db., dermatoblasts.
d.c.m., dorsal cell mass.
d.co.^{1}–*d.co.*^{2}, upper and lower portions of dorsal coelom.
d.d., dorsal diaphragm of blood-distributing apparatus (anterior portion of cephalic aorta).
d.d.c., definitive dorsal closure.
d.l., dorsal lamella of blood-distributing apparatus.
d.o., dorsal organ.
do., dorsal side.
dp., depression in femur.
dr., deutocerebrum.
dr.co., dorso-rostral pouch of coelom.
d.s.c., degenerating serosa cells.
d.w., dorsal wall of coelom.
E., embryo.
e., eye.
ect., ectoderm.
ej.d., ejaculatory duct.
em.mem., embryonic membranes.
emp., empodium.
ep., eye-plate.
er.^{1}–*er.*^{3}, epimeron of 1st to 3rd thoracic segments.
e.s., epineural sinus.
et.^{1}–*et.*^{3}, episternum of 1st to 3rd thoracic segments.
F., fatty tissue.
fl., follicle cells.
fr., femur.
g.c., genital cells.
g.cv., genital cavity.
g.fr., frontal ganglion.
gl., also *gl*^{1}, *gl*^{2}, galea.
go., gonad.
g.oc., occipital ganglion.
g.ph., pharyngeal ganglion.
gs., glossa.
g.vn., ventricular ganglion.
H., heart.
h., hypopharynx.
h.c., hepatic caecae.
h.l., head lobes.
h.s., horizontal septum.
hyp., hypodermis.
i.b., circum-intestinal blood sinus.
in.l., inner layer.
int.ap., intercalary appendage.
int.s., embryonic cuticle.
l., thoracic leg.
l.^{1}–*l.*^{3}, 1st to 3rd thoracic legs.
lb.^{1}–*lb.*^{3}, 1st to 3rd protocerebral lobes.
lbr., labrum.
lbs.^{1} and *lbs.*^{2}, 1st and 2nd lateral blood sinuses.
lc., lacinia.
l.f., lateral furrow in coelomic wall.
l.m., labral mesoderm.
l.mb., lateral myoblast plate.
l.mus., longitudinal muscles.
l.oc., lateral ocellus.
l.p., large yolk particles.

l.t., lateral wall of antennary coelom forming fatty tissue.
lt.gs., left glossa.
m.a., median thickened wall of antennary coelom.
mbs., mid-dorsal blood sinus.
md., mandible.
md.a., mandibular apodeme.
md.g., mandibular nerve ganglion.
md.m., mandibular mesoderm.
md.p., temporary inner process of mandible.
md.s., mandibular sternum.
me., median ectodermal ingrowth between protocerebral lobes.
mes., mesoderm.
m.g., mid-gut.
m.g.ep., mid-gut epithelium.
mic., probable micro-organisms.
ml., molar area.
ml. c., median cord.
mm., median mesoderm.
mo., mouth.
m.oc., median ocellus.
m.t., Malpighian tubules.
m.tr., median terminal wall of antennary coelom going to blood-distributing apparatus.
mus., muscle.
mx.^{1} and *mx.*^{2}, 1st and 2nd maxillae.
mx.^{1}*g.*, 1st maxillary nerve ganglion.
mx.^{2}*g.*, 2nd maxillary nerve ganglion.
mx.^{1}*m.*, 1st maxillary mesoderm.
mx.^{2}*m.*, 2nd maxillary mesoderm.
mx.^{1}*p.*, 1st maxillary palp.
mx.^{2}*p.*, 2nd maxillary palp.
mx.^{1}*s.*, 1st maxillary sternum.
mx.^{2}*s.*, 2nd maxillary sternum.
n.b., nerve coming from brain.
nb., neuroblasts.
nb.^{1}, daughter cells of neuroblasts (= ganglion cells).
n.c., nerve cord.
n.cn., nerve connective.
n.g., nerve ganglion.
n.gr., neural groove.
nl., neurilemma.
n.s., neural swelling.
nu., nucleus.
nu.^{1}, refractile bodies (? degenerating nuclei) in nerve connectives.
nur., neurospongium.
oe., oenocytes.
o.i.b., outer mesentery of circum-intestinal blood sinus.
op.g., optic ganglion.
op.l., optic lobe.
op.n., optic nerve.
ovp.^{8} and *ovp.*^{9}, lower and upper ovipositor valves.
P., proctodaeum.
p.c., pericardial cells.
p.d., pericardial diaphragm.
p.d.c., provisional dorsal closure.
pe.m., pre-oral mesoderm.
pf., palpifer.
pg., palpiger.
pgs., paraglossa.
phm., mesodermal covering of pharyngeal ganglia.
p.lat.s., primary lateral sternum.
p.m., proctodaeal membrane.
p.m.s., primary median sternum.
p.mes., proctodaeal mesoderm.
pn., aedeagus.
po.m., post-oral mesoderm.
p.p., posterior pole of egg.
pr., protoplasm.
prc., protocerebrum.
prc.i., invagination between lobes of protocerebrum.
prf., site where optic ganglion first acquires secondary connexion with eye-plate ; post-retinal fibres also arise here.
prm., prementum.
prp., paraproct.
pr.pr., protoplasmic processes.
p.s., posterior serosal patch.
p.terg., primary tergum.
p.w., proctodaeal wall.
p.y., primary yolk cells.
Q., ectodermal ingrowth at blind end of stomodaeum.
R., rectum.
r.n., recurrens nerve.
rt.gs., right glossa.
sap., supra-anal plate.
sb.b., suboesophageal body.
sb.c., suboesophageal commissure.
sb.g., suboesophageal ganglion.
scx., subcoxa.
s.d., salivary ducts.

se., serosa.
s.gl., subgalea.
sgp., subgenital plate.
sk., stalk of pleuropodium.
sl.i., invagination of salivary glands.
sm., submentum.
s.m., stomodaeal membrane.
s.mus., suspensory muscles of heart.
sp., spiracular invagination.
sp.^{1}–*sp.*^{10}, 1st to 10th spiracles.
s.p., small yolk particles.
spl.m., splanchnic mesoderm.
spl.m.^{1}, dorsal layer of splanchnic mesoderm (forming mid-gut musculature).
spl.m.^{2}, ventral layer of splanchnic mesoderm (forming outer mesentery of circum-intestinal blood sinus).
sr., secretion.
sr.i., spermathecal invagination.
s.s., serosal sac.
st., stomodaeum.
st.m., stomodaeal mesoderm.
stp., stipes.
s.y.c., secondary yolk cells.
t., trachea.
T^{1}., anterior tentorial invagination.
t.f., terminal filament.
t.g., terminal joint to leg.
th.^{1}*g.*–*th.*^{3}*g.*, 1st to 3rd thoracic nerve ganglia.
th.^{1}*s.*–*th.*^{3}*s.*, 1st to 3rd thoracic sterna.
th.^{1}*t.*–*th.*^{3}*t.*, 1st to 3rd thoracic terga.
ti., tibia.
t.l., lateral diverticulum of spiracular invagination.
t.m., medio-dorsal diverticulum of spiracular invagination.
t.m.^{1}, median diverticulum of spiracular invagination.
to., toothed area.
tr., trochanter.
trc., trito-cerebrum.
ts., tarsus.
ts.^{1}–*ts.*^{3}, 1st to 3rd tarsal joints.
ts.p., tarsal pads.
va., vacuole.
v.c.m., ventral cell mass.
v.co., ventral pouch of coelom.
ve., ventral side.
vg.i., vaginal invagination.
v.l., ventral lamella of blood-distributing apparatus.
v.s., ventral septum.
v.w., ventral wall of coelom.
w., clear area between ventricular ganglia.
w.a., thickened wall of cephalic aorta.
y., yolk.
y.c., yolk cells.
y.p., yolk-like particles in cells of suboesophageal body.

Plate 1

Fig. 1.—Transverse section of a 52-hours-old embryo across the second maxillary segment, showing the right and left halves of the inner layer. × 390.

Fig. 2.—Transverse section of a 56¼-hours-old embryo across the second maxillary segment, showing the formation of the coelomic cavities. (The provisional dorsal closure is not yet formed.) × 390.

Fig. 3.—Portion of a transverse section of a 75-hours-old embryo across the extreme distal (rostral) end of the second thoracic segment, showing the dorso-anal pouch of the first thoracic coelom and the median mesoderm (" Blutzellenlamelle "). × 245.

Fig. 4.—Portion of a transverse section of a 75-hours-old embryo across the middle of the second thoracic segment, showing the coelomic pouches. × 245.

Fig. 5.—Portion of a transverse section of a 94-hours-old embryo across the distal end of the second thoracic segment, showing the lateral (ventral) furrow in the coelomic wall. × 245.

Fig. 6.—Portion of a longitudinal-vertical section of a 59-hours-old embryo, showing the thoracic coelomic cavities. (The provisional dorsal closure is not shown.) × 160.

Fig. 7.—Transverse section of a 72-hours-old embryo across the ninth abdominal segment. The inner layer is not yet divided into definitive segments. × 225.

Fig. 8.—Transverse section across the inter-segment between the second and third abdominal segments of a 56¼-hours-old embryo, showing the median mesoderm. × 390.

Fig. 9.—Ditto, across the second abdominal segment, showing the appearance of the coelomic cavity. × 390.

Fig. 10.—Transverse section of a 75-hours-old embryo across the fourth abdominal segment, showing the separated coelomic cavities. × 270.

Fig. 11.—Portion of a longitudinal-vertical section of a 112-hours-old embryo across the third to sixth abdominal segments. × 230.

Fig. 12.—Frontal section of a 56¼-hours-old embryo showing the labral coelomic cavities. × 158.

Fig. 13.—Portion of a longitudinal-vertical section of a 59-hours-old embryo, showing the labral coelom. × 375.

Fig. 14.—Portion of a longitudinal-vertical section of an embryo during balstokinesis, showing the intercalary coelom. × 230.

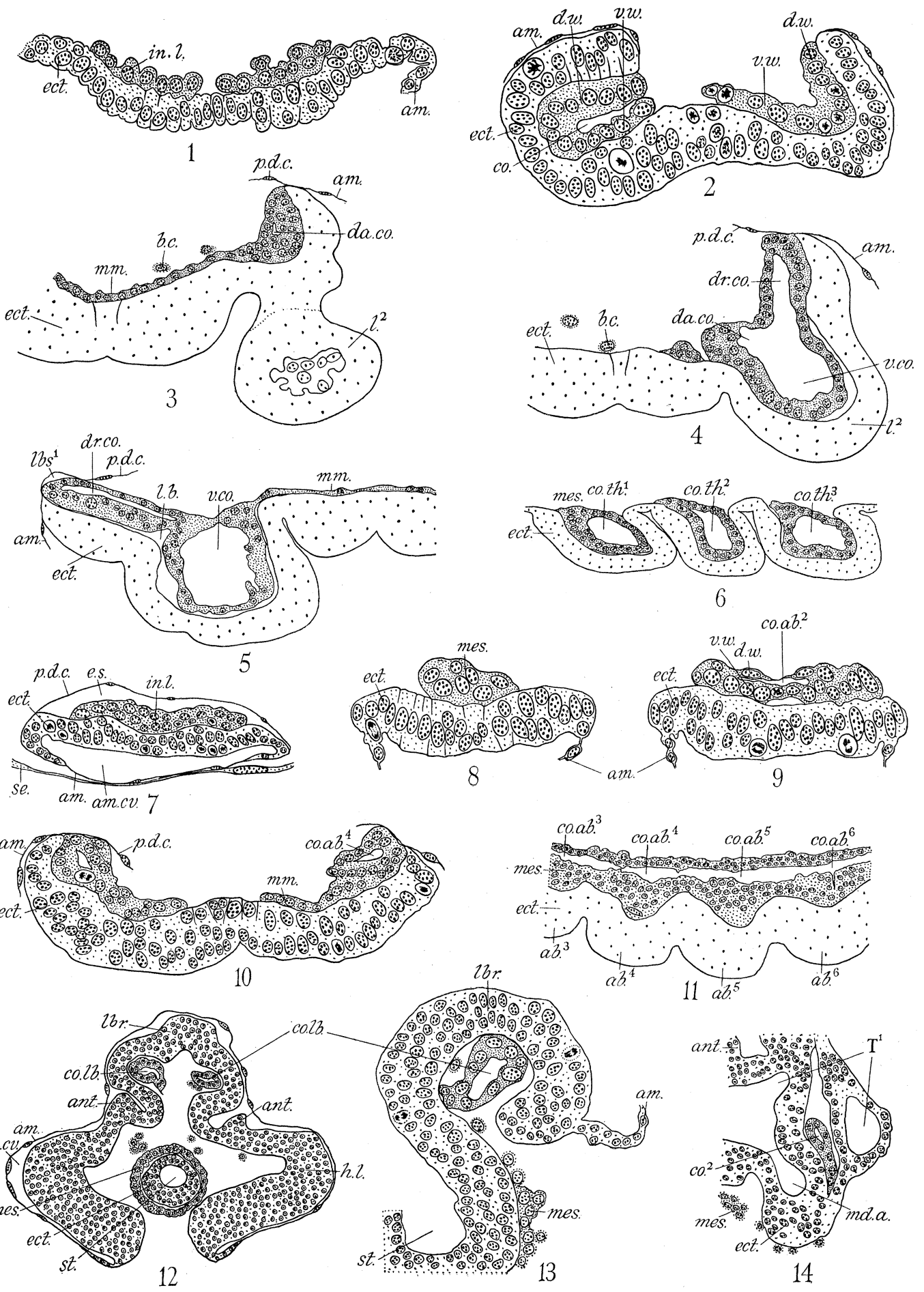
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Plate 2

Fig. 15.—Transverse section of a 59-hours-old embryo across the first maxillary segment. × 228.

Fig. 16.—Transverse section of a 75- to 80-hours-old embryo across the eleventh abdominal segment, showing the eleventh abdominal coelom. × 365.

Fig. 17.—A portion of the same section as in fig. 15, more magnified, showing the origin of the provisional dorsal closure. × 820.

Fig. 18.—Transverse section of a 75- to 80-hours-old embryo across the mandibular segment. Note the origin of the suboesophageal body from the mandibular mesoderm. × 110.

Fig. 19.—A portion of the same, more magnified. × 750.

Fig. 20.—Portion of the suboesophageal body, from a longitudinal-vertical section of a 94-hours-old embryo. Note the vacuoles in the cytoplasm. ×1660.

Fig. 21.—Ditto, from an embryo shortly after blastokinesis. Note the yolk-like particles in the cells. × 655.

Fig. 22.—Ditto, from an embryo one day after blastokinesis. Note the vacuoles and the black bodies in the cytoplasm. × 655.

Fig. 23.—Portion of a longitudinal-horizontal section of an embryo during blastokinesis, showing the suboesophageal body. × 67.

Fig. 24.—Portion of a longitudinal-vertical section of an egg two days after blastokinesis, showing the formation of the dorsal organ. The egg-wall is not shown. × 95.

Fig. 25.—The posterior serosal patch, from a longitudinal section of an egg two days after blastokinesis. × 240.

Fig. 26.—Mid-dorsal portion of a transverse section of embryo one day after blastokinesis, showing the degenerating amnion cells. × 610.

Fig. 27.—Portion of a transverse section of embryo shortly after blastokinesis, showing the invagination of the corpus allatum. × 380.

Fig. 28.—Ditto, but a little anterior. × 380.

Fig. 29.—Corpus allatum from a transverse section of embryo two days after blastokinesis. Note the mesodermal investment of the body. × 585.

Fig. 30.—Portion of transverse section of embryo shortly after blastokinesis, across the labial segment, showing the invagination of the salivary glands. × 245.

Fig. 31.—Portion of transverse section of embryo one day after blastokinesis, across the hypopharynx, showing the salivary ducts. × 160.

Fig. 32.—Section of a lobe of the salivary glands. (From a longitudinal section of embryo about to hatch.) × 610.

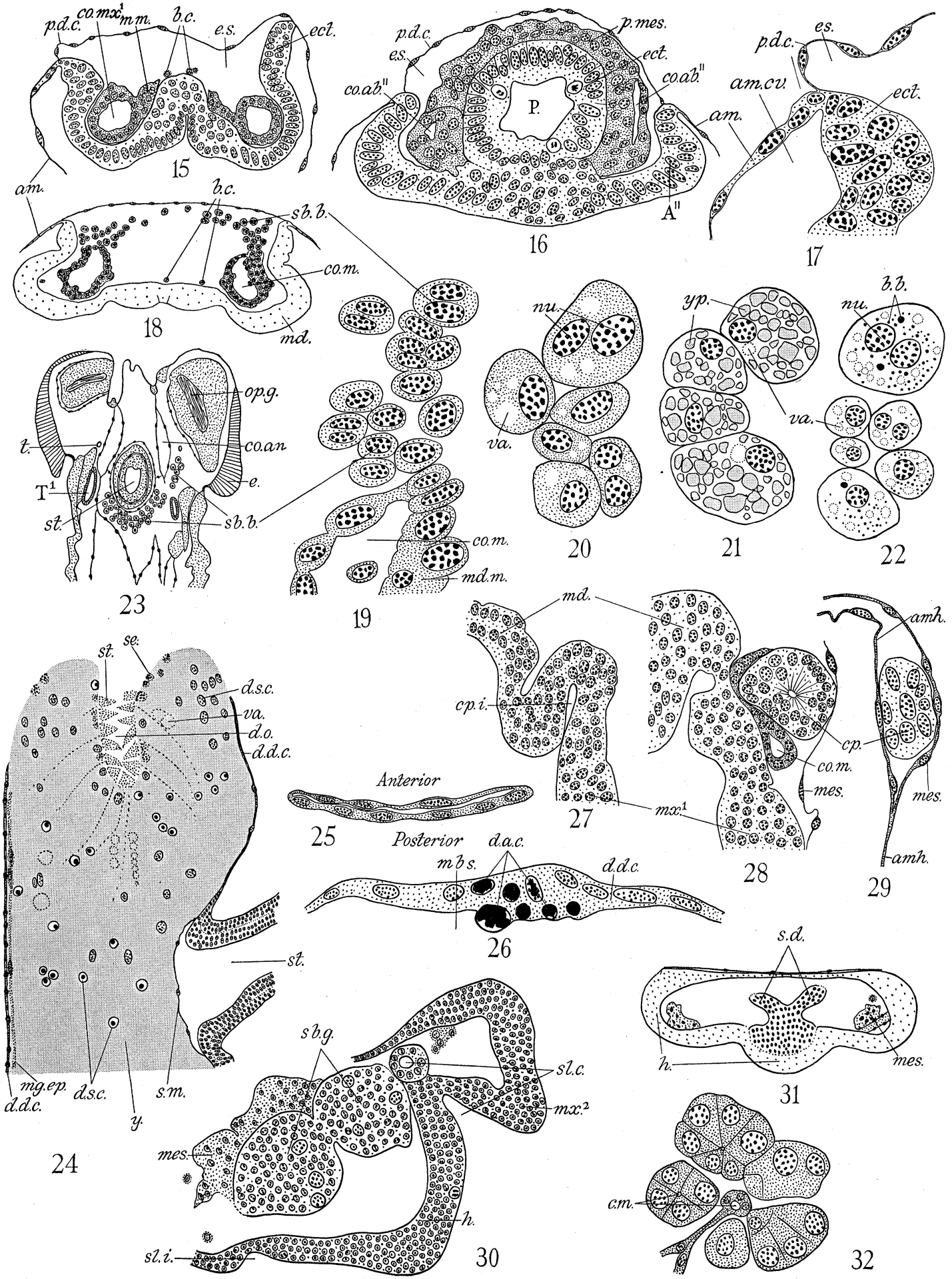
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Plate 3

Fig. 33.—Labrum of a 70-hours-old embryo. Dorsal view. × 155.
Fig. 34.—Ditto, from a 117-hours-old embryo. × 85.
Fig. 35.—Labrum of a recently hatched female nymph. Ventral view. × 42.
Fig. 36.—Antenna of a 70-hours-old embryo. × 65.
Fig. 37.—Ditto, from 100-hours-old embryo. × 65.
Fig. 38.—Ditto, from 128-hours-old embryo. × 65.
Fig. 39.—Ditto, from embryo shortly after blastokinesis. × 40.
Fig. 40.—Ditto, from embryo one day after blastokinesis. × 40.
Fig. 41.—Ditto, from embryo five days after blastokinesis. × 35.
Fig. 42.—Ditto, from freshly hatched male nymph. × 22.
Fig. 43.—Mandible of a 70-hours-old embryo. × 65.
Fig. 44.—Ditto, from 100-hours-old embryo. Note the small projection on the inner side of the mandible ; it disappears shortly afterwards. × 65.
Fig. 45.—Ditto, from embryo during blastokinesis. Note that the mandible is palp-like. × 65.
Fig. 46.—Ditto, from embryo one day after blastokinesis. Note that the inner wall of the mandible is very thick. × 40.
Fig. 47.—Ditto, from a freshly hatched male hopper. × 35.
Fig. 48.—First maxilla of a 70-hours-old embryo. × 65.
Fig. 49.—Ditto, from 100-hours-old embryo. × 65.
Fig. 50.—Ditto, from 112-hours-old embryo. × 65.
Fig. 51.—Ditto, from embryo during blastokinesis. × 65.
Fig. 52.—Ditto, from embryo two days after blastokinesis. × 40.
Fig. 53.—Ditto, from embryo four days after blastokinesis. × 40.
Fig. 54.—Ditto, from a freshly hatched male nymph. × 42.
Fig. 55.—Second maxillae of a 70-hours-old embryo. Ventral view. × 65.
Fig. 56.—Ditto, from 100-hours-old embryo. × 65.
Fig. 57.—Ditto, from embryo shortly after blastokinesis. × 42.
Fig. 58.—Ditto, from embryo one day after blastokinesis. × 42.
Fig. 59.—Ditto, from embryo five days after blastokinesis. × 42.
Fig. 60.—Ditto, from freshly hatched female nymph. × 42.
Fig. 61.—Ventral view of a portion of the head of an embryo during blastokinesis, showing the formation of the hypopharynx from the sterna of the mandibular and first and second maxillary segments. (The labrum is removed.) The sterna forming the hypopharynx have already fused together. × 35.
Fig. 62.—Ditto, of embryo two days after blastokinesis. × 35.
Fig. 63.—Ditto, of embryo three days after blastokinesis. (The mandible on the right has been partly dissected away.) × 35.
Fig. 64.—Second thoracic leg of a 70-hours-old embryo. Ventral view. × 65.
Fig. 65.—Ditto, of a 100-hours-old embryo. × 65.
Fig. 66.—Ditto, of a 120-hours-old embryo. × 65.
Fig. 67.—Ditto, of an embryo shortly after blastokinesis. (The subcoxa is not shown.) × 65.
Fig. 68.—Ditto, of an embryo one day after blastokinesis. × 40.
Fig. 69.—Ditto, of a freshly hatched male hopper. × 22.
Fig. 70.—Portion of side view of embryo 120 hours old, showing the basal segments of the thoracic legs. × 70.
Fig. 71.—Ditto, of embryo, one day after turning. × 35.
Fig. 72.—Ditto, of a freshly hatched female hopper. × 35.
Fig. 73.—Diagrammatic representation of a transverse section across the metathorax of an embryo shortly before blastokinesis, showing the origin of the terga and sterna. × 42.
Fig. 74.—Portion of a longitudinal-vertical section of an embryo during blastokinesis, showing the pleuropodium. × 227.

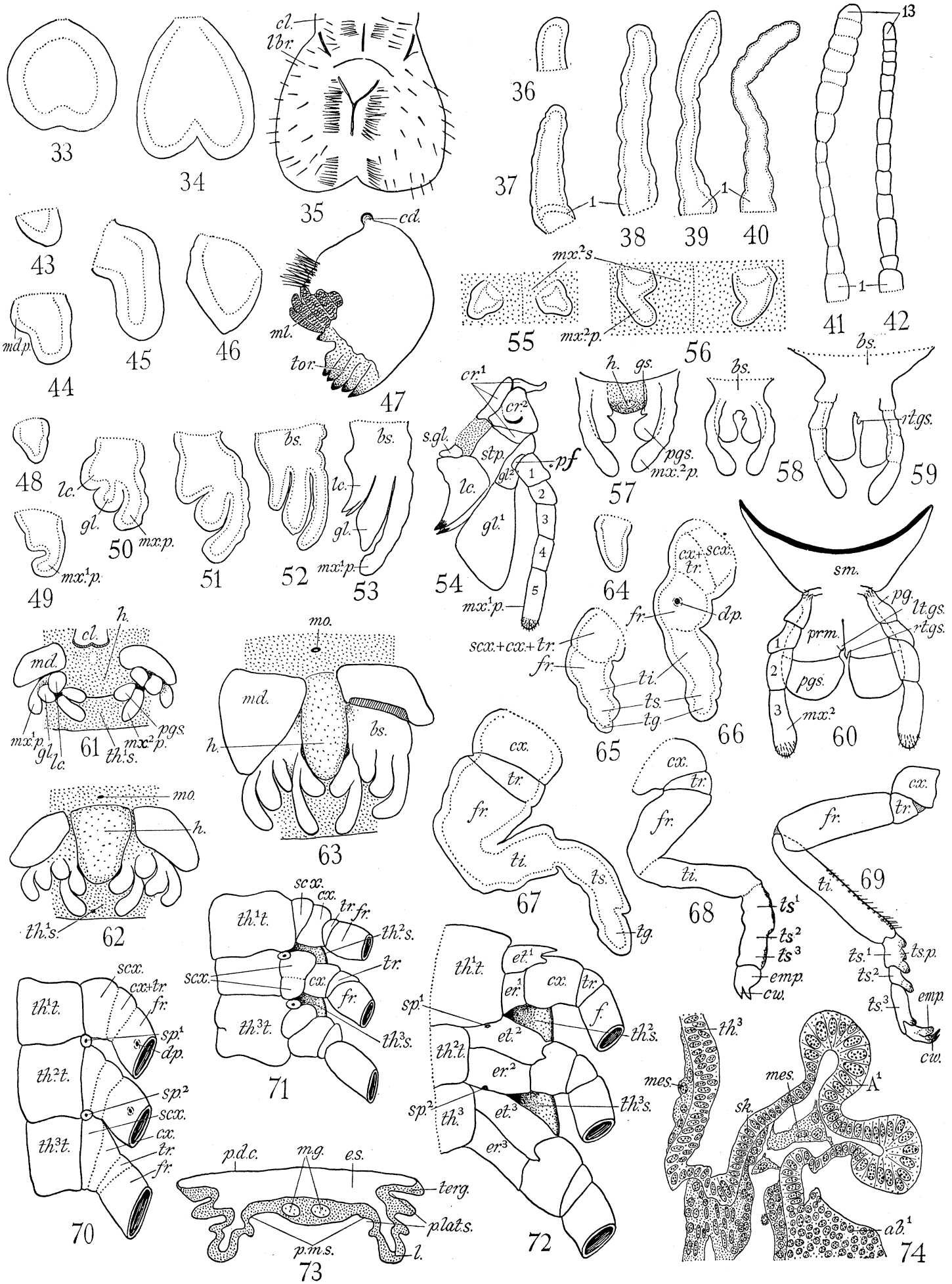
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Plate 4

Fig. 75.—Portion of transverse section of a 112-hours-old embryo across the fifth abdominal segment, showing the differentiation of the cardioblasts and the genital cells. × 250.

Fig. 76.—Transverse section of an embryo one day after blastokenisis, across the fourth abdominal segment. Partly schematic. × 93.

Fig. 77.—Portion of transverse section of an embryo two days after blastokinesis, across the distal region of the mesothorax, showing the connexion between the heart and the circum-intestinal blood sinus. × 670.

Fig. 78.—Portion of transverse section of an embryo two days after blastokinesis, across the abdominal region. Compare with fig. 77. × 390.

Fig. 79.—Ditto, of embryo five days after blastokinesis. × 157.

Fig. 80.—Portion of a transverse section of an embryo shortly after blastokinesis across the second maxillary region, showing the crescent-shaped cardioblast (*cf.* fig. 133*b*). × 880.

Fig. 81.—Diagrammatic representation of the cephalic aorta and associated parts of an embryo one day before hatching. Dorsal view. (Reconstructed from transverse sections.)

Fig. 82.—Portion of transverse section of an embryo one day before hatching, showing the dorsal diaphragm of the blood-distributing apparatus (anterior portion of the cephalic aorta). × 160.

Fig. 83.—Portion of a frontal section of the head of an embryo one day before hatching, showing the posterior portion of the cephalic aorta and the associated structures. × 270.

Fig. 84.—Transverse section of a 112-hours-old embryo across the anterior region of the first abdominal segment, showing the spiracular invagination. × 360.

Fig. 85.—Portion of transverse section of a 75- to 80-hours-old embryo a short distance behind the blind end of the stomodaeum, showing the provisional dorsal closure and the stomodaeal mesoderm. × 232.

Fig. 86.—Portion of a longitudinal-vertical section of an embryo during blastokinesis, showing the splanchnic mesoderm and associated structures. × 610.

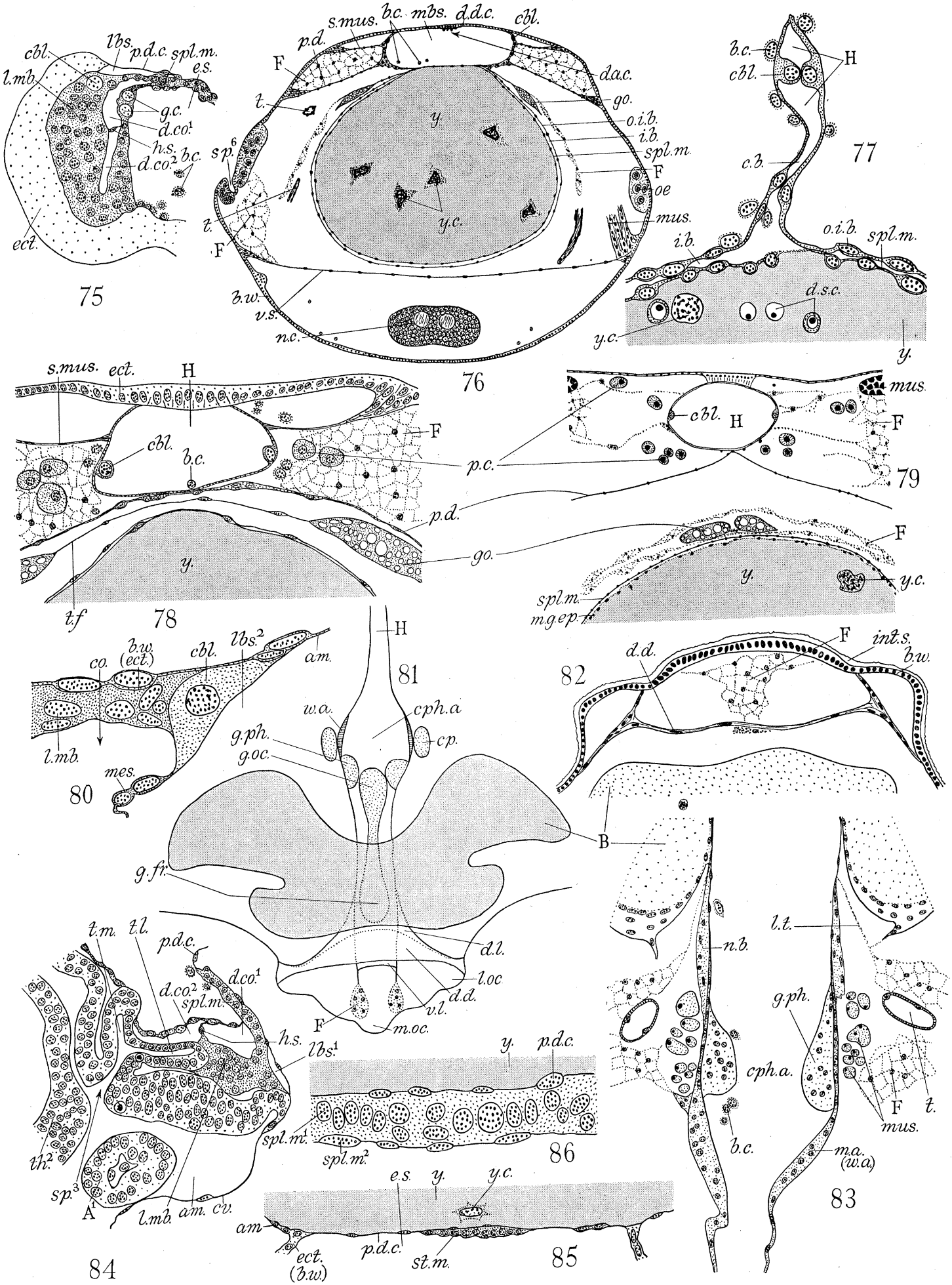
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Plate 5

Fig. 87.—Portion of transverse section of a 64-hours-old embryo across the second maxillary segment, showing the differentiation of neuroblasts. (The inner layer is not shown.) × 380.

Fig. 88.—Ditto, of a 75- to 80-hours-old embryo across the second thoracic segment. × 380.

Fig. 89.—Median portion of a transverse section of a 94-hours-old embryo across the intersegment between the second maxillary and the prothoracic segments, showing the median cord neuroblast. × 595.

Fig. 90.—Portion of transverse section of a 112-hours-old embryo across the second abdominal segment, showing ganglion formation. × 380.

Fig. 91.—Portion of transverse section across the head of a 75- to 80-hours-old embryo, showing the protocerebral lobes. The optic lobe has completely separated from the eye-plate (*cf.* fig. 94). × 160.

Fig. 92.—Portion of transverse section of a 120-hours-old embryo showing the antennary nerve. × 405.

Fig. 93.—Portion of transverse section of the head of a 53-hours-old embryo, showing the origin of the eye-plate and the optic lobe. × 400.

Fig. 94.—Ditto, of a 59-hours-old embryo showing the separation of the optic lobe and the differentiation of the other lobes of the protocerebrum. The optic lobe has not yet completely separated from the eye-plate (*cf.* fig. 91). × 270.

Fig. 95.—Portion of transverse section of an embryo shortly after blastokinesis, showing the eye-plate and the optic ganglion. × 245.

Fig. 96.—Portion of longitudinal-horizontal section of the first abdominal ganglion of an embryo one and half days after blastokinesis, showing the degenerating neuroblasts. × 595.

Fig. 97.—Median portion of transverse section of the extreme anterior end of an 80-hours-old embryo, showing the median ectodermal ingrowth between the protocerebral lobes. × 380.

Fig. 98.—Transverse section of a nerve connective between the first and second thoracic ganglia. Note the refractile bodies (? degenerating nuclei) embedded in the neurospongium. × 595.

Fig. 99.—Portion of transverse section of the dorsal stomodaeal wall of an embryo shortly before blastokinesis, showing the ventricular ganglia. × 385.

Fig. 100.—Portion of transverse section of an embryo shortly after blastokinesis, showing a portion of the antennary coelom and the associated structures. × 385.

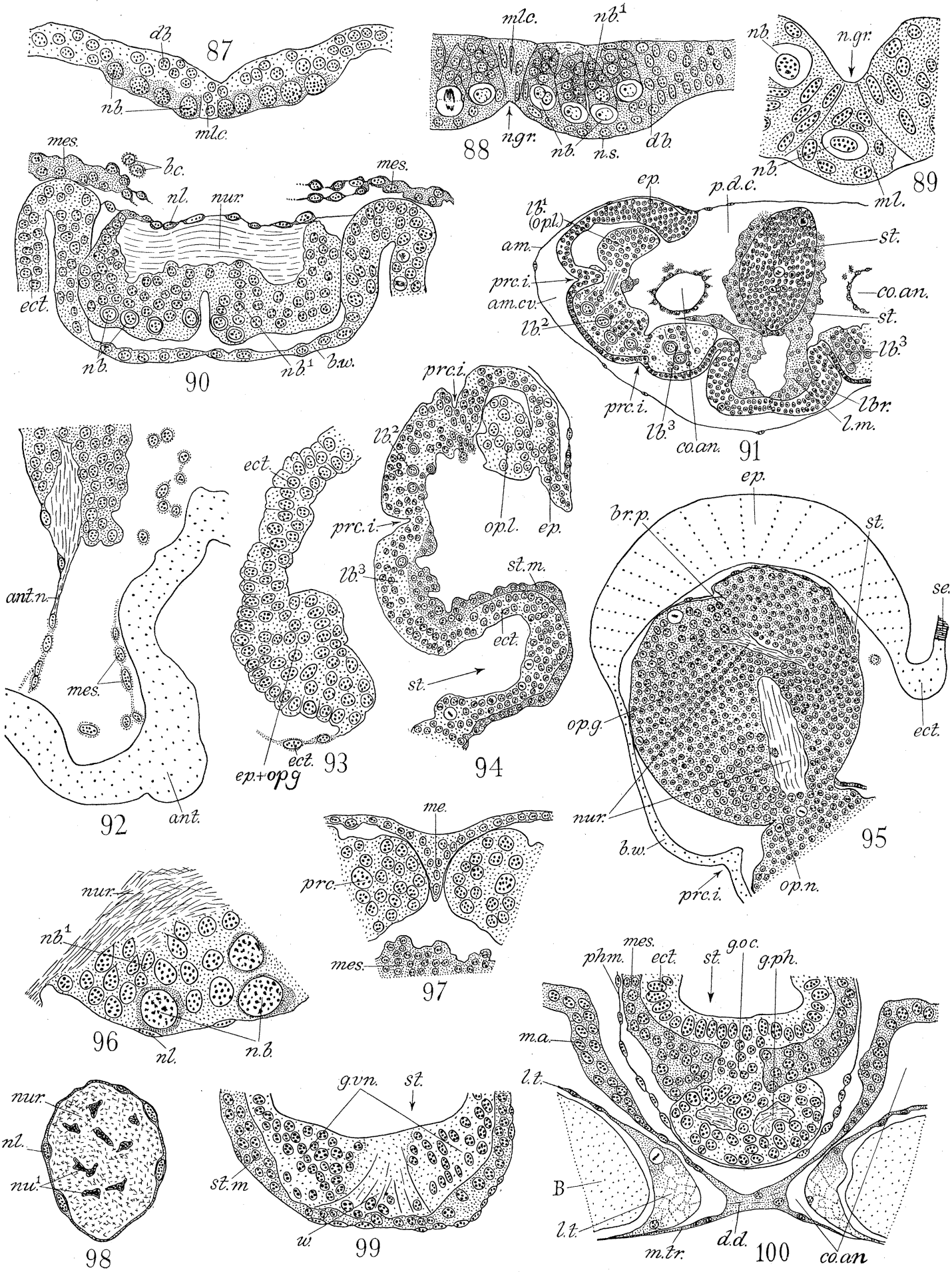
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Plate 6

Fig. 101.—Longitudinal-vertical section of a 75- to 80-hours-old embryo, showing the coelomic cavities. (Combined from several sections and partly schematic.) × 102.

Fig. 102.—Longitudinal-vertical section of a female embryo shortly after blastokinesis. (Combined from several sections and partly schematic.) × 73.

Fig. 103.—Portion of transverse section of a 120-hours-old embryo across the fifth abdominal segment. × 390.

Fig. 104.—Portion of transverse section of an embryo shortly after blastokinesis across the first abdominal segment. × 375.

Fig. 105.—Portion of median longitudinal-vertical section of a 52-hours-old embryo, showing the stomodaeal invagination. Note the ectodermal ingrowth at the blind end of the stomodaeum. × 275.

Fig. 106.—Ditto, of a $56\frac{1}{4}$-hours-old embryo. × 172.

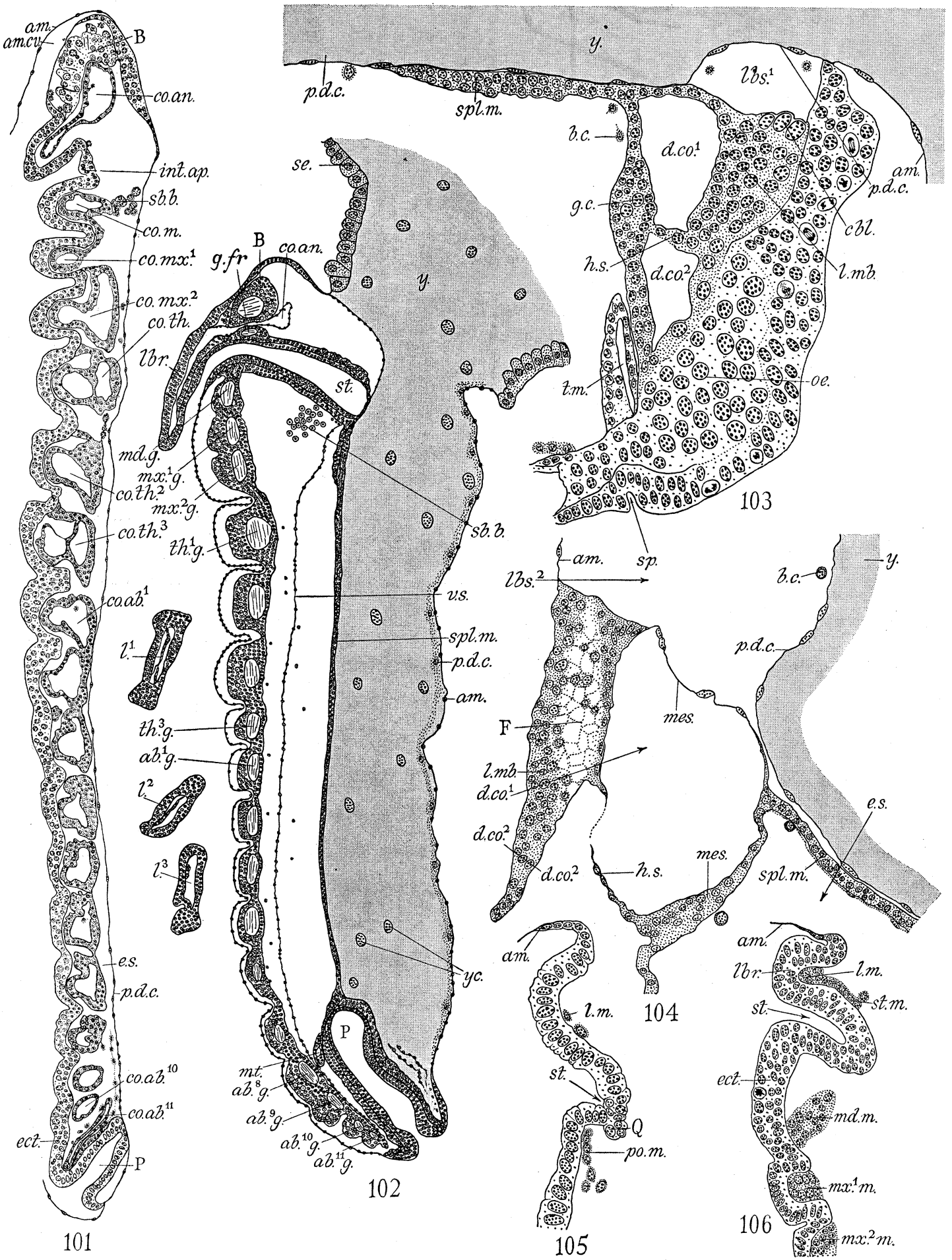
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Plate 7

Fig. 107.—Portion of median longitudinal section of a 59-hours-old embryo, showing the stomodaeum and its relation to the provisional dorsal closure. × 215.

Fig. 108.—Portion of a transverse section of a 72-hours-old embryo, showing the stomodaeum and its relation to the provisional dorsal closure. × 275.

Fig. 109.—Portion of a transverse section of a 70-hours-old embryo, showing the proctodaeum. × 280.

Fig. 110.—Portion of a transverse section of a 117-hours-old embryo, across the proctodaeal wall, showing the differentiation of a Malpighian tubule. × 650.

Fig. 111.—Portion of longitudinal-vertical section of an embryo one day after blastokinesis, showing the development of a Malpighian tubule. × 220.

Fig. 112.—Portion of longitudinal-vertical section of an embryo one day after blastokinesis across the proctodaeal region, showing the extent of the (ectodermal) mid-gut epithelium. × 245.

Fig. 113.—Ditto, of an embryo two days after blastokinesis. × 535.

Fig. 114.—Portion of longitudinal-vertical section across the mid-gut of an embryo five days after blastokinesis, showing the mid-gut epithelium. × 650.

Fig. 115.—Ditto, of a freshly hatched male nymph. × 535.

Fig. 116.—Portion of transverse section of an embryo one day after blastokiensis across the fourth abdominal segment, showing the relation of the circum-intestinal blood sinus to the heart. × 595.

Fig. 117.—Transverse section of male gonad of an embryo one day after blastokinesis. (From transverse section of embryo across the fifth abdominal segment.) × 610.

Fig. 118.—Ditto, of female gonad. (From transverse section of embryo across the sixth abdominal segment.) × 610.

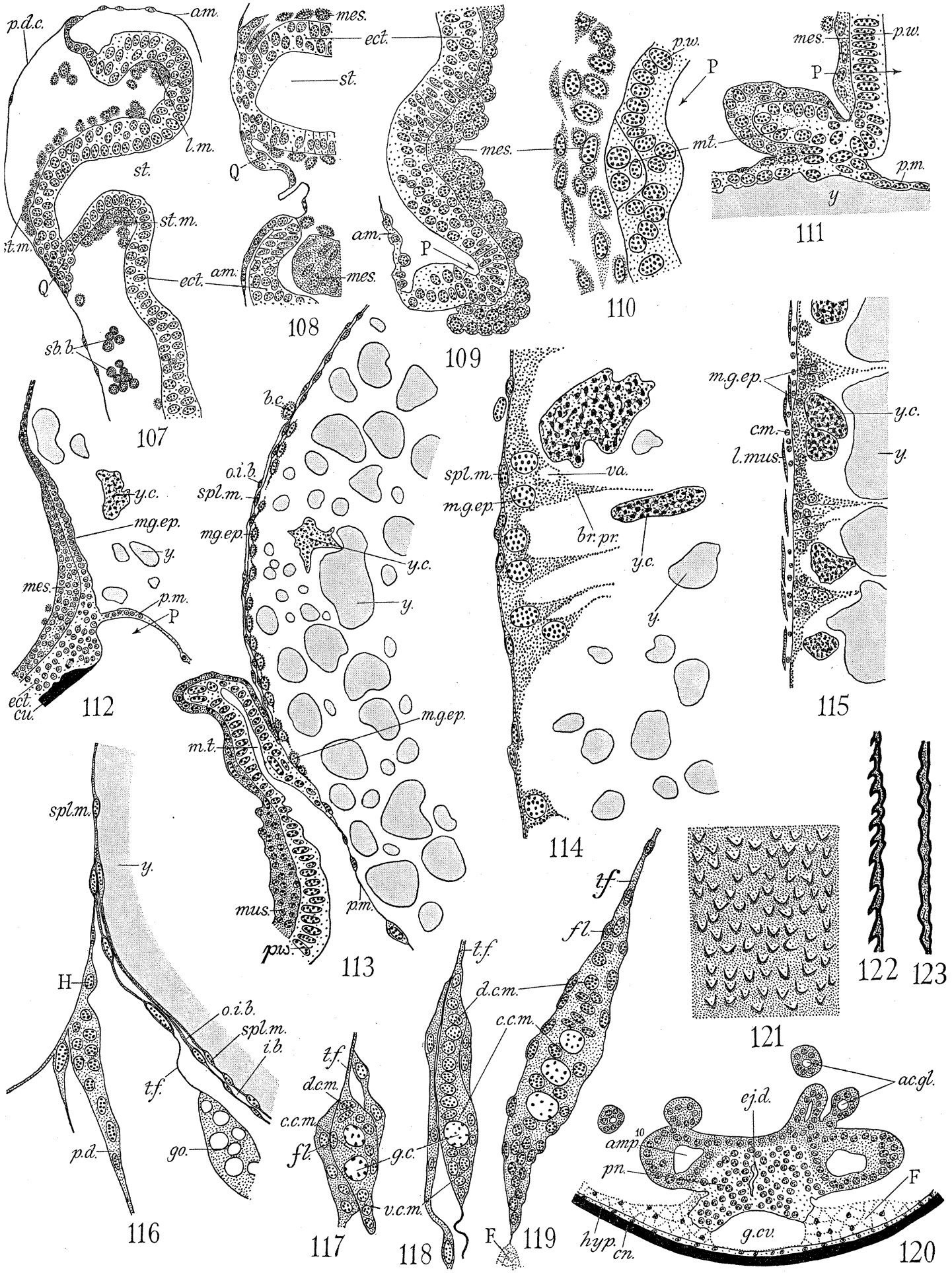
Fig. 119.—Ditto, from an embryo two days after blastokinesis. × 595.

Fig. 120.—Portion of transverse section of the posterior end of a freshly hatched male nymph, showing the formation of the aedeagus and the male accessory glands. × 350.

Fig. 121.—Portion of the embryonic cuticle from the thoracic region of an embryo almost about to hatch. Surface view. Note the hook-like outgrowths which are directed posteriorly. × 610.

Fig. 122.—Ditto, in longitudinal-vertical section. × 610.

Fig. 123.—Ditto, but at the cephalic region of the embryo. Note the absence of hook-like outgrowths (*cf.* fig. 122). × 610.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