EMBRYOLOGY OF THE RED COTTON BUG DYSDERCUS *CINGULATUS* (FABRICIUS) (PYRRHOCORIDAE: HETEROPTERA: INSECTA) III—.ORGANOGENY*

By
NEELAM TANDON
*School of Entomology, St. John's College, Agra****

I—INTRODUCTION

The following is a further account of the embryology of *Dysdercus cingulatus* (Fabricius) dealing with development from the time of germ layer formation, to the time those germ layers become differentiated into the Digestive system, Excretory system, Tracheal system and the Nervous system found in the first instar of the bug.

II—THE DIGESTIVE SYSTEM

The development of the alimentary canal begins with the formation of a stomodaeal invagination in the anterior region of the embryo at the 40th hour of incubation. The stomodaeal invagination gives rise to the pharynx, oesophagus and crop. The proctodaeal invagination follows about 6 hours later in the posterior region and gives rise to the hind-gut and the Malpighian tubules. The Malpighian tubules arise as evaginations from the blind anterior end of the proctodaeum. The alimentary canal of a fully formed embryo of *Dysdercus cingulatus* consists of (a) fore-gut, (b) mid-gut, and (c) hind-gut.

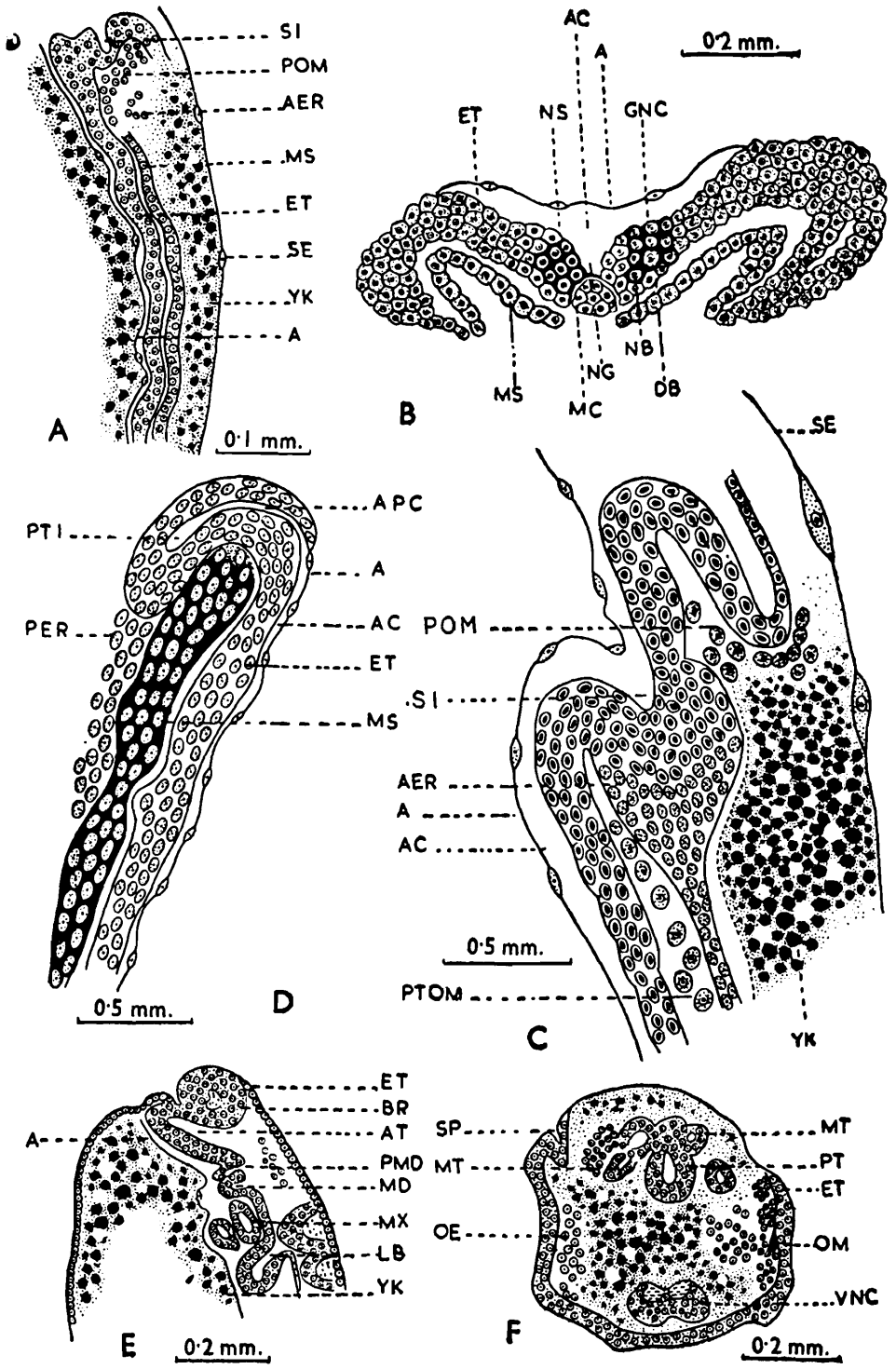
(a) *The Fore-Gut:* The ectodermal invagination to form the stomodaeum is the beginning of the fore-gut formation. It appears as a shallow ectodermal depression on the antero-ventral surface (Text-fig. 1, A, SI). This depression gradually deepens and comes to occupy a position between the mesodermal layer and the outer most serosa (Text-fig. 1, C, SI). Its external opening marks the position of the future mouth. A discontinuous layer of mesoderm extends all along the outer surface of the germ band, and a group of mesodermal cells are found lying immediately posterior to the stomodaeal invagination (Text-fig. 1, A, AER).

At first, the lumen of the stomodaeum is a shallow pit (Text-fig. 1, A, SI) which becomes gradually deeper and gets narrower after sometime. It thus assumes the form of an elongated blind tube (Text-fig. 4, A). Its wall is composed of densely packed columnar cells.

As the stomodaeal invagination deepens some of the mesodermal cells, present at the posteriorly growing blind end are pushed laterally into the cavity of the antenna, while others that still remain there separate from the posterior mesodermal layer, and form the anterior endoderm rudiment of the midgut (Text-fig. 1, A, SI, AER). The displaced mesodermal cells which were pushed into the cavity of the antenna by the deepening of the stomodaeum constitute the pre-oral mass of mesoderm (Text-fig. 1, A, C, POM).

---

*Part 2 of this series appeared in *Proc. Zool. Soc., Calcutta*, **23**: 119-137 (1970).
***Contribution No. 145 from the School of Entomology, St. John's College, Agra. *Rec. Zool. Surv. India*, **65** (1-4) [1967] 1971.



TEXT-FIG. 1. Organogeny of *Dysdercus cingulatus* (Fabr.)

Fig. A. L. S. of an egg of 40 hours, showing the stomodaeal invagination and the scattered mesodermal cells in front of it.

Fig. B. T. S. of an egg of 44 hours through the middle region showing the differentiation of neuroblasts and the formation of nerve swellings.

Fig. C. L. S. of an egg of 44 hours through the anterior end.

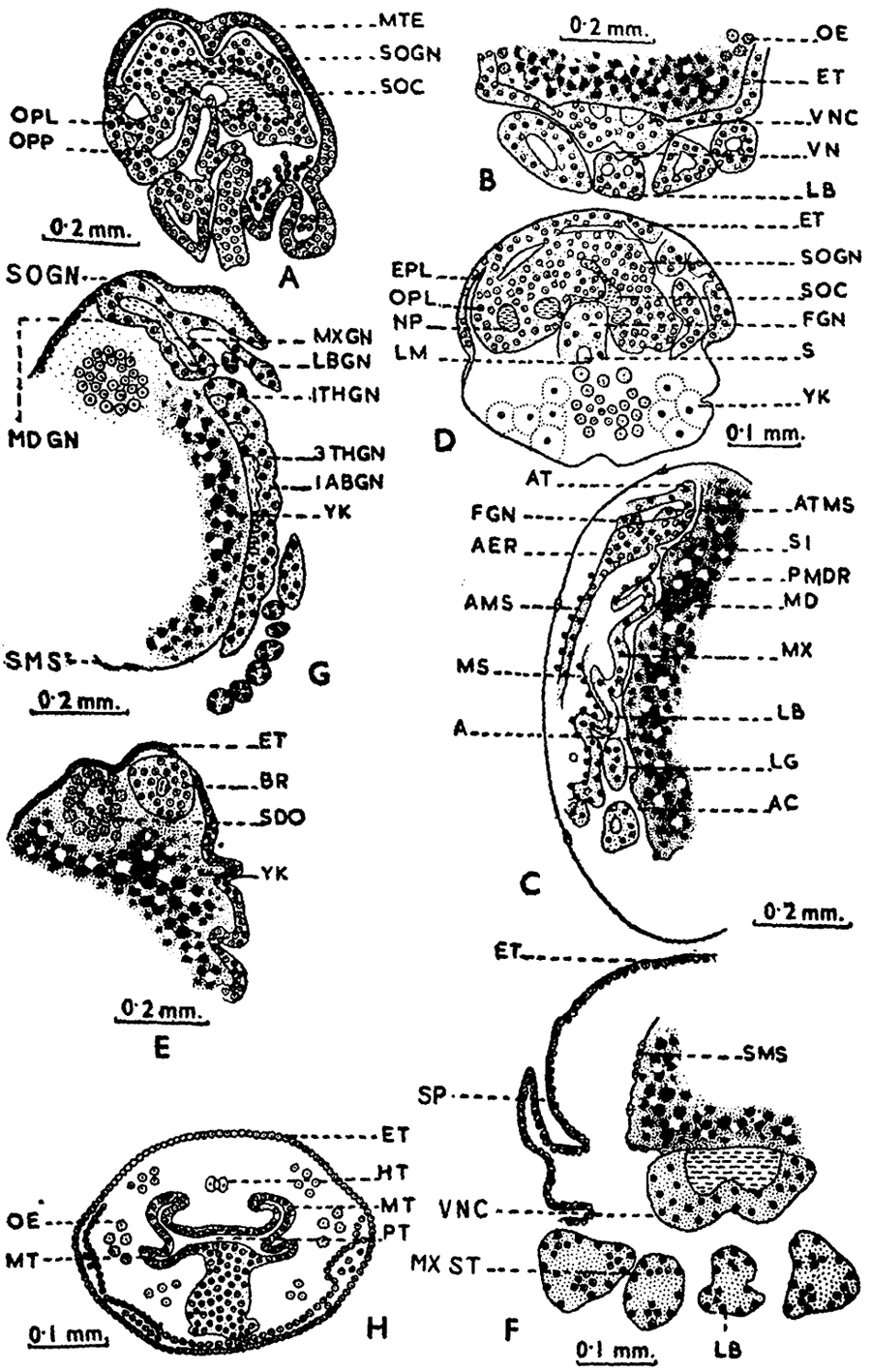
Fig. D. L. S. of an egg of 46 hours through the posterior end.

Fig. E. L. S. of an egg of 56 hours through the anterior end.

Fig. F. T. S. of an egg of 68 hours through the posterior end.

A little later, at the 44th hour of development the mass of cells that remained in front of the stomodaeum (anterior endoderm rudiment) becomes so closely associated with the stomodaeal invagination that it seems as if the anterior endodermal component is being proliferated from the stomodaeal invagination itself (*i.e.* from the ectoderm),

(Text-fig. 1, C, SI, AER). The anterior mid-gut rudiment extends out in the form of two narrow strands as far as the labial segment at the 68th hour of development (Text-fig. 2, C, AER, AMS).



TEXT-FIG. 2. Organogeny of *Dysdercus cingulatus* (Fabr.)

Fig. A. T. S. of an egg of 68 hours through the anterior end.
Fig. B. T. S. of an egg of 68 hours through the middle region to show the ventral notch.
Fig. C. L. S. of an egg of 68 hours showing the anterior mid-gut strands.
Fig. D. T. S. of an egg of 72 hours through the anterior end.
Fig. E. L. S. of an egg of 76 hours through the anterior end.
Fig. F. T. S. of an egg of 76 hours showing deepining of the spiracle into an elongated blind tube.
Fig. G. L. S. of an egg of 76 hours showing the supra oesophageal ganglion, and the mandibular, maxillary and labial ganglion.
Fig. H. T. S. of an egg of 80 hours through rectal region.

As the development of the embryo advances, the stomodaeum elongates and assumes the form of a definite channel, which after 100 hours of development is distinguishable into an anterior sac like pharynx, and a posterior narrow tubular oesophagus (Text-fig. 3, D, PH, O). After another 8 hours of development this tube further elongates and gets distended at its blind end to form the crop (Text-fig. 4, A, CR). It is worthwhile to note here that on the dorsal wall of the pharynx is present a group of small irregular cells which presumably give rise to the stomatogastric nervous system later (Text-fig. 2, C, FGN). The distal wall of the dilated crop thins down to a single layered, almost membranous wall called the limiting membrane. It forms a sort of partition between the cavity of the stomodaeum and the endodermal component of the mid-gut (Text-fig. 4, A, LM).

Thus the fore gut forms a definite channel after five days of development. It extends backwards between the supra and the sub-oesophageal ganglion. The fore gut remains short until blastokinesis is completed, after which its length rapidly increases and it grows in the anterior direction.

The stomodaeal musculature is derived from the preoral and partly also from the post-oral masses of mesoderm (Text-fig. I, C, POM, PTOM).

(b) *The Mid-gut:* The development of the mid gut can conveniently be studied by dividing the entire mid gut into an (i) anterior mid gut, and (ii) posterior mid gut.

(i) *The anterior mid-gut:* The anterior mid-gut rudiment arises as a mass of proliferating cells at the blind end of the stomodaeum after about 42 hours of development. As stated before, this mass of cells is derived from the anterior most cells of the inner layer, lying just in front of the blind end of the stomodaeal invagination. This group of cells becomes heaped up just in front of the stomodaeal invagination and forms a rounded swelling (Text-fig. 1, C, AER). These cells (of the anterior mid-gut rudiment) spread over the stomodaeum and become almost confluent with it, so much so, that they are almost indistinguishable from the ectodermal cells of the stomodaeum. At a slightly later stage, the anterior endoderm rudiment extends a little further posteriorly in the form of two thin ribbons. Mellanby (1936) in *Rhodnius prolixus* Stal and Butt (1949) in *Oncopeltus fasciatus* Doll and Seidel (1924) in *Pyrrhocoris apterus* Linn., have also recorded that the anterior mid-gut rudiment arises in the form of a mass of proliferating cells from the mesodermal layer. As development proceeds, the anterior endoderm rudiment (the mid gut rudiment) extends further to the posterior side. A thin layer of mesoderm intervenes between the rapidly growing anterior mesenteron and the germ band.

(ii) *The posterior mid-gut:* The posterior mid-gut rudiment arises at the 46th hour of development in the same way as the anterior one (Text-fig. 1, D, PER), *i.e.*, from the posterior portion of the mesodermal layer, which becomes so closely associated with the proctodaeal invagination, that it seems as the posterior mid gut rudiment is being proliferated from the ectodermal cells of the proctodaeum.

A very thick layer of mesoderm lies between the proctodaeal invagination and the germ band but it loses connection with the posterior mid-gut. rudiment, which in its turn grows anteriorly separately (Text-fig. 1, D, MS).

After 108 hours of development the anterior mid-gut strands grow posteriorly over the yolk and become invested externally by the splanchnic layer of mesoderm (Text-fig. 4, A, & 5, F, AMS, SMS). Similarly the posterior mid-gut strands also grow over the yolk towards the anterior side and come to lie in apposition to the outer splanchnic mesodermal layer (Text-fig. 4, B, PMS, SMS). Both the anterior and the posterior mesenteron strands growing towards each other over the yolk ultimately meet one another and become fused after about 116 hours of development, thereby enclosing the yolk from all sides (Text-fig. 5, A, MG, MGE). The two anterior and posterior mid-gut ribbons, whose cells were rather loosely arranged now form a compact epithelium, thus giving rise to a simple mid-gut. The mid-gut cells become enlarged and are recognized by their hyaline cytoplasm and a distinct nucleus.

In some cases as in *Melanoplus differentialis* Thomas, (Stuart, 1935) the yolk cells take part in the formation of the mid gut.

In *D. cingulatus*, though the primary yolk cells have been observed in the middle of the egg, in the early stages of development, they have not been observed to take part in the formation of the mid gut epithelium. They disappear at an early stage of development. The anterior and the posterior endoderm rudiments in this case arise from the anterior and posterior ends of the inner layer (mesoderm) respectively. The anterior and posterior mass of mesodermal cells become associated with the stomodaeum and proctodaeum respectively and form the anterior and posterior mid-gut (endoderm) rudiments. Hence the mode of formation of mid-gut in *D. cingulatus* is similar to that described by Seidel (1924) for *Pyrrhocoris apterus*, *Mellanby* (1936) for *Rhodnius prolixus* and Butt (1949) for *Oncopeltus fasciatus*. It is thus concluded that the anterior and posterior mid gut rudiments are mesodermal in origin in the case of *D. cingulatus*.

(c) *The Hind-Gut:* It arises as an ectodermal invagination at the posterior end of the germ band, at the 46th hour of development. It develops six hours after the formation of the stomodaeal invagination. The proctodaeal invagination elongates along the outer surface of the germ band towards the side of serosa (Text-fig. 1, D, PTI). It is known that in insects in general, the stomodaeal formation precedes the proctodaeal development as is the case in *D. cingulatus*, but Sehl (1931) in *Ephestia* and Farooqi (1963) in *Athalia proxima* Klug, record the reverse condition.

A mass of cells is present just in front of the blind end of the proctodaeal invagination. This represents the posterior mesenteron rudiment of the mid-gut (Text-fig. 1, D, PER), and is derived from the cells of the inner layer (mesoderm). The posterior endoderm rudiment becomes attached to the blind end of the invaginating proctodaeum and it appears that the ectodermal cells of the blind end of the proctodaeum are giving rise to the posterior mid-gut rudiment. The wall of the blind end forms a partition between the cavity of the proctodaeum and the component of the mid-gut.

At this stage, the lumen of the proctodaeal invagination is in direct continuation with the amniotic cavity (Text-fig. 1, D). In fact the dorsal wall of the proctodaeal invagination is continuous with the amnion itself (Text-fig. 1, D, APC). Thus the cavity enclosed posteriorly between the amnion and the germ band is known as the amnio-proctodaeal cavity, which in course of time will give rise to the proctodaeum proper.

The proctodaeum after the completion of the blastokinesis differentiates into a pyriform rectum, which communicates with the exterior through a small opening representing the future anal aperture.

The early development of the proctodaeum in *D. cingulatus* is very similar to that recorded in *Oncopeltus fasciatus,* by Butt (1949) and in *Pyrilla perpusilla* Walker by Sander (1956). In all the above mentioned cases the dorsal wall of the proctodaeum is amniotic in origin while the ventral wall is formed by the germ band. The musculature of the proctodaeum is derived from the dense mesodermal layer which lies in the last abdominal segment between the proctodaeum and the germ band (Text-fig. 1, D, MS). These cells spread over the walls of the growing proctodaeum and envelope it along its whole length.

The ectodermal wall between the proctodaeal lumen and the mid-gut ruptures only when the embryo is about to hatch. The partition between the stomodaeum and the mid-gut also ruptures at about the same time, thereby establishing a communication between the fore-gut and the hind gut through the mid-gut.

III—The Excretory System

The Development of Malpighian Tubules: The Malpighian tubules arise as hollow ectodermal outgrowths from the blind end of the proctodaeum at the 68th hour of development (Text-fig. 1, F, MT). There are two pairs of Malpighian tubules in *Dysdercus cingulatus.* At the 80th hour of development, they elongate considerably and appear as long narrow tubes. All of them open by a separate opening into the lumen of the proctodaeum (Text-fig. 2, H, MT). Each tubule pushes its way into the mesoderm surrounding the proctodaeum, which later on forms a thin envelope round each tubule.

In origin, the Malpighian tubules are ectodermal, for they arise as outgrowths of the proctodaeal wall, far back from the posterior mesodermal component of the mid-gut. Their ectodermal origin is confirmed by the presence of a thin ectodermal septum at the blind end of the proctodaeum, which separates their places of origin from the anteriorly lying mesodermal component. Mellanby (1936) in *Rhodnius prolixus* states that the Malpighian tubules arise from the proctodaeum close to its blind end, and that they appear to be ectodermal structures. The ectodermal origin of the Malpighian tubules has been recorded in other groups of insects by Carriere and Burger (1897) in *Chalicodoma muraria* Ratz, Wheeler (1889) in *Leptinotarsa decemlineata,* and by Nelson (1915) in *Apis* (Hymenoptera).

According to Henson (1932) in *Pieris brassicae* Linnaeus, the functional parts of the tubule are derived from the endoderm. Srivastava and Bahadur (1961) while describing the development of the Malpighian tubules in *Dysdercus koenigii* consider Henson's view

to be highly probable. In *D. cingulatus* no evidence has been found to substantiate the endodermal origin of the Malpighian tubules.

IV—THE TRACHEAL SYSTEM

The tracheal system of *Dysdercus cingulatus* consists of the spiracles, the spiracular invaginations and the tracheae. It first makes its appearance in the 56th hour stage as eleven pairs of ectodermal invaginations which mark the position of the spiracles. The paired invaginations arise before the process of blastokinesis has been completed, even before the development of the appendages is well advanced.

Out of the eleven pairs of spiracles the first three belong to the pro, meso and meta-thoracic segments (Text-fig. 3, G, SP. 1, SP. 2, SP. 3 and 4, F, 1THSP, 2THSP, 3THSP) and the rest eight to the first eight abdominal segments. According to Singh (1923) in the females of *Dysdercus cingulatus,* there is, in addition, one degenerate spiracle on the ninth abdominal segment which loses its connection with the trachea in the later stages and thus becomes closed. Hence, in both the sexes, there are no spiracular openings on the last two abdominal segments. The observation of Singh (1923) with regard to the presence of a spiracle on the 9th abdominal segment in the female, gets no support from the present embryological studies.

It has been noted that a little before the hatching of the insect, the prothoracic spiracle closes. Thus there are only ten pairs of functional spiracles in the first larval instar, which are retained in the adult insect also. Mellanby (1936) has observed three pairs of thoracic and eight pairs of abdominal spiracles in *Rhodnius prolixus.* She states that all these persist except the eighth abdominal, which soon closes.

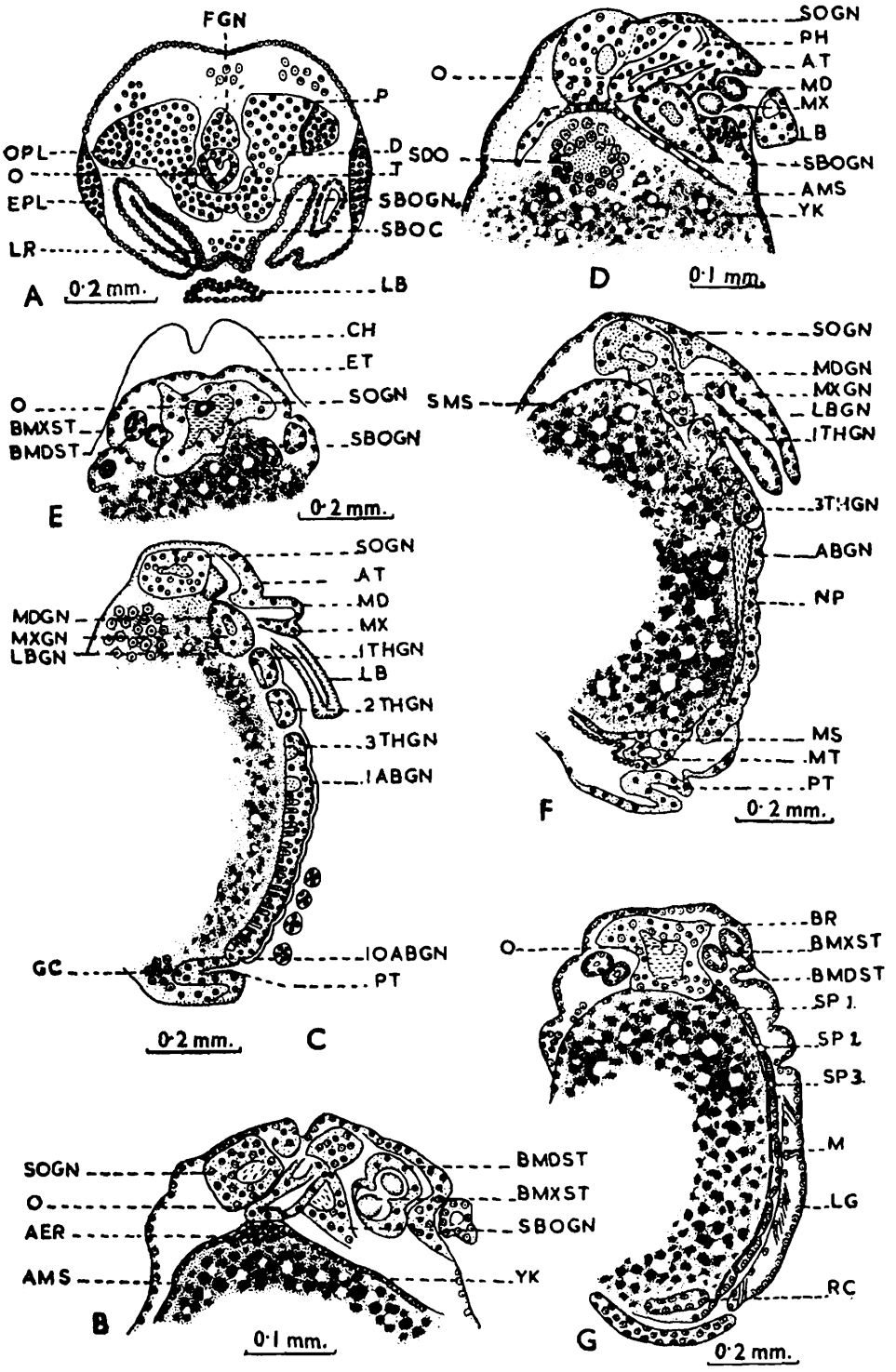
As already described in *D. cingulatus,* the first pair of thoracic spiracles close a little before the egg hatches. Thus out of the ten remaining pairs of spiracles, the first two pairs belong to the thorax and the rest, to the first eight abdominal segments.

It is interesting to note that during the later stages of development an anterior shifting of the thoracic spiracles occurs, as a result of which the mesothoracic spiracle comes to occupy a position between the pro- and the mesothoracic segment and the metathoracic spiracle moves forward to occupy a position between the meso- and metathoracic segment.

According to Singh (1923) in the adult insect, the thoracic spiracles are situated between the pro- and meso-thorax and between the latter and the metathorax. Grove (1909) and Davidson (1913) believe that the first pair of thoracic spiracles belong to the prothorax, while Murray (1914) and Savage (1914) state that they belong to the mesothoracic segment. During the course of the present investigations it has been observed that the first pair of functional spiracles belong to the mesothorax and the second to the metathorax.

A pair of abdominal spiracles are present near the anterodorsal corner of the first eight abdominal segments (Text-fig. 1, F).

As the embryo grows older, the spiracular invaginations which arose as slight ectodermal inpushings deepen to form a small blind elongated tube (Text-fig. 2, F). From the blind end of the



TEXT-FIG. 3. Organogeny of *Dysdercus cingulatus* (Fabr.)

Fig. A. T. S. of an egg of 80 hours through the anterior end.
Fig. B. L. S. of an egg of 84 hours through the anterior end.
Fig. C. L. S. of an egg of 88 hours showing the complete nervous system and the proctodaeal invagination at the posterior end.
Fig. D. L. S. of an egg of 100 hours through the anterior end.
Fig. E. T. S. of an egg of 100 hours through brain.
Fig. F. L. S. of an egg of 100 hours showing the fusion of abdominal ganglia.
Fig. G. F. S. of an egg of 104 hours showing the pro-, meso- and meta-thoracic spiracles.

spiracular tube, arise two well defined trachea simultaneously, one of which is directed towards the anterior end and the other towards the posterior end at the 116th hour of development (Text-fig. 5, C,

ANTR, PTR). The two longitudinal lateral tracheal trunks which run throughout the length of the body are connected to each other by ventral transverse tracheal commissures passing below the ventral nerve cord (Text-fig. 5, D, TTR). The author, therefore, believes that immediately after their origin from either side the ventral commissures give off small branches towards the dorso-anterior and ventro-posterior direction. The former branches ramify profusely over the viscera without forming a commissure and constitute the dorsal tracheal system, whereas the latter branches ramify below the viscera to form the ventral tracheal system.

The external opening of the spiracular invaginations which were earlier very wide, become reduced to narrow clefts. The head and the prothorax presumably receive their tracheal supply from the anterior branch of the first thoracic spiracle, while the posterior branch joins the longitudinal trunk.

V—THE NERVOUS SYSTEM

The nervous system begins to make its appearance at the 44th hour of development. The brain and the nerve cord are ectodermal in origin and develop from specialized ectodermal cells known as the neuroblasts. The neuroblasts become recognizable at an early stage of development, even before the segmentation of the germ band is initiated. They are differentiated on either side of the median portion of the germ band throughout its length (Text-fig. 1, B, NB) and are easily distinguished from the rest of the ectodermal cells, (known as the dermatoblasts) by their large size, a massive nucleus and a comparatively faintly stained cytoplasm.

(A) *The Ventral Nerve Cord:*

After 44 hours of development, before the neuroblasts are completely segregated, an invagination appears along the entire mid-ventral longitudinal line of the germ band. This invagination deepens to form the neural groove (Text-fig. 1, B, NG). Simultaneously, the neuroblasts multiply, as a result of which, two rows of swellings appear, one on either side of the neural groove. These are known as the neural swellings and follow a segmental arrangement (Text-fig. 1, B, NS). The neural swellings will form the segmental ganglia of the nerve cord later on. Thus, two parallel chains of nerve swellings result along the entire length of the embryo. The wedge shaped area which lies in between the neural swellings forms the median cord.

The ectodermal cells (dermatoblasts) which are situated beneath the neuroblasts, become crowded together and arrange themselves to form an outer layer, the dermatogen (Text-fig. 1, B, DB). Unlike the cells of the lateral cords, those of the median cord are not covered externally by the dermatoblasts. The cells of the median cord are narrow and columnar (Text-fig. 1, B, MC).

It has been observed that the neural swellings arise from 3 to 4 neuroblasts which become differentiated on either side of the neural groove. The neuroblasts now divide repeatedly to form a mass of daughter cells known as the ganglion cells (Text-fig. 1, B, GNC). The neuroblasts stop dividing further and the ganglion cells become

compact, and condense to form the ganglia. The ultimate fate of the parent neuroblasts is not known.

The median cord, as described before, is placed like a wedge between the two lateral cords (Text-fig. 1, B, MC). The neurogenic cells of the median cord are distinguished from the other nerve cells by their larger size and paler cytoplasm. The cells of the median cord take part in the formation of the nerve ganglion in combination with the segmental swellings of the two lateral cords.

The cells of the median cord give off fine fibres which form the transverse commissures. These fibres unite with the ganglionic fibres from the ganglion cells and thus establish a connection between the two members of the same segmental ganglionic pair.

As growth progresses the two lateral cords unite medially, leaving a temporary notch on the ventral side (Text-fig. 2, B, VN), which soon disappears, with the growth of the nervous tissue. During the subsequent development, the nerve cords become separated from the underlying ectoderm. The ganglia of the same segment fuse together to give rise to the segmental ganglion. In the intersegmental regions the two ventrally running lateral cords come in close approximation to one another, but can be easily distinguished from each other. These form the paired longitudinal connectives between the succeeding and the preceding ganglion. The transverse commissures between the ganglia of each pair become obliterated due to the consolidation of the two ganglionic halves but the line of fusion can still be observed. The paired lateral nerves arise from the lateral portion of the ganglia. At the side of the developing nerves, the ganglion cells produce fine fibres which become continuous with the fibre region of the ganglia on the one side and form the lateral nerve on the other (Text-fig. 5, B, LN).

In an 88 hour old embryo the nervous system of *D. cingulatus* consists of the supra-oesophageal ganglion, three gnathal, three thoracic and ten abdominal ganglia (Text-fig. 3, C SOGN, MDGN, MXGN, LBGN, 1THGN, 2THGN, 3THGN, 1ABGN. 10ABGN). It is interesting to note that in the adult *D. cingulatus*, the nervous system consists of a cerebral ganglia (supra-oesophageal ganglion), a suboesophageal ganglion and two thoracic ganglionic masses and the ventral nerve cord devoid of any abdominal ganglia. The presence of 10 abdominal ganglia and three thoracic ganglia during early embryonic stages, as mentioned above, gives an indication of the massive consolidation of the ganglia that has resulted in the adult condition. The triganglionic origin of the sub-oesophageal ganglionic mass (three gnathal ganglia) representing the mandibular, maxillary and labial ganglia, can be observed even at the 100th hour of development (Text-fig. 3, F, MDGN, MXGN, LBGN). The three gnathal ganglia later fuse to form the sub-oesophageal ganglionic mass. (Text-fig. 4, C, SBOGN).

At a slightly later stage of development, signs of fusion become evident. The first abdominal ganglion fuses with the third thoracic ganglion which is followed by the establishment of continuity of the neuropiles of the first three abdominal ganglia, which marks the first step towards the consolidation of abdominal ganglia (Text-fig. 2, G, 3THGN, 1, ABGN). At the 100th hour of development the neuropiles of all the abdominal ganglia become continuous (Text-fig. 3,

F, ABGN, NP), which gives the indication of fusion of all the abdominal ganglia.

Concentration of abdominal and thoracic ganglia occurs between 100 and 108 hours of development (Text-fig. 4, A). The abdominal part of the ventral nerve cord is pulled up into the thorax, which results in the complete absence of abdominal ganglia in the adult. In an 108 hour old embryo the nervous system consists of the supra-oesophageal ganglion, sub-oesophageal ganglion (Text-fig. 4, A, SOGN, SBOGN) and two thoracic ganglia (Text-fig. 4, A, 1THGN, 2THGN). Of the two thoracic ganglionic masses, the first belongs to the prothorax while the second represents the complex of meso, and metathoracic ganglionic masses with which have become fused the embryonic abdominal ganglia (Text-fig. 4, A).

Thus, at the time of hatching, the nervous system consists of a supra-oesophageal ganglion, a sub-oesophageal ganglion, two thoracic ganglionic masses and a ventral nerve cord which extends up to the posterior end of the abdomen.

(B) *The Brain:*

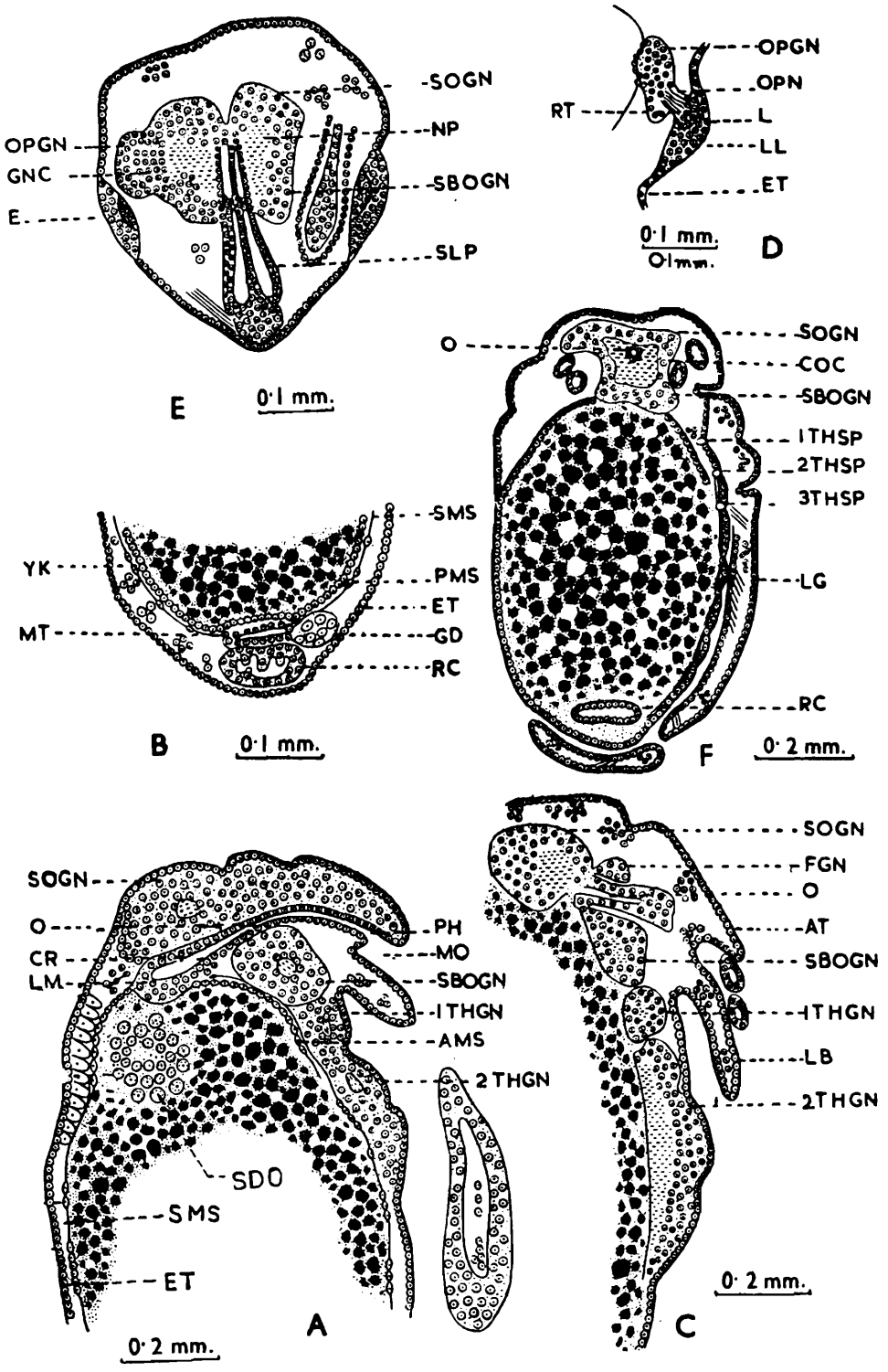
The brain of *Dysdercus cingulatus* is formed by the fusion of three pairs of ganglia, *viz.* protocerebrum, deutocerebrum and tritocerebrum (Text-fig. 3, A, P., D., T.). These three component ganglia of the brain, become defined on either side of the anterior end of the germ band at the same time, as the ventral ganglia make their appearence. The protocerebrum develops from the neuroblasts of the protocerebral segment. The deutocerebrum and the tritocerebrum develop from the neuroblasts in the antennary and premandibular segment respectively.

(i) *The Protocerebrum and the Optic Ganglion:* The protocerebral lobe of the brain is the largest of the three components and occupies a greater part of the head lobe (Text-fig. 3, A, P). The two lobes of the protocerebrum are connected medially by a narrow bridge through which a transverse band of nerve fibres traverse, giving rise to the supra-oesophageal commissure (Text-fig. 2, A & 5, E, SOC). The commissure arises partly from the cells of the protocerebral lobes and partly from a median thickening of the epidermis which retains its intimate relation with the protocerebral lobes till the commissure is completely formed (Text-fig. 2, A).

The protecerebral lobes can be distinguished into its three constituent lobes. The first, the second and the third lobes are separated from each other by a slight depression.

The ganglia of the brain retain their connection with the ectodermal wall till the end of the third day of development. Partial separation takes place at the 72nd hour of development, while complete separation takes place after 76 hours of development.

Optic Ganglion: At about the 68th hour of development the ectoderm opposite to the protocerebral lobe 3 becomes thickened to form a more or less round mass of cells. The peripheral cells of this mass arrange themselves in a single row, while in the rest of the mass they exhibit an irregular arrangement. This mass will give rise both to the optic ganglion and the optic plate (Text-figs. 2, A, OPL,



TEXT-FIG. 4. Organogeny of *Dysdercus cingulatus* (Fabr.)

Fig. A. L. S. of an egg of 108 hours through the anterior end.
Fig. B. L. S. of an egg of 108 hours through the posterior end.
Fig. C. L. S. of an egg of 108 hours showing the frontal ganglion above the stomodaeum.
Fig. D. T. S. of an egg of 108 hours showing the optic ganglion.
Fig. E. T. S. of an egg of 108 hours through the anterior end.
Fig. F. F. S. of an egg of 112 hours showing the thoracic ganglion.

OPP). After another four hours of development, the inner irregular mass (optic ganglion) begins to separate from the outer unilayered optic plate (Text-fig. 2, D, OPL, EPL), and later on the dermatogen loses its connection with the optic ganglion and becomes continuous with the optic plate. After 80 hours of incubation the separation of

the optic ganglion from the optic plate is complete (Text-fig. 3, A, EPL, OPL). The optic ganglion now fuses with the protocerebral lobe and loses its entity in the later stages.

In *Dysdercus cingulatus*, it has been observed that the cells of the peripheral thickened ectoderm divide and give rise to a large number of ganglionic cells, which are destined to form the optic ganglion. These ganglion cells in their turn form nerve fibres which become continuous with the fibre region of the protocerebral lobes (Text-fig. 4, E, GNC, OPGN).

(ii) *Deutocerebrum and Tritocerebrum:* The deutocerebral lobes of *D. cingulatus* are fairly large and occupy a position at the base of the antenna (Text-fig. 3, A, D). They do not extend so far laterally as the protocerebral lobes. The proto and deutocerebral lobes of the brain are at first widely separated from each other, but with the subsequent development, the deuto — cerebral lobes fuse with the protocerebrum. There is no transverse commissure in the deutocerebrum.

The tritocerebral ganglia (Text-fig. 3, A, T) are the smallest of the three lobes and lie in front of the mandibles and belong to the premandibular segment. They are in continuation with the deutocerebrum in front and with the mandibular ganglion behind. The tritocerebrum merges completely in the hinder margin of the deutocerebrum. The tritocerebral lobes are connected to each other by a transverse commissure known as the sub-oesophageal commissure (Text-figs. 5, E, SBOC).

The tritocerebrum also gives rise to the circumoesophageal connectives which unite it to the sub-oesophageal ganglionic mass (Text-figs. 5, E, COC).

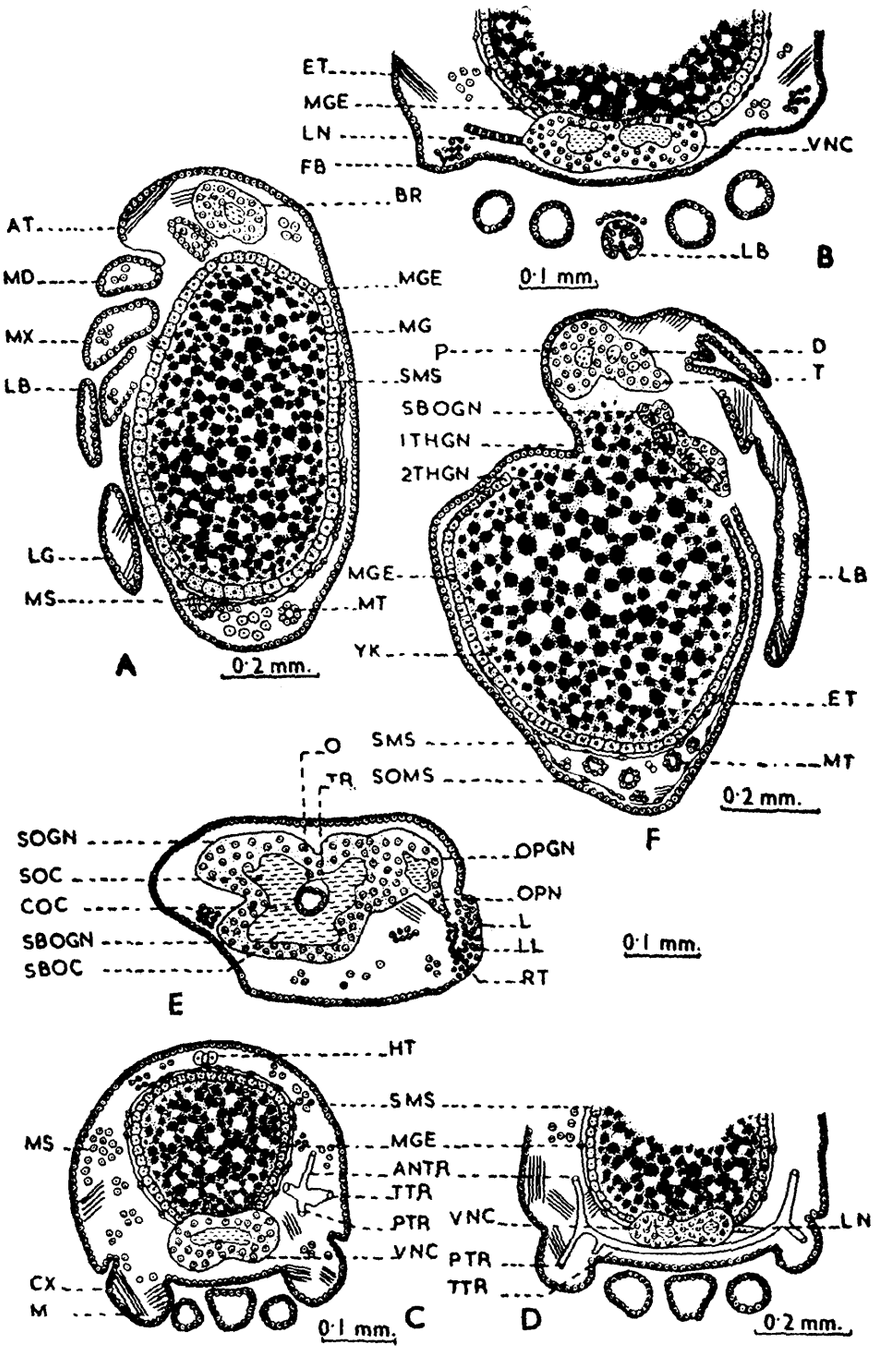
(C) *Sympathetic Nervous System:*

The sympathetic nervous system of *Dysdercus cingulatus* originates from a median thickening in the dorsal wall of the stomodaeum after 72 hours of development (Text-fig. 2, C, FGN). At this stage a large mass of cells is seen above the dorsal wall of the stomodaeum (Text-fig. 2, D, FGN). This mass of cells has not as yet assumed the form of true nerve cells. At the 108th hour of development these cells consolidate to form the frontal ganglion lying on the dorsal wall of the stomodaeum. It is soon constricted off from the stomodaeal wall and can be seen closely adhering to it (Text-figs. 3, A & 4, C, FGN).

After another 8 hours of development *i.e.*, at the 116th hour, the frontal ganglion gets completely severed off from the dorsal wall of the stomodaeum (Text-fig. 2, D, FGN). This mass of cells has not as yet assumed the form of true nerve cells. At the 108th hour of development these cells consolidate to form the frontal ganglion lying on the dorsal wall of the stomodaeum. It is soon constricted off from the stomodaeal wall and can be seen closely adhering to it (Text-figs. 3, A & 4, C, FGN).

After another 8 hours of development *i.e.*, at the 116th hour, the frontal ganglion gets completely severed off from the dorsal wall of the stomodaeum and is separated from it by the mesodermal layer that penetrates in between the two. The origin of the recurrent nerve,

the paired pharyngeal ganglia and the occipital ganglion could not be traced.



TEXT-FIG. 5. Organogeny of *Dysdercus cingulatus* (Fabr.)

Fig. A. L. S. of an egg of 116 hours showing the completely formed mid gut epithelium.
Fig. B. T. S. of an egg of 116 hours showing the origin of lateral nerve.
Fig. C. T. S. of an egg of 116 hours showing the anterior, posterior and transverse tracheal branches.
Fig. D. T. S. of an egg of 116 hours showing the anterior, posterior and transverse tracheal trunks.
Fig. E. T S. of an egg of 116 hours through the anterior end.
Fig. F. L. S. of an egg of 124 hours L. S. showing the proto-, deuto and tritocereberum, the sub-oesophageal ganglion and two thoracic ganglia.

In *Rhodnius prolixus,* Mellanby (1936) states that the sympathetic nervous system develops from a mass of cells lying in the mid dorsal part of the stomodaeum. The anterior part of this mass of cells gives rise to the frontal ganglion, while the posterior part forms the sympathetic ganglion. The two ganglia are connected by a recurrent nerve.

(D) *Development of the Eye:* At the 44th hour of development, the dorso-lateral areas of the ectoderm on either side of the brain, become thickened to form the common rudiment of the optic ganglion and the optic plate (Text-fig. 2, A, OPL, OPP). The outermost cells of this ectodermal thickening are arranged neatly in a single row, while the rest of the cells show an irregular arrangement.

After 72 hours of incubation the inner cell mass, destined to form the optic ganglion, separates from the outer layer (optic plate), which in its turn becomes continuous with the rest of the dermatogen (Text-figs. 2, A, D, & 3, A, EPL, OPL, OPP). The outer layer of the optic plate now thickens (Text-figs. 2, A, D & 3, A, EPL, OPP), and after 108 hours of development becomes transparent to form the convex lens of the eyes (Text-fig. 5, E, L). The cells underlying the lens arrange themselves neatly and constitute the lenticular layer (Text-fig. 4, D, 5, E, LL). The layer below the lenticular layer forms the retina, the cells of which are closely packed (Text-figs. 4, D & 5, E, L, LL, RT). The so formed structure of the eye remains unaltered during the entire embryonic development. While the structural differentiation of the cells of the eye is taking place, the peripheral cells of the optic ganglion send out long nerve fibres to the eye which together constitute the optic nerve (Text-figs. 4, D & 5, E, OPN).

VI—SYNOPTIC TABLE OF DEVELOPMENT AT DIFFERENT HOURS OF INCUBATION

State of development	*Incubation period*
The stomodaeal invagination appears on the outer surface of the germ band. The anterior and posterior cells of the mesodermal layer give rise to the anterior and posterior mid-gut rudiments.	40 hours
Neuroblasts appear. Two continuous rows of nerve swellings are formed.	44 hours
The proctodaeal invagination makes its appearance and the posterior mid-gut rudiment becomes distinguishable.	46-48 hours
The anterior and posterior mid-gut ribbons start growing posteriorly and anteriorly respectively.	50 hours
Eleven pairs of spiracular invaginations are formed.	56 hours
Malpighian tubules appear. Fusion of the two lateral nerve swellings takes place and the segmental ganglia are formed in all the segments. Brain enlarges. The common rudiment of the optic ganglion and the optic plate is differentiated.	68 hours
The optic ganglion becomes well differentiated. The rudiment of the sympathetic nervous system appears.	72 hours

State of development	
The abdominal ganglia show signs of fusion. The mandibular, maxillary and labial ganglion become distinct. The spiracular invaginations deepen and form a blind tube.	76 hours
The optic lobe becomes associated with the protocerebrum. Frontal ganglion is formed.	80 hours
Abdominal ganglia consolidate.	88 hours
Pharynx and oesophagus are formed.	100 hours
The oesophagus dilates to form the crop. The abdominal ganglia and the third thoracic ganglion fuse with the meso-thoracic ganglion. The lens, the retina of the eye are formed.	108 hours
Complete mid-gut is formed. An anterior, posterior and transverse tracheal branch arise from the blind end of the spiracular invagination.	116 hours
The fore,- mid,- and hind gut become continuous. The eyes appear as dark brown spots.	128 hours

VII—SUMMARY

1. The stomodaeal and proctodaeal invaginations arise as ectodermal invaginations of the germ band and grow towards the outer surface of the embryonic rudiment *i.e.* towards the side of the serosa.
2. The proctodaeal invagination is in direct continuation with the amniotic cavity in the early stages of development and hence it is known as the amnio-proctodaeal cavity.
3. The anterior and posterior mid-gut rudiments are derived from the anterior and posterior cell masses of the mesodermal layer.
4. The Malpighian tubules arise from the blind end of the proctodaeum and hence are ectodermal in origin. There are two pairs of Malpighian tubules, and each one of them opens by a separate opening into the lumen of the proctodaeum.
5. The tracheal system makes its appearance as eleven pairs of ectodermal invaginations, which represent the spiracles.
6. The first three pairs of spiracles belong to the three thoracic segments and the rest eight to the first eight abdominal segments respectively.
7. The pro-thoracic spiracle closes a little before the hatching of the egg and an anterior shifting of the meso- and metathoracic spiracles occurs.
8. The nervous system develops from the neuroblasts which are specialized ectodermal cells. The neuroblasts divide to give rise to two rows of neural swellings, which form the segmental ganglia of the nerve cord in each segment of the body.
9. The nervous system in the embryonic stages consists of a brain, a sub-oesophageal ganglion, three thoracic and ten abdominal ganglia.

10. At a later stage of development all the abdominal ganglia along with the third thoracic fuse with the second thoracic ganglion. Thus in the adult bug, the nervous system consists of the brain the sub-oesophageal ganglion and two thoracic ganglia only.

VIII—ACKNOWLEDGEMENTS

I take this opportunity of thanking Dr. T Singh, Professor of Zoology and Entomology, School of Entomology, St. John's College, Agra, for guidance and for facilities for work during the course of this work. I owe my thanks to Dr. Santokh Singh of the School of Entomology, for constant encouragement and for his very able advice in the preparation of this paper. I have also to thank Dr. M. S. Mani, and Dr. Shah M. Alam, Prof. and Head of the Zoology Department, Aligarh Muslim University, for useful suggestions.

IX—REFERENCES

BUTT, F. H. 1949. Embryology of milkweed bug *Oncopeltus fasciatus* (Hemiptera).—*Mem. Cornell Univ. agric. Exp. Stn.*, Ithaca, New York, 283, pp. 3-45.

CARRIERE, J. and O. BURGER. 1897. Die Entwicklungseschichte der mauerbiene (*Chalicodoma muraria* Fabr.) in Ei.—*Nova Acta. Leopoldina,* Leopoldina, 69, pp. 255-420.

DAVIDSON, J. 1913. Structure and biology of *Schizoneura lanigera* Hausmann.—*Q. Jl. microc. Sci.* London, 58, pp. 653-697.

FAROOQI, M. M. 1963. The embryology of the mustard sawfly, *Athalia proxima* Klug. (Tenthredinidae: Hymenoptera).—*Aligarh Musl. Univ. Publs.*, (Zoological Series) Aligarh, 5, pp. 1-59.

GROVE, A. J. 1909. Anatomy of *Siphonophora rosarum* Walker.—*Parasitology,* Cambridge, 2, pp. 1-25.

HENSON, H. 1932. The development of the alimentary canal in *Pieris brassicae* and the endodermal origin of the Malpighian tubules in insects.—*Q. Jl. microsc. Sci.*, London, 75, pp. 283-309.

HEYMONS, R. 1899. Beitrage zur Morphologie und Entwicklungs-geschichte der Rhynchoten.—*Nova Acta. Leopoldina.*, Leopoldina, 74, pp. 351-456.

MELLANBY, H. 1936. The later development of *Rhodnius prolixus.*—*Q. Jl. microsc. Sci.*, London, 79, pp. 1-42.

MURRAY, C. H. 1914. Notes on the anatomy of the bed bug. (*Acanthia lectularia* L.)—*Parasitology,* Cambridge, pp. 278-321.

NELSON, J. A. 1915. The embryology of the honey bee.—*Princeton Univ. Bull.*, Princeton, N. J., pp. 1-282.

SANDER, K. 1956. The early embryology of *Pyrilla perpusilla* Walker (Homoptera), including some observations on the late development.—*Aligarh Musl. Univ. Publs.*, (Zoological Series) Aligarh, 4 pp. 1-61.

SAVAGE, R. E. 1914. Respiratory system in *Monophlebus stebbingi* var *octocaudata.—Bull. ent. Res.*, London, 5 pp. 45-47.

SEHL, A, 1931. Furchung und Bildung der Keimanlage bei der Mehlmotte *Ephestia kuhniella,* nebst einer allgemeinen ubersicht uber den Verlauf der Embryonalentwicklung.—*Z. f. Morph. Okol. Tiere.,* Berlin, pp. 535-598.

SEIDEL, F. 1924. Die Geschlechts organe in der embryonalen Entwicklung von *Pyrrhocoris apterus.—Z. f. Morph. Okol. Tiere,* Berlin, 1 pp. 429-506.

SINGH, H. 1923. On the anatomy and bionomics of the red cotton bug, *Dysdercus cingulatus* Fabr.—*J. Asiat. Soc. Beng.,* Calcutta, 19 pp. 15-42.

SRIVASTAVA, U. S. AND BAHADUR, I. 1961. The Development of Malpighian Tubules in *Dysdercus koenigi* (Hemiptera: Pyrrhocoridae).—*Q. Jl. microsc. Sci.,* London, 102, pp. 347-360.

STUART, R. R. 1935. The development of the mid — intestine in *Melanoplus differentialis.—J. Morph.,* Philadelphia 58 pp. 419-438.

WHEELER, W. M. 1889. The embryology of *Blatta germanica* and *Doryphora decemlineata.—J. Morph., Philadelphia,* 3 pp. 291-386.

ABBREVIATIONS

A.—Amnion ; AC.—Amniotic cavity ; IABGN.—First abdominal ganglion ; 10ABGN.—10th abdominal ganglion ; AER.—Anterior endoderm rudiment ; AMS.—Anterior mid-gut strand ; APC.—Amnio-proctodaeal cavity ; AT.—Antenna ; ATMS.—Antennary mesoderm ; BMDST.—Base of the mandibular stylet ; BMXST.—Base of the maxillary stylet ; BR.—Brain ; CH.—Chorion ; CR.—Crop ; CX.—Coxa ; D.—Deutocerebrum ; DB.—Dermatoblasts ; E.—Eye ; EPL.—Eye plate ; ET.—Ectoderm ; FB.—Fat body ; FGN.—Frontal ganglion ; GC.—Germ cells ; GD.—Gonad ; GNC.—Ganglion cells ; HT.—Heart ; L.—Lens ; LB.—Labium ; LBGN.—Labial ganglion ; LG.—Leg ; LL.—Lenticular layer ; LM.—Limiting membrane ; LN.—Lateral nerve ; LR.—Labrum ; M.—Muscle ; MC.—Median cord ; MD.—Mandible ; MDGN.—Mandibular ganglion ; MG.—Mid-gut ; MGE.—Mid-gut epithelium ; MO.—Mouth ; MS.—Mesoderm ; MT.—Malpighian tubule ; MTE.—Median thickening of the ectoderm ; MX.—Maxilla ; MXGN.—Maxillary ganglion ; MXST.—Maxillary stylet ; NB.—Neuroblasts ; NG.—Neural groove ; NP.—Neuropile ; NS.—Neural swelling ; O.—Oesophagus ; OE.—Oenocytes ; OM.—Oblique muscles ; OPGN.—Optic ganglion ; OPL.—Optic lobe ; OPN.—Optic nerve ; OPP.—Optic plate ; PER.—Posterior endoderm rudiment ; PH.—Pharynx ; PMD.—Pcemandibular rudiment ; PMS.—Posterior mid-gut strand ; POM.—Pre-oral mesoderm ; PT.—Proctodaeum ; PTOM.—Post-oral mesoderm ; PTR.—Posterior trachea ; RC.—Rectum ; RT.—Retina ; S.—Stomodaqum ; SBOC.—Sub-oesophageal commissure ; SBOGN.—Sub-oesophageal ganglion ; SDO.—Secondary dorsal organ ; SE.—Serosa ; SI.—Stomodaeal invagination ; SLP.—Salivary piston ; SMS.—Splanchnic mesoderm ; SOC.—Supra-oesophageal cosmmissure ; SOGN.—Supra-oesophageal ganglion ; SP.—Spiracle ; SP_1, SP_2, SP_3—Spiracle 1, 2 & 3 ; T.—Tritocerebrum ; 1, 2 & 3 THGN.—First, Second and third thoracic ganglion ; 1, 2 & 3 THSP.—First, second and third thoracic spiracle ; TR.—Trachea ; TTR.—Transverse trachea ; VN.—Ventral notch ; VNC.—Ventral nerve cord ; YK.—Yolk.

Present Address: School of Tropical Medicine, Calcutta.