VI. EMBRYONIC ENVELOPES AND BLASTOKINESIS

(A) Embryonic envelopes.

In *D. indicus*, immediately after the differentiation of the endomesoderm, the embryonic envelopes are developed. The cells of the extra-embryonal layer assume a pronounced squamous shape and can be clearly distinguished from the cells of the germ band. At the twenty-third hour, the posterior part of the embryo sinks inward so that the extra-embryonal epithelium gets folded forwards on the ventral surface of the embryo (Fig. 33). At the same time the cells of the serosa elongate and become more or less spindle shaped. Due to the in-sinking of the embryo and elongation of the serosal cells, a post-amniotic fold is formed which grows over a small portion of the embryo at the posterior end. A similar fold appears anteriorly (Fig. 34), but it is not so pronounced (Fig. 35). During the sinking process the embryo remains connected everywhere to the extra-embryonal layer. As a result of head and tail folds, the amnion becomes separated from the serosa. Amniotic folds finally extend from all sides over the ventral surface of the embryo. When the folds of the amnion have completely overgrown the embryo a closed amniotic cavity is formed (Fig. 36). The amnion is at first composed of well defined rectangular cells, but soon the cells become stretched as the amnion is stretched over the ventral surface of the growing embryo. The outer layer forms the serosa (Fig. 37) which is continuous with the extra-embryonal layer and has no
part in the formation of germ layers. The cells of the
serosal layer are elongated with large spherical nuclei.
The serosa forms a closed sac which covers the whole surface
of the egg with one part extending over the surface of the
yolk and the other part over the ventral surface of the embryo.

In *D. indicus*, the yolk is seen penetrating between the
amnion and the serosa only at the time of formation of the
embryonic envelopes in the posterior region. But in later
stages it is not seen penetrating between the amnion and the
serosa and the embryo remains superficial during its further
development.

(B) **Segmentation and Appendages.**

(1) **Segmentation.**

The germ band shows superficial segmentation, at first
divided transversely in the endomesoderm which then becomes
evident in the ectoderm. The segmentation of the germ band
later reduces to ten, when the abdominal segmentation is tak-
is first initiated in the anterior region and then proceeds
backwards. The segmentation of the abdomen takes place only
become more pronounced. The number of segments taking part
when procephalic, gnathal and thoracic segments along with
into the formation of the head has been determined. Six
their appendages are well defined. Roughly, around twenty-
segments take part in the head development. The head segment-
fourth hour, the germ band first divides into two parts as
then plan based on the study of appendages, coelomic sacs,
protocephalon (primary cephalic) and protocorm (primary trunk)
and neurosomes is given in Table 1. (page 35)
(Fig. 38). The protocephalon is broader and conspicuous because
of its lateral lobes which give rise to the protocerebral seg-
ments. These lateral lobes enlarge and spread on the sides
of the yolk. The protocephalon will give rise later to
appendages of the head, thorax, and abdomen can be
labrum, mouth, eyes, and antennae.
In about thirty hours, the protocorm shows signs of segmentation (Fig. 39). It divides into a broad anterior part and a narrow posterior part. The front portion of the latter shows inconspicuous lines of further segmentation into six segments. The first three are the gnathal segments -- mandibular, first maxillary, and second maxillary. The remaining three segments give rise to the three thoracic segments -- prothorax, mesothorax, and metathorax.

The narrow posterior part shows the first indication of segmentation at about thirty-six hours. First two abdominal segments are well marked, lying immediately behind the third thoracic segment (Fig. 40). Further segmentation of the abdomen takes place when a feeble indication of division appears in the remaining portion of the abdomen at about forty-two hours.

The abdomen is finally divided into eleven segments which later reduce to ten. When the abdominal segmentation is taking place the gnathal as well as the three thoracic segments become more pronounced. The number of segments taking part into the formation of the head has been determined. Six segments take part in the head development. The head segmentation plan based on the study of appendages, coelomic sacs, and neuromeres is given in Table 1. (page 35)

(2) Appendages.

The appendages develop as small hollow evaginations of the ectodermal wall situated laterally. In the developing embryo appendages of the head, thorax, and abdomen can be
Table 1. Observations recorded on the head segmentation of *D. indicus*.

<table>
<thead>
<tr>
<th>No. of segments</th>
<th>Segment</th>
<th>Appendages</th>
<th>Coelomic sacs</th>
<th>Neuromeres</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Labrum</td>
<td>Labrum</td>
<td>Yes</td>
<td>Protocerebrum</td>
</tr>
<tr>
<td>2</td>
<td>Antennary</td>
<td>Antennae</td>
<td>Yes</td>
<td>Deutocerebrum</td>
</tr>
<tr>
<td>3</td>
<td>Intercalary</td>
<td>-</td>
<td>Yes</td>
<td>Tritocerebrum</td>
</tr>
<tr>
<td>4</td>
<td>Mandibular</td>
<td>Mandibles</td>
<td>Yes</td>
<td>Mandibular</td>
</tr>
<tr>
<td>5</td>
<td>First maxillary</td>
<td>First maxillae</td>
<td>Yes</td>
<td>First maxillary</td>
</tr>
<tr>
<td>6</td>
<td>Second maxillary or labial</td>
<td>Second maxillae</td>
<td>Yes</td>
<td>Labial</td>
</tr>
</tbody>
</table>

distinguished. The head appendages develop from the head lobes. The labrum arises in front of the stomodeaum as a pair of ventral lobes (Figs. 39 and 40). The two lobes come close to each other and eventually fuse to form a single flap-like structure overhanging the stomodeal invagination in later stages (Fig. 41). The antennae arise as two small backwardly directed papillae from the postero-ventral region of the antennary segment. Antennae are post-oral in the beginning; but with subsequent rapid growth of the anterior and lateral cephalic structures they are carried upwards and forwards and eventually come to lie in a pre-oral position (see Fig. 41).

The intercalary segment is seen merely as a pair of obscure
undulations. There are no appendages pertaining to this segment which has a conspicuous mass of mesoderma. A pair of mandibles arise from the mandibular segment. During the subsequent development the mandibles become pointed at their distal ends but are broad basally. The sickle-shaped mandibles lie on either side of mouth in a hinged pattern. Each of the mandibles is traversed by a fine canal. These are the strongest appendages on the head and therefore, the head is of mandibulate type. The mandibles become yellowish on the fourth and fifth day. The maxillary appendages become constricted into a large basal and smaller distal part. The distal lobe gives rise to the palp. The basal and distal condition is caused by a transverse constriction of the appendage. The maxillae come to occupy a postero-lateral position with respect to the mouth aperture. Their distal ends are directed towards the mouth. The second maxillae or labial appendages meet in the mid-line behind the mouth aperture. Their bases fuse together and the palps are directed towards the mouth. The cardo and mala will form from the proximal part. Chitinization of the head capsule occurs on the fourth day.

The small hollow ectodermal outgrowths of the thoracic appendages become conspicuous and extend backwards as the development proceeds. Each of these appendages gives rise to three segments corresponding to the coxa, femur, tibia. The trochanter becomes differentiated at a later stage. Each thoracic leg bears at the tip a claw-like structure. The abdomen consists of ten segments and it tapers towards the
posterior end. The last abdominal segment has a telescopic arrangement. The abdominal appendages arise as short ectodermal evaginations. These are hollow structures. In later life each such hollow structure of the first nine segments is penetrated by a fine trachea. Each of the first eight abdominal segments carries a pair of such abdominal appendages. The ninth segment, however, has two pairs. Each abdominal appendage is a small structure with fine hairy outgrowths. The last abdominal segment bears posteriorly two pairs of curved, chitinous and hook-like appendages.

(C) **Dorsal Closure of the Embryo and Secondary Dorsal Organ**

(1) **Dorsal closure of the embryo**.

The growing embryo needs nourishment, which is provided in the form of yolk globules. Constant growth of the embryo requires space, which is created while the food is consumed. By the end of twenty-three hours, the development of the amnion and serosa is well advanced (see Fig. 37). Around twenty-sixth hour due to the pressure exerted by the growing embryo, the amnion ruptures and fuses with the serosa along the midventral line (Figs. 42 and 43). The margins of the amnion and serosa remain adhered to each other for sometime. Later, due to the dorsal contraction of the serosa and upward growth of the embryo the serosa ruptures (Fig. 44), and all the food material i.e. yolk mass is enclosed by the embryo (Fig. 45). At the time of dorsal closure the amnion forms a provisional body wall on the dorsal side.
(2) **Secondary dorsal organ**.

During the process of dorsal closure the serosal cells become larger to form the secondary dorsal organ, a cluster of polygonal cells with spherical nuclei (Fig. 46). Formation of the secondary dorsal organ proceeds from posterior end to the anterior end. Later, it disappears with the complete degeneration of its cells in the surrounding yolk mass. The degeneration of the secondary dorsal organ takes place from the posterior end and proceeds simultaneously as the organ is being built up in the anterior side. No part of the secondary dorsal organ goes into the construction of the definitive body wall.

(3) **Blastokinesis**.

The delicate and thin extra-embryonal layer developed at the time of germ band formation is later differentiated into the serosa. The anterior and posterior parts of the germ band sink into the yolk mass, so that the head and tail folds, respectively, are formed (See Fig. 35). The germ band elongates towards the anterior side and the amnion becomes separated from the serosa. The amnion covers the entire ventral surface of the embryo (See Figs. 36 and 37). Further increase in length of the embryo results in rupture of the amnion mid-ventrally which ultimately joins the serosa (See Figs. 42 and 43). The anterior and posterior ends of the germ band grow towards the dorsal side. Later, the segmentation and appendages are formed (See Fig. 47). At the time of dorsal closure the germ band is shortened. The segmental furrows
become more conspicuous with the shortening of the germ band. The food for the constantly growing embryo is provided in the form of yolk granules, the absorption of which facilitates to accommodate the growing embryo. During the process of dorsal closure the whole yolk mass is enclosed by the growing embryo and towards the end of this process both the embryonic membranes disintegrate into the yolk mass. As the embryo develops the posterior portion grows towards the ventral side and the embryo becomes J-shaped (Figs. 48 and 49). Similarly, the head also moves toward the ventral side. The embryo elongates and becomes S-shaped (Figs. 51 and 52).

All these movements of the germ band such as in-sinking, lengthening, shortening and bending of head and tail regions are more specific and therefore, are considered as blastokinetic movements.