I. INTRODUCTION

Historical aspects of the development of phoronids are summarized by Selys-Longchamps (1907), Cori (1939), and Hyman (1959) and will not be considered here. The phylogenetic relationships of the phoronids, some of which are drawn from studies on embryonic and larval development (see Emig, 1976, 1982, 1985 for discussion), have been controversial. Only the more recent interpretations are included in this article and this has been done with a view to stimulate future investigations. The terminology, used here, is as proposed by Emig (1975).

II. MODE OF INSEMINATION

A. Sperm Transfer via Spermatophore

1. Types of spermatophore

Spermatophore formation is of general occurrence in phoronids (except in Phoronis ovalis in which lophophoral organs are absent). Some authors (e.g. Ikeda, 1903; Rattenbury, 1953; Silen, 1954) have observed a discharge of spermatozoa directly into the sea water, but this should be considered an exception.

Two types of spermatophores (Fig. 1) have been distinguished in phoronids (Zimmer, 1967; Emig, 1982). The A type consists of an ovoid mass of spermatozoa, about 130 by 75 μm in size; it is produced by small lophophoral organs, present only in members of burrowing or encrusting species (Phoronis ijimai, P. hippocrepia, P. australis) living in close proximity to each other (Fig. 1A and A'). The B type, described by Zimmer (1967) in Phoronopsis harmeri, is a spermatophore with two portions; it contains a spherical mass of spermatozoa (170 to 290 μm in diameter) to which is attached a wide spiral float of two or three turns (total length: 800 to
Fig. 1. A and A': Spermatophore of the A type \((Phoronis ijimai, \text{after Zimmer, 1964})\) with spermatozoa neatly aligned and some cellular debris at the broader end. B: Diagram of a spermatophore of the B type \((Phoronopsis harmeri, \text{after Zimmer, 1964})\). A and B are drawn on the same scale.

1,350 \(\mu\)m (Fig. 1B). This type of spermatophore is produced by all species with large lophophoral organs, membranous or glandular. All these species live separately embedded vertically in soft substratum. The lophophoral organs are considered by Entig (1985) as a phylogenetic character.

2. Transfer of spermatophore

The release of spermatophore was briefly described by Zimmer (1967): the tentacles are lowered and the spermatophore escapes by opening of the flaps of the lophophoral organs, greatly assisted by water and ciliary currents. No dependences or interactions exist between the sexes with respect to male spawning behaviour (Silén, 1954; Zimmer, 1967).

Spermatophores are relatively dense: those of the A type are probably collected by one of the nearest individuals (species with such spermatophore are all hermaphroditic). Type B spermatophores can float away, owing to the wide sail, via water currents which occur in the biotopes where phoronids live (Emig, 1973a). Undoubtedly, transport of sperm to the female or to hermaphroditic individual is effected by spermatophores, but the mechanism of insemination has not yet been clearly elucidated. It is most likely that the spermatozoal mass is first drawn into the lophophore of the recipient, and from there in some manner not yet understood into the metacoelom through the nephridial duct. Many observations support this view; the natural access to the body cavity is limited to the nephridiopore (Brooks and Cowles, 1905; Selys-Longchamps, 1907; Kume, 1953; Rattenbury, 1953; Forneris, 1959; Zimmer, 1967). By placing a spermatophore on the tentacles of a female specimen of \(Phoronopsis harmeri\), Zimmer (1972) observed lysis of the tentacular wall and passage of spermatozoa down the lumen of the tentacle into the metacoelom after perforation of the diaphragm. Further studies on sperm transfer are needed in view of the paucity of information.

III. FERTILIZATION

In Phoronida, internal fertilization appears to be the rule, judging from the presence of spermatozoa in the metacoelom of females of dioecious species, the development of isolated ova in the body cavity which alone undergo cleavage and embryonic development, and the occurrence of cleavage stages within the metacoelom (only seen in non-brooding species). One must also consider the production of spermatophores and of highly atypical spermatozoa, which always involve internal fertilization in other phyla (Franzén, 1956, 1977; also Volume II).

The oocytes, floating in the coelomic fluid, are at metaphase of the first meiotic division; the spindle lies normal to the surface of the oocyte (Fig. 2). The entry of spermatozoa takes place at this time, generally in the distal end of the metacoelom. But exceptions could be possible on the basis of observations of Silén (1954) and Ikeda (1901, 1903). No investigations seem to have been carried out on the...
fertilization process per se in phoronids and the presence of male nuclei within the ovum has only been seen by Rattenbury (1953).

IV. EMBRYONIC AND LARVAL DEVELOPMENT

A. Activation of the Ovum

The liberation of polar bodies occurs only when the ovum comes into contact with sea water, and never in the body cavity. The first polar body is expelled in about 15 minutes after the ova have been released into the sea water, and the second about 30 minutes later. The eggs are surrounded by a rather thick, crenulated membrane in type 3 species and only by a delicate hyaline membrane in type 2 species (Table 1).

Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Species name of the phoronic larva</th>
<th>Type of developmental pattern</th>
<th>Substratum</th>
<th>Spermatophore type</th>
<th>Nature of blastula and gastula</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phoronis ovalis</td>
<td>Not a true actinotroch</td>
<td>1</td>
<td>Hard substrate</td>
<td>No spermatophore</td>
<td>Gastula and gastrula</td>
</tr>
<tr>
<td>Phoronis hippocrepia</td>
<td>Hippocrepia</td>
<td>2</td>
<td>Burrowing or encrusting</td>
<td>Type A</td>
<td>Blastula thick-walled; blastocoeval quite small. Gastula with obliterated primary cavity</td>
</tr>
<tr>
<td>Phoronis australis</td>
<td>A. vancouverensis</td>
<td>2</td>
<td>Burrowing or encrusting</td>
<td>Type A</td>
<td>Blastula thick-walled; blastocoeval quite small. Gastula with obliterated primary cavity</td>
</tr>
<tr>
<td>Phoronis psammophila</td>
<td>A. sabatieri</td>
<td>2</td>
<td>Soft substrate</td>
<td>Type B</td>
<td>Blastula thin-walled; blastocoeval extensive</td>
</tr>
<tr>
<td>Phoronis pallida</td>
<td>A. pallida</td>
<td>3</td>
<td>Vertically embedded</td>
<td>Type B</td>
<td>Blastula and gastrula thin-walled; blastocoeval extensive</td>
</tr>
<tr>
<td>Phoronis harmeri</td>
<td>A. harmeri</td>
<td>2</td>
<td>?</td>
<td>Type B?</td>
<td>?</td>
</tr>
</tbody>
</table>

P. ovalis has an unusual larval development among the Phoronida; a careful description is given by Slén (1954). Type 1 species brood the eggs in parental tube and type 2 species on nidamental glands in the lophophoral concavity; type 3 species do not brood the eggs.

B. Cleavage

The egg undergoes its first cleavage a few minutes after the liberation of the second polar body (Fig. 2). The segmentation is similar in all phoronid species studied (no information is available on Phoronis pallida, Phoronopsis alboadulata, and Phoronopsis californica) and is total, equal, or somewhat subequal. The cleavage is of the radial (not of the spiral) type, but according to Zimmer (1964), the term 'biradial' is more appropriate for the 16-cell and subsequent stages.

In type 3 eggs, after the four-cell stage, variations often appear in the orientation of the blastomeres producing fortuitous figures of spiral appearance in arrangement of the blastomeres. These apparent spiral patterns in Phoronida are only secondarily derived from a true radial type (Zimmer, 1964; Emig, 1974, 1977a; Herrmann, 1986). The occurrence of such anomalies is the result of a compression of the blastomeres within the egg membrane under diverse effects, though some authors (Ikeda, 1901; Rattenbury, 1954) tend to consider the cleavage as 'spiral'.

The divisions of the blastomeres are not always synchronous and take place around the animal-vegetal axis (Roule, 1900; Ikeda, 1901; Brooks and Cowles, 1905; Selys-Longchamps, 1907). Incidentally, the segmentation of eggs, described by Brooks and Cowles (1905), is of Phoronis muelleri and not of P. architecTa (= P. psammophila) (cf. Emig, 1977b). Sometimes, eggs undergo cleavage while they are still in the body cavity. This abnormal feature occurs only in species of type 3 (Table 1).

C. Blastula

In type 2 species, the eggs develop to the blastula stage between 13 and 36 hours whereas in type 3 species, with a lesser volume of yolk, the development is more rapid (see Fig. 8). In both types, the seventh (128-cell) or eighth (256-cell) stage results in a coeloblastula which is more or less ciliated, has a smooth contour, and is composed of long, cone-shaped, homogenous cells. In the late blastula of Phoronopsis harmeri (cf. Zimmer, 1964), a thickening of the animal pole gives rise to the apical plate at the gastrula stage. The egg membrane is loose at least while the cilia begin to appear.

The blastocoeal arises from the segmentation cavity at about the 8-cell stage; no cells have been found in the blastocoeal. In type 2 species (Table 1), the blastula is thick-walled enclosing a very small blastocoeal which is disc-shaped rather than spherical; in type 3 species, the wall is thin and the cavity extensive.

D. Gastrulation

At the vegetal pole, a flattening called the 'gastral plate' invaginates generally in typical embyro. This process affects the entire vegetal hemisphere and gives rise to a gastrula with a large blastopore. The gastrulae of type 3 species retain their extensive blastocoeal whereas those of type 2 species obliterate their small primary cavity. The walls of the archenteron are closely pressed against the ectoderm; this stage is attained 30 to 90 hours after the egg release, less rapidly in type 2 species.
The number of tentacles increases in type 3 (B) (see Table 1). The arrows indicate the polar axis of the egg.

The cup-shaped archenteron changes into a tubular canal by fusion of its lateral lips along the ventral midline; a narrowing of the blastopore occurs as the gastrula elongates. Rapid growth of the ectoderm in the anterior region leads to the formation of a preoral lobe (characteristic of the actinotroch) which grows to overhang at first the blastopore and is subsequently bent forward above the ventral surface to form a vestibule. An ectodermal thickening (the apical plate) on the preoral lobe represents the incipient nervous ganglion. The cilia of the apical plate are longer than those of other ectodermal regions. The apical plate seems to be the only nervous tissue apparent in the gastrula. At the postero-ventral region, thickening of the ectoderm leads to the formation of a circular tentacular ridge; the first pair of tentacles buds off as isolated mesodermal cells within the blastocoel; these cells form the initial mesoderm into preoral lobe, where the first coelomic cavity, the protocoel, arises (Fig. 3). The mesoderm cells may proliferate and simply line the blastocoelic space of the preoral lobe: this formation arises by mesodermal wandering in Phoronis immai, P. muelleri, and P. psammophila. Or, the cells can aggregate in a mass which is rapidly arranged in the form of a vesicle to line the blastocoel in the preoral lobe: this type of formation occurs as a schizocoel in Phoronopsis harmeri. In the second phase, the mesoderm proliferates from the two ventro-lateral archenteric areas and the mesodermal cells form a mass from which later arises the metacoel in the postero-lateral regions. The blastocoel fills all the remaining larval space. Herrmann (1980, 1986), investigating Actinotrocha brachiiata, described a rapid formation of the three coelomic spaces, protocoel, mesocoel, and metacoel, in that order. In gastrula of type 2 species, the elaboration of the mesoderm is difficult to follow because of the intimate contact between the walls of the epidermis and of the archenteron; the blastocoel reappears with the development of the preoral lobe and the tentacular ridge. The formation of mesoderm stops when the archenteric cells become almost regular. Mesoderm formation in Phoronida is considered to be of the modified enterocoelous type.

By this time, the embryo has entered the actinotroch stage.

E. Organogenesis

1. Preoral lobe

The preoral lobe is a characteristic structure of the actinotroch. The entire surface of the lobe is ciliated, particularly along the free margin where a belt of cilia is constituted, and at the apical plate, especially in larvae of type 3 species. This latter fact could be explained by the attachment of the apical plate to mucus secretions of the nidamental glands of brooding species (type 2).

The vestibule is formed by overgrowth of the preoral lobe on a portion of the ventral epidermis. In the gastrula stage, the internal part of this vestibule invaginates and gives rise to the oesophagus (Fig. 3). The preoral lobe represents the protostome with its own coelomic cavity, the protocoel.

2. Tentacular ridge

At the first actinotroch stage, the larva shows one or two pairs of tentacles arising by evagination from an ectodermal thickening. The number of tentacles increases regularly in pairs with new ones added dorsally. They develop obliquely, and on each side of the midventral region. The longest tentacles are located ventrally (see Figs. 6 and 7). The number of definitive larval tentacles varies with species, from 12 to about 42 (cf. Emig, 1982). In species with a small number of tentacles they are short and stubby; in others, they are slender and graceful. The tentacles are one of the main locomotory and alimentary organs of the actinotroch.
Both the preoral lobe and the adult epistome have a role in the feeding process. However, by a different mechanism, both can close the entrance to the digestive tract. In one species (Actinotrocha branchiata), adult tentacles do not usually appear until the larva has had about 20 larval tentacles; they arise as evaginations under the bases of the larval tentacles (see Fig. 7). In other known species, the larval tentacles seem to show a basal thickening of the tentacular epithelium, often for about half the length; the distal parts of the larval tentacles are cast off during metamorphosis. In his description, subsequently confirmed by Forneris (1959) and Herrmann (1980), Ikeda (1901) writes, “The rudiments of the adult tentacles make their appearance as bud-like ectoblastic thickenings immediately below the base of the larval tentacles” (Fig. 4).

3. Protonephridia

The nephridial pit appears close to the anus in a postero-ventral position in the gastrula as an ectodermal invagination that bifurcates on each side of the larval intestine. The primordium of the nephridia has sometimes been misidentified and considered as a coelomic primordium (Fig. 3). The rapid elongation of the trunk in the actinotroch separates the primordium into two canals each of which comes further forward and opens laterally, one to each side of the intestine, by a tiny pore beneath the insertion of the tentacles. The common duct disappears (Figs. 4 and 5).

The nephridial canals are heavily ciliated and furnished at their inner blind end with solenocytes formed almost at the two-tentacle actinotroch stage. How solenocytes are formed is not known but an ectodermal origin seems possible (Hay-Schmidt, 1987). In well-developed actinotrochs, the solenocytes lie in the blastocoelic preseptal cavity.

4. Metasomal sac

The metasomal sac develops, between the two leaves of the ventral mesentery in which it is suspended, as an epidermal thickening of the ventral midline that progressively invaginates to grow as a conspicuous sac. This sac bends upon itself around the alimentary tract in the metacoel where it occupies the largest space (sometimes virtually all the coelom) in the fully developed actinotroch (Figs. 4 and 7). In the wall of the metasomal sac of actinotrochs, the layers are disposed in a fashion inverse to that of the adult body wall. Internally to this sac is the epidermis which includes some glandular cells; the mesoderm layer lying outside becomes muscular and forms first a circular sheet covering the epidermis and then a longitudinal sheet that differentiates into bundles. The metasomal sac is also surrounded by a coelomic lining. In the fully developed state, the epidermis of the metasomal sac is highly glandular.

5. Perianal ciliated ring

The perianal ciliated ring, formed by ectodermal thickening around the anus, is heavily ciliated (Fig. 4). The differentiation of the ring, which already begins in the gastrula, progresses rapidly during the first actinotroch stage. The perianal ciliated
general diffuse basi-epithelial plexus, as in the adult; a U-shaped apical plate which represents the larval ganglion in the centre of the dorsal side of the preoral lobe; three long nerves arising from the ganglion and proceeding anteriorly in parallel along the middorsal region of the preoral lobe, and supplying the pyriform organ; the pyriform organ, which appears shortly before metamorphosis (well developed in *Actinotrocha branchiata*, but much less apparent or absent in other species); a major nerve ring issuing from the pyriform organ or from the three nerves along the free margin of the preoral lobe; a collar nerve ring, with nerves to tentacles.

7. Digestive tract

The larval digestive tract with its three major divisions, which arise during the gastrula stage, lengthens with the elongation of the larval trunk. The oesophagus, ectodermal in origin, shows dense ciliation and numerous gland cells; the mouth is large, surrounded by its musculature. As in the adult, there is no abrupt epidermal transition. In some species, a valve occludes the entrance to the stomach, at the level of the blastopore (Figs. 3 and 6 B-C).

The stomach, of endodermal origin as the intestine, begins just posterior to the septum. Anteriorly, the stomach grows into one or two prominent diverticula (absent in young actinotrochs) lying ventrolateral to the oesophagus and with a highly vacuolized epithelium. The function of the diverticula is unknown but is probably related to the ingestion of food. The stomach can be divided into a major cavity above and a minor cavity below; the latter is funnel-shaped and heavily ciliated and serves to induce a current that rotates the alimentary particles often surrounded by a mucous cord. A strong sphincter separates the lower part of the stomach from the intestine. The intestine in turn communicates with the exterior posteriorly in the centre of the trunk floor by anus, surrounded by a perianal ring.

Becker (1937), who studied digestion in *Actinotrocha branchiata*, may be consulted for a description of the epithelium of the digestive tract.

8. Development of the coelomic cavities

Early investigators have often expressed divergent views on the formation and arrangement of body cavities in the larva. The presence of metacoel and mesocoel has been widely recognized since the study of Ikeda (1901), but the existence of the protocoel was not established until the work of Zimmer (1964) though Masterman (1900) did refer to it. The mode of formation of the three coelomic cavities appears to vary with the species in phoronids (see Emig, 1982).

(a) Protocoel

The U-shaped protocoel almost fills the preoral lobe. Its size varies with the species, but in general it extends between the upper and the lower walls of the preoral lobe. A septum separates this cavity from the blastocoelic collar space just behind
the apical plate. It seems that all previous investigators did recognize the presence of such a septum but could not decide whether it was complete or incomplete. The protocol is retained throughout the larval life.

(b) Metacoel

The metacoel (or trunk coelom) originates dorsally, at an early actinotroch stage, from a single U-shaped row of cells forming a solid mass that undergoes schizocoely. The ends of the trunk coelom fold around the digestive tract and meet on the ventral midline to establish the definitive ventral mesentery uniting the trunk wall to the intestine and stomach. In some species, the presence of a dorsal mesentery (whose erosion later results in a single coelom) suggested to some investigators that the metacoel originates from a pinching off of paired posterior vesicles. The metacoel gradually extends in a forward direction to the posterior limit of the tentacular ridge where an oblique septum is formed as a separation between the coelom and the blastocoelic collar cavity. This septum achieves the status of a mesentery just prior to metamorphosis by an intimate contact of the mesocoel with the metacoel (Figs. 3 and 4).

(c) Mesocoel

Also named ‘collar coelom’, the mesocoel appears between the gastrula and actinotroch stages (Fig. 8). Its origin has not been described; it probably arises as a schizocoel from a mesoderm mass posterior to the tentacles. The mesocoel develops as a U-shaped structure, interrupted dorsally, just above the septum on the inner side of the tentacles. The collar cavity, which is in the form of a wide blastocoelic space lined by some mesodermal cells and with isolated transverse muscle bands during most of the larval stage, is reduced by the growth of the mesocoel into a narrow space surrounding the gut in front of the septum (Fig. 4).

The muscular system.

The actinotrochs are provided with a complex muscular system which varies in the different known species. The muscle cells are apparently derived from mesoderm cells. Through most of its length, the digestive tract is only poorly provided with musculature. The main muscles of the body are shown in Fig. 6 B—D. The muscular array of the actinotroch needs a great deal of attention by future investigators.

10. Circulatory system

No functional circulatory system occurs in the actinotroch. In fully developed actinotrochs only one of the two longitudinal blood vessels, the median one, appears on the dorsal midline of the stomach and extends from the pylorus to the diaphragm. The presence of a second vessel, suggested to be present by some authors, seems incompatible with the disposition of the vessel in adults (Emig, 1973b). According to Herrmann (1980), the lateral vessel arises between two layers of the ventral mesentery just before metamorphosis. At the level of the pylorus is a bunch of short cœca as evaginations of the mesodermal lining. These structures, blastocoelic in origin, are developed in the space between the stomach wall and the coelomic lining associated with the collar space, and are lined by mesodermal cells of the wall of the metacoel, as in adults (Emig, 1977c). Posteriorly, the median vessel becomes undefined and passes into the ordinary splanchnic mesodermal lining.

The third component of the larval circulatory system consists of one to four solid masses (see Emig, 1982) of blood corpuscles which lie in the collar space and generally adhere to the stomach walls (Fig. 4). The erythrocytes gradually assume a red colour. The number and disposition of the blood masses seem to be a species characteristic of the actinotrochs and, thus, could be used for their identification. The origin of the erythrocytes is presently elusive: it may be said that the masses are differentiated from the splanchnic cells covering the stomach or arise from the mesodermal masses which later give rise to the mesocoel. Confirmation is needed of the origin of the endothelial cells in the blood vessels.

F. Embryonic Nutrition

Our knowledge of the embryonic nutrition of actinotrochs is far from satisfactory because only short and incomplete observations have been made by previous workers, such as Lebour (1922), Becker (1937), Veillet (1941), Thorson (1946), Forneris (1959), and Herrmann (1976). Actinotrochs can eat flagellates (e.g. *Peridinium trochoideum*), diatoms (mostly *Coscinodiscus*), and larvae of lamellibranchs. Sielen (1954) had little success in rearing actinotrochs with diatoms, chloromonads or *Nitschia*, but better results were obtained by changing the sea water once or twice a day. No food is taken in by the larva during the brooding. In both adult and actinotroch, digestion is intracellular.

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**Fig. 8. Diagram of the three types (see Table 1) of embryonic and larval development in Phoronida (a—g, stages of Fig. 7). The formation of blastula (B), gastrula (G), metasomal sac (MS), blood mass (BM), dorsal blood vessel (DV), and the onset of metamorphosis (M) are shown. In some species, characteristic pigmentation spots appear at about the four-tentacle stage and are of prime importance in identifying the various species.**
In just-metamorphosed animals, the first food consists of cast-off organs, such as tentacles and preoral lobe. The presence of a midventral ciliated groove, described by Roule (1900) and Masterman (1900) as leading to the mouth for about half the length of the trunk, has not been found by subsequent investigators and can be considered an artifact. The same may be said of the ‘atrial grooves’, described by Masterman (1900) as leading into the dorso-lateral corners of the mouth.

The feeding currents seem to be created by ciliated belt of the preoral lobe and by ciliary bands on the tentacles (cf. Emig, 1982). A comparative study of the feeding mechanism of the actinotroch and adult would be of interest.

G. Larval Development and Settlement

The duration of larval development averages 18 to 21 days in all known actinotrochs, but not *Phoronis ovalis* which is a curious exception (Fig. 8, type I). According to Silén (1954), the length of the actinotroch stage, from about the four-tentacle stage to metamorphosis, is approximately 12 to 14 days in non-brooding as well as brooding species, but the latter have a shorter pelagic life. *P. ovalis*, which has only a four-day-long pelagic life, shows developmental patterns which are not far, I believe, from direct development.

*Actino/rocha branchiata*, the best known phoronid larva, is often used as an example to illustrate morphological development (Fig. 7) involving a rapid elongation of the trunk (that reaches about half the length of the larva, or more) and an increase in the number of tentacles. The body of the larva, ready to metamorphose, becomes opaque. However, in other species such as *A. pallida* and *A. hippocrepia*, the more mature actinotrochs are hard to distinguish (Silén, 1954).

A familiar constituent of the plankton, the actinotroch larva seems to be photopositive (Silén, 1954), but water movements, particularly waves or strong currents, tend to break down this response that is more rapid as the larva swims nearer to the sea surface (Herrmann, 1976). The mature larva, just ready to undergo metamorphosis, becomes negatively phototactic (Cori, 1939; Silén, 1954), an observation not confirmed by Zimmer (1964) and Herrmann (1976). Yet, this larva responds positively to the typical substrate of the adult which seems to be found with precision; no previous workers have taken into consideration the particular relation which could exist between the factors initiating larval sinking and the settlement on suitable substrates (in some species between 50 and >200 m deep). The sinking appears to be induced by bacteria or chemical substances in the phytoplankton, activating the larva (Herrmann, 1976, 1979). At the bottom the metamorphosis may be induced by bacteria and/or ions, as is known in other animal groups.

While the larva is going down to the bottom, the preoral lobe of the actinotroch is contracted and becomes rounded. The protruding tip is the pyriform organ in species where this structure occurs, and the apical plate in others, though in the latter the possibility of the existence of a pyriform organ cannot be entirely excluded. The tip enters by direct contact into the suitable substratum and metamorphosis is invariably induced. The main function of the pyriform organ (probably also the apical plate in some species) appears to be selection of a favourable site for metamorphosis and to start the transformation process. This organ seems to be only associated with ecological behaviour of the Phoronida and is no indicator of true evolutionary relationships.

At this time, the larva ceases to be ciliated. By violent muscular contraction, the metasomal sac evaginates vertically downward into the soft bottom and produces a tube by means of sticky secretions from the numerous epidermal gland cells. On a hard substratum, the newly evaginated trunk does not enter but remains outside. It is then rapidly surrounded by a thin hyaline tube and the animal begins to burrow into the hard bottom (Silén, 1954).

H. Larval Metamorphosis

Several authors, for example, Roule (1900), Selys-Longchamps (1907), Cori (1939), Veillet (1941), Silén (1954), Zimmer (1964, 1978), and Herrmann (1976, 1979, 1980), have studied the peculiar metamorphosis of the actinotroch, but in general only the external characteristics. The metamorphosis is usually complete in about five to 30 minutes. Thus, in a very short period of time the actinotroch passes from a highly adapted pelagic stage to a slender benthic organism, organized as a tubicolous adult (Fig. 9).

![Fig. 9. Settlement on soft substratum (A) and some stages (B, C) in metamorphosis of *Actino/rocha bran­chiata*. D: An adult specimen of *Phoronis muelleri*, about one day after the beginning of the metamorphosis. The arrows indicate the polar axis of the egg. (See also Figs. 2 and 3.)](image)

As the sharp preoral lobe comes in contact with a suitable substratum (Fig. 9A), the trunk first shows a compression and rapidly evaginates its metasomal sac by strong muscular contractions, especially by the ventral muscle bands. In this sac which is the incipient adult trunk, the digestive tract, attached by the ventral
mesentery, moves forward to take its adult position (Fig. 9B). The metacoel is retained. The larval ventral mesentery connecting the outer convex wall of the U-shaped alimentary tract with the body wall in the adult is named ‘oral mesentery’ on the descending branch and ‘anal mesentery’ on the ascending branch (i.e. intestine). The adult lateral mesenteries are only secondarily differentitated.

Differentiation now starts of the epidermis of the posterior part of the metasome into ampulla. The mouth and anus are brought into close proximity. No description of the formation of the prestomach has been given. The diverticula become indistinguishable from the rest of the stomachal epithelium during the considerable elongation of the entire tract when the metasome everts. That the adult intestine is formed of endodermal cells is confirmed by studies on regeneration by Emig (1972). The origins of the digestive system of the adult are controversial. It may be that the larval intestine and anus give rise to those of adults and the larval trunk with the perianal ring disintegrates little by little after a few hours (Fig. 9D). Or, during the elongation of the adult metasome the larval anus, perianal ring, and an important part of the dorsal and ventral epidermis are drawn inside and the distal part of the intestine arises as a proctodaeum.

Concomitantly, the preoral lobe and the distal part of the tentacles (or the whole larval tentacles in Actinotrocha branchiata) shrink and are cast off and ingested. These structures still persist as fragments and the mesocoel also is partly retained. The preoral lobe, which in the form of a small bleb derived from the internal part of the vestibular epidermis, bends over dorsally into a fold between the mouth and the anus, encircled by the lophophore. Thus arises the epistome with its own coelomic cavity (the procoelom) in continuity with the larval protosome. The larval ganglion is included in the part of the preoral lobe that has been cast off; it does not therefore give rise to the adult ganglion which later arises as a thickening of the adult ring nerve. The entire nerve ring probably originates from the larval one.

Formation of the diverticula from the mesocoel occurs already as buds. They rapidly increase in length. In A. branchiata, however, the definitive tentacles arise in the late larval stage to become the adult lophophore; the larval tentacles are then swallowed and ingested (Fig. 9C). The new lophophore, elevated around the mouth, is functionally suited for food gathering. New tentacles are constantly budded on the dorsal side between the mouth and the anus.

Transformation of proonephridia with solenocytes into metanephridia (‘mixonephridia’, according to Goodrich’s (1945) classification) merits greater attention in future studies on evolutionary speculations and relationships of the phoronids (Emig, 1973b). Only one point has not been contested since Caldwell (1882): the solenocytes become detached from the larval ducts and fall into the incipient lophophoral vessel. Most investigators (e.g. Ikeda, 1901; Menon, 1902; Goodrich, 1903; Cowles, 1904; Brooks and Cowles, 1905; Shearer, 1906; Selys-Longchamps, 1907) believe that the larval ducts are retained and form the adult nephridia by funnel openings into the metacoelom. The funnels are only secondarily acquired and are possibly of mesodermal origin. The larval nephridiopores have shifted dorso-laterally on the anal papilla owing to a mechanical narrowing of the dorsal surface of the body during metamorphosis.

Finally, the circulatory system becomes suddenly functional. The collar cavity, surrouned by mesocoel, gives rise to a single lophophoral vessel that is divided, about 12 hours later, into an afferent and an efferent lophophoral vessel. It sends a small vessel into each lophophoral tentacle.

The blood masses, located in collar cavity, break apart allowing the erythrocytes to enter the vessels. The second longitudinal vessel (the lateral vessel) now proceeds from the lophophoral vessel as a slit in the splanchopleure on the left side of the descending digestive tube and broadly communicates with the median vessel in the space between the stomach wall and the coelomic lining; this space is the primordium of the stachmal blood plexus. The median vessel, present since the actinotroch stage, becomes separated from the stomach wall and unites the incipient blood plexus with the lophophoral vessel; it is contractile exhibiting peristaltic waves (Fig. 9D). The circulatory system becomes closed.

I. Factors Influencing Embryonic and Larval Development

During the entire course of development in phoronids, particularly during the pelagic life, an external source of nutrition seems to be necessary for differentiation and growth. Actinotrochs are able to thrive even when food is in short supply or under other unfavourable conditions, but their development is delayed. Older larvae store food and are thus able to survive temporary periods of starvation.

The length of the pelagic life is also related to the finding of a suitable substratum where the adult populations are generally living. The increase, observed in the number of tentacles in some Actinotrocha branchiata (from about 30 to 42), could be explained by this lengthening of the pelagic life.

V. PARENTAL CARE OF EGGS AND YOUNG

Some phoronid species (e.g. Phoronis hippocrepia, P. iijimai, P. australis, P. psammpophila) exhibit brooding behaviour. The ova are swept through the nephrine into the nidamental glands (accessory sex glands) where they are attached by a mucous secretion to form the brood mass in the lophophoral concavity. Insertion of the larvae to the mucous cord generally occurs in their apical plate region. During brooding, the embryos do not gather food; the amount of yolk contained in eggs (diameter: 80 to 130 µm) is sufficient to take the larva to a stage when it is ready to escape. Silén (1954) suggests that in non-brooding species the amount of yolk contained in eggs (diameter: 50 to 70 µm) is too small to allow a strictly lecithotrophic mode of development, but this notwithstanding, the larval size in the two egg types is about the same at the end of the period of embryonic development.

The larva, completely ciliated, liberates itself from the parent and begins its pelagic
existence. At this stage, tentacles are only incipient in *P. psammophila*, but two to four tentacles are present in *P. hippocrepia* and *P. ijimai*, and six to eight in *P. australis*.

Among phoronids, *P. ovalis* shows an unusual type of parental care: the eggs are retained in the tube of the adult until they hatch out as ciliated, slug-like larvae which lead a short pelagic existence before becoming adults (Silen, 1954).

### VI. CONCLUSION

It is well known that developmental patterns provide interesting clues to phylogenetic relationships of animal groups. Several problems of the phylogeny and development of phoronids have been solved (see Emig, 1982, 1985) but more careful work is needed on other aspects, for example, the protonephridia -metanephridia relationships and the differentiation of the mesocoel and metacoel. Differences between various species in morphology, differentiation, and pattern of metamorphosis of the actinotroch also deserve more careful study inasmuch as they have often been a source of misunderstanding to earlier investigators.

In phoronids, Emig (1985) considered several reproductive patterns as phylogenetic characters: for example, gonads, development patterns, and the larval state. Plesiomorphic characters include dioecism, direct egg release, and the presence of misunderstanding to earlier investigators.

In phoronids, Emig (1985) considered several reproductive patterns as phylogenetic characters: for example, gonads, development patterns, and the larval state. Plesiomorphic characters include dioecism, direct egg release, and the presence of misunderstanding to earlier investigators.

### REFERENCES


