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Embryology of Phoronida

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SYNOPSIS Fertilization in the Phoronida appears to be internal. Three different types of eggs were found: (1) Eggs rich in yolk, about 125 μ in diameter, which are retained in the parent's tube, without a true pelagic life; (2) Eggs moderately rich in yolk, about 100 μ in diameter, brooded up to the actinotroch stage in the lophophoral concavity owing to the nidamental glands, with a more or less long pelagic life; (3) Eggs, yolk-poor, about 60 μ in diameter, which are directly discharged into sea-water and which have a long pelagic life.

Cleavage in the Phoronida is total, equal or subequal. The pattern is typically radial though biradial in some stages, but there are instances in which the blastomeres exhibit a spiral appearance.

The gastrula arises generally by emboly. The blastocoel is extensive in embryos of type 3 (see above) and virtually obliterated by wall compression in type 2. The blastopore is reduced to an anterior remnant.

The differentiation of the ectoderm leads to the formation of the preoral lobe, the apical plate, the tentacular ridge, the nephridial anlage, the oesophagus (issued from the posterior part of the vestibule) and the mouth which does not originate as a stomodeum; the blastopore is located between oesophagus and stomach.

Differentiation of the archenteron (endoderm) produces the stomach, the intestine and the anus which opens by perforation of the ectoderm, without formation of a proctodeum. The anus appears to be independent of the blastopore.

The mesodern originates as isolated cells proliferated from the anterior and ventrolateral areas of the archenteron, in two phases. The mesoderm is formed in a modified enterocoelous manner. The protocoel is produced first from the anterior archenteric wall and occupies the cavity of the preoral lobe; the metacoel originates from the ventrolateral mesodermal proliferations. The mode of formation of these cavities seems to vary with species.

INTRODUCTION

The embryonic development of several species in the phylum Phoronida have been studied. Because of some controversies arising from studies on the embryology of this group, a review of fertilization, cleavage, and early development of the embryo is presented as well as recent studies performed on *Phoronis psammophila* Cori, *Phoronis ijimai* Oka, and *Phoronia australis* Haswell.

FERTILIZATION

Only two basic types (Table 1) of lophophoral organs are developed in male and hermaphroditic species (Figs. 1a, 2, 3d) and represent elaborate accessory male reproductive organs (accessory spermatophoral organs). Their function is secretion of spermatophoral membranes and formation of the spermatophores (Zimmer, 1967). The spermatozoa in the coelom are concentrated near the nephridia by the currents produced by the nephridial funnels and compacted within the ascending nephridial branches. The aggregates of spermatozoa are extruded through the nephridiopores into the lophophore and the accessory spermatophoral organs form spermatophores which are released into sea-water (Zimmer, 1967; Emig, 1973*b*).

In females and hermaphroditic species, the spermatophores or spermatozoa ascend to the metacoelom through the nephridia (Rattenbury, 1953) or in one case by a pore through the tentacular wall of the lophophore and perforation of the diaphragm (Zimmer, 1972). The presence of spermatozoa in the coelom of females (in dioecious species) has suggested protandry to some authors (Roule, 1900*a*; Torrey, 1901; Brooks and Cowles, 1905;

TABLE 1. *Characteristics of the reproductive biology and embryonic development of Phoronida.*

Type	Species	Sexuality	Lophophoral organs	Nidamental glands	Brooding pattern	Diameter of eggs (in μ)	Egg-release	
1	*Phoronis ovalis*	? MF M & F	Absent	Absent	Retain eggs in parental tube	125	in one time	?
2	*P. hippocrepia*	MF	Small	2a	Embryos in paired lophophoral masses	100	continuous	*Blastula*: thick-walled, with blastocoel quite small. *Gastrula*, after emboly: with obliterated primary cavity.
	P. ijimai	MF	Small	2a	Embryos in paired lophophoral masses	100	continuous	
	P. australis *P. buskii*	MF	Small	2b	Embryos on mucous cord	100-130	continuous	
	P. bhadurii	?	?	2 (?)	Eggs retained in the lophophore	?	?	
	P. psammophila	M & F	Large, glandular	2c	Embryos in single lophophoral mass	80-120	discontinuous	
3	*P. architecta* (?)	M & F	Large, glandular	Absent	No brooding	100	continuous (more or less)	*Blastula and gastrula*: thin-walled, with extensive blastocoel.
	P. muelleri	M & F	Large glandular	Absent	No brooding	50-65		
	P. pallida	MF	Large, glandular	Absent	No brooding	50-70		
	Phoronopsis harmeri	M & F	Large, membranous	Absent	No brooding	60-65		
?	*Ph. albomaculata*	M & F	Large	?	?	100	?	?
	Ph. californica	(?)M & F	Large, membranous	?	?	?		

M, male; F, female; MF, hermaphrodite; 2a, 2b, 2c, see text.

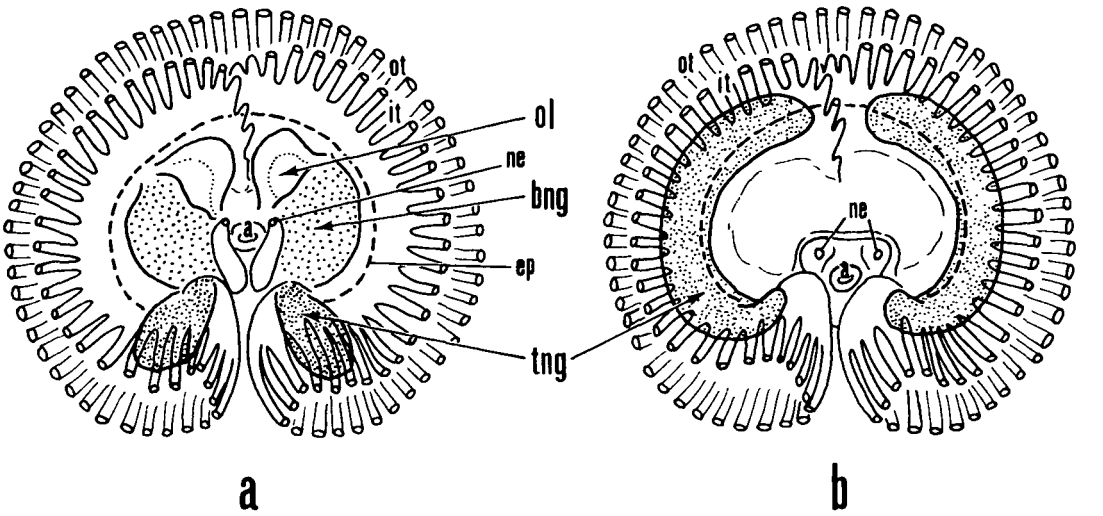


FIG. 1. Looking into the lophoral cavity of mature *Phoronis* with accessory sex glands; A. *Phoronis hippocrepia* with type 2a nidamental glands; B. *Phoronis psammophila* female type 2c. bng, basal nidamental gland; tng, tentacular nidamental gland; ol, lophophoral organ (=accessory spermatophoral organ); a, anus; ep, epistome; ne, nephridiopore; it, inner tentacles; ot, outer tentacles.

Pixell, 1912; Cori, 1939); however, there is no evidence to suggest that *Phoronis muelleri, P. psammophila, Phoronopsis harmeri* (and probably *Phoronopsis albomaculata, Phoronopsis californica*) are other than dioecious (Table 1).

Internal fertilization occurs in *Phoronis hippocrepia, P. ijimai* [*P. vancouverensis* (Emig, 1971)], *P. australis, P. psammophila, P. muelleri,* and *Phoronopsis harmeri* (Kowalevsky, 1867; Selys-Longchamps, 1907; Kume, 1953; Rattenbury, 1953; Forneris, 1959; Zimmer, 1964; Emig, 1974). External fertilization could occur in *P. ijimai* and *P. australis* (Ikeda, 1901, 1903), *P. pallida* (Silén, 1954), *P. muelleri* (Selys-Longchamps, 1907; Silén, 1954), *P. psammophila* (Roule, 1900*a*; Brooks and Cowles, 1905).

Thus, fertilization appears to be either internal and external in Phoronida; yet, it is difficult to understand the adaptive value of external fertilization when considering the existence of spermatophore and the production of spermatozoa of a highly modified type (Franzén, 1956; Zimmer, 1972). These two features are typically involved with internal fertilization in other phyla (Franzén, 1956). Cross-fertilization, not autofertilization, probably takes place in hermaphroditic species (Silén, 1954). Other workers have recognized possibilities of both self- and cross-fertilization (Kowalevsky, 1867; Forneris, 1959). However, the question of autogamy in hermaphroditic species remains unresolved. It appears that there are no interactions between the sexes with respect to spawning behavior in *Phoronis psammophila, P. ijimai* and *Phoronopsis harmeri* (Zimmer, 1964; Emig, personal observations).

The oocytes, liberated from the ovary in the coelomic fluid, are generally at metaphase of the first meiotic division. Each oocyte is surrounded by a delicate hyaline membrane. The penetration of spermatozoa probably at the primary oocyte stage takes place in the body cavity. Subsequently, the maturation divisions occur either within the metacoelom or after release through the nephridia. In a few cases, cleavage stages have been seen within the coelomic cavity (Selys-Longchamps, 1907; Rattenbury, 1953; Forneris, 1959), generally in species without brood patterns.

SPAWNING

According to Brooks and Cowles (1905), Rattenbury (1953), Silén (1954), the egg-laying usually takes place at night. But

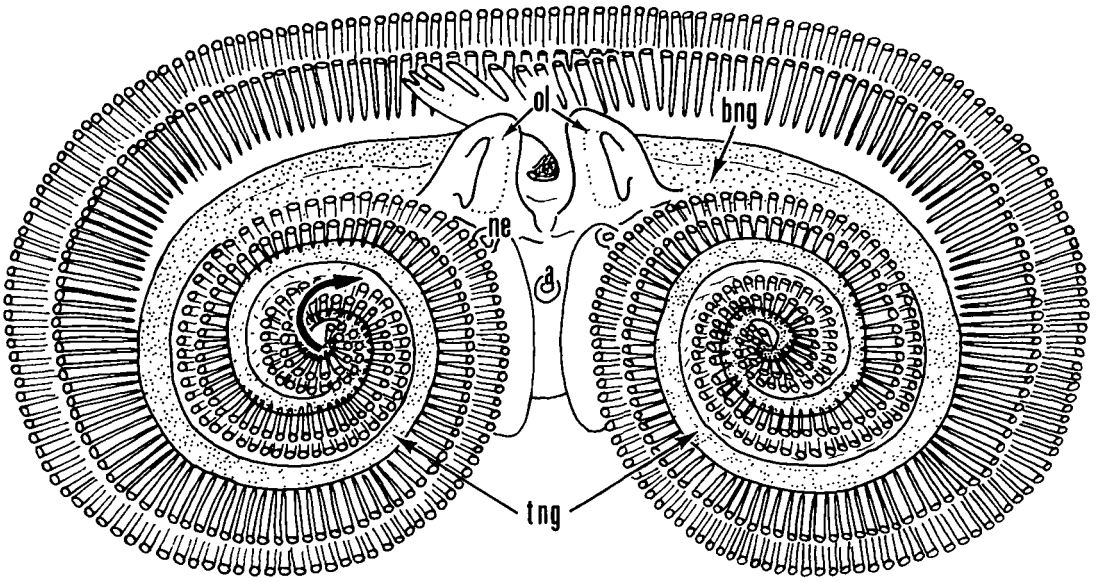


FIG. 2. Mature *Phoronis australis*, viewed from the distal end, with accessory sex glands (nidamental glands of type 2b). Abbreviations as in Figure 1.

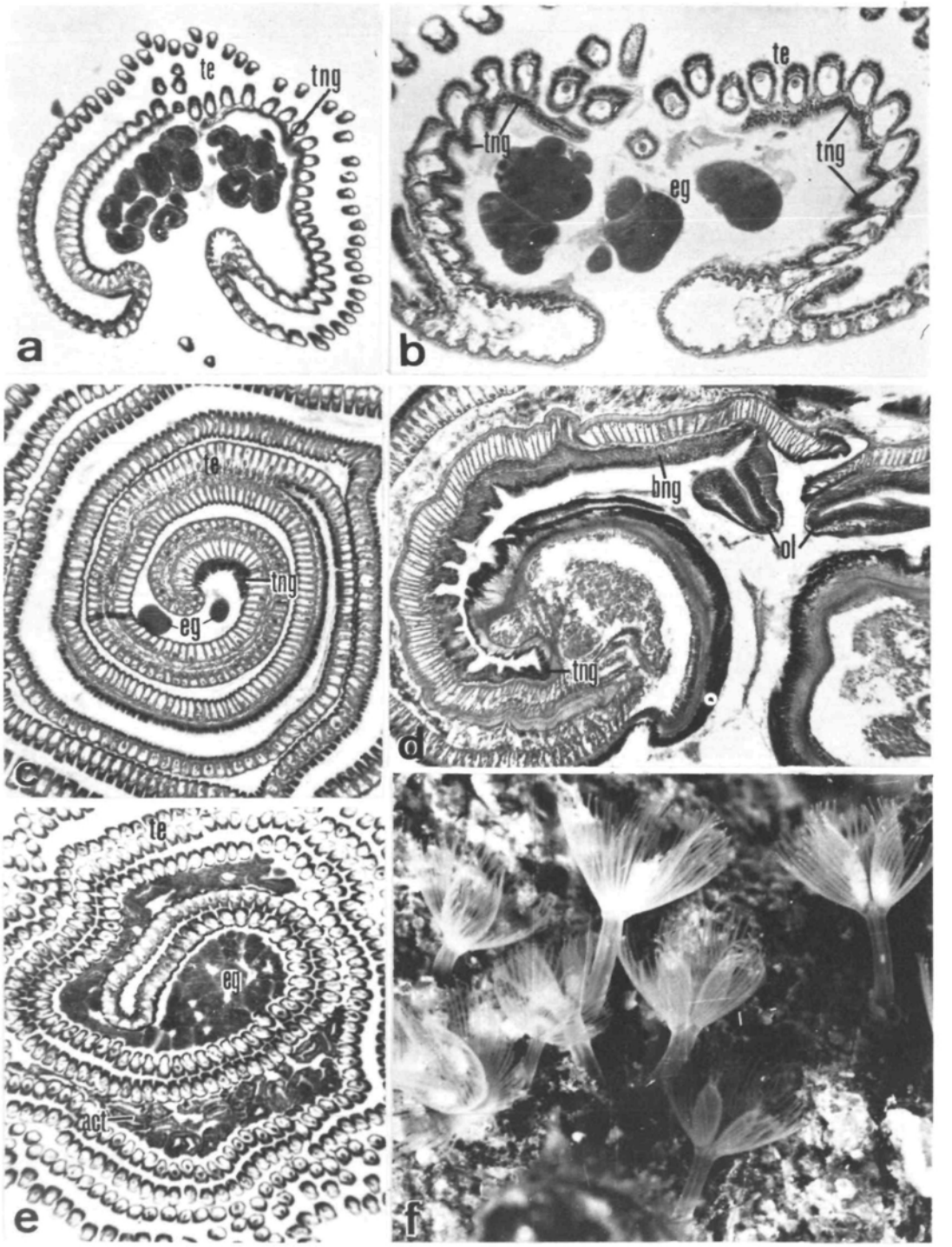
Forneris (1959), Zimmer (1964), and Emig (1974) have observed the release of ova at all hours of the day and night. The eggs in Phoronida are shed through the nephridia directly into the ambient sea-water or into the lophophoral concavity where ova and embryos are brooded (Table 1).

In the majority of species, spawning is more or less continuous over a number of days (Silén, 1954; Zimmer, 1964); the only known exceptions are *Phoronis ovalis* (Silén, 1954) in which spawning occurs once, and *P. psammophila* (Emig, 1974) in which it may be periodic. According to Silén (1954), a maximum of about 500 eggs are shed during the season by one individual of *Phoronis muelleri* or *P. pallida*; in *P. hippocrepia*, this number probably does not exceed a total of 100. Zimmer (1964) observed one specimen of *P. ijimai* releasing between 5 and 30 eggs per day for as long as 32 days while in *Phoronopsis harmeri* the maximum number is about 500 eggs per day.

In species which brood, the ova are swept onto the nidamental glands, where they are attached by secreted mucous to form the brood mass (Fig. 3). The function of the nidamental gland is to attach recently shed ova to the embryonal masses and maintain the integrity of these masses (Zimmer, 1967). Nidamental glands are of three types (Table 1): *type 2a*: developed on the floor of the lophophoral concavity (adjacent to the lophophoral organs) and on the inner surface of those tentacles to which the two embryo masses are attached (Figs. 1a, 3f); *type 2b*: limited to the floor of the lophophoral concavity (adjacent to the lophophoral organs) with extension along several coils of the lophophore at the inner surface of the tentacles, two embryo masses (Figs. 2, 3c-e); *type 2c*: formed by the fusion of the tentacles of the inner row of the lophophore, a single mass of embryos (Figs. 1b, 3 a-b).

Three different types of development (Table 1) can be correlated with egg size (Silén, 1954; Emig, 1974). *Type 1*: eggs are 125 μ in diameter and rich in yolk; *P. ovalis*, the only representative known, retains its eggs in the tube of the adult until

FIG. 3. a) and b) *Phoronis psammophila*: cross-section through the lophophore at level of the nidamental glands and the single brood mass (a: embryos at gastrula stage; b: formation of the brood mass after egg-release). c), d) and e) *Phoronis australis*: cross-section through the lophophore at different levels; eggs occur in the inner coil (c, e) while the older stages (up to actinotroch) are exterior (e). f) *Phoronis*



hippocrepia: lophophore of mature animals bearing two masses of embryos within the lophophoral concavity.
act, actinotroch; bng, basal nidamental gland; eg, egg; lo, lophophoral organ (=accessory spermatophoral organ); te, tentacles; tng, tentacular nidamental gland.

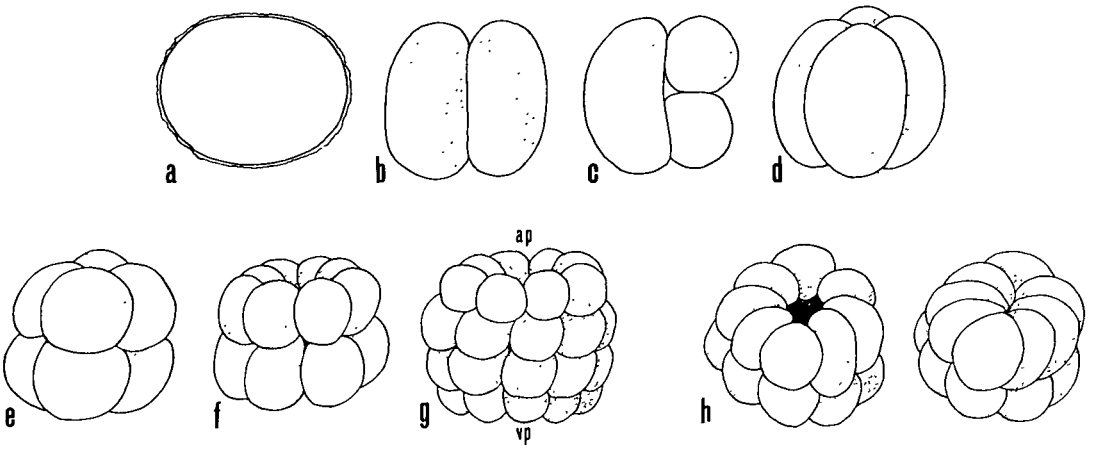


FIG. 4. Egg cleavage of a phoronid with brooding pattern *(Phoronis psammophila)*, in lateral view (except c: polar view) of the different stages (b, 2-cell; c, transitory 3-cell; d, 4; e, 8; f, 16; g, 32; h,16-cell stage in animal and vegetal pole views.

they become ciliated, slug-like larvae. *Type 2*: eggs are approximately 100 μ in diameter, moderately rich in yolk; with a period of brooding of the embryos within the lophophoral concavity of the adult. *Type 3*: eggs are yolk poor and about 60 μ in diameter. These eggs are shed directly into the sea water.

No correlation between body size and egg size has been established; nor does egg size and egg number seem to correlate (Silén, 1954). As regards the spawning pattern, the species which brood or retain their eggs and embryos (type 1 and 2) possess larger eggs (Emig, 1974), but there is no correlation between the amount of yolk and the duration of brood protection or the developmental stage reached before release (Silén, 1954). The diploid (2n) number of chromosomes for phoronid species range from 12 to 16 (Emig, 1974).

CLEAVAGE PATTERNS

Segmentation is similar in *Phoronis ovalis* (Zimmer, 1964), *P. hippocrepia* (Foettinger, 1882), *P. ijimai* (Ikeda, 1901; Zimmer, 1964), *P. australis* (Kume, 1953), *P. muelleri* (Selys-Longchamps, 1907), *P. psammophila* (Brooks and Cowles, 1905; Emig, 1974), and *Phoronopsis harmeri* (Zimmer, 1964). The eggs usually undergo first cleavage from 15 minutes to one hour after their release. However, in some cases, the segmentation begins in the metacoelom.

The first cleavage is meridional (in a plane perpendicular to the long axis of the egg) and divides the egg into two equal or nearly equal blastomeres (Fig. 4b).

The second cleavage is also meridional (including the animal-vegetal axis), but perpendicular to the first (Fig. 4d). It divides the two cells into four approximatively equal ones. The cleavage of one blastomere usually precedes that of the other and a transitory 3-cell stage is seen (Fig. 4c). At the 4 cell-stage, there is some variation in the orientation of the blastomeres in a few species (Rattenbury, 1954; Zimmer, 1964). After the second cleavage, the spindle axes always occur between a 90° angle, parallel or perpendicular to the polar axis. Immediately before the second and the subsequent cleavages the blastomeres cling together and the embryo assumes a spherical shape with an irregular contour.

The third cleavage divides each of the blastomeres equatorially into two plates of four cells each. This cleavage is slightly unequal, the cells at the animal pole being smaller in general (Fig. 4e). The divisions are not always synchronous in all cells, but take place one blastomere after another around the animal-vegetal axis; this fact can explain the various stages described by

Roule (1900*a*), Ikeda (1901), Selys-Longchamps (1907). At the 8-cell stage the corresponding blastomeres of the vegetal and animal quartets may be oriented directly above one another (Fig. 4). This third cleavage results in a variety of cell arrangements, especially in *Phoronopsis harmeri* (Rattenbury, 1954; Zimmer, 1964), but no variation in cell "pattern" is seen in *Phoronis psammophila* (Emig, 1974).

The fourth cleavage is in a meridional plane, dividing the blastomeres into two plates of eight cells each arranged above one another as in the preceding cleavage. At the animal pole an opening leading into the segmentation cavity may be present between the blastomeres (Fig. 4f, 4h). A similar opening is less frequent at the vegetal pole and, if present, is smaller.

The fifth cleavage is latitudinal resulting in four plates of eight blastomeres each (Fig. 4g). At the animal pole a discrete opening into the segmentation cavity is surrounded by the octet of smaller cells; the larger blastomeres at the vegetal pole are frequently arranged in a bilateral pattern.

In subsequent stages, the successive cleavages are probably alternately meridional and latitudinal, but the asynchrony of the divisions and the absence of precise cellular "landmarks" render further observations impractical.

At the blastula stage, the embryos are ciliated. The blastula of adult type 2 (Table 1) is thick-walled and the blastocoel is quite small (Fig. 6a), that of adult type 3 has thin walls and an extensive blastocoel (Fig. 7a).

In species with nidamental glands of type 2a and 2b, the brood masses are formed by the continuous release of eggs over a period of time; new eggs push the older ones distally and simultaneously the young actinotrochs escape; in *Phoronis australis* (Figs. 2, 3c, 3e), the eggs are attached on a mucous cord near the nidamental glands (type 2c) from the inner coil to the exterior, the older stages being distal. In type 2c, the single lophophoral mass is formed by a massive and rapid egg-release (Figs. 3a-b): all embryos are at the same development stage or slightly older at the distal end of the lophophore; a new mass is formed again after the escape of the preceding mass.

DISCUSSION OF SEGMENTATION IN PHORONIDA

The segmentation in the phylum Phoronida is total, equal or subequal (the animal cells are slightly smaller than those of the vegetal pole in the latter case).

The cleavage of Phoronida is of the radial type (Foettinger, 1882; Roule, 1900*a*; Masterman, 1900; Brooks and Cowles, 1905; Cori, 1939; Kume, 1953; Zimmer, 1964; Emig, 1974) and not spiral (Ikeda, 1901; Rattenbury, 1954). Reasons for considering the cleavage as spiral were given by Rattenbury who suggested that the occurrence of such a blastomere arrangement was the result of compression of cells within the egg-membrane. This compression produces variants of the radial pattern; occasionally, anomalies of radial or biradial pattern appear derived from typical radial segmentation. It seems that a spiral appearance does not ordinarily occur in brooding species. The apparent spiral patterns in Phoronida is secondarily derived from a true radial type, for the following reasons (Zimmer, 1964, Emig, 1974): (1) The radial pattern is subject to variations that suggest a spiral cleavage pattern. In contrast, the spiral segmentation possesses an apparent stability and deviations towards radial features are virtually unknown in other phyla. (2) In the case of these modifications, the spiral arrangement results from the compression of the blastomeres under diverse effects. It should be mentioned that spiral arrays of blastomeres in normal cleavage are well known in the "deuterostomes." (3) The cleavage spindles oscillate between a 90° angle, generally parallel with or perpendicular to the animal-vegetal axis. (4) The blastomere arrangement into two and four tiers of eight cells each (at 16- and 32-cell stages) and the superposition of the cells directly above one another (from the 8-cell stage) result from the alternation of meridional and latitudinal cleavage planes (Fig. 4).

The cleavage patterns of Phoronida are briefly compared below with those of the

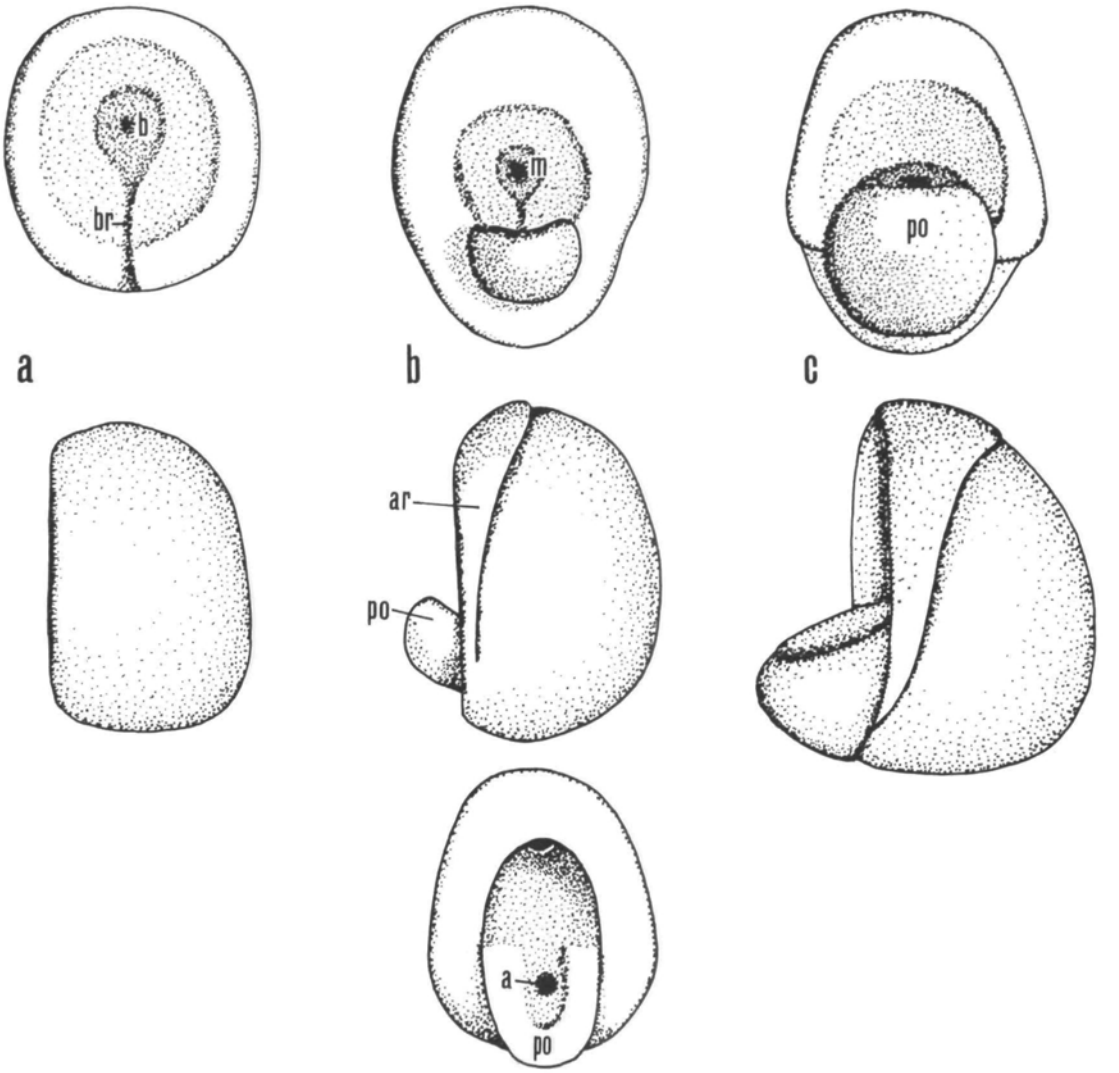


FIG. 5. Some stages of the embryonic development of *Phoronis ovalis* (after Silén, 1954). a) Newly released larva in ventral and lateral view. b) Larva 2 days after liberation: ventral, lateral and oblique anterolateral views. c) Larva 3-4 days after liberation in ventral and lateral view.
a, anus; ar, anterior rim; b, blastopore; br, blastoporal raphe; m, mouth; po, posterior outgrowth.

other Lophophorate phyla. The cleavage of Bryozoa is generally equal or subequal, but sometimes with larger cells in the vegetal hemisphere; the cleavage pattern is usually of a radial type, or is biradial in some species with cells more or less alternating. The 16-cell stage is composed of two plates of 8 cells each, as in Phoronida. At the 32-cell stage, the blastomere arrangement often consists of two plates of sixteen cells, but appears fundamentally as four tiers of 8-8-16-4 respectively.

The cleavage of Brachiopoda is practically equal and generally of a radial type, sometimes irregular (Percival, 1953) or with spiral cleavage (Conklin, 1902). At 16-cell and 32-cell stages, the blastomere arrangement is of two plates of eight and sixteen cells each in *Lingula* (Yatsu, 1902) or of two and four tier octets in *Terebratalia* (Zimmer, 1964; Long, 1964).

All three Lophophorate phyla present a radial or biradial cleavage that is equal or subequal. The segmentation of the Pho-

ronida corresponds more closely to that of Brachiopoda, especially in its tendency for irregularity of cleavage and differs from that of Bryozoa in details of the array of the blastomeres.

Regulative potential of Phoronida has been investigated only by Zimmer (1964): isolated blastomeres of *Phoronis ijimai* and *Phoronopsis harmeri* at 2-cell stage produce complete but diminutive embryos. In *P. ijimai* each blastomere of 4-cell stage regulates to form an atentaculate actinotroch, if not blocked at gastrulation.

DEVELOPMENT OF THE GASTRULA

At the vegetal pole, the gastrula shows a flattening which may be called the gastral plate (Figs. 6a, 7a). This plate invaginates in typical emboly or by bending of the two germ-layers (ectoderm, endoderm) after flattening of the whole embryo (all intermediates of these two processes occur, but the first is more general: Figs. 6b, 7b, 8a). These processes affect the entire vegetal hemisphere and give a gastrula with a large blastopore. The embryo rapidly acquires bilateral symmetry.

The gastrula in species of type 3 possesses a spacious primary cavity whereas the gastrula in species of type 2 (Table 1) has a virtually obliterated blastocoel (Emig, 1974), with the walls of the archenteron closely pressed against the ectodermal cells (Figs. 6, 7, 8).

The lateral lips of the blastopore fuse from posterior towards the anterior with reduction in diameter of the blastopore and conversion of the hemispherical archenteron into a tubular canal (Figs. 6, 7, 8). Concomitantly, the gastrula elongates in the antero-posterior axis. The blastopore is reduced to an anterior remnant and assumes an oval or triangular shape. Then the line of the blastoporal fusions disappears; the site of this raphe is the ventral midline. The blastopore remains as the connection between ectoderm and endoderm (Figs. 6d, 7d, 8c).

The external development of *Phoronis ovalis* with its considerable variations has been studied by Silén (1954) (Fig. 5). The embryo leaves the parent's tube as a slug-

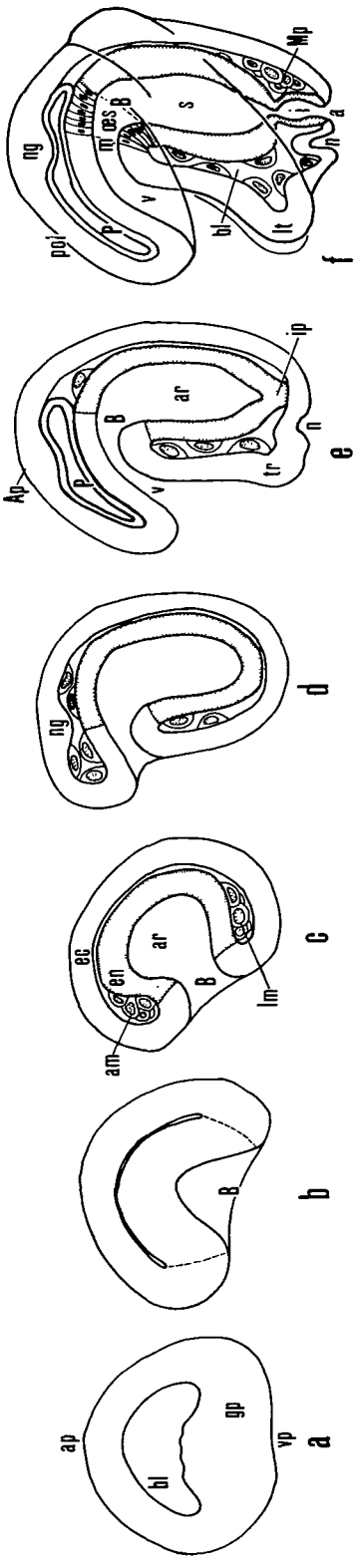


FIG. 6. Development of the gastrula of *Phoronis psammophila* in lateral view. a, anus; am, anterior mesoderm; Ap, apical plate; ap, animal pole; ar, archenteron; B, blastopore; bl, blastocoel; ec, ectoderm; en, endoderm; gp, gastral plate; i, intestine; ip, intestine primordium; lm, lateral mesoderm; lt, larval tentacle; m, mouth; Mp, metacoel primordium; n, nephridia primordium; ng, nervous ganglion; oes, oesophagus; ov, oesophagal valve; P, protocoel; pol, preoral lobe; s, stomach, tr, tentacular ring; v, vestibule; vp, vetetal pole.

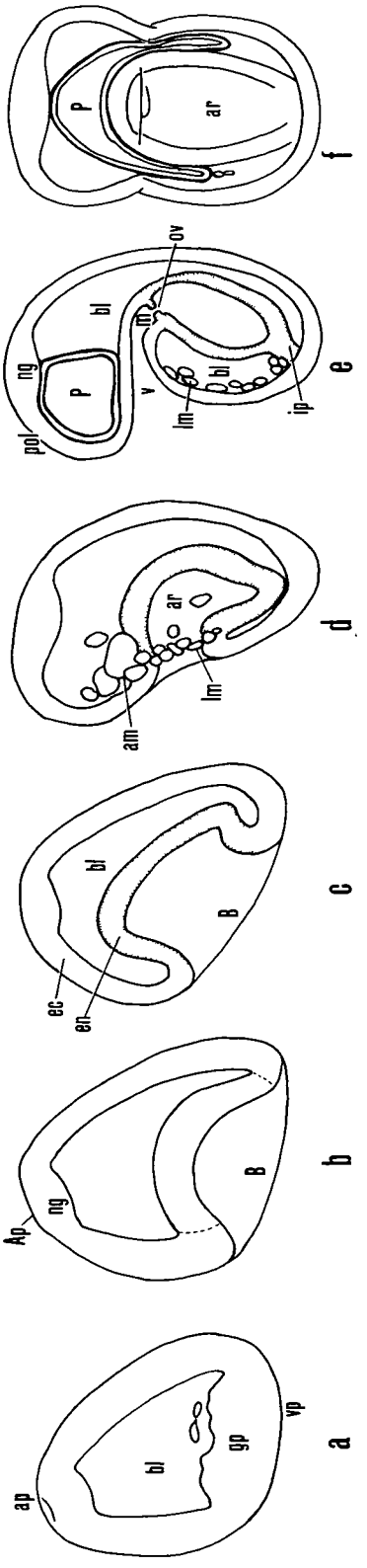


FIG. 7. Development of the gastrula of *Phoronopsis harmeri* in lateral view, except f, which is in frontal view (reconstructed from Zimmer, 1964). Abbreviations, see Figure 6.

like larva. For about 24 hours of their pelagic life the larvae have a distinct rim along the anterior region; this rim is probably the preoral lobe (Fig. 5b). With the growth of the anterior region, the blastopore acquires a central position on the ventral side. At the posterior end, a blunt outgrowth (probably the trunk) is formed and the anus opens on this projection (Figs. 5b, c).

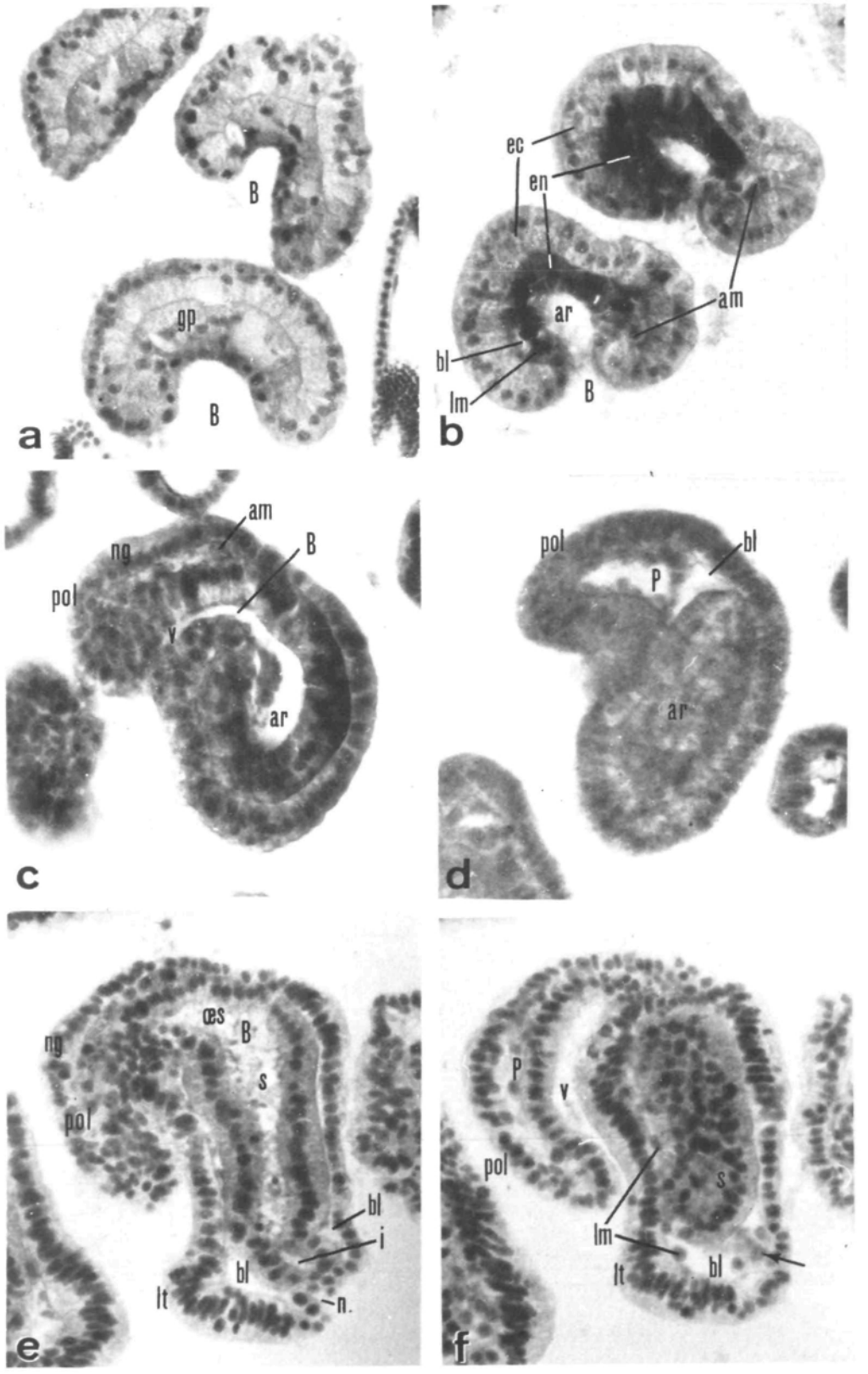
In the species with brood protection, the embryos are attached within the brood mass by an aggregation or a cord of mucus from the nidamental glands and inserted at the apical plate region of the preoral lobe (Zimmer, 1964). The embryos break free from the parent and begin their pelagic existence, at a stage of actinotroch with incipient tentacle formation in *Phoronis psammophila*, with two or four tentacles in *P. hippocrepia* and *P. ijimai,* and with six or eight tentacles in *P. australis* (and *P. Buskii*).

Differentiation of the ectoderm

The rapid growth of the ectoderm in the anterior region leads to the formation of the preoral lobe. With this development and the elongation of the gastrula, the blastocoel is reestablished (especially in the anterior region) in the larva of type 2 (Figs. 6c-d, 7c-d, 8b-c). The preoral lobe, characteristic of the *Actinotrocha*, grows ventrally and posteriorly to overhand first the blastopore and then a part of the ventral surface. The overgrowth of the ventral surface by the lobe lines an ectodermal cavity abutting on the blastopore (Figs. 6, 7, 8c) is called a vestibule.

An ectodermal thickening which is the apical plate occurs at the distal region of the preoral lobe and represents the incipient nervous ganglion of the larva (Figs. 6,

FIG. 8. *Phoronis psammophila*. a) Section of early gastrula, with embolic invagination of the gastral plate; the blastocoel is obliterated. b) Closing of the blastopore and mesoderm formation. c) Longitudinal section of a gastrula, with incipient preoral lobe. d) as c, with the protocoel. e) and f) Longitudinal sections of an older gastrula; the arrow indicates the metacoel primordium. Abbreviations see Fig. 7.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7, 8). At the onset of gastrulation the apical plate of *Phoronopsis harmeri* appears at the animal pole, directly over the gastral plate (Fig. 7); later this plate is shifted anterior to the blaspore (Zimmer, 1964). The cilia of the apical plate are longer than those of the other regions of the ectoderm. According to Zimmer (1964), this plate is the only nervous tissue apparent in the embryos during the lecithotropic growth.

At the postero-ventral region, a thickening of the ectoderm leads to the formation of the tentacular ridge that runs obliquely around the body (Figs. 6e-f, 8c-f). This ridge is most highly developed in its ventral portions; its cells are columnar, heavily ciliated, with elongate nuclei. The ciliation of the tentacular ring is longer and more dense than that of the rest of the epidermis; it shows a metachronal synchrony (Zimmer, 1964). The tentacles arise as evagination of the tentacular ridge (Emig, 1972*b*, 1973*a*). The first pair of tentacles evaginates adjacent to the ventral midline and successive pairs are formed in the dorsal directions.

The primordium of the nephridial ducts originate as an ectodermal invagination at the postero-ventral region of the embryo that leads to a small hollow ectodermal tube (Fig. 6e-f, 8e). The latter gives rise to the larval protonephridia. The nephridial pit appears shortly before the opening of the anus. The single duct bifurcates into paired lateral tubes. Their communication with the exterior is by a short common canal, but this is lost with further development and each tube opens separately on each side of the intestine. The solenocytes appear at the distal end of each nephridial tube; their origin has not been precisely determined. The development of the larval trunk begins generally at the actinotroch stage.

Formation of the digestive tract

After the emboly of the gastral plate, nuclei of the ectodermal cells elongate and lie near the middle of the cells; the endodermal cells (archenteron) keep their oval nuclei but change biochemically so as to modify the histological staining characteristics (Figs. 7b-c).

With the elongation of the gastrula and the reduction of the blastopore, the cup-shaped archenteron changes into a tubular canal (Figs. 6, 7, 8); its wall is less and less in contact with the ectoderm, so a blastocoelic space reappears in later gastrulae of type 2. The blastopore marks the separation between the ectodermal vestibule and the archenteron (Masterman, 1900; Roule, 1900*a*; Selys-Longchamps, 1902, 1907; Emig, 1974). As supposed by Brooks and Cowles (1905) and Hyman (1959) and as described by Emig (1974), and contrary to the opinion of Selys-Longchamps (1907), the mouth does not originate as true stomodeum in Phoronida: A slight penetration of the posterior part of the vestibule into the body takes the place of a stomodeal invagination; this penetration pushes inside the blastopore (Figs. 6e-f, 8e). The posterior part of the vestibule becomes the oesophagus, the mouth is formed later. In *Phoronis psammophila* (Emig, 1974) the blastopore marks the separation of the ectodermal oesophagus and the endodermal stomach. Thus, the blastopore does not become the mouth of the larva. In *P. ijimai* and *Phoronopsis harmeri* an annular diaphragm marks the entrance to the stomach and is also the possible site of the blastopore (Fig. 7e)

The posterior part of the archenteron grows to the posterior pole of the embryo and becomes a cell column which is the larval intestine (Figs. 6e, 7e, 8e). The endodermal cells come into contact with the ectoderm which is then perforated without any formation of a proctodeum: the intestinal and ectodermal cells join together to establish the anus (Fig. 6f). A similar process occurs in regeneration of the anus (Emig, 1972*b*, *c*; 1973*a*). The anus of Phoronida appears as a neo-formed structure, independent of the blastopore (Schultz, 1897; Shearer, 1906; Emig, 1974); the opening of the anus occurs in a region corresponding to the posterior pole of the gastrula, dorsal to the gastral plate in the first stage of the gastrula (Figs. 6, 7).

The intestine is separated by a pyloric valve from the anterior region of the ar-

chenteron which is now the expanded larval stomach. Both stomach and intestine are derived from the original archenteric invagination and so are of endodermal origin.

Formation of the mesoderm

Recent interpretation of mesoderm formation (Emig, 1974) corroborates the observation of many earlier workers (Table 2). Initially, archenteric cells of the anterior region are budded off as isolated cells of initial mesoderm into the blastocoel (Figs. 6c-d, 7d, 8b). The mesodermal cells then aggregate and later become organized occupying most of the space of the blastocoel of the preoral lobe (Fig. 8c). In *Phoronopsis harmeri* the mesoderm cells are budded from the gastral plate at the beginning of the emboly; these cells form a U-Shaped mass anterior and lateral to the archenteron (Zimmer, 1964). The second phase of mesoderm formation occurs at the time of fusion of the blastoporal lips: the mesoderm proliferates from paired ventrolateral archenteric areas and migrates along the walls of the blastocoel. Although the mesoderm has a double origin, its three sites of formation are probably more or less contiguous (Figs. 6d-f, 7d-f, 8e-f). When the archenteric cells become quite regular, no cell budding of mesoderm occurs.

The mesoderm is not evolved from archenteric diverticula. Caldwell (1885) and Masterman (1900, 1901) suggested that there are true diverticula without communication with the archenteron and that the mesoderm originates from a true or from a modified enterocoelous type. However, Roule (1900*b*) considered that the initial mesoderm forms an incomplete lining of the blastocoelic cavity. Cori (1939) concluded that the mesoderm development is neither enterocoelous nor teloblastic. Yet, the formation of mesoderm by cell proliferation in Phoronida appears to be a variation of the enterocoelous method (Dawydoff, 1928; Hyman, 1959; Emig, 1974). This formation is comparable to that of some Archimerata (Emig, 1975).

In the other Lophophorate phyla, the origin of mesoderm is uncertain. In brachiopods, mesoderm originates by proliferation of the lateral walls of the archenteron into two cell masses with later schizocoelous development (Yatsu, 1902); this pattern does not differ significantly from the enterocoelous method (Conklin, 1902; Plenk, 1913; Percival, 1944; Long, 1964). Origin of the mesoderm in the Bryozoa has not been established.

Formation and initial development of body cavities

The opinions of earlier investigators are often divergent on the formation and arrangement of the body cavities. Their statements are briefly considered below in comparison with recent observations (Emig, 1974).

The blastocoelic cavity reappears at the anterior pole of the gastrula with the development of the preoral lobe; the mesodermal cells formed by budding are organized in a vesicle which rapidly fills most of the space of the blastocoel along the walls of the preoral lobe (Figs. 6, 7, 8c-d). The formation of the epithelial wall of this vesicle appears to form in two ways. (1) The mesoderm cells proliferate and simply line the walls of the blastocoel, which is limited to the preoral lobe: this method seems to occur in *Phoronis ijimai* and *P. psammophila* (Fig. 8c-d) and the formation arises by mesodermal wandering (Zimmer, 1973; Emig, 1974); (2) The cell aggregation may develop an internal cavity and its expansion fills the blastocoel in the preoral lobe: this latter method seems to occur in *Phoronopsis harmeri* and the formation is a schizocoel (Zimmer, 1964).

The single cavity of the preoral lobe appears to be the first coelomic space, the protocoel. Its size varies within the phoronid species from most of the space of this lobe to only its ventral half. Until the work of Zimmer (1964), the existence of the protocoel was not considered, except by Masterman (1900) who described a protocoel in the preoral lobe originating from a single anterior archenteric diverticula (Table 2). Yet, some authors considered that the spacious preoral lobe cavity is completely or incompletely lined with

TABLE 2. *Origin of the mesoderm and coelomic cavities formation in different species of Phoronida.*

Species	Authors	Origin of Mesoderm: Blastula wall	Archenteron: General	Archenteron: Anterior	Archenteron: Lateral	Archenteron: Ventral or dorsal or posterior	Nephridial anlage	Origin of preoral lobe cavity: Wandering	Origin of preoral lobe cavity: Schizocoely	Origin of metacoel: Wandering	Origin of metacoel: Schizocoely
Phoronis hippocrepia	Kowalevsky (1867)	x									
(see also Selys-Longchamps and Cori)	Foettinger (1882)	x[b]	x[b]								
	Caldwell (1882, 1885)				x		x		AD		x
Phoronis ijimai	Ikeda (1901)		x	x		x	(x)	x		x	
	Zimmer (1964, 1973)		x	x	x			x			x
Phoronis buskii	Masterman (1897, 1900)			x	x	x			AD		AD
Phoronis psammophila	Roule (1890, 1900)		x		(x)	x		x			
(see also Selys-Longchamps and Cori)	Cowles (1904)		x	x	x		x		(x)		(x)
	Brooks and Cowles (1905)		x	x	x		x	x		x	
	Shearer (1906)		x	x	x		x	x			x
	Emig (1974)		(x)	x	x			x			(x)
Phoronopsis harmeri	Rattenbury (1954)			x	x			x			
	Zimmer (1964)		x	x	x				x		
Diverse species	Selys-Longchamps (1902)		x	x	x		x				
	Selys-Longchamps (1904, 1907)		x	x	x					x	
	Cori (1939)		x		x						x
	Schultz (1897)		x	x		x					
	Metchnikoff (1882)[c]		x[a]								

[a] blastula cells forming endoderm.
[b] issued from blastula cells from ectoderm or endoderm.
[c] Metchnikoff, E., 1882. Vergleichend-embryologische Studien. 3. Ueber die Gastrula einiger Metazoa. Z. Wiss. Zool. 37:286-313.

mesoderm cells (Roule, 1890, 1900*a*; Ikeda, 1901; Cowles, 1904; Brooks and Cowles, 1905; Shearer, 1906; Rattenbury, 1954) and that this cavity is horseshoe-shaped (Fig. 7f). Selys-Longchamps (1907) considered the anterior cavity haemocoelic.

By its development, the protocoel of *Phoronis ijimai* largely fills the preoral lobe and afterwards this protocoel is obliterated by approximation of the two surfaces of the lobe. In *Phoronopsis harmeri* (Zimmer, 1964), the protocoel is formed by the anterior part of the U-shaped coelomic cavity (Fig. 7f). Near the end of the lecithotrophic stage, this cavity persists only as a small remnant, not obliterated but retained throughout larval life (Zimmer, personal communication). In *Phoronis psammophilia*, the two horns of the preoral lobe cavity are slightly developed posteriorly on either side of the blastopore(Brooks and Cowles, 1905; Shearer, 1906; Emig, 1974); these horns are continued in the two ventrolateral areas by isolated cells (the mesodermal lateral proliferations are not organized in masses, but the mesodermal cells wander along the blastocoelic walls—Figs. 6d-f, 8e-f). As, in the preceding species, a temporary existence of the anterior cavity has been observed (Brooks and Cowles, 1905; Shearer, 1906).

The trunk coelom (or metacoel) in *Phoronis ijimai* originates from a single U-shaped row of cells that proliferate to form a solid mass (Zimmer, personal communication) and then undergoes schizocoely (Zimmer, 1973). Ikeda, (1901) considered that the metacoel is probably formed by cells lining the trunk space. In *Phoronopsis harmeri* (Zimmer, 1964), no trunk coelom is developed and no mesodermal aggregation is present at the end of lecithotrophic development. Thus, it seems that there is only the small protocoelic remnant at this time and the blastocoel fills all other larval space. In *Phoronis psammophila*, a mass of mesodermal cells, issued from the postero-lateral proliferation areas, appears dorsally near the anus around the intestine (Figs. 6f, 8f); from this mass arises the metacoel as a schizocoel (Emig, 1974; Shearer, 1906). Selys-Longchamps (1907) implied that the trunk coelom is formed by mesodermal cell wandering along the blastocoelic walls, but as did Roule (1890, 1900*a*) he considered that the gastrula possesses no coelom, the whole cavity is still blastocoelic. Cowles (1904), and Brooks and Cowles (1905) probably confused the solenocytes of the protonephridia with the mesodermal aggregation and described the metacoel primordium only in *Phoronis psammophila*. According to Caldwell (1882) and Cori (1939), the metacoel in one *Phornonis hippocrepia* originates posteriorly from paired dorsal sacs, formed by aggregations of isolated mesodermal cells. Masterman (1900) stated that in *Phoronis buskii* the trunk arises from a paired archenteric diverticula on the dorsolateral areas of the blastocoel.

In summary, it seems possible that the mode of the formation of the coelomic cavities varies with the species (Table 2). The third coelomic cavity, that of the collar (mesocoel), appears only shortly before metamorphosis. The other space retains its embryonic status, that of a surviving blastocoel.

CONCLUSIONS

Two remarks are necessary on the previously listed features. First, too much phylogenetic significance has been given to the origin of the mouth and anus: these two features present many deviations in the Protostomia and Deuterostomia and cannot be considered with certainty as criteria for the separation of the two superphyla. (Jagersten, 1955; Brien, 1970; Emig, 1974). Secondly, coelom formation in the Phoronida has parallels in deuterostomic phyla such as the Hemichordata and the Echinodermata and must be considered in relation to the origin of the mesoderm from which the coeloms are derived. These features have been considered in a recent study on the phylogenetic position of Phoronida and Archimerata (Emig, 1975): the phylum Phoronida agrees with the pathway of Chordata, so the statements of proceeding investigators (Young, 1962; Zimmer, 1973; Emig,

1973*a*, 1974) are corroborated, contrary to the opinion of many earlier zoologists which related the Phoronida to the "Prostomia."

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