Adv. Mar. Biol., Vol. 19, 1982, pp. 1–89.

THE BIOLOGY OF PHORONIDA

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I. Introduction

Since the last decade, the view that the Phoronida form a "minor phylum" has changed on account of their world-wide distribution, their ecological interest and their phylogenetic relationships. Known since the Devonian, the Phoronida, an exclusively marine group, are regarded as a class of the phylum Lophophorata (Emig, 1977a). As a result of the development of ecological investigations, our knowledge of the biology of the Phoronida has advanced in different disciplines. It is only recently that the variability in the taxonomic characteristics has become sufficiently known to establish the systematics of those phoronid species which are currently recognized (Emig, 1971a, 1974a, 1979). Larval development and the systematics of the actinotroch larvae also need detailed study. The extensive controversies concerning the phylogenetic relationships of the Phoronida have been in general due to lack of knowledge of embryonic and larval morphology and development. In addition, some basic aspects of the biology of the Phoronida still need to be studied in detail. Thus, the aim of the present review is to stimulate questions which have to be answered in future investigations, and have become necessary since the previous reviews by Cori (1939) and Hyman (1959).

II. Systematics

The possession of common characters, especially that of the lophophore, proves an affinity between Brachiopoda, Bryozoa (Ectoprocta) and Phoronida, which is implied by several authors by referring them to Lophophorate phyla. Others, including myself (Emig, 1977a), group them to form a phylum Lophophorata, of which each group then constitutes a class. As suggested by Hyman (1959), the name Tentaculata, proposed by Hatschek (1888), "is unfortunate, for tentacles occur in many unrelated animal groups",

and has to be rejected; only the name Lophophorata should now be used.

The diagnosis of the class Phoronida is as follows (Emig, 1977a): free-living, solitary, in a cylindrical tube of their own secretion; three body parts in larval and adult forms (archimeric regionalization); presence of a lophophore; trunk slender and cylindrical with an end-bulb, the ampulla; U-shaped digestive tract; nervous centre between mouth and anus, a ring nerve at the basis of the lophophore, one or two giant nerve fibres; metanephridia; closed-type circulatory system with red blood corpuscles.

In the Phoronida only two genera—*Phoronis* Wright 1856 and *Phoronopsis* Gilchrist 1907—and some ten species are currently recognized. The former genus is identified by the absence of the epidermal collar-fold below the lophophore, while the genus *Phoronopsis* has such a collar-fold (Fig. 1). The following characteristics are used to distinguish the species: habitat, lophophore shape, nephridial morphology, number of giant nerve fibres, longitudinal muscle formulae, gonads and accessory sex glands, when available. Some other additional features are sometimes used: absence of one or two lateral mesenteries, unusual trunk muscle disposition and differences in the circulatory system (Emig, 1974a). On the bases of all those taxonomic characteristics the systematics of the adult species have been established and several previously described species may therefore be considered as synonyms (Table I). For accurate identification adult phoronids need histological sections at different levels of the animal, usually the whole of the anterior region and posterior third of the trunk, both of which contain the main taxonomic features. Phoronids must be fixed quickly to prevent lophophore autotomy. Good results are obtained with Bouin's fixative, paraffin wax embedding, sectioning at 7 μm and Azan staining after Heidenhain's method (Emig, 1971a, 1979).

In several recent papers on Phoronida, particularly of American investigators, some synonyms (*Phoronis architecta*, *P. vancouverensis*, *Phoronopsis viridis*) are still cited as species: such usage should cease so as to avoid confusion and misinterpretation, or the species status must be established by a new description on the basis of the cited taxonomic features.

The larva of Phoronida, named *Actinotrocha* by Müller (1846), was described before the discovery of the adult form. But the International Commission of Zoological Nomenclature accepted as valid the name *Phoronis*; thus the actinotroch keeps a separate name considered as a technical one, which is sometimes still different from

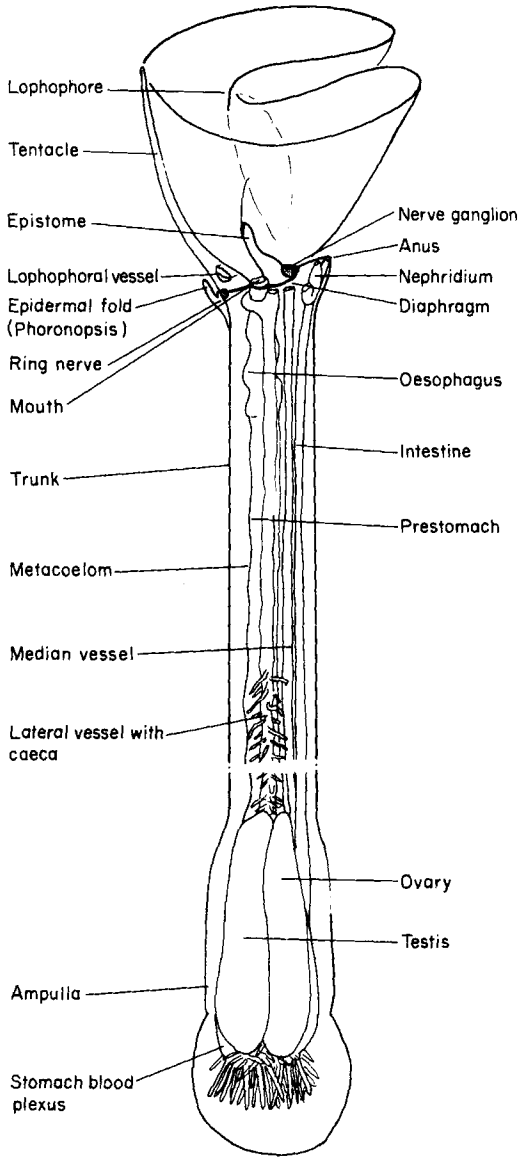

FIG. 1. Diagram of a phoronid, showing the main anatomical features.

the adult species name (Silén, 1952). A first review of the *Actinotrocha*, related to the adult form, with taxonomic characteristics is proposed and discussed in Section IV, B.

TABLE I. CLASS OF PHORONIDA: ADULT SPECIES, WITH SYNONYMS, AND RELATED ACTINOTROCH LARVAE

Genus	*Species*	*Synonyms*	Actinotrocha*
Phoronis Wright 1856	*ovalis* Wright, 1856		Not an actinotroch: Silén, 1954a
	hippocrepia Wright, 1856	*gracilis* *kowalevskii* *caespitosa* *capensis*	*A. hippocrepia* Silén, 1954a
	ijimai Oka, 1897	*vancouverensis*	*A. vancouverensis* Zimmer, 1964
	australis Haswell, 1883 (? *bhadurii* Ganguly and Majumdar, 1967)	*buskii*	
	muelleri Selys-Longchamps, 1903		*A. branchiata* Müller, 1846
	psammophila Cori, 1889	*sabatieri* *architecta*	*A. sabatieri* Roule, 1896
	pallida Silén, 1952		*A. pallida* Silén, 1952
Phoronopsis Gilchrist, 1907	*albomaculata* Gilchrist, 1907		
	harmeri Pixell, 1912	*pacifica* *viridis* *striata*	*A. harmeri* Zimmer, 1964
	californica Hilton, 1930		

*The adult form of *Actinotrocha wilsoni* has not yet been established while some larval forms remain unknown.

III. REPRODUCTION AND EMBRYONIC DEVELOPMENT

A. *Sexual patterns and gonad morphology*

Phoronid species are obviously either hermaphrodite or dioecious (Table II, Fig. 3) though several previous authors, such as Roule (1900), Torrey (1901), Brooks and Cowles (1905), Selys-Longchamps (1907), Pixell (1912) and Cori (1939), suggested a possible protandric condition owing to the presence of spermatozoa in the metacoelom and around the ovary of females, or to the apparent succession of male–female over the reproductive period. Such a possibility can be ruled out; the presence of spermatozoa in females results from

internal fertilization which occurs in all phoronid species. A considerable range of gonad maturation occurs among the individuals of a population over the whole reproductive period (Fig. 2); evidence for protandry has never been found.

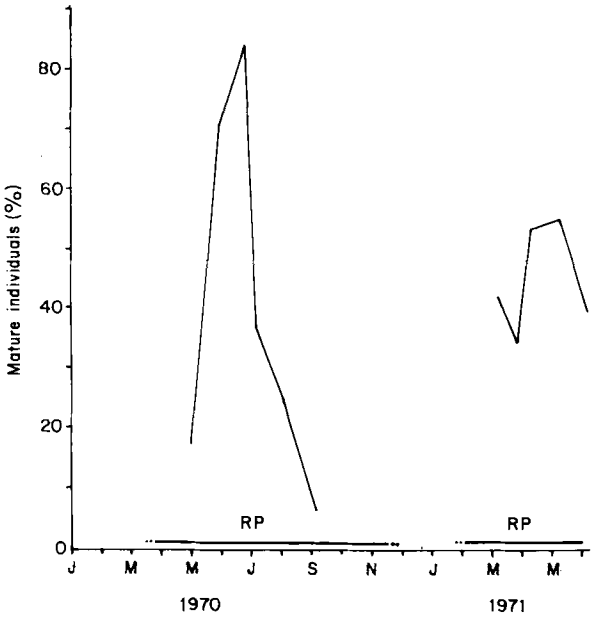

FIG. 2. Distribution (in %) of mature individuals in a population of *Phoronis psammophila* over one half year (Marseilles, Prado Beach at 4 m deep). The present data (unpublished) were obtained during the study of Emig and Emig (1975).

The gonads are applied to the lateral blood vessel and its large caeca in the left oral cavity of the metacoelom at stomach level and in the ampulla (Figs 1 and 3). They are intimately associated with the vasoperitoneal tissue. In hermaphrodite species, the testis lies on the oral side of the lateral vessel and the ovary on the anal side (Fig. 3b). In *Phoronis pallida* this disposition can be reversed (Silén, 1952; Emig, 1969). Ovary and testis are very close to each other, being only separated by a narrow distinct vasoperitoneal cell layer; both are clearly simultaneously active in one animal (Fig. 3b). In dioecious species (Fig. 3c, d), the gonads can extend into the right oral cavity of the metacoelom, where a secondary lateral blood vessel generally occurs, and which is also filled by vasoperitoneal tissue, and sometimes extends into the anal cavities. The sexes cannot be distinguished externally, although the ampulla seems sometimes whitish in males.

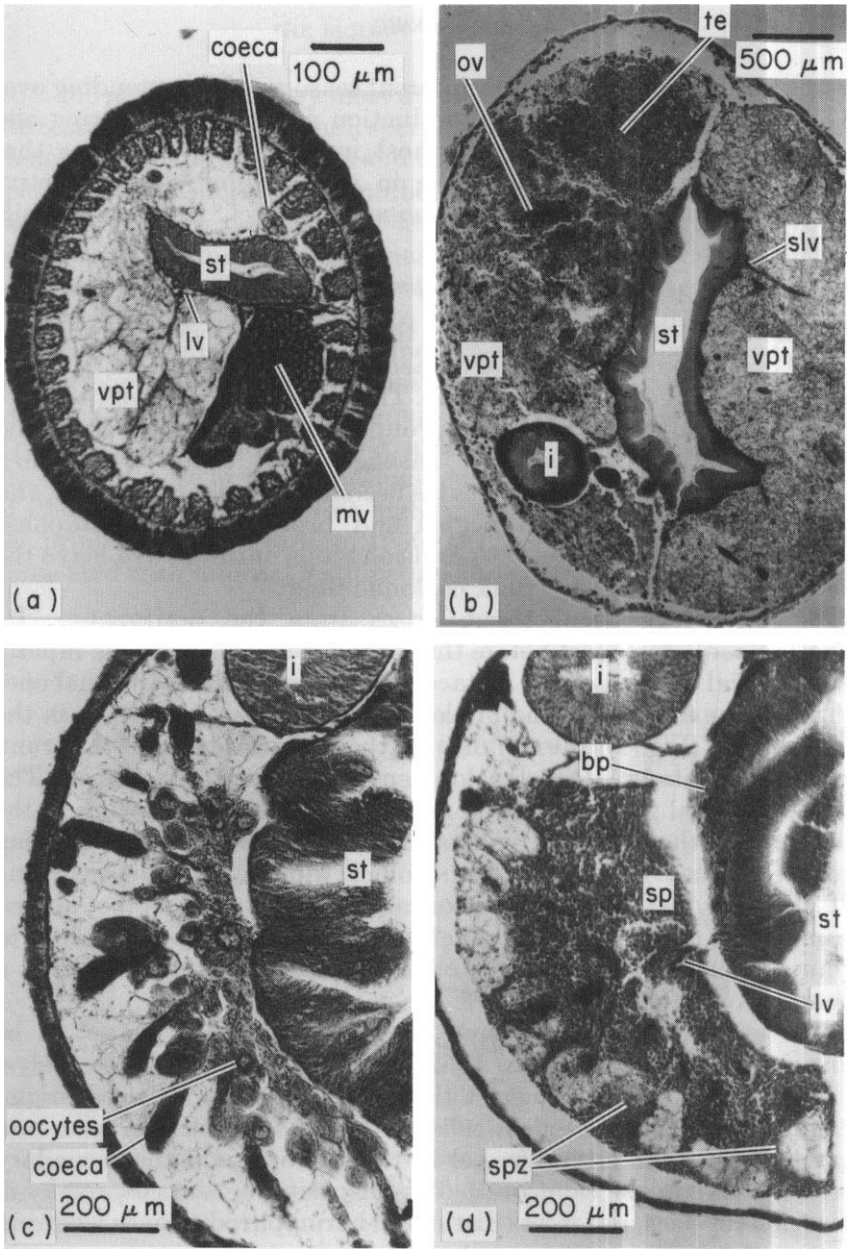

FIG. 3. Cross-sections at the gonad level. (a) *Phoronis australis*: development of vasoperitoneal tissue around the lateral vessel; (b) *P. australis*: gonad maturation in a hermaphroditic species, showing the important development of the vasoperitoneal tissue in all coelomic compartments, presence of the secondary lateral vessel; (c) *P. psammophila*: mature female; (d) *P. psammophila*: mature male. bp: blood plexus; i: intestine; lv: lateral blood vessel; mv: median blood vessel; ov: ovary; slv: secondary lateral vessel; sp: spermatids; spz: spermatozoa; st: stomach; te: testis; vpt: vasoperitoneal tissue.

Gonads become mature at different seasons, often extending over 8–10 months. The peak of reproduction occurs in late spring and summer (Fig. 2), according to most investigators. It seems that individuals which metamorphose in spring show a reproductive period in autumn, in *Phoronis psammophila* (cf. Emig and Emig, 1975).

B. *Oogenesis*

The ovary differentiates from the peritoneum along the lateral blood vessel and its capillary caeca which seem to be of great importance in gonad development. The germ cells in different stages of development are arranged in groups around and along the blood caeca. They grow inside the vasoperitoneal tissue which then degenerates gradually. The oocytes become somewhat flattened, and the first meiotic division begins and proceeds to a metaphase arrangement; at this stage the division stops until the ova leave the ovary to enter into the trunk coelomic fluid.

The vasoperitoneal tissue arises from the peritoneum. Its development starts just before that of the gonads. The tissue rapidly fills the oral cavities of the metacoelom and sometimes the anal ones through the numerous small holes distributed here and there in the mesenteries (Fig. 3). It extends over the posterior third of the trunk and reaches its greatest development at the breeding season. The vasoperitoneal tissue is considered as a nutrient layer owing to the richness of the yolk-like substance which nourishes the growing oocytes while at the same time the follicle widens. After the spawning of the oocytes, the vasoperitoneal tissue is said to be almost eliminated, and a new reproductive cycle can begin. According to Ohuye (1943), the vasoperitoneal tissue seems also to be a hematopoietic organ.

Several authors considered the vasoperitoneal tissue to be unpaired (Cori, 1939; Silén, 1952; Forneris, 1959), but, like Selys-Longchamps (1907), I suggest that this tissue has a paired origin, coming from the peritoneal cells of the blood vessels in each oral cavity (along the lateral vessel in the left oral and the secondary lateral vessel in the right oral). This disposition occurs especially in dioecious species, but is less distinct in hermaphrodite ones where an unpaired origin cannot be excluded.

C. *Spermiogenesis*

Spermiogenesis, like oogenesis, develops within the vasoperitoneal tissue. The male germ cells arise in the wall of the blood-vessels

from the peritoneum; they meet first near the lateral vessel, anlage of the testis. At this stage, small spermatogonia and oogonia are almost identical in shape and aspect and cannot be distinguished. Then, the spermatogonia increase in number, around and between the large caeca; they aggregate more or less loosely to one another to form either radial strings or small masses containing cells at about the same stage (Fig. 3b, d). The development process of spermiogenesis has never become known owing to the great difficulty in following the germinal cell sequence. The formed spermatozoa appear usually on the periphery of the testis in cohesive clumps: heads are together and tails free, both being of about equal length (Ikeda, 1901; Silén, 1952; Franzén, 1956; Zimmer, 1972; and my own unpublished observations). As those previous authors found, the V-shaped spermatozoa of Phoronida (Fig. 4) are of a highly "modified" type (in contrast to the primitive type: Franzén, 1956, 1977). Such a sperm structure is connected with internal fertilization and spermatophore production.

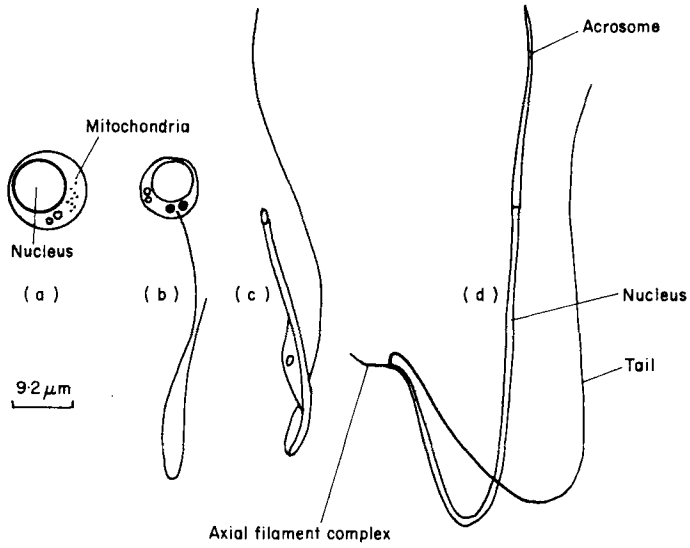

FIG. 4. Spermatogenesis of *Phoronis pallida*: (a)–(c) spermatids; (d) sperm (after Franzén, 1956).

D. *Release of spermatozoa*

Mature spermatozoa break away from the testis into the metacoelom and aggregate into a loose spherical mass near the nephridial funnels by currents created by their heavy ciliation. The sperm mass is compacted within the nephridial ducts where

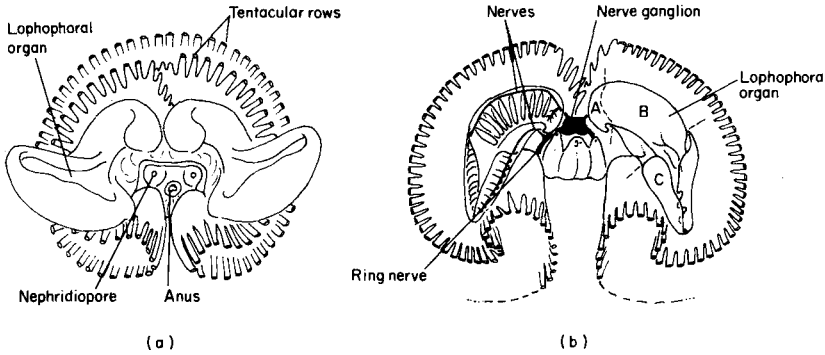

FIG. 5. Lophophoral organs (accessory spermatophoral organs). (a) Looking into the lophophoral concavity of a mature *Phoronis psammophila* with large and glandular lophophoral organs (after Emig, 1979); (b) lophophoral concavity of a mature *Phoronis harmeri* with large and membranous organs showing their innervation (left side) and their morphology with the three regions demarcated by dotted lines (right side) (after Zimmer, 1964). The small lophophoral organ type is represented in Fig. 7.

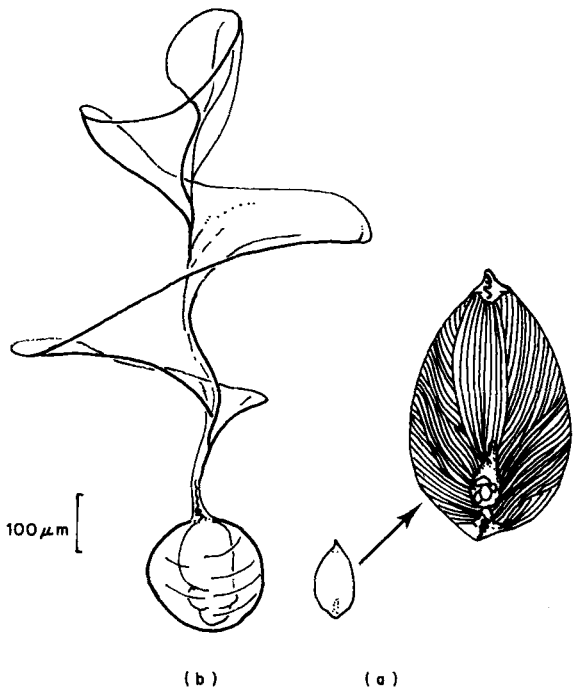

FIG. 6. Spermatophores: (a) of type A (*Phoronis ijimai*); (b) of type B (*Phoronopsis harmeri*) (after Zimmer, 1964).

orientation of the spermatozoa occurs, and is then extruded through the nephridiopore along the spermatic groove to the lophophoral organs where the spermatophore gradually takes shape. Nephridia serve also as gonoducts, as Dyster (1859) first observed. Cross-fertilization seems to be the rule; according to Zimmer (1964), the maturation of the spermatozoon is probably dependent on secretion from either the nephridia or the lophophoral organs, which could provide a mechanism for the avoidance of self-fertilization.

The term "lophophoral organs" has previously been used to describe all glands which occur in the lophophoral concavity. Many hypotheses have been put forward as to their possible functions (sensory: Caldwell, 1882; McIntosh, 1888; Selys-Longchamps, 1907; Gilchrist, 1907; secretory: Benham, 1889; Masterman, 1900; sensory and secretory: Forneris, 1959; Silén, 1954b; selection of sand grains for tube formation: Andrews, 1890); also correlations with gonad development have been suggested by Brooks and Cowles (1905), Selys-Longchamps (1907), Gilchrist (1907), Silén (1952) and Hyman (1959). The true function of the "lophophoral organs" has only

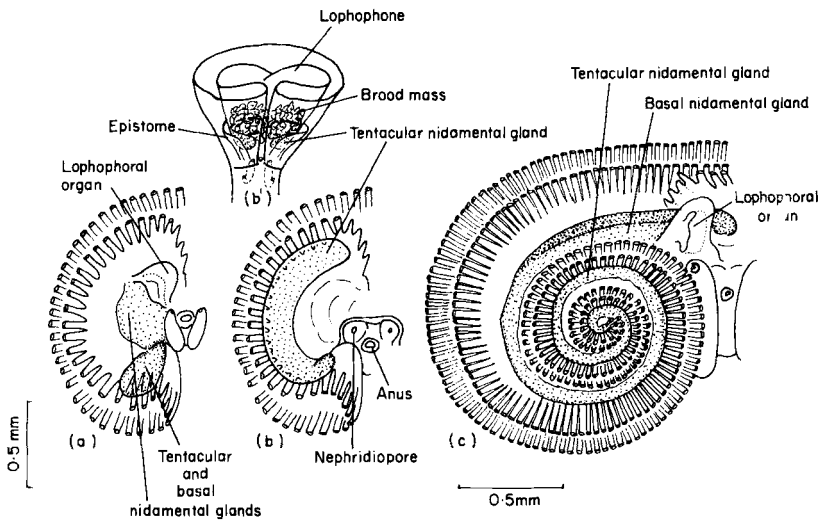

FIG. 7. Nidamental glands: looking into the lophophoral concavity of mature phoronids with brooding patterns, viewed from the distal end. (a) Nidamental glands of type 2a (*Phoronis hippocrepia*, *P. ijimai*), developed on the floor of the concavity and on the inner tentacle row at the inner side of the horseshoe-shaped end (respectively basal and tentacular nidamental glands); (b) of type 2c (*Phoronis psammophila*), formed along the inner tentacle row; (b') anal view of the anterior body part showing the position of the brood mass in the lophophoral concavity; (c) of type 2b (*Phoronis australis*), extended from the floor of the concavity into the several coils of the lophophore at the inner surface of the inner tentacles (after Emig, 1977b).

TABLE II. SUMMARY OF THE MAIN PATTERNS OF THE DEVELOPMENTAL BIOLOGY IN PHORONIDA

Species	*Sexes*	*Egg types*	*Diameter in μm*	*Number per individual up to*	*Release*	*Spermatophore types*
Phoronis ovalis	♂♀?	1	125	40	In one time	No spermatophore(?)
Phoronis hippocrepia	♀	2	85–100	100	Continuous	Type A
Phoronis ijimai	♀		90–110	400	Continuous	
Phoronis australis	♀		100–130	300	Continuous	
Phoronis psammophila	♂♀		80–120	400	Periodic	
Phoronopsis albomaculata	♂♀	?	100	?	?	(Type B?)
Phoronis muelleri	♂♀	3	50–65	500	Continuous	Type B
Phoronis pallida	♀		50–70	500		
Phoronopsis harmeri	♂♀		60–65	1000		
Phoronopsis californica	♂♀	?	?	?	?	(Type B?)

recently been discovered by Zimmer (1967): the general term lophophoral organs overlaps the male and female accessory sex glands, respectively lophophoral organs (sensu stricto) and nidamental glands (in brooding species). The development of both sex glands is correlated with gonad maturation.

The lophophoral organs (s.s.) may be small (Fig. 7a, c) or large (glandular or membranous; Fig. 5a, b) and occur in males and hermaphrodite species, but are usually lacking in *Phoronis ovalis* (Table II). They secrete the spermatophoral membrane and assist in spermatophore formation which is of general occurrence in Phoronida. However, several authors (Ikeda, 1903; Rattenbury, 1953; Silén, 1954a) have observed direct release of spermatozoa into the sea water, but that seems to be exceptional. In Phoronida, two types of spermatophores can be distinguished (Zimmer, 1967; Emig, 1980). The A type is an ovoid mass of spermatozoa produced by small

Types of developmental patterns	*Oviposition and embryonic development*	Actinotrocha *species*	*Pelagic life*	*Settlement on*
1	Brooding in parental tube during 4–5 days	Not a true actinotroch	Short stage 4 days Creeping stage 3 days	
2	Brooding on nidamental glands during about 7–8 days	*A. hippocrepia* *A. vancouverensis* ? *A. sabatieri*	9–14 days (after brooding period)	Hard substrate (burrowing or encrusting
(?)	?	?	?	
3	Direct release into the ambient sea water (no brooding) entirely pelagic existence	*A. branchiata* *A. pallida* *A. harmeri*	18–22 days	Soft substrate (embedded vertically)
?	?	?	?	

lophophoral organs (Table II; Fig. 6a) which is produced by burrowing or encrusting hermaphrodite species which are all living in intimate dense populations. The B type is a large spermatophore in two parts, a spherical mass of spermatozoa to which is attached a wide spiral float (Table II; Fig. 6b). This type seems to be formed by species with large lophophoral organs, living embedded vertically in soft bottoms, often in sparse populations. The spermatophores are greatly assisted in their escape by water and lophophoral ciliary currents: those of A type are probably rapidly collected by one of the nearest individuals and those of B type can float away to other, sometimes far distant specimens.

E. *Fertilization*

The transport of the sperm to female or hermaphrodite species is effected by means of the spermatophore. The main mechanism of

insemination seems to be the penetration of the sperm mass into the metacoelom through the nephridial duct: this is the natural access to the ovary. It is corroborated by many observations of previous investigators, such as Brooks and Cowles (1905), Selys-Longchamps (1907), Kume (1953), Rattenbury (1953). Forneris (1959) and Zimmer (1967). Nevertheless, Zimmer (1972) observed the drawing into the lumen of a tentacle downwards to the ovary after perforation of the diaphragm.

Fertilization in Phoronida appears to be internal. The presence of spermatozoa in the metacoelom and around the ovary of females (in dioecious species) has suggested protandry to several authors (see Section I, A). As indicated above, cross-fertilization seems to be a rule in hermaphroditic species. Fertilization occurs in the trunk coelom usually just after the egg escapes from the ovary.

F. *Spawning*

The ova rise into the nephridial funnels and are discharged into the lophophoral concavity through the nephridia: spawning usually takes place at all hours of the day and night. In the majority of the phoronid species it is more or less continuous over a number of days; however, spawning may be periodic in *Phoronis psammophila* (cf. Emig, 1974b, 1977b) and only once in *Phoronis ovalis* (cf. Silén, 1954a). The ova are directly released into the ambient sea water, or brooded in nidamental glands or in the distal end of the tube in *Phoronis ovalis* (Table II). Species with brooding patterns produce and release less eggs and the egg number decreases while the egg size increases; however, Silén (1954a) suggested that the estimated number also increases with the body volume. The function of the nidamental glands which occur only in brooding species is the attachment of the ova (by means of mucous secretion) to the embryonic masses and the maintenance of the integrity of these brood masses. According to Zimmer (1964) and Emig (1977b) the nidamental glands are of three types (Table II), which are illustrated in Fig. 7.

G. *Embryonic Development*

Only when the egg comes in contact with sea water does it start the expulsion of the polar bodies and the subsequent developmental stages. Phoronids show three different types of egg development (Table II; Fig. 8). The segmentation is similar in all species: total,

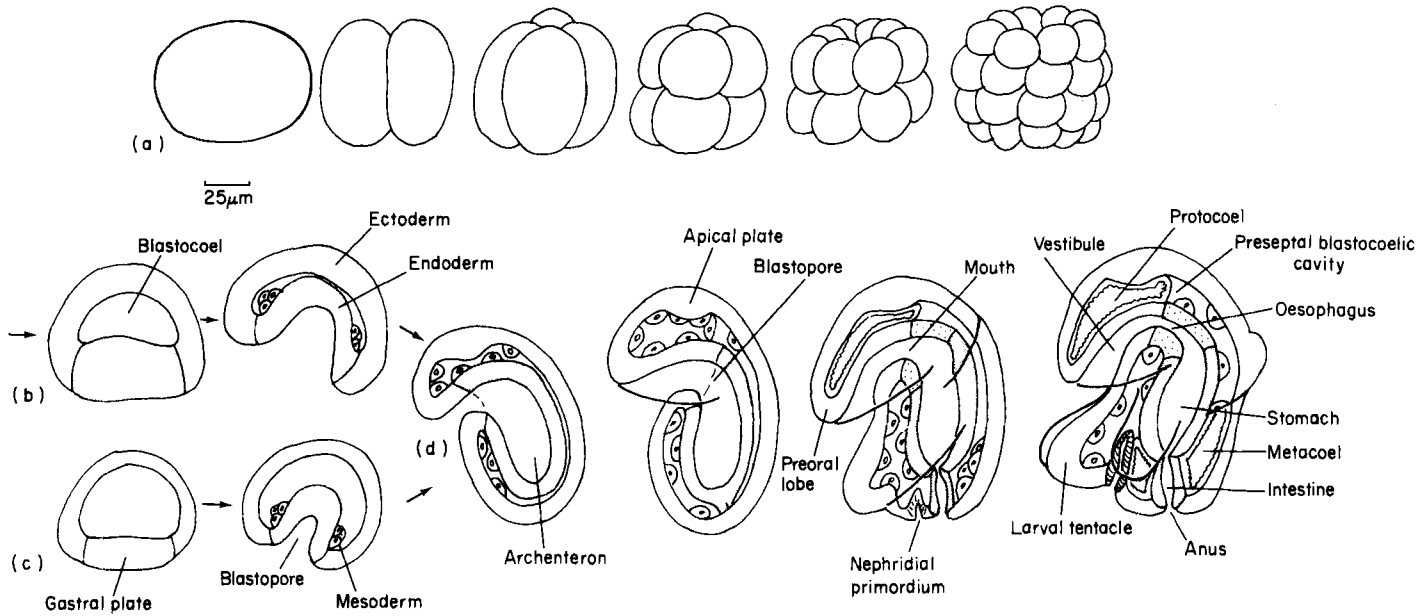

FIG. 8. Egg cleavage and embryonic development in Phoronida. (a) Egg cleavage in species of type 2 (see Table II); (b) blastula and gastrulation of developmental type 2. and (c) of type 3; (d) some stages of gastrula development (after Emig, 1974b, 1977b, 1979).

equal or subequal, and the cleavage is of typically radial type, though biradial in some stages. However, in egg developmental type 3, there occurs sometimes an apparent spiral arrangement which is induced by compression or variations in the orientation of the blastomeres (Zimmer, 1964; Emig, 1974b, 1977b), and also egg cleavage within the metacoelom which must be considered as an abnormal pattern.

The development reaches the blastula stage (Fig. 8b, c), a thick-walled ciliated coeloblastula in type 2 and a thin-walled one in type 3, but in both types the blastocoel has about the same diameter (35–40 μm).

The gastrula arises by a typical invagination (Fig. 8). During this process the gastrula of type 2 virtually obliterates its blastocoel by wall compression, while this cavity remains extensive in type 3. With the elongation of the archenteron, the embryo acquires a new bilateral symmetry perpendicular to the polar axis of the egg. At the gastrula stage (Fig. 8d), the differentiation of the archenteron (endoderm) produces a stomach and an intestine, the exterior opening of which, the anus, arises by perforation of the ectoderm without the formation of a proctodaeum. The oesophagus is produced by an ectodermal penetration of the posterior part of the vestibule: this process pushes inside the blastopore which remains as the boundary between the ectodermal oesophagus and the endodermal stomach (Fig. 8d). The mouth marks later the entrance into the digestive tract. The anterior ectoderm differentiates (a characteristic feature of the phoronid larva) the preoral lobe, on which an epidermal thickening leads to the nervous ganglion. In brooding species, the embryos are attached to the mucous cord of the nidamental glands by the apical area of the preoral lobe. At the postero-ventral region the tentacular ridge appears, and below in the midline the primordium of the protonephridia develops as an ectodermal invagination (Fig. 8d).

According to the recent interpretation of the mesoderm origin (cf. Emig, 1977b), the site and mode of mesoderm proliferation in Phoronida show marked similarities to the enterocoelous mode: the mesoderm originates as isolated cells proliferated from the anterior and ventro-lateral areas of the archenteron in two phases. The pattern does not differ significantly from this latter mode and must be considered as a modified enterocoelous type. The differentiation of mesoderm begins in the gastrula, but only one coelomic cavity occurs, the protocoel. This arises from the anterior mesoderm cells either as a schizocoel (in *Phoronopsis harmeri*: Zimmer, 1964) or by mesodermal wandering (in *Phoronis ijimai* and *P. psammophila*:

Zimmer, 1964; Emig, 1974b; *P. hippocrepia*). The protocoel largely fills the preoral lobe (Fig. 8d). Several mesodermal cells budded off from the lateral archenteric areas proliferate to form in the posterior end of the gastrula a solid mass which later gives rise to the metacoel. With the development of the gastrula the blastocoelic cavity reappears rapidly in embryos of type 2.

The embryos of brooding species escape from the brood masses with incipient tentacles, up to about six in number, according to the species, usually at the beginning of the larval stage.

H. *Embryonic nutrition*

The ova of types 1 and 2 are apparently supplied with sufficient yolk to last until the pelagic life without food; in non-brooding species (type 3), the amount of yolk is too small to allow a lecithotrophic mode of life during the same period of time: in all three types the larval size is about the same at the end of this period (Silén, 1954a). Thus, during pelagic existence embryo and larva ingest diverse organisms (as flagellates, diatoms, small larvae, etc). Digestion is always intracellular. The mode of embryonic nutrition has so far only been established by short and incomplete observations by several previous investigators, so that new careful studies are obviously needed on this topic.

IV. Actinotroch Larvae

A. *General Account*

The characteristic phoronid larva is termed *Actinotrocha* (or actinotroch) which must only be used as a technical name of the larval forms as stated by Silén (1952) in a footnote. The actinotroch has a pelagic existence: swimming near the sea surface for several days (Table II). The larva is a familiar constituent of the plankton, with a world-wide distribution. Only *Phoronis ovalis* is a curious exception (Silén, 1954a). The actinotroch seems to be photopositive, but its position at the sea surface depends upon the water movements, which if they are strong induce the larva to sink down (Hermann, 1976).

The general form and the gross structure of the *Actinotrocha* are familiar, established by several authors and also given in textbooks (e.g. Hyman, 1959; Emig, 1979, 1980). Thus, they are only briefly described here to facilitate the understanding of the different larval stages (Fig. 9) and the processes of metamorphosis.

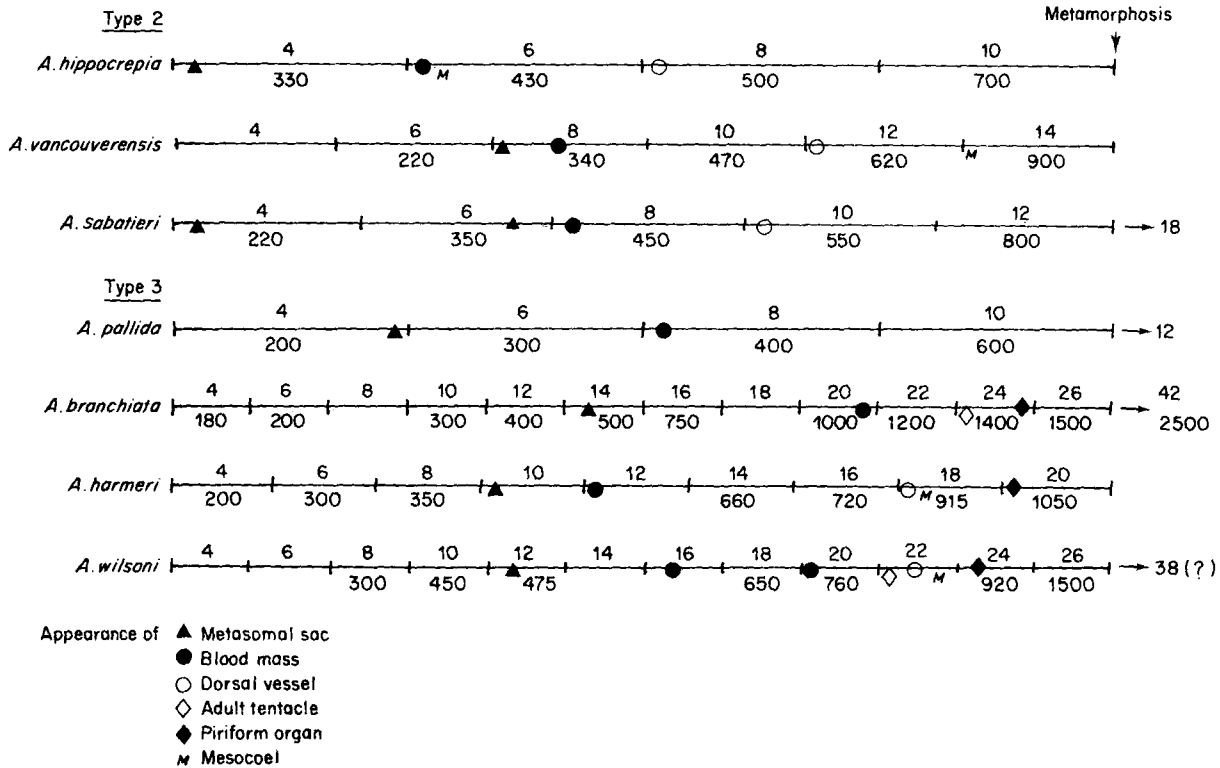

FIG. 9. Developmental stages of the known actinotroch species, with indication of the stage number (by number of larval tentacles: upper level, of the body length in μm: lower level) and of the appearance of the main features (by specific signs). See also Figs 12–19 where are represented the main larval stages in lateral view, without the ciliation of the perianal ring.

During development, the actinotroch elongates the larval trunk which ends in the perianal ciliated ring and increases regularly its number of tentacles. Both structures, tentacles and perianal ciliated ring, are the main locomotory organs of the larva, whilst the tentacles and the preoral lobe have feeding functions. The tentacles develop obliquely on each side of the midventral region, the longest being ventral; their maximum number varies with the species, but also somewhat within each species according to local ecological conditions, especially food availability. The definitive adult tentacles arise either as thickenings of the wall of the larval ones or as eversions under the bases of the larval tentacles (Figs 10, 19, 20). The preoral

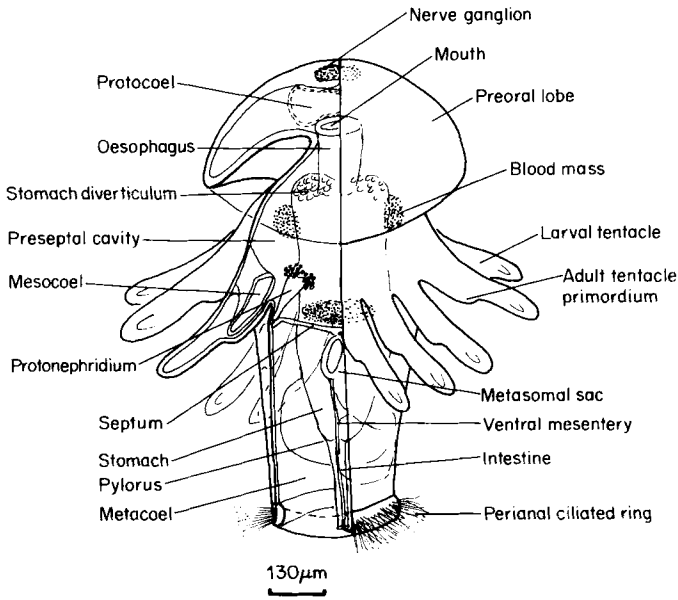

FIG. 10. Diagram of the ventral view of a mature *Actinotrocha sabatieri*, showing the internal anatomy.

lobe which overhangs the mouth like a hood is a characteristic feature of the actinotroch; it is entirely ciliated with a belt of cilia along the free margin and a strongly ciliated area (especially in larva of type 3) in the centre of the dorsal (anterior) surface of the preoral lobe at the site of the apical plate, which is the larval nervous ganglion. The remaining epidermal body surface is also ciliated, especially the tentacles and the perianal ring. Just behind the mid-ventral tentacles there is an ectodermal invagination which gives rise to the metasomal

sac. This sac develops between the two leaves of the ventral mesentery and grows to occupy the largest space of the metacoel, sometimes virtually all the coelom (Fig. 10). The protonephridia originate by a single ectodermal invagination that bifurcates rapidly into two separate canals opening laterally on each side of the intestine by a tiny pore just behind the tentacles and the trunk septum (Fig. 8d, 10, 11). At the closed proximal end of each nephridial canal arise solenocytes arranged in one to three clusters and lying in the blastocoelic preseptal cavity. In Phoronida the body is divided into

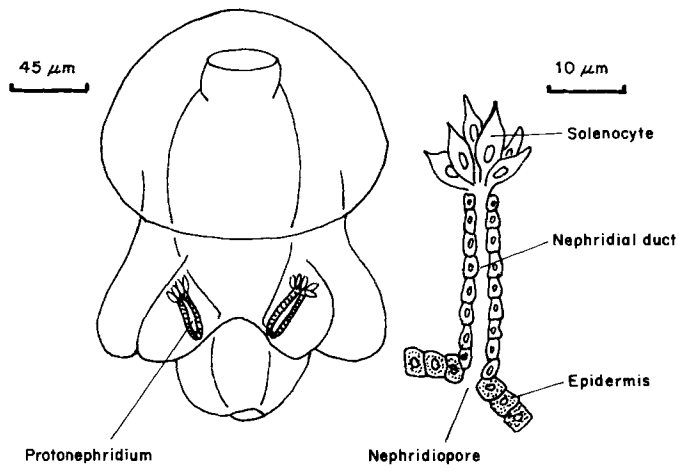

FIG. 11. Protonephridium in a young actinotroch (*Actinotrocha hippocrepia*): disposition in the larva and cross-section (after Emig, 1980).

three major archimeric regions each with its own unpaired coelomic cavity. At first, the U-shaped protocoel occurs by schizocoely or cell wandering in the space of the preoral lobe (or protosome) and is separated from the blastocoelic collar space (or blastocoelic preseptal cavity) by a septum (preoral septum) just behind the apical plate (Fig. 10). According to Zimmer (1978) the extensive protocoel which occupies the cavity of the preoral lobe in the gastrula degenerates to persist only as a small vesicle situated between the apical plate and the oesophagus near the limit of the preoral lobe in the actinotroch stage. Then the metacoel (or trunk coelom) undergoes schizocoely; it establishes a ventral mesentery which unites the trunk wall to the digestive tract and anteriorly, at the level of the tentacles, a definitive septum (or trunk septum) which assumes the status of a mesentery with the development of the mesocoel (or collar coelom).

Between the preoral septum and the trunk a blastocoelic cavity persists until late in the actinotroch development (Fig. 10). The mesocoel develops into a horseshoe shape (probably by schizocoelic formation according to Ikeda, 1901; Goodrich, 1903) within the blastocoelic space over the trunk septum in well-developed larvae. The digestive tract has elongated with the trunk development and consists of three divisions: the oesophagus opening by the mouth; the stomach in three portions: anteriorly one or two vacuolated diverticula, then a large cavity and posteriorly a small funnel-shaped heavily ciliated cavity entering the intestine by a pylorus, and the intestine opening by the anus in the centre of a ciliated ring (Fig. 10). One to four solid masses of blood corpuscles appear in the blastocoelic collar space. Their number and disposition are used in the identification of actinotroch species. In the fully developed larva there is a dorsal blood vessel, the incipient median vessel, and at the site of the pylorus a bunch of short blood caeca. The circulatory system is not functional in the actinotroch. The muscle arrangement and the nervous system are complex and vary in the different species. Several actinotroch species are provided with a piriform organ which appears shortly before metamorphosis (Fig. 20a) and is supplied by three long nerves from the ganglion. Several actinotroch species show from about the four tentacle stage a characteristic pigmentation of prime importance in identification (Figs 13, 14).

B. *Development of the actinotroch species*

The main developmental stages of the different known actinotroch species are shown in Figs 9 and 12–19, together with some characteristics helpful in their identification.

The duration of the whole larval development averages probably 19–21 days in all species. Silén (1954a) suggested that the length of the actinotroch stage, elapsing between four-tentacle to metamorphosis, is about 12–14 days without difference between brooding and non-brooding phoronid species; only *Phoronis ovalis* is an exception (Table II).

A brief description of each actinotroch species follows and possible synonyms are proposed. It is suggested that the description of a number of actinotrochs is due to different interpretations by previous investigators who have mostly studied *A. branchiata*, to an unintentional misunderstanding of statements by earlier workers, and to the fact that the early workers recognized about 20 phoronid species where there are presently about ten. There is no doubt that

our knowledge of actinotroch species is far from satisfactory and the following list of actinotrochs needs particular attention in the future and probably some modifications, and also additions will have to be made.

1. *Larva of* Phoronis ovalis

The sexual reproduction of *Phoronis ovalis* has only been described by Silén (1954a). The embryo escapes from its tube in a gastrula stage about 4–5 days after the egg release. Its transformation and differentiation is so different from that of other phoronid larvae that this embryo cannot be called an actinotroch, as suggested by Silén (1954a). The development is more direct: the planktonic existence is almost omitted and the short pelagic life of about 4 days serves for larval dispersal exclusively, and no true metamorphosis occurs after a creeping period of about 3–4 days. The whole development elapsing from the egg release to the transformation to the adult phoronid is of about 12–13 days.

The external morphological characteristics of the larva of *P. ovalis* are shown in Fig. 12.

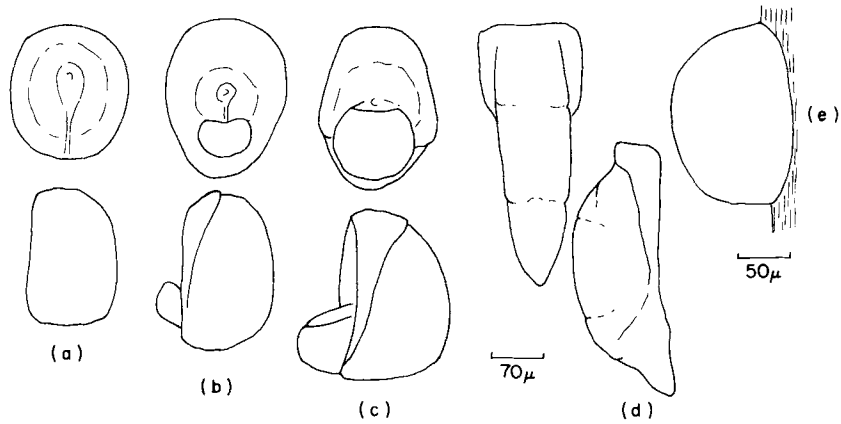

FIG. 12. Larval development of *Phoronis ovalis* (after Silén, 1954a). (a) Larva just escaped from the parental tube, in ventral and lateral view; (b) 2 days after liberation; (c) 3 days after liberation; (d) after 5 days, creeping stage; (e) just attached larva, 7 days after liberation, in lateral view.

2. *Larva of* Phoronis hippocrepia: Actinotrocha hippocrepia

The larva of *Phoronis hippocrepia* Wright, 1856, was discovered by Silén (1954a), and since found by Forneris (1959).

The body of *Actinotrocha hippocrepia* is opaque; its pigmentation consists of very small pigment granules (dark brown in reflected light) probably contained in the epidermal cells. The granules are distributed in distinct patches at certain fixed points of the body which increase in number from the four-tentacle stage to the last actinotroch stage (Fig. 13).

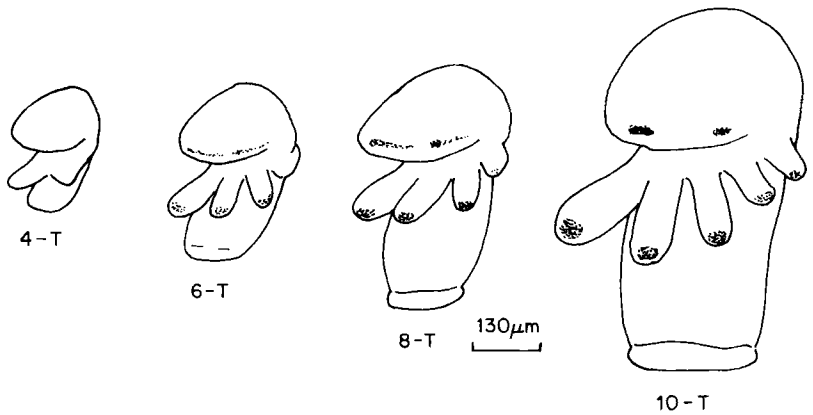

FIG. 13. Developmental stages of *Actinotrocha hippocrepia*, with its characteristic pigmentation.

A. hippocrepia possesses two ventral blood masses which fuse in the oldest specimens at the level of the oesophagus, but blood globule clusters on each side of the trunk are situated near the insertion of the tentacles. The stomach diverticulum is unpaired. The tentacles are not more than ten in number; no adult tentacles occur (Fig. 9).

According to Silén (1954a) and Forneris (1959), *A. hippocrepia* is very similar to *A. pallida* in general appearance and behaviour and it is difficult to distinguish between the larvae unless they are placed side by side. However, the characteristic pigmentation of *A. hippocrepia* is the main feature for identification, as is the number of blood masses.

3. *Larva of* Phoronis ijimai: Actinotrocha vancouverensis

Actinotrocha vancouverensis has been described by Zimmer (1964), especially its main developed stages. This larval form is the larva of *Phoronis ijimai* Oka, 1897 (synonym: *Phoronis vancouverensis* Pixell, 1912; established by Emig (1971b) and confirmed in Emig (1977c)).

A. vancouverensis has a opaque body which is heavily pigmented (two pairs of pigment patches on the preoral lobe, a rather uniform distribution on the collar, only interrupted at the tentacles, uniform

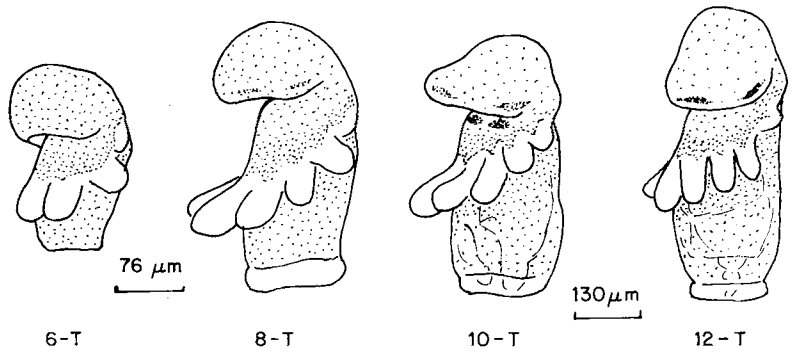

FIG. 14. Main development stages of *Actinotrocha vancouverensis* showing the characteristic pigmentation (after Zimmer, 1964).

but variable in density on the trunk, see Fig. 14). There is a single blood mass on the anterior ventral surface of the stomach. The maximum number of tentacles is 14 in larvae ready to metamorphose, without indication of adult tentacles.

The species A of the four actinotroch types described by Ikeda (1901) cannot be considered as the larval form of *Phoronis ijimai* especially in view of the presence of two masses of blood corpuscles. It seems also that any larva found by this author belongs to *A. vancouverensis*.

4. *Larva of* Phoronis psammophila: Actinotrocha sabatieri

Actinotrocha sabatieri, discovered by Roule (1896) and described by this author in 1900 and by Selys-Longchamps (1907), is the larva of *Phoronis psammophila*. It has been recently studied by Veillet (1941) and Herrmann (1977). After the writing of the present paper, Herrmann (1979) published a note on the larval development and metamorphosis of *Phoronis psammophila*, results of which confirmed most of my own observations on *A. sabatieri*.

A. sabatieri is large and transparent. Pigmentation occurs until the six-tentacle stage; at first two pigment masses are located on both sides of the apical plate and later at the distal end of the tentacles. Herrmann (1979) considers that the pigment amoebocytes may represent a nutrient reserve used by the larva during a period of food shortage. The larva does not develop more than 12 larval tentacles. The adult tentacle are represented by a thickening of the wall of the larval tentacles at the end of the ten-tentacle stage. Three blood masses are distributed, two on each side of the stomach diverticulum

(which is unpaired), and one, unpaired, on the ventral midline just above the insertion of the tentacles (Figs 10, 15). Herrmann (1979) shows the metasomal sac and the perianal ciliated ring during the eight-tentacle stage, the stomach diverticula and the blood masses at the ten-tentacle stage, and the adult tentacles and two longitudinal blood vessels along the stomach during the 12-tentacle stage.

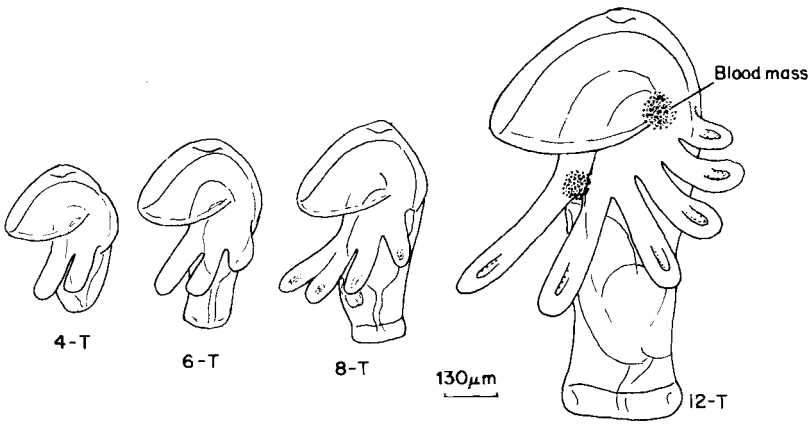

FIG. 15. Main stages of *Actinotrocha sabatieri*.

According to various authors, several actinotroch species are to be considered as synonyms of *A. sabatieri*. However, the name *sabatieri* has been retained because this actinotroch has the best complete description and is without doubt the larval form of *P. psammophila*. The characteristics of *Actinotrocha metschnikoffi* discovered by Metschnikoff (1869, 1871) have been established by Selys-Longchamps (1907), all being similar to those of *A. sabatieri*: 0·6 mm long, up to 16 larval tentacles with anlage of the adult ones as thickenings at the interior bases of the larval tentacles and three blood masses of characteristic disposition. On *A. metschnikoffi*, the statement of Roule (1900) that probably only one actinotroch species occurs in the Mediterranean Sea must be refuted as suggested by Selys-Longchamps (1907), especially because several phoronid species live here and consequently several actinotroch species. *Actinotrocha wilsoni A*, which was named by Selys-Langchamps (1907), is described by Wilson (1881), Cowles (1904a) and Brooks and Cowles (1905) and belongs probably to *A. metschnikoffi* (presently *A. sabatieri*); it is about 1 mm long; has up to 18 larval tentacles with definitive ones as thickenings; has no piriform organ; pigmentation is present especially as spots at the bases of the tentacles; has blood

masses until about the 12-tentacle stage, but there are only two of these masses, disposed ventro-laterally to the stomach. *Actinotrocha hatscheki*, figured by Hatschek (1891), has been briefly described by Selys-Longchamps (1907); all known features are similar to those of *A. sabatieri*, especially in the maximum number of tentacles (up to 16), no piriform organ and two stomach diverticula. Another species, *Actinotrocha ashworthi*, described by Selys-Longchamps (1907) belongs, I believe, to *A. sabatieri*: it is 0·65 mm long, has about 20 tentacles with anlage of adult ones and three masses of blood corpuscles. Steuer (1933) found two larval forms one of which has the following main characteristics: it is about 0·6 mm long; has up to 16 tentacles and three blood masses: this form seems to be related to *A. sabatieri*. Recently, the larval form considered by Zimmer (1978) as that of *Phoronis architecta* (which species is a synonym of *P. psammophila* according to Emig, 1972a, 1977c) is thought to be related to *Actinotrocha branchiata* (see following paragraph).

5. *Larva of* Phoronis muelleri: Actinotrocha branchiata

Actinotrocha branchiata was discovered near Helgoland by Müller (1846), who considered this animal to be an adult. The adult form named *Phoronis* was described in 1856 by Wright on the English coast. The transformation of this actinotroch into *Phoronis muelleri* was established by Selys-Longchamps (1903). The other main works on *A. branchiata* are from Selys-Longchamps (1907), Silén (1954a), Emig (1973a), Siewing (1974a) and Herrmann (1976). Recently, Zimmer (1978) related a larva to *Phoronis architecta*, but this larva belongs to *Actinotrocha branchiata*, which confirmed the confusion introduced by Brooks and Cowles (1905), and discussed by Emig (1977c), between *P. muelleri* and *P. psammophila* which may both be mixed in the same locations.

Actinotocha branchiata is a transparent larva with numerous pigmented amoebocytes; yellow pigments are located at the base of the tentacles, around the preoral lobe and near the ciliated perianal ring. This larva, the largest known in phoronids, grows to an unusual size (about 2 mm in length), and the larval tentacle number increases to 42. Paired vacuolated stomach diverticula are present, as are two ventral blood masses just above the nephridial site, lateral to the stomach. The two masses originate at about the 20-tentacle stage and usually fuse just before metamorphosis. The adult tentacles arise as independent eversions under the bases of the larval ones until the larva has usually about 22 (Figs 9, 16, 20).

The larva which is ready to metamorphose from about the 24-tentacle stage (Fig. 20) becomes opaque, although a protruding tip called the piriform organ appears on the preoral lobe (anteriorly to the apical plate, between the latter and the ventral free margin of the lobe). Herrmann (1976) suggested that the function of the piriform organ is to select a suitable substratum for larval settlement and then to induce the processes of metamorphosis. According to Emig (1980)

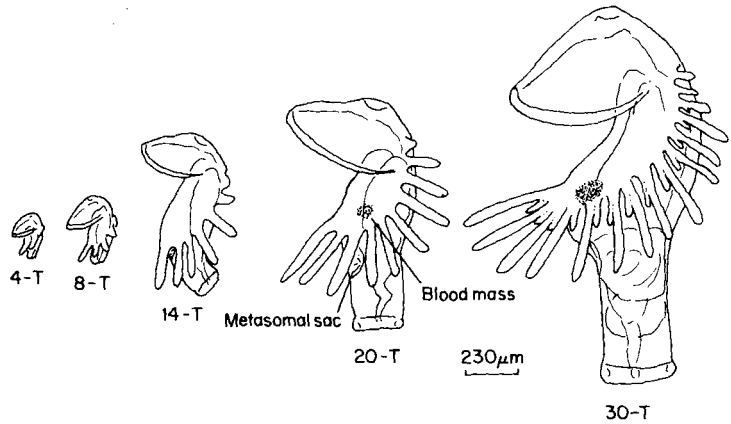

FIG. 16. Some developmental stages of *Actinotrocha branchiata*.

the piriform organ seems to be related to larval ecological behaviour and has no evolutionary relationships within the Lophophorata or with related phyla. The larva can induce metamorphosis without the piriform organ being present (Fig. 9). The length of pelagic life can be prolonged by lack of food or other unfavourable conditions which may delay development in *A. branchiata*; the increase of the number of tentacles could then be explained by the lengthening of the pelagic life; the same statement seems to be true of the other actinotroch species, especially *Actinotrocha sabatieri*.

All actinotrochs collected by Browne (1895, 1900) and studied by Selys-Longchamps (1907) belong to *A. branchiata*; the specimens named *A. brownei* are of the same species just beginning their metamorphosis. Schepotieff (1906) described two forms which are both probably related to *A. branchiata*. Similarly the first larva identified by Steuer (1933) belongs to the latter species. The form B of the species established by Ikeda (1901) could be a synonym of *A. branchiata* and probably also the form D which seems to be an abnormal stage in metamorphosis.

6. *Larva of* Phoronis pallida: Actinotrocha pallida

The adult form of *Actinotrocha pallida*, a larva known since Schneider (1862), has recently been described by Silén (1952), under the name *Phoronis pallida*. Other information on the larva is given by Selys-Longchamps (1903, 1907), Silén (1954a) and Zimmer (1964).

A. pallida is small, opaque, yellowish-white, provided with a considerable amount of yellowish pigment located in the apices of the epidermal cells (no pigment in the apical plate); there are no pigmentiferous amoebocytes (Figs 9, 17). The stomachal diverticulum is unpaired. There is only one blood mass in a paired

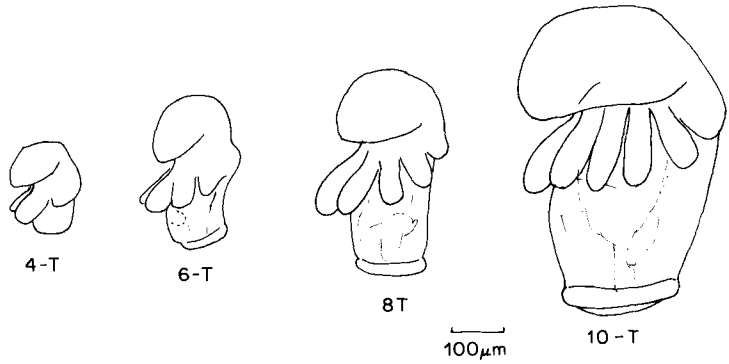

FIG. 17. Developmental stage of *Actinotrocha pallida*.

aggregation united in the midline in the fore ventral part of the stomach. The larva ready to metamorphose exhibits a maximum number of ten tentacles, but sometimes two additional tentacles appear just before metamorphosis. At this stage, the metasomal sac occupies virtually the whole of the trunk coelom. It seems that the extensive pigmentation and the highly colourful body distinguish *A. pallida* from the other actinotroch species (see discussion in *A. hippocrepia*).

7. *Larva of* Phoronopsis harmeri: Actinotrocha harmeri

A. harmeri is the larva of *Phoronopsis harmeri*: this larva has been described by Zimmer (1964) under the name *Actinotrocha A* and recent unpublished observations have confirmed this parental relationship. Zimmer (1978) established that there was no difference between the larvae of *Phoronopsis harmeri* and *Phoronopsis viridis*; it must be remembered that both species are considered as synonyms

(Marsden, 1959; Emig, 1971a, 1979) although Zimmer's (1978) opinion has never been further supported.

A. harmeri is large, transparent, without epidermal pigmentation; only concentrated yellow pigmented amoebocytes occur in characteristic locations: margin of the preoral lobe, tentacles, metasomal sac, collar ring muscle, oesophagus and perianal ciliated ring. There are two pairs of blood masses which are located as follows: one disc-shaped pair in the dorso-lateral corners of the preoral lobe and one pair elongate in the collar, ventro-laterally at the site of the third tentacles (Figs 9, 18). The larva is ready to metamorphose at the 20-tentacle stage without the presence of adult tentacles. Zimmer (1964)

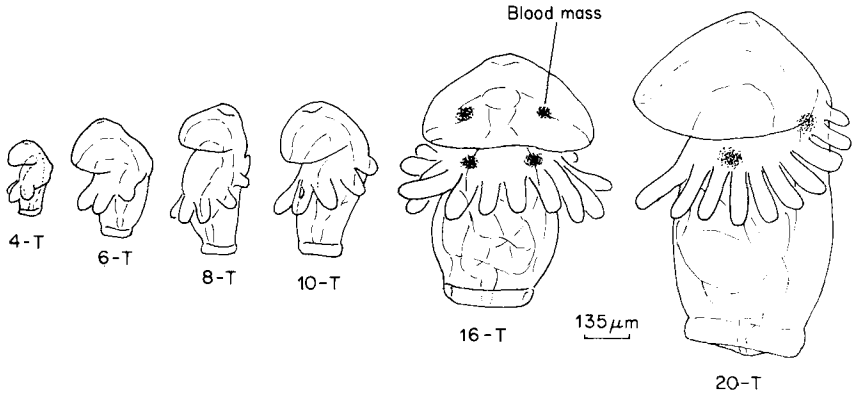

FIG. 18. Main developmental stages of *Actinotrocha harmeri* (four-tentacle larva to 16-T after Zimmer, 1964).

suggested that a piriform organ could be present shortly before metamorphosis, but it does not possess the remarkable extensibility of that organ in *Actinotrocha branchiata*.

The species named *Actinotrocha ikedai A* by Selys-Longchamps (1907) has been studied by Ikeda (1901) who considered it to be the larva of *P. ijimai*. According to its characteristics, this larva is mostly similar to *A. harmeri*: short and thick body; 1–1·5 mm long; about 16 tentacles; metasomal sac at about the eight-tentacle stage and the two pairs of blood masses at the 14-tentacle stage, one pair of these masses covering the stomach diverticulum, the other pair ventro-laterally in front of the septum on both sides of the stomach.

8. *Larva of an unknown adult*: Actinotrocha wilsoni

Under this name is described the "species B" of Wilson (1881). The adult form of *Actinotrocha wilsoni* is presently unknown, but it could

be suggested that the larva belongs to *Phoronopsis albomaculata* on the basis of the similarities with *Actinotrocha harmeri*. Selys-Longchamps (1907) and Forneris (1959) have studied the present form B which they considered to be a distinct larva. However, a synonymy with *A. harmeri* cannot be excluded.

The pigmentation of the body is diffuse, not in amoebocytes. Pigment spots are located in the preoral lobe, on the inferior face of the larval tentacles and in the perianal ciliated ring. The stomach protrudes usually into paired diverticula, but this is not invariable. The piriform organ is present in front of the apical plate in larvae ready to metamorphose. At the latter stage, the actinotroch shows up to 26 larval tentacles, and definitive ones independent of the larval tentacles. Four masses of blood corpuscles occur, two dorso-lateral at the level of the oesophagus and two ventro-lateral to the stomach (Figs 9, 19).

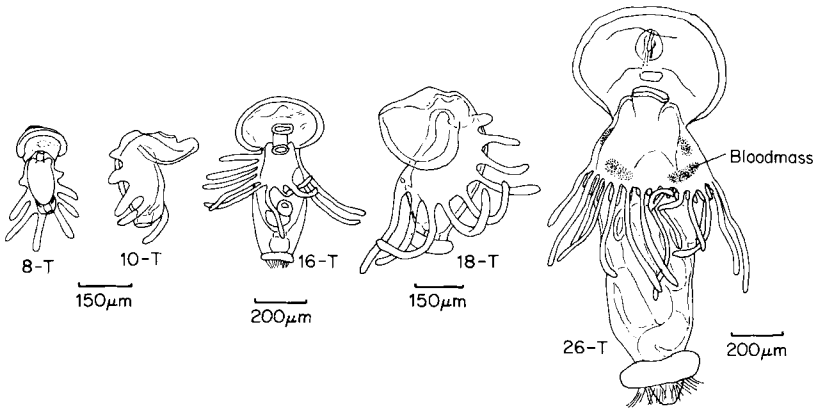

FIG. 19. Some developmental stages of *Actinotrocha wilsoni* (after Forneris, 1959). The 26-tentacle larva is fully developed with 20 adult tentacles, ventral view.

The characteristics of *Actinotrocha menoni X*, given by Selys-Longchamps (1907) based on a few specimens collected by Menon (1902), are similar to those of *A. wilsoni*: an oval body with a large preoral lobe; about 1·40 mm long; 44 tentacles; four blood masses: two lateral to the stomach just above the septum and two dorso-lateral in the fore-part of the stomach. The same suggestion is made for *Actinotrocha bella* whose description by Forneris (1959) is very similar to that of *A. wilsoni*, but the former larva as with *A. menoni X* could have delayed development as indicated by the high number of tentacles.

9. *Other described actinotroch species*

Several actinotroch species are insufficiently characterized; most of them have been established by Selys-Longchamps (1907): *Actinotrocha gegenbauri*, *A. sheareri*, *A. selysi*, *A. dubia*, *A. olgae*, *A. henseni*, *A. gardineri* and *A. goodrichi* after description of Goodrich (1903), *A. spauldingi* after Spaulding (1906), *A. haswelli A* and *B* according to Haswell (1893), *A. ikedai C* after Ikeda (1901), and *A. menoni A*, *B*, *C* after the description by Menon (1902). *Actinotrocha chata*, recently discovered by Forneris (1959), is probably the ten-tentacle stage of a known species.

C. *Larval settlement and metamorphosis*

When the actinotroch is mature and ready to undergo metamorphosis, the metasomal sac is completely developed; the larva becomes opaque and negatively phototactic (Cori, 1939; Silén, 1954a). On the latter point, however, Zimmer (1964) and Herrmann (1976) do not agree. The actinotroch sinks to the bottom; this behaviour seems to be induced by bacteria or chemical substances as metamorphosis proceeds (Forneris, 1959; Herrmann, 1976). Such behaviour is known from the literature in other zoological groups. During settlement, the preoral lobe becomes round and the piriform organ protrudes (sometimes sharply as in *Actinotrocha branchiata*)

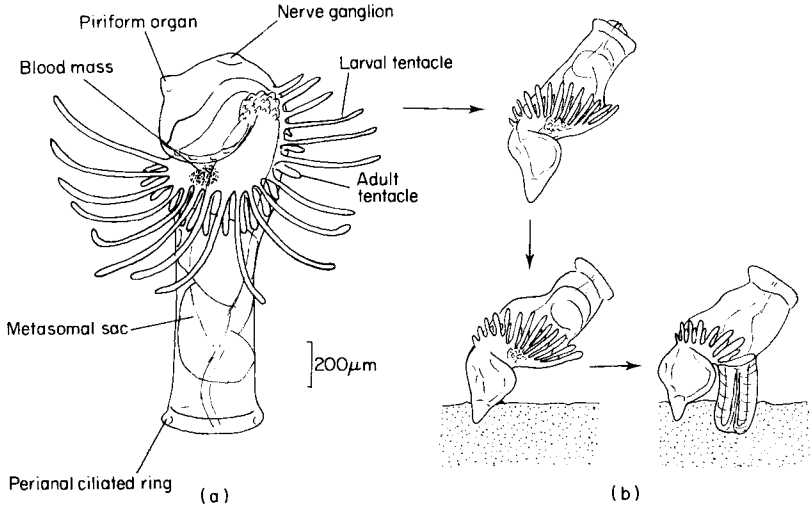

FIG. 20. *Actinotrocha branchiata*. (a) Larva ready to metamorphose, with adult tentacles and piriform organ; (b) settlement and beginning of the metamorphosis process (eversion of the metasomal sac into the soft sediment).

(Fig. 20) in species possessing such a structure; in other species the preoral lobe may be pointed, the anterior tip being the apical plate. The preoral lobe enters directly into contact with a suitable bottom and metamorphosis is invariably induced. The piriform organ or apical plate have at this time the function of selecting a favourable substratum and probably of starting the process of metamorphosis.

The cilia cease to beat and through violent muscular contraction the metasomal sac is suddenly fully evaginated, passing vertically downwards into the soft sediment where it rapidly secretes a tube (Figs 20b, 21); on hard substrata the animal begins to burrow into the bottom after the secretion of a thin hyaline tube (Silén, 1954a).

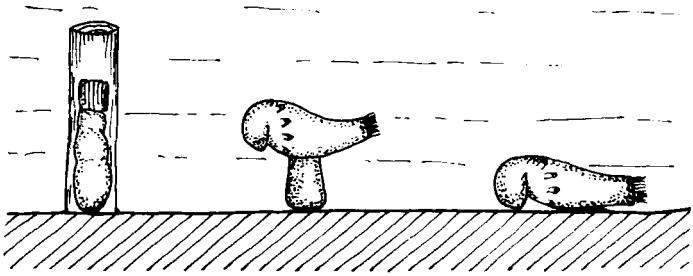

FIG. 21. Settlement and metamorphosis of *Actinotrocha hippocrepia* on hard calcareous substratum, in upright position (after Silén, 1954a). This author described also (not shown) the metasome evagination in horizontal plane, with the tube and adult consequently adnate.

In view of the fundamental importance of the relationship between the adult phoronid and the substratum and its associated fauna, the actinotroch can, but probably with only a small chance of success, search for a suitable bottom, and metamorphosis then seems not to be delayed for long. When the settlement of larvae occurs within adult phoronid aggregations, which seem attractive to actinotrochs, the nearest-neighbour distances are not limiting in the settlement which occurs randomly (Fig. 22) (Ronan, 1978; personal observations on *Phoronis hippocrepia*, *P. ijimai*, *P. australis*, *P. psammophila*). Close n-n distances need a stratification of the lophophores to provide a fully tentacular expansion, which is especially observed in clumps of burrowing or encrusting forms. Such a disposition in suspension feeders always requires some water currents to bring food. The turbidity of the sea water is not a factor affecting the abundance of the phoronids. Figure 22 is comparable with the curves published by Ryland (1976, Fig. 35) on Bryozoa. Similar figures would probably be established for hard-substratum species. The nearest-neighbour

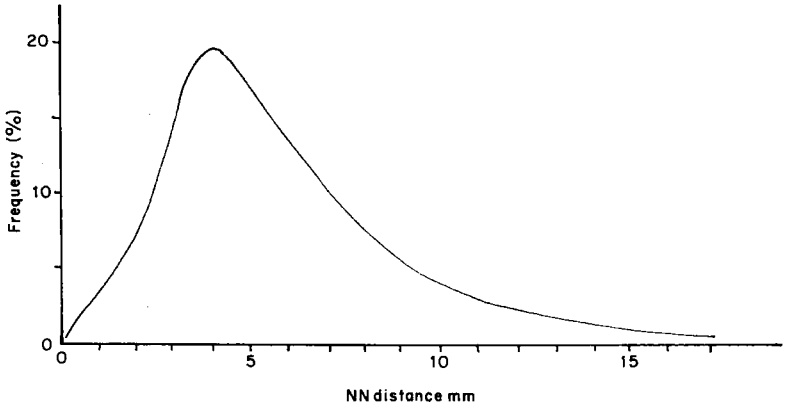

FIG. 22. Frequency distribution of the nearest-neighbour distances in nine intertidal aggregations of *Phoronis harmeri* (established after the data of Table I of Ronan, 1978).

distances in *Phoronis psammophila* were, however, never less than the space required to expand two adjacent lophophores completely (Emig, 1966), even in a high density of about 18000 individuals m^{-2}. According to Ollivier *et al.* (1977), *Phoronopsis harmeri* may avoid locations near large deposit feeders; similar observations were made by me with filter-feeders (Emig, 1966). On the other hand, the presence of phoronid aggregations prevents the settlement of larvae and adults of the associated fauna, particularly of tube-builders.

D. *Metamorphosis*

In all published works, metamorphosis has been studied imperfectly (see Roule, 1900; Ikeda, 1901; Selys-Longchamps, 1907; Cori, 1939; Veillet, 1941; Silén, 1954a; Herrmann, 1976). The actinotroch passes from a highly adapted pelagic form to a slender benthic organism organized as a tubicolous adult in a very short period of time, about 5–30 min. The adult organization arises from larval structures and only certain of the larval structures break down. In fact, metamorphosis is "catastrophic" in regard to the rapid formation of all adult structures which begin by the rotation through about 90° of the larval axis to assume a new adult axis (parallel with the polar axis of the egg) arising by the eversion of the metasomal sac (Figs 20, 23). This sac, which is thus the wall of the adult trunk, evaginates entirely, drawing down the digestive tract attached by the ventral mesentery in the adult position. The posterior end of the sac differentiates into the ampulla. During the

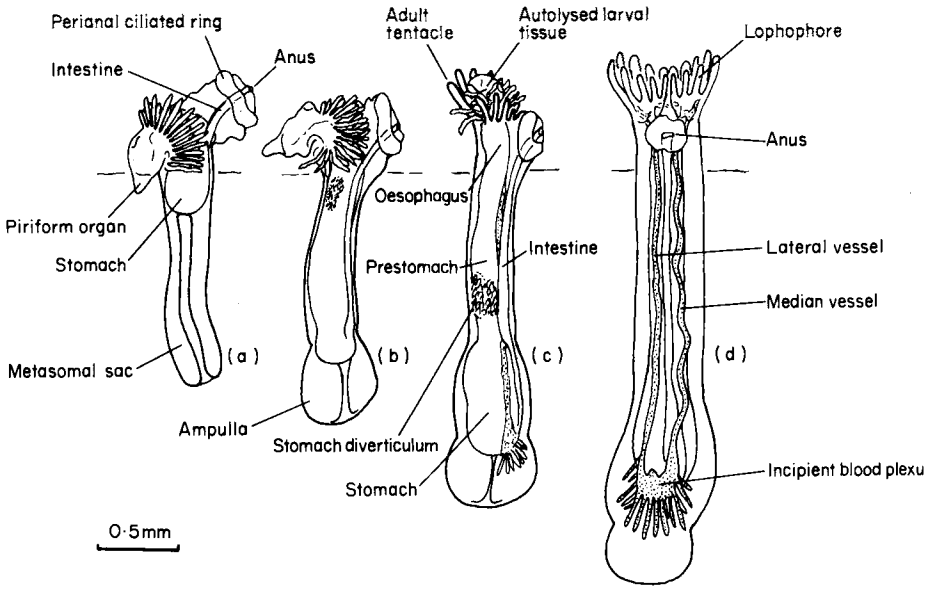

FIG. 23. Main metamorphosis stages in *Actinotrocha branchiata* (see also Fig. 20) from the evagination of the metasomal sac to a juvenile *Phoronis muelleri*. (a) About 1 min after settlement; (b) about 3 min; (c) about 8 min; (d) about 1 day after the beginning of the metamorphosis.

evagination mouth and anus are brought into close proximity. The preoral lobe and the larval tentacles shrink and are mostly cast off and ingested (they represent the first food intake of the adult). The definitive adult tentacles are elevated around the mouth in the functional position for food gathering. The circulatory system also becomes functional. Internal and some external changes are briefly considered below and particular attention is given to the transformation from the larval to the adult status of the main organs (Fig. 23).

The processes of metamorphosis retain the archimeric disposition of the larval body, but the borders of the three body regions of the adult and their coelomic cavities will have other relationships owing to the axis rotation, while the dorsal body side is largely reduced (Figs 24, 25, Table III). Such dispositions have been largely discussed by Emig (1973a, 1976a, b, 1977b). The differentiation of the epistome has been the subject of controversy; most previous investigators stated that the epistome does not arise from the larval lobe, which is refuted by Wilson (1881), Caldwell (1882), Schultz (1903), Meek (1917) and Zimmer (1964). The recent studies of Siewing (1974) and Zimmer (1978) confirm the opinion of Roule (1896) that the preoral

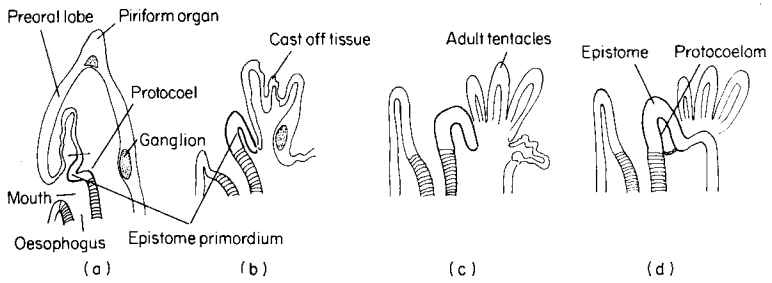

FIG. 24. Diagram of the differentiation of the epistome during the metamorphosis of *Actinotrocha branchiata* (after some photographs and description of Siewing, 1974 and of Zimmer, 1978). Successive stages from the preoral fold (incipient epistome) at the first stage of the metamorphosis to the epistome of an individual in which the casting off of the autolized larval tissue is complete.

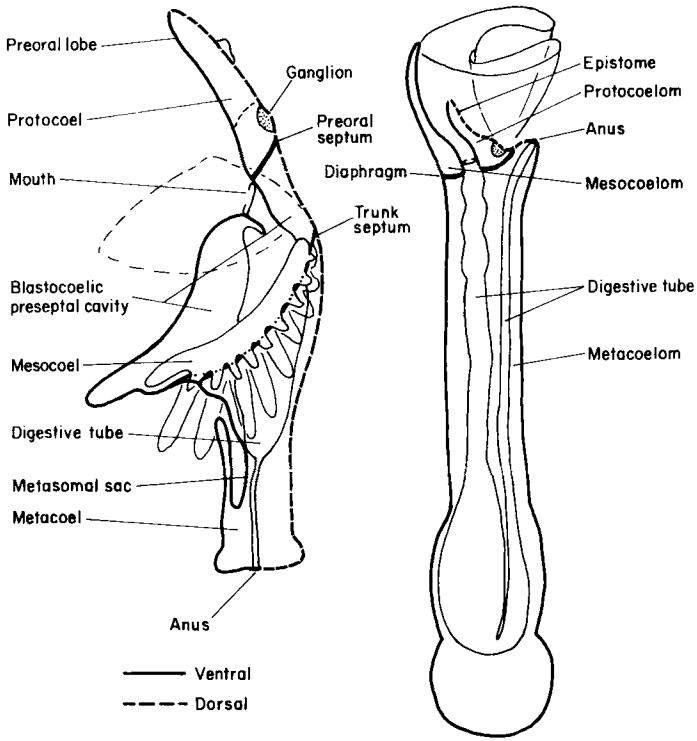

FIG. 25. Diagram of the archimeric structure of an actinotroch just before metamorphosis and of a phoronid, showing the disposition of the coelomic cavities and the ventral and dorsal sides.

lobe shrinks and is cast off, but a small bleb issuing from the internal part of the vestibule is retained as a remnant of the lobe (Figs 23, 24). This fold, partly containing the protocoel, bends dorsally to fuse with the lophophore and trunk epidermis and soon differentiates (Fig. 24) into the adult epistome. The delimitation of the epistome and of its coelomic cavity was established by Emig and Siewing (1975). The larval nervous ganglion, and the piriform organ if present, are not retained; the adult ganglion appears later in the dorsal wall of the epistome (Fig. 25) as a thickening of the adult nerve ring which probably originates from the larval collar ring nerve (Emig, 1976a).

The larval tentacles or their distal portions are swallowed and ingested. The adult tentacles or the basal buds are elevated around the mouth in the lophophore; the new tentacles arise then on the dorsal side between mouth and anus. The mesocoel is horseshoe-shaped with an enlargement in each tentacular bud. The trunk septum has now the status of a mesentery and becomes the adult diaphragm which separates the pro- and meso-coelom from the meta-coelom (Table III).

TABLE III. ARCHIMERIC DIVISION OF THE LARVAL BODY AND ITS HOMOLOGY IN THE ADULT STRUCTURE (TERMINOLOGY ACCORDING TO EMIG, 1975)

	Actinotroch	*Phoronid*
1. Prosome	Preoral lobe +Protocoel	Epistome +Protocoelom
	Preoral septum	
2. Mesosome	Collar +Mesocoel	Mesome (or lophophore) +Mesocoelom
	Blastocoelic collar space Preseptal cavity	Lophophororal blood vessel
	Trunk septum	Diaphragm
3. Metasome	Trunk +Metacoel	Metasome (or trunk) +Metacoelom

By strong muscular contractions (Fig. 20b) the larval trunk evaginates the metasomal sac which is then the wall of the adult trunk provided with all layers (epidermis, basiepithelial nervous plexus, basal lamina, circular and longitudinal muscle layers, peritoneum). The posterior part of the adult trunk becomes rapidly an enlargement or ampulla (Fig. 23). The metacoel is retained and now named metacoelom separated distally from the pro- and meso-coelom by the diaphragm, a complete mesentery derived from the

larval trunk septum. The trunk contains the largest coelomic cavity with the most internal adult organs.

During the evagination of the metasomal sac, the whole larval digestive tract, which is attached by the single ventral mesentery, moves downwards to take the adult position, and at the same time mouth and anus are brought into close proximity, whilst the larval walls of the collar (except definitive tentacles) and of the trunk shrink and disintegrate little by little around both openings (Fig. 23). The digestive tract is now divided into a descending branch with successively an oesophagus, and an elongate stomach which differentiates gradually into a prestomach and a stomach, and a slender ascending branch represented by the intestine. As observed by Herrmann (1976), the larval stomach diverticula degenerate in the prestomach epithelium (Fig. 24b, c). The ventral mesentery of the actinotroch becomes the oral mesentery and the anal one in the adult form, connecting the trunk wall with the U-shaped digestive tract. No description of the differentiation of the median and lateral mesenteries is given. Their ontogenesis may be compared with the regeneration process (Emig, 1972b, c, 1973a).

The protonephridia with solenocytes are transformed into metanephridia in the adult, classified as mixonephridia by Goodrich (1945). Such a transformation needs much further attention (Emig, 1973a). At metamorphosis, the solenocytic cells fall into the blastocoelic space and the two larval nephridal tubes narrow the anus on either side in a dorso-lateral position. Most previous investigators stated that the larval ducts are retained and the internal coelomic funnels are secondarily acquired probably from mesodermal cells. Nevertheless, Ikeda (1901), Cowles (1904b), Brooks and Cowles (1905) and Cori (1937) suggested that the larval ducts degenerate totally or partly. It is interesting to note that during regeneration the nephridia originate entirely from mesodermal cells. The differentiation of the nervous system is largely unknown. According to Silén, (1954b) no larval nervous structures remain in the adult. Selys-Longchamps (1907) stated that the giant nerve fibre is differentiated in the metasomal sac in the late actinotroch stage.

Finally, the circulatory system becomes functional. The lophophoral vessel is produced from the reduction of the blastocoelic collar space, as described first by Wilson (1881) and since generally confirmed. Both afferent and efferent vessels that together form the lophophoral vessel differentiate about 12 h later and send capillaries into the tentacles. The blood masses break rapidly apart in the blastocoelic space and the erythrocytes are distributed throughout

the whole system. The median vessel (or dorsal vessel of the actinotroch) develops rapidly into a large vessel which unites the incipient stomach blood plexus to the lophophoral vessel, whilst the second longitudinal vessel, the lateral, originates as a splanchnic slit along the left side of the descending branch of the digestive tract (Fig. 23). The latter vessel unites the lophophoral vessel to the stomach plexus. Now, the circulatory system is of the closed type and the train of peristaltic waves begins. The differentiation of this system obviously needs to be studied in the different actinotroch species, and the regeneration processes compressed (Emig, 1973d). Then, it is probable that more information will be obtained regarding the evolution of the circulatory system. Selys-Longchamps (1907) and Emig (1973d) considered the two lateral vessels to be primitive. The right branch of the lateral vessel and the second lateral vessel on the right side of the stomach blood plexus are considered to be remnants of the second lateral vessel. In *Phoronis ovalis* the two lateral vessels are represented in the metasome (Emig, 1969).

It seems that the divergent descriptions of previous authors on some processes of the metamorphosis can be explained by the probable occurrence of abnormal phenomenona during experimental metamorphosis or development under the microscope.

V. Ecology

All phoronids are tubicolous and free living within their tubes. They may be found singly or in masses of many individuals, embedded vertically in soft bottoms or buried in, or encrusting on, hard substrata, including the special position of *Phoronis australis* within tubes of cerianthids. The best investigations on ecology and sampling are obtained by means of Scuba diving, especially on hard biotopes, and by the use of suction samplers (Emig, 1971a, 1977d; Emig and Lienhart, 1966, 1971).

A. *Tube*

The tube of Phoronida is secreted by epidermal gland-cells, recently studied by Pourreau (1979) in *Phoronis psammophila*. Two cell types actively secrete the tube (Fig. 26). The acidophilic A cells secrete mucopolysaccharides which constitute the two thinner but compact peripheral layers whose thickness varies little compared to that of the central basophilic layer. This is secreted by the basophilic

B cells which produce sulphomucopolysaccharides; its thickness varies considerably along the tube and consists of numerous very thin parallel coats. A third less frequent type of cell, the B^1 cell, also

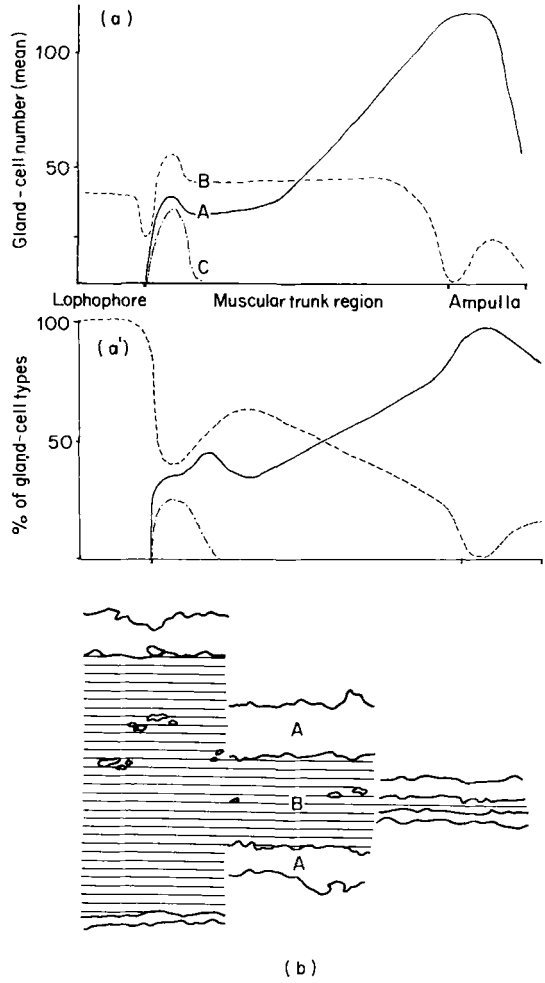

FIG. 26. (a) Distribution of the epidermal gland cells along the body wall of *Phoronis psammophila*. A: acidophilic cells—mucopolysaccharides; B: basophilic cells—acid mucopolysaccharides; C: C cells—acidophilic nature (from Pourreau, 1979). Recent observations on *Phoronis hippocrepia* reveal the presence of A and B cell types in the major length of the lophophore. (a') Relative abundance of the epidermal gland cell types (in %) along the body wall of *P. psammophila* (from C. Pourreau, unpublished results); (b) some aspect of the tube laying in relation to the thickness of the tube. A: acidophilic coating layer; B: basophilic coating layer (from Pourreau, 1979). The main thickness of the tube is about 10 μm.

basophilic in nature and secreting protein, probably participates in tube formation. On the external surface of the tube, substratum elements adhere, particularly in soft sediments (various grains, debris, detritus), which cover the whole tube in a single layer. The above description of those epidermal gland cells does not agree with the descriptions given by several previous workers (Selys-Longchamps, 1907; Marcus, 1949; Lönöy, 1954; Forneris, 1959), but confirms the incomplete short work of Hyman (1958) who identified only a positive reaction on the outer layers. A fourth type (C cells), named "corps en massue" by Selys-Longchamps (1907), occurs in the anterior part of the trunk, especially just below the lophophore (Fig. 26). According to Pourreau (1979), their function is probably lubrication to permit rapid motion in and out of the tube. The distribution of all epidermal cell types is represented on a diagram (Fig. 26). In the anterior trunk where all A, B and C cells are abundant, active secretion allows repair of the upper part of the tube (about 2–3 cm), which is easily damaged during bad weather by water movement. The posterior half of the ampulla has mostly a mechanical function either in substratum burrowing or in anchorage of the animal within its tube, which explains the reduced density of gland-cells. Tube secretion cannot be restricted to any particular area of the body, all parts of which are involved in the tube building process.

Observations on tube secretion in the aquarium revealed that a fragile and transparent membraneous coat generally surrounds first the base of the ampulla, then it becomes visible anterior to the ampulla and particularly in the lophophoral region. The ampulla remains uncovered for a longer period of time but is finally also covered by the coat. The phoronid moves freely within its newly formed tube. The substratum particles adhere to the viscous tube.

The length of the tube varies according to the extended size of the body (about five times longer than the contracted size) of the phoronid species and to the type of substratum. The smallest occurs on hard substrata, particularly in shells, and the largest on sandy bottoms. Such differences can also be observed within the species according to the burrowing potential of the substratum. The greatest recorded length and diameter of the tube in the different species may be summarized as follows: *P. ovalis*: 3 cm, 0·4 mm; *P. hippocrepia*: 8 cm, 2 mm; *P. ijimai*: 10 cm, 2 mm; *P. australis*: 18 cm, 5 mm; *P. muelleri*: 12 cm, 1·5 mm; *P. psammophila*: 19 cm, 2 mm; *P. pallida*: 14 cm, 1·5 mm; *Phoronopsis albomaculata*: 15 cm, 2 mm; *Phoronopsis harmeri*: 22 cm, 4 mm; *Phoronopsis californica*: 45 cm, 5 mm.

In soft sediments the phoronids burrow downwards posterior end first; active burying is accomplished by hydrostatic pressure changes of the coelomic fluid and aided by contractions of the metasomal muscles (Fig. 27). After about only 8–

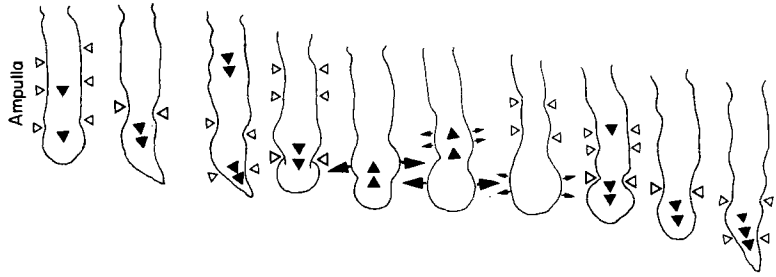

FIG. 27. Hydraulic pressure changes in the ampulla of *Phoronis psammophila* during the burrowing process (from C. Pourreau, unpublished observations). → Swelling movement; ▲ motion of hydraulic fluid; Δ muscle contraction.

24 h the lophophore remains out of the substrate. On the other hand, the animal moves toward the sediment surface by a similar action in the anterior part of the body (lophophore). During both movements the tube is concomitantly being secreted, and during this sticky phase various particles of the immediate environment adhere to the tube, which therefore reflects the nature of the substratum. The coating of particles can vary from fine mud to coarse sand grains, with sometimes numerous fragments, e.g. of shells, algae, sponge spicules, test of Foraminifera, or urchins, coral, etc., and fine pebbles. There was a great amount of controversy among previous authors concerning the selection of substratum particles for the tube. Some authors argued that the phoronid selects the particles, i.e. Andrews (1890) who named *P. architecta* (synonym of *P. psammophila*) on a possible grain selection. Other authors such as Selys-Longchamps (1907), Hyman (1959), Emig (1971), say, on the contrary, that the particles adhere randomly to the sticky tube without specific sorting of grains by the animal. This latter statement has been confirmed by Pourreau (unpublished data) on *P. psammophila*. No significant differences occur between the two grain size curves of the tube and sediment composition, which confirms the observations of Emig (1971a, 1973b). In all species embedded in soft sediment the posterior end of the tube always shows a small opening (Fig. 28a).

We have no information on boring species, but it is likely that a similar method is used, namely by ampulla movements probably assisted by chemical action on the substratum. Each individual lives

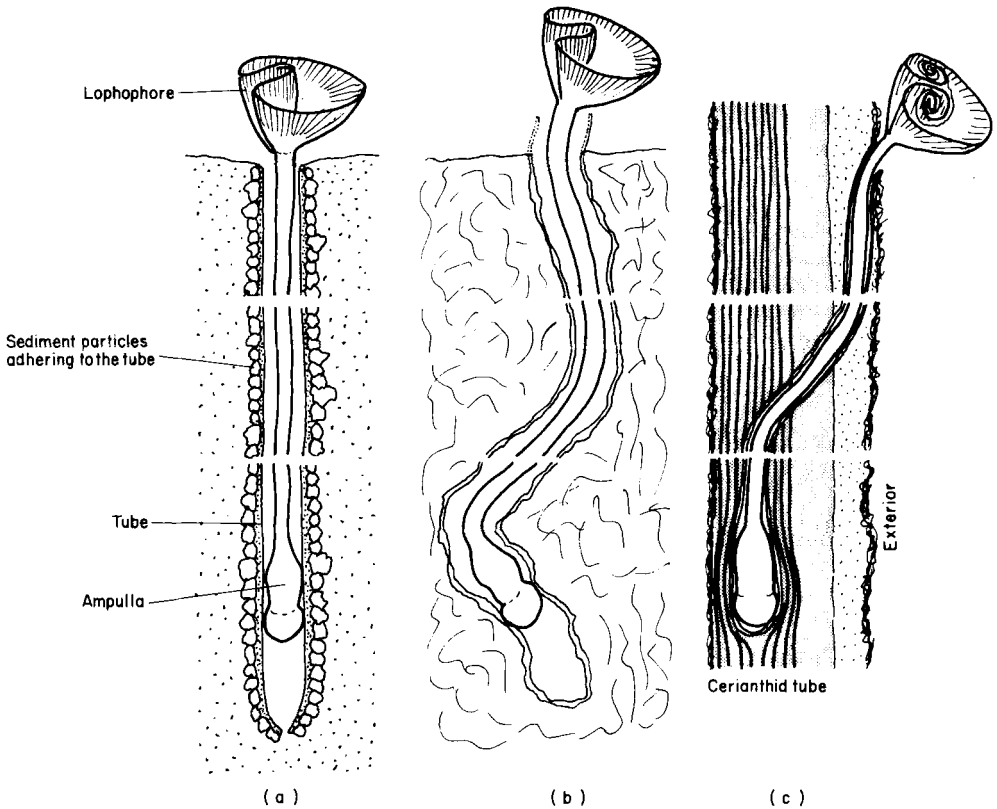

FIG. 28. Diagrams of the position of Phoronida in the substrata. (a) Embedded vertically in soft sediment; (b) burrowing in hard substrate; (c) *Phoronis australis* living in the tube wall of cerianthids (after Emig *et al.*, 1972).

in its own burrow which is lined by a yellowish membrane that sometimes projects and is then covered with debris (Fig. 28b). The perforated hard substrata are of different kinds in *Phoronis ovalis*, *P. hippocrepia* and *P. ijimai*. They generally live in empty mollusc shells, sometimes in living ones, but also in barnacles, *Caryophyllia*, *Lithothamnion*, coral rubble and rocks (lime- sand- and calcarous stones), and logs (see Emig, 1973b). The burrows in shells are generally parallel with the shell layers between the periostracum and the pearl layer; distally the tube becomes perpendicular to the shell surface and the lophophore protrudes. The posterior end of the tube is thus in a cul-de-sac. *P. hippocrepia* and *P. ijimai* can also be encrusting, forming turf-like masses composed of many intertwined individuals. Such clumps adhere to pilings, logs, ledges, soft

sediments, rocks, often in crevices, in rather quiet water. The tubes are covered by particles (mud, sand grains, faeces, debris, algae) and within the entangled tubes sometimes occur molluscs, ascidians, polychaetes, ophiuroids, actinians or other animals. Burrowing of encrusting forms may depend upon the nature of the environment (hydrodynamics, desiccation, presence of other boring animals).

Brazilian specimens of *Phoronis ovalis* sometimes show "cuticular processes" around the posterior end of the tube about 0·50 mm long (Marcus, 1949; Lönöy, 1954; Forneris, 1959; Voigt, 1975). Such extensions are not explained, but are not related to the presence of *Cliona* (cf. Voigt, 1975), as supposed by Marcus (1949).

Phoronis australis, in its own tube, occurs in the tube-wall of cerianthids, which must be considered as a "hard" substratum, and thus displays a unique association. In Madagascar the tube-wall of *Cerianthus maua* may be divided into five distinct layers (Fig. 28c): the ampulla of *P. australis* is always located in the fourth, the hardest one; the phoronid tube passes across the other three layers and the lophophore projects externally (Emig *et al.*, 1972).

B. *Biotopes*

The main results of my review on the ecology of Phoronida (Emig, 1973b) are summarized here with the addition of more recent work (cited below) and of recent unpublished observations (particularly on the west coast of Panama, vicinity of Marseille and in the Indian Ocean). All generally confirm the previous studies. The vertical zones whose nomenclature is used in the present review are given according to Pérès (1967).

Phoronis ovalis. The density is great owing to the small body size of this species; it reaches 150 individuals/cm^2. The bathymetric distribution is at present from low tide mark to about 50 m. *Phoronis ovalis* lives usually in coraligenous and detritic communities between 20 and 50 m (Fig. 29b). Recently specimens have been recorded in shallow waters by Stancyck *et al.* (1976), Scelzo (1976) and Emig and Bailey-Brock, (1980), and in greater depths by Emig (1977c).

Phoronis hippocrepia. Like the former species, *P. hippocrepia* has a patchy distribution which can reach about 57 000 individuals/m^2, from the intertidal zone to 55 m. Individuals observed between 0 and 10 m live preferably in turbid or shady conditions, in harbours (Emig and Bailey-Brock, 1980), and under overhangs and in cave entrances (Fig. 29b). In similar conditions, Ocharan (1978) recorded *P.*

hippocrepia (in burying form) in two locations (Bañagues and El Puntal) on the northern Atlantic Spanish coast. The mean density is about 91 000 individuals/m^2, but it reached 5·7 individuals/cm^2 over 13 cm^2. This species occurs in shallow depths under rather strong water motion. A list of the associated fauna and flora is given by this author.

Phoronis ijimai. This species is usually known in the encrusting form living in similar conditions to the former species. The density in encrusting clumps can be greater than where it occurs as a boring form. The bathymetric distribution ranges from low tide mark to about 10 m. Emig (1977c), on the basis of recent observations in San Juan Island (U.S.A.), confirmed the synonymy of *Phoronis vancouverensis* with *P. ijimai*. Recently, this species has been located by Haderlie and Donat (1978) on piles on the east side of the wharf in Monterey Harbor (California) where *P. ijimai* covers a large area of the pile surface between 0·50 and 7 m deep; a list of the associated fauna is given by these authors.

Phoronis australis. The burrowing habit of this species is characteristic. In general it occurs in groups of 20–50 individuals and sometimes up to 100 per tube in the tube-wall of cerianthids (Coelenterata, Anthozoa). The recorded depth range is from the low tide mark to more than 36 m (Emig, 1977c; Emig *et al.*, 1977). The known identification of the cerianthid species are *Pachycerianthus fimbriatus* by McMurrich (1910), *Cerianthus maua* by Emig *et al.* (1972), *C. membranaceus* by Emig (1977c), *C. filiformis* by Ishikawa (1977); all other investigators indicated *Cerianthus* sp.

Phoronis muelleri. This species is characteristic of muddy bottoms, with a sandy, sometimes a coarse, fraction, over a large recorded depth range, from 1 to 390 m (Fig. 29). Anadon and Anadon (1973) discovered a specimen in a depth of 0·60 m, whilst Holthe (1973, 1977) described *P. muelleri* as abundant all over the Borgenfjorden, from 10 to 25 m, and in Trondheimsfjorden usually from 10 to 50 m (mostly 20–25 m) with some locations at 100 m and one at 208 m. Thomassin and Emig (1980) sampled *P. muelleri* during the "Benthedi-Expedition" from 5 to 390 m, most individuals being collected between 16 and 30 m. These records confirm the common range of *P. muelleri* as 10–50 m, usually 15–30 m (Fig. 29b). The density can reach 3000 individuals/m^2; this number is recorded by Barnes and Coughlan (1972) in "mud on clay" (probably related to a *Macoma-*

community) where *P. muelleri* is regarded as the indicator of this type of bottom. According to Buchanan *et al.* (1978), *Phoronis muelleri* lives in a silty area along the Northumberland coast from about 20 to 85 m, where an *Amphiura filiformis–A. chiajei* community occurs mainly on mud (*A. chiajei* subcommunity) and muddy sand (*A. filiformis* subcommunity) (Buchanan, 1963). *Phoronis muelleri* is ubiquitous and a top ranked species over the entire area. The seasonal recruitment reaches a maximum between September and November, and the greatest mortality follows between November and January.

Phoronis psammophila. It occurs generally in shallower waters, from low tide mark to 8 m, with extension to 20 m and, as recently reported, to 25 m (Emig *et al.*, 1977). The greatest density of this species is 18 000 individuals/m^2, reached in fine well-sorted sand at 4–6 m depth, although occurrences are also mentioned from mud to shelly coarse sand with a fine sand fraction, as well as in *Zostera* or *Cymodocea* sea-meadows, and polychaete reefs. In the Mediterranean benthic populations, *P. psammophila* live mostly in the biocoenoses of fine well-sorted sand and of superficial muddy sands in sheltered areas which show several facies as sea-meadows (Pérès, 1967). In the other areas it occurs in *Venus–Abra alba* and in *Macoma baltica* communities, in the *Tellina* boreal lusitanic community intertidally in fine sand at densities of 60–150 individuals/m^2 (Vieitez, 1977), and in several types of sandy bottom (Thomassin and Emig, 1980; Emig and Bailey-Brock, 1980). The distribution of this species often overlaps some other phoronid species, particularly *P. muelleri*, *P. pallida* and *Phoronopsis albomaculata* (Fig. 29a). The presence of *P. muelleri* in the type locality of *Phoronis architecta* (= *P. psammophila*, synonymy established by Emig, 1972d) is a confirmation of the mixing of these two species under a single name "*P. architecta*" by Brooks and Cowles (1905). This confusion led Emig (1977c) to attribute to "*P. architecta*" some characteristics of *P. muelleri*, especially in reproductive strategy. In areas of high density (mean about 15 000 individuals/m^2), the spatial patterns are a uniform general distribution, but as the individual number per square metre decreases a patchy distribution appears perhaps caused by asexual reproduction, actinotroch settlement, presence of suspension feeders, etc. The expanded lophophores can cover more than the half of the sediment surface. The nearest-neighbour distances always remain greater than the space required to provide for full expansion of adjacent lophophores; thus, an overlying of lophophores has never been observed.

Phoronis pallida. This species occurs in fine sand to clayed sand, in shallower waters (1–14 m). The greatest density is 74 000 individuals/m^2. Emig *et al.* (1977) recorded *P. pallida* mainly in fine sand from 2 to 25 m with the highest abundance near 15 m in Port Philip Bay, and from 3 to 8 m in the other Australian waters (Fig. 29). Thomassin and Emig (1980) described *P. pallida* living exclusively in fine sand from 0 to 13 m with the maximal density (about 20 individuals/m^2) between 6 and 13 m.

Phoronopsis albomaculata. The general occurrence is in soft sediments from sandy mud to clogged coarse sand with a fine fraction, from subtidal areas to about 55 m (Fig. 29). The only cited density gives 37–70 individuals/m^2 (Thomassin and Emig, 1980).

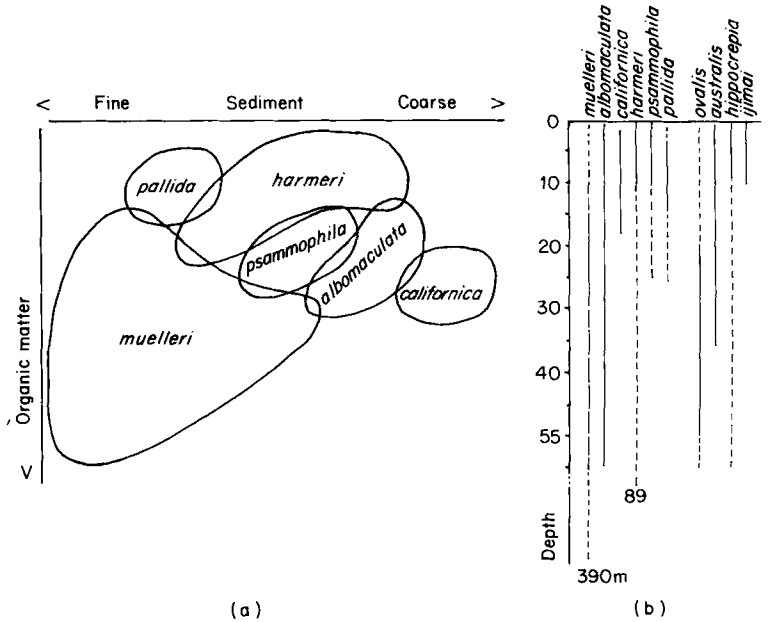

FIG. 29. (a) Diagram of a possible relationship between the different species living in soft substrate and the sediment particles and the organic matter based on our present knowledge of the distribution of Phoronida (modified, after Thomassin and Emig, 1980); (b) distribution of the phoronid species in relation to the depth (after Emig, 1979, completed).

Around Madagascar (Thomassin and Emig, 1980), *Phoronopsis albomaculata* is generally recorded in coarse sand communities under bottom currents, characterized by *Asymetron* (or sometimes *Branchiostoma*); but in the Brisbane River and in Port Philip Bay

(Australia) (Emig *et al.*, 1977) this species has been collected in silty and muddy sand from 2 to 25 m, abundant in locations from here to 15 m. Like *Phoronis pallida*, the present species is often mixed with *Phoronis muelleri* and *P. psammophila* which is considered to be an overlapped distribution. However in Port Philip Bay there is great resemblance between the distribution of *P. psammophila* and that of *Phoronopsis albomaculata*. More investigations are necessary on the preferrred biotopes of the latter species (Fig. 29a).

Phoronopsis harmeri lives in soft sediments, sand to mud, sometimes with a coarse fraction, and has recently been found in *Zostera* beds (Emig *et al.*, 1977), from the intertidal zone to 89 m deep, with a common range from 0 to 12 m (Fig. 29). Depths are cited by Emig (1977c) from different geographical areas. *Phoronis harmeri* is locally abundant, up to 28 000 individuals/m^2 particularly in fine sandy bottoms. The highest density in a *P. harmeri* population, about 68 000–93 000 individuals/m^2, was established by Ollivier *et al.* (1977, Fig. 79) in spring 1972, but the population suffered high mortality by heavy predation (60 000 adults/m^2 by June). In some Californian areas, *Phoronopsis harmeri* shows a uniform distribution over the littoral region of the flats, slightly less dense on the upper and lower edges of the intertidal zone where the sediment is coarser. The average annual population of *P. harmeri* probably remains rather constant. But, according to Ronan (1978), the population of *P. harmeri* shows density variations of 0–22 000 individuals/m^2 along the intertidal zone. The phoronids are aggregated in discrete clusters which are largest in area and individual density in sand with particles less than 250 μm, and rare or absent in greater sediment particles. The mean distance between two individuals in fine sediment is 5·4 mm with a range of 1–25 mm (Fig. 22) and the most common distances are between 3 and 7 mm (frequency about 74%): the mean distance is roughly half the diameter of the expanded lophophore (Ronan, 1978).

Phoronopsis californica. It occurs from mud to coarse sands, from 0 to 17 m in depth (Fig. 29).

C. *Ecological effects*

In general, temperature and salinity are not limiting factors since the range normally encountered in the distribution of Phoronida is such that they can be regarded as eurythermal and euryhaline

animals. Nevertheless, some species are only recorded from tropical and subtropical regions. Phoronids are able to live in water with small amounts of oxygen. During summer 1971, Simon and Dauer (1977) studied a massive outbreak of red tide and its results on a sandy intertidal habitat in Tampa Bay (Florida); they pointed out that *Phoronis psammophila* appeared to be completely unaffected by the red tide; before the occurrence the mean density was $3/m^2$, 1 month afterwards $1/m^2$ and 2 years later $23/m^2$.

The effects of the tropical storm "Agnes" led to a delayed decrease in abundance of *Phoronis psammophila*, living in shallow sand bottoms of Chesapeake Bay. This was probably a response to the effect of lowered salinity (below 10‰) for over a week (Boesch *et al.*, 1976). Since the hurricane passed during the reproductive period of the phoronids this may have been a recruitment failure. The population had recovered a year after the spawning period (spring to autumn), see Fig. 30a which is to be compared with the curve published by Virnstein (1979), Fig. 30b, and with my own observations on gonad maturations (Fig. 3).

All phoronids are suspension feeders which demand water movement. If the currents are strong their distribution is limited, especially in or below the intertidal zone (Emig, 1971a). The spatial

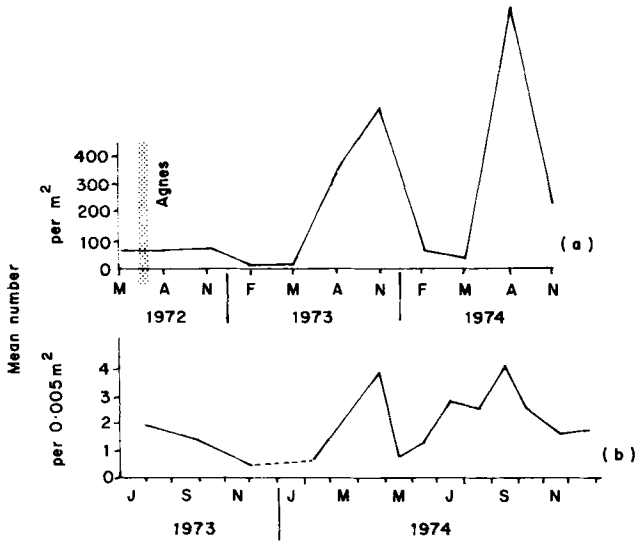

FIG. 30. (a) Change in the mean density of *Phoronis psammophila* showing significant changes at the 3 m deep sand bottom stations in the lower York River, prior to and after the passage of the tropical storm Agnes (21 June 1972) (after Boesch *et al.*, 1976); (b) monthly abundance patterns of *Phoronis psammophila* in natural uncaged sediments (after Virnstein, 1979).

distribution can be modified by different factors: predation, associated fauna (filter-feeders; burrowing and digging animals) and asexual reproduction which occurs in all phoronids.

The occurrence of the species of Phoronida in their preferred substrata and benthic communities has been described above. The depth range, the vertical distribution and their possible relationships between the different species are summarized in Fig. 29.

The presence of numerous tubicolous phoronids in soft sediments reduces erosion of the substratum and thus stabilizes the sediment and its infauna. The burrowing species have a destructive action on shells; in living animals, as in *Caryophyllia smithi* (cf. Hiscock and Howlett, 1975), the phoronids may cause death by structural damage.

D. *Predators of Phoronida*

The predators of Phoronida are not well known, yet phoronids do form a significant proportion of the diet in more animals than is generally supposed. They may provide an abundant food supply in areas of high density. Emig (1973b) estimated that the biomass of *Phoronis psammophila* was about 45 g/m^2 wet-weight (15 g dry weight) for 15 000 individuals, the anterior part of the body being about 3 g and 1 g (wet and dry weights respectively) for this number of animals.

The defence against many predators is a very rapid retraction into the inner part of the tube where the animal is anchored by means of its ampulla.However, the response to a slight disturbance (Emig, 1966) is only a folding of the lophophore near the tube opening. The anterior part of the body with the lophophore (which protrudes over the surface, sometimes up to 3 cm, particularly in burrowing or encrusting species) is the most vulnerable to attack by predators. Phoronids can, however, rapidly regenerate the lost part in 2 or 3 days (Emig, 1972c; unpublished observations on *Phoronis ijimai* and *Phoronopsis harmeri*). The tube should offer some protection from predators (Virnstein, 1979).

Phoronids occur in the guts of fishes which are able to remove an animal from its tube. Other observations seem to indicate predation on small animals by nematodes. Of predators on phoronids, the gastropods are the best known. Attacks by the nudibranch *Hermissenda crassicornis* removed only a few of the tentacles but sometimes the entire lophophore (Ronan, 1978). Ollivier *et al.* (1977) indicated high mortality rates in *Phoronopsis harmeri* populations

which decrease by about 60% after June, probably due to predation by *Hermissenda crassicornis* which is then very abundant: the adult phoronid abundance patterns may be strongly influenced by predators. According to Virnstein (1979), the abundance of *Phoronis psammophila* is apparently not significantly regulated by predators such as crabs or fishes. The opposite observations of those authors suggest that the predation on phoronids obviously needs further study, particularly that by fish and gastropods, probably the most important consumers. My opinion is supported by my own incomplete observations on predation of *P. psammophila* in a high density area.

E. *Geographical distribution*

The geographical distribution of the Phoronida is well known in several substantial areas of all oceans and seas (Fig. 31), and our knowledge has increased recently as benthic studies have developed. Since the exhaustive review of Emig (1973b, completed in 1977c), new localities have been cited by Barnes and Coughlan (1972), Voigt (1975), Holthe (1973, 1977), Scelzo (1976), Vieitez (1977), Emig *et al.* (1977), Vieitez and Emig (1979), and Emig and Bailey-Brock (1980), Thomassin and Emig (1980); and recently new locations have been recorded from China (Tsingtoa: *P. ijimai*, *P. australis*); the latter species occurs also on the west coast of Australia (off Geraldton) and in Florida (St Lucie); from Panama (especially Naos, Culebra, Perlos Islands: *Phoronis muelleri*, *P. psammophila*, *P. hippocrepia*, *Phoronopsis albomaculata* and *P. harmeri)*; from Mexico (Vera-Cruz: *P. hippocrepia*) and this species occurs also near Marseille (Gulf of Fos; Calanque of Morgiou); from the U.S.A. (Humboldt Bay, Morro bay, Santa Barbara: *Phoronopsis harmeri*; Port Aransas: *P. muelleri*). *Phoronis psammophila* also occurs in the Bahamas, Bermuda and in France (Cortiou near Marseille; Gulf of Morbihan).

In general, phoronids have a world-wide distribution as indicated in Fig. 31, and most of the species can be considered as cosmopolitan, particularly *P. muelleri*, *P. hippocrepia* and *P. psammophila*. Some species, such as *P. australis*, *Phoronopsis albomaculata* and *P. californica*, seem to be restricted to the tropics.

VI. Fossil Phoronida

Several authors suggested that tubes or tubicolous burrows in fossil records belong to Phoronida (Fenton and Fenton, 1934;

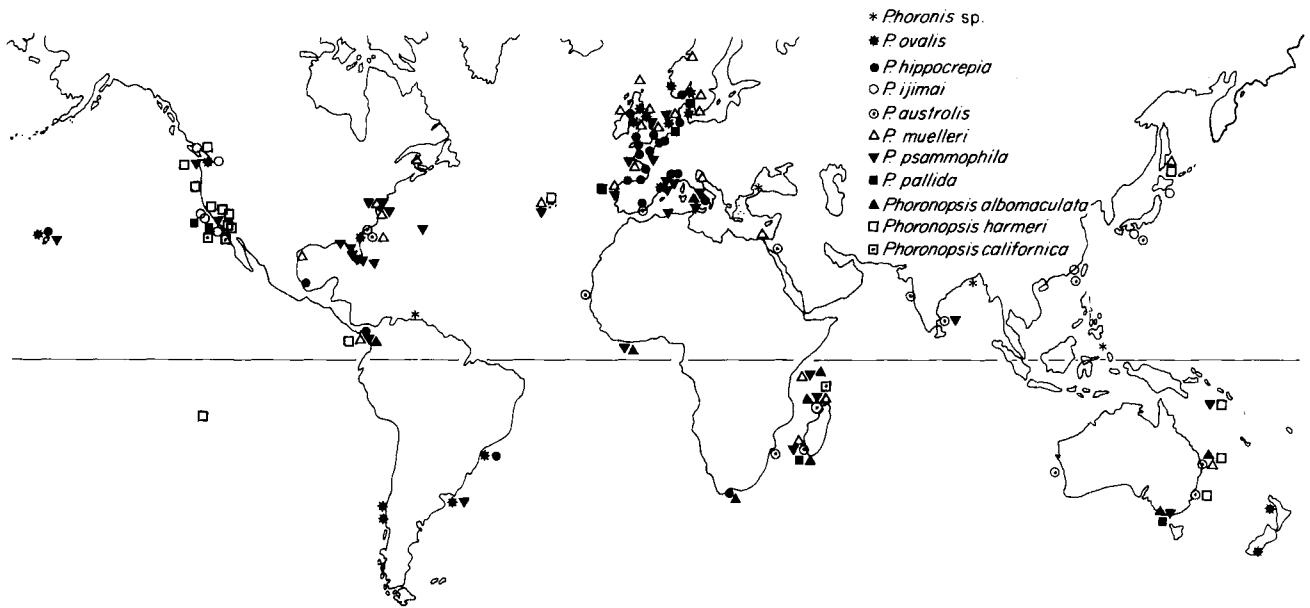

FIG. 31. Geographical distribution of Phoronida (after Emig, 1979, completed).

Avnimelech, 1955; Josey, 1959; Voigt, 1972; Mackinon and Biernat, 1970). Recently, Voigt (1975) has proved the identity of species of the genus *Phoronis* with the ichnogenus *Talpina* v. Hagenow, 1840, confirmed in 1978. The *Talpina* burrowed in such diverse calcareous substrata as calcareous algae, echinids, mollusc shells and rostra of Belemnites (Fig. 32). The fossil phoronid burrows seem to have been present since Devonian times. Voigt gives criteria used for the discrimination of the phoronid burrows from other similar ones such as those of Thallophytes, sponges, Bryozoa or "worms". The frequent presence of agglutinating Foraminifera surrounding the opening of

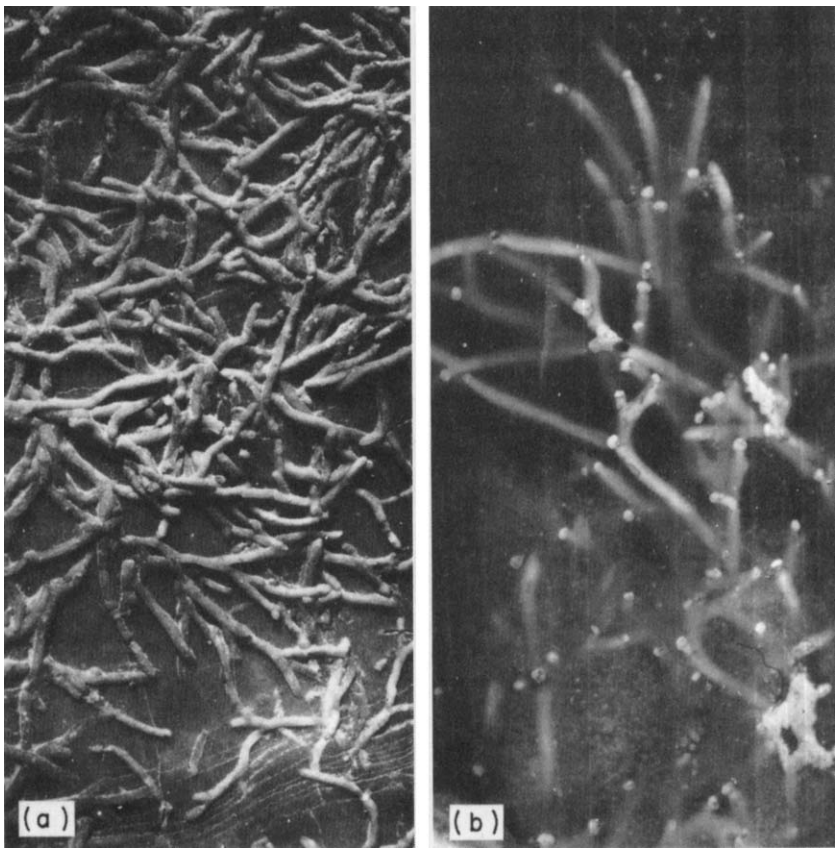

FIG. 32. (a) *Talpina gruberi* Mayer, in diagenetically destroyed aragonitic layer of shells from Muschelkalk (Trias) (× 5·5) (photo. Prof. Dr E. Voigt, reproduced with his permission); (b) *Talpina ramosa* v. Hagenow, in *Belemnella lanceolata* (Maastrichtian Lüneburg) (× 5·2) (from E. Voigt, 1972, Table 3, Fig. 1).

the tube of a worm-like fossil animal provisionally determined as *Phoronopsis* and suggesting commensalism between both fossil organisms (Voigt, 1970) in Upper Maastrichtian, has never been confirmed in recent observations on Phoronida. Tubes of the ichnogenus *Talpina ramosa* which occur frequently within the guards of *Belemnella* and *Belemnitella* (cf. Voigt, 1972) are described within the cavities probably originating from diagenetically destroyed aragonitic corals of the Maastrichtian chalk-tuff (Voigt, 1978).

VII. Feeding

Phoronida are suspension feeders capturing particulate matter, detritus or small organisms from the water by means of the lophophore, but it is not yet known if they show feeding preferences. However, food is also available in the form of dissolved organic matter. It is obvious that our knowledge is fragmentary and that the feeding biology of Phoronida needs research in a variety of ways.

A. *Lophophore and epistome*

The definition of a lophophore given by Hyman (1959) and recently completed by Emig (1976c) is as follows: "A lophophore is defined as a tentaculated extension of the mesosome (and its cavity the mesocoelom) that embraces the mouth, but not the anus, and its main functions are feeding, respiratory and protective".* The latter author pointed out that the term lophophore is limited to the phylum Lophophorata (Brachiopoda, Bryozoa, Phoronida: Emig, 1977a), and cannot be replaced by any other terms.

The general form of the lophophore of Phoronida is well known (Emig, 1971a, 1976c, 1979). Briefly, it is bilaterally symmetrical, supported by a collagenous "skeleton" which is an enlargement of the basal lamina. The lophophore shape assumes a greater complexity with increase of the tentacle number in relation to the general size of the species (Table IV; Figs 1, 5, 7), which suggests a dimensional relation between food-gathering, respiratory capacities and metabolic requirements.

The arrangement of the cilia of the tentacles is shown in Fig. 33. Mucous gland cells (B cells: see Section V, A) occur in the latero-frontal surfaces of the tentacles. There is no evidence that mucus

* In the present section only the feeding function will be described whilst the respiratory one will be considered in the following section on the circulatory system.

TABLE IV. MAIN CHARACTERISTICS OF THE LOPHOPHORE OF PHORONIDA

Species	*Lophophore shape*	*Maximal number of tentacles*
Phoronis ovalis	oval	28
P. hippocrepia	Horseshoe	190
P. muelleri	Horseshoe	100
P. psammophila	Horseshoe	130
P. pallida	Horseshoe	140
Phoronopsis albomaculata	—Or sometimes	160
Phoronis ijimai	slightly coiled	230
Phoronopsis harmeri	Up to 2 coils	400
Phoronis australis	3·5 coils	1600
Phoronopsis californica	Helicoidal up to 5 coils	1500

plays any role in food capture (Bullivant, 1968b; Strathmann, 1973; Emig, 1976c), but it is associated in the particle rejection mechanism when the particles are bound into strands by mucus.

According to the observations of Emig and Béchérini (1970), Emig (1976c) and Gilmour (1978), it could be suggested that the feeding position of the lophophore is somewhat different in species with a horseshoe-shaped lophophore than in those with a coiled one, as shown in Fig. 33, and the water currents seem to be deflected in different ways. Nevertheless, the adult phoronids always orient their lophophores into the prevailing water current, and when currents change direction, the phoronids can rapidly re-orientate to maintain the food-catching surface of the lophophore in the water flow.

The mouth, located at the bottom of the lophophoral cavity, is covered on the dorsal side by a lip extended along the inner tentacle row, with its own coelomic cavity the protocoelom. This lip is called the epistome (or protosome, first of the three body regions; Figs 1, 25). The anal side of the epistome is sparsely ciliated whereas the oral side shows a dense ciliation (Fig. 33b). The epistome is involved in feeding (Selys-Longchamps, 1907; Pross, 1978). Gilmour (1978) supporting Masterman (1896, 1900) speculates that the function of the epistome is "involved in the rejection of inedible material and acceptance of food particles during suspension feeding", which is similar to the function of the labial palps in bivalves and the gill slits of chordates (Gilmour, 1979).

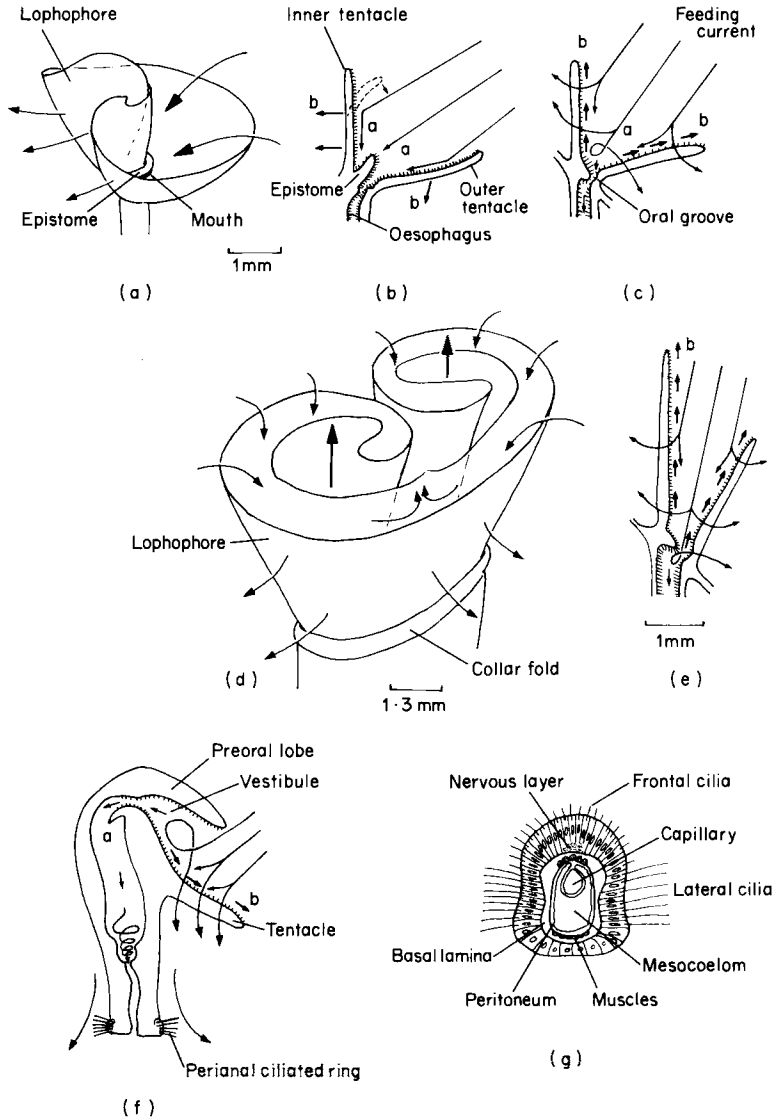

FIG. 33. Diagrams of the suspension feeding in Phoronida. (a) Feeding position of *Phoronis psammophila* showing the water currents according to the studies of Emig and Béchérini (1970; Fig. 7) and Emig (1976c, Fig. 4b); (b) section of the lophophore of *Phoronis psammophila* with feeding currents past tentacles: (a) capture of food particles on frontal surface, (b) rejection of inedible particles through the lophophore; the diagram represents also the tentacle flicking; (c) water flow in the lophophore of *Phoronis ijimai* (from Gilmour, 1978) (a), (b), see above); (d) feeding position of *Phoronopsis harmeri* with water currents (after Gilmour, 1978, modified); (e) longitudinal section of the lophophore of *Phoronopsis harmeri*, with the particle motion (from Gilmour, 1978) (a), (b), see above); (f) longitudinal section of an actinotroch with currents (interpreted from Figs 1 and 3 of Gilmour, 1978) and motion of the ingested food particles (from own unpublished observations); (g) cross-section of a tentacle of an adult phoronid.

B. *Mechanisms of feeding*

After several studies on food-gathering methods, it has been found that the manner in which phoronids capture particles from suspension is difficult to determine; the various modes of food selection which have been suggested for Phoronida are summarized below.

The first observations were made by Masterman (1900) who suggested that the cilia of the inner surface of the tentacles cause currents of food and water to pass downwards towards the mouth, the outer surface of the tentacles having a non-ciliated epithelium.

Bullivant (1968a, b) pointed out that the mechanism of feeding of Phoronida and other Lophophorata can be termed as "impingement feeding" in analogy with the impingement particle separation used in industrial processes: the sharp deflection of the water currents through the lophophore causes particles to be thrown towards the mouth. Strathmann (1973) believed that impingement would not be effective for particle capture considering the slow speed of the feeding currents and the high density of the food particles in the sea water. The author suggested that food-gathering occurs by an induced feeding current of the lateral cilia of the tentacles, transporting the particles along the frontal surface of the tentacles to the mouth, and by means of local reversals of the lateral cilia as a result of contact of the cilia with passing particles (Fig. 33b). But according to Ryland (1976) the co-ordination of such local reversal must be fairly complex in Bryozoa, and the same problem seems to exist in Phoronida. The inward flicking of the distal part of the tentacles may serve sometimes to transfer particles into the central feeding current and can also be considered as a feeding mode (Fig. 33b). The particles, sometimes nearly 100%, are trapped within the lophophoral concavity; however, some particles are allowed to pass between the tentacles and expelled in the out-flowing current (Strathmann, 1973; Emig, 1976c).

Gilmour (1978) who has examined *Phoronis ijimai* (as have Strathmann (1973) and Pross (1974)), and *Phoronopsis harmeri*, observed a different particle selection and rejection method: the edible material is carried towards the mouth onto the epistome by an incoming water current created by the lateral cilia of the tentacles which beat with a dexioplectic metachronal rhythm. The particles may be transported down to the bases of the tentacles where they are collected by the cilia of the oral surface of the epistome and by the oral groove, to converge in two lateral streams in the midline of the epistome to pass into the mouth. The epistome, particularly visible in

species with a coiled lophophore, shows a midline oral groove (own unpublished observations) directed towards the mouth.

Heavy inedible particles are expelled by the beat of the frontal cilia to the tips of the tentacles (Fig. 33c, e) in the out-going current. Gilmour (1978) assumed that Phoronida are able simultaneously to accept food particles by a filtration mechanism and reject inert ones by an impingement mechanism; such a theory contradicts the previous models. Particle selection is probably purely mechanical based on both weight and size (Emig, 1976c) and depends on impingement or inertial impaction (Gilmour, 1978).

According to the speculations of Pross (1974), recapitulated in 1978, the epistome has the function of raising the lophophore which leads to closure of the oesophagus. The epistome concentrates the particles which are carried by the feeding current as a food-filtrate which passes into the digestive tube by contraction of trunk muscles. Such theoretical statements obviously need experimental corroboration, and Gilmour (1978) noted that the epistome is simultaneously involved "in acceptance of food and rejection of solid waste material and allows the escape of excess water travelling towards the mouth with food particles". The opinions of the two former authors were put forward earlier by Selys-Longchamps (1907, p. 90) and Cori (1939).

Gilmour (1978) also made observations on the food selection of the actinotroch larvae: the tentacles (larval ones?) of old larvae are provided with ciliated epidermal cells which are similar to those of adult phoronids as well as to those described in *Rhabdopleura* by Dilly (1972). The lateral cilia beat with a dexioplectic metachronal rhythm and so assist the cilia of the perianal ring in driving water (Fig. 33f): the flow in the ventral region is deflected in the vestibule, observed at first by Lebour (1922), where it swirls and the particles are collected and swept to the oesophagus by the cilia of the inner surface of the preoral lobe, while the flow in dorsal and lateral regions is weaker. The frontal cilia beat an antiplectic metachronal rhythm to discharge the heavy particles into the out-going currents. Thus, based on Gilmour's observations, it can be suggested that the (larval) tentacles and those of the adult lophophore have similar functions in food selection and rejection of inedible material, although the disposition in larva and adult is opposite (Fig. 33).

C. *The alimentary canal*

The digestive tract of Phoronida is U-shaped and its four component parts are represented in the Figs 1 and 25.

1. *Oesophagus*

The oesophagal epithelium originates from the ectoderm in the actinotroch, whilst during asexual reproduction the regeneration of the oesophagus occurs by "metaplasia" of the prestomach cells to assume ectodermal status (Emig, 1973c). The oesophagus, lying immediately internal to the mouth, is lined by a highly ciliated columnar epithelium with numerous gland cells of acid mucopolysaccharide secretion. This epithelium is very similar to and continous with that surrounding the mouth, i.e. the basal epithelium of the outer tentacle row and of the oral side of the epistome (see also Fig. 26). In *Phoronis ijimai*, the histochemical results published by Vandermeulen and Reid (1969) disclose an activity of phosphatases and esterases in the oesophagus, which are associated with the digestive processes. These authors showed also the occurrence of lipid droplets surrounded by digestive enzyme films. I agree with the statements of Vandermeulen (1970) that the oesophagus aids in food ingestion and conduction of the foodmass. This is due to a dense ciliation, mucus secretion, and also to numerous longitudinal muscle fibres and some circular ones, together with enzyme synthesis indicated by phosphatase and esterase activity.

2. *Prestomach*

The oesophagus passes rapidly into the prestomach, sometimes called the proventriculus. This is the longest part of the descending branch of the digestive tract, characterized by a broader tube and a simple small and weakly ciliated epithelium, except along the median blood vessel where there is a deep ciliated groove. The prestomach has a weak musculature with circular fibres and some longitudinal ones.

Emig (1968) described under the electron microscope two cell types in *Phoronis psammophila*. The first one is laterally ciliated, its apical cell membrane often showing microvillous projections. Small granules (up to 0·3 μm in diameter) bounded by a single membrane are confined in the apical cell region and small rounded vesicles (up to 0·1 μm) frequently associated with the apical membrane have a pinocytotic function. The mitochondria occur always in the supranuclear position. Lipid bodies sometimes appear in the basal region of the cells.

The apical membrane of the cells of type 2, which are club-shaped, shows no cilia or microvilli. These cells are characterized by rough endoplasmic reticulum (or ergastoplasm) throughout the whole

cytoplasm, and by granules, up to 0·8 μm in diameter (probably zymogen granules), surrounded by a single membrane, frequently associated with the ergastoplasm. The hypothesis that the two types are distinct or that they are the same is discussed by Emig (1968). In the prestomach of *Phoronis ijimai*, Vandermeulen (1970) described one cell type which shows the characteristics of both previous types, in which the small PAS-positive granules (up to 0·5 μm in diameter), located in the apical region of the cells, show an intense activity of phosphatases and esterase (Vandermeulen and Reid, 1969). According to the two latter authors, the histochemical staining discloses also the distribution of lipid already discribed in the oesophagus.

Often, another cell type occurs in the basal region of the prestomachal cells, as well as in the intestine (Emig, 1968; Vandermeulen, 1970; unpublished observations on all phoronid species), generally near the attachment of the mesenteries where these cells can be numerous. The cells contain numerous very electron-dense granules (up to 1 μm in diameter), chromaffin-like ones, which are bounded by a single limiting membrane and separated from this membrane by a clear space.

According to Cori (1890), Becker (1938), Hyman (1959), Emig (1968) and Vandermeulen (1970), the prestomach has a primordial role in digestion by secretion of enzymes supported by secretion of zymogen granules and phosphatase and esterase activity; the enzymes are mixed with the foodmass by the beating of the cilia of the prestomach groove. This seems to be its main function, as well as the conduction of this mass towards the stomach, aided by the wall muscles of the prestomach. Its second role is in absorption and storage of lipid and digestive products suggested by the lipid bodies within the cells and by esterase activity, and by the presence of pinocytotic vesicles.

3. *Stomach*

The prestomach passes imperceptibly into the stomach in which the ciliated groove extends over a long part. This latter structure exists in all phoronid species and is not, as stated by Vandermeulen (1970), due to a misinterpretation. The stomach is much larger relative to the other regions of the digestive tube. It appears to lack muscular investment and externally is surrounded by a blood-plexus with a wall structure of type 1 described in the following section. The stomach continues to the ampulla where it ends in a sphincter, the

pylorus, and passes into the intestine. The food mass is moved in the stomach by ciliary action.

The stomach epithelium in *Phoronis psammophila*, described by Emig (1967), consists of very tall columnar cells, with an apical microvillous border and paired cilia. From the apical part to the basal one, different regions can be distinguished in each cell: the apical zone contains numerous excretory vesicles (up to 0·5 μm in diameter), zymogen-like granules (up to 1·5 μm in diameter) and pinocytic vesicles; then, a mitochondrial zone with the Golgi apparatus and lysosomes; a zone with lipid bodies (up to 1 μm in diamater), interrupted by the nucleus; sometimes mitochondria occur basally. In about the middle part of the stomach occur one or more horizontal girdles of gland-cells (of mucus secretion).

In *Phoronis ijimai*, Vandermeulen (1970) pointed out that prestomach and stomach epithelia "do not differ significantly from each other ultrastructurally and histochemically", which does not agree with the above observations on *Phoronis psammophila*. Vandermeulen and Reid (1969) suggested that there is extracellular digestion in the stomach as well as in the prestomach owing to phosphatase activity and to a lesser extent esterase activity.

The presence of a single bulging, vacuolated syncytium or of a paired syncytial mass, which appeared capable of phagocytosis and intracellular digestion, has been cited by different authors (Becker, 1938; Cori, 1939; Marcus, 1949; Silén, 1952; Lönöy, 1954; Emig, 1967); many recent observations lead to the conclusion that such structures occur only in animals in a poor state of preservation and were never seen in phoronids fixed immediately after sampling.

The main functions of the stomach in *Phoronis psammophila* are in absorption and storage of products of digestion which pass into the blood at this level, and secondarily in enzyme production. The absorptive function is provided by the microvilli which increase the absorptive surface by 30–60 times (Emig, 1967). In *Phoronis ijimai*, Vandermeulen (1970) considered the above second function as the primary one.

Both intracellular and extracellular digestion occur in Phoronida. It seems that extracellular digestion takes place particularly in the prestomach and intracellular digestion in the stomach. However, in *Phoronis ijimai*, Vandermeulen (1970) indicated that ingested food particles travel in less than a minute down to the stomach where they remain for up to half an hour; thus, extracellular digestion occurs in prestomach and stomach, and absorption in the intestine. Is the rate of food passage different between the phoronid species, as well as the

length of time necessary for particle passage through the alimentary system?

4. *Intestine*

The intestine, which is separated from the stomach by the pylorus, represents the whole ascending limb of the digestive tube; its proximal part, located in the ampulla, has a greater diameter and its epithelium is taller, surrounded by longitudinal muscle fibres, while the major part of the intestine is a slender tube with a similar longitudinal muscle arrangement. The intestine is ciliated throughout its length.

In *Phoronis psammophila*, Emig (1968) described one type of intestinal cell; a second type occurs basally, similar to that mentioned in the paragraph on the prestomach. The intestinal cells are ciliated, with a microvillous apical border. Single membrane-bound secretory granules (0·2–0·3 μm in diameter), numerous vesicles (up to 0·2 μm in diameter) particularly abundant in the apical region and in the microvilli, and mitochondria are present in the supranuclear region of the cells. Lysosomes occur in all intestinal cells. The nucleus is located basally. Lipid bodies are more frequent in the proximal hindgut part.

In *Phoronis ijimai*, Vandermeulen (1970) defined two intestinal cell types in the proximal part of the intestine: gland cells with sulphated mucopolysaccharide secretion. Gland cells are also described in the intestine of *Phoronis australis* by Ohuye (1943); however, they were never observed in *P. psammophila*. No phosphatase activity nor presence of lipid has been demonstrated, only traces of esterase activity in the intestine (Vandermeulen and Reid, 1969).

The intestine has a primarily absorptive function (Vandermeulen, 1970), which, except in the proximal part, seems less important in elaboration of faecal pellets, which are rejected by a combination of ciliary and muscular action through the anus, situated on an anal papilla. The anus is encircled by a tall, probably glandular, epidermis.

The function of the basal cell type in the prestomach and in the intestine may, according to Vandermeulen (1970), be a neurosecretory control of digestive processes.

D. *Food particles ingested by Phoronida*

Possible food types, nature and abundance, available to Phoronida are largely unknown. Various authors suggest algae,

diatoms, flagellates, peridinians, small invertebrate larvae, detritus, etc. Future studies are needed on the food sources of phoronid species.

E. *Uptake of dissolved organic matter*

The direct uptake of dissolved organic compounds, through the epidermis, by marine invertebrates, including suspension feeders, is now generally considered a normal process of nutrition (cf. Emig and Thouveny, 1976). However, the importance of this food source is not yet known for Phoronida, except in *Phoronis psammophila*, which is able to remove actively amino-acids from natural concentrations in the sea water. The experiments on ^{14}C-valine uptake by *Phoronis psammophila*, reported by Emig and Thouveny (1976), show polyphasic kinetics of uptake at external concentrations higher than 1·5 μM (Fig. 34). This process through the trunk wall and leads to an

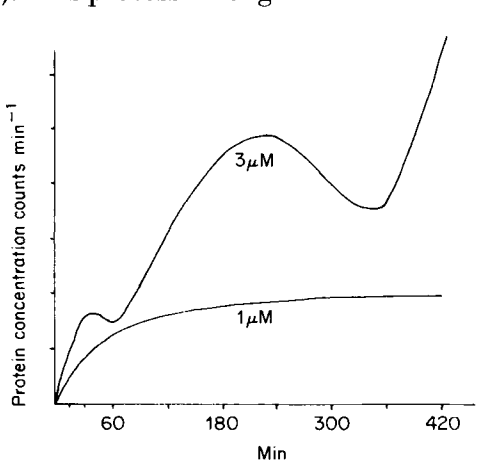

FIG. 34. Kinetics of ^{14}C-valine uptake at two external concentrations in *Phoronis psammophila* in winter (after results of Emig and Thouveny, 1976).

internal accumulation of amino-acids. The internal concentration is twice in winter and 7–20 times in summer that of the external medium. The seasonal variations suggest the intervention of an active transport which occurs only during the summer time, which is confirmed by temperature experiments and the action of ATP inhibitors on amino-acid absorption.

The tube of phoronid species is not a significant barrier to uptake of dissolved organic matter from the surrounding medium. The cilia of the epidermal cells produce an exchange of water within the tube.

In species embedded in soft sediments the rear end of the tube has a small opening (Fig. 28a).

VIII. Circulatory System

Knowledge from earlier sources has been summarized by Selys-Longchamps (1907), Cori (1939) and Hyman (1959). Interesting recent work and observations will be discussed in the following account.

A. *General structure*

The circulatory system of Phoronida is of the closed type, with red blood corpuscles (erythrocytes). In all species except *Phoronis ovalis*, there are two longitudinal trunk vessels (Fig. 35), a median

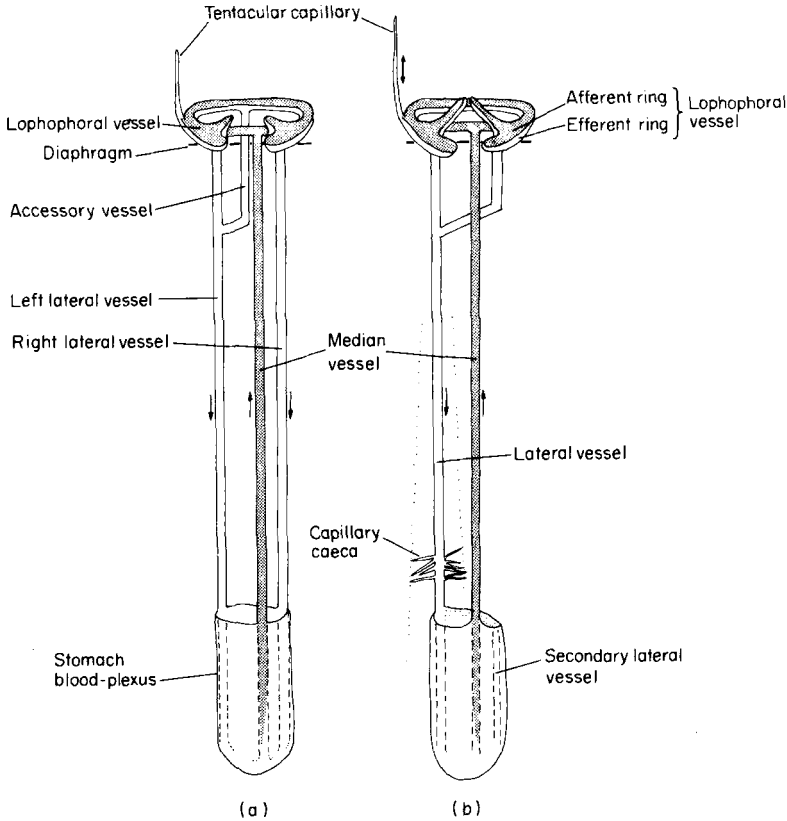

FIG. 35. Circulatory system in (a) *Phoronis ovalis*, and (b) other phoronid species (from Emig, 1979).

vessel, arising from the extensive stomach blood plexus, and a lateral vessel, originating from the lophophoral vessel by two branches (a left and a right one) which unite at the oesophageal level. Both longitudinal vessels communicate through the blood plexus and the lophophoral vessel. The lateral vessel gives rise along most of its length to numerous blind-ending diverticula called capillary caeca. At the level of the blood plexus, where the caeca are somewhat larger, they are particularly well developed along the lateral vessel, the secondary lateral vessel, which occurs only in the plexus (Fig. 35), and on the posterior end of the plexus (Figs 1, 3, 35). In *Phoronis ovalis* (Fig. 35), three longitudinal vessels occur, a median vessel and two lateral ones. The left lateral vessel has an oral branch called the "accessory" vessel, along the oral mesentery. The lophophoral vessel, following the shape of the lophophore, is composed of closely applied afferent and efferent branches; at the junction of both branches a tentacular capillary arises and ascends in each tentacle (Figs 1, 35). More details on the general structure of the circulatory system and of its regeneration are given by Selys-Longchamps (1907) and by Emig (1971a, 1972b, c).

B. *Circulation and function*

The median afferent vessel contains venous blood and is the main blood vessel (Figs 35, 37). The flow is produced by peristaltic waves along the vessel.

Regular rhythmic contractions, about 4–16/min, are performed by the strong muscular layer of the blood vessel wall (Wright, 1856; Selys-Longchamps, 1907; Bethe, 1927). Bethe (1927) pointed out that the waves originate at a point where the median vessel arises from the blood plexus. The blood passes from the median vessel through the T-shaped vessel into the afferent branch of the lophophoral vessel, and then fills each highly contractile tentacular capillary.

Up and down movement of the erythrocytes within the tentacular capillary occurs in "strings" which undergo very rapid acceleration caused by the blood flow; each "string" is always preceded by a single blood corpuscle, 20–30 μm in front of the "string". The erythrocytes are often distorted by the small diameter of the capillaries (Fig. 36). The blood remains stationary for some seconds before the capillary empties by a strong muscular contraction, from the tip basally, into the efferent branch through a valve located in the proximal part of the capillary at the level of the

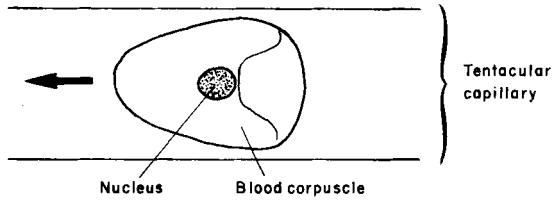

FIG. 36. Distortion of an erythrocyte by friction along the capillary wall during blood flow (from Emig, 1966).

junction between the afferent and efferent branches of the lophophoral vessel. The frequency of contractions in the tentacles is 7–13/min (Bethe, 1927; Emig, 1966). In general, no coordination can be seen between the flow in neighbouring capillaries which contract autonomously.

The respiratory gas exchange takes place while the erythrocytes are in the tentacles (Fig. 37). There is no doubt as to the respiratory

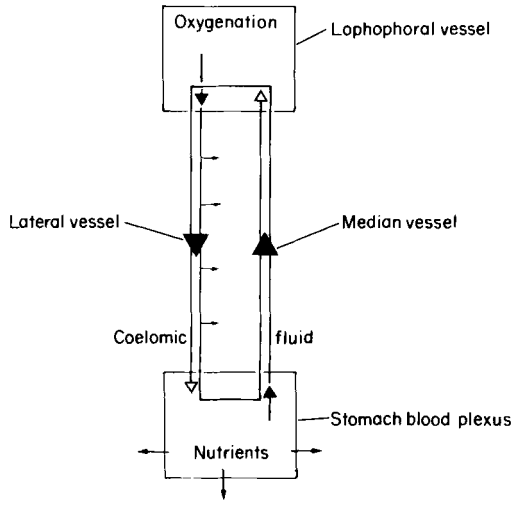

FIG. 37. Diagram of the main function of the circulatory system. The gaps have to be completed in the future.

function of the lophophore in Phoronida (Emig, 1976c). This important function, like that of nutrition, is implied in the rapid regeneration of this organ and its circulatory apparatus after autotomy or removal by predators. Such process have been observed in several phoronid species (Emig, 1972b, c, and unpublished studies on *Phoronis ijimai*, *P. hippocrepia* and *Phoronopsis harmeri*).

From the lophophoral vessel, the blood descends into the lateral vessel. In both vessels, the muscular contractions are weaker and less regular than in the median vessel.

The lateral vessel is efferent and filled by arterial blood. Along most of its course this vessel gives off numerous generally simple capillary caeca, extended particularly in the oral coelomic compartments, and sometimes in the anal ones, of the metacoelom. The caeca show, like the tentacular capillaries, autonomous contractions and they empty by a sudden contraction with a frequency of 3–10/min, each contraction is followed by a longer period of relaxation during which the caeca fill again. Bethe (1927) suggested that the function of the caeca is similar to that of the capillaries of the vertebrates. My opinion is that the gas distribution to the different organs is provided by means of the coelomic fluid after gas-exchange between this fluid and the blood of the caeca, the vessels and the plexus (Fig. 37). The circulation of the coelomic fluid is induced by the muscular contraction of the body wall. This opinion was expressed by Selys-Longchamps in 1907.

The circulatory system also distributes the digestive products, the uptake occurring between the digestive tube and its blood plexus. The nutrients would be distributed like gases, with the coelomic fluid assisting (Fig. 37). Nutrients reach the germ cells for use during gametogenesis by means of the blood caeca to which these cells lie adjacent but probably the coelomic fluid serves also as a means of distribution of dissolved nutrients to the gonads. Selys-Longchamps indicated a third function, namely storage of lipids.

A reverse blood flow or to and fro movements may occur during disturbance, and always during the first regeneration stages before the junction of the two longitudinal trunk vessels.

C. *Wall structure of the circulatory apparatus*

The results of recent studies on the wall structure of the vessels and capillaries by Kawaguti and Nakamichi (1973) on *Phoronis australis*, by Emig (1977e) on *P. psammophila* and by Storch and Herrmann (1978) on *P. muelleri* are summarized below.

1. *Type 1*

The walls of the capillaries and the blood plexus consist, from the interior to the exterior, of endothelial cells, a thin basal lamina and peritoneal cells (Fig. 38). However, the blood is frequently in direct

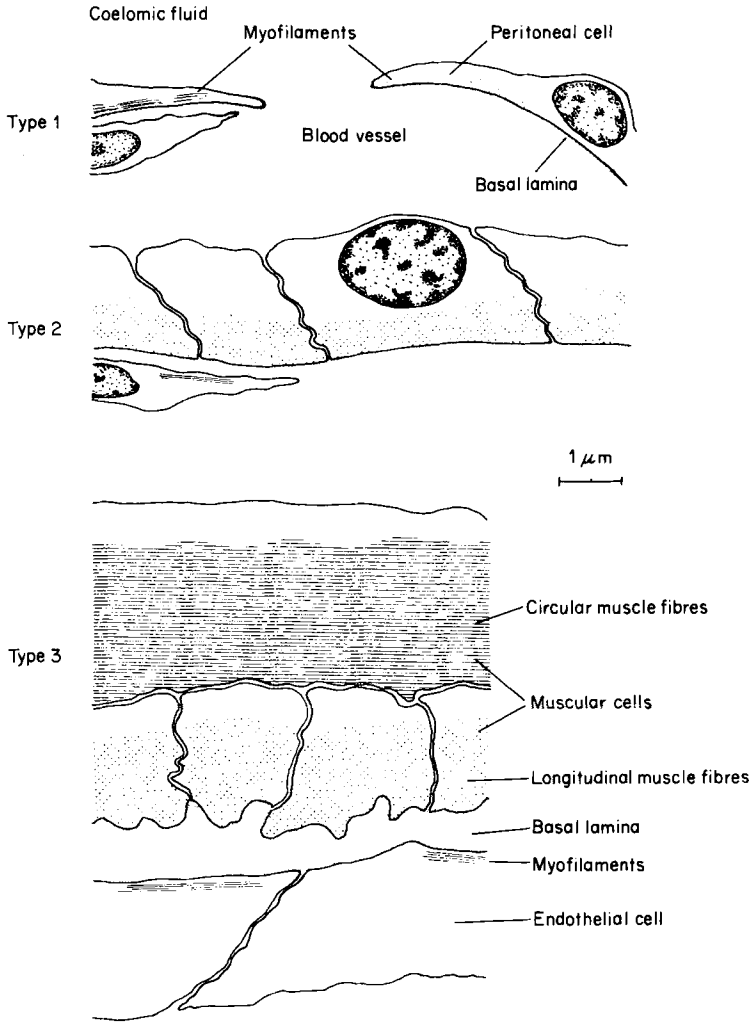

FIG. 38. Diagram of the wall types of the circulatory apparatus in *Phoronis psammophila*.

contact with the basal lamina, the endothelium being sparsely distributed. In some areas, the peritoneal cells, or both endothelium and peritoneum, are lacking and then the basal lamina directly faces the lumen of the capillary. Such regions are especially favourable for exchanges between blood and coelomic fluid. The thickness of the walls of Type 1 is about 1–4 μm, that the basal lamina is of about 0·1 μm (0·2–0·5 μm in the plexus at the bases of the stomach cells).

In peritoneal cells there are often bundles of myofilaments, located near the basal lamina. The myofilaments run mostly longitudinally in extended capillaries; they are of 10–35 nm in diameter. According to Kawaguti and Nakamichi (1973), the bundles of myofilaments occur in various positions in concentrated capillaries. These authors discriminate also between two kinds of cells, muscle cells and peritoneal ones, but they frequently observed peritoneal cells containing muscle fibres.

2. *Type 2*

Type 2 (Fig. 38), the most common in the circulatory system, occurs particularly in the broader parts of the longitudinal trunk vessels. The wall is thicker than in the former type owing to a higher external layer of muscle cells, but no peritoneum lining is observed. The muscle fibres are almost longitudinal; in *Phoronis psammophila* circular muscle fibres are rarely observed covering the former cell layer. The thickness of the basal lamina is of about 0·1–0·3 μm. The endothelium is sometimes wanting. Small bundles of myofilaments appear in some endothelial cells; they are very thin and almost scattered, and circular.

3. *Type 3*

The walls of the longitudinal trunk vessels show important muscular layers in some regions which are responsible for the blood circulation. Such a structure occurs in the distal part of the median vessel.

The wall has a thick outer muscular layer (Fig. 38). The longitudinal muscle fibres are intimately connected with the basal lamina. In *Phoronis australis*, Kawaguti and Nakamichi (1973) describe only a longitudinal muscle layer with cross-striated fibres, while in *P. psammophila* two smooth muscle layers occur, an outer circular one and a longitudinal one, which together reach 6 μm in thickness (Emig, 1977e). The basal lamina shows a folded belt of 0·3–1 μm in thickness. The endothelium covering is continuous, of about 3 μm thick. The endothelial cells often contain bundles of myofilaments.

4. *Podocytes in* Phoronis muelleri

Podocytes which show radiating processes ramify in many pedicels interconnected by slit membranes (Fig. 39); they are often

encountered in the coelomic lining of different metasomal blood vessels in *Phoronis muelleri* (cf. Storch and Herrmann, 1978). These cells contain myofilaments near the basal lamina, and they are

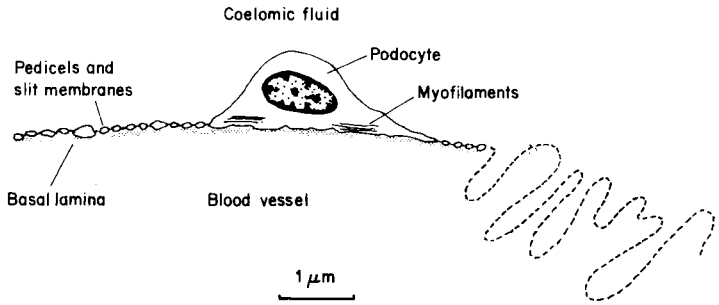

FIG. 39. Diagram of podocyte lining of a blood vessel of *Phoronis muelleri*. The dotted line shows an area with infoldings of the wall.

involved in the formation of the fenestration of the vessels. The wall structure appears to be related to the type 1 described above. The presence of such structures very similar to podocytes, only known in *P. muelleri*, is confirmed by the unpublished observations of Mattisson (personal communication).

The capillary caeca are lacking on the major part of the lateral vessel of *P. muelleri*, which suggests that their exchange function is here performed by the podocytes, which are known from different excretory organs as sites of ultrafiltration.

D. *Blood corpuscles*

The blood of phoronid species is composed of a colourless plasma containing solitary leucocytes (which have never been seen in the blood of *Phoronis psammophila* and their occurrence is considered by the present author as uncertain) and red corpuscles, the pigment of which is a kind of haemoglobin, originally established by Lankester and confirmed since by several authors (Cori, 1890, 1937; Ohuye, 1943; Lönöy, 1954; Emig, 1966). Recently, Garlick *et al.* (1979) studied the intracellular haemoglobin of *Phoronopsis harmeri* which is composed of four unique polypeptide chains, two of which can combine to form hetero- and homodimers and two of which do not associate at all. The four chains all have molecular weights of about 16 900 and they have been characterized by amino-acid composition, tryptic peptide patterns and the amino-acid sequence of the NH_2 terminal segment. The authors have determined the oxygen

equilibrium of a dimeric fraction at pH 7·5 and 20°C, and the pressure of half saturation which is 2·3 mm Hg.

The erythrocytes are generally approximately spherical, up to 12 μm in diameter. Their nuclei, about 3 μm in diameter, are located rather eccentrically; the dense coloured cytoplasm contains haemoglobin, Golgi apparatus, lysosome-like granules whose numbers increase in old cells, vesicles, some mitochondria which often surround the nucleus, and a poor ergastroplasm (Fig. 40). Mattisson

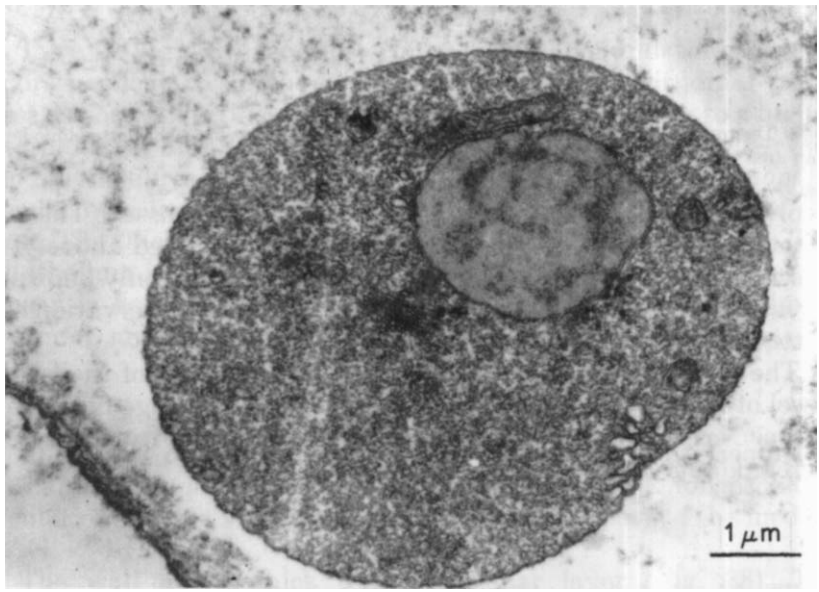

FIG. 40. General view of an erythrocyte of *Phoronis psammophila*. The Golgi apparatus lies near the nucleus, which shows some nuclear pores. Near the outer membrane occur microvesicles, which apparently coalesce to form larger ones; they are probably pinocytotic vesicles.

(unpublished results) has shown the occurrence of a marked endocytotic activity indicating a function of defence like that of white blood cells of higher organisms. In his ultrastructural studies, Mattisson has found a transport of mitochondria into the nucleus of the erythrocytes. Such an engulfing of mitochondria by the nucleus has also been reported to occur during spermiogenesis in the crustacean family Trogulidae by Juberthie and Manier (1977).

Cori (1890) pointed out that the red corpuscles possibly arise from the endothelial cells of the blood vessels. This origin was corroborated

by Ohuye (1942) in *Phoronis australis*: the endothelial gives rise to the erythrocytes and to the leucocytes. However, the observations of a similar origin of the blood cells, arising from the peritoneal lining and from the vasoperitoneal tissue (particularly during regeneration: Ohuye, 1943), are untrustworthy and need more detailed studies in the future.

It is of great interest to compare the structures of the wall and blood corpuscles of the Phoronida with those of other invertebrate groups, whose vascular systems up to now have been little studied, to establish possible relationships and probable phylogenetical evidence. It is suggested that the wall structure of type 1 is for low blood pressure which allows uptake and exchange of gases or food, while in type 3 strong muscular contractions pump blood around the whole system.

IX. Phylogenetic Relationships of Phoronida

The phylogenetic position and relationships of the Phoronida since their discovery have been the subjects of extensive controversial speculations. In the light of recent interpretations based on new information, particularly on developmental patterns and larval morphology, it is now generally agreed that the Lophophorata, to include Brachiopoda, Bryozoa and Phoronida, should have phylum status (Emig, 1977a). The position of the Phoronida within the Lophophorata, one of the most interesting groups in the phylogeny of the animal kingdom, as well as the relationships of the Lophophorata within the Chordata trend, and particularly in the Archimerata assemblage, will be discussed in relation to phylogenetic arguments expressed in recent studies (Valentine, 1975; Siewing, 1976; Emig, 1976b, 1977a; Farmer, 1977; Nielsen, 1977; Zimmer, 1978; Gilmour, 1979). Immediately, it may be suggested that the Phoronida share a larger proportion of evolved features than in the other lophophorate groups, and that the Lophophorata form a close-knit group with strong similarities deserving reassessment as possible ancestors from which the other Archimerata groups may have evolved.

A. *Archimeric subdivisions, morphological adaptations and phylogenetic relationships*

In general, Archimery (= Oligomery, Paurometamery, Trimery, ...) is defined by three body regions, prosome, mesosome and metasome, each with its own paired or unpaired coelomic cavity.

Recent findings (see Section III) lead to a general agreement that the fundamental pattern in Phoronida is the regionalization of the larval and adult body into three archimeric parts, each with an unpaired coelom (Fig. 25); their disposition is somewhat different in actinotroch and adult (Emig, 1976a). Archimery in Brachiopoda is fully anticipated in the larvae of Inarticulates, while in adult Articulates only the meso- and metasome are already developed, as well as in Bryozoa, in which only the Phylactolema show the presence of an epistome. The archimeric subdivision in the Lophophorata is one of the characteristics that no longer justifies their larvae being regarded as a modified trochophore; instead these larvae, especially actinotrochs, are to be related to the Dipleurula-type, which corroborates my previous opinion (Emig, 1976b).

1. *Prosome*

The preoral lobe of the actinotroch is homologous with the epistome, both structures being equivalent to the prosome, and homologous with similar structures in Brachiopoda and Bryozoa. The origin of the coelomic cavity of the preoral lobe is entirely independent from that of the other coeloms in the actinotroch; in the juvenile adult, a discrete protocoel is retained throughout metamorphosis as the protocoelom, the cavity of the epistome (Fig. 24). A small communication is formed between the protocoelom and the mesocoelom in adult forms (Emig and Siewing, 1975). Zimmer (1978) suggested that a remarkable parallel exists between the fates of the preoral lobe of phoronids and asteroids. The preoral lobe and epistome of lophophorates function in food-collecting and escape of excess water during feeding (see Section VII). Gilmour (1979) pointed out that the epistome is similar in internal structure to the proboscis of Hemichordata: the gill-slits originate from an epistome-like structure of a lophophorate ancestor, which is compatible with the present speculations. Such a structure, according to the same author, has become elaborated into a system of folds and grooves which may become fused to form a series of water pores, precursors of the gill-slits of chordates, as was first suggested by Masterman (1896). The actinotroch, like the other lophophorate larvae, retains the apical plate (larval nervous centre) which is lost during metamorphosis (Fig. 24) and does not serve as the primordium of the adult nervous ganglion, which is also located in the prosome (Emig, 1976a, b); this is corroborated by recent findings (Siewing, 1974; Zimmer, 1978; see also Section IV).

In actinotrochs the selection of a suitable substrate during settlement is accomplished by the piriform organ, or by the apical plate in species which lack this structure (Figs 20, 21). In the bryozoan cyphonaute larva the similar function is performed by the vibratile plume at the anterior end of the piriform organ, a complex of glandular cells whose function seems to be enigmatic (Farmer, 1977). In both larval types the piriform organ and the apical plate are united by a cord. Emig (1980) suggested that the piriform organ seems only to be associated with the ecological behaviour of the actinotroch without having any true evolutionary relationship.

2. *Mesosome*

The mesosome of the adult phoronids, surrounding the prosome (Figs 1, 25, 33), is represented by the lophophore, whose definition and functions have been discussed in Sections II, VII and VIII. Through its definition, the lophophore has an important phylogenetic significance (Emig, 1976c). The mesosome contains also the mouth, the ring nerve, the lophophoral vessel and accessory sex glands. The mesocoel differentiates in the collar region of the actinotroch, generally in the late larval stage, the remaining collar space being blastocoelic (Figs 9, 10, 25; Table II). Clark (1964) and Trueman (1968) argued that the tentacular apparatus or proboscis are secondary modifications in the acquisition of a burrowing habit, toward a sessile mode of life, and in this way, the retractable lophophore of the Bryozoa is interpreted by Farmer *et al.* (1973) as a coadaptation to colonial life. The evolutionary model of the lophophore, convincingly discussed by Cowen (1974), should only be applied to the Chordate trend.

Emig (1974a) pointed out that phoronid brooding species with a lecithotrophic larval stage are derived secondarily from forms which shed their eggs directly into the sea water, involving a long pelagic stage. The former pattern is considered as a more adapted reproductive strategy in Phoronida; brooding tends to reduce the pelagic phase which minimizes losses from larval predation and reduces larval mortality. The present argument needs further investigation in relation to spermatophore production and habitat (all burrowing species have brooding patterns). A similar view on Bryozoa has been expressed by several authors (e.g. Emig, 1976b; Farmer, 1977), considering the planktonic larva cyphonaute as an archaic and presumably primitive type, while, in contrast, Silén (1944) believed brooding forms to be primitive in Bryozoa. Recently,

Strathmann (1978) pointed out that Oligomera do not re-acquire a planktotrophic larval phase once it is lost, the loss being accompanied by an extensive loss of larval structures used in feeding, and that a secondarily acquired larval planktotrophy may not be as effective in permitting reduced egg size and hence greater fecundity. These arguments confirm our former statement.

Phoronida in their lack of cephalization, and as regards the disposition of their nervous system (Emig, 1976b), may be considered as "Epineuriens": the nervous system is basiepithelial and has shared similarities with those of the Hemichordates and Echinoderms, while relationships with the Spiralia have been disproved. In the genus *Phoronopsis*, the epidermal collar fold at the basis of the lophophore (Fig. 1) leads to a primitive neurulation and may be considered as an evolutionary process which has to be compared with the collar nervous cord of Hemichordata and with the radial nerve of Echinodermata.

3. *Metasome*

The metasome is the main locomotory organ of the Phoronida, adapted to a larval pelagic existence (or to a creeping life in the larva of *Phoronis ovalis*) and in the adult to a sedentary or sessile mode of life (see Sections II and VII). The adult trunk, and particularly its ampulla, is used to form a living burrow and may be homologous with similar structures, such as adhesive organ and pedicle which occur in other Archimerata groups. It shows a secondary internal subdivision into four cavities separated by mesenteries (one or two are lacking respectively in *Phoronis muelleri* and *P. ovalis*). Similar subdivisions occur in the Hemichordate *Cephalodiscus* and Ptychoderidae.

A convincing correlation between the archimeric condition and the adult tubicolous habit has been put forward by several authors, which is corroborated by the fact that the evolution of a coelomic cavity (primitively a hydrostatic skeleton) is closely tied to the acquisition of a burrowing habit (Clark, 1964; Trueman, 1968). Recent phylogenetic arguments refuted the opinion of Remane (1950) that the oligomerous condition represents a primary adaptation of early coelomates; this leads to the rejection of the term Archicoelomata introduced by Masterman (1898) and used by German workers.

Structures contained in the metasome have phylogenetic implications. The adult digestive tract of Phoronida is U-shaped, bringing the anus anteriorly to lie close to the mouth and reducing to

a remnant the dorsal side of the trunk (Fig. 25). The mouth orginally occupied an antero-ventral position and the blastopore has at no time the function of a mouth, both structures evolving independently (Williams, 1960). The Protostomia–Deuterostomia theory, initially proposed by Grobben (1908), and used for classification by phylogenetic relationships has been refuted by many previous zoologists (e.g. Lovtrup, 1975; Siewing, 1976; Emig, 1976b); this old concept is not in conformity with modern embryological findings and can no longer be upheld.

Protonephridia with solenocytic cells occur in the actinotroch, metanephridia in the adult phoronid (Figs 1, 11); the relationship of both structures has been discussed by Emig (1973a, 1976b) and future investigators have to try to reach conclusions on nephridial evolution in Phoronida. In this way, the arguments of Wilson and Webster (1974), that the evolution of the blood vascular systems of moderate pressure provides an alternative muscle-powered filtration force, and other forms of kidney have evolved to replace the protonephridium, may be accepted in Phoronida (see Section VIII). The apparent structural similarities in protonephridia would be the result of convergent evolution imposing a conformity based on functional requirements. Protonephridial terminal organs are divided into three or four different groups which are probably not interrelated, and the protonephridia are assumed to be homologous throughout the groups in which they occur (Wilson and Webster, 1974). As in actinotrochs, the lancelot *Branchiostoma* (Cephalochordata) possesses protonephridia with a number of solenocytes. However, in general very little is known of the way in which solenocytic cells function. Wilson and Webster (1974) give evidence to support the early notion of Goodrich (1945) that protonephridia in Kamptozoa (Endoprocts) conformed to the general platyhelminth pattern. This is another argument to refute Nielsen's (1977) conclusion that Bryozoa and Kamptozoa stem from a common ancestor.

B. *Other phylogenetic expression*

In Phoronida, as in the other Archimerata groups, the egg cleavage is of the radial type, total and subequal. The differentiation of the mesoderm occurs by a derived enterocoelous method, considered as a primitive stage of enterocoely (Emig, 1976b, 1980), which may be a general pattern in the Chordate lineages. In recent studies on Bryozoa, Zimmer and Wollacott (1977) described the

arising of mesenchymal cells from ectodermal tissue, specifically the epidermal blastema (apical disc). Such cells occur throughout the blastocoel of the bryozoan larvae, and the adult coelomic cavities become defined through the rearrangement of these cells, while the mesodermal lining of the basal part or of all ectodermal derivatives become peritoneum after metamorphosis.

The ribosomal RNA of *Phoronis australis*, *Lingula anatina* and *Terebratalia coreana* studied by Ishikawa (1977) may be of the "protostomiate" type with respect to thermal stablity and molecular size. However, the opinion of Ishikawa (1977) that the ribosomal RNA's molecular characteristics support the peculiarity of the embryology has to be refuted since he was not aware of recent embryological findings on Lophophorata. That the lophophorate ribosomal RNA is distinct from that of Echinodermata is not an adequate reason for opposing the combination of the Archimerata groups. Phylogenetic speculation based on this biochemical aspect needs more information.

In relation to the intracellular haemoglobin, Garlick *et al.* (1979) concluded with caution that the *Phoronopsis* Hb–Ia sequence appears to be evolutionarily far from Protostomia and Deuterostomia and perhaps about equidistant from each group.

C. *Relation of the Phoronida to the other Lophophorata*

There is general agreement that the Brachiopoda, Bryozoa and Phoronida share a large proportion of structures, with strong similarities in morphology and embryology, so as to constitute a closely related group, the Lophophorata. Although they have often been regarded as independent phyla, there is no reason to detach the three groups from one another. They constitute not only a phylogenetic assemblage but also a natural systematic unit which, as a taxon, deserves the status of a phylum (Emig, 1977a), the Brachiopoda, Bryozoa and Phoronida being classes (Fig. 41). The Lophophorata have the same well-defined characteristics as the other Archimerata phyla (Fig. 42).

The strong similarities shown by the three lophophorate classes are indicative of common ancestry and the relation of the Phoronida to the Brachiopoda and Bryozoa will be considered in the light of recent proposals, and particularly the question whether the Phoronida may be placed nearest to the ancestral stock (e.g. Hyman, 1959; Farmer *et al.*, 1973; Valentine, 1975; Farmer, 1977) or be

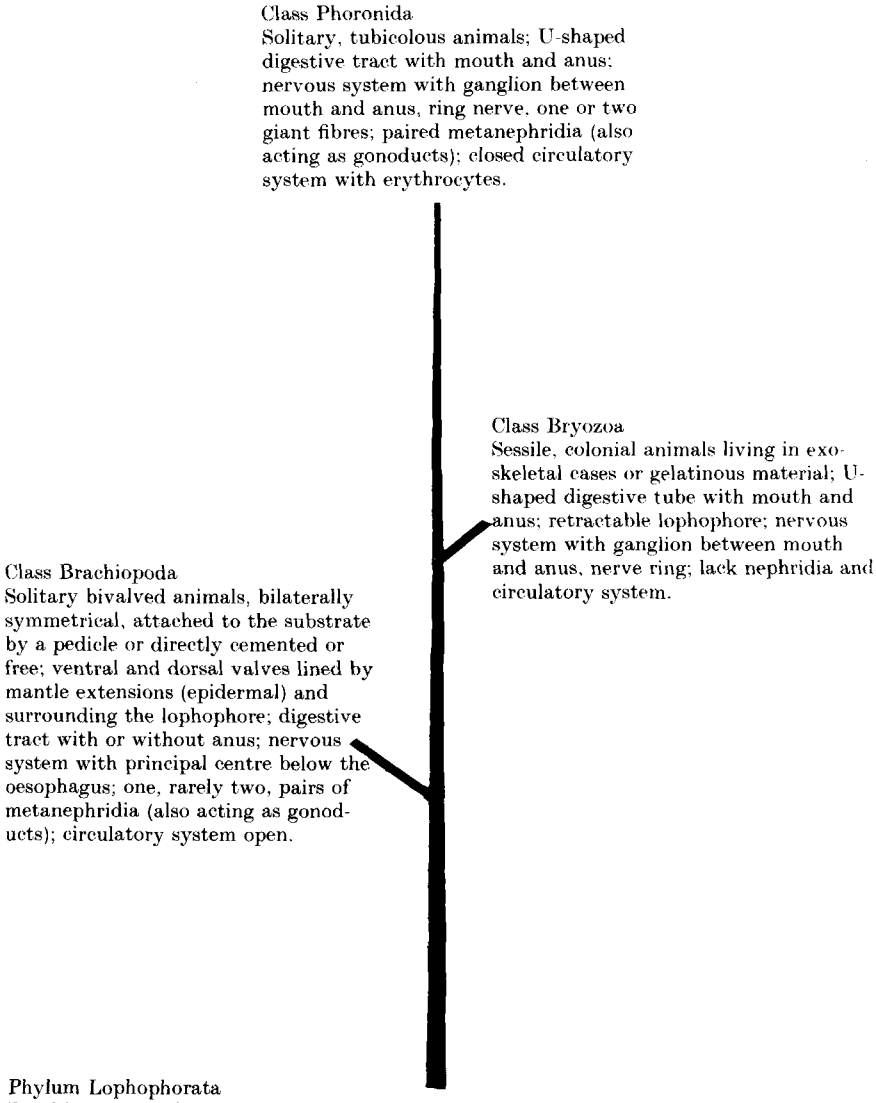

FIG. 41. The taxonomic and systematic relations between the Lophophorata, established on the basis of a phylogenetic reconstruction.

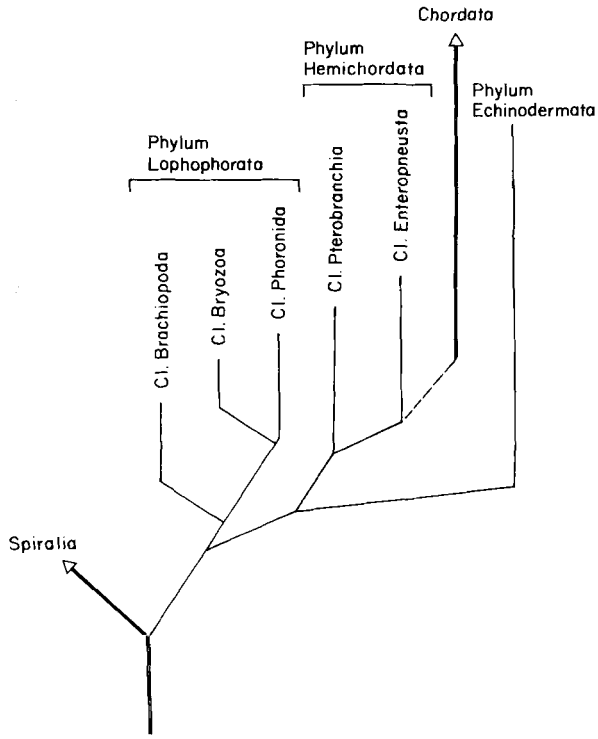

FIG. 42. Phylogenetic classification of the Archimerata phyla and their relationships, and their position in the animal kingdom.

regarded as the most evolved within the Lophophorata (Emig, 1976b).

Clark (1964) argued that the primitive function of the coelom was to act as a hydrostatic skeleton in burrowing and in this way the Lophophorata were derived from an infaunal ancestor of tubicolous habit to which the coelom is a functional necessity. Valentine (1975) estimated that this adaptive radiation probably occurred in the late Precambrian time. Another interesting argument concerns the modes of respiration (Cowen, 1974) and feeding (Webb, 1969) which become adaptive in the Lophophorata by development of a lophophore. Thus, speculation on the ancestral form suggests a soft-bodied infaunal vermiform burrow-dwelling animal, with a tentacle crown for feeding and respiration, and a fluid-filled coelomic space in trunk and tentacles (probably meso- and metasome) to produce an archimeric body plan. This ancestor lacked a skeleton and the time of its origin is unknown and perhaps unknowable.

Speculation as to radiation from the ancestral morphological form can only be based on the structure of existing animals so leading to consistent phylogenetic reconstructions. The prolophophorate form evolving from the Precambrian fauna would be of a small size in the absence of highly evolved organ systems. Presumably under environmental changes it developed a semi-epifaunal and epifaunal mode of life, or kept an infaunal one, with increase in size and in morphological complexity. This population gave rise to three successive evolutionary branches: the Brachiopoda arose first, then the Bryozoa and the Phoronida appeared successively, the Lophophorata being considered as monophyletic (Fig. 41). In other words, the common ancestral stock gave rise to the Brachiopoda and the Bryozoa as blind branches, then continued along its main line of evolution to the Phoronida. Valentine (1975) proposed that inarticulate brachiopods developed on soft substrata, subsequently radiating onto solid ones (craniids) and back into infaunal lingulids, while Articulates evolved from an ancestry which lacked a pedicle on hard substrata which later led to species which reinvaded soft sediments. The second lineage, the Bryozoa, may have followed a pathway of miniaturization and colony formation leading to the loss of some organ systems (nephridia, circulatory system) by adaptation and evolutionary divergence (Jebram, 1973; Farmer, 1977). According to morphological and behavioural features, *Phoronis ovalis* appears as the phoronid approaching nearest to the bryozoan lineage (Silén, 1952; Emig, 1969, 1976b; Farmer, 1977). This species is also the most primitive of the Phoronida and the oldest known phoronid fossil (see Section VI). On similarities with a phylogenetic basis the Phoronida may appear to show the highest degree of evolution, especially in fulfilling their life cycle and by their reproductive strategy, which emphasize the advantage of a rapid metamorphosis and regeneration (of the anterior body part and in asexual propagation). Phoronida also stand nearest to the Pterobranchia (Hemichordata).

Brachiopoda may have evolved in the latest Precambriam times; the Bryozoa are known since the Ordovician and Phoronida since the Devonian.

Each lophophorate class has assumed a selection of the optimal reproductive method (planktotrophic, pelagic lecithotrophic, non-pelagic lecithotrophic) for the opportunistic use of the habitat by the adult. Controversy exists in tracing the evolutionary trend of the actinotroch from a cyphonaute ancestor (Jägersten, 1972). Conversely the actinotroch may be the ancestral form for the

Bryozoa, particularly of the cyphonaute from which the other bryozoan larvae are modified or altered forms (Farmer, 1977). The fact that the cyphonaute larva is highly adapted for an extended pelagic existence (up to 2 months) appears to be a more primitive condition compared with actinotroch types (see foregoing pages). On the other hand, the larva of *Phoronis ovalis* approaches in many respects the morphology of some bryozoan larvae. The study of the development and anatomy of this larva will probably resolve the present controversy. However, it seems reasonable to imagine an intermediate form from which both actinotroch and cyphonaute were derived. In any event the lophophorate evolution proposed in this paragraph is incompatible with Nielsen's (1977) arguments that the Bryozoa originated from the Kamptozoa (= Endoprocta), arguments which have been refuted by Emig (1976b, c) and Farmer (1977) and which cannot be retained in the Archimerata concept.

D. *Relation of the Lophophorata to the other related Phyla*

The following phylogenetic reconstruction of the relationships of the Lophophorata in the animal kingdom is based on adaptive transformations brought to light in the present review on the biology of Phoronida and by several investigators during the last decade (for bibliography refer to, e.g. Jollie, 1973; Valentine, 1975; Emig, 1976b; Siewing, 1976).

The phyla with archimeric body regionalization have several homologous features; they may be considered as a monophyletic assemblage, called Archimerata by Emig (1976b). The term Archicoelomata, initially proposed by Masterman (1898), has been rejected earlier in the present review on the basis of recently published arguments. One major homologous character appears to be the mesosome and its coelomic cavity, whose derivatives take the form of tentacular outgrowths and arms to the ambulacral system. Stephenson (1976) agreed with Nichol's hypothesis (1967) that the echinoderms originate from a lophophorate animal but he stated that the tentacles of the lophophore have to be considered homologous with the echinoderm tube feet. The Archimerata assemblage brings together the Lophophorata, the Hemichordata and the Echinodermata, which all stemmed from a common lophophorate ancestor. In other words, it is suggested that the Lophophorata may be a possible ancestor of the Chordata (Fig. 42), which gave rise, on the one hand, to the Echinodermata, which evolved as a blind branch, and, on the other hand, to the Hemichordata and Chordata; the latter is a

hypothesis which is generally agreed upon; this is in contrast to the speculative hypothesis of Gutmann and Bonik (1978). The Phoronida show similarities to the Pterobranchia, which are generally admitted to be more primitive than Enteropneusta.

A close relationship between Hemichordata and Chordata has been generally acknowledged, but the ideas of the different authors on the prochordate ancestor vary. Recently Welsch and Welsch (1978) investigated the suggestion of homology of the preoral ciliary groove of Enteropneusta (Hemichordata) and the Hatscheck's pit of *Branchiostoma* (Acrania) with the vertebrate adenohypophysis, and this was neatly confirmed by them.

In accordance with Ulrich (1972) and Siewing (1976), the Archimerata group should not be considered only as a phylogenetic concept but also as a natural systematic unit. It does not represent a central group in the Coelomata classification as was proposed by Siewing (1976, Fig. 13). This corroborates my former opionin (Emig, 1976b) that the Archimerata lie at the base of the Chordata stem of which they are primitive precursors and that they show very few, even no, similarities with the Spiralia.

To summarize these speculations, the Lophophorata, and particularly the Phoronida, are allied with the Chordata stem of which they represent an early evolutionary offshoot. It appears beyond doubt that they are allied neither to the Spiralia, nor to some central position between the Spiralia and Chordates.

X. References

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