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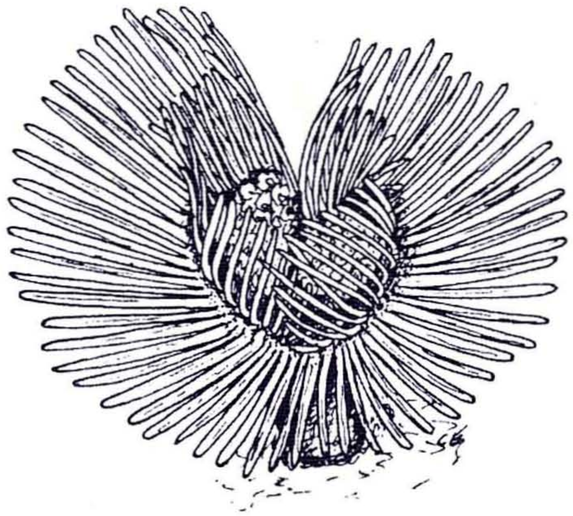
edited by Doris M. Kermack and R.S.K. Barnes
No. 13

British and Other Phoronids

C.C. Emig



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A NEW SERIES
Synopses of the British Fauna
No. 13
Edited by Doris M. Kermack and R. S. K. Barnes

BRITISH AND OTHER PHORONIDS

Keys and Notes for the Identification of the Species

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Foreword

Phoronids are a small, but widely distributed, group of benthic marine animals. For the first time in English, Dr Emig has provided keys and descriptions to enable not only the British species to be identified but also all other known species. The size of this synopsis and a glance at the maps show that little is known of these tube-dwelling, worm-like invertebrates. It is also the reason for the editors decision to extend the coverage of this synopsis to include full descriptions of species of phoronids occurring outside British waters. The author and editors are anxious to receive new records of localities with phoronids, so that the group may become better known and understood.

This *Synopsis* bears the names of two Editors and is the first, of what we hope will be many, to be produced by the Estuarine and Brackish-water Sciences Association and the Linnean Society of London. In 1976, the former decided to solicit small monographs on those groups of aquatic organisms for which modern keys were not available in English. Rather than produce a series in parallel to the *Synopses of the British Fauna* (New Series), EBSA accepted the invitation of the Linnean Society to collaborate with them. Thus, though produced on behalf of the two organizations, this and subsequent volumes will continue the numbering of the existing series as well as the format, with its now well-known features of simple illustrations of each species described, spaces left for owner's notes and a waterproofed cover.

The Estuarine and Brackish-water Sciences Association and the Linnean Society are grateful to Dr Emig for the care he has taken to follow the synopsis format and yet extend the geographic range of his work, all this in a language other than in his native tongue, French.

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A Synopsis of British and Other Phoronids

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CONTENTS

Introduction

Phoronids are an exclusively marine group of lophophorate animals which secrete and live freely in a chitinous cylindrical tube. They may be found, singly or in masses of many individuals, buried in or encrusting rocks and shells, or embedded in soft sand, mud or fine gravel.

Several authors regard them as constituting a separate phylum, the Phoronida; but others, including myself (Emig, 1977c), group them with the two other lophophorate groups, the Bryozoa and Brachiopoda, to form the phylum Lophophorata, of which phoronids then constitute a class.

Only two genera—*Phoronis* Wright (one of the numerous epithets of the Egyptian goddess Isis) and *Phoronopsis* Gilchrist—and some ten species are currently recognized. It is only recently that it has been appreciated that many of the characteristics hitherto used to distinguish the species are variable, and that several species are therefore of dubious status (Emig, 1971b, 1974; Emig *et al.*, 1978). All species have a wide geographical range, although only those of the genus *Phoronis* are represented in the British marine fauna. The first phoronids to be discovered were the two burrowing "worms" described by Wright (1856) from the British coast (Inchkeith; Ilfracombe), but it was not until 1867 that Kowalevsky showed that Wright's *Phoronis* was the adult form of the larva from near Heligoland previously described by Müller (1846) under the name *Actinotrocha*. Separate names for the larvae are sometimes still used.

The biology of phoronids has been reviewed by Selys-Longchamps (1907), Cori (1939) and by the present author (Emig, 1966–1978). The terminology used in this synopsis follows Emig (1975). Descriptive terms are defined in a glossary on p. 51.

General Organization

Phoronids have a vermiform **body** with a terminal **lophophore**, which is an important and characteristic structure found in phoronids, brachiopods and bryozoans (Fig. 1). It can be defined as "a tentacular extension of the mesosome (and its cavity, the mesocoelom) that embraces the mouth, but not the anus, and its main functions are feeding, respiration and protection".

The shape of the bilaterally symmetrical lophophore varies greatly, but it is a characteristic and fairly constant feature within each phoronid species. Five main groups can be established on the basis of the lophophore structure (Fig. 2), ranging from those which are oval (11–28 tentacles) to those which are helicoidal with more than 1500 tentacles. The number of **tentacles** increases with the age of the animal and is somewhat variable within a given species. New tentacles arise in the middle of the inner row (Fig. 3), between the mouth and the anus (i.e. the dorsal side). Apart from the site of tentacle proliferation, the tentacles are of about the same length, except in *Phoronis muelleri*, where the tentacles of the outer row also become shorter at the oral side (Fig. 2B). The latter disposition must not be confused with a similar configuration resulting from regeneration (see p. 20). In the genus *Phoronis* the lophophore is not demarcated from the metasome or trunk, whereas in *Phoronopsis* an epidermal **collar-fold** occurs at the base of the lophophore (Fig. 2D, F).

The **body** is composed of three sections (Fig. 1)—**prosome, mesosome** and a long **metasome**—each containing its own coelom—**protocoelom, mesocoelom, metacoelom**. The prosome forms the **epistome**, a fold extending from the ends of the lophophore along the inner row of tentacles and overhanging the **mouth** dorsally. It appears to support the lophophore and may participate in food intake. The protocoelom communicates with the mesocoelom; each cavity is unpaired, as is the metacoelom. The mesosome bears the lophophore, the

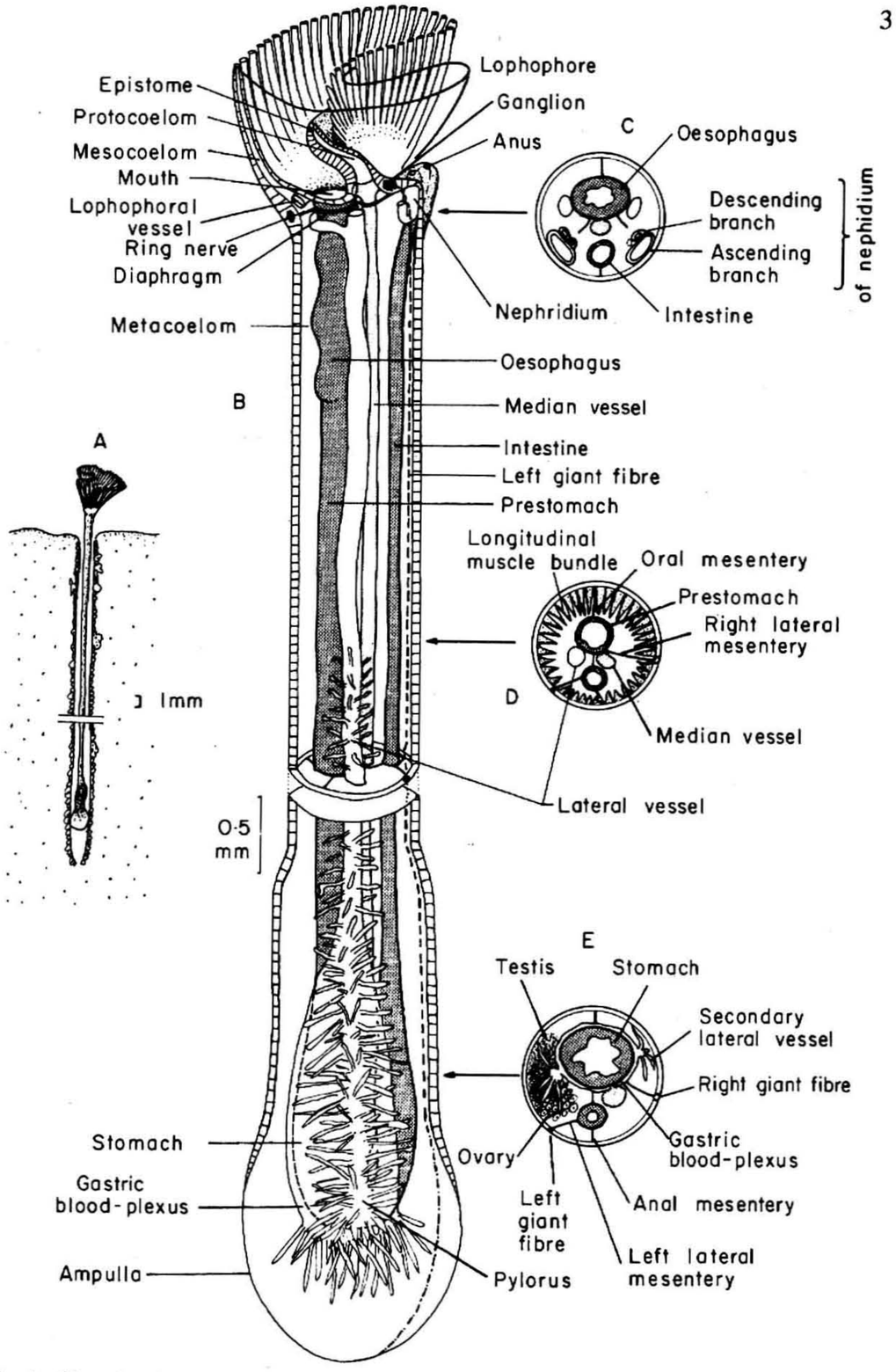


FIG. 1. A, Sketch of a phoronid in its tube, embedded in soft sediment. B, Diagram of *Phoronis* showing the main anatomical features. C, Cross-section of the metasome at the nephridial level. D, Cross-section of the metasome in the muscular region. E, Cross-section of the metasome in the ampulla.

mouth lying between its two rows of tentacles and the **accessory sex glands** (Figs 1B; 3). The metasome (or **trunk**) is slender and cylindrical, uniform in diameter except for the posterior end (or **ampulla**), which is enlarged into an end-bulb used for anchorage (Fig. 1A, B). A transverse septum or **diaphragm**, located behind the lophophore base, separates the mesocoelom from the metacoelom; a **nerve ring** occurs at this level (in the collar-fold in *Phoronopsis*). **Nephridia, gonads, circulatory system, longitudinal muscle bundles** and **giant nerve fibres** are important distinguishing characters situated in the metasome (Figs 1B; 4; 5A, B). The metacoelom may be divided by mesenteries into four compartments, left oral; right oral; left anal and right anal (see p. 12).

The **digestive tract**, which extends throughout the trunk, is U-shaped bringing the **anus** close to the **mouth** and shortening the animal's dorsal surface (Fig. 1B). The descending branch opens at the crescentic mouth, overhung dorsally by the epistome, then passes into the **oesophagus** with heavily ciliated thick walls. The **prestomach** follows; it is the longest part and is lined with a thin, ciliated epithelium and passes insensibly into the **stomach**, which is thick walled and surrounded by a **blood-plexus**. The **pylorus** is a muscular constriction between stomach and **intestine**. The latter forms the whole ascending tube, which is slender and long and ends in the anus.

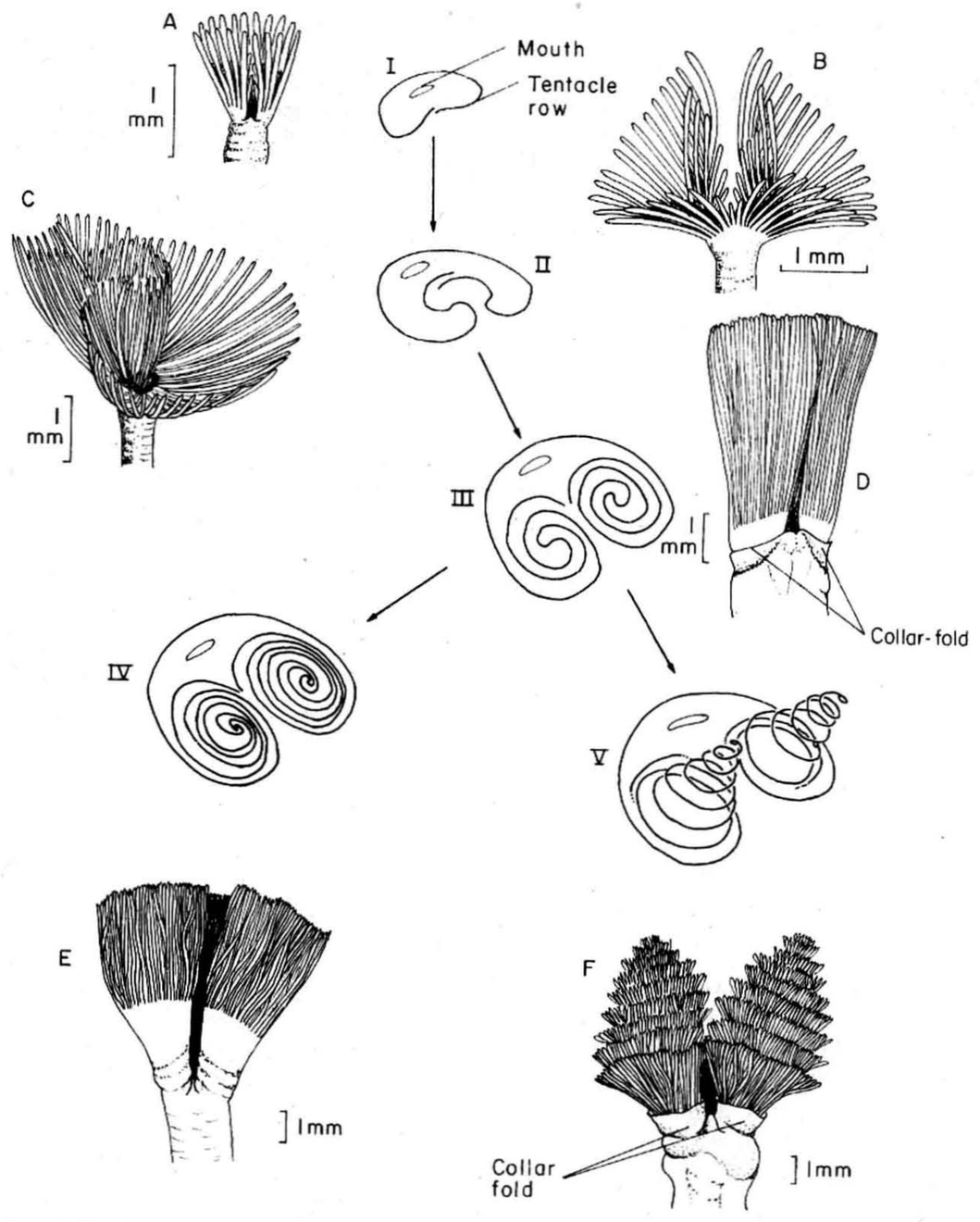
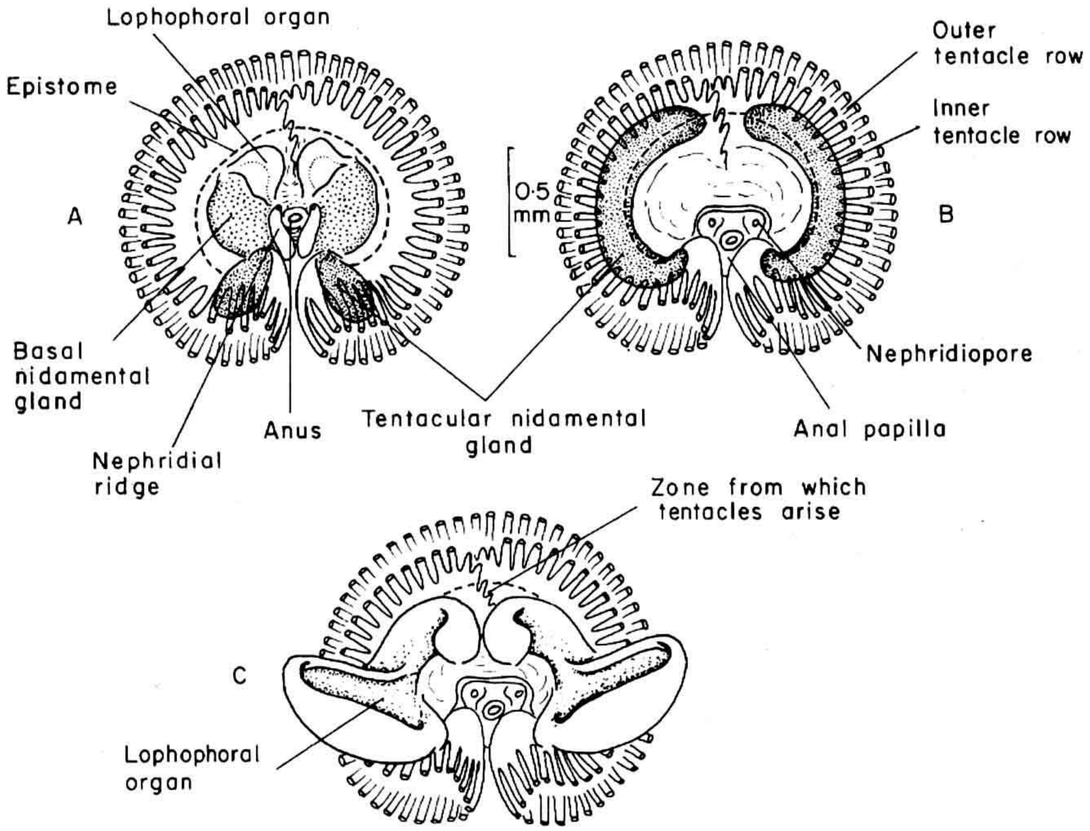


FIG. 2. Variation in lophophore shape. A, Oval (*Phoronis ovalis*). B, Horseshoe-shaped, with short oral tentacles (*P. muelleri*). C, Horseshoe-shaped, with tentacles of equal length (*P. psammophila*) [*P. hippocrepia, P. ijimai* and *Phoronopsis albomaculata* are similar, although slight coiling may occur in the two latter species]. D, Spiral, with 1·5–2·0 coils (*Phoronopsis harmeri*). E, Spiral, with 2·5–3·5 coils (*Phoronis australis*). F, Helicoidal, with 4–5 coils (*Phoronopsis californica*). A, D-F, Anal view; B, Oral view; C, Lateral view.



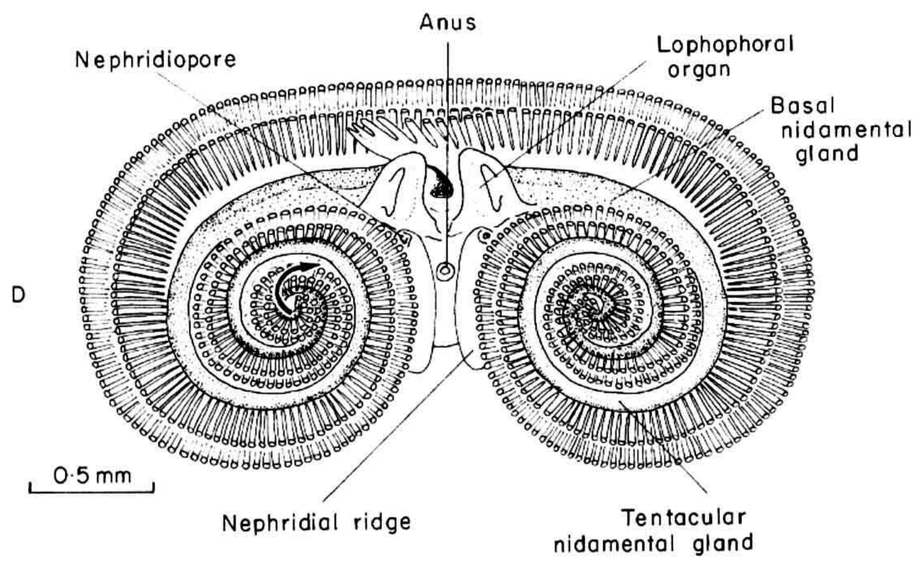


FIG. 3. The lophophoral concavity of mature phoronids, showing the accessory sex glands. A, *Phoronis hippocrepia* ♂. B, *P. psammophilia* ♀. C, *P. psammophila* ♂. D, *P. australis* ♂.

TABLE 1. Main characteristics of nephridia of phoronids

Species	Funnel	Descending branch	Nephridiopore on	Nephridiopore aperture	Group No.
P. ovalis	1	absent	anal papilla	anus level	1
P. muelleri	1	present	anal papilla	anus level	2
P. psammophila				below anus	
Ph. albomaculata				below anus (on collar-fold)	
P. hippocrepia	2 anal:larger oral: smaller	absent	nephridial papilla	above or anus level	3
P. ijimai					
P. australis					
P. pallida	2 anal slightly larger than oral	present	anal papilla	anus level	4
Ph. harmeri	2 anal: smaller oral: larger			below anus (on collar-fold)	
Ph. californica	2 anal: larger oral: smaller			below anus (on collar-fold)	

The paired excretory organs are **nephridia**, located on either side of the intestine in the anterior part of the trunk, at the level of attachment of the lateral mesenteries (Figs 1B, C; 4A). A nephridium is usually a U-shaped tube (though the descending arm is lacking in some species) which opens into the metacoelom by one or two **funnels** and discharges its contents to the exterior via a **nephridiopore**. When two funnels are present, they are separated by the lateral mesentery and one opens in the oral metacoelomic compartment (**oral funnel**) and the other in the anal metacoelomic compartment (**anal funnel**). Usually the nephridiopores are located on the **anal papilla** on each side of the anus at its level or below (Figs 3B; 4A), except in group 3 (Table 1) where the nephridiopores is situated on the **nephridial ridge** above the anus level (Fig. 3A). In *Phoronopsis* the anal papilla appears as an enlargement of the collar-fold and the nephridiopore opens in the epidermal invagination. The morphological characteristics of the nephridia are of taxonomic importance as indicated in Table 1; diagnostic features are the number of funnels (one or two), the presence or absence of a descending branch, and the location of the nephridiopore. Thus four groups can be established which are represented in Fig. 4, and summarized in Table 1.

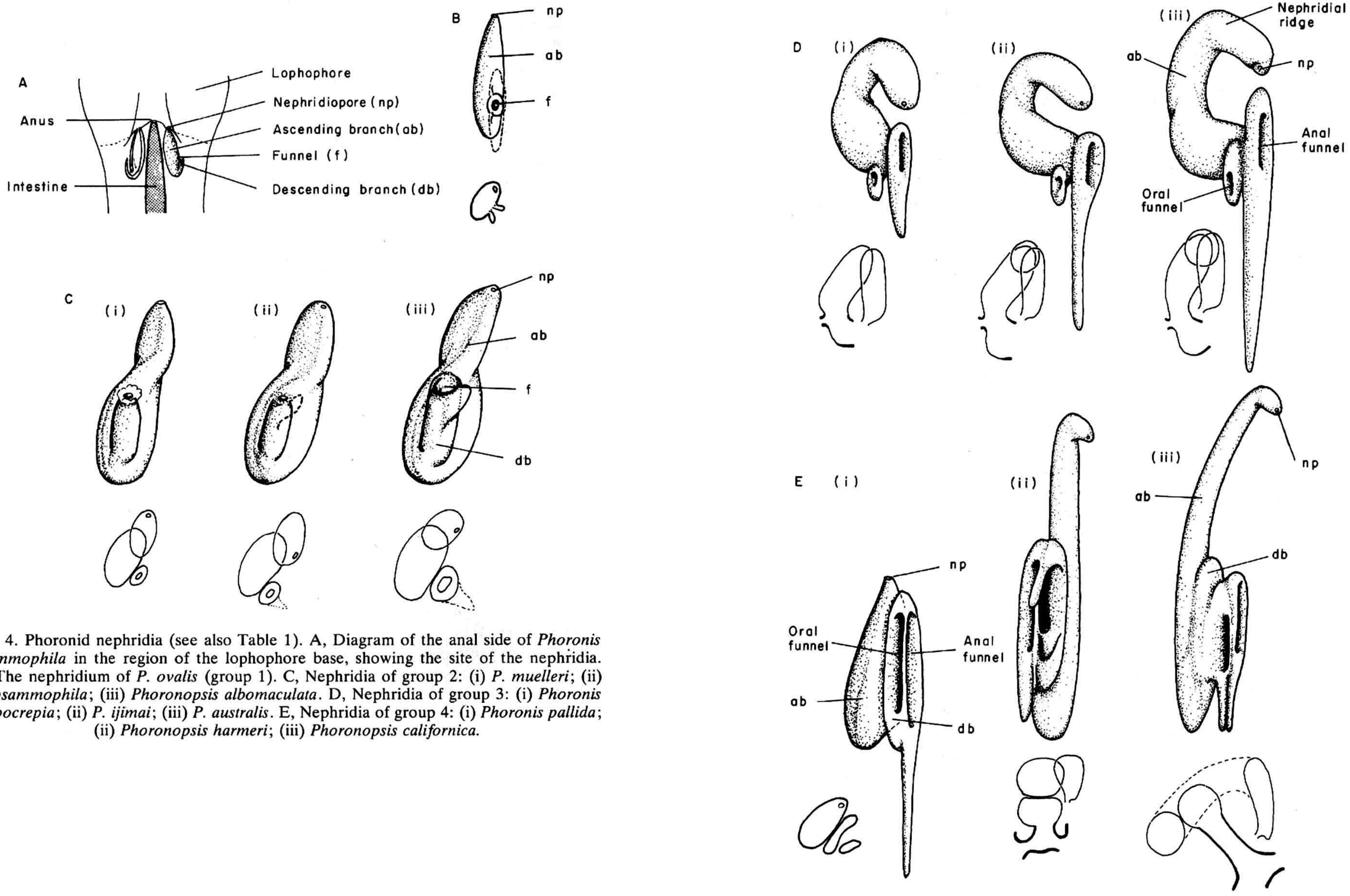


FIG. 4. Phoronid nephridia (see also Table 1). A, Diagram of the anal side of *Phoronis psammophila* in the region of the lophophore base, showing the site of the nephridia. B, The nephridium of *P. ovalis* (group 1). C, Nephridia of group 2: (i) *P. muelleri*; (ii) *P. psammophila*; (iii) *Phoronopsis albomaculata*. D, Nephridia of group 3: (i) *Phoronis hippocrepia*; (ii) *P. ijimai*; (iii) *P. australis*. E, Nephridia of group 4: (i) *Phoronis pallida*; (ii) *Phoronopsis harmeri*; (iii) *Phoronopsis californica.*

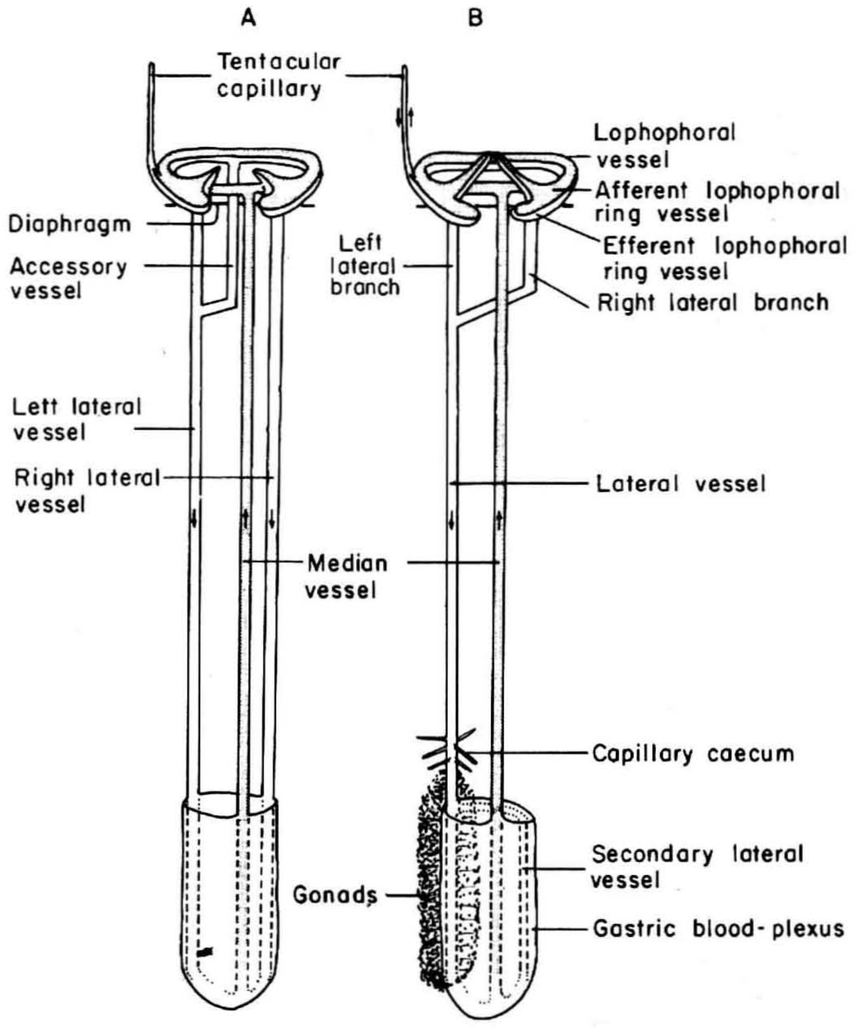


FIG. 5. Circulatory system in (A) *Phoronis ovalis*, and (B) other phoronid species.

Phoronids have a closed **circulatory system**, containing **red corpuscles**. In the trunk, this system comprises two **longitudinal vessels**, an afferent **median** one arising from the extensive **blood-plexus** on the stomach wall and an efferent **lateral** one issuing from the **lophophoral vessel**. The two trunk vessels communicate through the blood-plexus and the lophophoral vessel. The lateral vessel shows blind-ending **capillary caeca**, especially in the posterior body part (Figs 1B, E; 5B). *Phoronis ovalis*, however, has three longitudinal trunk vessels: a median one and two lateral vessels (left and right); at the level of the oesophagus, an **"accessory" vessel** near the oral mesentery unites the lophophoral vessel with the left lateral vessel (Fig. 5A).

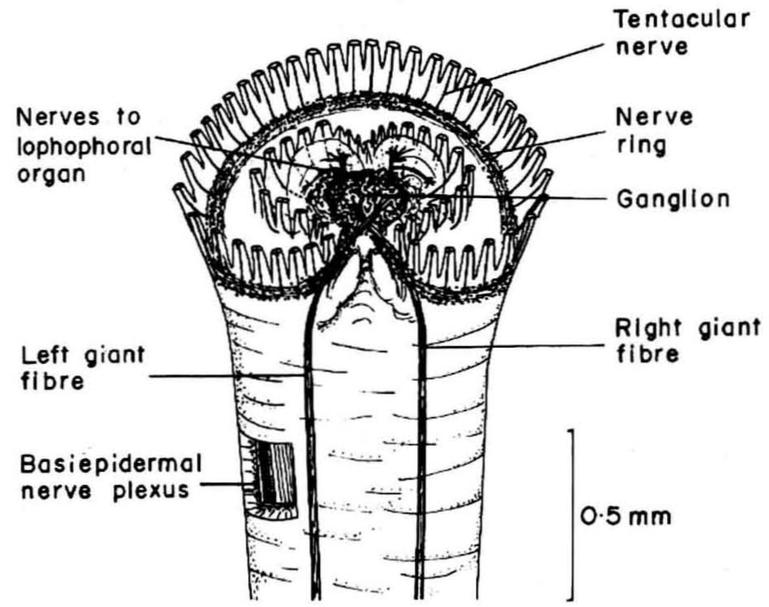


FIG. 6. Diagram of the phoronid nervous system (modified from Silén, 1954b).

The **nervous system** of the phoronids lies within epithelial tissue. The main nerve centre or **ganglion** is located in the epidermis of the epistome between the mouth and anus and gives off a **nerve ring** at the level of the diaphragm and one or two **giant nerve fibres** on the right and left side along the site of attachment of the lateral mesenteries (Figs 1B, D, E; 6). Giant fibres are absent in *Phoronis ovalis*. *P. hippocrepia, P. ijimai* and *P. australis* have two giant fibres, whilst in the genus *Phoronopsis* only the left fibre runs the full length of the animal, the right one ends at the nephridial level. *Phoronis psammophila, P. muelleri* and *P. pallida* have but a single, left, giant fibre.

The **trunk wall** consists of **epidermis**, with a **basal nervous layer, basal lamina, two muscle layers** (a thin outer one of **circular** fibres and an inner well-developed **longitudinal** muscle layer), and **"peritoneum"** (mesodermal cell layer) (Figs 6; 7A(i), C). The arrangement of the longitudinal muscle bundles relative to the four sub-divisions of the metacoelom formed by the mesenteries is represented by the conventional **formula** of Selys-Longchamps (1907):

	oral mesentery	
left lateral mesentery	left oral coelom | right oral coelom	right lateral mesentery
	left anal coelom | right anal coelom	
	anal mesentery	

The variations of this formula in the different species of phoronids have been studied in detail. In *Phoronis ovalis* the lateral mesenteries are absent, so no formula can be given, whilst in *P. muelleri* the absence of the left lateral mesentery is indicated by a dotted line. The number of muscle bundles may vary within certain limits in a single species, being dependent upon such factors as habitat or locality. This number also varies in several species from the anterior to the posterior part of the muscular region of the trunk. The muscle fibres are arranged in two patterns, **bushy** or **feathery** (Fig. 7A). *Phoronis pallida* possesses an unusual arrangement of trunk musculature (Silén, 1952); the circular muscle layer forms three thick sphincters and the longitudinal muscle layer shows six zones dependent on the degree of development of the marginal and central muscle fibres (Fig. 7B, C).

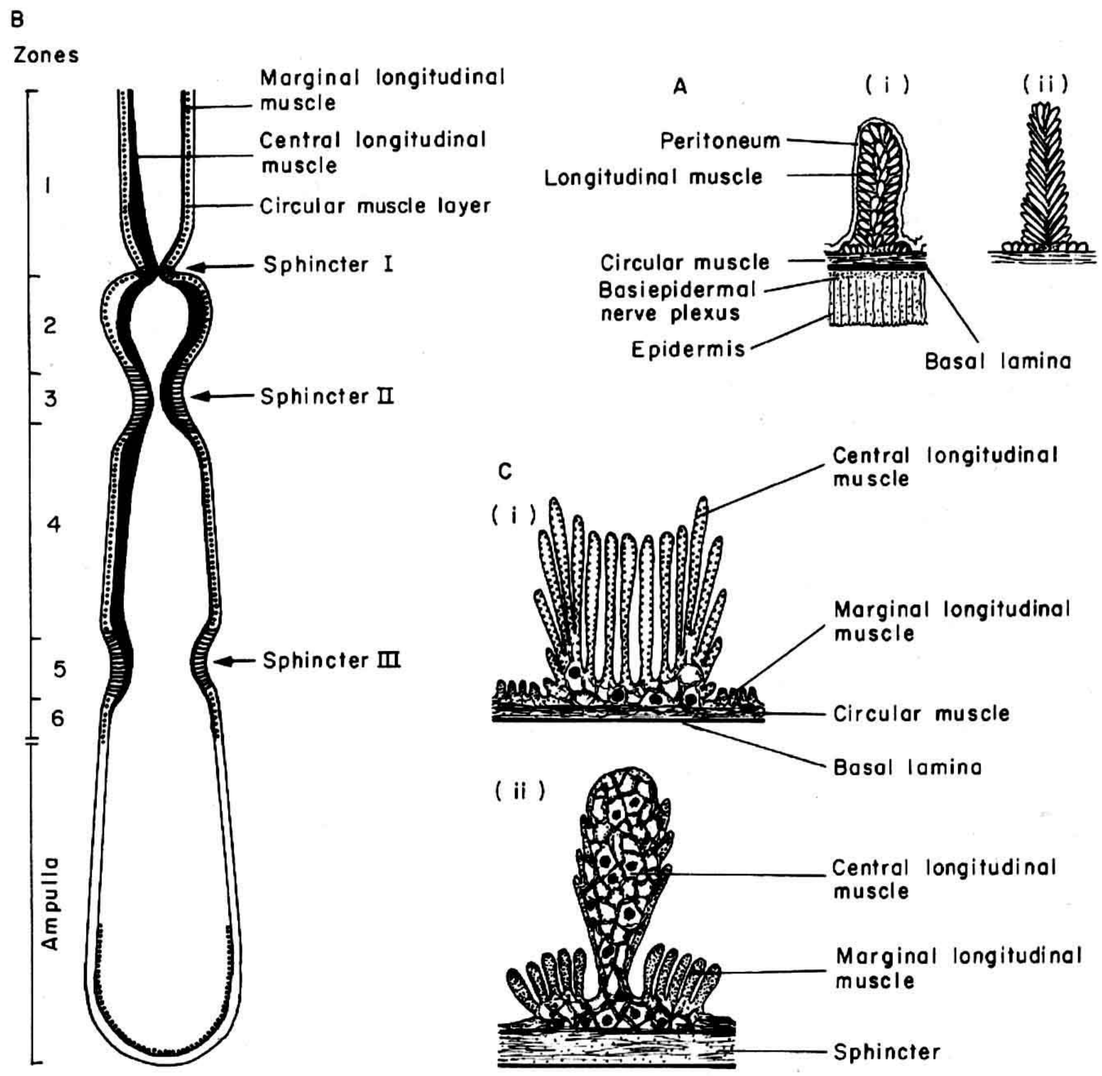


FIG. 7. A, Cross-sections of longitudinal muscle bundles (i) bushy shape (with section of the trunk wall); (ii) feathery shape. B, Scheme of the muscle arrangement in *Phoronis pallida* (after Silén, 1952). C, Sections of longitudinal muscle strips of *P. pallida* (i) from zone 4, and (ii) from zone 3 (after Silén, 1952).

Phoronids are **hermaphrodite** or **dioecious**: the **gonads** are applied to the lateral blood vessel and its capillary caeca in the left oral cavity of the metacoelom at stomach level and in the ampulla (Figs 1E; 5). In hermaphrodite species, the testis lies on the oral side of the lateral vessel and the ovary on the anal side. In *P. pallida* this disposition can be reversed. In dioecious species, the gonads can extend into the right oral cavity of the metacoelom, where a secondary lateral blood vessel generally occurs in the extensive blood-plexus (Figs 1E; 5). Two groups of **accessory sex glands** appear in the lophophore during gonad maturation (Fig. 3). The first, the **lophophoral organs**, may be small or large (glandular or membraneous) and occur in males and hermaphrodite species in the lophophoral concavity. They secrete the spermatophoral membranes and so assist in spermatophore formation, but are usually lacking in *Phoronis ovalis*. The second group are the **nidamental glands**, although these are only present in species which brood their eggs. These are of three types and their function is the attachment of the ova to the embryonic masses and the maintenance of the integrity of these brood masses.

Type *a* are developed on the floor of the lophophoral concavity and on the inner surface of those tentacles to which the two embryo masses are attached; e.g. in some hermaphrodite brooding species such as *Phoronis hippocrepia* and *P. ijimai* (Fig. 3A).

Type *b* are restricted to the floor of the lophophoral concavity with an extension along the coils of the lophophore on the inner surface of the tentacles and associated with the two embryo masses; e.g. *Phoronis australis* (Fig. 3D).

Type *c* are formed by the fusion of the inner row of lophophore tentacles and the single embryo mass; e.g. as in the dioecious brooding *Phoronis psammophila* (Fig. 3B, C). The other phoronid species do not brood, although no information is available on *Phoronopsis californica* and *Phoronopsis albomaculata*.

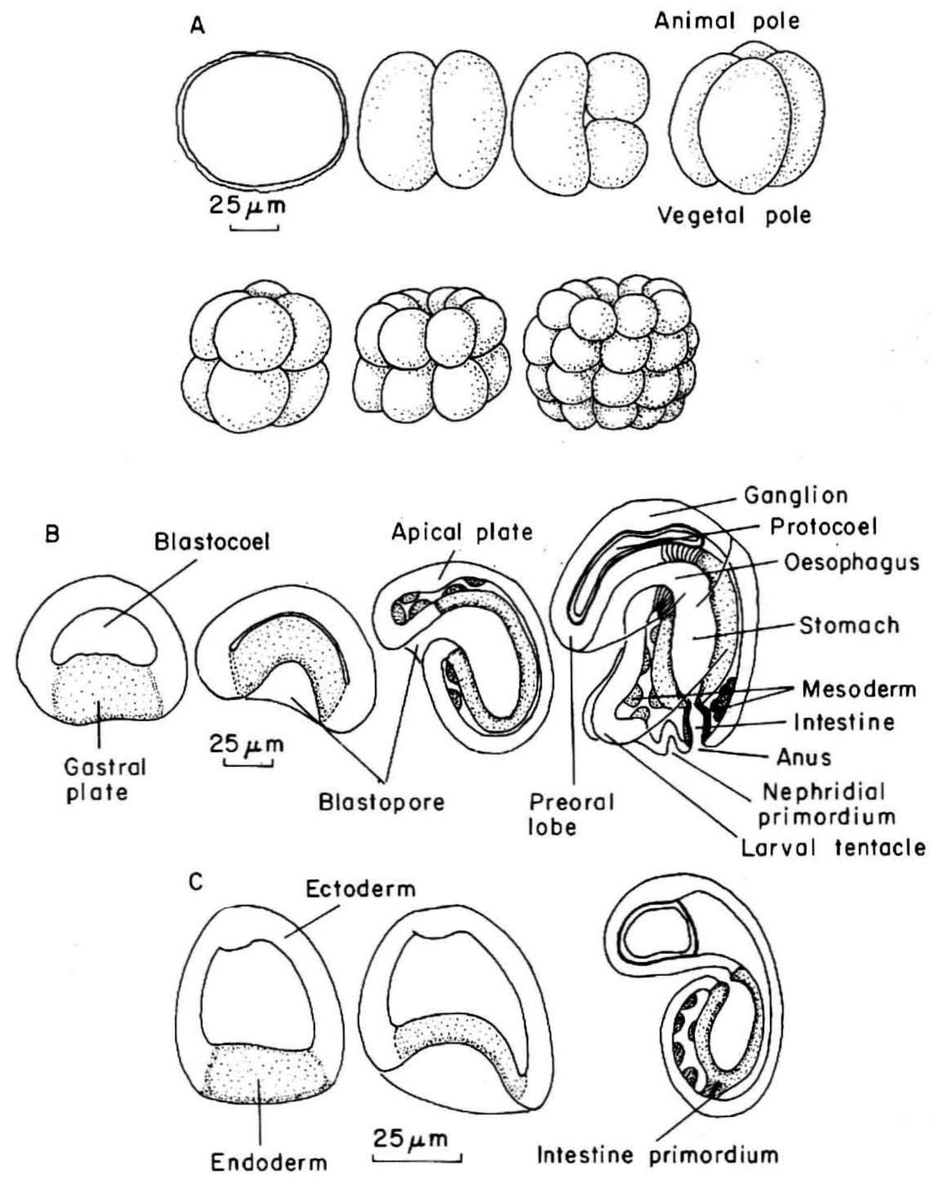


FIG. 8. A, Egg cleavage in phoronids. B, Some stages of gastrula development (egg developmental type 2). C, Some stages of gastrula development of type 3.

Biology

Life History

Phoronids generally breed from spring to autumn over a fairly long period. The spermatozoa are congregated near the nephridial funnels, compacted within the nephridia and extruded through the nephridiopores to the lophophoral organs to form the spermatophores. The latter gain access to the metacoelom of the females or hermaphrodite species inwards through the nephridial tube. Fertilization is internal and cross-fertilization takes place in hermaphrodite species. The oocytes are liberated from the ovary into the coelomic fluid and released after fertilization to the exterior via the nephridia acting as gonoducts. They may be swept onto the nidamental glands in the lophophoral concavity where they are attached by mucus to form a brood mass in brooding species, or shed freely into the ambient sea-water in the other species.

Phoronids show three different types of egg development:

(1) eggs which are heavily yolked, about 125 μm in diameter and retained within the tube of the adult until they become ciliated slug-like larvae with no true pelagic life (Fig. 12), e.g. *Phoronis ovalis*;

(2) eggs which are moderately rich in yolk, about 100 μm in diameter and brooded in the lophophoral concavity on the nidamental glands until the actinotroch stage so that there is a fairly short larval stage, e.g. *Phoronis hippocrepa, P. ijimai, P. australis, P. psammophila* (and probably *Phronopsis albomaculata* on the basis of the diameter of its eggs);

(3) eggs which are small, about 60 μm in diameter and shed directly into the surrounding sea-water. These have a long pelagic larval life, e.g. *Phoronis muelleri, P. pallida* and *Phoronopsis harmeri*.

Egg cleavage is total, equal or subequal. The pattern is typically **radial** though biradial in some stages (Fig. 8A), but there are instances in which the blastomeres exhibit a spiral appearance (especially in the small lightly yolked eggs of type *3*). The gastrula arises by **emboly**. The **blastocoel** is extensive in embryos from small eggs (type *3*) but virtually obliterated by wall compression in those from medium sized eggs (type *2*) (Fig. 8C, D). The **blastopore** is reduced to an anterior remnant, located between the oesophagus and stomach. Differentiation of the **archenteron (endoderm)** produces the stomach and intestine, but not the oesophagus, whilst that of the **ectoderm** leads to the formation of the pre-oral lobe, apical plate, nephridium primordium and oesophagus (Fig. 8C, D). The anus opens by perforation of the ectoderm, without the formation of a **proctodaeum**. The **mesoderm** originates as isolated cells proliferated from the anterior and ventrolateral areas of the archenteron in two phases and its formation is considered to be a modified **enterocoelous type**. The mode of formation of the coelomic cavities varies with the species. The **protocoel** or larval cavity of the **pre-oral** lobe is produced from the anterior mesodermal area; the **metacoel** originates from the ventrolateral mesodermal proliferation; whilst the third larval coelomic cavity, the **mesocoel**, appears only shortly before metamorphosis.

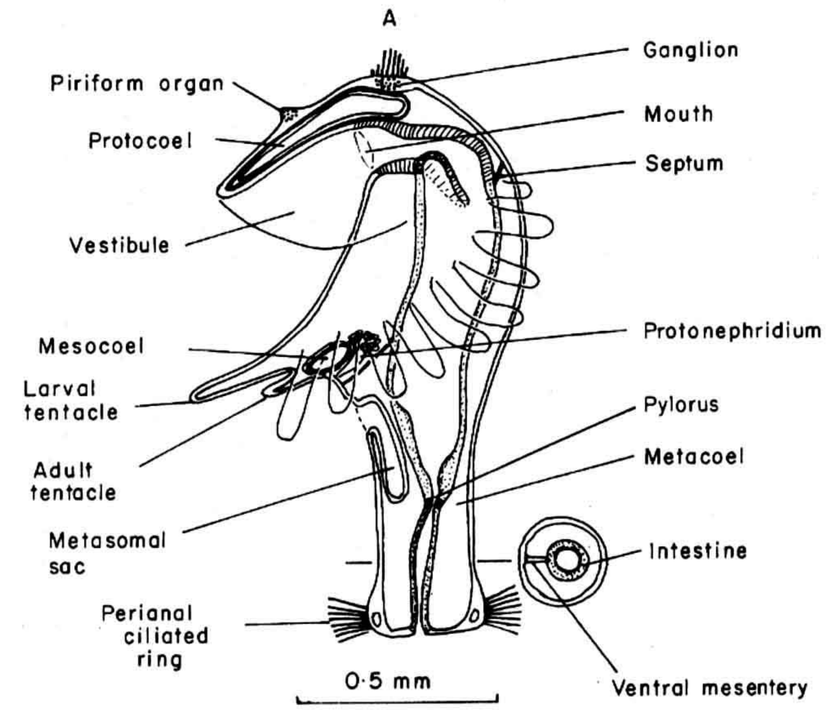


FIG. 9. A, Diagram of an actinotroch (*Actinotrocha branchiata*) near its metamorphosis. B, The main stages of the metamorphosis of *Actinotrocha branchiata* (after Herrmann, 1976, with modifications).

The larva takes up a planktonic life, developing a ciliated ring round the anus. **Tentacles** arise as an evagination of the tentacular ridge; the first pair from the ventral midline with further successive pairs formed dorsally. The fully developed free-swimming larva is called an **actinotrocha** or actinotroch and has a fairly characteristic appearance (Figs 9A; 10). It is not known in some species of phoronids. The **metasomal sac**, red corpuscle masses, blood vessel primordium, the **piriform-organ**, and mesocoel, and in some species, the adult tentacles below the larval ones, become visible before metamorphosis.

The pelagic existence of the actinotroch ends with a rapid (10–15 min) and "catastrophic" metamorphosis, which is activated by bacteria. This process begins with the evagination of the metasomal sac, then follows the pulling of the digestive tract into a U-shape, important tissue transformations (especially in the preoral lobe and in the perianal ciliated ring), the start of the blood circulation, and metamorphosis finally ends with the settlement of the young phoronid adult upon the sea-bottom (Fig. 9B).

All phoronid species show asexual reproduction, usually by transverse fission about the middle of the trunk, but *Phoronis ovalis* also reproduces by budding and autotomy of the lophophores (Fig. 11).

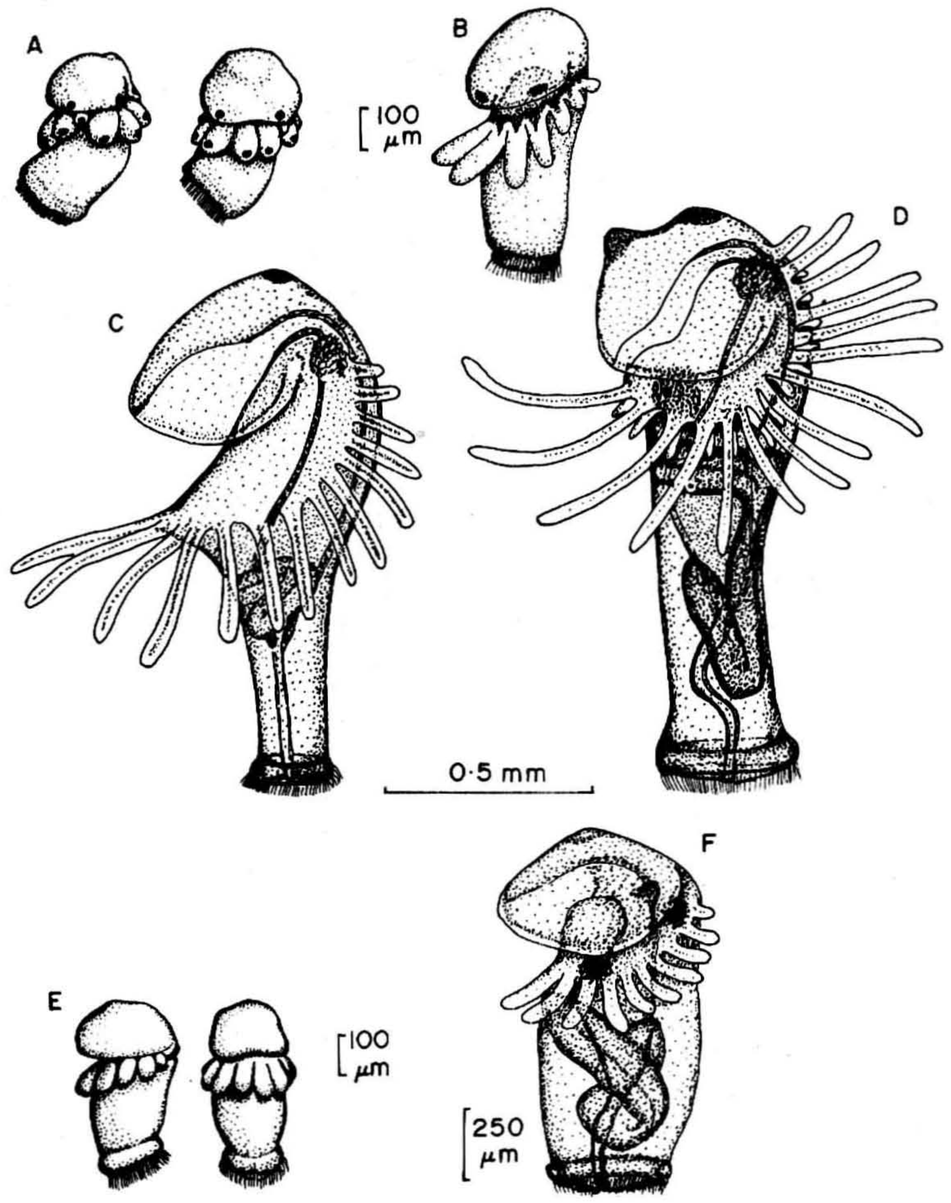


FIG. 10. A, *Actinotrocha hippocrepia* with five tentacle pairs and pigment spots (after Silén, 1954a), lateral and ventral views. B, *Actinotrocha vancouverensis* (the larva of *P. ijimai*) with seven pairs of tentacles and characteristic pigmentation. C, *Actinotrocha branchiata* as a fully developed larva with 15 pairs of tentacles and a small metasomal sac. D, *Actinotrocha branchiata* just before metamorphosis, with the adult tentacles below the larval ones, and the piriform organ. E, *Actinotrocha pallida* with five tentacle pairs (after Silén, 1954a), lateral and ventral views. F, *Actinotrocha harmeri*, fully developed with ten pairs of tentacles.

Feeding

Phoronids are suspension-feeders. Collection of food particles is one of the functions of the lophophore. The cilia on its tentacles create a feeding current, which transports the particles along their frontal surface down to the mouth at the bottom of the lophophoral cavity. Food particles are generally phytoplankton and other unicellular organisms, and also detritus. Rejected particles fall between the tentacles and pass away from the mouth. Recent experiments have revealed direct uptake of amino-acids through the epidermis in *Phoronis psammophila*. This uptake displays seasonal variations, with a maximum in summer.

Tube Building

The characteristically rigid tube of a phoronid consists of layers of chitin to which particles of sediment and debris from the animal's immediate environment adhere. Chitin is secreted by epidermal gland cells especially concentrated in the ampulla and over the anterior part of the body. The cells of the ampulla secrete the basic tube and lengthen it as the occupant grows, whilst the anterior gland cells repair the mouth region, i.e. that part of the tube most exposed to damage from current action, abrasion by sediment, etc.

When freshly produced, the secretion is fluid, transparent and sticky, but on contact with water it hardens. It is during the sticky phase that sand grains, shell fragments, minute stones, sponge spicules, etc. become attached. The coating of sedimentary particles therefore reflects the nature of the substratum in which the phoronid lives and can vary from fine mud particles and algae to coarse sand grains with shell fragments and fine pebbles.

Enemies and Regeneration

The predators of phoronids are not well known but they probably include fishes, gastropods and nematodes. The reaction of a phoronid to a predator is a very rapid retraction down into the tube out of harm's way. Should the anterior part of the body be taken by the predator, the phoronid can rapidly regenerate the lost part in two or three days. This type of "animal grazing" may provide an important food source. For example, the biomass of *Phoronis psammophila* is about 45 g/m^2 wet weight (15 g dry weight) for 15 000 individuals; the weight of the anterior region is about 3 g and 1 g (wet and dry weights respectively) for the same number of animals.

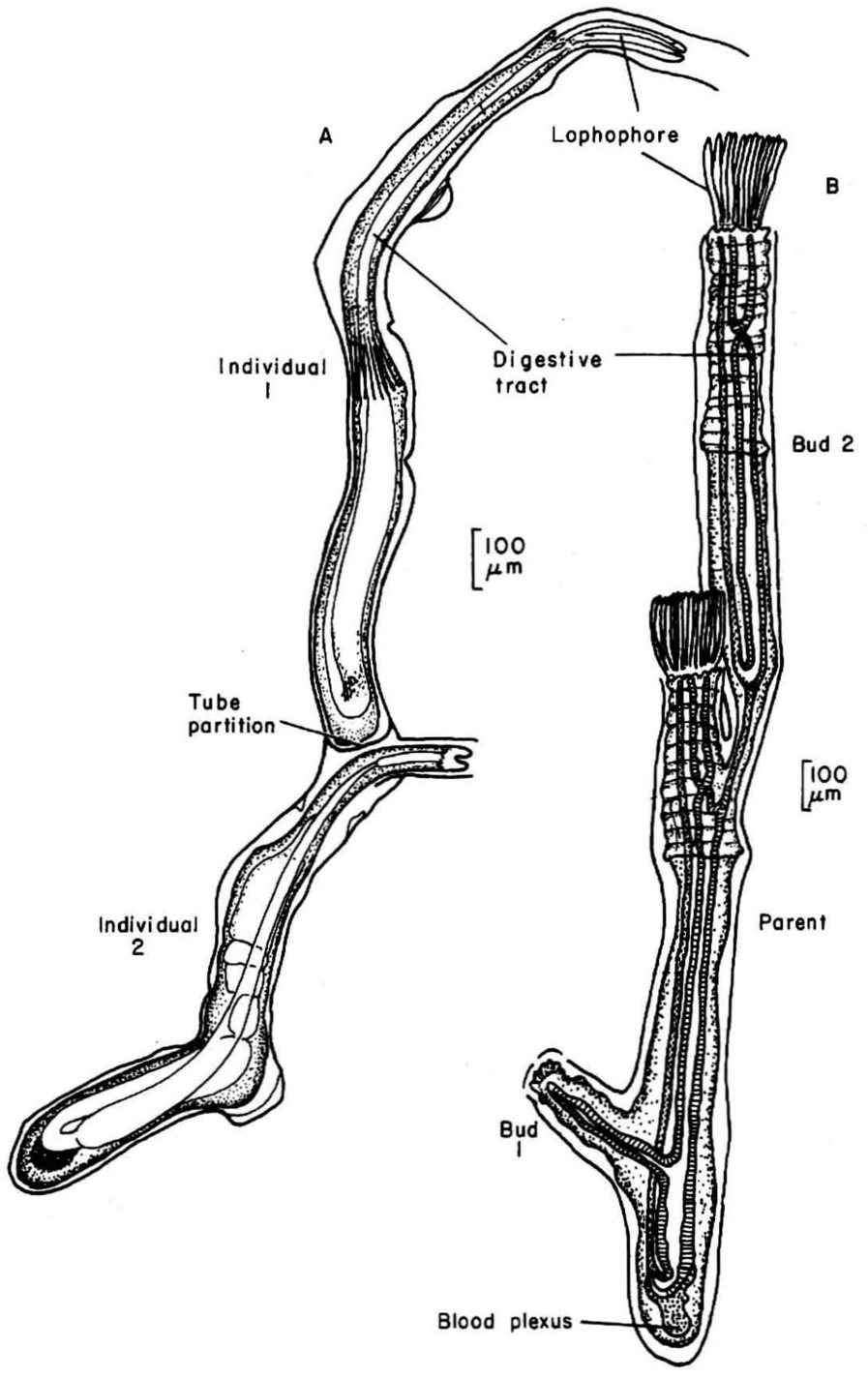
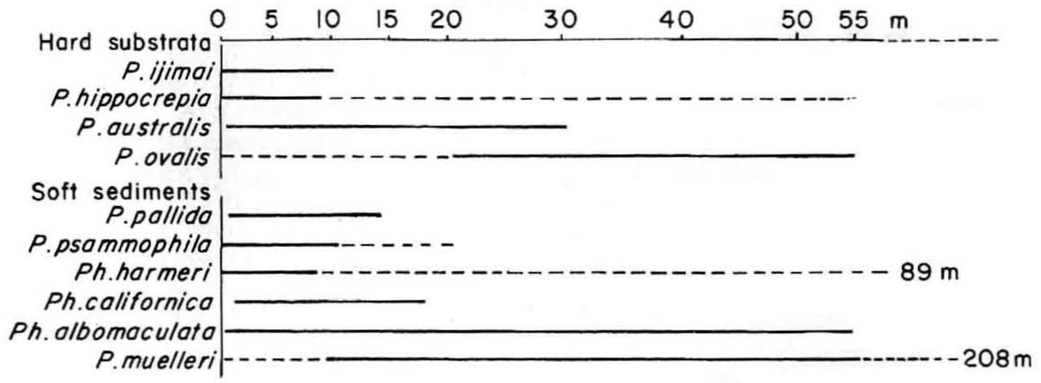


FIG. 11. Asexual reproduction in *Phoronis ovalis* by (A) transverse fission (after Harmer, 1917) and (B) budding (after Marcus, 1949).

Ecology

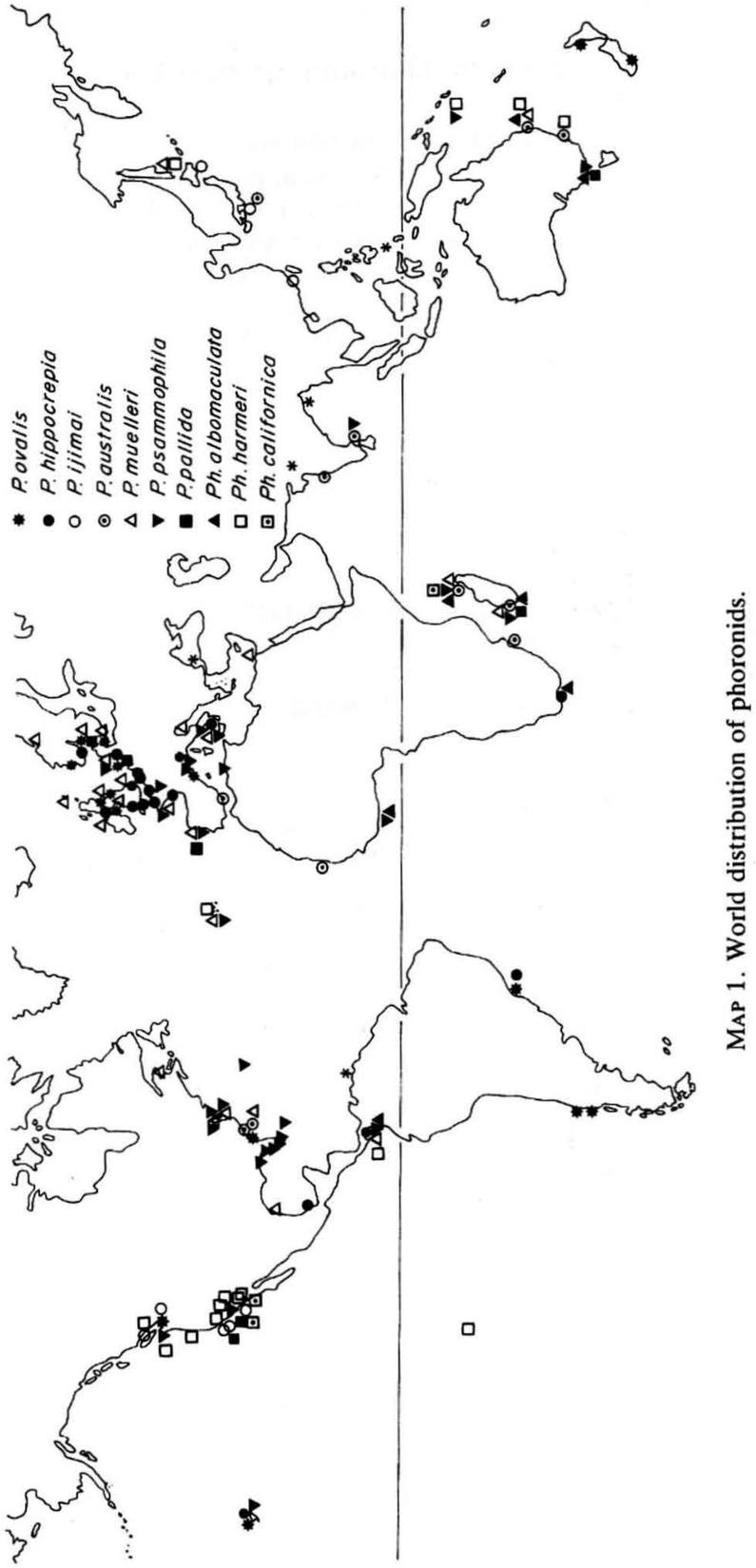
TABLE 2. Distribution of phoronids in relation to depth and substratum.



All phoronids are tubicolous but live free within their tubes. *Phoronis ovalis*, *P. hippocrepia* and *P. ijimai* burrow into rocks or mollusc shells: their tubes are generally membraneous and curved. *P. hippocrepia* and *P. ijimai* may occur in two forms, burrowing or encrusting, depending upon the nature of the environment. *Phoronis australis* displays a unique association with cerianthid anemones: numerous individuals (about 20–100), each in their own chitinous tube, occur in the tube-wall of the cerianthids. All other phoronid species live in sand encrusted tubes generally embedded vertically in soft sediments (mud to coarse sand). The distribution of the different species is shown in Table 2. Phoronids are present from the intertidal zone to about 200 m depth.

World Distribution

Phoronids have a world-wide distribution: they are known in all oceans and seas and are not uncommon in favourable situations. In some habitats they are very abundant (15 000–20 000 individuals/m^2). Most species are probably cosmopolitan (Map 1).



MAP 1. World distribution of phoronids.

Collection, Preservation and Examination

Phoronids can be collected most easily by Scuba-diving on rocky substrata; whilst on soft muddy or sandy bottoms, the best apparatus is a suction sampler (Emig and Lienhart, 1966; Emig, 1977d). Phoronids must be fixed quickly to prevent lophophore autotomy. The best fixative appears to be Bouin, although specimens stored for more than 8–10 years are usually impossible to identify because of tissue deterioration.

For accurate identification histological slides should be prepared from different levels of the animal, usually the whole of the anterior region and the posterior third of the trunk. The following routine has produced good results for histological examination of specimens:

(1) Bouin's Fixative	24 h
(2) dehydration in 95% alcohol	1 h
100% alcohol	1 h
three changes of toluene	15 min each
(3) wax-impregnation: three changes of paraffin	40 min each
(4) embed in paraffin wax	
(5) section at 7 μm	
(6) Azan stain, using Heidenhain's method.	

Classification

CLASS PHORONIDA

Phoronis ovalis Wright
Phoronis hippocrepia Wright
Phoronis muelleri Selys-Longchamps
Phoronis psammophila Cori
Phoronis pallida Silén

The following do not occur in British or adjacent waters, but as this is such a small group of animals, it has been decided to include them as an appendix to the Systematic part.

Phoronis ijimai Oka
Phoronis australis Haswell
(?*Phoronis bhadurii* Ganguly and Majumdar)
Phoronopsis albomaculata Gilchrist
Phoronopsis harmeri Pixell
Phoronopsis californica Hilton

Key to Adults of Species Occurring in British or Adjacent Waters*

1. Lophophore oval-shaped (nephridia with one funnel; no lateral mesenteries) ..... *Phoronis ovalis* (p. 28)

Lophophore horseshoe-shaped **2**

2. Nephridia with two funnels **3**

Nephridia with one funnel **4**

3. Nephridia without descending branch, ascending one with two horizontal chambers; two giant fibres; burrowing or encrusting habit
Phoronis hippocrepia (p. 32)

Nephridia U-shaped, i.e. ascending and descending branches about the same length; one giant fibre; unusual muscle disposition
Phoronis pallida (p. 42)

4. All mesenteries present; nephridiopore below anus
Phoronis psammophila (p. 40)

Left lateral mesentery lacking; prebuccal and post anal tentacles of the same length; lateral tentacles longer ..... *Phoronis muelleri* (p. 36)

Note: identification should always be verified by reference to the following species descriptions.

* See also Tables 1 and 3.

TABLE 3. Summary of the main taxonomic characteristics of phoronids from British and adjacent waters

Species	Habitat	Length up to (mm)	Lophophore shape	Nephridia	Giant fibres (diameter in μm)		Composite and mean muscle formulae		Hermaphrodite or dioecious	Nidamental glands	Lophophoral organs	Egg developmental type[a]
P. ovalis	hard substrata	15	oval		absent	14–39	left coelom: 7–21 right coelom: 7–19	29=15/14	?	absent	absent	1
P. hippocrepia	hard substrata	100	horseshoe	See Table 1	2 (left 4–10) (right 1–7)	24–43	$\frac{7–15}{3–7} \mid \frac{7–16}{3–10}$	$32=\frac{11}{5} \mid \frac{11}{5}$	♀	type a	small	2
P. psammophila	soft sediments	190	horseshoe		1 (7–27)	25–53	$\frac{7–19}{4–11} \mid \frac{7–17}{4–11}$	$34=\frac{11}{6} \mid \frac{11}{6}$	♀ ♂	type c	large glandular	2
P. muelleri	soft sediments	120	horseshoe (tentacles shorter at oral side)		1 (7–40)	18–30	$\frac{5–13}{2–6} \mid \frac{5–11}{3–6}$	$24=\frac{9}{3} \mid \frac{9}{3}$	♀ ♂	absent	large glandular	3
P. pallida	soft sediments	140	horseshoe		1 (10–20)	17–19	$\frac{5–6}{4} \mid \frac{5}{3–4}$	$18=\frac{5}{4} \mid \frac{5}{4}$	♀	absent	large glandular	3

[a] See p. 16

Systematic Part

Genus PHORONIS Wright, 1856

Absence of the epidermal collar-fold below the lophophore.

Phoronis ovalis Wright, 1856

(Figs. 5A; 11; 12A-D)

Phoronis ovalis: Wright, 1856; Harmer, 1917; Meek, 1917; Cori, 1939; Brattström, 1943; Silén, 1952, 1954a, 1955; Lönöy, 1954; Bruce *et al.*, 1963; Emig, 1969b, 1971b, 1973c, 1974

The whole animal ranges in length up to 15 mm, but is generally about 4–6 mm, with a diameter of 0·15–0·35 mm. The anterior body part is retractable into a very strongly developed ampulla. The animal is transparent, sometimes pigmented a brownish colour on the distal portion of the tentacles or over the whole body. The oval-shaped lophophore possesses about 11 to 28 tentacles which are 0·3–1·2 mm long (Fig. 12B). The nephridia are straight ascending ducts with a single small internal funnel which can be enlarged on maturation of the gonads (Fig. 12C). Distally, the nephridiopore opens on the anal papilla at the anus level. Giant fibres are absent, although sometimes a left and a right one about 2·5 μm in diameter seem to be present. As the two lateral mesentries are lacking, a conventional formula of longitudinal muscles bundles cannot be established; the composite formula is [14–39]: left coelom 7–21 and right coelom 7–19; and the mean formula 29 = 15/14. At present, information on gonads is contradictory: is *P. ovalis* hermaphroditic or possibly dioecious? The lophophoral organs are absent and no brooding occurs. The larva of *P. ovalis* is not a true actinotrocha; the embryo leaves the parental tube as a slug-like larva for a short pelagic life (Fig. 8B). *P. ovalis* has great potential for asexual propagation by transverse fission, budding, or automized lophophores (Fig. 11).

Other taxonomic characters are: absence of lateral mesenteries, and presence of an "accessory" blood vessel and of two lateral longitudinal blood vessels (Fig. 5A).

P. ovalis generally burrows into empty and decayed shells of a variety of molluscs, but also into rocks (limestone) or *Balanus*. Its thin, membraneous, hyaline tubes are curved in various ways and closely applied to the inner surface of the burrows; they are disposed parallel to the shell surface at different depths in the shell material beneath the periostracum. At its distal end, the tube becomes perpendicular to the shell surface, generally the external face, and opens to the exterior. The diameter of the majority of tubes is about 0·25–0·30 mm. As a result of the small size of *P. ovalis* and its great potential for asexual propagation, its density can be up to 1 500 000/m^2; it seems that this species reaches its greatest density in thick and large shells.

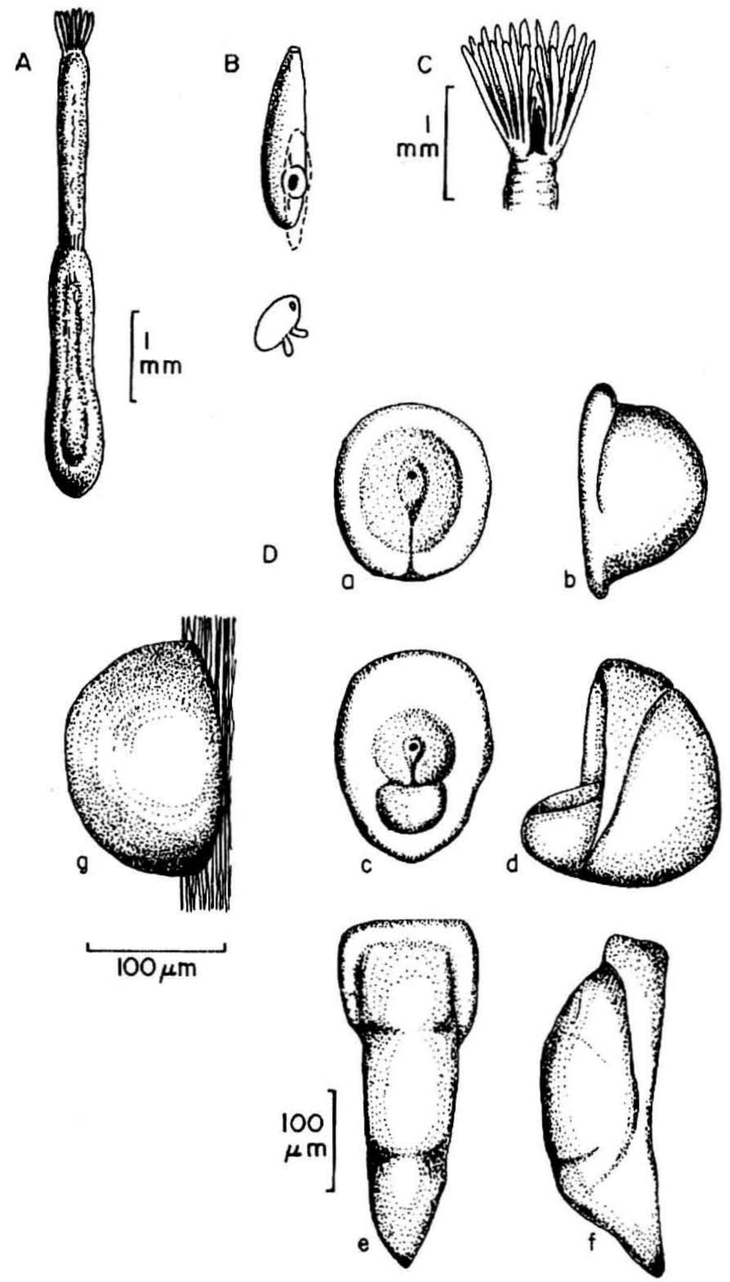
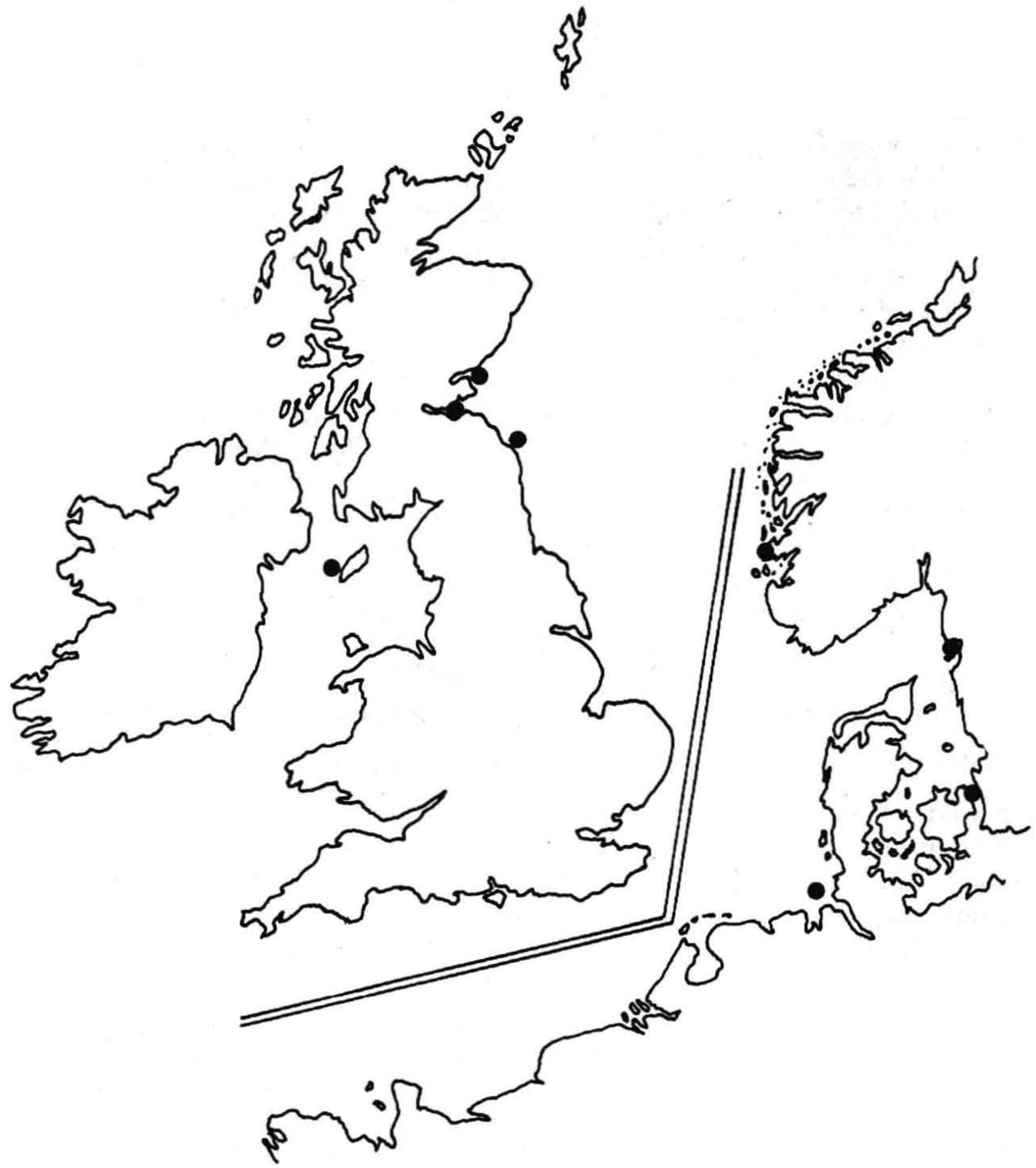


FIG. 12. *Phoronis ovalis*. A, Whole animal. B, Nephridium. C, Lophophore. D, Main stages of larval development from the newly escaped larva (a, b) to settlement on the substratum (g) (after Silén, 1954a).

P. ovalis has been recorded from the low tide mark to about 55 m, but it lives preferentially at 20–50 m depth (Table 2). Records of this species in British waters are shown in Map 2; it has also been recorded from Hawaii (Kanoehe Bay); USA (Washington State; Georgia); Chile (Tumbes; Mehuin); Brazil (Porchat Island; Lazaro); France (Cap Béar); Germany (Heligoland); Sweden (Ven Island; Gullmar Fjord); Norway (Bergen); New Zealand (Piha; Otago).



MAP 2. Distribution of *Phoronis ovalis* in British and adjacent waters.

Phoronis hippocrepia Wright, 1856

(Figs. 3A; 13A–D)

Phoronis hippocrepia: Wright, 1856; Dyster, 1859; Kölliker, 1864; Giard, 1879; Garstang, 1891; Selys-Longchamps, 1903, 1907; Hartlaub, 1904; Theel, 1907; Cori, 1932; Silén, 1952, 1954a; Naylor, 1965; Emig, 1970, 1971b, 1973c, 1977b; Hiscock and Howlett, 1975
Phoronis (*Crepina*) *gracilis* Van Beneden, 1858; Wright, 1859
Phoronis caespitosa Cori, 1889, 1890
Phoronis kowalevskii Benham, 1889
Phoronis capensis Gilchrist, 1907; Emig, 1971b

At its longest *P. hippocrepia* is about 100 mm, with a diameter of 0·3–1·5 mm. The colour is greenish-grey, yellowish or fleshy. The lophophore bearing the tentacles is horseshoe-shaped with the ends turned medially; the tentacles are 50–150 in number and 2–3 mm in length (Figs 13B; 3A). Nephridia have two funnels, with the anal larger than the oral; the descending branch lacks and the ascending one forms two horizontal chambers, the upper one is the nephridial ridge, on which opens the nephridiopore above or at the anus level (Fig. 13C). Two giant fibres are present one on the left (4–10 μm in diameter) and one on the right (1–7 μm in diameter) (Fig. 6); they occur at the attachment of the lateral mesenteries to the body wall. The composite formula of longitudinal muscles is [24–43] $\frac{7\text{–}15 \mid 7\text{–}16}{3\text{–}7 \mid 3\text{–}10}$; and the mean formula is $32 = \frac{11 \mid 11}{5 \mid 5}$; the longitudinal muscle bundles are of bushy type (Fig. 7A(i)). *P. hippocrepia* is hermaphrodite, male and female tissue developing at the same time in one animal. This species broods the embryos in paired lophophoral masses, the nidamental glands being of type *a*, i.e. on the floor of the lophophoral concavity and on the inner surface of those tentacles to which the embryo masses are attached (Fig. 3A, 13B). Spawning is continuous, the addition of new eggs to the brood masses pushing the older ones distally whilst simultaneously the young actinotrochs escape. Asexual propagation occurs by transverse fission.

The larva of *P. hippocrepia* is *Actinotrocha hippocrepia*, described by Silén (1954a): the larva ready for metamorphosis is about 0·7 mm long, possesses five pairs of tentacles and two sanguinary globules which fuse in older actinotrochs; and its pigmentation is characteristic—small dark-brown grains are assembled at certain fixed points of the body (Fig. 13D).

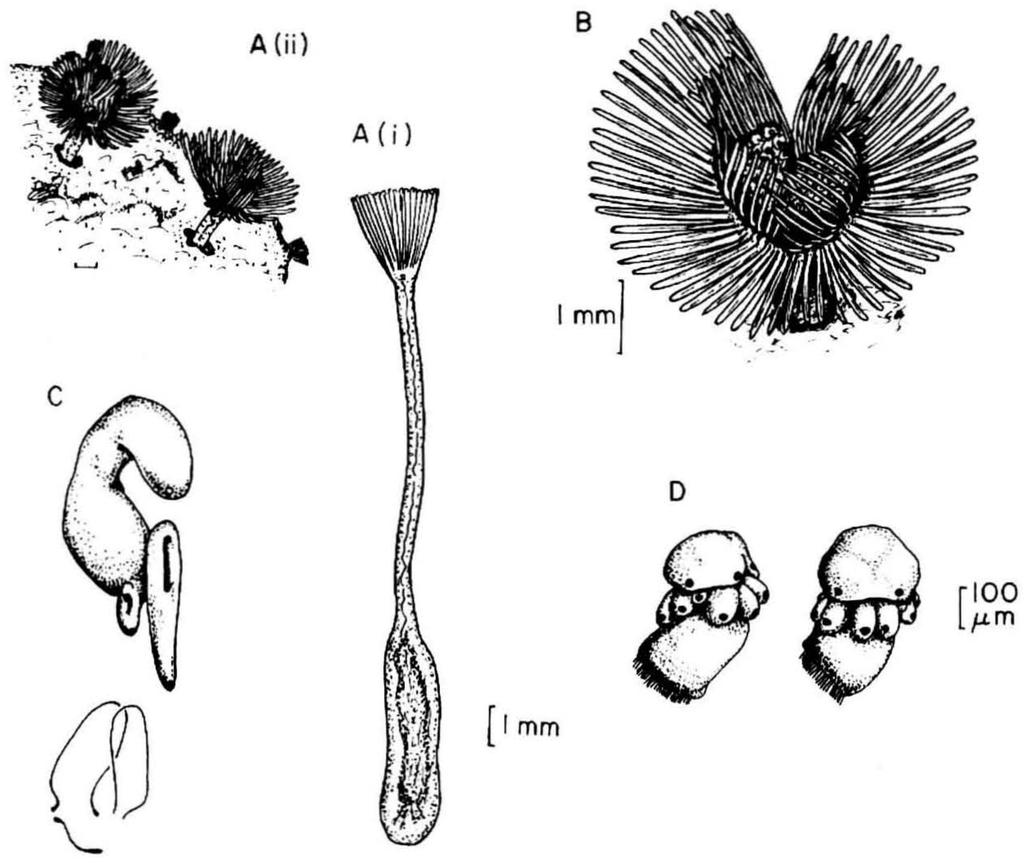


FIG. 13. *Phoronis hippocrepia*. A, Whole animal (i) out of tube (ii) *in situ*. B, Lophophore, showing two masses of embryos within the lophophoral concavity. C, Nephridium. D, Lateral and ventral views of actinotroch larva (after Silén, 1954a).

P. hippocrepia is a burrowing or encrusting species, the two forms inhabiting similar substrates (rocks, empty mollusc shells, *Caryophyllia*, *Lithothamnium*, wood). The tubes are sinuous, tangled and membraneous in the burrowing forms, and covered by diverse debris and fragments, sand and mud in encrusting populations. It seems that *P. hippocrepia* occurs in one or other form according to the pattern of water movements, the dessication stresses, or the presence of boring animals, such as *Polydora*. It has a bathymetric range from the intertidal zone, near the low tide mark, to 48 m deep (but generally 0–10 m, see Table 2); its density can reach more than 20 000 individuals/m^2. *P. hippocrepia* lives generally with other animals under poor conditions of illumination (sciaphilous fauna), occurring in algal communities and occasionally in concretionary hard substrata with sessile algae and animals ("coralligenous" community).

This species has a wide distribution; its occurrence in Britain is shown in Map 3, and it is otherwise known in Hawaii (Kanoehe Bay); Panama (W. coast); Mexico (Vera-Cruz); Brazil (Cananeia: Porchat Island); France (Étang de Berre; Marseilles; Arcachon; Roscoff; Tatihou; Wimereux); Belgium (Ostende); Germany (Heligoland); Sweden (Gullmar Fjord); Italy (Naples); South Africa (False Bay).

MAP 3. Distribution of *Phoronis hippocrepia* in British and adjacent waters.

Phoronis muelleri Selys-Longchamps, 1903

(Fig. 14A–D)

Phoronis muelleri: Selys-Longchamps, 1903, 1907; Meek, 1917; Gustafson, 1936; Brattström, 1943; Silén, 1952, 1954a; Judges, 1953; Jones, 1956; Bruce *et al.*, 1963; Dörjes *et al.*, 1970; Emig, 1970, 1971b, 1973a, c; Pearson 1970; Barnes and Coughlan, 1972; Gage, 1972a, b; Siewing, 1974; Holthe, 1977

The complete animals are usually about 5–12 cm long and 0·2–1 mm in diameter. The colour is yellowish, reddish or pink; occasionally the lophophore bears spots. The lophophore is in the form of a horseshoe, with the ends sometimes slightly turned medially. The tentacles range in number from about 40 to 98 and have a length of about 1–2 mm, but they become shorter in the middle of the oral side (Fig. 14B). Such a disposition is also observed in all phoronid species during lophophore regeneration and must not be mistaken for the normal lophophore of *P. muelleri*. Each nephridium ends at a single funnel in both the oral and anal compartments of the metacoelom at lateral mesentery level; it possesses a descending and an ascending branch which opens by the nephridiopore on the anal papilla at the anus level (Fig. 14C). There is a large conspicuous giant nerve fibre (7–40 μm in diameter) on the left side of the trunk, external to the normal site of the left mesentery, which is absent in *P. muelleri*, except at the nephridial level. The lack of the latter mesentery is indicated in the muscle formulae by a dotted line. The composite formula of longitudinal muscle bundles (which are of feathery type, see Fig. 7A(ii)) is: $[18–30]\begin{matrix}5–13\\ \vdots\\ 2–6\end{matrix}\cdot\left|\begin{matrix}5–11\\ \vdots\\ 3–6\end{matrix}\right.$, the mean combination being $24=\begin{matrix}9\\ \vdots\\ 3\end{matrix}\cdot\left|\begin{matrix}9\\ \vdots\\ 3\end{matrix}\right.$. *P. muelleri* is dioecious; the lophophoral organs are large and glandular; no brooding occurs and the ova are shed freely in the sea-water. This species shows asexual propagation by transverse fission.

The larva of *P. muelleri* is *Actinotrocha branchiata*, which was described before the discovery of the adult; this actinotroch is also the best known phoronid larva. *A. branchiata* is an unusual size (up to 2 mm in length) and the tentacle number reaches 16 pairs. The body is transparent, with pigmentiferous amoebocytes; there is a single pair of blood masses. Specimens ready to metamorphose show definite tentacles below the larval ones (Figs 9B; 10D; 14D).

P. muelleri is characteristic of muddy bottoms, with a sandy, sometimes a coarse fraction, and it is found in more or less straight tubes of fine, cemented, sand grains, vertically and entirely embedded in the sediment. Often, the anterior part of the tube is covered with mud, not sand. The bathymetric range varies from 0·6 to 208 m, but the common range is 10–50 m (Table 2). *P. muelleri* occurs in different communities (especially in those of *Amphiura* and of terrigenous muddy bottoms); its density can reach 3000 individuals/m^2.

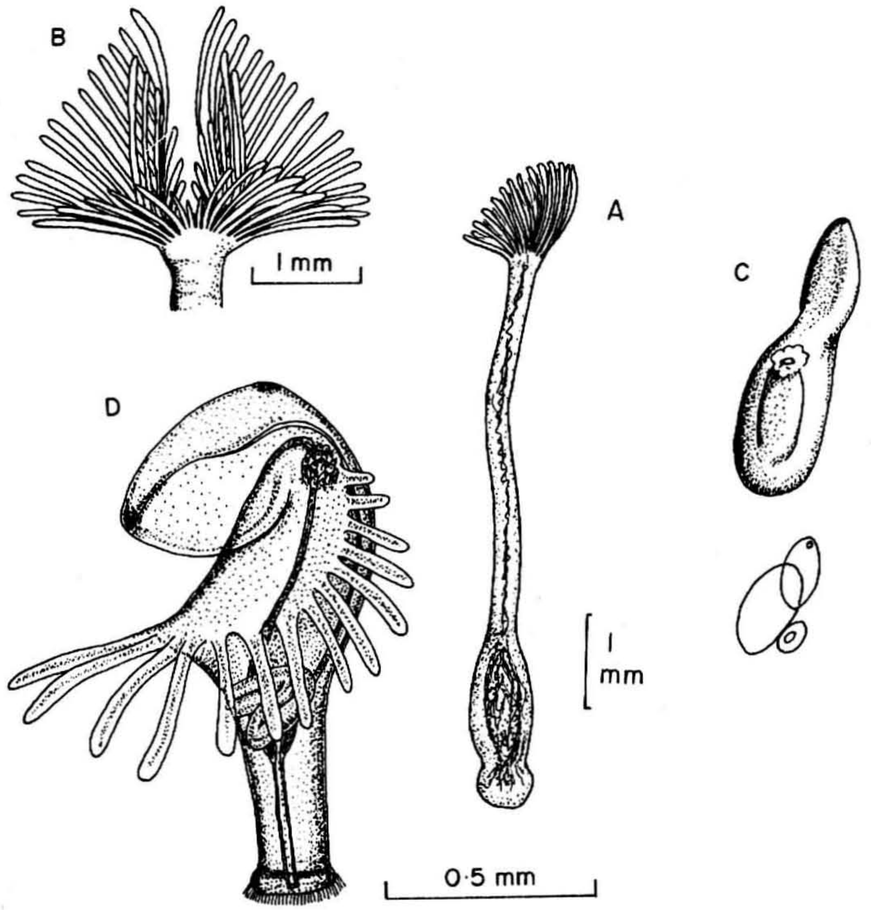


FIG. 14. *Phoronis muelleri*. A, Whole animal. B, Lophophore. C, Nephridium. D, Actinotroch larva.

P. muelleri has a world-wide distribution; the British records are shown in Map 4. *Actinotrocha branchiata* occurs in some British locations where the adult phoronid is unknown (Map 4); this larva is cited by Selys-Longchamps (1907), Browne (1895). The other world records of *P. muelleri* are from Panama (W. coast); East coast of North America; Azores; Spain (Vigo); France (Oleron Island); Germany (Heligoland; German Bight); Sweden (Ven Island; Gullmar Fjord); Norway (Bergen); Italy (Gaeta); Yugoslavia (Leme); Egypt (Alexandria); Madagascar (Tulear; Nosy-Bé); USSR (Kamchatka); Australia (Moreton Bay).

MAP 4. Distribution of larval and adult *Phoronis muelleri* in British and adjacent waters.

Phoronis psammophila Cori, 1889

(Fig. 15A–C)

Phoronis psammophila: Emig, 1969a, 1971b, 1973a, c; Ollivier, 1969
Phoronis sabatieri Roule, 1889; Emig, 1968
Phoronis architecta Andrews, 1890; Emig, 1969a, 1971b, 1977a

In extended size, *P. psammophila* ranges from 80 to 190 mm in length and 0·5 to 2 mm in diameter. The trunk colour is pink, whilst the lophophore is transparent with white spots, sometimes coloured in yellow, red or green. The lophophore is horseshoe-shaped with the ends turned medially; its tentacle number varies from 60 to 130, the tentacles ranging from 1·5 to 2·5 mm in length (Figs 3B, C; 15B). Each nephridium opens into both oral and anal compartments of the metacoelom by a single funnel, very markedly developed during the reproductive period. It shows a descending and an ascending branch which ends on the anal papilla by the nephridiopore, below the anus (Figs 1C; 3B, C; 4A; 15C). The single left giant nerve fibre is very large: about 7–27 μm in diameter. A very thin fibre is rarely found on the right side. The longitudinal muscle formula varies as follows: [25–53] $\frac{7\text{–}19 \mid 7\text{–}17}{4\text{–}11 \mid 4\text{–}11}$, the mean formula is $34 = \frac{11 \mid 11}{6 \mid 6}$. Longitudinal muscle bundles are of feathery type (Fig. 7A(ii)). *P. psammophila* is dioecious; the gonads are developed along the stomach on the capillaries of the lateral blood vessel (and sometimes along the secondary lateral vessel—Fig. 1E). The females brood their embryos in a single brood mass in the lophophoral concavity: the nidamental glands are of type *c* (Fig. 3). The wide embryo mass is accumulated at a single time by a massive, rapid egg-release, so all embryos are at the same stage of development, and a new mass is formed again after escape of the preceding one. *P. psammophila* asexually propagates by transverse fission.

The larva of *P. psammophila* is unknown.

This species typically occurs in sandy sediments, but can also be found in sandy mud, sand with a coarse fraction, sea meadows, and polychaete reefs. The chitinous tube is generally straight and covered by sand grains (Fig. 15A). *P. psammophila* is found from the intertidal zone to about 20 m depth, although usually between 4 and 7 m (Table 2). The highest known density is about 17 000 individuals/m^2. It lives mostly in fine well-sorted sand, but also in superficial muddy sand bottoms (*Venus-Abra alba* and *Macoma baltica* communities).

P. psammophila, still unknown in British waters (Map 5), is cosmopolitan and has been recorded from Hawaii (Kaneohe Bay); Pacific coast of USA and Panama; East coast of USA; Bermuda; Bahamas; Azores; Ivory Coast (Grand Bassam); Algeria (Castiglione); Italy (Messina; Naples; Gaeta); France (Marseilles region; Étang de Thau; Morbihan; Dinard); Germany (German Bight); Madagascar (Tulear; Nosy-Bé); India (Porto-Novo); Australia Melbourne); Solomon Islands.

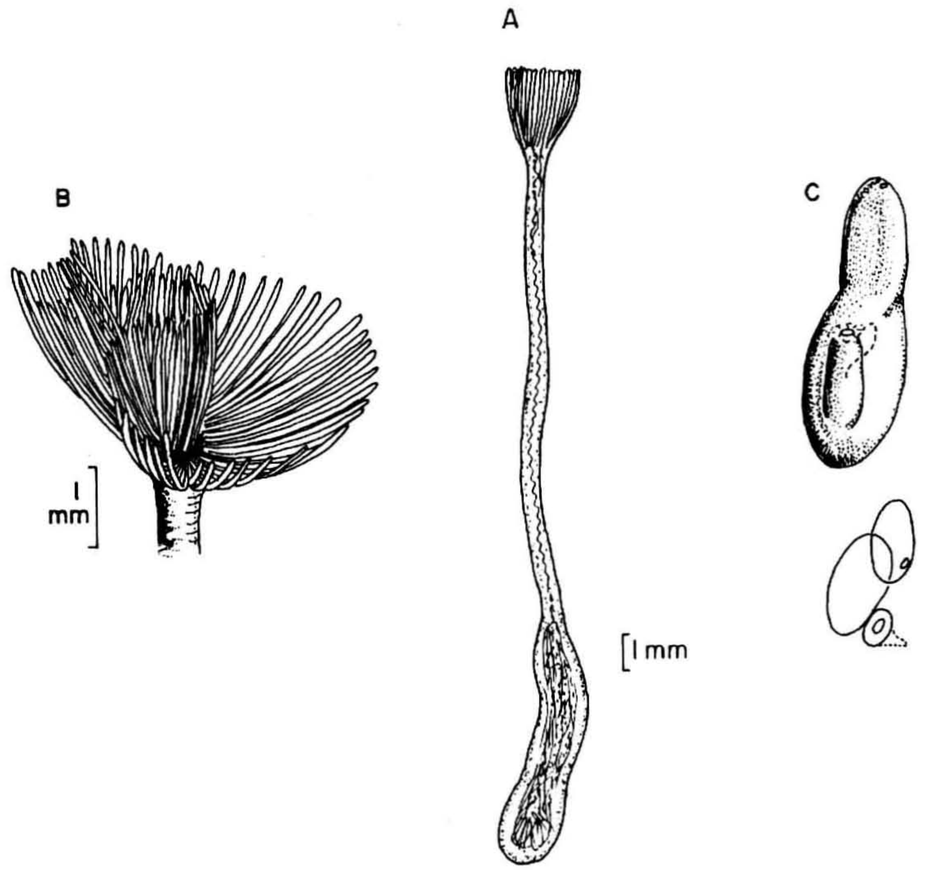


FIG. 15. *Phoronis psammophila*. A, Whole animal. B, Lophophore. C, Nephridium.

Phoronis pallida Silén, 1952

(Figs. 7B; 16 A–E)

Phoronis pallida: Schneider, 1862; Silén, 1952, 1954a; Emig, 1969b, 1973c

The whole animal reaches a length of 140 mm and ranges in diameter between 0·3 and 1 mm. Its colour is pink-yellowish. The horseshoe-shaped lophophore possesses between 50 and 140 tentacles, each about 2·5 mm long (Fig. 16B). *P. pallida* possesses paired nephridial funnels, the anal one being slightly larger than the oral one; both ascending and descending branches have the same length. The nephridiopore opens on the anal papilla at the anus level (Fig. 16C). The single (left) giant fibre is very large (diameter about 10–20 μm). The composite formula of the longitudinal muscle bundles is: [17–19] $\frac{5\text{–}6 \mid 5}{4 \mid 3\text{–}4}$, and the mean formula is $18 = \frac{5 \mid 5}{4 \mid 4}$. *P. pallida* is the only phoronid with such a constant number of longitudinal muscles. The same trunk musculature also shows another characteristic feature, unusual in phoronids: circular muscles with three strong horizontal sphincters, and longitudinal muscles divided into six zones (Figs 7B; 16D). *P. pallida* is an hermaphrodite: male and female reproductive tissues developing at the same time in one animal are disposed near the stomach respectively on the oral and anal side of the lateral blood vessel, but often also in the reverse position. This species discharges its ova directly into the sea-water; the lophophoral organs are large and glandular.

The larva of *P. pallida* is *Actinotrocha pallida*, which is small (maximum 0·6 mm long), with five pairs of tentacles. Its body is opaque, yellowish white, and shows a single blood mass (Fig. 16E).

P. pallida occurs in sand or clayed sand, from 1 to 14 m depth (Table 2); its density can reach about 74 000/m^2. No other information has been published on this species. As yet unknown in British waters, *P. pallida* occurs in Sweden (Map 5); Spain (Vigo); USA (California); Germany (German Bight); Madagascar (Tulear); Australia (Melbourne).

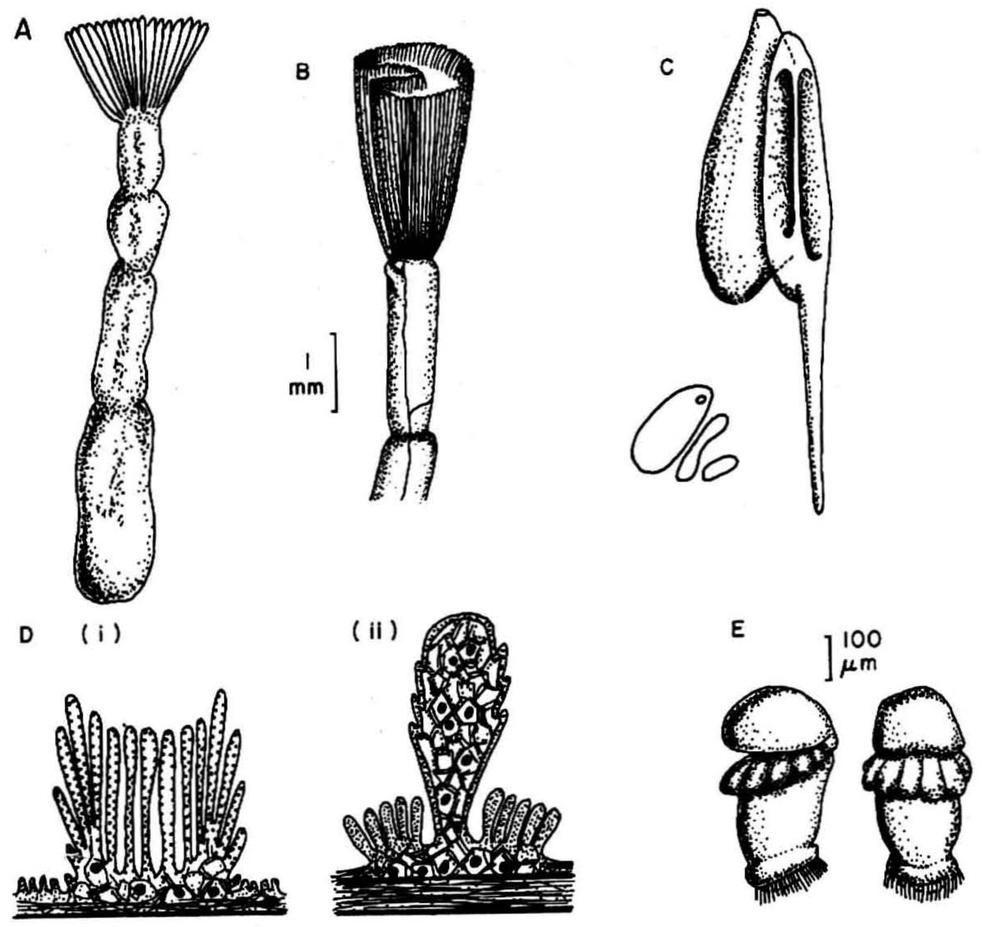
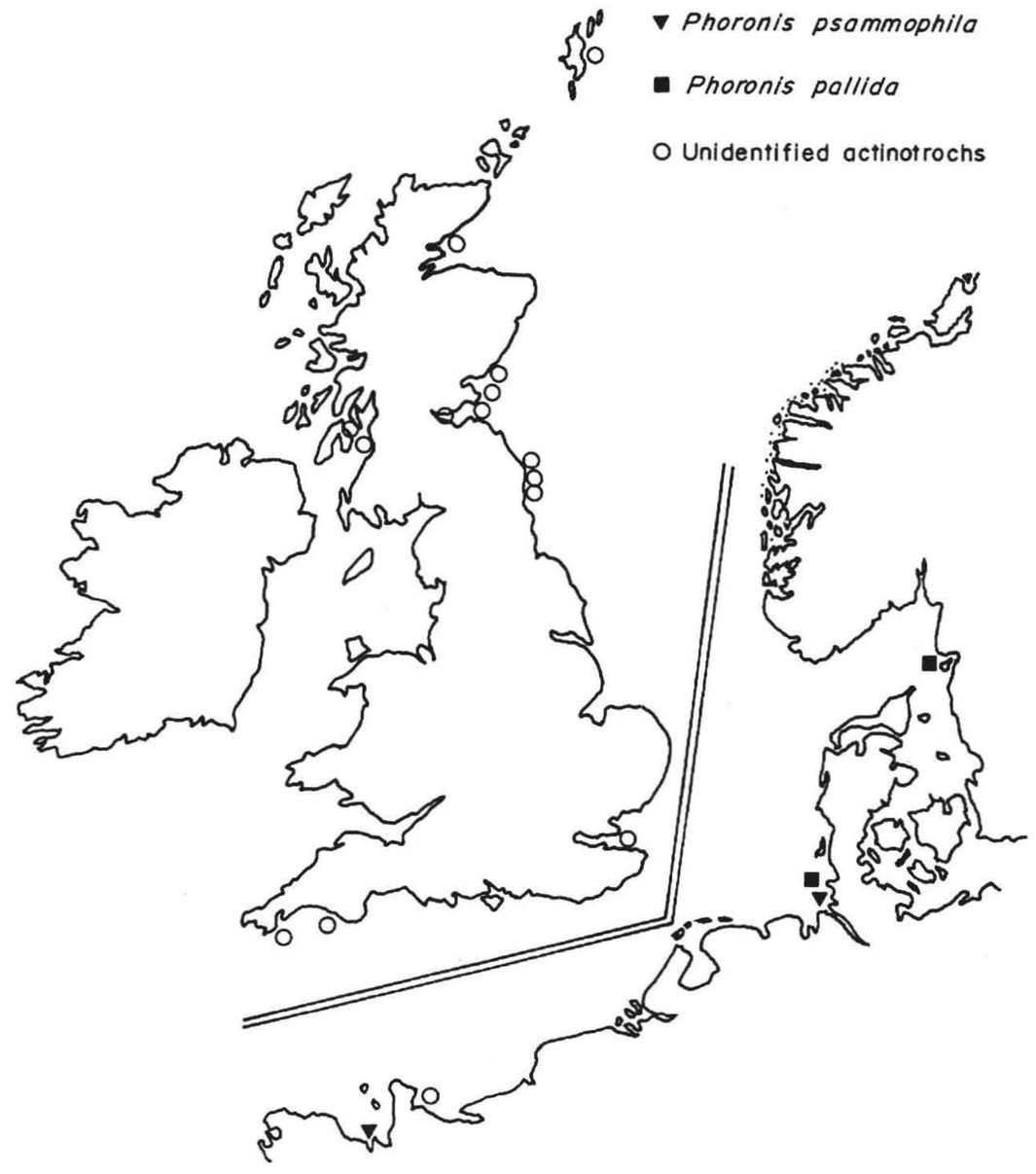


FIG. 16. *Phoronis pallida*. A, Whole animal. B, Distal end of contracted specimen (after Silén, 1952). C, nephridium. D, Sections of longitudinal muscles in zones III and IV (after Silén, 1952). E, Lateral and ventral views of the actinotroch (after Silén, 1954a).

Actinotrocha sp.

Except *Actinotrocha branchiata* (see *Phoronis muelleri*), all other phoronid larvae recorded on the British coasts have not been identified or their identity is doubtful.

Their distribution is shown on Map 5, from data in Cobbold (1858), Cunningham (1886), Herdman (1886), Shrubsole (1886), McIntosh (1886), Barstang (1891), Browne (1895, 1900), Meek (1917), etc.



MAP 5. Distribution of *Phoronis psammophila, P. pallida* and unidentified actinotrochs in British and adjacent waters.

Appendix

Species of phoronids absent from British and adjacent waters.

Phoronis ijimai Oka, 1897

Phoronis ijimai: Oka, 1897; Ikeda, 1901; Emig, 1971a, 1977a
Phoronis vancouverensis Pixell, 1912; Marsden, 1959; Zimmer, 1967; Emig, 1971a, 1977a, b

Length of the extended body up to 120 mm; diameter 0·5–2 mm. Colour pink to transparent, sometimes with white spots on the lophophore. Lophophore horseshoe-shaped or spiral with up to one coil; tentacles 70–230 in number and 2–5 mm long. Nephridia with two funnels (anal large and oral small); descending branch absent; nephridiopore on nephridial ridge opening above or at anus level (Fig. 4D(ii); Table 1). Giant nerve fibres two (one left 3–10 μm in diameter; one right 2–8 μm). Longitudinal muscle bundles of bushy type:

[37–69] $\frac{10–32 \mid 13–31}{2–14 \mid 3–13}$; mean formula $56 = \frac{20 \mid 22}{7 \mid 7}$. *P. ijimai* is hermaphrodite; nidamental glands of type *a*; lophophoral organs small: embryos brooded in paired lophophoral masses; egg developmental type is *2*. Asexual reproduction by transverse fission.

The larva is *Actinotrocha vancouverensis*. The actinotroch ready for metamorphosis is about 0·8 mm long, possesses seven pairs of tentacles, no adult tentacles, only one blood mass, and shows a characteristic pigmentation (Fig. 10B).

P. ijimai is an encrusting (occasionally a burrowing) species on rocks, wood, or soft sediments such as sand or mud, living in turf-like masses with many intertwined tubes, from 0 to 10 m depth; its habitat seems to be similar to that of *Phoronis hippocrepia*. Its density reaches 20 000 individuals/m^2.

It has been recorded from Canada (Vancouver Island); USA (San Juan Archipelago, California); China (Amoy); Japan (Akkeshi Bay; Tokyo Bay).

Phoronis australis Haswell, 1883

Phoronis australis: Haswell, 1883; Benham, 1889; Emig and Marche-Marchad, 1969; Emig *et al.*, 1972; Emig, 1973c, d, 1977a; Emig *et al.*, 1978
Phoronis buskii McIntosh, 1888; Masterman, 1900

Body length up to 200 mm; diameter 2–5 mm. Colour of anterior body part black, deep reddish or pink. Lophophore spiral with 2·5 to 3·5 coils on each side (Fig. 2E); tentacles 400–1600, 5–16 mm long, the bases of the tentacles being connected together for about $\frac{1}{4}$ of their total length. Nephrida with two funnels (anal large, oral small); descending branch lacking; nephridiopore on nephridial ridge, opening above the anus or at its level (Figs 3D–4D(iii)). Giant nerve fibres two (one left 5–11 μm in diameter; one right 3–13 μm). Longitudinal muscle bundles of bushy type: [43–87] $\frac{15–29 \mid 13–27}{4–17 \mid 5–17}$; mean formula $64 = \frac{22 \mid 22}{11 \mid 9}$. *P. australis* is hermaphrodite: nidamental glands of type *b* and lophophoral organs small; embryos brooded on mucous cord (Fig. 3D); egg development type *2*.

The larva is unknown. Asexual propagation by transverse fission.

P. australis burrows into the tube-wall of cerianthids, forming a commensal association with the anthozoan. Its bathymetric range is 0–30 m, and its density is up to 100 per cerianthid tube. It has been recorded from USA (Georgia); Senegal (Somone); Spain (Almeria); Israel (Eilat); Mozambique (Inhaca Island); Madagascar (Tulear; Nosy-Bé); India (Port Okha; Krusadai Island); Japan (Misaki); Australia (Moreton Bay; Sydney); China.

Genus PHORONOPSIS Gilchrist, 1907

Presence of the epidermal collar-fold below the lophophore.

Phoronopsis albomaculata Gilchrist, 1907

Phoronopsis albomaculata: Gilchrist, 1907; Emig, 1973c, d, 1977a; Emig *et al.*, 1978

Length up to 150 mm, 0·5–2 mm in diameter. Colour yellowish with lophophore pigmented with white spots. Lophophore horseshoe-shaped or spiral with one coil; tentacles 70–160 and 2–3 mm long. Nephridia with a single funnel, a U-shaped tube, the nephridiopore below the anus on the anal papilla opening in the epidermal invagination (Fig. 4C(iii); Table 1). A single giant nerve fibre on the left side, 15–35 μm in diameter; the right one ends at the nephridial level. Longitudinal muscle bundles of feathery type: [46–102] $\frac{14–33 \mid 15–33}{7–20 \mid 7–16}$; the mean formula $72 = \frac{23 \mid 23}{14 \mid 12}$. *Phoronopsis albomaculata* is dioecious; lophophoral organs large and glandular, probably nidamental glands. Asexual reproduction by transverse fission.

The larva is unknown.

The epidermal invagination, below the lophophore, is about 0·1 mm, well-marked on the anal side.

Phoronopsis albomaculata occurs in soft sediments from clogged coarse sand to sandy mud, from 0 to 45 m depth. It lives in straight tubes of cemented sand grains, vertically embedded in the sediment. This species is especially found in coarse sand under strong bottom currents. It has been recorded from Panama (Pacific coast); Ivory Coast; Madagascar (Tulear; Nosy-Bé); South Africa (False Bay); Australia (Melbourne; Moreton Bay).

Phoronopsis harmeri Pixell, 1912

Phoronopsis harmeri: Pixell, 1912; Marsden, 1959; Mamkaev, 1962; Zimmer, 1967; Emig, 1967, 1971b, 1973c, 1977a
Phoronis pacifica Torrey, 1901; Ledig, 1919; Emig, 1971b
Phoronopsis viridis Hilton, 1930a; Marsden, 1959; Emig, 1971b
Phoronopsis striata Hilton, 1930a; synonymy established on unpublished data by the present author

Length of the extended body up to 220 mm, diameter 0·6–4 mm. Colour greenish to pink, with tentacles sometimes white pigmented. Lophophore spiral with 1·5 to two coils on each side; tentacles 100–400 in number, 2–5 mm long (Fig. 2D). Nephridia with two funnels (anal smaller, oral larger), U-shaped tube, nephridiopore below the anus on the anal papilla opening in the collar invagination (Fig. 4E(ii); Table 1). Giant nerve fibre on the left side (20–60 μm in diameter), the right ends at nephridial level. Longitudinal muscle bundles of feathery type: [75–145] $\frac{20–49 \mid 23–55}{12–28 \mid 11–26}$; mean formula $113 = \frac{37 \mid 37}{21 \mid 18}$. *Phoronopsis harmeri* is dioecious; lophophoral organs large and membranous; nidamental glands absent, no brooding, and eggs shed directly into the sea (egg developmental type *3*). Asexual propagation by transverse fission.

The larva of *Phoronopsis harmeri* is *Actinotrocha harmeri*. This actinotroch is ready for metamorphosis when about 1 mm long; it possesses ten pairs of tentacles, no adult tentacles, four blood masses, no distinctive dense epidermal pigmentation. The piriform-organ is not present at the beginning of metamorphosis.

The collar invagination is very distinct round the lophophore basis (Fig. 2D).

Phoronopsis harmeri lives in straight sand-encrusted tubes, vertically disposed in soft sediments (sands to mud, sometimes with a coarse fraction), from the intertidal zone to 89 m deep (common range: 0–12 m; Table 2); it is locally abundant with up to 28 000 individuals/m^2. It has been recorded from the Pacific coast of North America and Panama; Cook Island; Azores; Australia (Moreton Bay; Sydney); Solomon Islands; USSR (Sakhalin Island).

Phoronopsis californica Hilton, 1930

Phoronopsis californica: Hilton, 1930b; Emig, 1973c, d

Length of extended body reaches more than 450 mm, diameter 2·5–5 mm. Colour of body orange to brown; lophophore orange, red, grey, or greenish. Lophophore helicoidal-shaped with 4–5 coils on each side; lophophore length 5–7 mm (Fig. 2F); tentacles more than 1500 in number, 2–2·5 mm long. Nephridia with two funnels (anal larger than oral), U-shaped tube, nephridiopore below the anus on anal papilla opening in the collar invagination (Fig. 4E(iii); Table 1). Giant nerve fibre on the left side (70–80 μm in diameter); the right one ends at nephridial level. Longitudinal muscle bundles of feathery type: [180–243] $\frac{53\text{–}81 \mid 56\text{–}79}{35\text{–}54 \mid 29\text{–}40}$; the mean formula $211 = \frac{66 \mid 66}{44 \mid 35}$. *Phoronopsis californica* is dioecious; lophophoral organs large and membranous; no information on nidamental glands and egg type.

The larva is unknown.

The collar-fold is about 1 mm deep, well-marked round the lophophore (Fig. 2F).

Phoronopsis californica occurs from mud to coarse sands, from 0 to 17 m depth, living in vertically embedded, sand or gravel-encrusted tubes. It is known from the USA (southern California) and Madagascar (Nosy-Bé).

Glossary of Special Terms

ACCESSORY SEX GLANDS: Represented by the lophophoral organs and the nidamental glands.
ACTINOTROCHA (or actinotroch): Technical name of the larval form in Phoronida.
AMPULLA: Posterior end-bulb of the trunk.
APICAL PLATE: Larval sensory organ on the preoral lobe.
ARCHENTERON: Embryonic digestive tract (endoderm).
BLASTOCOEL: Primary body cavity.
BLASTOPORE: Invagination pore between the two first primordial layers, ectoderm and endoderm.
COELOM: Secondary body cavity, bounded on all sides by mesoderm and filled with fluid.
COLLAR-FOLD: Epidermal invagination at the basis of the lophophore (used as generic criterion).
DIAPHRAGM: Complete transverse septum which separates the mesocoelom from the metacoelom, and the protocoelom from the metacoelom.
ECTODERM: First primordial cell layer.
EMBOLY: Invagination of the vegetative pole, differentiating endoderm.
ENDODERM: Second primordial cell layer.
ENTEROCOELOUS METHOD OF MESODERM FORMATION: By outpouching of the archenteron wall (in Phoronida, mesoderm formation by budding off archenteric cells is considered as a modified enterocoelous type).
EPISTOME: Lip along the inner tentacle row, covering the mouth from the dorsal side.
EXOSKELETON: Hardened epidermal secretions (chitinous tube in phoronids).
FUNNEL: Internal opening of metanephridium into the coelom.
GIANT NERVE FIBRE: Longitudinal lateral nerve, consisting of a single fibre.
LOPHOPHORAL CAVITY: Space between the inner and the outer tentacle row; its bottom is occupied by the mouth.
LOPHOPHORAL CONCAVITY: Space limited by the inner tentacle row.
LOPHOPHORAL ORGANS: Pair of glandular pockets; are accessory spermatophoral organs.
LOPHOPHORATA: Phylum, including Brachiopoda, Bryozoa, Phoronida. Its definition: Benthic enterocoelous coelomates, characterized by the lophophore. Body generally regionated into three parts (prosome, mesosome, metasome), each containing its own coelomic cavity. Nervous system basiepithelial, without cephalization. Secretion of an exoskeleton. Egg cleavage radial and total. Coelom originated from archenteric wall, by a modified enterocoelous method. Larva related to the dipleurula type.
LOPHOPHORE: Tentaculated extension of the mesosome (and its cavity, the mesocoelom) that embraces the mouth, but not the anus, and its main functions are feeding, respiration, and protection.

MESENTERY: Sheet composed of a double layer of peritoneum.
MESOCOEL: Larval coelomic cavity of the larval mesosome.
MESOCOELOM: Coelomic cavity of the mesosome of the adult phoronid (also called lophophoral coelom).
MESODERM: Third primordial cell layer (arising by a modified enterocoelous type in Lophophorata).
MESOSOME: Second body section, especially formed by the lophophore in adult and the tentacular collar in actinotroch.
METACOEL: Coelomic cavity of the larval trunk (metasome).
METACOELOM: Coelomic cavity of the trunk (metasome) of the adult phoronid.
METASOMAL SAC: Primordium of the adult trunk wall in fully developed actinotroch; it evaginates at metamorphosis.
METASOME (or trunk): Third body section, containing the digestive tract, gonads, nephridia, main circulatory system.
NEPHRIDIUM: Excretory organ (also gonoduct: serving for discharge of sex cells from coelom to exterior). In actinotroch, it is closed at its inner end (protonephridium) and open at its inner end in adult phoronid (metanephridium).
NEPHRIDIOPORE: Exterior opening of a nephridium.
NIDAMENTAL GLAND: Brooding glandular organ.
PERITONEUM: Mesodermal epithelium lining the metacoelom.
PHORONIDA: Class of the phylum Lophophorata. Its definition: solitary animals, living in a chitinous tube. U-shaped digestive tract, with mouth and anus. Nervous system with main centre between mouth and anus, nerve ring, one or two giant fibres. Two metanephridia, also gonoducts. Circulatory system of closed type, with red corpuscles (haemoglobin).
PIRIFORM-ORGAN: Sensory and nervous organ, which appears just before the metamorphosis (in *Actinotrocha branchiata*).
PREORAL LOBE: Hood which overhangs ventrally the mouth in actinotroch (considered as prosome).
PROCTODAEUM: Ectodermal termination of the posterior opening of the archenteron.
PROSOME: First body section, represented by the preoral lobe in actinotroch and by the epistome in adult phoronid.
PROTOCOEL: Coelomic cavity of the larval preoral lobe.
PROTOCOELOM: Coelomic cavity of the epistome.
RADIAL CLEAVAGE: Radial egg symmetry because the meridional division planes pass through the polar axis (animal-vegetative poles).
SEPTUM: Membrane closing the metacoel anteriorly.
TRUNK (or Metasome): Third body section containing the digestive tract gonads, nephridia and main vessels of the circulatory system.

References

A general account of phoronids can be found in *Traité de Zoologie* Vol. V, Ed. P. P. Grassé (Masson, Paris; 1959) and in *The Invertebrates* Vol. V by L. H. Hyman (McGraw-Hill, New York; 1959).

ANDREWS, E. A. 1890. On a new American species of the remarkable animal *Phoronis*. *Ann. Mag. nat. Hist.* **5,** 445–449.

BARNES, R. S. K. and COUGHLAN, J. 1972. The bottom fauna of the Blackwater estuary: the macrofauna of the area adjacent to Bradwell nuclear generating station. *Essex Naturalist* **33,** 15–31.

BENEDEN, P. VAN 1858. Note sur un annélide céphalobranche sans soies, désigné sous le nom de *Crepina*. *Ann. Sci. nat.* **10,** 11–23.

BENHAM, W. B. 1889. The anatomy of *Phoronis australis*. *Q. Jl microsc. Sci.* **30,** 125–158.

BRATTSTRÖM, H. 1943. *Phoronis ovalis* Wright, eine für die skandinavische Fauna neue Phoronide aus Øresund. *Acta Univ. Lund* (Unders. Øresund) **39** (2), 1–17.

BROWNE, E. T. 1895. On the changes in the pelagic fauna off Plymouth during September 1893 and 1895. *J. mar. biol. Ass. U.K.* **4,** 168–173.

BROWNE, E. T. 1900. The fauna and flora of Valencia Harbour on the west coast of Ireland. *Proc. R. Ir. Acad.* **5,** 667–693.

BRUCE, J. R., COLMAN, J. C. and JONES, N. S. 1963. *Marine fauna of the Isle of Man*. Liverpool University Press, 224 pp.

COBBOLD, T. S. 1858. On a probably new species or form of *Actinotrocha* from the Firth of Forth. *Q. Jl microsc. Sci.* **6,** 50–52.

CORI, C. J. 1889. Beitrag zur Anatomie der *Phoronis* Inaug. Diss. Prag, 48 pp.

CORI, C. J. 1890. Untersuchung über die Anatomie und Histologie der Gattung *Phoronis*. *Z. wiss. Zool.* **51,** 480–568.

CORI, C. J. 1932. Phoronidea. *Die Tierwelt der Nord- und Ostsee* (Ed. Grimpe and Wragler) **7** (2), 101–132.

CORI, C. J. 1939. Phoronidea. *Bronn's Kl. Ordn. Tierreichs* **4** (4), 1–183.

CUNNINGHAM, J. T. 1886. *Tornaria* and *Actinotrocha* of the British coasts. *Nature, Lond.* **34,** 361.

DÖRJES, J., GADOW, S., REINECK, H. E. and BIR SINGH, I. 1970. Sedimentologie und Makrobenthos der Nordgründe und der Aussenjade (Nordsee). *Senckenberg. marit.* **2,** 31–59.

DYSTER, F. D. 1859. Notes on *Phoronis hippocrepia*. *Trans. Linn. Soc. Lond.* **22,** 251–256.

EMIG, C. C. 1966. Anatomie et écologie de *Phoronis psammophila* Cori (Golfe de Marseille et environs; Étang de Berre). *Rec. Trav. St. mar. Endoume* **40,** 161–248.

EMIG, C. C. 1967. Considérations sur la systématique des Phoronidiens. II. *Phoronopsis harmeri* Pixell, 1912. *Bull. Mus. Hist. nat., Paris* **39,** 984–991.

EMIG, C. C. 1968. Présence de *Phoronis psammophila* Cori: la bioconenose des Sables Fins en Mode Calme. *Bull. Soc. zool. Fr.* **93,** 115–125.

EMIG, C. C. 1969a. Considérations sur la systématique des Phoronidiens. III. *Phoronis psammophila* Cori, 1889, et *Phoronis architecta* Andrews, 1890. *Bull. Mus. Hist. nat., Paris* **41,** 312–327.

EMIG, C. C. 1969b. Considérations sur la systématique des Phoronidiens. VIII. *Phoronis pallida* (Schneider) Silén, 1952. IX *Phoronis ovalis* Wright, 1856. *Bull. Mus. Hist. nat., Paris* **41,** 1531–1542.

EMIG, C. C. 1970. Remarks on the systematics of Phoronidea. IV. Notes on the ecology, morphology and taxonomy of *Phoronis mülleri. Mar. Biol.* **5,** 62–67.
EMIG, C. C. 1971a. Remarques sur la systématique des Phoronidea. X. Notes sur l'écologie, la morphologie et la taxonomie de *Phoronis ijimai* et *Phoronis vancouverensis. Mar. Biol.* **8,** 154–159.
EMIG, C. C. 1971b. Taxonomie et systématique des Phoronidiens. *Bull. Mus. Hist. nat., Paris (Zool.)* **8,** 469–568.
EMIG, C. C. 1972a. Réproduction asexuée chez *Phoronis psammophila* Cori. *Mar. Biol.* **13,** 247–258.
EMIG, C. C. 1972b. Régénération de la région antérieure de *Phoronis psammophila* Cori (Phoronida). *Z. Morph. Tiere* **73,** 117–144.
EMIG, C. C. 1973a. Notes sur l'écologie et la taxonomie de *Phoronis muelleri* (Phoronida). *Naturaliste canad.* **100,** 421–426.
EMIG, C. C. 1973b. Les processus de l'ontogenèse, comparés à ceux de la régénération des Phoronida. *Z. Morph. Tiere* **75,** 329–350.
EMIG, C. C. 1973c. Écologie des Phoronidiens. *Bull. Ecol.* **4**(4), 339–364.
EMIG, C. C. 1973d. Phoronidiens de Madagascar. *Téthys suppl.* **5,** 9–24.
EMIG, C. C. 1974. The systematics and evolution of the phylum Phoronida. *Z. zool. System. Evol.-Forsch.* **12** (2), 128–151.
EMIG, C. C. 1975. Terminology in Phoronida. *Zool. Scripta* **4,** 37–40.
EMIG, C. C. 1976a. Phylogenèse des Phoronida. Les Lophophorates et le concept des Archimerata. *Z. zool. System. Evol.-Forsch.* **14,** 10–24.
EMIG, C. C. 1976b. Le lophophore—structure significative des Lophophorates (Brachiopoda, Bryozoa, Phoronida). *Zool. Scripta* **5,** 133–137.
EMIG, C. C. 1976c. Disposition et délimitation des cavités coelomiques chez les Phoronidiens (Lophophorates). *C. r. Acad. Sci., Paris* **282,** 1445–1447.
EMIG, C. C. 1977a. Notes sur la localisation, l'écologie et la taxonomie des Phoronidiens. *Téthys* **7** (4), 357–364.
EMIG, C. C. 1977b. Embryology of Phoronida. *Am. Zool.* **17,** 21–38.
EMIG, C. C. 1977c. Un nouvel embranchement: les Lophophorates. *Bull. Soc. zool. Fr.* **102** (4), 341–344.
EMIG, C. C. 1977d. Un nouvel aspirateur sous-marin, à air comprimé. *Mar. Biol.* **43** (4), 379–380.
EMIG, C. C. and EMIG, A. 1975. Étude des variations du nombre et de la répartition des muscles longitudinaux chez *Phoronis psammophila* Cori. *J. exp. mar. Biol. Ecol.* **17,** 23–31.
EMIG, C. C. and LIENHART, R. 1966. Un nouveau moyen de récolte pour les substrats meubles infralittoraux: l'aspirateur sous-marin. *Rec. Trav. St. mar. Endoume* **42,** 115–120.
EMIG, C. C. and MARCHE-MARCHAD, I. 1969. Considérations sur la systématique des Phoronidiens. VII. *Phoronis australis* Haswell, 1883. *Bull. Mus. Hist. nat., Paris* **41,** 1244–1251.
EMIG, C. C. and THOUVENY, Y. 1976. Absorption directe d'acide aminé chez *Phoronis psammophila. Mar. Biol.* **37,** 69–73.
EMIG, C. C., HERBERTS, C. and THOMASSIN, B. A. 1972. Sur l'association de *Phoronis australis* (Phoronida) avec *Cerianthus maua* (Ceriantharia) dans les zones récifales de Madagascar. *Mar. Biol.* **15,** 304–315.
EMIG, C. C., BOESCH, D. F. and RAINER, S. 1978. Phoronida from Australia. *Rec. Austr. Mus.* **30,** (16), 455–472.
GAGE, J. 1972a. A preliminary survey of benthic macrofauna and sediments in Lochs Etive and Creran, sea-lochs along the west coast of Scotland. *J. mar. biol. Ass. U.K.* **52,** 237–276.

GAGE, J. 1972b. Community structure of the benthos in Scottish sea-lochs. I. Introduction and species diversity. *Mar. Biol.* **14** (4), 281–297.
GARSTANG, W. 1891. *Phoronis* at Plymouth. *J. mar. biol. Ass. Plymouth* (2) **2,** 77–78.
GARSTANG, W. 1892. Notes on the invertebrate fauna of Plymouth for 1892. *J. mar. biol. Ass. Plymouth* (2) **2,** 335–339.
GIARD, A. 1879. *Phoronis hippocrepia. Bull. Sci. Nord* **10,** 24.
GILCHRIST, J. D. 1907. New forms of the Hemichordata from South Africa. *Trans. S. Afr. phil. Soc.* **17,** 151–176.
GUSTAFSON, G. 1936. Distribution of *Phoronis mülleri* on the Swedish west coast. *Ark. Zool., Stockh.* **28B,** 1–6.
HARMER, S. F. 1917. On *Phoronis ovalis. Q. Jl microsc. Sci.* **62,** 115–148.
HARTLAUB, C. 1904. Bericht über eine zoologische Studienreise nach Frankreich, Grossbritanien und Norwegen, ausgeführt in Frühjahr 1902. *Wiss. Meeresunters.* (*Abt Helgoland*) **5,** 97–106.
HASWELL, W. A. 1833. Preliminary note on an Australian species of *Phoronis* (Gephyrea tubicola). *Proc. Linn. Soc. N.S.W.* **7,** 606–608.
HERDMAN, W. A. 1886. *Actinotrocha* on the British coasts. *Nature, Lond.* 34, 587.
HERRMANN, K. 1976. Untersuchungen über Morphologie, Physiologie und Ökologie der Metamorphose von *Phoronis muelleri* (Phoronida). *Zool. Jb. Anat. Bd* **95,** 354–426.
HILTON, A. W. 1930a. Phoronidea from the coast of Southern California. *J. Entomol. Zool. Claremont* **22,** 33–35.
HILTON, A. W. 1930b. A new *Phoronopsis* from California. *Trans. Am. microsc. Soc.* **49,** 154–159.
HISCOCK, K. and HOWLETT, R. M. 1975. The ecology of *Cariophyllia smithi* Stokes and Broderip on south-western coasts of the British Isles. In *Underwater Research* (Ed. E. A. Drew, J. N. Lythgoe and J. D. Woods). Academic Press, London and New York, pp. 319–334.
HOLTHE, T. 1977. Investigation of the level-bottom macrofauna of Trondheimsfjorden, Norway. *Gunneria* **28,** 1–20.
IKEDA, I. 1901. Observations on the development, structure and metamorphosis of *Actinotrocha. J. Coll. imp. Univ. Tokyo* **13,** 507–592.
JONES, M. L. 1956. The fauna and biomass of a muddy sand deposit off Port Erin I.O.M. *J. Anim. Ecol.* **25,** 217–252.
JUDGES, E. C. 1953. Occurrence of *Phoronis mülleri* in the Irish Sea. *Nature, Lond.* **172,** 409.
KÖLLIKER, A. 1864. Kurzer Bericht über einige im Herbst 1864 an der Westküste von Schottland angestellte vergleichend-anatomische Untersuchungen. *Würzb. nat. Z.* **5,** 232–250.
KOWALEVSKY, A. 1867. Anatomie und Entwicklung von *Phoronis. Mem. Acad. Imper. St-Petersburg* **10.**
LEDIG, R. 1919. General structure of *Phoronis pacifica. J. Entomol. Zool. Claremont* **11,** 55–57.
LÖNÖY, N. 1954. Comparative anatomical study on *Phoronis ovalis* Wright from Norwegian, Swedish and Brazilian waters. *Univ. Bergen Årb.* (*nat. Rekke*) **2,** 1–23.
MCINTOSH, W. C. 1886. *Actinotrocha* on the British coasts. *Nature, Lond.* **34,** 468.
MCINTOSH, W. C. 1888. Report on *Phoronis buskii* n. sp., dredged during the voyage of HMS Challenger, 1873–1876. *Voyage HMS Challenger Zool.* **27** (75), 1–27.
MAMKAEV, I. V. 1962. On Phoronida from the Far-East (in Russian). *Issledov. Dal'nevost. Morei USSR* **8,** 219–237.
MARCUS, E. 1949. *Phoronis ovalis* from Brazil. *Bolm. Fac. Filos. Ciênc. Univ. S. Paulo* (*Zool.*) **14,** 157–170.

MARSDEN, J. C. 1959. Phoronidea from the pacific coast of North America. *Can. J. Zool.* **37,** 87–111.
MASTERMAN, A. T. 1900. On the Diplochorda. 3. The early development and anatomy of *Phoronis buskii* McIntosh. *Q. Jl microsc. Sci.* **43,** 375–418.
MEEK, A. 1917. On the Phoronidea. *Rep. Dove mar. Lab. Cullercoats* **6,** 33–48.
MÜLLER, J. 1846. Bericht über einige neue Thierformen der Nordsee. *Arch. Anat. Physiol.* **1846,** 101–104.
NAYLOR, E. 1965. Biological effects of a heated effluent in docks at Swansea, S. Wales. *Proc. Zool. Soc., London* **144,** 253–268.
OKA, A. 1897. Sur une nouvelle espèce japonaise du genre *Phoronis*. *Annotnes zool. jap.* **1,** 147–150.
OLLIVIER, M. T. 1969. Étude des peuplements de Zostères, Lanice et Sabelles de la région dinardaise. *Téthys* **1,** 1097–1138.
PEARSON, T. H. 1970. The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch on the west coast of Scotland. 1. The physical environment and distribution of the macrobenthic fauna. *J. exp. mar. Biol. Ecol.* **5,** 1–34.
PIXELL, H. 1912. Two new species of Phoronidea from Vancouver Island. *Q. Jl microsc. Sci.* **58,** 257–284.
ROULE, L. 1889. Sur une nouvelle espèce méditerranéenne du genre *Phoronis*. *C. r. Acad. Sci., Paris* **109,** 195–196.
SCHNEIDER, A. 1862. Ueber die Metamorphose der *Actinotrocha branchiata*. *Arch. Anat. Physiol.* **1862,** 47–65.
SELYS-LONGCHAMPS, M. DE. 1903. Ueber *Phoronis* und *Actinotrocha* bei Helgoland. *Wiss. Meeresunters. (Abt. Helgoland)* **6,** 1–56.
SELYS-LONGCHAMPS, M. DE. 1907. *Phoronis. Fauna Flora Golf Neapel* **30,** 1–280.
SHRUBSOLE, W. H. 1886. *Actinotrocha* of the British coasts. *Nature, Lond.* **34,** 439.
SIEWING, R. 1974. Morphologische Untersuchungen zum Archicoelomatenproblem. 2. Die Körpergliederung bei *Phoronis muelleri* Selys-Longchamps (Phoronida) Ontogenese-Larva-Metamorphose-Adultus. *Zool. Jb. Anat.* **92,** 275–318.
SILÉN, L. 1952. Research on Phoronida of the Gullmar Fiord area (West coast of Sweden). *Ark. Zool.* **4** (4), 95–140.
SILÉN, L. 1954a. Developmental biology of Phoronidea of the Gullmar Fiord area. *Acta Zool., Stockh.* **35,** 215–257.
SILÉN, L. 1954b. On the nervous system of *Phoronis*. *Ark. Zool.* **6** (1), 1–40.
SILÉN, L. 1955. Autotomized tentacle crowns as propagative bodies in *Phoronis*. *Acta Zool., Stockh.* **36,** 159–165.
THEEL, H. 1907. Om utvecklingen af Sveriges zoologiske hafsstation Kristineberg och om djurlifvet i angränsande haf och fiordar. *Ark. Zool.* **4** (5), 1–123.
TORREY, H. B. 1901. On *Phoronis pacifica* sp. nov. *Bull. Biol. mar. biol. Lab., Woods Hole* **2,** 282–288.
WRIGHT, T. S. 1856. Description of two tubicolar animals. *Proc. R. Soc. Edinb.* **1,** 165–167.
WRIGHT, T. S. 1859. Note sur la *Crepina* de M. van Beneden. *Ann. Sci. nat.* (4) **11,** 150.
ZIMMER, R. L. 1967. The morphology and function of accessory reproduction glands in the lophophores of *Phoronis vancouverensis* and *Phoronopsis harmeri*. *J. Morph.* **121,** 159–178.

Index of Genera and Species

For species and genera the correct names are in *italics*; synonyms are in roman.