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The systematics and evolution of the phylum Phoronida

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With 23 figures

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The phylum Phoronida consists of two genera (*Phoronis* and *Phoronopsis*) and some eleven species, exclusively marine and entirely free-living. This phylum must be considered as primitive Deuterostomia (ZIMMER 1964; EMIG 1973 b). Phoronid taxonomy has been studied by several authors (BENHAM 1889; CORI 1890; SELYS-LONGCHAMPS 1907). CORI (1939) listed sixteen species, omitting *Phoronopsis californica*, but his account is unsatisfactory and does not make any mention of the degree of morphological variation. Since then *Phoronis pallida* has been described by SILÉN (1952) and *Phoronis bhadurii* by GANGULY and MAJUMDAR (1967). The dubious validity of some species has been commented on by SILÉN (1952) and MARSDEN (1959), but at this time the taxonomy of *Phoronida* obviously needs revision. The author (EMIG 1971 b) studied the degree of variation of all taxonomic characters and concluded that several species can be considered as synonyms owing to the variability of many of these features (Tables 1, 2). In the present work study of several of these characters is completed or confirmed.

I. Taxonomic characters

Phoronid taxonomy is based on external and internal anatomy, the latter being studied by means of serial cross sections. The characters are listed and discussed below.

Table 1

All described species of the phylum Phoronida has been listed with date and type-locality

1856	*Phoronis ovalis* Wright (a)	Inchkeith (Great-Britain)
	Phoronis hippocrepia Wright (a)	Ilfracombe (Great-Britain)
1858	*Phoronis (Crepina) gracilis* Van Beneden (a)	Ostende (Belgium)
1883	*Phoronis australis* Haswell (a)	Port-Jackson (Australia)
1888	*Phoronis buskii* McIntosh	Philippines
1889	*Phoronis kowalevskii* Benham (a)	Neapel Harbor (Italia)
	Phoronis caespitosa Cori (a)	Neapel Harbor (Italia)
	Phoronis psammophila Cori (a)	Messina (Italia)
	Phoronis sabatieri Roule (a)	Etang de Thau (France)
1890	*Phoronis architecta* Andrews (a)	Beaufort N. C. (U.S.A.)
1897	*Phoronis ijimai* Oka (a)	Misaki (Japan)
1901	*Phoronis pacifica* Torrey	Puget Sound (U.S.A.)
1903	*Phoronis muelleri* Selys-Longchamps (a, b)	Helgoland (Germany)
1907	*Phoronis euxinicola* Selys-Longchamps (= nomen nudum)	Sebastopol (U.S.S.R.)
	Phoronis capensis Gilchrist	False Bay (South Africa)
	Phoronopsis albomaculata Gilchrist (a)	False Bay (South Africa)
1912	*Phoronis vancouverensis* Pixell (a)	Vancouver Island (Canada)
	Phoronopsis harmeri Pixell (a)	Vancouver Island (Canada)
1930	*Phoronopsis viridis* Hilton (a)	Moro Bay, Calif. (U.S.A.)
	Phoronopsis striata Hilton	Moro Bay, Calif. (U.S.A.)
	Phoronopsis californica Hilton (a)	Balboa Bay, Calif. (U.S.A.)
1952	*Phoronis pallida* Silén (a)	Gullmar Fiord (Sweden)
1967	*Phoronis bhadurii* Ganguly and Majumdar	Digha, Bengal (India)

according to the International Rules of Zoological Nomenclature
a. species studied by the author; b. this species must be written *muelleri* and not *mülleri*

Table 2

Genus and species of the phylum Phoronida

(see also Table 1)

Genus	Species	Synonyms, proposed by
Phoronis	*ovalis*	
	hippocrepia	*gracilis* Wright, 1859; Silén, 1952 *kowalevskii* Selys-Longchamps, 1907; Emig, 1971 b *caespitosa* Cori, 1890 *capensis* Emig, 1971 b
	ijimai	*vancouverensis* Emig, 1971 a
	australis	
	buskii	(? with *P. australis*)
	bhadurii (?)	
	muelleri	
	psammophila	*sabatieri* Emig, 1968 *architecta* Emig, 1972
	pallida	
Phoronopsis	*albomaculata*	
	harmeri	*viridis* Marsden, 1959 *pacifica (Phoronis)* Emig, 1971 b ? *striata*
	californica	

Table 3

Distribution of Phoronida after the vertical zonation and the possible relationships of the species (between brackets the preferential substratum of each species), except Phoronis buskii (sand with pebbles) and Phoronis bhadurii (mixture of sand and mud)

	Hard substrata	Soft substrata	
Infralittoral zone	*Phoronis hippocrepia* (rocks, shells) *Phoronis ijimai* (rocks) *Phoronis australis* (tube-wall of cerianthid)	*Phoronis psammophila* (fine well-sorted sands) *Phoronis pallida* (sand, muddy sand) *Phoronopsis harmeri* (sand)	*Phoronopsis albomaculata* (clogged coarse sand) *Phoronopsis californica* (mud; coarse sand)
Circalittoral zone	*Phoronis ovalis* (mollusc shells)	*Phoronis muelleri* (mud and sandy clay)	

1. Biotope

All phoronids inhabit a cylindrical tube made of their own secretion in which they can move freely. The occurence of *Phoronida* in benthic communities has been discussed by Emig (1973 c) and these are reported in the separate diagnoses. Phoronids are present from the intertidal zone to 140 m in depth. Two or three species can be occasionally found together. This phylum lives in two different substrates.

a. Hard substrata

Phoronis ovalis, Phoronis hippocrepia and sometimes *Phoronis ijimai* burrow into rocks and mollusc shells; their tubes are membranous and curved (Table 3). *P. hippocrepia* and *P. ijimai* may present two forms, a burrowing and an encrusting – form (Fig. 1 a), depending on environmental factors (hydrodynamic action, nature of substratum, associated fauna). *Phoronis australis* displays a unique association, inquilinism, with cerianthid; in their own chitinous tubes, numerous individuals (Fig. 1 c, 11) occur in the tube-wall of cerianthid (Emig and al. 1972).

b. Soft substrata

Each individual of all other species lives in its sand-encrusted tube embedded vertically in soft bottom, usually mud, fine or coarse sand (Fig. 1 b; Table 3).

2. Length

The length of the body varies within a single species and in the same individual. During sampling or fixation, phoronids contract together and their total length falls

to 1/3 or 1/5 of natural size one. The whole length of a phoronid matches the length of its tube (SELYS-LONGCHAMPS 1970; EMIG 1968). The diameter of the body varies also: in diagnoses we give two numbers, the first being the smallest diameter below the lophophore, the second the largest one in the ampulla.

3. Colour

The coloration varies sometimes within a single species, in the same locality or in different localities.

4. Collar fold

The absence or presence of an epidermal collar fold at the basis of the lophophore is used to separate the two genera *Phoronis* and *Phoronopsis* (Fig. 14, 22, 22).

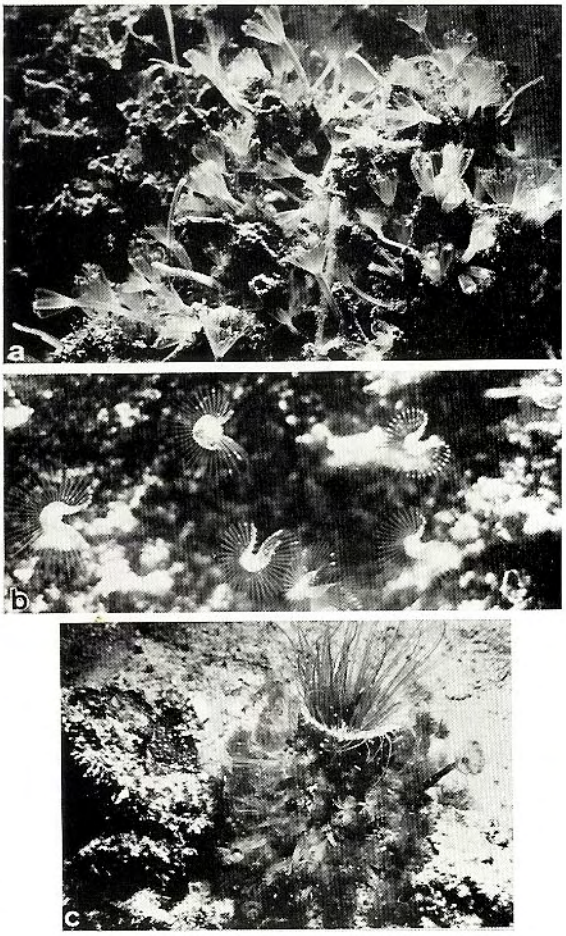


Fig. 1 a–b. Phoronis hippocrepia: encrusting-form (a), *Phoronis psammophila* (b), *Phoronis australis* (c): numerous individuals in the tube-wall of *Cerianthus maua*

5. Lophophore and tentacles

The shape of the lophophore is characteristic and seems to be a constant feature within each species. Phoronids are divided into 5 groups on the basis of the lophophore structure. The number of tentacles increases with the complexity of lophophore shape, but this number can also vary within a single species (Table 4).

6. Nephridia

The paired nephridia of *Phoronida* are classified as metanephridia. They are situated in dorsal position under the lophophore, on either side of the intestine and anal papilla (Fig. 10). Each nephridium is usually a U-shaped tube, with a descending branch (except several species: Table 5) and an ascending branch, opening into the metacoelom by means of one or two funnels and outside by the nephridiopore on the anal papilla or on the nephridial ridge (or papilla).

From study of nephridial evolution, I conclude that their development is linked to the maturation of gonads (nephridia are gonoducts). In young individuals, the nephri-

Table 4

Taxonomic characteristics of the lophophore of Phoronida

Shape	Species	Number of tentacles
Oval-shaped (Fig. 6)	*Phoronis ovalis*	15–28
Horseshoe-shaped; tentacles of the outer row being shorter at the oral side (Fig. 14)	*Phoronis muelleri*	40–98
Horseshoe-shaped with the end turned medially in the lophophoral concavity (Fig. 8)	*Phoronis pallida*	50–140
	Phoronis psammophila	60–130
	Phoronopsis albomaculata	70–126
	Phoronis hippocrepia	50–150
	Phoronis ijimai	72–226
Spirally-shaped with 1.5 to 2 coils on each side (Fig. 19)	*Phoronopsis harmeri*	100–400
Spirally-shaped with 2.5 to 3.5 coils on each side (Fig. 12)	*Phoronis australis*	600–1000
	Phoronis buskii	1000
Helicoidally-shaped with 4 to 5 or more coils on each side (Fig. 21, 22)	*Phoronopsis californica*	1500 or more

dial epithelium is generally thin and the funnel small; sexually mature adults have developed nephridia, the funnels of which are prolonged longitudinally along the lateral mesenteries to a relatively great length or surrounded by expanded edges (Emig 1971 b).

Nephridia are not subject to any variation in their shape and have an obvious taxonomic significance. According to the morphological features of nephridia, the phoronid species may be classified into five categories (Table 5).

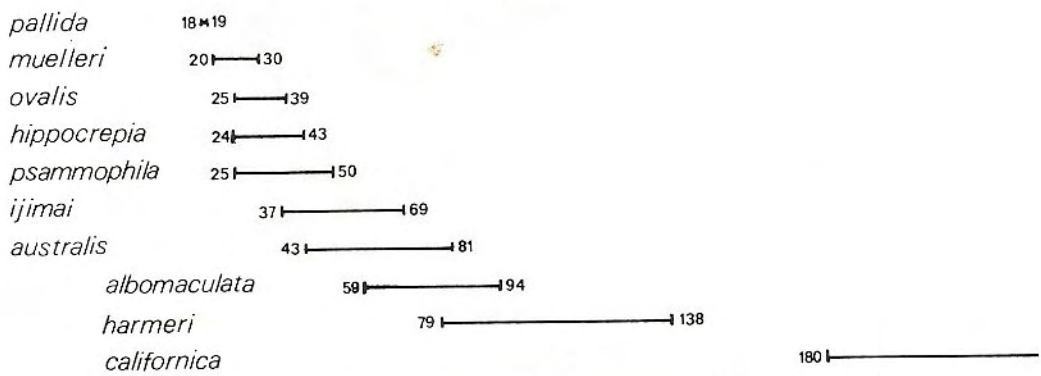


Fig. 2. Variations of the longitudinal muscle numbers in *Phoronida*

7. Nervous system

The nervous system of *Phoronida* was studied by Selys-Longchamps (1907), Cori (1939) and recently by Silén (1954). Most phoronid species present generally one giant fiber on the left side only, at the attachment of the left lateral mesentery (Fig. 4), but in few species two giant fibers exist, left one and right one at the site of attachment

Table 5

Main characteristics of nephridia of phoronid species (1-4: Phoronis; 5: Phoronopsis)

Category	1.	2.		3.			4.	5.		
Species	*ovalis*	*muelleri*	*psammophila*	*hippocrepia*	*ijimai*	*australis*	*pallida*	*albomaculata*	*harmeri*	*californica*
Type	1 funnel	1 funnel		2 funnels			2 funnels	2 funnels		
aperture of funnels	anal-oral	anal-oral		anal: larger oral: smaller			anal lightly larger than oral	anal: smaller oral: larger		anal: larger oral: smaller
descending branch	absent	± short		absent			as long as A	long (= 1/2 of A)		long (= 1/3 of A)
ascending branch (A)	single	single		in 2 horizontal chambers	single, ± curved	single curved	single	single		
nephridiopore on	anal papilla	anal papilla		nephridial papilla			anal papilla	anal papilla (on the epidermal fold)		
aperture of nephridiopore	anus level	anus level	below anus	above anus or anus level			anus level	below anus		
epithelium	thin	thin		thin	± thick	thick	thin	± thick	thick	thin
figure	7	15 a	15 b	9 a	9 b	9 c	16	18 a	18 b	18 c

Table 6

Number and diameters of giant nerve fibers in the muscular region of the metasoma of Phoronida

Species	Left giant fiber (diameter in μ)		Right giant fiber (diameter in μ)	
P. ovalis	absent or 1 ?	2.5	absent or 1 ?	2.5
P. hippocrepia	1	4–10	1	1–7
P. ijimai	1	3–10	1	2–8
P. australis	1	5–11	1	3–13
P. psammophila	1	7–27	rarely rudimentary one	
Ph. albomaculata	1	15–24	present only down to nephridial level, is absent below	
Ph. harmeri	1	20–60		
Ph. californica	1	70–80		
P. pallida	1	15–20		
P. muelleri	1	7–40		

Table 7

Longitudinal muscle formulae of phoronid species

(n. i.: number of studied individuals; (a) see also Emig 1972, 1973 a)

Species	Composite formula		Mean Formula		n. i.
P. pallida	18–19	$\frac{5–6 \mid 5}{4 \mid 4}$	18 =	$\frac{5 \mid 5}{4 \mid 4}$	12
P. muelleri	20–30	$\frac{7–13 \mid 7–11}{2–5 \mid 3–5}$	24 =	$\frac{9 \mid 9}{3 \mid 3}$	216
P. ovalis	25–39	left coel. 12–21 right coel. 13–19	31 =	$^{16}/_{15}$	62
P. hippocrepia	24–43	$\frac{7–15 \mid 7–16}{3–7 \mid 3–10}$	32 =	$\frac{11 \mid 11}{5 \mid 5}$	160
P. psammophila (a)	25–50	$\frac{7–19 \mid 7–17}{4–11 \mid 4–9}$	34 =	$\frac{11 \mid 11}{6 \mid 6}$	2459
P. ijimai	37–69	$\frac{10–32 \mid 13–31}{2–14 \mid 3–13}$	56 =	$\frac{20 \mid 22}{7 \mid 7}$	182
P. australis	43–81	$\frac{17–29 \mid 14–27}{4–16 \mid 5–11}$	64 =	$\frac{22 \mid 22}{11 \mid 9}$	38
Ph. albomaculata	59–94	$\frac{18–32 \mid 17–30}{11–18 \mid 10–15}$	72 =	$\frac{23 \mid 22}{14 \mid 13}$	35
Ph. harmeri	79–138	$\frac{20–48 \mid 23–55}{12–27 \mid 11–26}$	113 =	$\frac{37 \mid 37}{20 \mid 19}$	42
Ph. californica	180–243	$\frac{53–81 \mid 56–79}{35–54 \mid 29–40}$	211 =	$\frac{66 \mid 66}{44 \mid 35}$	13

of the right lateral mesentery (Fig. 3 b–d). Giant fibers are altogether absent from *Phoronis ovalis* (FORNERIS 1959). In the genus *Phoronopsis* the right fiber is only present down to nephridial level and is absent below (Table 6).

8. Longitudinal muscles

The number of muscle bundles may vary within certain limits in one species. The muscle formulae vary from locality to locality or (and) from biotope to biotope, usually from the anterior to the posterior part of the muscular region of the metasome within one individual (EMIG 1971 b).

The arrangement of longitudinal muscle bundles relative to the four subdivision of the metacoelom is represented by the conventional formula of SELYS-LONGCHAMPS (1907) as follows (Fig. 3, 4):

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

For each species we give the composite muscle formula and a mean formula (Table 7). Owing to the absence of the lateral mesenteries in *Phoronis ovalis,* no formula can be etablished. In *Phoronis muelleri* the absence of the left mesentery is indicated by a dotted line. *Phoronis pallida* possesses an unusual arrangement of the musculature (Fig. 4 c, 17): the circular muscle layer forms 3 thick sphincters and the longitudinal muscle layer presents 6 zones according to the degree of development of the marginal and central muscle of a same strip (SILÉN 1952).

Muscles bundles are stated to be often taller and more numerous an the left side

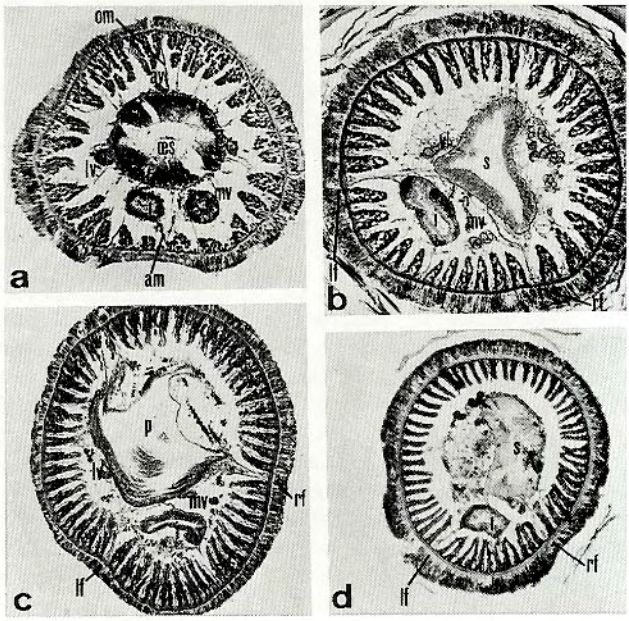


Fig. 3. Cross sections through the muscular body region. (a) *Phoronis ovalis:* section in the anterior body part showing the "accessory" vessel and the absence of the lateral mesenteries (1 mm = 6,9 μ); (b) *Phoronis hippocrepia* (1 mm = 17 μ); (c) *Phoronis australis* (1 mm = 47 μ); (d) *Phoronis ijimai* (1 mm = 66 μ). am = anal mesentery; av = "accessory" vessel; i = intestine; lf = left giant fiber; llm = left lateral mesentery; lv = lateral vessel; mv = median vessel; oes = oesophagus; om = oral mesentery; p = prostomach; rf = right giant fiber; rlm = right lateral mesentery; s = stomach

especially in the left oral coelom in *Phoronis muelleri* (Fig. 4 a), *Phoronis psammophila* (Fig. 4 b), *Phoronopsis albomaculata* (Fig. 4 d) or they are generally tallest on the oral side in the other species (Fig. 3; 4 e, f).

This taxonomic feature must be used with caution on account of the degree of variation normally found within the different species (Fig. 2; Table 7).

9. Gonads

Phoronids are hermaphroditic or dioecious; the gonads are applied to the lateral blood vessel in ampulla. In hermaphroditic species, the ovary occurs on dorsal side of the lateral vessel, the testis on its ventral side, but in *Phoronis pallida* the relation can be reversed (Silén 1952; Emig 1969). The lophophoral organs (s. l.) of *Phoronida* are proved to be accessory sex glands (Zimmer 1967): female nidamental glands facilitate the temporary brooding of embryos, male accessory spermatophoral organs (lophophoral organs, s. s.) are in spermatophore elaboration.

In hermaphroditic brooding species (Table 8) each mature adult has a pair of lophophoral organs and nidamental glands. In *Phoronis hippocrepia* and *Phoronis ijimai* the nidamental glands (type 2 a) are developed on the floor of the lophophoral concavity and in the inner surface of those tentacles to which the embryo-masses are attached (Fig. 10). In *Phoronis australis* and *Phoronis buskii* the nidamental glands (type 2 b) are limited to the floor of the lophophoral concavity; this glands secrete a mucous cord which retains the embryos (Masterman 1900).

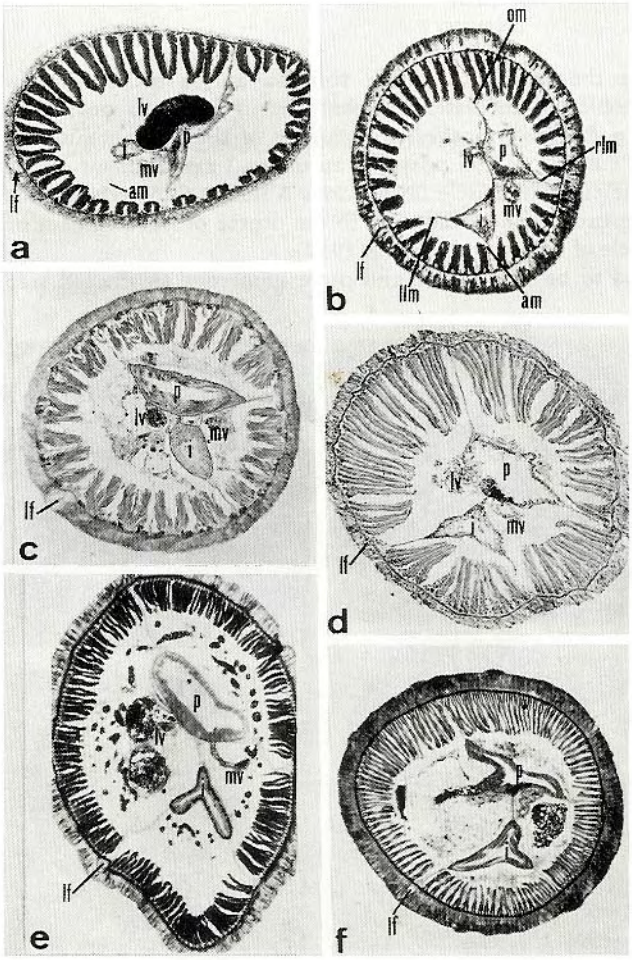


Fig. 4. Cross sections through the muscular body region. (a) *Phoronis muelleri* (1 mm = 19 μ), the left lateral mesentery is absent; (b) *Phoronis psammophila* (1 mm = 30 μ); (c) *Phoronis pallida*, section in zone 4 (1 mm = 12 μ); (d) *Phoronopsis albomaculata* (1 mm = 12 μ); (e) *Phoronopsis californica* (1 mm = 38 μ); (f) *Phoronopsis harmeri* (1 mm = 39 μ). (see abbr. Fig. 3)

Table 8

Characteristics of gonads and accessory sex glands

(After ZIMMER 1964, modified and completed)

Species	Type	Sexuality	Nidamental glands	Lophophoral organs	Brooding pattern
P. ovalis	1 ?	MF M & F	Absent	Absent	Retain eggs in parental tube
P. hippocrepia	2	MF	2 a	Small	Embryos in paired lophophoral masses
P. ijimai	2	MF	2 a	Small	– id –
P. australis	2	MF	2 b	Small	Embryos on mucous cord
P. buskii	2	MF	2 b	Small	Embryos on mucous cord
P. bhadurii	?	?	2	?	Eggs retained in the lophophore
P. psammophila	2	M & F	2 c	Large glandular	Embryos in single one or paired lophophoral masses
P. muelleri	3 ?	M & F	Absent	Large glandular	No brooding
P. pallida	3	MF	Absent	Large glandular	No brooding
Ph. albomaculata	? ?	M & F	?	Large	?
Ph. harmeri	3	M & F	Absent	Large membranous	No brooding
Ph. californica	? ?	M & F	?	Large membranous	?

In dioecious brooding *Phoronis psammophila*, the female possesses nidamental glands of type 2 c (all type are according to ZIMMER 1964; Table 8), on each side of the lophophore, formed by the fusion of the most of the tentacles of the inner whorl. The embryos are brooded in a single mass or two masses.

The other phoronid species have no brooding pattern (Table 8), the ova are shed freely in water; females lack accessory sex glands, but in males the lophophoral organs are present. *Phoronis ovalis* alone is not likely to possess lophophoral organs; hitherto FORNERIS (1959) described a small median lophophoral organ, but this seems unlikely according to ZIMMER (1964). Information on the presence or absence of accessory sex glands are lacking in *Phoronopsis albomaculata* and *Phoronopsis californica;* investigation on the former species has been recently performed by EMIG (1973 a).

10. Other characteristics

Especially *Phoronis ovalis* and *Phoronis muelleri*, if we except the unusual musculature arrangement of *Phoronis pallida*, present additional characteristics with regard to the other phoronid species. This characteristics are indicated in diagnosis, but the differences of the circulatory system between *Phoronis ovalis* and the other species may be described below.

The circulatory system of *Phoronida* is a closed type. They are two longitudinal vessels in the trunk (Fig. 4, 5 a): the median vessel (afferent) arising from the blood plexus on the stomach-wall and the lateral vessel (efferent) proceeding from the lophophoral ring vessel. Median and lateral vessels communicate in the blood plexus in ampulla and in the lophophoral vessel. At the basis of the lophophore, the horseshoe-shaped lophophoral ring vessel is formed by two vessels placed side by side

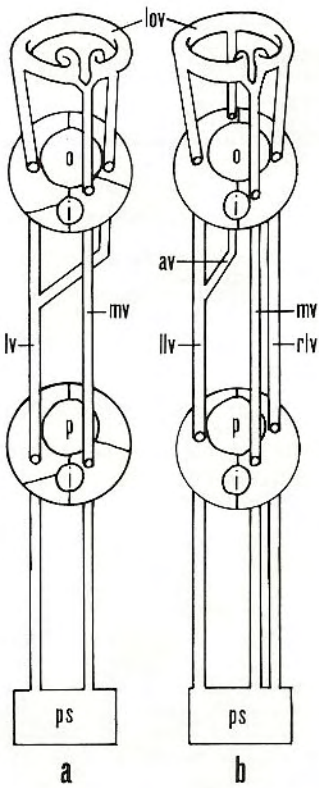


Fig. 5. Diagrams of the circulatory system in the metasoma, (b) in *Phoronis ovalis,* (a) in the other species (the secondary lateral vessel is not represented). av = "accessory" vessel; i = intestine; lov = lophophoral ring vessel; lv = lateral vessel; llv = left lateral vessel; mv = median vessel; o = oesophagus; p = prostomach; ps = blood plexus of the stomach-wall; rlv = right lateral vessel

SELYS-LONGCHAMPS 1907). The lateral vessel at the oesophagus-level and on its each side is composed by two branches (Fig. 5 a).

In *Phoronis ovalis* Marcus (1949) mentions the presence of a third vessel, called "accessory" vessel: this vessel and the two branches of the lateral vessel unite at the level of the oesophageal valve and form one lateral vessel. On the contrary, LÖNÖY (1954) says that the lateral vessel and "accessory" vessel do not unite, but reach separately to the ampulla. EMIG's description (1969) differs from MARCUS' and LÖNÖY's conclusions as regards to the extension of this vessel: the "accessory" vessel situated near the oral mesentery (Fig. 3 a, 5 b) unites at the oesophageal valve with the left lateral vessel; two lateral vessels are present in the metasoma on each side of the descending branch of the alimentary canal (Fig. 5 b).

11. Conclusions

A review of all taxonomic characters indicates that the phylum *Phoronida* may be divided into 5 major categories.

1. *Phoronis ovalis* seems to be defined by the absence of the lateral mesenteries and probable absence of giant fibers, by asexual reproduction (transverse fission and budding); the lophophore is single, oval-shaped; nephridia are poorly developed and consist of one ascending branch with one funnel. This species possesses an unusual circulatory system and an oesophageal valve.
2. *Phoronis hippocrepia, P. ijimai, P. australis* are characterized by nephridia of type with two funnels and without descending branch, the nephridiopore opening on nephridial papilla, two giant fibers and simultaneously hermaphroditic gonads. Embryos are brooded in paired lophophoral masses or on mucous cord.
3. *Phoronis psammophila* and *P. muelleri* are distinguishable from the other categories by their nephridia of one funnel type and a descending branch. They possess one left giant fiber and longitudinal muscle bundles are taller and usually more numerous on the left side.
4. *Phoronis pallida* possesses remarkable longitudinal and circular muscle layers (6 different body zones and 3 horizontal sphincters), a constant number of longitudinal muscle bundles ($18 = \frac{5|5}{4|4}$), nephridia of type with two funnels and an equal length of the descending and ascending branches.

5. The genus *Phoronopsis* seems to be adequately defined by the epidermal collar fold on the base of the lophophore, nephridia of type with two funnels and a long descending branch, one left giant fiber (right fiber only present down to the nephridia level), numerous longitudinal muscle bundles.

Principal taxonomic features appear to be shape of lophophore and morphology of nephridia. *Our categories may be etablished with only one character, the nephridia,* which underlines its taxonomic importance. However the study of all taxonomic features is indispensable to determine a phoronid species with certainty. The fixation after sampling should be rapid because phoronids usually autotomized their lophophore and in this case determination is impossible.

II. Diagnoses of species

Genus *Phoronis* Wright, 1856: absence of the collar fold below the lophophore.

1. Phoronis ovalis Wright, 1856

Biotope: burrowing into mollusc shells, rocks, *Balanus;* density up to 150 individuals in sq. centimeter; depth from 0 to 50 m (with reference to mean lower water as 0); living in coralligenous and coastal detritic populations.

Length: up to 15 mm (0.25 to 0.35 mm in diameter); anterior body part retractable into a very developed ampulla.

Colour: transparent, sometimes brownish pigmented only at the distal portion of the tentacles or over the whole body.

Lophophore: oval-shaped (Fig. 6).

Tentacles: 15–28 (0.3 to 1.2 mm long).

Fig. 6 (left). Phoronis ovalis. oval-shaped lophophore – *Fig. 7 (right). Phoronis ovalis.* Diagram of a nephridium. A = ascending branch; f = funnel; n = nephridiopore – *Fig. 8 (centre).* Diagram of the horseshoe-shaped lophophore

Nephridia: one small funnel; descending branch absent; nephridiopore on the anal papilla, opening at the anus level (Fig. 7).

Giant fibers: absent; sometimes one on the left and one on the right (about 2.5 μ in diameter).

Longitudinal muscles (Fig. 3 a): [25–39] left coelom: 12–21 right coelom: 13–19 $31 = {}^{16}/_{15}$

Gonads: hermaphroditic or dioecious; lophophoral organs absent; no brooding.

Larva: is *not Actinotrocha.*

Asexual propagation: by transverse fission and budding, by autotomized tentacle crowns.

Other characters: absence of lateral mesenteries (Fig. 3 a); presence of an "accessory" vessel and two lateral vessels, right one and left one (Fig. 3 a, 5 b); presence of an oesophageal valve.

Distribution: Great-Britain, Sweden, Norway, Germany, France, Brazil, Chile, New-Zealand, North America (pacific coast).

2a. Phoronis hippocrepia Wright, 1856

Synonyms:

Phoronis (Crepina) gracilis Van Beneden, 1858.
Phoronis kowalevskii Benham, 1889.
Phoronis caespitosa Cori, 1889.
Phoronis capensis Gilchrist, 1907.

Biotope: burrowing into or encrusting on rocks, shells, wood, *Lithothamnion*, coral; density up to 22,000 ind./m²; depth from 0 to 55 m; living in infralittoral photophilic algal populations (occasionally in coastal detritic bottoms or enclaves of circalittoral biocoenosis); Fig. 1 a.

Length: up to 100 mm (0.2 to 1.5 mm in diameter).

Colour: greenish-grey, yellowish or transparent.

Lophophore: horseshoe-shaped with ends turned medially (Fig. 8).

Tentacles: 50–150 (2–3 mm long).

Nephridia: 2 funnels, anal larger, oral smaller; descending branch absent; ascending branch forms 2 horizontal chambers; nephridiopore on nephridial papilla opening above or at anus level (Fig. 9 a).

Giant fibers: 2 fibers, one left (4–10 μ in diameter) and one right (1–7 μ in diameter), Fig. 3 b.

Longitudinal muscles (Fig. 3 b): [24–43] $\frac{7\text{–}15 \mid 7\text{–}16}{3\text{–}\ 7 \mid 3\text{–}10}$ $32 = \frac{11 \mid 11}{5 \mid 5}$

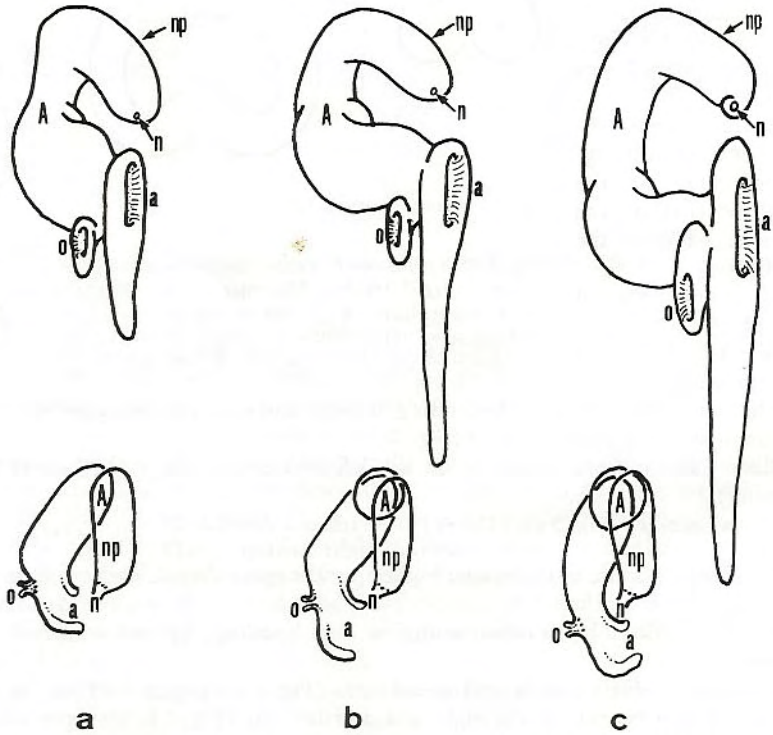


Fig. 9. Diagrams of a nephridium of *Phoronis hippocrepia* (a), *P. ijimai* (b), *P. australis* (c). A = ascending branch; a = anal funnel; D = descending branch; f = funnel; n = nephridiopore; np = nephridial papilla; o = oral funnel

Gonads: hermaphroditic; lophophoral organs small, nidamental glands 2a type; embryos in paired lophophoral masses.
Larva: *Actinotrocha hippocrepia.*
Asexual propagation: by transverse fission.
Distribution: Great-Britain, France, Belgium, Germany, Sweden, Italy, Brazil, South Africa.

2b. Phoronis ijimai Oka, 1897

Synonym:
Phoronis vancouverensis Pixell, 1912.
Biotope: encrusting or occasionally burrowing in rocks, sands, wood; depth from 0 to 8 m; density up to 15,000 ind./m²; living in similar biotope as *Phoronis hippocrepia.*
Length: 30–100 mm (0.5 to 2 mm in diameter).
Colour: pink to transparent, sometimes presence of white pigment in the lophophore.
Lophophore: horseshoe-shaped with the ends turned medially (Fig. 8, 10).
Tentacles: 72–226 (2–5 mm long).
Nephridia: 2 funnels, anal larger, oral smaller; descending branch absent; nephridiopore on nephridial papilla opening above or at the anus level (Fig. 9b, 10).
Giant fibers: 2 fibers (Fig. 3d), one left (3–10 μ in diameter) and right one (2–8 μ in diameter).
Longitudinal muscles (Fig. 3d): [37–69] $\frac{10\text{–}32}{2\text{–}14}\left|\frac{13\text{–}31}{3\text{–}13}\right.$ $56 = \frac{20}{7}\left|\frac{22}{7}\right.$
Gonads: hermaphroditic; lophophoral organs small, nidamental glands 2a type; embryos in paired lophophoral masses (Fig. 10).
Larva: *Actinotrocha vancouverensis.*
Asexual propagation: by transverse fission.
Distribution: Japan, North America (pacific coast).

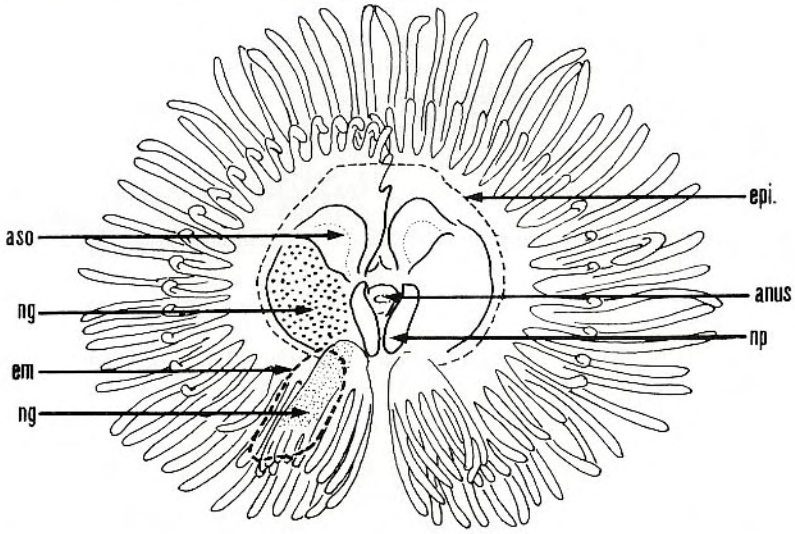


Fig. 10. Diagram of mature *Phoronis ijimai* viewed from the distal end (after Zimmer 1967). aso = accessory spermatophoral organ (= lophophoral organ); em = position of brooded embryos; epi = epistom; ng = basal and tentacular nidamental glands; np = nephridial papilla

2c. Phoronis australis Haswell, 1883

Biotope: burrowing into tube-wall of cerianthid (Fig. 1 c; 11); depth from 0 to 30 m; association (= inquilinism) *Phoronis*-cerianthid; density up to 100 into one cerianthid tube.
Length: 50–200 mm (2–5 mm in diameter).
Colour: anterior body part black, deep reddish or pink.
Lophophore: spirally-shaped with 2.5 to 3.5 coils on each side (Fig. 12).

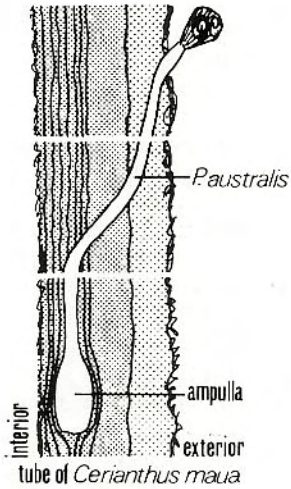


Fig. 12. Phoronis australis. Spirally-shaped lophophore

Fig. 11. Position of *Phoronis australis* in the tube-wall of *Cerianthus maua* (the tube of *P. australis* is not represented) after EMIG and al. 1972

Tentacles: 600–1000 (5–16 mm long); the basis of the tentacles are connected together for about one quarter or one third of their total length (Fig. 13).
Nephridia: 2 funnels, anal larger, oral smaller; descending branch absent; nephridiopore on nephridial papilla, opening above the anus or at its level (Fig. 9 c).
Giant fibers: 2 fibers (Fig. 3 c), one left (5–11 μ in diameter) and one right (3–13 μ in diameter).
Longitudinal muscles (Fig. 3 c): [43–81] $\frac{17\text{–}29}{4\text{–}16} \Big| \frac{14\text{–}27}{5\text{–}11}$ 64 = $\frac{22}{11} \Big| \frac{22}{9}$
Gonads: hermaphroditic; lophophoral organs small; nidamental glands 2 b type; embryos on mucous cord.
Larva: unknow.
Asexual propagation: by transverse fission.
Distribution: Australia, Japan, India, Madagascar, Moçambique, Senegal.

Phoronis buskii McIntosh, 1888

Information on *Phoronis buskii* is limited to that in type description (MCINTOSH 1881, 1888). This species lives in sand encrusted tubes in sandy bottom (18–37 m depth) and shows similar characteristics to *Phoronis australis*. Their identity may be considered as possible.
Distribution: Philippines.

Phoronis bhadurii Ganguly and Majumdar, 1967

Phoronis bhadurii is poorly described by GANGULY and MAJUMDAR (1967). This species lives in a mixture of sand and mud in the intertidal zone and possesses a spirally-shaped lophophore (3 coils on each side), 1406 tentacles (6–8 mm long). The length is 58–94 mm and the eggs are present in the tentacles. Other informations lack. According to the other species, *Phoronis bhadurii* may be related to *Phoronis buskii* or considered as a new species of the genus *Phoronopsis* afters its figures.
Distribution: India.

Fig. 13 (left). Phoronis australis. Anal view of the anterior body part – *Fig. 14 (right). Phoronis muelleri.* Oral view of the anterior body part (after CORI 1939)

3a. Phoronis muelleri Selys-Longchamps, 1903

Biotope: mud to sand bottom (sometimes with coarse fraction); depth from 2 to 140 m; density up to 540 ind./m²; living in biocoenosis of coastal detritic, b. of terrigenous mud, in *Amphiura*-communities.
Length: 50–120 mm (0.2 to 1 mm in diameter).
Colour: yellowish, reddish or pink; occasionally lophophore with spots.
Lophophore: horseshoe-shaped with tentacles of the outer ring being shorter at the oral side (Fig. 14).
Tentacles: 40–98 (about 1 mm long).
Nephridia: 1 funnel; short descending branch; nephridiopore opening at the anus level on the anal papilla (Fig. 15 a).
Giant fiber: 1 on the left side, 7–40 μ in diameter (Fig. 4 a).
Longitudinal muscles (Fig. 4 a): $[20–30]\ \frac{7–13}{2–5}\left|\frac{7–11}{3–5}\right.\quad 24 = \frac{9}{3}\left|\frac{9}{3}\right.$
Gonads: dioecious; lophophoral organs larger glandular; nidamental glands absent; no brooding.
Larva: *Actinotrocha branchiata.*
Asexual propagation: by transverse fission.
Other characters: absence of the left lateral mesentery below the left nephridium (Fig. 4 a).
Distribution: Germany, Great-Britain, Sweden, France, Italia, Yugoslavia, Egypt, the Azores, Canada, USSR (Far East), Madagascar, USA (E Coast).

3b. Phoronis psammophila Cori, 1889

Synonyms:
Phoronis sabatieri Roule, 1889.
Phoronis architecta Andrews, 1890.
Biotope: Fine sand to mud (sometimes with coarse fraction), reefs of polychaetes, sea-meadows; depth from intertidal zone to 20 m; density up to 17,000 ind./m²; living

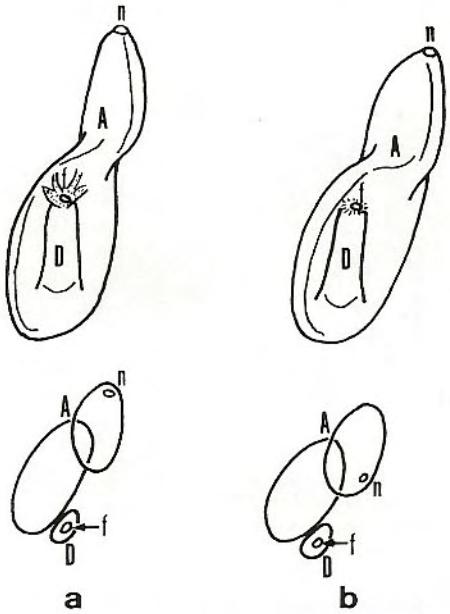


Fig. 15. Diagrams of a nephridium of *Phoronis muelleri* (a) and *P. psammophila* (b). (see abbr. Fig. 9)

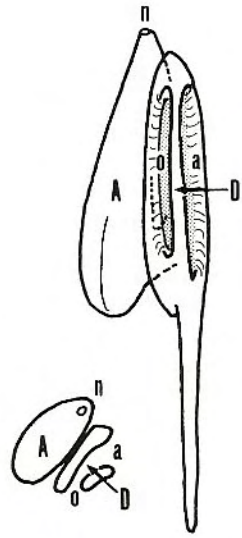


Fig. 16. Diagram of a nephridium of *Phoronis pallida* (see abbr. Fig. 9)

in biocoenosis of fine well-sorted sand, b. of superficial muddy sands and in *Venus-*, *Albra alba-* and *Macoma baltica*-communities.

Length: 60–190 mm (0.5 to 2 mm in diameter).

Colour: lophophore transparent with white spots (pigment), sometimes lophophore yellow, red or green; body pink.

Lophophore: horseshoe-shaped with the ends turned medially (Fig. 1 b, 8).

Tentacles: 60–130 (1.5 to 2.5 mm long).

Nephridia: 1 funnel; short descending branch; nephridiopore on the anal papilla opening below the anus (Fig. 15 b).

Giant fibers: only 1 on the left side, 7–27 μ in diameter (Fig. 4 b); rarely one very thin on the right side.

Longitudinal muscles (Fig. 4 b): $[25–50]\ \frac{7–19}{4–11}\Big|\frac{7–17}{4–\ 9} \qquad 34 = \frac{11}{6}\Big|\frac{11}{6}$

Gonads: dioecious; lophophoral organs large glandular; nidamental glands 2 c type; embryos in a single one or in 2 masses in the lophophore; except probably *P. architecta:* no brooding patterns.

Larva: unknow.

Asexual propagation: by transverse fission.

Distribution: Italy, France, Germany, Algeria, Ivory Coast, the Azores, North America, Madagascar, India.

4. Phoronis pallida Silén, 1952

Biotope: sand, clayed sand; depth from 1 to 12 m; density up to 74,000 ind./m².

Length: up to 140 mm (0.3 to 1 mm in diameter).

Colour: pink-yellowish.

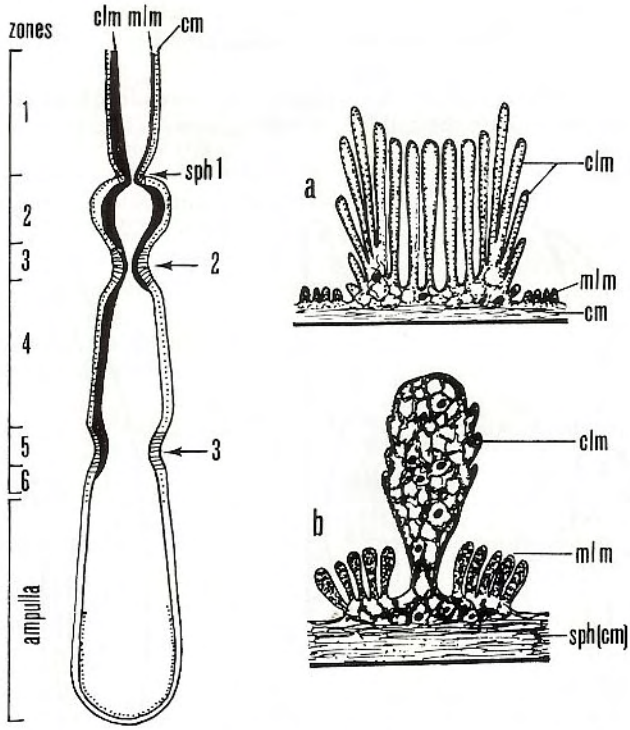


Fig. 17. Diagrams of arrangement of muscles in *Phoronis pallida* and of sections of longitudinal muscle strip, from zone 4 (a) and zone 3 (b) after SILÉN (1952). clm = central longitudinal muscle; cm = circular muscle; mlm = marginal longitudinal muscle; sph = sphincter

Lophophore: horseshoe-shaped (Fig. 8).
Tentacles: 50–140 (about 2.5 mm long).
Nephridia: 2 funnels, anal slightly larger than oral; descending branch as long as ascending branch; nephridiopore on the anal papilla opening at the anus level (Fig. 16).
Giant fiber: 1 on the left side, 15–20 μ in diameter (Fig. 4 c).
Longitudinal muscles (Fig. 4 c): [18–19] $\frac{5-6}{4}\left|\frac{5}{4}\right.$ $18 = \frac{5}{4}\left|\frac{5}{4}\right.$
Gonads: hermaphroditic; lophophoral organs large glandular; nidamental glands absent; no brooding.
Larva: *Actinotrocha pallida.*
Other characters: unusual musculature arrangement (Fig. 4 c, 17), circular muscles present 3 strong horizontal sphincters, longitudinal muscles divide into 6 zones.
Distribution: Sweden, North America (W coast).
Genus *Phoronopsis* Gilchrist, 1907: presence of a collar fold below the lophophore.

5a. Phoronopsis albomaculata Gilchrist, 1907

Biotope: clogged coarse sand to sandy mud; depth from any meters to 45 m; living in populations of coarse sands under bottom currents, with *Asymetron.*
Length: 80–150 mm (0.5 to 2 mm in diameter).

Colour: lophophore pigmented with white spots; body yellowish.
Lophophore: horseshoe-shaped with the ends turned medially (Fig. 8).
Tentacles: 70–126 (2–3 mm long).
Nephridia: 2 funnels, anal smaller, oral larger; long descending branch; nephridiopore opening below the anus on the collar in the invagination (Fig. 18 a).

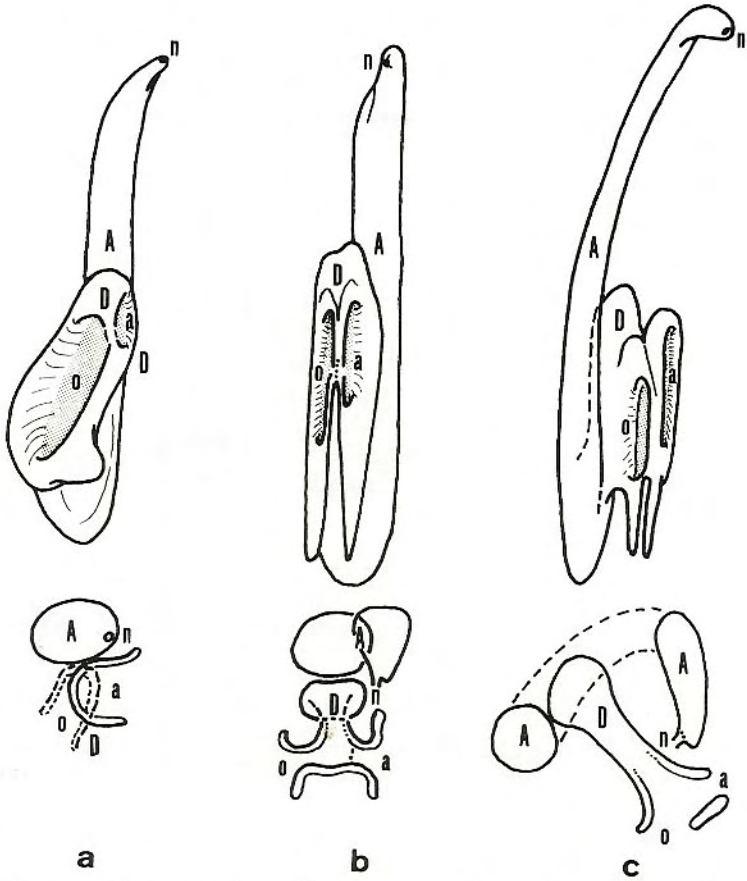


Fig. 18. Diagrams of a nephridium of *Phoronopsis albomaculata* (a), *harmeri* (b), *californica* (c). (see abbr. Fig. 9)

Giant fibers: 1 on the left side, 15–24 μ in diameter (Fig. 4 d); the right fiber only present down to the nephridial level and is absent below.

Longitudinal muscles (Fig. 4 d): $[59–94]\ \frac{18–32}{11–18}\left|\frac{17–30}{10–15}\right.$ $\quad 72 = \frac{23}{14}\left|\frac{22}{13}\right.$

Gonads: probably dioecious; lophophoral organs large.
Larva: unknow.
Asexual propagation: by transverse fission.
Invagination: about 0.1 mm.
Distribution: South Africa, Madagascar, Ivory Coast.

5b. Phoronopsis harmeri Pixell, 1912

Synonyms:

Phoronis pacifica Torrey, 1901.
Phoronopsis viridis Hilton, 1930.
? *Phoronopsis striata* Hilton, 1930.

Biotope: sands to mud (sometimes with coarse fraction); depth from intertidal zone to 89 m; density up to 28,000 ind./m².

Length: 40–220 mm (0.6 to 4 mm in diameter).

Colour: greenish with tentacles white-pigmented.

Lophophore: spirally-shaped with 1.5 to 2 coils on each side (Fig. 19, 20).

Tentacles: 100–400 (2–5 mm long).

Nephridia: 2 funnels, anal smaller, oral larger; long descending branch; nephridiopore opening below the anus on the collar in the invagination (Fig. 18 b).

Giant fibers: 1 on the left side, 20–60 μ (Fig. 4 f); the right fiber fading at right nephridial level.

Longitudinal muscles (Fig. 4 f): [79–138] $\frac{20\text{–}48 \mid 23\text{–}55}{12\text{–}27 \mid 11\text{–}26}$ 113 = $\frac{37 \mid 37}{20 \mid 19}$

Gonads: dioecious; lophophoral organs large, membranous; nidamental glands absent; no brooding.

Larva: *Actinotrocha A.*

Invagination: very distinct (Fig. 20).

Distribution: North America (W coast), USSR (far east), Cook Islands, the Azores.

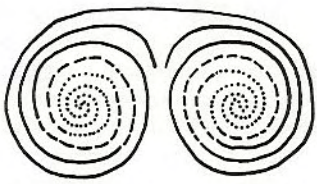
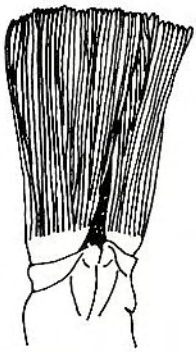
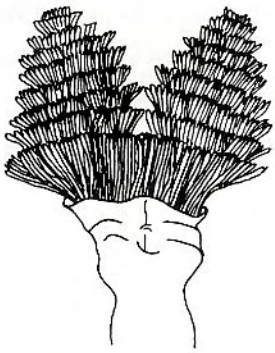


Fig. 19 (left). Phoronopsis harmeri. Spirally-shaped lophophore – *Fig. 20 (right). Phoronopsis californica.* Helicoidal-shaped lophophore





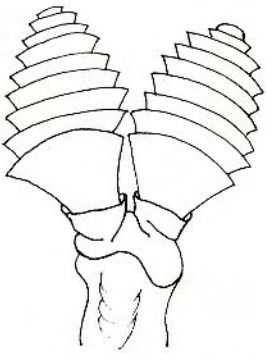


Fig. 21 (left). Phoronopsis harmeri. Anal view of the anterior body end – *Fig. 22 (centre and right). Phoronopsis californica.* Oral and anal view of the anterior body end, showing the helicoidal-shape of the lophophore

5c. Phoronopsis californica Hilton, 1930

Biotope: mud to coarse sands; depth any meters to 17 m; living in biocoenosis of coarse sands and fine gravels under bottom currents, with *Branchiostoma*.
Length: 220 to more than 450 mm (2.5 to 5 mm in diameter).
Colour: lophophore orange, red, grey, greenish; body orange to brown.
Lophophore: helicoidal-shaped with 4 to 5 coils on each side, 5–7 mm long (Fig. 21, 22).
Tentacles: more than 1500, 2 to 2.5 mm long (Fig. 22).
Nephridia: 2 funnels, anal larger, oral smaller; long descending branch; nephridiopore opening below anus on the collar fold in the invagination (Fig. 18 c).
Giant fibers: 1 on the left side, 70–80 μ in diameter in the body (Fig. 4 e); the right one only present down to the nephridial level and is absent below.
Longitudinal muscles (Fig. 4 e): [180–243] $\frac{53–81 \mid 56–79}{35–54 \mid 29–40}$ 211 = $\frac{66 \mid 66}{44 \mid 35}$
Gonads: dioecious (probably); lophophoral organs large, membranous.
Larva: unknow.
Invagination: about 1 mm.
Distribution: North America (California), Madagascar (Nosy-Bé).

III. Discussion

The suggestion made by both MARSDEN (1959) and SILÉN (1952) that *Phoronida* can be divided into four or five subgroups respectively is supported by my studies. However, in my opinion, the most probable natural subdivision of the Phoronida differs from the arrangement suggested by these authors except with respect to the 2 well-defined categories, *Phoronis ovalis* and *Phoronis pallida* (Table 9).

Refering to table 9, SILÉN grouped *Phoronis psammophila* with his category 2, but MARSDEN places it with a different species assemblage in his category 3 which also includes *Phoronis muelleri* and genus *Phoronopsis*. MARSDEN (1959) stated of this

Table 9

Subdivision of the phylum Phoronida

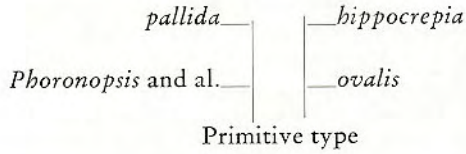
(The categories 3 and 4 are considered respectively 4 and 2 in MARSDEN's paper)

Category	SILÉN (1952)	MARSDEN (1959)	EMIG
1.	*Phoronis ovalis*	*Phoronis ovalis*	*Phoronis ovalis*
2.	*Phoronis hippocrepia* *Phoronis australis* *Phoronis psammophila*	*Phoronis hippocrepia* *Phoronis ijimai* *Phoronis australis*	*Phoronis hippocrepia* *Phoronis ijimai* *Phoronis australis*
3.	*Phoronis muelleri*	*Phoronis muelleri* *Phoronis psammophila* Genus *Phoronopsis*	*Phoronis muelleri* *Phoronis psammophila*
4.	*Phoronis pallida*	*Phoronis pallida*	*Phoronis pallida*
5.	Genus *Phoronopsis*		Genus *Phoronopsis*

group that "accumulation of more information in the future may justify its subdivision". I feel that this subdivision is necessary: my reasons for making a new arrangement (col. 3, Table 9) derive largely from comparative morphology of nephridia. *Phoronopsis* is also distinguished adequately by the occurrence of an annular fold.

Both SILÉN (1952) and MARSDEN (1959) contemplated etablishing separate genera for each of their species groups to give their the same status as *Phoronopsis*. Althrough I may ultimately adopt this suggestion, it would be premature to set up separate genera at this time. On the one hand this would complicate the systematics of the *Phoronida* and make it difficult for non-specialist to allocate generic names; on the other hand, without studies of the *Actinotrocha*-larva our understanding of relationships within the *Phoronida* remains imperfect.

MARSDEN (1959) concluded his study by constructing an evolutionary scheme which depicted all four groups as derived from a single primitive type (see MARSDEN's diagram below):



My suggestions as to phylogenetic relationships are based on the study of various aspects of adult morphology. Each character considered can be traced from a simple to a more complex condition. For example: – lophophore (from a simple circle of tentacles to a complicated tentacle crown, as in *Brachiopoda*); – nephridia (Table 5), the duplication of the nephrostomes is a secondary phenomenon and the simple funnel and the absence of either one or both of the lateral mesenteries correspond to a primitive condition (SILÉN 1952; EMIG 1973 b); – number and arrangement of longitudinal muscles (Table 7; Fig. 3, 4); – giant fibres (Table 6), SELYS-LONGCHAMPS (1907) concludes that "le nerf latéral est un organe primitivement pair", and in my opinion the presence of two giant fibres is a primitive feature; – gonades (Table 8), from hermaphrodism to dioecism.

A possible scheme of relationships between the various phoronid species has been etablished by a comparison using the above mentioned characters (Fig. 23). This scheme is very close to that produced by MARSDEN (1959). *Phoronis ovalis closest to the primitive* type is a morphologically less complex than category 2; this species of both categories are burrowing into or encrusting on hard substrates. The species of all other categories live in

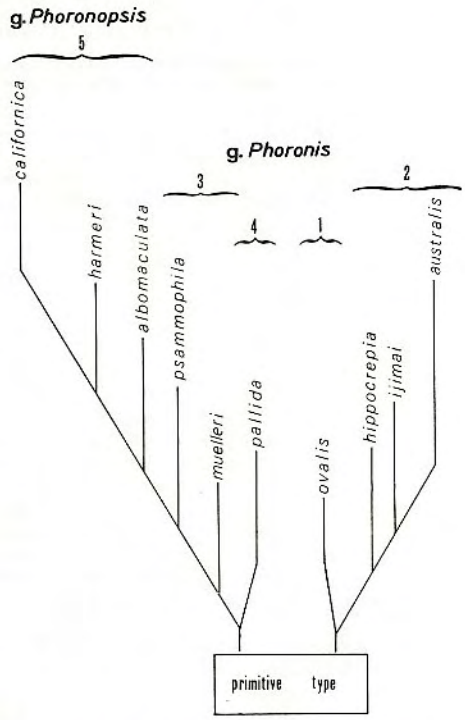


Fig. 23. Possible scheme of the phylogeny of the species of *Phoronida*

vertical tubes in soft substrates and are more closely related to one another by morphological similarities than they are to the two preceeding categories.

The recognition of the phylum *Phoronida* as primitive members of *Deuterostomia* is based on the study of ZIMMER (1964) and EMIG (1973 b).

Summary

The taxonomic characters of the *Phoronida* are briefly described with their degree of variation. A diagnosis is etablished for each species. The phylum *Phoronida* (2 genera *Phoronis* and *Phoronopsis*) can be divided into five categories (1. *Phoronis ovalis;* 2. *Phoronis hippocrepia, P. ijimai, P. australis;* 3. *Phoronis muelleri, P. psammophila;* 4. *Phoronis pallida;* 5. Genus *Phoronopsis: albomaculata, harmeri, californica*). The characteristics of each category are discussed. An evolutionary scheme with relationships between the various phoronid species has been etablished by a comparison using the taxonomic characters.

Zusammenfassung

Systematik und Evolution von Phoronida

Die taxonomischen Merkmale der Phoroniden werden kurz geschildert und ihre Variabilität festgehalten. Für jede Art wird eine Diagnose gegeben. Auf Grund verschiedener Merkmale kann man die die Gattungen *Phoronis* und *Phoronopsis* umfassenden Phoroniden in 5 Kategorien unterteilen: 1. *Phoronis ovalis;* 2. *Phoronis hippocrepia, Ph. ijimai, Ph. australis;* 3. *Phoronis muelleri, Ph. psammophila;* 4. *Phoronis pallida;* 5. *Phoronopsis* mit den Arten *albomaculata, harmeri, californica.* Die für jede dieser Kategorien bestimmenden Merkmale werden diskutiert. Ein Diagramm der Phylogenese der Phoroniden wird, fußend auf der Evolution der taxonomischen Merkmale innerhalb der Gruppe, ausgearbeitet.

Résumé

Systématique et Evolution des Phoronidiens

Les caractères taxonomiques des phoronidiens sont brièvement exposés et leurs variations ont été portées dans divers tableaux. Une diagnose a été établie pour chaque espèce. D'après l'étude de leurs divers caractères, les différentes espèces de phoronidiens, comprenant deux genres *Phoronis* et *Phoronopsis,* peuvent être réunies en 5 catégories (1. *Phoronis ovalis;* 2. *Phoronis hippocrepia, P. ijimai, P. australis;* 3. *Phoronis muelleri, P. psammophila;* 4. *Phoronis pallida;* 5. Genre *Phoronopsis: albomaculata, harmeri, californica*). Les caractères propres à chacune de ces catégories sont discutés. Un diagramme de la phylogenèse des espèces de phoronidiens a été établi d'après l'évolution des caractères taxonomiques.

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Appendix

In a recent study on Phoronida from Australia I have studied *Phoronopsis albomaculata:* this species possesses nephridia with *one funnel* and not 2 as the possibility has been described (dotted line in Fig. 18 a). So that the nephridia of *Phoronopsis albomaculata* present the same morphology as these of *Phoronis psammophila* and it are of category 2 (and not 5).

Phoronis ijimai and *Phoronopsis albomaculata* can present also a spirally-shaped lophophore with one coil on each side.