Phylogenetic systematics in Phoronida (Lophophorata)

By C. C. Emig

Abstract

Cladistic methods are used to analyse phylogenetic relationships within the Phoronida. Eleven characters, which may be present in an apomorphic or derived condition, are as follows: ecological habit; shape of longitudinal muscle; number of giant nerve fibres; number of coelomic funnels of nephridia; number of nephridial branches; development of nephridial epithelium; type of lophophoral organs; collar fold; gonads; developmental patterns, and larva. Some of the other characters need further investigation to establish their phylogenetic usefulness. These 11 characters have been used for constructing a tree of phylogenetic interrelationships of phoronid species. Two sister-groups are recognized, one of boring species and the other of soft-sediment living species. *Phoronis ovalis* and *P. muelleri* are considered to be primitive in each group respectively, and the genus *Phoronopsis* as the most advanced among the sediment-dewellers.

The Phoronida are sedentary, benthic suspension feeders, with a vermiform body enclosed in a secreted tube in which they move freely. They share together with the Brachiopoda and Bryozoa a ciliated lophophore which functions as a food-gathering and respiratory organ (e. g. EMIG 1976 a). According to the adaptive model proposed by FARMER et al. (1973) and VALENTINE (1975), infaunal tubicolous ancestors gave rise in the early Cambrian to both the Brachipoda and the Bryozoa. The Phoronida closely resemble the presumed common ancestor of the lophophorates, which is called Protolophophorate by EMIG (1984). The poor record of soft-bodied phoronids provides limited information of the time at which the lineage arose; burrows and borings attributed to phoronids are known since the Devonian (see EMIG 1982, for a review) and possibly the late Precambrian (VALENTINE 1977).

The Phoronida, while retaining the general ancestral form, have evolved as a monophyletic group. Their common characters establishing monophyly have been discussed previously by EMIG (1976 b, 1982); they will not be taken in consideration herein. The small diversity of phoronids (10 species in two genera) reflects constraints imposed by their adaptative strategy. All species have a broad geographical distribution, mostly world-wide.

Several taxonomic arrangements of phoronid species have been suggested by SILÉN (1952), MARSDEN (1959), and EMIG (1974). The aim of these authors was to construct an evolutionary scheme from a primitive type, based on an empirical approach of the character relationships. The goal of the present paper ist to construct a cladogram showing phylogenetic relationships within the Phoronida.

Character analysis

The analysis utilizes the taxonomic characters used to identify phoronid species; these characters have been established and discussed previously (EMIG 1971, 1974, 1979, 1982). Study of most characters requires histological serial cross-sections. The characters utilized

are as follows: mode of life; absence or presence of a collar fold; shape of the lophophore; morphology of nephridia; shape and formula of longitudinal muscle bundles; number (one or two) of giant nerve fibres; gonads and accessory sex glands, and developmental patterns. Three species have additional features (muscle arrangement, circulatory system, lack of lateral mesenteries). The phylogenetic significance of all these characters are discussed below, and features considered to have phylogenetic implications within the group Phoronida are listed on Tables 1 and 2.

1. Modes of life and muscle arrangement

Most phoronid species are infaunal, vertically embedded in soft sediments, living sometimes in sparse populations. Some, however, bore, generally in mollusc shells and rocks, or like *Phoronis australis* in cerianthid tube walls; and the species *Phoronis hippocrepia* and *P. ijimai* which normally bore, encrust hard substrates under still environmental conditions (EMIG 1973 a, 1982). According to the general assumptions of VALENTINE (1977), CLARCK (1977), SALVINI-PLAWEN (1982), the phoronid body was primitively employed for burrowing in soft sediments and sustaining the animal in its infaunal mode of life (EMIG 1984). This life-style is regarded as plesiomorphic, whereas boring in hard substrates and epifaunal habits are regarded as apomorphic.

Two main types of cross-sectional shape of the central longitudinal muscle bundles occur in phoronids (EMIG 1974), not three as stated by CORI (1939). These two types can be called feather-shaped and bush-shaped (Fig. 1). The feather-shaped type is observed in all sediment-dwellers, with some variation in disposition related to the number of muscle bundles in the various species. The peculiar disposition of longitudinal muscles in *Phoronis pallida* described by SILÉN (1952) is obviously a modified version of the feather-shaped type; SILÉN's reasons for considering it as not referable to any other type are contradicted by the fact that muscle bundles in other phoronid species show a similar feature just below the lophophore or in the ampulla. Nevertheless, the body wall muscles in *P. pallida* are differentiated to a degree unique in the Phoronida, especially the circular muscles which form three thick sphincters (SILÉN 1952); such a structure, whose function is unknown, is not reported in any other species, all of them have the same circular muscle system (including boring species), that leads to consider the muscle system of *P. pallida* as a derived version of the feather type (Fig. 1).

The bush-shaped type occurs in the boring species (Fig. 1). *Phoronis ovalis*, like all other phoronid species, shows marginal longitudinal muscles, which SILÉN (1952) failed to observe. The function of the longitudinal muscles is to draw the animal down into the basal part of its tube. Because sediment-dwellers always have a much longer tube than borers, it seems assuming
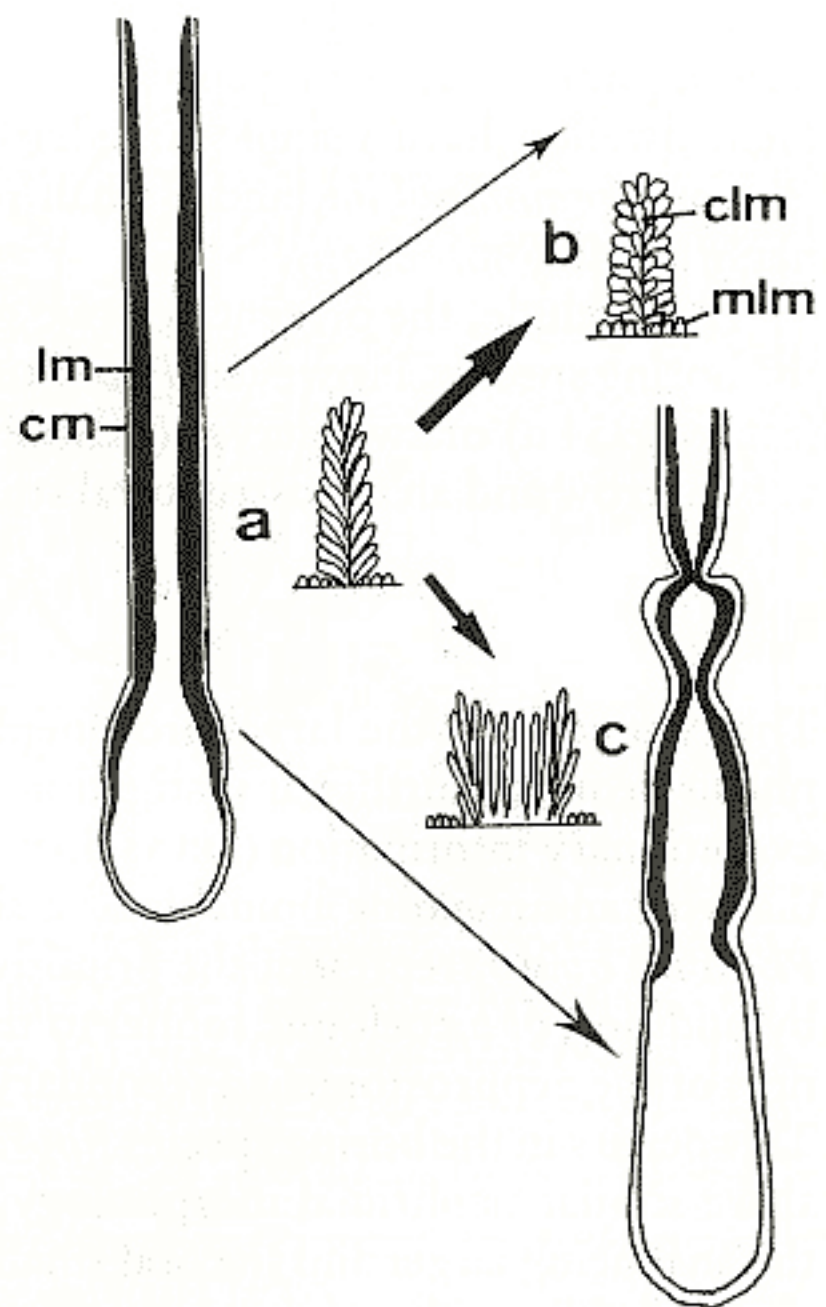

Fig. 1. Development of the longitudinal muscle bundles (lm) and circular muscles (cm) along the metasome of all phoronid species (a), except *Phoronis pallida* (c, after SILÉN 1952), and cross-sections of those bundles; feather-shaped (a) in sediment-dwellers, except derived condition (c) in *P. pallida*; bush-shaped (b) in boring species. (clm = central longitudinal muscles; mlm = marginal longitudinal muscles)

that muscle shape is related to mode of life, the bush-shape of borers being derived relative to the feather-shape of sediment-dwellers.

The number of longitudinal muscle bundles varies widely in phoronid species, except for *Phoronis pallida* which has a constant number of muscles. Muscle number may be related to size in general. In smaller species the number of bundles is constant along the body wall of each individual, while in larger species which always have more muscles, muscle number increases from the lophophore level down to the ampulla (EMIG 1971; EMIG and EMIG 1975). Often the number of longitudinal muscles and their distribution in the body (according to the conventional muscle formula) characterize different populations of the same species. Conversely, individuals of different species may show the same muscle formula.

It seems obvious that this character is homoplasic or and without apparent phylogenetic significance.

2. Number of giant nerve fibres

The giant nerves, issuing from the ganglion and extending along the body wall, are one or two in number. SELYS-LONGCHAMPS (1907) argued that the giant nerves were originally paired, a view which is shared by SILÉN (1954 a) and EMIG (1974). In favour of this opinion, SILÉN concluded that the right giant nerve fibre in Phoronida decussates in the same way as that described for other invertebrate groups but decussation of a single fibre is a feature peculiar to the Phoronida. It is always the right nerve which is lacking or rudimentary in phoronids; boring species have two nerves, the right one is always smaller. Sediment-dwellers have a single large left fibre, with a vestigial right fibre observed rarely in *Phoronis psammophila*, and a small remnant of the right fibre down to the level of the nephridia in *Phoronopsis*.

To conclude, the presence of two giant nerves is a plesiomorphic condition, shared by the boring species. However, *Phoronis ovalis* remains problematic: there is either no nerve (SILÉN 1954 a) or two nerves (FORNERIS 1959; EMIG 1971). When nerves exist, they are very narrow and an ultrastructural study is needed.

3. Nephridia

The change from the larval protonephridia to the adult metanephridia during metamorphosis requires further investigation. However, adult nephridial morphology provides evolutionary information (SELYS-LONGCHAMPS 1907; SILÉN 1952; EMIG 1973 b). Nephridia with an ascending branch and a simple coelomic funnel, or nephrostome, as seen in *Phoronis ovalis*, represent the primitive condition which is probably reached in the adult by addition of a coelomic funnel to the larval protonephridial tube (Fig. 2). The doubleness of the nephrostome is a secondary phenomen (SILÉN 1952), i. e. an apomorphic state. This occurs in the boring species *Phoronis hippocrepia*, *P. ijimai*, and *P. australis*. These all share similar nephridial morphology, with two funnels, well-defined morphologically, the anal being larger and the oral smaller (EMIG 1979) (Fig. 2).

Nephridia with two branches, descending and ascending, and a *single* funnel, as seen in *Phoronis muelleri*, *P. psammophila* and *Phoronopsis albomaculata*, can be derived from the plesiomorphic condition by addition of a descending branch (Fig. 2). The acquisition of two funnel-shaped nephridia by *Phoronis pallida*, *Phoronopsis harmeri*, and *Phoronopsis california* is directly derived from the former nephridial state by development of the nephridial epithelium surrounding the opening of the descending branch; this leads to a two-funnel morphology which is always more prominent during the reproductive period, when the nephridia act as gonoducts (EMIG 1971, 1979) (Fig. 2). A similar development may occur weakly in *Phoronis psammophila* and in *Phoronopsis albomaculata*, but it never reaches a two-funnel shape. It has not been in *Phoronis muelleri* or in boring species in
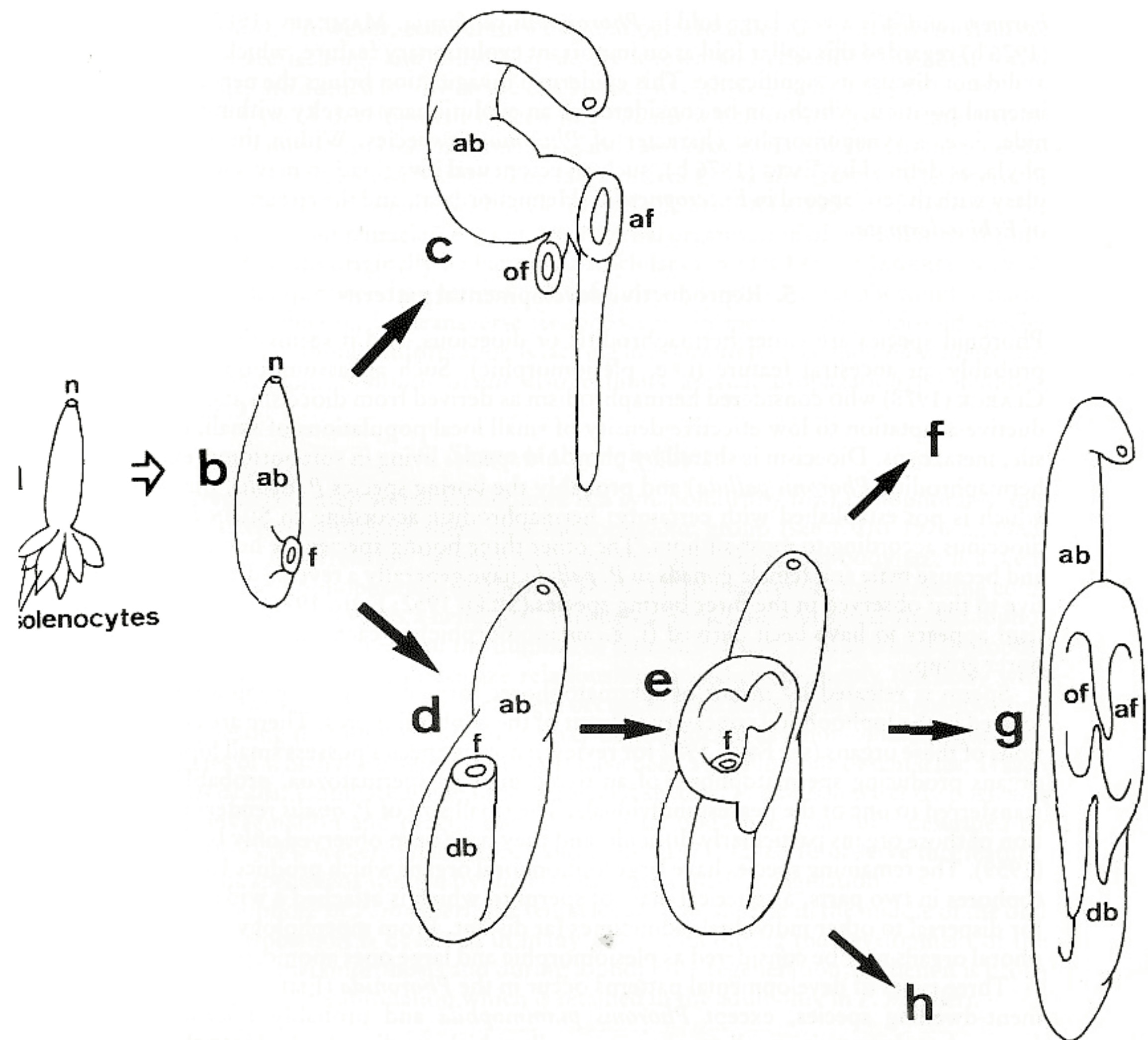
Fig. 2. Phylogenetic relationships of phoronid nephridia. a: Larval protonephridium which occurs in all larvae (n = nephridiopore); b: Nephridium with single branch ascending (ab) and single coelomic funnel (f) (*Phoronis ovalis*); c: Nephridium with a curved ascending branch and two funnels (af = anal funnel; of = oral funnel) (*P. hippocrepia, P. ijimai, P. australis*); d: Nephridium with two branches, descending (db) and ascending (ab), and a single funnel (f) (*P. muelleri*); e: Same type with development of nephridial epithelium surrounding the funnel, particularly during the reproductive period (*Phoronis psammophila; Phoronopsis albomaculata*); f, g, h: Derived state leading to "two-funnel" types (f. *Phoronis pallida*; g: *Phoronopsis harmeri*, represented; h: *Phoronopsis californica*) (see text for discussion, and EMIG 1979)

which the two-funnel morphology is quite different. Development of the nephridial epithelium appears to be an apomorphic feature among the sediment-dwellers, but its exact form is specific to each species (Fig. 2).

4. Collar fold

The presence of an epidermal collar fold below the lophophore characterises the genus *Phoronopsis*. This fold is slightly developed, often only on the anal side, in *Phoronopsis albomaculata*, but a deep invagination occurs around the lophophore in *Phoronopsis*

harmeri, and it is a very large fold in *Phoronopsis california*. MAMKAEV (1962) and EMIG (1976 b) regarded this collar fold as an important evolutionary feature, which SILÉN (1954 a) did not discuss its significance. This epidermal invagination brings the nerve ring in an internal position, which can be considered as an evolutionary novelty within the Phoronida, i. e. a synapomorphic character of *Phoronopsis* species. Within the archimerate phyla, as defined by EMIG (1976 b), such an ectoneural invagination may suggest homoplasy with the collar cord in *Enteropneusta* (Hemichordata), and the circumoral nerve ring of *Echinodermata*.

5. Reproductive developmental patterns

Phoronid species are either hermaphroditic or dioecious, and it seems that dioecism is probably an ancestral feature (i. e. plesiomorphic). Such an assumption is made by CLARCK (1978) who considered hermaphrodism as derived from dioecism and as a reproductive adaptation to low effective density of small local populations of small, often sessile, metazoans. Dioecism is shared by phoronid species living in soft bottoms (except the hermaphroditic *Phoronis pallida*) and probably the boring species *P. ovalis*, the status of which is not established with certainty: hermaphroditic according to SILÉN (1952) but dioecious according to most authors. The other three boring species are hermaphroditic, and because male and female gonads in *P. pallida* have generally a reverse disposition relative to that observed in the three boring species (SILÉN 1952; EMIG 1971), hermaphrodistism appears to have been derived (i. e. autapomorphic) in each sediment-dweller and borer group.

Sperm is released by means of spermatophores formed in two lophophoral organs, located in the lophophoral concavity in front of the nephridiopores. There are two conditions of these organs (see EMIG 1982 for review): boring species possess small lophophoral organs producing spermatophores of an ovoid mass of spermatozoa, probably rapidly transferred to one of the nearest individuals. The small size of *P. ovalis* renders the detection of those organs particularly difficult, and they have been observed only by FORNERIS (1959). The remaining species have large lophophoral organs which produce large spermatophores in two parts, a spherical mass of sperm to which is attached a wide spiral float, for dispersal to other individuals sometimes far distant. From morphology, small lophophoral organs may be considered as plesiomorphic and large ones apomorphic.

Three types of developmental patterns occur in the *Phoronida* (EMIG 1982). The sediment-dwelling species, except *Phoronis psammophila* and probably *Phoronopsis albomaculata*, have quite small eggs, poor in yolk, which are directly shed into the sea and undergo a complete planktotrophic development. This is a primitive condition in *Lophophorata*, as in many other invertebrate groups (JÄGERSTEN 1972; STRATHMANN 1978; JABLONSKI and LUTZ 1983).

The two other developmental patterns involve brooding and large eggs rich in yolk. At first, *Phoronis hippocrepia*, *P. ijimai*, *P. australis*, and *P. psammophila*, the embryos are brooded within the lophophoral concavity on nidamental glands up to the first actinotroch stages (EMIG 1982). *P. hippocrepia* and *P. ijimai* have similar nidamental glands (basal ones on the floor of the lophophoral concavity and tentacular ones on the inner tentacle row at the inner side of the horseshoe-shaped end of the lophophore). *P. australis* extends the glands from the floor of the concavity into the several coils of the lophophore at the inner surface of the inner tentacles. *P. psammophila* develops the glands along the inner tentacle row around the lophophoral concavity. The presence of basal and tentacular glands and a continuous release of embryos in the three boring species seems to favour a common origin for the brood patterns, that is a synapomorphic character within the borer-group, while tentacular glands and a periodic release in *P. psammophila* appear to be autapomorphic in the dweller-group. In these brooding species, life as part of the

plankton is short. However, comparative morphological studies on the actinotroch larvae of phoronids are lacking, and only 7 larvae are known and related to the adult form. Further studies are needed before larvae can be used in a phylogenetic analysis.

The third type of development is seen in *P. ovalis* which probably in relation to its small size (5–15 mm long) lacks nidamental glands and broods its embryos in the parental tube, a peculiar feature in brooding. The larva differs externally from the actinotroch, being completely lecithotrophic, without a true pelagic life (Silén 1954 b). However, this creeping larva, without tentacles, exhibits the internal organisation of the actinotroch, this suggests that *P. ovalis* originally had an actinotroch larva (Silén 1954 b; Jägersten 1972) from which its unique brooding pattern evolved independently of other phoronid species.

Asexual reproduction by transverse fission occurs in most of the phoronid species (Emig 1972, 1979); though information is lacking in *Phoronis pallida* and *Phoronopsis californica*. In addition, *Phoronis ovalis* also exhibits asexual propagation by budding (Marcus 1949).

6. Shape of the lophophore

The occurrence of a mesosomal lophophore is a synapomorphy for Lophophorates, one of the characters establishing them as a monophyletic group (see Emig 1976 a, 1982; Rowell 1982). A correlation between shape of the lophophore and body size is a well-known feature in Lophophorates (Mundy et al. 1981). In Phoronida, the increasing complexity from an oval towards a helicoidal, through a horseshoe and spiral-shaped lophophore, is related to an increase of the number of tentacles (Emig 1976 a) which is proportional to body size. Such a shape-size relationship, necessary to supply the body with adequate food and respiratory gas exchange, occurs in both boring and sediment-dwelling species suggesting that lophophore shape may be considered as a homoplasous transformation series of which the original state must have been a simple circle of tentacles, as seen in *Phoronis ovalis*. Compared with other phoronid species, *P. ovalis* apparently possesses a peculiar invagination and evagination of the distal body part, carefully described by Harmer (1917). However, Silén (1952) and Emig (1971) failed to observe this feature, far none of the specimens studied by them shared any sign of invagination.

In the lophophore of *P. muelleri*, the tentacles become shorter in the middle of the oral side. Such a disposition is observed in many Phoronida during the development of the lophophore after metamorphosis and during lophophore regeneration; in them it is probably an ontogenetic recapitulation which is retained in the adult only in *P. muelleri*.

7. Absence of lateral mesenteries

The absence of lateral mesenteries in the body (absent from both sides in *Phoronis ovalis* but the left side only in *P. muelleri*) is considered as rather primitive by Silén (1952), who argued that they indicate phyletically late structures in view of their absence in the actinotroch-larva and late development in the adult. This interpretation was not entirely supported by Emig (1973 a), who suggested that their absence may rather be the result of a secondary reduction. A solution to this problem is at present impossible either in respect of ontogeny or phylogeny (Emig 1973 a).

8. Circulatory system

The general circulatory system (see Emig 1982, for review) is similar in all species, except *Phoronis ovalis* which in addition possesses an accessory vessel and a right lateral vessel along the trunk. These features might be interpreted as representing a primitive condition, reduced secondarily in the other species, which show only a remnant of the right lateral vessel in the blood-sinus (surrounding the stomach) and below the lophophore a short

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branch uniting the left lateral vessel. Recent ultrastructural studies have revealed some different structures in the vessel of *P. muelleri*, *P. psammophila*, and *P. australis*, but their significance cannot be assessed before further comparative studies, especially on *P. ovalis*.

Discussion

To analyse the characters considered within the phoronid species, the use of out-group, i. e. brachiopods or bryozoans, was of poor help to investigate and justify the character state polarity, plesiomorphic or apomorphic. The absence of specific comparison with the out-group, a standard problem sometimes to bring the argument convincing, is specified by the fact that most of characters within the Phoronida look quite different in both related phyla, Brachiopoda and Bryozoa, to be really used in our decision concerning the character condition within the Phoronida. In spite of this, simple comparison with out-group was utilised when available.

At least, 11 characters have been retained for phylogenetic inferences among the phoronid species; they are summarized on Table 1. From the results of this table, a data set of species and coded characters was constructed. This has been done in Table 2, determining the divergence index used to construct the three (Fig. 3) according to the method recently proposed by EMIG (1985). The Phoronida are divided into two sister-groups,
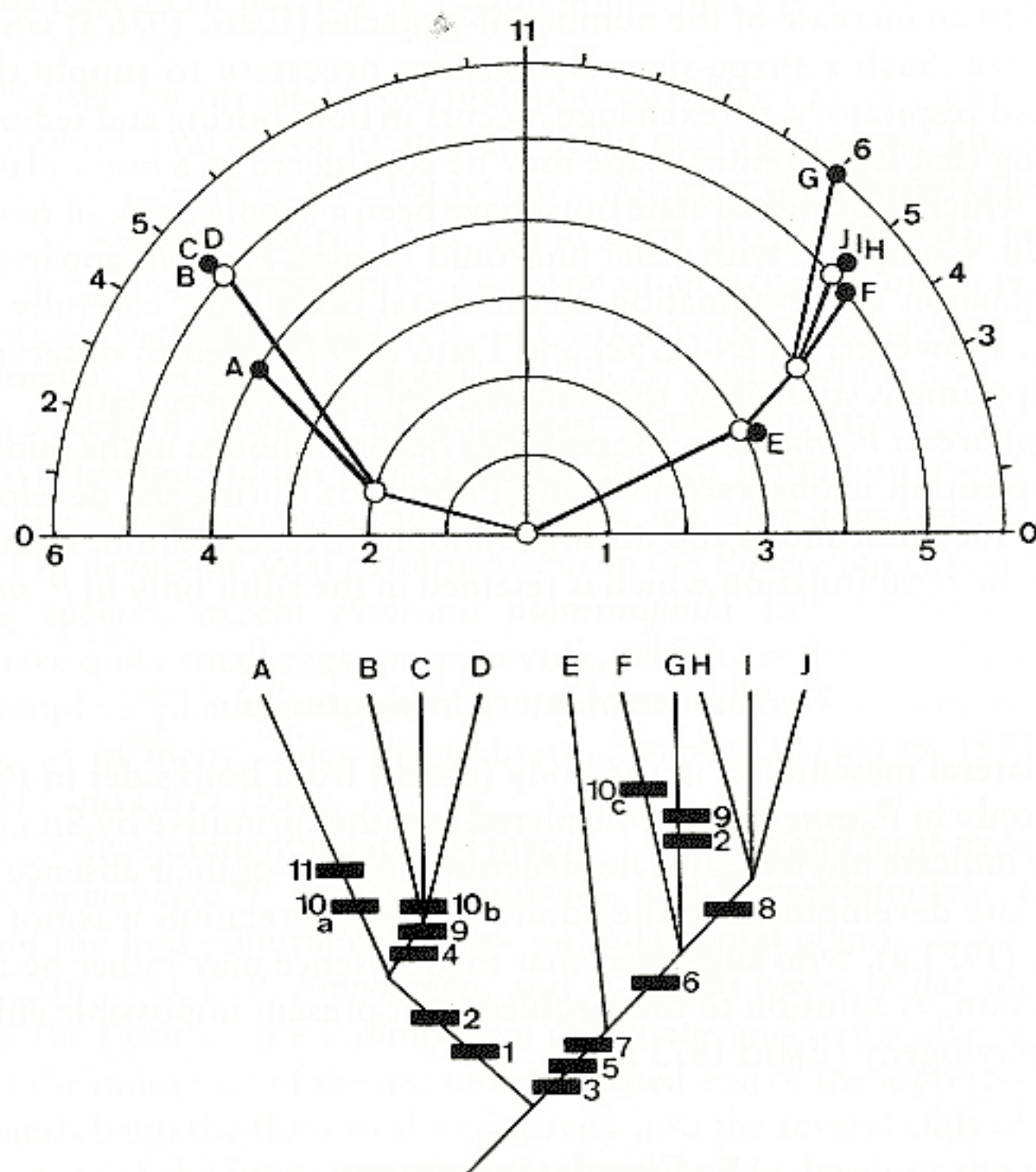

Fig. 3. Phylogenetic analysis of the interrelationships of phoronid species, using the method proposed by EMIG (1985) on Wagner tree: species are indicated by black circles and each is plotted on the intersection of the concentric semicircle and the centripetal line, that both equal the divergence index of the species (Table 2); ancestral species, indicated by open circles, are placed by the same manner according to the number of apomorphies shared by their descendants. Black bars are apomorphies, and character numbers correspond to characters shown in Tables 1 and 2

Table 1

Characters used to analyse the phylogenetic interrelationships of phoronid species

(Brooding patterns a: *Phoronis ovalis*; b: *P. hippocrepia, P. ijimai, P. australis*; c: *P. psammophila*; see text)

Characters	Plesiomorphic	Apomorphic; derived
1. Habits	infaunal in soft sediments	boring or epifaunal on hard substrates
2. Shape of longitudinal muscle bundles	feathery	bushy; *pallida*-condition
3. Number of giant nerve fibres	two	one
4. Coelomic funnels of nephridia	one	two
5. Nephridia branches	one ascending	two ascending and descending
6. Development of nephridial epithelium	absent	present
7. Lophophoral organs	small	large
8. Collar fold	absent	present
9. Gonads	dioecious	hermaphroditic
10. Developmental patterns	direct release	brooding patterns: a, b, c
11. Larva	actinotroch	creeping

Table 2

Divergence analysis from data of Table 1

The characters are coded as 0 plesiomorphic, 1 apomorphic or derived. Information is lacking on *Phoronis bhadurii* which is not included in the present list. DI = divergence index

Characters	ovalis A	hippocrepia B	ijimai C	australis D	muelleri E	psammophila F	pallida G	albomaculata H	harmeri I	californica J
1	1	1	1	1	0	0	0	0	0	0
2	1	1	1	1	0	0	1	0	0	0
3	0	0	0	0	1	1	1	1	1	1
4	0	1	1	1	0	0	0	0	0	0
5	0	0	0	0	1	1	1	1	1	1
6	0	0	0	0	0	1	1	1	1	1
7	0	0	0	0	1	1	1	1	1	1
8	0	0	0	0	0	0	0	1	1	1
9	0	1	1	1	0	0	1	0	0	0
10	1a	1b	1b	1b	0	1c	0	0	0	0
11	1	0	0	0	0	0	0	0	0	0
DI	4	5	5	5	3	5	6	5	5	5

one composed of boring species and the other of sediment-dwelling species. Both groups have evolved independently in separate ways from the common ancestral species.

The arguments of SILÉN (1952) that *P. ovalis* in all probability stands against all other phoronids as a primitive type is not demonstrated here, even if some general primitive features such as small size, oval lophophore, simplicity of nephridia are retained. On the other hand, developmental patterns and asexual reproductions are advanced characteristics, as assumed by SILÉN (1954 b). Instead, the most primitive species may be *P. muelleri* which retains most of the plesiomorphic characters of the Phoronida; furthermore, it gen-

erally lives on muddy bottoms, always in sparse populations, and has the greatest depth range. However, both species (*P. ovalis* and *P. muelleri*) are demonstrated as primitive in their respective groups.

The remaining boring species (*P. hippocrepia*, *P. ijimai* and *P. australis*), sharing a common ancestor with *P. ovalis*, possess similar characters (e. g. nephridia morphology, hermaphroditic reproduction, brooding patterns) that suggests a common ancestral species. *P. hippocrepia* may be most closely-related, and *P. australis* the most distantly-related, as indicated by its peculiar boring substrate (cerianthid tube walls), large size and related spirally-coiled lophophore, and more developed nidamental glands.

Within the sediment-dweller group, *P. muelleri* is the most primitive, and all the other dwelling species have evolved from a common ancestor to which *P. psammophila* may be most closely-related. *P. pallida* has accumulated many autopomorphies indicative of its independent evolution. In species of *Phoronopsis*, *Phoronopsis albomaculata* shows such morphological similarities with *Phoronis psammophila* that the two species may sometimes be distinguishable only by the presence or absence of the collar fold. An important problem remaining unanswered is whether or not *Phoronopsis albomaculata* broods its embryos; brooding is suggested by EMIG (1982) because the same egg size occurs in both *Phoronis psammophila* and *Phoronopsis albomaculata*. Finally, *Phoronopsis albomaculata* may be most closely-related to the common ancestral species of this genus, and *Phoronopsis california* most distantly-related, as indicated by its large size (the largest within the Phoronida) and related helicoïdally-coiled lophophore.

The scheme of interrelationships in phoronid species (Fig. 3) differs in some way from those given by SILÉN (1952), MARSDEN (1959), and EMIG (1974). Furthermore, SILÉN (1952) suggested a possible subdivision of *Phoronis* into several genera, that is not supported in the present analysis. Both MARSDEN (1959) and EMIG (1974) have recognized two main categories, that are species with boring habits and species with sediment-dwelling habits, and the former category has been divided in *Phoronis ovalis* and *P. hippocrepia*-group. However, all three authors considered *P. pallida* as a divergent species within the dweller-group, and *P. psammophila* as related to *P. muelleri*, rather than to the *Phoronopsis* genus. Finally, more recent investigation on the analysed characters, developed during the last ten years, have led to the construction of the present tree (Fig. 3). Nevertheless, some characters need further comparative studies to establish their phylogenetic usefulness, particularly the larva features.

Zusammenfassung

Vorschlag für ein phylogenetisches System der Phoronida (Lophophorata)

Unter Heranziehung von 11 Merkmalen, die jeweils bezüglich ihrer Plesiomorphie oder Apomorphie bewertet werden, wird ein kladistisches System der Phoronida entworfen. Die herangezogenen Merkmale sind: Habitat (Weichbodenbewohner oder Besiedler harter Substrate), Ausbildung der Längsmuskulatur, Längsnerven in einfacher oder doppelter Ausbildung, Zahl der Nephrostome an den Metanephridien, Form des Nephridialkanals, Vorhandensein oder Fehlen des Nephridialepitheliums, Form der Lophophore, Ausbildung oder Fehlen einer Ringfalte unter dem Lophophor, Geschlechtsverhältnisse (Gonochorismus oder Hermaphroditismus) und Entwicklung (Eier und Larven). Um weitere Merkmale für eine phylogenetische Auswertung zu benutzen, bedarf es noch entsprechender Untersuchungen und Analysen. Nach den 11 ausgewerteten Merkmalen lassen sich die Phoroniden in zwei durch eine Anzahl von Apomorphien charakterisierte Schwestergruppen aufteilen. Die eine Gruppe umfaßt die Weichbodenbewohner, die andere die in härteren Substrat bohrenden Vertreter. *Phoronis ovalis* kann als der ursprünglichste Vertreter der einen, *Phoronis muelleri* als der ursprünglichste der anderen Gruppe gelten. Die Gattung *Phoronopsis* stellt die am meisten abgeleitete Gruppe der Phoronida dar.

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Author's address: Dr. CHRISTIAN C. EMIG, Station Marine d'Endoume, Rue de la Batterie-des-Lions, F-13007 Marseille