

## General Introduction

With eleven valid species, Phoronida constitutes a small group of exclusively marine coelomate animals. According to Hyman (1959) Phoronida are grouped within Bryozoa (Ectoprocta) and Brachiopoda as Tentaculata or Lophophorata. The monophyly of the Tentaculata (Cohen 2000, Cohen & Weydmann 2005, Lüter 2000) lacks sufficient support and the phylogenetic position of the taxa constituting it within the Bilateria (see Lüter & Bartolomaeus 1997, Adoutte *et al.* 2000, Giribet *et al.* 2000, Zrzavý 2001, Giribet 2002, Zrzavý 2003) remains controversial. This uncertainty primarily results from incongruity of the morphological and molecular data.

All representatives of the phoronids are sessile and live in tubes consisting of chitin, in which they can move and anchor themselves by antagonistic muscle activity and by the aid of the trunk coelom that functions as a hydroskeleton (Hyman 1959). Phoronids feed on organic material, which they filter out of the water column with their perioral tentacles. Morphologically, the tentacles originate from a horseshoe shaped ridge, the lophophor. The lophophor contains the tentacle coelom or mesocoel, which surrounds the oesophagus and sends extensions into the tentacles. The mouth opening is situated in the center of the tentacular ridge. The epistome, which is a muscular lobe that is used to push the infiltrated particles into the mouth opening, overhangs the mouth opening (Pross 1974). Entering the mouth the food particles are passed through the U-shaped gut by ciliary action. The gut opens to the outside via the anus, which is situated on a small anal papilla just outside the tentacular ridge. The nephropori of the metanephridia that drain the trunk coelom or metacoel are located on the left and right sides of the anal opening. The metanephridial ducts serve a dual function as gonoducts during periods of reproduction (Goodrich 1903).

Thus, adult phoronids can be readily divided into three distinctive outer parts; an anterior epistome, the tentacular region, and an elongated posterior trunk. Classic light microscopical investigations allocate at least one coelomic lumen to each of the body regions (Masterman 1898, Zimmer 1964, Emig 1974, Siewing 1974). In the species with pelagic larvae the tripartition of the outer body is developed early in life. The pelagic larva is called Actinotrocha and it possesses a prominent episphere, which overhangs the mouth, a tentacular region, and an elongated posterior hyposphere or trunk. During metamorphosis, which is initiated by the evagination of a metasomal tube developed during larval life, these three body regions are restructured and transformed into the adult organization (Herrmann 1979, Bartolomaeus 2001).

The origin and changes during embryonic development of the unpaired coelomic cavities

during metamorphosis have been investigated more often than the coeloms themselves (Caldwell 1885, Roule 1890, Roule 1900, Kowalewsky 1867, Schultz 1897, Masterman 1900, Ikeda 1901, de Selys-Longchamps 1902, 1907, Shearer 1906, Brooks & Cowles 1905, Cori 1939, Rattenbury 1954, Zimmer, 1964, 1980, Emig 1977a, Herrmann 1986, Santagata 2004). However, conclusions drawn from these investigations describe the origin of the mesoderm in different ways (Tab. 1). Nevertheless, there is general agreement that mesoderm formation is divided into two phases. In addition, the exact time and the location of cell proliferation are described differently, sometimes even for the same species (Tab. 1).

**Tab. 1:** Origin of mesoblasts in different phoronid species.

Origin of mesoblasts	from gastral plate before gastrulation			1) no data 2) Brooks and Cowles (1905) 3) Caldwell (1883) 4) Cori (1939) 5) Emig (1977a) 6) Freeman & Martindale (2002) 7) Herrmann (1986) 8) Ikeda (1901) 9) Kowalewsky (1867) 10) Malakhov & Temereva (1999) 11) Masterman (1900) 12) Rattenbury-Marsden (1954) 13) Roule (1890, 1900) 14) Santagata (2004) 15) de Selys-Longchamps (1902) 16) de Selys-Longchamps (1907) 17) Schultz (1897) 18) Shearer (1906) 19) Zimmer (1964, 1980)
		from the archenteron:		
		from around the blastopore	from the entire surface	
<i>Phoronis ovalis</i>	1	1	1	
<i>Phoronis hippocrepi</i>	9 <sup>a</sup>	3,4	4	
<i>Phoronis ijimai</i>	8 <sup>c</sup>	8,10	8	
Syn.: <i>P. vancouverensis</i>	!6,19 <sup>c</sup>	6,19	19	
Syn.: <i>Phoronis buskii</i>			11 <sup>b</sup>	
<i>Phoronis psammophila</i>	!13 <sup>c</sup>	5,16	13,16,18	
<i>Phoronis pallida</i>	!14		13	
<i>Phoronis muelleri</i>	7,15 <sup>c</sup> ,17 <sup>a</sup>	16	16,17	
<i>Phoronopsis harmeri</i>	19	5		
Syn.: <i>Phoronopsis viridis</i>			12	
<i>Phoronis architecta</i>	2 <sup>c</sup>	2 <sup>c</sup>	2	

**Legend:** ‘!’: presence denied, *a*: single cells dispensed into blastocoel, *b*: enterocoelous diverticula, *c*: data obtained from the figures.

According to Zimmer (1964, 1980) and Emig (1974), the cells of the first phase of mesoderm proliferation accumulate in the anterior area of the embryo within the fast differentiating episphere. In this area the cells constitute the epithelial lining of the coelom, thus forming the protocoel, whose persistence varies within the different species (Zimmer, 1964, 1980, Emig 1974, Herrmann 1986). Later in development, cells originating from the posterolateral region migrate between the sheets of the ecto- and endoderm of the hyposphere, accumulate in this area and diverge to form the trunk coelom or metacoel (Zimmer 1964, 1980, Emig 1974). This chronological separation of the differentiation of the anterior mesoderm and the development of the metacoel has been known for a long time (e.g. Caldwell 1882, Ikeda 1901). Recent investigations showed that the metacoel is formed by cells that

proliferate from material of the archenteron, i.e. the cells are considered enterocoelic in origin (Malakhov & Temereva 1999). For the prospective mesoderm cells of the episphere on the other hand, origin from the endoderm-ectoderm border is likely, so that it remained unclear so far, whether these cells were ectodermal or endodermal in origin (Freeman & Martindale 2002, Santagata 2004).

So far, development of the coelom has been studied only for those phoronid species that exhibit a pelagic mode of larval life. Investigations of the coelomogenesis of the lecithotrophic larva (Silén 1952) from *Phoronis ovalis* Wright, 1856 are missing. However, since a lecithotrophic larva likely represents the ground pattern condition of the brachiopods (Haszprunar *et al.* 1995, Lüter 1998, 2000), data from this larva are important for the evaluation of the basal relationships of the Tentaculata.

The specific organization of the adult and larval body of the Phoronida, as well as the arrangement of the coelomic cavities were interpreted by Masterman (1898) as an argument for a close relationship between the Deuterostomia and the Phoronida and as a vestige of a pelagic ancestor, with four gastral pouches and radial symmetry. Masterman (1898) regarded the blastocoelic space as a paired coelom, the larval protonephridia as coelomoducts, assumed paired coelomoducts in the larval proto- and metacoel, and interpreted the stomach diverticula as homologs of the Notochord (Masterman 1898). Despite these severe misinterpretations, this archicoelomate concept of Mastermann survived and has been expanded by Remane and his students (e.g. Ulrich 1972, Pross 1980, Siewing 1980) and continues to influence the discussion about the coelomate origin of the Bilateria (Herrmann 1997; Dewel 2000, Temereva *et al.* 2006). Independently of the archicoelomate concept, the trimeric organisation of the coelom and the endodermal origin of the mesoderm are interpreted as evidence of a common origin of the tentaculate taxa and the Deuterostomia (Ax 1989, Ax 1995, Nielsen 2000). The mesosomal lophophore is often discussed as a possible autapomorphy of the Tentaculata/Lophophorata (Hyman 1959, Emig 1977b). However, a similar tentacular feeding apparatus is also found in the Crinoida and in the Pterobranchia (e.g. Jefferies 1986). Together with the trimeric body organization, the Lophophore is therefore considered as an autapomorphy for the Radialia by several authors (e.g. Hennig 1966, Ax 1989, Nielsen 2000). The Radialia-hypothesis is furthermore supported by the occurrence of the “upstream-collecting mechanism“ (Nielsen 1987) of the feeding systems in both larvae and adults. This “upstream-collecting mechanism“ is only found in the Phoronida, Brachiopoda, Echinodermata, and Hemichordata (Nielsen 1999, Nielsen 2000, Nielsen 2002). New ultrastructural investigations on the origin of the mesoderm and the coelomogenesis in brachiopods led to the hypothesis that this Brachiopoda constitutes the sister group to the deuterostomes (Lüter 1998, 2000); while bryozoans and

phoronids branch off independently from the stemlineage of the Radialia, rendering the Tentaculata (= Lophophorata) paraphyletic. According to this study, the brachiopods and the deuterostomes share together the origin of the mesodermal cells from the archenteron as an apomorphic character and, moreover have composite metanephridia in common that develop directly without protonephridia as an intermediary stage (Lüter 2000).

Molecular analyses provide evidence for a completely different phylogenetic relationship of brachiopods, bryozoans and phoronids. Phylogenetic analyses of 18S rRNA sequences suggest a close relationship of the monophyletic tentaculate taxa with annelids and molluscs (Halanych *et al.* 1995, Cohen *et al.* 1998a, 1998b, Cohen 2000). The phoronids and brachiopods together constitute a monophylum in all analyses. Halanych *et al.* (1995) proposed the phoronids as sister group to the articulate brachiopods and grouped the inarticulate brachiopods together with molluscs and annelids. In another analysis of molecular sequence data Cohen (2000) and Cohen & Weydmann (2005), however, found that the phoronids together with the inarticulate brachiopods represent the sister taxon to the articulate brachiopods. According to Cohen (2000) the phoronids are nested within the brachiopods and the taxon comprising the thus paraphyletic brachiopods and the Phoronida is called Phoroniformea. However, mapping the morphological data on this “molecular” tree leads indeed to incomprehensible conflicts (Lüter & Bartolomaeus 1997).

In the present study, the development of the larva of *P. ovalis* is investigated on an ultrastructural level. So far, only descriptions of the external anatomy of the ontogeny of this species exist (Harmer 1917, Silén 1954, Zimmer 1991). According to Emig (1969), the horseshoe-shaped lophophore and the pronounced asexual mode of reproduction, as well as the lack of giant nerve fibers encountered in this species indicate an ancestral organization within Phoronida. Because it has convincingly been argued that a lecithotrophic larva is most parsimoniously reconstructed for the ground pattern of brachiopods (Haszprunar *et al.* 1995, Lüter 1998), the lecithotrophic larva of *Phoronis ovalis* suggests an ancestral condition for phoronids as well. Therefore, *Phoronis ovalis* could constitute the sister group to the rest of the phoronids and knowledge of its detailed anatomy is potentially decisive for character interpretation within Phoronida.

The second focus of this study is on the relationship among the Phoronida. A morphological data matrix of the Phoronida is generated using data from this study, as well as data taken from literature. Morphological characters from the Brachiopoda are added, using data from Carlson (1995) and Lüter (1998). This study tests the Phoroniformea hypothesis sensu Cohen (2000) and Cohen & Weydmann (2005) from a morphological point of view. The results of the cladistic analysis are used to establish a phoronid ground plan. This is the first time a cladistic analysis over a whole phylum on species level is conducted.

## Literature

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