Morphological and molecular affinities of Phoronida and Brachiopoda

Introduction

The Phoronida Hatschek, 1888 comprise eleven species assigned to the genera *Phoronis* Wright, 1856 and *Phoronopsis* Gilchrist, 1907. They possess characteristic features such as a wormlike body that secretes a chitinous tube in which the animal lives, burrowed in the substrate. A ciliary anterior tentacle crown that is held into the water column to capture food and giant nerve fibres running alongside the body that allow the animal a rapid retraction of its entire body represent further characteristic features. Phoronids possess a biphasic life cycle, with the pelagic actinotroch larva that develops into a juvenile phoronid via a catastrophic metamorphosis.

So far, the only systematic study on phoronids has been published by Emig (1985). However, with only ten species and eleven characters examined, the taxon-sampling and the amount of characters analyzed in this study are very limited. This and the use of many a priori assumptions about the evolution of the characters cast doubts on the validity of the results. Thus, hitherto no comprehensive phylogenetic analysis of phoronid relationships exists.

Since their first discovery in 1878, the relationship of the Phoronida to other metazoan taxa could not be resolved. Most of the time, the phoronids are considered to represent a sister group of the brachiopods (Ax 1989). Their grouping in a taxon called "Tentaculata" (*sensu* Hatschek 1888) or "Lophophorata" (*sensu* Hyman 1959) together with the Bryozoa (Ectoprocta) and Brachiopoda was well accepted by subsequent textbook authors, and found support in systematic considerations on the phylogenetic position of the Phoronida by Emig (1977, 1984, 1997) and Zimmer (1997). The presumed position of the Lophophorata is basal within the Radialia (Jefferies, 1986; Ax 199, Ax, 2000). In their analysis on the phylogeny of brachiopods, Cohen (2000) and Cohen & Weydmann (2005) suggest a position of the Phoronida within the brachiopod clade; as sister group of the Craniida, with the name Phoroniformea.

The use of molecular data in phylogenetic studies, applied by Halanych *et al.* (1995) for resolving the phylogeny of the metazoa, moved and divided the taxon lophophorata from their basal position in the radialian clade to a position within the Spiralia, establishing a new taxon called Lophotrochozoa.

Numerous subsequent studies, involving more taxa and more and other genes, gave further support to these results. Although the morphological characters contradict these findings, the taxon Lophotrochozoa is now widely accepted in the literature and textbooks (but see Lüter & Bartolomaeus 1997).

The present study does not claim to comprehensively represent the phylogeny of Phoronida, but, by its content and scope, provides a minimal test of the monophyly and content of the phoronid clade. This study will elucidate some of the morphological synapomorphies of the Phoronida, and test whether phoronids constitute a taxonomic group in between the brachiopods as suggested by Cohen (2000), Cohen & Weydmann (2005). To accomplish this, a morphological data matrix of the Phoronida is generated using data from literature as well as from own investigations. For the test of monophyly of brachiopods, the data matrix is extended by the molecular data used by Cohen & Weydmann (2005) and analyzed using parsimony. In order to increase the accuracy of the phylogenetic analysis, all species of the Phoronida are sampled (Wiens 1998). On the basis of this analysis, the phoronid ground plan is estimated that will, in a following step, allow the inference of the phylogenetic position of the Phoronida within the Metazoa via an intuitive method sensu Yeates (1995).

Material and Methods

Examined Taxa

The present investigation was undertaken using an exemplar approach (Yeates 1995, Wiens 1998, Prendini 2001), with all eleven individual species used as terminals for the Phoronida. Although there are 14 phoronid species described (see Emig 1982, Temereva & Malakhov 1999, Santagata & Zimmer 2000), only eleven species are supposed to be valid (Emig 1967, 1982), because the data for *Phoronis badhuri* Ganguly & Majumdar, 1967 and *Phoronis svetlana* Temereva & Malakhov, 1999 are insufficient and therefore the validity of both species uncertain. *P. vancouverensis* Pixell, 1912 is a junior synonym of *P. ijimai* Oka, 1897 (Emig 1967), as well as *Phoronopsis harmeri* Hilton, 1930 is synonymous with *Phoronopsis viridis* (Marsden, 1959). The larva „Actinotrocha A" described by Zimmer (1964) is assigned to the adult species *Ph. harmeri*, whereas the larva "Actinotrocha wilsoni B" Brooks & Cowles, 1905 is assigned to the adult species of *Ph. albomaculata* Gilchrist, 1907.

The choice of exemplars in the analyses of molecular data is limited and determined by the availability of DNA data for each specimen. Some potentially important species are

represented solely by morphological data, such as all but one *Phoronopsis*. Molecular data for *P. pallida* Silén, 1952 are missing as well (Tab. 2).

For convenience, the genus *Phoronis* will be abbreviated with '*P.*', whereas *Phoronopsis* will be abbreviated with '*Ph.*'.

According to Cohen & Gawthrop (2005), the phoronids are closely related or even group within the Brachiopoda, and form the Phoroniformea; therefore species from all five major groups of the Brachiopoda are included in the analysis. Three related outgroups are chosen; two Bryozoa, two Crinoida, one Kamptozoa, one Polyplacophora, as well as one polychaete species.

Molecular Data

The choice of genes used for phylogenetic analysis is a crucial factor determining the level of resolution obtained from a molecular phylogenenetic study (Giribet 2002). The 18S

Tab. 2: List of terminal taxa included in this analysis

Terminal taxon	*Higher taxon*	*Gene length*	*GenBank Acc.-No.*
Pedicellina cernua	Kamptozoa	1720	U36273
Lanice conchilega	Polychaeta	1816	X79873
Acanthochitona crinita	Polyplacophora	1763	AF120503
Antedon serrata	Crinoida	1679	D14357
Metacrinus rotundus	Crinoida	1759	AY275898
Alcyonidiumgelatinosum	Bryozoa	1813	X91403
Cristatella mucedo	Bryozoa	1775	AF025947
Plumatella repens	Bryozoa	1813	U12649
Discinisca cf. tenuis	Brachiopoda	1769	AF202444
Glottidia palmeri	Brachiopoda	1750	AF201744
Lingula anatina	Brachiopoda	1749	U08331
Notosaria nigricans	Brachiopoda	1752	U08335
Neocrania anomala	Brachiopoda	1753	U08328
Platidia anomioides	Brachiopoda	1771	AF025933
Terebratalia transversa	Brachiopoda	1767	AF025945
Terebratella sanguinea	Brachiopoda	1748	U08326
Terebratulina retusa	Brachiopoda	1753	U08324
Phoronopsis viridis (=harneri)	Phoronida	1765	AF123308
Phoronis australis	Phoronida	1767	AF119079
Phoronis psammophila	Phoronida	1768	AF025946
Phoronis hippocrepia	Phoronida	1751	U08325
Phoronis ijimai	Phoronida	1769	AF202113
Phoronis muelleri	Phoronida	1766	
Phoronis ovalis	Phoronida	1759	

rRNA gene is used in this study, because it covers the most phoronid species. Two complete 18S rRNA genes from *P. muelleri* and *P. ovalis* are sequenced and included in this study. Specimens of P. muelleri were sampled off Helgoland in August 2001, and *P. ovalis* specimens were sampled in the Gullmar Fjord in Kristineberg/Sweden in November 2001. 18S rRNA was extracted from specimens using Qiagen DNeasy™ Tissue Kit (Qiagen GmbH, 40724 Hilden). PCR amplification of the 18S rRNA was performed according to manufacturer's instructions, in two overlapping fragments of ~900 bp and ~1800 bp respectively, using modified primers from Giribet *et al.* (1996) by using standard cycle sequencing protocols. The 25 µl reaction mixture for amplification of the 18S rRNA contained 12.5 µl Qiagen Taq PCR Master Mix (Qiagen GmbH, 40724 Hilden), 1 µl Template-DNA, 2 µl of each primer, and 7.5 µl H_2O. Amplifications were carried out using an Eppendorf Mastercycler gradient (Eppendorf GmbH, 22331 Hamburg). The following PCR temperature file was used: 95˚C for 90 s as initial denaturation step; 35 thermocycles at 94˚C for 30 s for denaturation, annealing at 45-50˚C for 60 s, and extension at 72˚C for 180 s; final extension at 72˚C for 8 min. After detection by gel electrophoresis the products were purified with the Qiaquick PCR Purification Kit (Qiagen GmbH, 40724 Hilden). Sequencing of all amplified fragments in both directions was carried out by the IIT Biotech/Bioservice of the University of Bielefeld. Overlapping fragments of the 18S rRNA were combined by using BioEdit (Hall 1999). Disagreement among these fragments was corrected in reference to the original chromatograms.

The accession numbers of additional sequences are obtained from EMBL/GenBank (http://www.ncbi.nlm.nih.gov) (Tab. 1).

Morphological Data

Morphological characters referring to larval and adult morphology of the species analyzed in this study were compiled from literature and put together with data from own investigations on *P. muelleri* Selys-Longchamps, 1903 and *P. ovalis* Wright, 1893. Morphological data for the brachiopods were taken from the data matrix generated by Carlson (1995) and Lüter (1998). Characters for Polychaeta, Crinoida, and Kamptozoa were obtained from Nielsen (1995), Nielsen *et al.* (1996), and Brusca & Brusca (2003).

A total of 133 characters were compiled into the morphological data matrix (see Appendix A), containing 43 characters specific to Phoronida, 79 characters specific to Brachiopoda, and 11 characters specific to the outgroups. Forty-five of the characters are coded binary and 88 are coded as multi-state characters. Composite coding was preferred over binary coding in order to minimize the occurrence of inapplicable or missing entries (Maddison

1993) and to account for the dependency of characters, for example the lateral mesenteries in the trunk of the phoronids and number of nephridial funnels, the type of larva, and presence or absence of adult tentacles. All multi-state characters were treated as unordered (Fitch 1971), thereby preventing *a priori* assumptions of character state order. The data set contains 175 unknown characters (5.98%), and 10 inapplicable characters (0.34%). Many of the characters used are well known in phoronid taxonomy and are listed in detail in the result section. Brachiopod characters as well as outgroup characters are not explicitly described here.

Phylogenetic analysis

The present study incorporates two different datasets: 18S rRNA data and morphological data. Sequence alignment is a problematic procedure: Every mismatch and every gap (as well as every gap extension) requires a cost model. A similar cost model is required by the phylogenetic analysis. It would be controversial to use different cost models in the sequence alignment and in the phylogenetic analysis. The confidential approach is to use the *direct optimization alignment* (DOA) method described by Wheeler (1996, 1999), which creates a unique set of putative homologies and is implemented in POY (Wheeler *et al.* 2003). All Molecular sequences were basically aligned using CLUSTAL W (Thompson *et al.* 2000) as implemented in BioEdit (Hall 1999). The sequences were subdivided to separate the conserved and variable regions before the searches. They were divided into smallest possible unambiguously recognizable homologous regions as described in Giribet *et al.* (2000), resulting in 47 unaligned data matrices as input files for POY.

Character weighting is controversial (Vogt 2002). Differential weighting, involving the use of multiple cost ratios (parameter sets) can, however, be used to assess the extent to which different analysis parameters affect phylogenetic conclusions. This so-called sensitivity analysis (Fitch & Smith 1983, Wheeler 1995) is performed to test the robustness of internal nodes under different parameters.

$$ILD = \frac{Length_{combined\ set} - \Sigma\ Length_{individual\ sets}}{Length_{combined\ set}} \qquad \text{Equation 1}$$

A measurement for the congruence of datasets is the *Incongruence Length Difference* test (ILD) (Mickewich & Farris 1981, Farris *et al.* 1995). The ILD value is calculated from the length of each tree obtained in the individual analysis as shown in equation 1. The ILD measures the extent to which two or more data sets result in different trees, with a higher score

indicating greater incongruence or more conflict among the data partitions. The datasets are analyzed both separate and combined in POY (ver. 3.0.11; Wheeler *et al.* 2003) using the complete sequence from all 47 fragments. The parametric values of the sensitivity analysis include transversion (tv) to transitions (ts) cost ratios 0.5:1 – 8:∞, and substitution to gap ratios 0.5:0-4:16 (Tab. 3). Morphological weight was applied as the product of tv and ts or equal to the transversion cost if ts = zero (Tab. 3). The analysis in POY was conducted using the following parameters: *prmaxtrees*: 2, *tbrmaxtrees*: 2, *fitchtrees*, *holdmaxtrees*: 50, *buildtbr*, *buildmaxtrees*: 2, *replicates*: 16, *ratchettbr*: 25, *ratchetpercent*: 10, *ratchetseverity*: 3, *ratchettrees*: 2, *treefuse*, *fuselimit*: 10, *fusemingroup*: 5, *fusemaxtrees*: 100, *slop*: 10, *checkslop*: 10. Altogether a parametric space consisting of 24 individual parameter sets was analyzed. To examine the support of individual nodes, bremer support values (Bremer 1988) as well as jackknife values (Farris *et al.* 1996) with 1000 replicates are calculated from each dataset (18S rRNA, morphological, and combined). The results of the sensitivity analysis are graphically displayed using "Navajo rugs", a graphical plot where the parameter space is represented as a grid with parameters represented in two axes (Wheeler 1995).

Most parsimonious trees for each dataset are calculated using PAUP* (ver. 4.0b10; Swofford 2002). A branch and bound search algorithm under equal weighting is chosen to calculate minimal length trees. Node support is calculated using jackknifing with 1000 replicates and heuristic search with 100 replicates of random addition sequence. The implied alignment with the parameter set that, according to the sensitivity analysis, minimized incongruence among the two partitions is used in this part of the phylogenetic analysis. Morphological character tracing is performed in the program MacClade (ver. 4.08; Maddison & Maddison 2000). When ambiguity is present, the ACCTRAN transformation is chosen for placement of the most parsimonious character transformation.

In order to make this morphological analysis directly comparable to the analysis of Cohen & Weydmann (2005), all outgroups, except for the chiton, which Cohen & Weydmann (2005) used, are excluded. Furthermore, all "brachiopod specific characters" are also excluded from this analysis. The resulting character matrix contains 18 taxa (11 phoronid, 6 brachiopods, and 1 chiton). The characters 46-51, 59-60, 62-66, and 68-96 are excluded from this analysis.

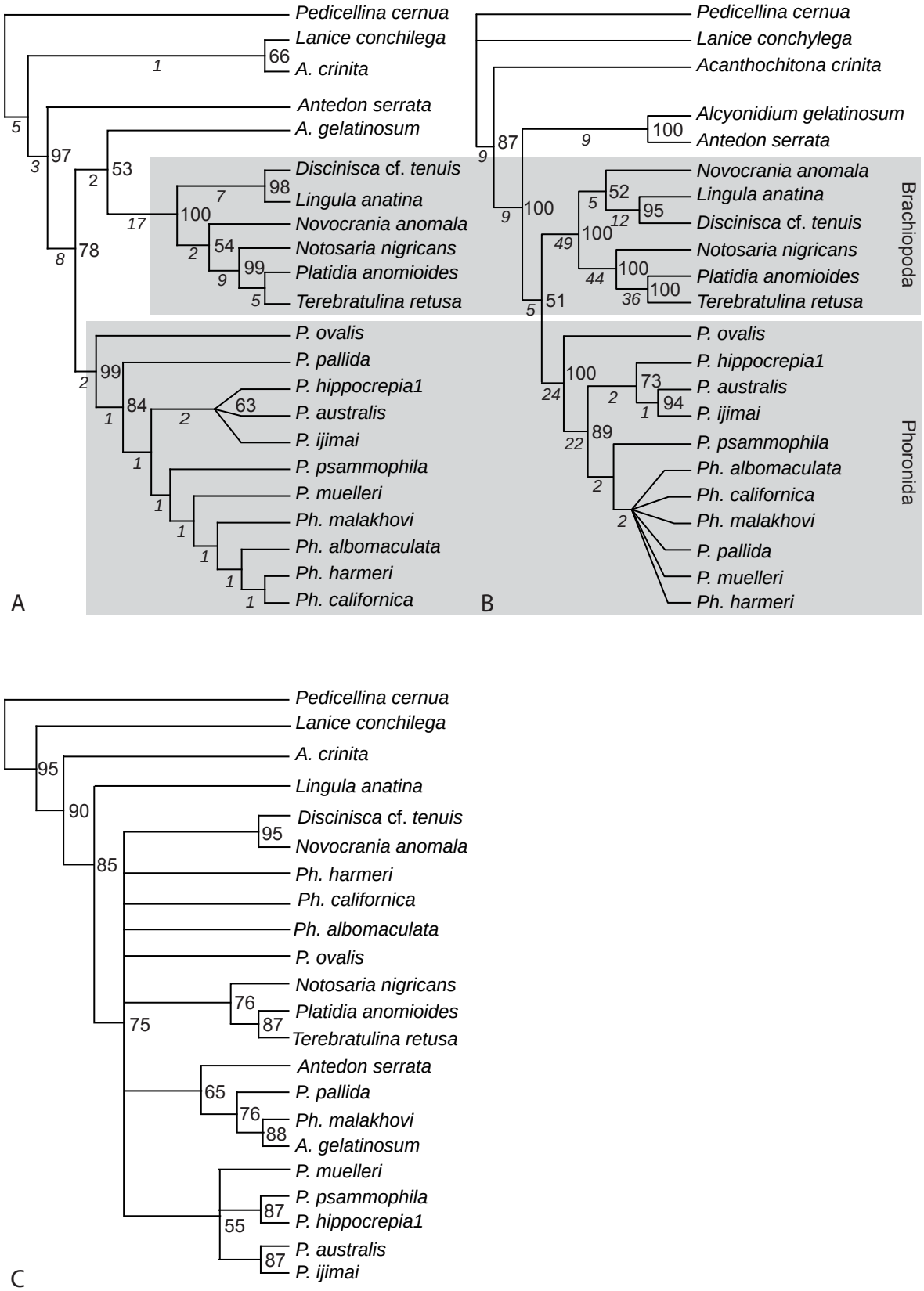

Fig. 16: A Strict consensus tree obtained from three parsimonious trees based on morphological data. Tree length 347. **B** Strict consensus tree of 19 parsimonious trees from the combined branch and bound analysis in PAUP* with tree length 1392. **C** 50% majority rule consensus tree obtained from 1000 trees using parsimony with the molecular data. Tree length 874. Values on each node indicate jackknife frequencies; values under each clade show bremer support values. Trees are rooted using *Pedicellina cernua* as outgroup.

Results

Morphological data

Regarding the Phoronida, 43 morphological characters have been coded, containing 39 parsimony-informative characters. For the Brachiopoda 74 characters were taken from Carlson (1995) and Lüter (1998) with 56 parsimony informative characters in total for this taxon. Altogether, the morphological matrix contains 133 characters with 114 parsimony-informative characters. The uninformative characters have been retained in the analysis because at least some have the potential to become informative, as additional information is made available. Branch and bound analysis in PAUP* yields three equally parsimonious trees of length 347, with a consistency index (CI) of 0.82, and a homoplasy index (HI) of 0.18 (Fig. 16 A). In these trees, the Phoronida are monophyletic with a jackknife support (js) of 99 and *P. ovalis* as the sister group species to all other phoronids. *P. hippocrepia*, *P. ijimai*, and *P. australis* comprise a monophyletic taxon (js=63). In the following, this monophylum will be called the P. hippocrepia-group. In each of the three trees, the position of *P. hippocrepi*a differs in relation to *P. ijimai* and *P. australis*. The position of the remaining taxa is stable throughout the three trees, with *P. pallida* as sister group to the P. hippocrepia-taxon and the remaining phoronids (js=84). Although these remaining groups of the Phoronida receive a jackknife support below 50, the topology of their relationships is still shown as this topology represents the best tree found in this analysis, because *Phoronopsis* is solved as a monophyletic group. In the brachiopods a good supported monophylum of Lingulacea and Discinacea (js=98) constitutes the sister group to the remaining articulate brachiopods and craniids (js=100) (Fig. 16 A). In this clade, the craniids are basal to the articulate brachiopods (js=54) and the articulate brachiopods have the Rhynchonellida basal to the Terebratulacea and Terebratellacea (js=99), whereas the latter having a jackknife support of 98.

The Bryozoa constitute the sister group of the Brachiopoda (js=53). Together with the Phoronida these three taxa constitute a monophylum (js=100). Not a single tree contains the Phoronida as ingroup of the Brachiopoda ("Phoroniformea") *sensu* Cohen (2000), Cohen & Weydmann (2005). Looking at the morphological characters for the Phoronida in detail, from the 43 characters coded from phoronid literature and own observations on the Phoronida, 20 have consistency indices of 1.0, 22 have consistency indices between zero and 1.0, indicating that the states have evolved more than once. One character (30) is constant (see below: description of characters).

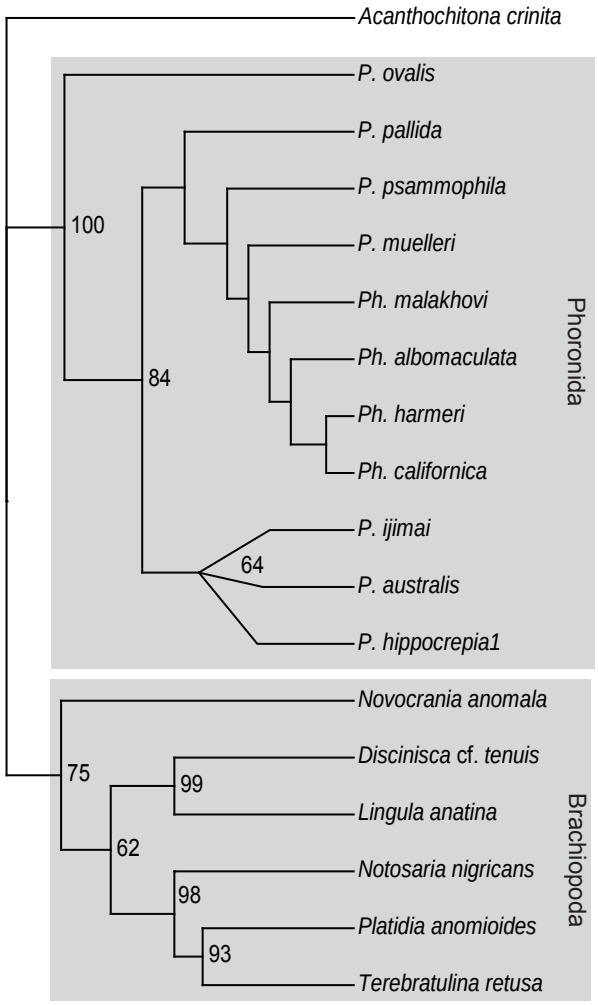

Fig. 17: Morphological tree with only one distantly related outgroup (*Acantochitona crinita*) and brachiopod specific characters (mantle and shell) excluded from analysis. Strict consensus tree from parsimony analysis in Paup*, obtained from 6 trees of equal length (177 steps). Jackknife support from 1000 replicates on each supported node.

Combined data

The combined morphological and molecular 18S rRNA analysis in PAUP* using branch and bound with equal weighting and parsimony as the optimality criterion results in 19 equally shortest trees with a branch length of 1392 (Fig. 16 B). Of the 1947 morphological and molecular characters used, 344 are parsimony-informative. All characters are unordered. The Phoronida are monophyletic throughout all three trees (js=100), with *P. ovalis* as sister group species to the remaining phoronids (js=89). Regarding jackknife values, the remaining phoronids are not well supported (i.e. under the 50% threshold). Exceptions represent the P. hippocrepia-clade with *P. australis* and *P. ijimai* as sister group species (js=94), and *P. hippocrepia* forming the sister group species to these two species (js=74). Bremer support values indicate a second monophyletic taxon, which constitutes a sister group to the P. hippocrepia-clade: Here *P. psammophila* forms the sister group species to the unresolved clade of *P. muelleri*, *P. pallida* and the *Phoronopsis* species. In 8 of the 19 equally parsimonious trees, brachiopods constitute the sister group to the phoronids (js=51),

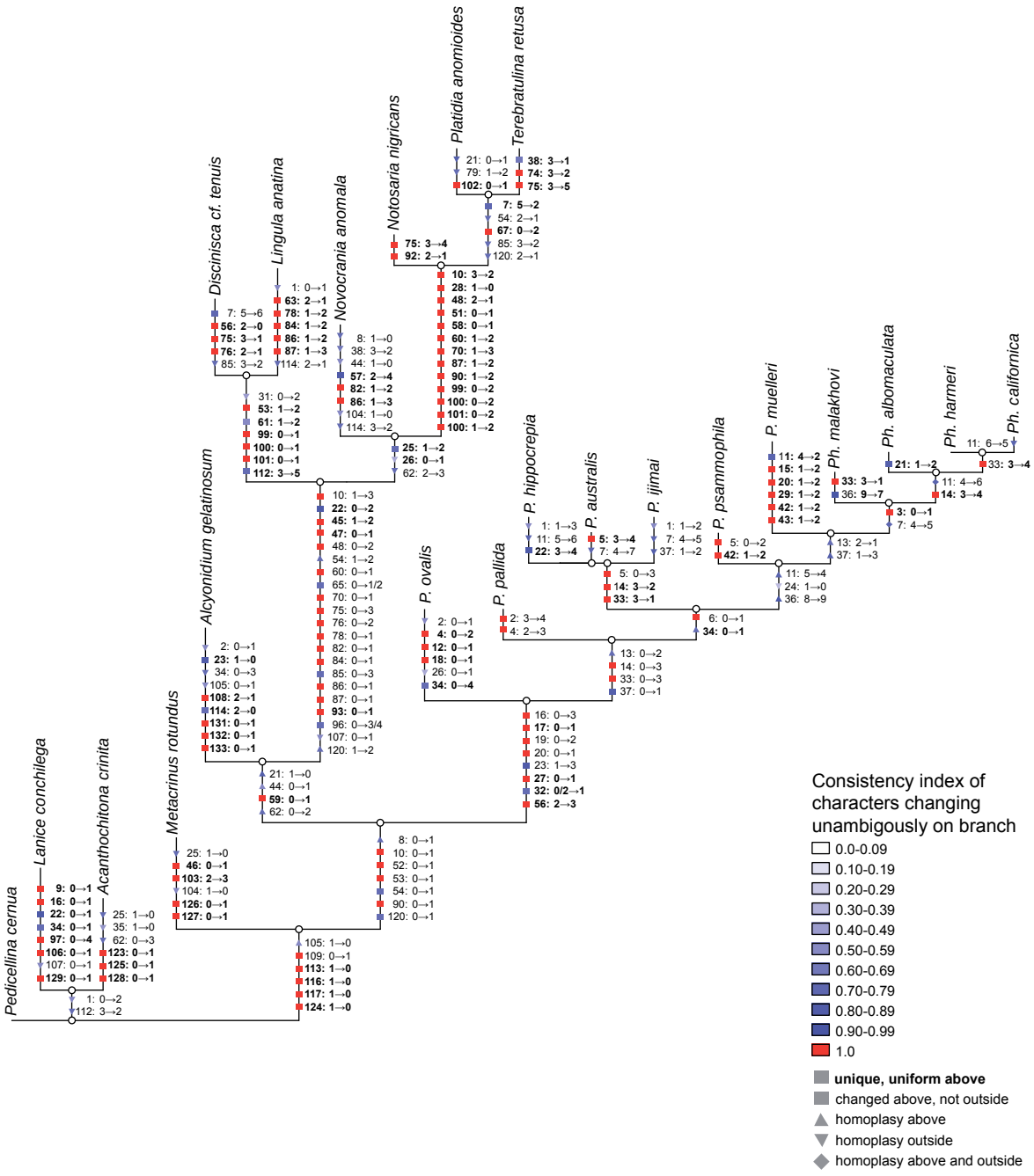

Fig. 18: Tracing of characters changing unambigously on the branches as obtained from MacClade and ACCTRANS on the tree obtained by branch and bounch search in Paup* using the morphological data of the Phoronida and Brachiopoda (see fig. 15A). Tree length 346 steps.

having crinoids and bryozoans as sister group (js=100). In the remaining 11 of the trees, crinoids and bryozoans form the sister group of the Phoronida. The chiton is always the sister group to the monophylum (bryozoan + crinoid (brachiopods + phoronids)) (js=89).

Tab. 3: Cladogram lengths and Incongruenc Length Differences (ILD-values) for analyses of different parameter sets. ILD = Lcomb–(Lmorph + L18S)/Lcomb. Minimum ILD value in bold.

Gap cost	TV/Gap Transversion		Transition	TV/TS	Morph weight	Length morph	Length 18s	Length combined	ILD
1	1	1	2	0.5	1	189	1024	1248	0.0280
2	1	2	2	0.5	2	378	1238	1710	0.0550
4	1	4	2	0.5	4	756	1485	2450	0.0853
8	1	8	2	0.5	8	1512	1942	3902	0.1148
1	**2**	**0.5**	**2**	**1**	**2**	**378**	**1226**	**1646**	**0.0255**
1	1	1	1	1	1	189	766	989	0.0344
2	1	2	1	1	2	378	892	1375	0.0764
4	1	4	1	1	4	756	1121	2101	0.1070
8	1	8	1	1	8	1512	1577	3554	0.1308
1	2	0.5	1	2	2	378	942	1369	0.0358
2	2	1	1	2	4	756	1143	2035	0.0668
4	2	2	1	2	8	1512	1389	3198	0.0929
8	2	4	1	2	16	3042	1845	5489	0.1130
16	2	8	1	2	32	6048	2736	10069	0.1276
2	4	0.5	1	4	8	1512	1512	3178	0.0485
4	4	1	1	4	16	3024	1888	5273	0.0685
8	4	2	1	4	32	6048	2381	9231	0.0869
16	4	4	1	4	64	12096	3278	17031	0.0973
32	4	8	1	4	128	24192	5038	32619	0.1039
1	2	0.5	0	inf	2	378	556	1015	0.0798
1	1	1	0	inf	1	189	368	622	0.1045
2	1	2	0	inf	2	378	488	994	0.1288
4	1	4	0	inf	4	756	709	1722	0.1492
8	1	8	0	inf	8	1512	1149	3174	0.1616

Sequence data

The implied alignment of the 22 18S rRNA sequences in POY with the 18S rDNA data set using the parameter set for gap-cost:transversion:transition = 1:2:2 that minimizes incongruence among the molecular and morphological data sets has 1,680 positions. Overall, the data matrix consists of 1,204 constant characters (72%), 268 variable positions (16%), and 190 parsimony informative positions (11%). The parsimony analysis yields over 1,000 equally parsimonious trees with each a score of 874. The 50%-majority rule consensus tree obtained from the 1,000 trees is displayed in Fig. 16 C. Neither phoronids nor brachiopods are supported as monophyletic clades; they are placed in an unresolved group consisting of phoronids, brachiopods and the crinoid. With a jackknife support of 95 the lingulids represent the sister group to this brachiopod/phoronid/crinoid clade (Fig. 16 C).

A Monophyletic taxon consisting of Brachiopoda and Phoronida:

	0.5:1	0.5:2	0.5:4	0.5:∞	1:0.5	1:1	1:2	1:4	2:0.5	2:1
ILDs	**0.0255**	0.0358	0.0485	0.0798	**0.0280**	0.0354	0.0668	0.0685	0.0550	0.0764
18S rDNA	57	/	/	/	54	/	/	/	/	/
Combined		/	/	/	/	/	/	/	/	/
Morphol.	76	76	75	76	72	74	75	73	77	73

B Phoronida monophyletic:

	0.5:1	0.5:2	0.5:4	0.5:∞	1:0.5	1:1	1:2	1:4	2:0.5	2:1
ILDs	**0.0255**	0.0358	0.0485	0.0798	**0.0280**	0.0354	0.0668	0.0685	0.0550	0.0764
18S rDNA	100	96	/	99	96	99	/	/	98	/
Combined	94	96	90	95	91	96	89	76	94	90
Morphol.	99	99	99	99	99	99	99	99	99	99

C Radialia:

	0.5:1	0.5:2	0.5:4	0.5:∞	1:0.5	1:1	1:2	1:4	2:0.5	2:1
ILDs	**0.0255**	0.0358	0.0485	0.0798	**0.0280**	0.0354	0.0668	0.0685	0.0550	0.0764
18S rDNA	/	/	/	/	/	/	/	/	/	/
Combined	/	/	/	/	/	/	/	/	/	/
Morphol.	99	99	99	99	99	99	99	99	99	99

D *P. ovalis* sistergroup to remaining Phoronida:

	0.5:1	0.5:2	0.5:4	0.5:∞	1:0.5	1:1	1:2	1:4	2:0.5	2:1
ILDs	**0.0255**	0.0358	0.0485	0.0798	**0.0280**	0.0354	0.0668	0.0685	0.0550	0.0764
18S rDNA	87	84	73	/	99	88	95	71	92	87
Combined	98	79	83	/	98	83	72	55	83	73v
Morphol.	83	83	81	83	83	83	81	82	81	81

Fig. 19: Four stability plots ("Navajo rugs") from the analysis of the Phoronida and Brachiopoda as revealed by the 24 analysis with different parameter sets for transversion/transition and transversion/gap-cost ranging from 0.5:0.5 up to 8:∞ (compare tab. 3, 4). The trees which the parameter set that minimizes incongruence among the two partitions are shown in fig. 15B, C. Solid squares represent monophyly for the taxon in question, open squares indicate paraphyly; shaded squares represent monophyly in some but not all of the shortest trees. The Number in each square represent the jackknife support for this particular split.

Phoroniformea

The analysis conducted with a reduced dataset, which only one distantly related outgroup and all brachiopod specific characters excluded from the analysis, add up to six shortest trees, each 117 steps long, with a consistency-index of 0.76, and a homoplasy index of 0.23. Compared to the former analysis, the phylogenetic position of the Phoronida is not changed within this analysis (Fig. 17); they constitute the sister group to the brachiopods, both groups appear monophyletic, with a strong support for each clade (js=99 for phoronids, js=75 brachiopods). The main difference compared to the former analysis is the position of *Novocrania anomala*: The craniid here represent the sister group to the remaining brachiopods. (js=75) (Fig. 17).

Mapping the characters on the likelihood tree from Cohen & Weydmann (2005: Fig. 2) yields 308 necessary changes and a consistency index of 0.82 (data not shown). The same characters mapped on the most parsimonious tree of the former analysis using the full dataset (Fig. 16 A) require 289 character state changes and has a consistency index of 0.88 (Fig. 18). To explain the position of the phoronids as sister group of the inarticulate brachiopods, one needs to assume 24 unique character states for articulates, and three homoplastic characters outside the articulates. The inarticulate brachiopods need four unique changes and two inside the Inarticulata. The phoronids need 13 unique changes with one additional homoplastic character, which changes in the phoronids, whereas the tree obtained under parsimony conditions needs eight unique changes in the Phoronida and twenty in Brachiopoda, with two additional homoplastic characters inside (Fig. 18).

Character congruence

Using direct optimization, the results of the ILD test are reported in Table 3. For the com-

Tab. 4: Parametric space used in the sensitivity analysis. Colored are the values with the lowest ILD. Black: ILD>0.09, orange: ILD<0.09, red: ILD<0.05, red bold: ILD < 0.03.

tv/ts / tv/gap	**0.5**	**1**	**2**	**4**	∞
8	8-1-2	8-1-1	16-2-1	32-4-1	8-1-0
4	4-1-2	4-1-1	8-2-1	16-4-1	4-1-0
2	2-1-2	2-1-1	4-2-1	8-4-1	2-1-0
1	**1-1-2**	1-1-1	2-2-1	4-4-1	1-1-0
0.5		**1-2-2**	1-2-1	2-4-1	1-2-0

bined analysis of all data, the parameter set 1-2-2 results in the lowest incongruence, at an ILD of 0.0255 (Tab. 3, 4). The stability of certain nodes in the trees obtained by the parsimonious analysis is tested under different parameters for gap and transversion/transition costs (Fig. 19). A monophyletic origin of brachiopods and phoronids is only supported by the morphological dataset with jackknife values for this specific node ranging from 73 to 77 (Fig. 19 A). With two parameter sets this node is also supported by the molecular data, the 1-2-2 and 1-1-2 parameter sets respectively. The jackknife values, however, are rather low. The monophyletic origin of the Phoronida is well supported by all three datasets, with the morphological data having jackknife values of 99 in all parameter sets and the combined analysis jackknife values between 76 and 96. The sequence data supports this split in 6 out of the 10 analyses. Here the monophyletic origin of the phoronids is supported with jackknife values ranging from 96 to 100 (Fig. 19 B). A monophyletic clade Radialia is supported only by the morphological data (js=99, Fig. 19 C). The species *P. ovalis* is the the sister group of the remaining phoronids in all data used under almost all parameter sets; only with the costs set to 1-2-0 there is no support for this position of *P. ovalis*. Molecular data supports this position of *P. ovalis* with jackknife values between 71 and 99. In the analyses using both molecular and morphological data, the values are similar to the former, whereas the morphological jackknife values range between 81 and 83 (Fig. 19 D).

Character descriptions

The following section represents a description of the characters used in this analysis. The characters referring to phoronids are described in detail, whereas for brachiopod and outgroup characters are taken from the literature. For these characters, only the respective references are provided - no detailed description will be given. Consistency index and retention index for each character are given in square brackets as obtained from PAUP* for the consensus-tree (Fig. 16 A), as well as the percentage of missing data for each individual character in the matrix.

1. **Substrate/Attachment:** (0) attached to hard substrate; (1) in soft substrate; (2) sedentary on soft substrate; (3) boring in hard substrate. Two Phoronids are boring in hard substrate: *P. ovalis* (Harmer 1917), and *P. hippocrepia* (Selys-Longchamps 1903). *P. ijimai* lives sedentary on soft substrate (Oka 1897), the other phoronids are building their tubes in soft substrate. This is described by Haswell (1883) for *P. australis*, Selys-Longchamps (1903) for *P. muelleri*, Andrews (1890) for *P. architecta* (syn. *P. psammophila*), Silén (1952) for *P. pallida*, Gilchrist (1907) for *Ph. albomaculata*, Pixell (1912) for *Ph. harmeri,* and Hilton (1930) for *Ph. californica*. The Brachiopoda are sessile on hard or in soft substrate (Carlson 1995) [0.5, 0.7, 0.0%].

2. **Mode of life:** (0) solitary; (1) colonial [0.5, 0.0]. Only *P. ovalis* has a colonial organization (Harmer 1917). For brachiopods: (Carlson 1995, char. 59) [0.5, 0.7, 0.0%].
3. **Collar fold:** (0) absent; (1) present. All species of the genus *Phoronis* lack this character. A collar fold is only present in *Phoronopsis* as described by Pixell (1912) for *Ph. harmeri*, Emig *et al.* (1977) for *Ph. albomaculata*, and Hilton (1930) for *Ph. californica* [1.0, 1.0, 0.0%].
4. **Metasoma sharp divided into two regions:** (0) absent; (1) present. Only *P. ovalis* has this character (Harmer 1917) [1.0, 0.0, 0.0%].
5. **Nidamental gland:** (0) absent; (1) present; (2) tentacular; (3) basal und tentacular; (4) basal und tentacular spirally coiled. The nidamental gland is defined by Zimmer (1964) as the "continuous strips of glandular epithelium that extends laterally around the bases of the tentacular whorls". Basal and tentacular: Zimmer (1964) for *P. hippocrepia*, *P. vancouverensis* (syn. *P. ijimai*); tentacular: *P. psammophila* (Emig 1966); basal and tentacular spirally coiled: *P. australis* (Emig, 1971); all other phoronids lack nidamental glands (Zimmer 1964; Emig 1971, Emig *et al.* 1977) [1.0, 1.0, 4.5%].
6. **Amoebocytes:** (0) absent; (1) present. *P. hippocrepia* (Emig 1982), *P. ijimai* (Emig 1982), *P. muelleri* (Silén 1954), *P. psammophila* (Brooks & Cowles 1905 for *P. architecta*), and *Ph. harmeri* (Zimmer 1964) have amoebocytes. *P. ovalis* (own observations) and *P. pallida* (Silén 1954) are lacking this character. In the remaining phoronids, the state of this character is unknown [1.0, 1.0, 18.2%].
7. **Lophophore:** (0) absent; (1) circle (trocholophe); (2) lateral arms multi-lobed (plectolophe); (3) paired arms arising from central arm (spirolophe); (4) horseshoe-shaped; (5) arms coil counter-clockwise; (6) arms coil clockwise; (7) counter-clockwise forming a spiral; (8) counter-clockwise multi-coiled. The lophophore as defined by Hyman (1959) and Emig (1976) is a unique feature in bryozoans, brachiopods and phoronids (Hyman 1959). The shape of the tentacle bearing lophophore varies greatly among brachiopods, phoronids and bryozoans. The bryozoans' posses the simplest form, a circular arm, from which the tentacles arise. The lophophore has either a so-called spirolophed or plectolophed condition (Hyman 1959; Rudwick 1970). The spirolophed lophophore has two arms, with can coil into complex spirals. In phoronids, craniids, inarticulates and rhynchonellids they coil counter-clockwise, whereas in discinisc brachiopods they coil in clockwise direction (Hyman 1959). In phoronids the amount of complexity of coiling is coded as well. In crinoids there is no lophophore; tentacles arise directly from the anterior body. Brachiopods: Carlson (1995, char. 35) [0.727, 0.625].
8. **Epistome:** (0) absent entirely; (1) with coelomic cavity; (2) continous with the tentacle coelom; (3) compact filled with muscles. In *P. ovalis* (Gruhl *et al.* 2005) and *P. muelleri*

(Bartolomaeus 2001) the epistome is continuous with the tentacle coelom. This is also true for the bryozoan *Plumatella repens* (I. Wegener, pers. comm.). In brachiopods, the median tentacle of *Lingula anatina* is compact and filled with muscles (Lüter 1998, 2000a) [0.667, 0.75, 4.5%].

9. **Number of nephridial funnels and lateral mesenteries:** (0) absent; (1) absent one nephridial funnel; (2) one with one nephridial funnel; (3) two with one nephridial funnel; (4) two with two nephridial funnels; (5) two with one funnel in males, and two funnels in females. This character is closely associated with the number of nephridial funnels: A simple funnel is found in the four species *P. ovalis*, *P. psammophila*, *P. muelleri*, and *Ph. malakhovi*. *P. ovalis* has no lateral mesenteries (Harmer 1917, Silén 1952), the left lateral mesentery is absent below the level of nephridia in *P. muelleri* (Silén 1952). In contrast, *P. psammophila* (Silén 1952) as well as *Ph. malakhovi* (Temereva 2000a), have two lateral mesenteries. Nephridia with two funnels occur only in species with two lateral mesenteries. The funnels are dissymmetrical; having the anal funnel larger than the oral one in *P. pallida* (Silén 1952), *P. ijimai* (Emig 1974b), *P. australis* (Emig & Marche-Marchad 1969), *Ph. californica* (Emig & Plante 1969). The remaining species have the proportion of the funnels inverted; the oral one larger than the anal as described by Temereva & Malakhov (2001) for *Ph. harmeri*, Emig & Thomassin (1969) for *Ph. albomaculata*, and Emig (1968) for *P. hippocrepia* [1.0, 1.0, 0.0%].
10. **Tentacle (lophophore) coelom:** (0) no lophophore; (1) one coelomic space per arm; (2) two coelomic spaces per arm; (3) more than two coelomic spaces per arm. Phoronids have one coelomic space per arm; brachiopods have two or more coelomic spaces per arm (Carlson 1995 char. 39) [1.0, 1.0, 0.0%].
11. **Lateral mesenteries:** (0) absent; (1) absent one nephridial funnel; (2) one with one nephridial funnel; (3) two lateral mesenteries; (4) two with one nephridial funnel; (5) two with two nephridial funnels; (6) two with two nephridial funnels: great anal, small oral; (7) two with two nephridial funnels: small anal, great oral. Harmer (1917) for *P. ovalis*; Silén (1952) for *P. pallida*; Temereva & Malakhov (2001) for *Ph. harmeri*; Emig *et al.* (1977) for *Ph. albomaculata*; Temereva (2000b) for *P. malakhovi*; Marsden (1959) for *P. architecta* [0.714, 0.667, 0.0%].
12. **Oesophagial valve:** (0) absent; (1) present. *P. ovalis* has a valve in the oesophagus (Lönöy 1954). All other phoronid species lack this character [1.0, 0.0, 0.0%].
13. **Stomach diverticula in larva:** (0) absent; (1) paired (2) unpaired. This character is absent in *P. ovalis* (own observations) and *Ph. harmeri* (Zimmer 1964 for Actinotrocha A). Paired stomach diverticula are found in the larva of *P. muelleri* (Selys-Longchamps 1903) and *Ph. albomaculata* (Brooks & Cowles 1905 for Actinotrocha wilsoni B). Three species have unpaired stomach diverticula: *P. hippocrepia*, *P. pallida*, and *P. psammo-*

phila (Emig 1982). The state of the stomach diverticula in the remaining Phoronids is unknown [0.667, 0.667, 18.2%].

14. **Giant fibers:** (0) absent; (1) present (2) two lateral; (3) one on left side; (4) one left, and right one only until level of right nephridia. Giant nerve fibers are present in all phoronid species except for *P. ovalis* (own observations). These can be either one or two fibers located in the epidermis at the site of attachment of the lateral mesenteries. *P. pallida* (Silén 1952), *P. muelleri* (Selys-Longchamps 1903), *P. architecta* (syn. *P. psammophila*, Brooks & Cowles, 1905) and *Ph. malakhovi* (Temereva 2000a) have only one left fiber, *P. hippocrepia* (Silén 1952), *P. ijimai* (Pixell 1912 for *P. vancouverensis*), and *P. australis* (Emig & Marche-Marchad 1969) have both fibers, whereas in *Ph. albomaculata* (Emig & Thomassin 1969), *Ph. californica* (Hilton 1930) and *Ph. harmeri* (Pixell 1912) the right one is only posterior until the level of the right nephridia [1.0, 1.0, 0.0%].
15. **Longitudinal vessels with blind ending ceacae:** (0) absent; (1) two; (2) three. Phoronids have longitudinal vessels with blind ending caecae. The number of these vessels and the allocation of the blind ending caecae are coded here. *P. ovalis* is the only phoronid species with three vessels (Lönöy 1954) composed out of one median vessel and two longitudinal vessels. All other Phoronids have two; one median and one lateral vessel (Wright 1856, Brooks & Cowles 1905, Pixell 1912, Silén 1952, Emig 1969b). Blind ending ceacae are distributed in all phoronids throughout the length of the trunk, only in *P. muelleri* the cacea are restricted to the proximal part of the trunk (Selys-Longchamps 1903) [1.0, 1.0, 0.0%].
16. **Arrangement of the circular muscles in body wall:** (0) no circular muscles in body wall; (1) present; (2) circular layer continuous throughout the trunk; (3) two separate circular layers; (4) three circular sphincters in the trunk. The circular muscles in the trunk of phoronids are arranged in two separate layers. In *P. pallida,* there are three additional sphincters in the trunk, dividing the longitudinal muscles in four compartments (Silén 1952) [1.0, 1.0, 0.0%].
17. **Typical longitudinal muscles:** (0) absent; (1) present. Longitudinal muscles arranged in single bands run throughout the trunk coelom in all phoronid species (Silén 1952, Emig 1985). All other taxa considered here are lacking this feature [1.0, 1.0, 0.0%].
18. **Nonmuscular region:** In *P. ovalis* the proximal end of the body and ampulla has no muscles (Harmer 1917) [1.0, 0.0, 0.0%].
19. **Constant number of longitudinal muscles:** In all phoronid species except for *P. pallida* the number of longitudinal muscles varies between the populations (Emig, 1974b) [1.0, 1.0, 0.0%].

20. **Pigmentation:** All phoronid species have pigmentation. *P. muelleri* has a star-like pigmentation (Selys-Longchamps 1903) [1.0, 1.0, 0.0%].
21. **Protonephridia:** (0) absent; (1) in larva; (2) in larva: canal branches; (3) in both larva and adult. Protonephridia are retained in the Polyplacophora during metamorphosis, therefore both larva and adult possess protonephridia (Strathmann, 1987). In polychaetes the larvae possess protonephridia; in some derived taxa the adults have protonephridia (Bartolomaeus & Ax 1992). Phoronid larvae have protonephridia (Emig 1982, Bartolomaeus 1989b; this study). In *Ph. albomaculata* the canal branches (Brooks & Cowles 1905: for A. wilsoni B), all other phoronid species have a single canal. The condition of *Ph. californica* is unknown, but a protonephridium can be assumed in the larva, as all other phoronids have one. Brachiopods have no protonephridia (Nielsen 1991, Lüter 1998, own observations on *Novocrania anomala*). Kamptozoa, Bryozoa as well as crinoids have no protonephridia, neither in the adult nor in the larva (Brusca & Brusca 2003) [0.75, 0.8, 0.0%].
22. **Metanephridia:** (0) absent; (1) type A; (2) type B (composed); (3) composed with ascending branch only; (4) composed with ascending branch only and divided into two chambers; (5) composed with two branches. The metanephridia in adult phoronids, brachiopods and echinoderms are formed out of an ectodermal channel with a mesodermal funnel, the type B (Bartolomaeus 1989b, Lüter 1998, Brusca & Brusca 2003). In Annelida the metanephridial channel and funnel are formed completely out of a single solid anlage (Bartolomaeus 1989a, Bartolomaeus & Ax 1992, type A). Bryozoans have no excretory structures. Their excretion is thought to occur over the whole body wall (Mukay *et al.*, 1997). The metanephridium of molluscs has evolved independently (see Lüter 1998) and is therefore coded as 'absent'. Crinoids have no excretory organs (Ruppert & Balser 1986) [1.0, 1.0, 0.0%].
23. **Nephridiophore:** (0) absent; (1) simple opening in body wall; (2) on nephridial papilla; (3) on anal papilla on the level of the anus; (4) on anal papilla below the level of the anus. Three different locations of the nephroporus in Phoronida can be distinguished: either on the anal papilla at the level of the anus or below the level of the anus or on a nephridial papilla located above the level of the anus. *P. ovalis* (Lönöy 1954), *P. pallida* (Silén 1952), and *P. muelleri* (Emig 1969b) belong to the first group with the nephroporus located on the level of the anus. *P. psammophila* (Emig 1968), *Ph. albomaculata* (Emig & Thomassin 1969), *Ph. californica* (Emig & Plante 1969), *Ph. harmeri* (Pixell 1912), and *Ph. malakhovi* (Temereva 2000a) have the nephroporus located below the level of the anus; whereas a separate nephridial papilla is formed in *P. hippocrepia* (Emig 1968), *P. ijimai* (Emig 1974b), as well as in *P. australis* (Emig 1969b) [0.8, 0.875, 0.0%].

24. **Sexes:** (0) dioecious; (1) hermaphrodite. All *Phoronis* species except *P. muelleri* (Emig 1970) and *P. psammophila* (Emig 1969a) are described to be hermaphroditic (*P. hippocrepia*, *P. ovalis*, *and P. pallida*: Silén (1952); *P. ijimai* and *P. australis*: Emig (1971). All four *Phoronopsis* species considered here are dioecious (*Ph. albomaculata*: Gilchrist (1919); *Ph. californica*: Hilton (1930); *Ph. harmeri*: Zimmer (1964); *Ph. malakhovi*: Temereva (2000a)). Brachiopods: Carlson (1995, char. 6) [0.25, 0.5, 4.5%].
25. **Gametes:** (0) develop from body tissues; (1) develop and stay in body cavity; (3) develop in body cavity and move to mantle canals. Brusca & Brusca (2003), brachiopods: Carlson (1995, char. 9) [0.667, 0.75, 0.0%].
26. **Egg size:** (0) small 50-100 µm; (1) large 110-200 µm. Egg size is relatively large in species with brood protection, and small in species with direct release of the embryos. *P. hippocrepia* (Silén 1952) and *P. ijimai* (Zimmer 1964 for *P. vancouverensis*) have small eggs with a diameter of 100 µm. *P. ovalis* has eggs with the size of 125 µm (Silén 1952). *P. muelleri* (Selys-Longchamps 1903: 50µm), *P. pallida* (Silén 1952: 70 µm), and *P. psammophila* (Emig 1982: 80-120 µm), as well as *Ph. harmeri* (Zimmer 1964: 60-65 µm) on the other hand have small eggs. The egg size of the remaining phoronid species is unknown. Brachiopods: Carlson (1995, char. 7) [0.333, 0.5, 40.9%].
27. **Sperm:** (0) simple; (1) V-shaped [0.667, 0.75, 4.5%]. All phoronids have V-shaped sperm (Emig 1982) [1.0, 1.0, 0.0%].
28. **Sperm morphology:** (0) ect aquasperm (small acrosome, short midpiece, long falgellum); (1) ent aquasperm (large acrosome, >1 mitochondrion). Carlson (1995, char. 8) [1.0, 1.0, 27.3%].
29. **Spermatophors:** (0) absent; (1) type A; (2) type B. *P. muelleri* is the only phoronid species with type A spermatozoa (Emig 1982). All other Phoronida have type B spermatozoa (Zimmer 1964, Emig 1982, Brusca & Brusca 2003) [1.0, 1.0, 27.3%].
30. **Spermrelease:** (0) at once; (1) continuous; (2) periodic. [/, /, 77.3%].
31. **Development:** (0) lecithotroph; (1) planktotroph with initial lecitotrophic stages; (2) planktotroph (Lüter 1998; this study), [0.4, 0.625, 13.6%].
32. **Origin of mesoderm:** (0) ectomesoderm; (1) border of ecto- and endoderm; (2) archenteron. (Lüter 2000a, Peterson & Eernisse 2001, Freeman & Martindale 2002, this study), [0.667, 0.875, 22.7%].
33. **Lophophoral organ:** (0) absent; (1) present; (2) small; (3) large and glandular; (4) large and membranous. This is the lophophoral organ *s. str.* from Zimmer (1964:214) describing the glandular pocket medially on the floor of the lophophoral concavity. It is formed during the reproductive period in Phoronida. In four species it is large and glandular: *P. muelleri* (Selys-Longchamps 1903), *P. pallida* (Silén 1952), *P. psammophila* (Emig

1974b), and *P. albomaculata* (Zimmer 1964). Temereva (2000a) shows a not exactly specified lophophoral organ for *Ph. malakhovi*. A small lophophoral organ is described in three species: *P. hippocrepia* (Silén 1952), *P. vancouverensis* (syn. *P. ijimai*) (Zimmer 1964), and *P. australis* (Emig 1971). Both *Ph. harmeri* and *Ph. californica* have large and membranous organs (Hilton 1930, Zimmer 1964) [1.0, 1.0, 0.0%].

34. **Asexual Reproduction:** (0) absent; (1) present; (2) transverse fission; (3) budding; (4) transverse fission and budding. *P. ovalis* has asexual reproduction by lateral budding (Marcus, 1949) and transverse fission (Harmer 1917). *P. hippocrepia* (Selys-Longchamps 1907), *P. ijimai* (Marsden 1959), *P. australis* (Emig 1974b), *P. muelleri* (Silén 1952), *P. psammophila* (Emig 1972), *Ph. albomaculata* (Gilchrist 1919) show asexual reproduction by transverse fission. *P. pallida* (Silén 1952) and *Ph. harmeri* (Temereva & Malakhov 2004) have no asexual reproduction [0.667, 0.667, 9.1%, 0.0%].

35. **Brood protection:** (0) absent; (1) present; (2) in tube of the adult; (3) on nidamental gland: Except for the three species *P. muelleri* (Selys-Longchamps 1903), *P. pallida* (Silén 1952), and *Ph. harmeri* (Zimmer 1964) all other representatives of the Phoronida show some sort of brood protection. Of these, *P. ovalis* is the only species to brood their embryos in the parental tube (Silén 1954). The remaining phoronid species brood their embryos on nidamental glands in the lophophoral concavity (*P. hippocrepia*: Silén (1952); *P. ijimai*: Emig 1971; *P. australis*: Ikeda, 1902; *P. psammophila*: de Selys-Longchamps (1903), Emig (1971)). Unfortunately, the state of this character in the remaining three *Phoronopsis* species is unknown. Brachiopods: Carlson (1995, char. 12) [0.429, 0.556, 13.6%, 0.0%].

36. **Larval type:** (0) absent; (1) present; (2) brachiopod larva; (3) pelagic juveniles; (4) trochophore; (5) phoronid larva; (6) slug-like larva; (7) actinotrocha-type; (8) actinotrocha without adult tentacles in late larval stage; (9) actinotrocha with adult tentacles in late larval stage. *P. ovalis* has a slug-like larva without tentacles (Silén 1954; this study). The remaining phoronids have an actinotroch larva with larval tentacles. *P. muelleri* (Emig 1982), *P. psammophila* (Herrmann 1979), and *Ph. albomaculata* (Brooks & Cowles 1905 for A. wilsoni B) develop adult tentacles shortly before metamorphosis. *P. hippocrepia* (Emig 1982), *P. ijimai* (Zimmer 1964 for *P. vancouverensis*), *P. pallida* (Santagata & Zimmer 2002), and *Ph. harmeri* (Zimmer 1964) have no adult tentacles. The knowledge about the development of *Ph. malakhovi* is patchy, but it has an actinotroch larva (Temereva 2000a). Brachiopods: Carlson (1995, char. 13), Lüter (1998) [0.875, 0.889, 9.1%].

37. **Number of larval tentacles at competence:** (0) no larval tentacles; (1) <13; (2) 13-20; (3) >20. From the eight phoronid species with known larva three have larva with less than 13 tentacles (*P. hippocrepia* and *P. pallida* (Silén 1954), *P. psammophila* (Her-

rmann 1979)). *P. ijimai* (Zimmer 1964 for *P. vancouverensis*) and *Ph. harmeri* (Zimmer 1964) have 13 to 20 tentacles. *P. muelleri* (Selys-Longchamps 1903) and *Ph. albomaculata* (Brooks & Cowles 1905 for A. wilsoni B) have more than 20 tentacles. *P. ovalis* has zero tentacles at competence (Silén 1954) [0.75, 0.75, 13.6%].

38. **Larval sense organs:** (0) absent; (1) present; (2) present as papillae or cilia; (3) present as pigment spots or eye spots. All phoronid species have larval sense organs (Silén 1954; Temereva 2000a), except for *P. ovalis* (this study). Brachiopods: Carlson (1995, char. 15) [0.6, 0.714, 9.1%].
39. **Eversible sense organ, Pyriform organ:** (0) absent; (1) present. An eversible sense organ is present in *P. hippocrepia* (Santagata 2002a), *P. muelleri* (Emig 1982), *Ph. harmeri* (Zimmer 1964). All other phoronid species lack this character: *P. ovalis* (this study), *P. pallida* (Santagata 2002a), *P. psammophila* (Herrmann 1979a), *Ph. albomaculata* (Brooks & Cowles 1905 for A. wilsoni B). In *P. ijimai*, *P. australis*, *P. malakhovi*, and *Ph. californica* the presence of an eversible sense organ is unknown [0.333, 0.0, 13.2%].
40. **Larval blood corpuscle masses:** (0) absent; (1) one; (2) two; (3) three; (4) four. Except for *P. ovalis* (this study), all phoronid species have blood corpuscles masses in their larva. *P. ijimai* (Zimmer 1964) and *P. pallida* (Silén 1954) have one. *P. hippocrepia* (Silén 1954), *P. muelleri* (Silén 1954), and *P. psammophila* (Herrmann, 1979) have two blood corpuscle masses, whereas four occur in the larvae of *Ph. albomaculata* (Brooks & Cowles 1905 for A. wilsoni B) and *Ph. harmeri* (Zimmer 1964). The state of *P. australis*, *Ph. californica*, and *Ph. malakhovi* is unknown [0.75, 0.75, 13.6%].
41. **Metamorphosis after extrusion of invaginated tube:** (0) absent; (1) present. The eversion of the metasomal tube during metamorphis is a feature unique to all phoronids, although some bryozoan larvae exhibit a similar character [0.5, 0.889, 9.1%].
42. **Juvenile tentacles:** (0) no juvenile tentacles; (1) modified larval; (2) basal thickenings; (3) separate set. The actinotrocha of *P. muelleri* develops juvenile tentacle short before metamorphosis as separate set from the larval tentacles (Selys-Longchamps 1903). *P. psammophila* on the other hand has the juvenile tentacles developed out of basal thickenings from the larval tentacles in the competent larva (Herrmann 1979). All other phoronid species have the juvenile tentacles developed from modified larval tentacles: *P. hippocrepia*, *P. ijimai*, *P. pallida*, and *Ph. harmeri*: Santagata (2002a), *Ph. albomaculata*: Brooks & Cowles (1905 for A. wilsoni B), with the exception of *P. ovalis*, which has no larval tentacles (Silén 1954; this study). The state of *P. australis*, *Ph. californica*, and *Ph. malakhovi* is unknown [1.0, 1.0, 22.7%].
43. **Juvenile lophophore:** (0) no lophophore; (1) adds new tentacles from only one place in the lophophore; (2) adds tentacles from two places. *P. muelleri* adds juvenile ten-

tacles from dorsad and vendrad in the lophophore (Selys-Longchamps 1903). All other phoronid species add the juvenile tentacles from dorsad (Santagata 2002a). The state of *P. australis*, *Ph. californica*, *Ph. albomaculata*, and *Ph. malakhovi* is unknown [1.0, 1.0, 54.5%].

44. **Separation between tentacle- and trunk coelom:** (0) distinct regionation; (1) imperfect separation. Brachiopods: Carlson (1995, char. 22) [0.5, 0.8, 0.0%].
45. **Muscular system:** (0) absent; (1) circular muscles overlied by longitudinal muscles; (2) single fibers). Brachiopods: (Carlson 1995) [1.0, 1.0, 0.0%].
46. **Number digestive diverticula (liver):** (0) absent entirely; (1) present; (2) two (one pair); (3) three (one pair plus one unpaired); (4) four (two pairs, two ducts); (5) more than four (from 6 to 16 pairs); (6) one (unpaired); (7) four (one pair plus two unpaired, four ducts). Brachiopods: Carlson (1995, char. 44) [1.0, 1.0, 0.0%].
47. **Mantle:** (0) absent; (1) present. Brachiopods: Carlson (1995, char. 24) 1.0[, 1.0, 0.0%].
48. **Mantle epithelium:** (0) no mantle epithelium; (1) continous posterior; (2) completely divided. Brachiopods: Carlson (1995, char. 25) [1.0, 1.0, 0.0%].
49. **Mantle rudiment from larva:** (0) no mantle epithelium; (1) not reversing; (2) reverse metamorphosis; (3) reverse embryogenesis; (4) reverse pelagic development. Brachiopods: Carlson (1995, char. 5) [1.0, 1.0, 0.0%].
50. **Mantle groove separating the inner and outer lobes of mantle edge:** (0) no mantle; (1) absent; (2) present in marginal canal; (3) present in terminal branches of mantle canal system. Brachiopods: Carlson (1995, char. 28) [1.0, 1.0, 0.0%].
51. **Secondary ganglion dorsal to the gut:** (0) absent; (1) present. Brachiopods: Carlson (1995, char. 52) [1.0, 1.0, 0.0%].
52. **Number of rows of tentacles per side in adult lophophore:** (0) no lophophore; (1) one row (unpaired) throughout ontogeny; (2) two rows (paired) post-trocholophe stage only; (3) two rows throughout ontogeny. Brachiopods: Carlson (1995, char. 37) [1.0, 1.0, 0.0%].
53. **Median tentacle of lophophore:** (0) no lophophore; (1) absent throughout ontogeny; (2) present initially, then lost later in development. Brachiopods: Carlson (1995, char. 38) [1.0, 1.0, 0.0%].
54. **Internal musculature in adult lophophore arms:** (0) brachial muscles absent or weakly supported; (1) brachial muscles strongly supported. Brachiopods: Carlson (1995, char. 40) [0.67, 0.83, 0.0%].
55. **Lophophore muscles:** (0) no lophophore; (1) absent; (2) present. Brachiopods: Carlson (1995, char. 55) [0.5, 0.6, 0.0%].

56. **Blood vascular system:** (0) absent entirely; (1) present and closed; (2) present and open; (3) intermediate state between open and closed; (4) lakunar system. Brachiopods: Carlson (1995, char. 47) [1.0, 1.0, 0.0%].
57. **Heart:** (0) absent; (1) present; (2) single heart present; (3) diffuse (several parts of the blood vessels are contractile); (4) multiple hearts present; (5) metamere. Brachiopods: Carlson (1995, char. 48) [0.8, 0.8, 4.5%].
58. **Muscle type:** (0) columnar muscles; (1) tendinous muscles. Brachiopods: Carlson (1995, char. 57) [1.0, 1.0, 68.2%].
59. **External muscles that attach body to external casing:** (0) absent (body moves by internal muscles and hydrostatic change); (1) present (move body with respect to zooecia or valves) . Brachiopods: Carlson (1995, char. 53) [1.0, 1.0, 0.0%].
60. **Muscle system with respect to mineralized valves:** (0) no valves; (1) complex; (2) simple. Brachiopods: Carlson (1995, char. 54) [1.0, 1.0, 0.0%].
61. **Mineralized skeleton:** (0) absent; (1) calcium carbonate; (2) calcium phosphate. Brachiopods: Carlson (1995, char. 61) [0.5, 0.71, 0.0%].
62. **Shell formation time:** (0) no shell; (1) embryonic; (2) larval; (3) postlarval. Brachiopods: Carlson (1995, char. 62) [0.67, 0.83, 0.0%].
63. **First formed shell mineralized as:** (0) no valve; (1) one valve that later folds and splits into two valves; (2) two valves throughout ontogeny; (3) two valves present only in larvae; absent in adult. Brachiopods: Carlson (1995, char. 63) [1.0, 1.0, 0.0%].
64. **Ventral valve growth:** (0) no valve; (1) holoperipheral throughout ontogeny; (2) hemiperipheral to holoperipheral (switches very early in ontogeny, at metamorphosis); (3) hemiperipheral (switches later in ontogeny, post-juvenile); (4) hemiperipheral throughout ontogeny. Brachiopods: Carlson (1995, char. 64) [1.0, 1.0, 0.0%].
65. **Dorsal valve growth:** (0) no valve; (1) holoperipheral; (2) hemispheral. Brachiopods: Carlson (1995, char. 65) [0.67, 0.75, 0.0%].
66. **Shell structure:** (0) no shell; (1) punctate (canicular); (2) punctate (punctae); (3) punktate (endopunctate); (4) pseudopunctate. Brachiopods: Carlson (1995, char. 68) [1.0, 1.0, 0.0%].
67. **Spicules (mesenchymal) in mantle and body wall and lophophore tissue:** (0) absent; (1) uncommon (present in some taxa); (2) common (present in most taxa). Brachiopods: Carlson (1995, char. 69) [1.0, 1.0, 0.0%].
68. **Valves articulation:** (0) no valve; (1) not in contact, and rotate only slightly about an obscure hinge axis; (2) in contact, and rotate about a hinge axis located on valves. Brachiopods: Carlson (1995, char. 72) [1.0, 1.0, 0.0%].

69. **Hinge line:** (0) no valve; (1) strophic; (2) astrophic. Brachiopods: Carlson (1995, char. 73) [1.0, 1.0, 0.0%].
70. **Pair of teeth and sockets:** (0) valve absent; (1) valve present, but teeth and sockets absent; (2) present and non-interlocking; (3) present and interlocking. Brachiopods: Carlson (1995, char. 74) [1.0, 1.0, 0.0%].
71. **Shape of ventral valve beak:** (0) no valve; (1) flat; (2) rounded; (3) pointed; (4) absent. Brachiopods: Carlson (1995, char. 86) [1.0, 1.0, 0.0%].
72. **Ventral valve beak length:** (0) valve absent; (1) extends barely beyond dorsal valve beak; (2) extends well beyond dorsal valve beak. Brachiopods: Carlson (1995, char. 87) [1.0, 1.0 0.0%].
73. **Ventral valve cardinal area:** (0) valve absent; (1) absent; (2) present as pseudointerarea; (3) present as interarea; (4) present as palintrope. Brachiopods: Carlson (1995, char. 88) [1.0, 1.0, 9.1%].
74. **Width of ventral valve cardinal area:** (0) valve absent; (1) very narrow to obsolete; (2) wide to narrow; (3) exceptionally wide. Brachiopods: Carlson (1995, char. 89) [1.0, 1.0, 4.5%].
75. **Orientation of ventral valve cardinal area:** (0) valve absent; (1) procline; (2) catacline; (3) apsacline; (4) orthocline; (5) anacline. Brachiopods: Carlson (1995, char. 90) [1.0, 1.0, 4.5%].
76. **Shape of ventral valve cardinal area:** (0) valve absent; (1) straight; (2) curved. Brachiopods: Carlson (1995, char. 91) [1.0, 1.0, 4.5%].
77. **Ventral valve beak ridges:** (0) valve absent; (1) absent; (2) poorly defined; (3) well defined. Brachiopods: Carlson (1995, char. 92) [1.0, 1.0, 0.0%].
78. **Ventral valve umbo:** (0) valve absent; (1) open; (2) solid. Brachiopods: Carlson (1995, char. 93) [1.0, 1.0, 0.0%].
79. **Median septum in ventral valve:** (0) valve absent; (1) absent; (2) small, inconspicous or poorly developed. Brachiopods: Carlson (1995, char. 94) [0.67, 0.67, 4.5%].
80. **Dental plates:** (0) valve absent; (1) absent; (2) small and simple; (3) large and exaggerated. Brachiopods: Carlson (1995, char. 95) [1.9, /, 18.2%].
81. **Chamber in ventral valve for reception of pedicle base:** (0) valve absent; (1) absent; (2) present. Brachiopods: Carlson (1995, char. 96) [1.0, 1.0, 4.5%].
82. **Delthyrial pedicle opening:** (0) valve absent; (1) present at some stages in ontogeny; (2) absent entirely. Brachiopods: Carlson (1995, char. 97) [1.0, 1.0, 0.0%].
83. **Delthyrial pedicle opening present in ventral valve:** (0) valve absent; (1) slit or foramen; (2) foramen enclosed by deltidial plates; (3) (gap or notch (subapical), open

delthyrium); (4) groove running along pseudointerarea. Brachiopods: Carlson (1995, char. 98) [1.0, 1.0, 4.5%].

84. **Notothyrium:** (0) valve absent; (1) absent; (2) present and open. Brachiopods: Carlson (1995, char. 99) [1.0, 1.0, 4.5%].
85. **Dorsal valve beak shape:** (0) valve absent; (1) flat; (2) rounded and indistinct; (3) pointed and distinct. Brachiopods: Carlson (1995, char. 100) [0.67, 0.75, 0.0%].
86. **Width of dorsal valve cardinal area:** (0) valve absent; (1) absent; (2) narrow to obsolete; (3) well developed and fairly wide. Brachiopods: Carlson (1995, char. 101) [1.0, 1.0, 4.5%].
87. **Orientation of dorsal valve umbo and cardinal area:** (0) valve absent; (1) central; (2) marginal; (3) terminal. Brachiopods: Carlson (1995, char. 102) [1.0, 1.0, 0.0%].
88. **Median septum in dorsal valve:** (0) valve absent; (1) absent; (2) present, but weak and poorly developed; (3) present, strong and well developed. Brachiopods: Carlson (1995, char. 103) [1.0, 1.0, 9.1%].
89. **Hinge plates:** (0) valve absent; (1) absent; (2) present. Brachiopods: Carlson (1995, char. 104) [1.0, 1.0, 13.6%].
90. **Calcareous lophophore support:** (0) no lophophore; (1) absent entirely; (2) present as projection from cardinalia; (3) present as ridges on dorsal valve floor. Brachiopods: Carlson (1995, char. 105) [1.0, 1.0, 0.0%].
91. **Loop:** (0) no lophophore; (1) short, from cardinalia only; (2) long, from cardinalia and medium septum. Brachiopods: Carlson (1995, char. 107) [1.0, /, 18.2%].
92. **Relative size of muscle scars in ventral valve:** (0) valve absent; (1) small; (2) medium; (3) large. Brachiopods: Carlson (1995, char. 108) [[1.0, 1.0, 0.0%].
93. **Muscle platforms:** (0) valve absent; (1) absent entirely; (2) present in ventral valve only. Brachiopods: Carlson (1995, char. 109) [1.0, 1.0, 0.0%].
94. **Cardinal process:** (0) valve absent; (1) small lobe; (2) medium to large lobe; (3) long, wide process. Brachiopods: Carlson (1995, char. 110) [1.0, 1.0, 13.6%].
95. **Shape of mantle canal markings:** (0) valve absent; (1) baculate; (2) bifurcate; (3) pinnate; (4) saccate; (5) lemniscate. Brachiopods: Carlson (1995, char. 111) [1.0, 1.0, 0.0%].
96. **Distribution of mantle canal markings on dorsal valve only:** (0) valve absent; (1) equidistributate; (2) ineqidistributate; (3) apocopate; (4) isolated. Brachiopods: Carlson (1995, char. 112) [0.67, 0.75, 0.0%].
97. **Larval setae:** (0) none; (1) one pair; (2) two pairs; (3) three pairs; (4) setae not in bundles. Brachiopods: Nielsen (1991), Carlson (1995, char. 16), Lüter (1998), Lüter, 2000b [1.0, 1.0, 0.0%].

98. **Adult setae during ontogenesis:** (0) absent; (1) present. Brachiopods: Lüter 2000b 0.5, 0.75, 0.0%].

99. **Origin of pedicle:** (0) Pedicle absent; (1) ventral mantle invagination; (2) from larval rudiment. Brachiopods: Carlson (1995, char. 31) [1.0, 1.0, 0.0%].

100. **Pedicle:** (0) absent; (1) present in latest larval stage, juvenile, and adult; (2) present in juvenile and adult only; (3) present in larval stages only. Brachiopods: Carlson (1995, char. 30) [1.0, 1.0, 0.0%].

101. **Pedicle characteristics:** (0) absent entirely; (1) Coelomate and muscular; (2) compact, not muscular. Brachiopods: Carlson (1995, char. 101) [1.0, 1.0, 0.0%].

102. **Vesicular bodies:** (0) absent; (1) present. Brachiopods: Lüter (1998) [1.0, /, 9.1%].

103. **Primary symmetry:** (0) asymmetrical; (1) radial; (2) bilateral (with cephalization); (3) bilateral larvae metamorphose into pentaradial adults (cephalization secondarily lost). All taxa in this analysis are bilateral, except for the Crinoida, which metamorphose into pentaradial adults (Brusca & Brusca 2003) [1.0, /, 0.0%].

104. **Chitin:** (0) absent (in shell, periostracum, and elsewhere); (1) present (in shell, pedicle, cuticle or outer body tube). Brachiopods: Carlson (1995, char. 71) [0.5, 0.0, 0.0%].

105. **Ciliation:** (0) monociliated; (1) multiciliated. Brusca & Brusca (2003) [0.5, 0.67, 0.0%].

106. **Teloblastic segmentation:** (0) absent; (1) present. Brusca & Brusca (2003) [1.0, /, 0.0%].

107. **Chaetae in larvae and adults:** (0) absent; (1) present. Brachiopods: Carlson (1995, char. 29) [0.5, 0.83, 0.0%].

108. **Ciliated feeding tentacles:** (0) absent; (1) perioral; (2) perioral with mesocoel inside tentacles; (3) perioralanal [1.0, 1.0, 0.0%].

109. **Single band cilias for feeding:** (0) absent; (1) absent in larvae, present adults. Brusca & Brusca (2003) [1.0, 1.0, 0.0%].

110. **Number of coelomic cavities in early larval stages:** (0) one pair; (1) two pairs; (2) five (two pairs plus one unpaired); (3) one unpaired. Brachiopods: Carlson (1995, char. 23), Lüter (1998), Lüter 2000a, this study [0.75, 0.0, 18.2%].

111. **Primary, cerebral ganglion:** (0) supraenteric (dorsal to gut); (1) subenteric (ventral to gut); (2) lacking entirely. Brachiopods: Carlson (1995, char. 51) [0.67, 0.86, 4.5%].

112. **Gut and position of anus:** (0) absent; (1) present; (2) straight, anus posterior; (3) u-shaped, curves up, anus dorsal; (4) u-shaped, curves down, anus ventral; (5) u-shaped, curves laterally to the right side, anus to the right (Nielsen 1991). Brachiopods: Carlson (1995, char. 43) [1.0, 1.0, 0.0%].

113. **Cleavage:** (0) total radial; (1) other. Brusca & Brusca (2003) [1.0, 1.0, 27.3%].
114. **Gastrulation:** (0) delamination; (1) invagination without epiboly; (2) invagination with epiboly. Brachiopods: Carlson (1995, char. 2) [0.67, 0.0, 22.7%].
115. **Fate of blastopore:** (0) forms adult mouth; (1) forms adult anus; (2) blastopore closes during embryogeny, mouth and anus form elsewhere. Brusca & Brusca (2003) [0.67, 0.83, 22.7%].
116. **Entomesoderm derives from a single (mesentoblast) cell, typically the 4d cell:** (0) absent; (1) present. Brusca & Brusca (2003) [1.0, 1.0, 22.7%].
117. **Trochoblasts:** (0) absent; (1) present. Brusca & Brusca (2003) [1.0, 1.0, 13.6%].
118. **Brachiopod fold:** (1) absent; (1) present. Nielsen (1991), Cohen *et al.*, (2003) [0.5, 0.75, 0.0%].
119. **Larval ciliary band:** (0) absent; (1) upstream ciliary sieving; (2) downstream. Nielsen, 2005 [1.0, 1.0, 9.1%].
120. **Tentacle arrangement:** (0) tentacles absent; (1) along both sides of arm axis; (2) on only one side of arm axis. Brachiopods: Carlson (1995, char. 36) [0.67, 0.83, 0.0%].
121. **Nervous system:** (0) below epidermis of body wall (subepidermal); (1) within epidermis of body wall (intraepidermal) . Brachiopods: Carlson (1995, char. 50) [, 18.2%].
122. **With synaptic nervous system:** (0) arranged as pentamerous network; (1) concentrated ventrally or ventrolaterally; (2) reduced, diffuse, but with circumoesophagial nerve ring. Brusca & Brusca (2003) [1.0, 1.0, 0.0%].
123. **Gonopericardial system:** (0) absent; (1) present. Brusca & Brusca (2003) [1.0, /, 0.0%].
124. **Sheets of subepidermal muscles:** (0) present, derived at least in part from archenteric mesoderm; (1) present, and derived at least in part from 4d mesoderm. Brusca & Brusca (2003) [1.0, 1.0, 0.0%].
125. **Mantle shell glands produce calcareous spicules or shells:** (0) absent; (1) present. Brusca & Brusca (2003) [1.0, /, 0.0%].
126. **Stereome ossicular skeletal system:** (0) absent; (1) present. Brusca & Brusca (2003) [1.0, /, 0.0%].
127. **Water vascular system:** (0) absent; (1) present. Brusca & Brusca (2003) [1.0, /, 0.0%].
128. **Radula:** (0) absent; (1) present. Brusca & Brusca (2003) [1.0, /, 0.0%].
129. **Unique annelidan head of presegmental prostomium and peristomium:** (0) absent; (1) present. Brusca & Brusca (2003) [1.0, /, 0.0%].
130. **Visceral mass in cup-shaped calyx:** (0) present; (1) absent. Brusca & Brusca (2003) [1.0, /, 0.0%].

131.Formation of brown bodies: (0) absent; (1) present. Brusca & Brusca (2003) [1.0, /, 0.0%].

132.Funiculus: (0) absent; (1) present [1.0, /, 0.0%].

133.Orifice closed by sphincter: (0) absent; (1) present [1.0, /, 0.0%].

Discussion

The phylogenetic position of the Phoronida has been the topic of controversial opinions (Emig 1977, 1984, Jefferies 1986, Ax 1989, Halanych et al. 1995, Emig 1997, Lüter & Bartolomaeus 1997, Zimmer 1997, Ax 2000). The striking difference between larval and adult morphology leads to several misinterpretations regarding their evolutionary background. The relationship of the actinotroch larva to the adult phoronid has been unknown for at least 20 years. It was Hatschek (1888), who first grouped the phoronids, together with Bryozoa and Brachiopoda, into a taxon which he called "Tentaculata". This name has been rejected by Hyman (1959), who united the three taxa under the name Lophophorata, due to their unique lophophore which she defined as a tentacle bearing ridge of the anterior body, surrounding the mouth and not the after and containing a coelomic lumen. This definition has been refined by Emig (1977). Regarding the systematic relationship of the eleven phoronid taxa itself, there have been only sparse phylogenetic analyses so far (Emig 1985).

The Phoronida are monophyletic in almost all datasets analyzed (Fig. 16A, B). A sister group relationship between Brachiopoda and Phoronida could only be shown with the 18S rRNA dataset. In all other analyses the Brachiopoda and Phoronida appear paraphyletic. The three species *P. hippocrepia*, *P. australis* and *P. ijimai* are well supported in all analyses (Fig. 16). The patterns presented in the clades correspond to the evolutionary trend applied to the evolution of Phoronida, implying they have gradually changed from fewer tentacles to more tentacles (Emig 1985).

Ground pattern of the Phoronida

A ground pattern for the Phoronida is established by a mixture of autapomorphic and plesiomorphic characters, where the state of each character in the ground pattern is determined by the state of the respective character in the outgroup – the brachiopods respectively. The reconstruction of the ground pattern for the phoronids is based on the parsimonious tree obtained in the morphological analysis (Fig. 16 A, Fig. 18).

Phoronids dwell inside their chitinous tubes embedded *in soft sediment* like, for instance *P. muelleri* or *Ph. californica*, or in hard substrate, as *P. ovalis* or *P. hippocrepia*. Emig (1984, 1985) assumes a primarily soft-bottom dwelling mode of life, following general assumptions of other authors. But this is not supported by this analysis: the state of this character is unclear regarding the ground pattern of phoronids.

They *live solitary*; the colonial organization of *P. ovalis* boring in shells is derived, as all other phoronids and the brachiopods are solitary which represents therefore the plesiomorphic condition.

The secretion of an outer casting is done by an area around the lophophore, whereas the brachiopods secrete their bivalved shell by the mantle epithelium and the bryozoans by their epithel.

Phoronids have *no mantle or mantle epithelium* and no mineralized skeleton, as the brachiopods (with the exception of the phosphatic lingulids). The secretion of a *chitinous tube* must therefore be autapomorphic for the phoronids.

The stemlineage representative has a *lophophore with paired arms*, arising from a central arm, like in brachiopods and bryozoans. The *lophophore is horseshoe shaped*; an autapomorphy for the phoronids.

The lophophore encircles the central mouth opening, which is overlapped by the epistome and bears ciliated feeding tentacles, with a coelomic cavity inside the tentacles. This is shared with brachiopods, just as the inner morphology of the epistome: *The coelom of the tentacles also extends into the epistome* and is therefore continuous with the tentacle coelom (Lüter 1998, 2000, Gruhl *et al*. 2005). This is plesiomorphic for the phoronids.

The *coelom of the adults is divided into two compartments*, the anterior tentacle coelom, which surrounds the mouth opening and extends into the tentacles, and the posterior trunk coelom, which contains the intestine as well as the gonads. *Two coelomic cavities are plesiomorphic* for the Phoronida, since Brachiopoda also possess such two coelomic compartments (Lüter 1998, 2000a, own observation on *Novocrania anomala*).

Except for *P. ovalis*, all phoronids have *one or two lateral mesenteries*. The presence and the number of lateral mesenteries are closely related with the presence or absence of the giant nerve fibers and the number of nephridial funnels. The absence of lateral mesenteries in *P. ovalis* yields to the presence of only *one nephridial funnel and the absence of giant nerve fibers* in the ground pattern of the Phoronida.

The paired and composed metanephridia (Bartolomaeus 1989b) are also developed in brachiopods and are therefore plesiomorphic. The phoronid nephridium in the ground pattern has either an ascending branch or straight duct only, as in *P. ovalis*, *P. australis*, *P. hippocrepia*, and *P. ijimai*, or consists of an ascending and descending branch, like in *P. muelleri*, *P. psammophila* and the *Phoronopsis*. Emig (1985) assumes a metanephridium with an ascending branch or U-shaped duct and a simple coelomic funnel as shown in *P. ovalis* as primitive condition for the Phoronida. In the brachiopods *Terebratulina retusa* and *Novocrania anomala*, the nephridial duct is straight and connects the nephridial funnel with the nephridiopore. The nephridial funnel is situated in the metacoel and the nephridiopore opens into the mantle cavity of the lateral body wall (Lüter 1995). Therefore the existence of *one straight nephridial duct or one ascending nephridial duct connecting the nephrostome with the nephridiopore* can be assumed as plesiomorphic for the phoronids.

All taxa this analysis considers a nephridiopore that is a simple opening in the body wall. In phoronids the *nephridiopore is situated on the anal papilla above the level of the anus*.

The circulatory system in all phoronid species is closed, with numerous capillaries in the region of the stomach and the gonads. Brachiopods also possess vessels, but they do not form a closed circulatory system. The bryozoans have no blood vascular system. Thus the *closed blood vascular system* is autapomorphic in the ground pattern of the Phoronida.

There is no heart present, but several parts of the median blood vessel are contractile. There could be either three longitudinal vessels, as realized in *P. ovalis*, or two, as realized in the remaining phoronids. The longitudinal vessels have blind ending cacae.

The muscular system consists of two separate circular layers in the body wall and inner longitudinal muscles, which vary in number and are differentiated into series of longitudinal muscles extending throughout the trunk. The *two circular muscle layers*, as well as the *specialized longitudinal muscles* are autapomorphic for the phoronids.

Phoronids are primarily *hermaphroditic*, a derived feature; *gametes develop in the vasiperitoneal tissue and stay in the trunk coelom*, same as in brachiopods (and polychates). Only in bryozoans gametes develop from the body tissue.

The *sperm is V-shaped* (autapomorphic), the *eggs are small* (50-100µm). *No spermatophores* were present in the stemlineage of phoronids, as all outgroup taxa chosen are lacking this feature and the state in *P. ovalis* is unknown. The absence of spermatophores is supported by the *absence of lophophoral organs* in the ground pattern of phoronids, which is necessary to build spermatophores (Zimmer 1964).

Although *P. ovalis* asexual reproduces by transverse fission and lateral budding, it is parsimonious to assume the *sexual reproduction* in the ground pattern of phoronids, since brachiopods, crinoids and chitons reproduce only sexually, and *P. pallida* is reported to reproduce sexually only (Silén 1952).

Except for the inarticulate brachiopods, *P. pallida* as well as the derived phoronids, all other phoronids exhibit some sort of *brood protection*, which therefore can be assumed for the ground pattern of Phoronida as well. Primarily, brood protection must have occurred in the tube of the adult, like in *P. ovalis*, because nidamental glands, the other location where brood protection in the Phoronida occurs, evolved later in the Phoronida.

A larva is present in all taxa, and should therefore belong to the stem species of Phoronida. As the initial development of the phoronid species is *lecitothrophic* (see this study), the planctotrophic actinotroch larva must have been evolved within the phoronids, and a larva resembling the slug-like *P. ovalis* larva can be assumed for the ground pattern of the phoronids. This larva has sense organs, however, an eversible sense organ like in the cyphonautes of bryozoans (Ryland 1970) is missing. The same is true for larval tentacles (this study) and adult tentacles being formed prior to metamorphosis (this study).

Since the nephridial duct becomes U-shaped during metamorphosis in phoronid species that have an actinotroch larva (Bartolomaeus 1989b), the straight nephridial duct in *P. ovalis* may indicate a different mode of metamorphosis, i.e. not by means of everting the metasomal tube and subsequently turning the hyposphere into a U-shape. Actually, a metasomal sac has never been recorded in *P. ovalis* (this study) Blood corpuscle masses also evolved later in the phoronid clade. Since brachiopods are either missing this feature, an *invaginated metasomal sack must be unique for the actinotrocha larva* and is not present in the larva in the ground pattern of the Phoronida.

The phoronid larvae possess *paired protonephridia* (Emig 1982, Bartolomaeus 1989a, this study). *Mesoderm originates from the border of the ecto- and endoderm* (Lüter 2000a, Freeman & Martindale 2002, this study). In early larval stages, there is *one unpaired coelomic* cavity or one single compact coelomic anlage (this study). This is plesiomorphic, as the brachiopods have one unpaired coelomic anlagen in the early larval stages as well (Lüter 1998, 2000a, Grobe, Lüter & Bartolomaeus in prep.); the state in bryzoans is unknown.

Evolution of characters within Phoronida

The evolution of characters within Phoronida turned out to be difficult to trace. Most of the morphological features are autapomorphic for the Phoronida, like for instance the spe-

cialized longitudinal muscles, the nephridial ducts, the size and shape of the lophophore. *Phoronopsis* species tend to cluster in a monophyletic group, as indicated by the bremer support values. Possible autapomorphies are the collar fold and the lophophoral arms' coiling in counterclockwise direction (Fig. 18).

Several characters argue for the basal position of *P. ovalis*, and the monophyletic origin of the P. hippocrepia-clade. The close relationship of the latter three species is hypothized also by Ikeda (1901), Marsden (1959) and Emig (1974a). The sister group relationship of *P. pallida* to the remaining phoronids is supported by two characters (Fig. 18). But there is no significant jackknife support for this phylogenetic relationship, likewise the monophyletic origin of *Phoronopsis* and the phylogenetic position of *P. muelleri* and *P. psammophila* receives no jackknife support (Fig. 16 A). The combined analysis approved the basal position of *P. ovalis*. Considering the analysis of molecular data alone, there is only little phylogenetic signal in the 18s *rRNA* dataset to resolve the phylogeny of the phoronids (Fig. 16 C).

The Phoroniformea hypothesis

The result of Cohen & Weydmann (2005) suggests a sister group relationship of the Phoronida with the inarticulate brachiopods. Using 18S rRNA data alone an unresolved bush consisting of phoronids, brachiopods and the crinoid is obtained, indicating the low resolution of the 18S rRNA dataset (this study). In order to explain the position of the Phoronida in the Brachiopoda shown by Cohen & Weydmann (2005) under the parsimonious aspect, the Phoronida should share more characters with the inarticulate craniids than with the brachiopods as a whole or the articulate brachiopods respectively. Brachiopods have a large number of characters, that are not shared with the phoronids and which are regarded as autapomorphic (see Nielsen, 2002).

In this study, a reduced dataset with a similar species sampling and a reduced character set did not prove the monophyletic origin of the inarticulate brachiopods and the Phoronida under parsimonious conditions. The costs for mapping the characters of this study on the tree obtained by Cohen & Weydmann (2005) are higher than those revealed when mapping them on the most parsimonious tree obtained in this study (Fig. 16 A), (308 vs. 289 character state changes). The additional changes to explain the tree from Cohen & Weydmann (2005) obtained under likelihood conditions are (1) the origin of the mesoderm (char. nr. 32): the phoronids changed from entodermal origin of mesodermal cells to origin of the mesodermal cells from the border of the ecto- and endoderm; (2) the number of rows per side in adult lophophore (char. nr. 52): the phoronids have only one row, whereas all

brachiopods have two. (3) the third additional change is the blood vascular system: brachiopods have an open vascular system, phoronids evolved with a closed blood vascular system. (4) the transformation from an organic shell/tube bearing brachiopod/phoronid ancestor to a chitinous tube and or mineralized shell involves much more transversions, than just incorporate some calcite into the external casting: brachiopods for instance, have a muscle system that attach the body to the external valves, phoronids do not attach their body to their external tube.

On the other hand, phoronids and inarticulate brachiopods share two characters, which indicate a sister group relationship between these two taxa. (1) the long ciliated tentacles of the planctonic larva form a postoral horseshoe near the apical organ, which becomes the adult tentacle after metamorphosis; at least in some taxa of phoronids and in the inarticulate brachiopods. (2) the metanephridia of both taxa have long ciliated funnels, which also serve as gonoducts (Nielsen 2002). The stem species of the phoronids may be wormlike, like today's phoronids, or may look similar to a brachiopod, as the brachiopod folding (Nielsen 1991; Cohen *et al.* 2003) suggests. The latter hypothesis requires further assumptions, as the brachiopod fold demands the animal to bend on the ventral side and secrete the valves from the dorsal surface, as in brachiopods. The metamorphosis of the phoronids brings the ventral side in contact with the surface, the dorsal side is shortened, and the secretion of the tube is done by the ventral surface (Nielsen 2002). Due to these striking differences, a common brachiopod fold is therefore rejected for both taxa.

Cohen & Weydmann (2005) only map morphological characters on their tree, and did not perform a morphological analysis. The results from this analysis shows that the morphological data are incompatible with the molecular data. The analysis of Cohen & Weydmann (2005) is well-founded, but the resolution of the 18S RNA data is not sufficient to resolve the phylogeny of Brachiopoda and Phoronida.

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