

Is the Aplacophora monophyletic? A cladistic point of view

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Abstract: The systematic position and monophyly (versus paraphyly) of the two aplacophoran taxa, Solenogastres (also called Neomeniomorpha or Ventroplicida) and Caudofoveata (or Chaetodermomorpha) has been a subject of long debate. Also the plesiomorphic versus apomorphic (paedomorphic) condition of several aplacophoran features has been argued for over a century. A cladistic analysis has been undertaken to address these questions or at least to identify the specific lack of knowledge and necessary studies. Outgroup comparison of character states is generally limited, because many relevant organ systems (*e. g.* buccal apparatus, mantle cavity, gonopercardial system, osphradia) do not exist in any possible molluscan outgroup; thus the polarity of these characters cannot be inferred *a priori* to the analysis. Based on current knowledge and available data, the arrangement {Solenogastres [Caudofoveata (Polyplacophora and Conchifera)]} is the most parsimonious one, and the Aplacophora form a basic, paraphyletic assemblage. Accordingly, several aplacophoran features can be reasonably regarded as plesiomorphic for Mollusca. The monophyly of Testaria (Polyplacophora and Conchifera) is very well supported by several characters, contradicting recent ideas about a monophyly of Aculifera (Polyplacophora and Aplacophora). In particular ontogenetic data are badly needed to improve the understanding of aplacophoran relationships and of the ancestral features of the Mollusca as a whole.

Key Words: Mollusca, Aplacophora, phylogeny, inapplicable characters

The origins and interrelationships of the Mollusca and its seven to eight extant primary clades ("classes") has been a matter of debate over a century. Detailed historical reviews have been provided by various authors (*e. g.* Ghiselin, 1988; Haszprunar, 1996a). This contribution focuses on the most recent discussions.

Based on morphological and molecular characters the systematic position of the phylum Mollusca is now fairly well settled among the Spiralia (taxa with spiral-quartet cleavage) or in more recent reviews (*e. g.* Adoutte *et al.*, 2000) among the "Lophotrochozoa" (taxa with ciliary trochi or a lophophore). The long-lasting debate between "turbellarian-like" versus "annelid-like" ancestors has been resolved in favour of a coelomate (*i. e.*, derived from 4d-blastomere, but not eucoelomate, *e. g.*, Salvini-Plawen and Bartolomaeus, 1995) molluscan condition and a non-segmented body plan - at least in the opinion of the present and most recent authors (*e. g.* Haszprunar, 1996a; Haszprunar and Schaefer, 1997b; Haszprunar and Wanninger, 2000; Table 1). Whereas molecular studies remain ambiguous, analyses of phenotypical characters suggested the Kamptozoa (Entoprocta) or the Sipuncula as the direct sister group of the Mollusca (Haszprunar, 1996a; Scheltema, 1993, 1996; but see Jenner and Schram, 1999).

Broad agreement exists on the monophyly of all conchiferan molluscan classes, Monoplacophora

(Tryblidia), Bivalvia, Scaphopoda, Gastropoda, and Cephalopoda. However, there is still considerable debate about the status and phylogenetic position of the aculiferan taxa, Caudofoveata (Chaetodermomorpha), Solenogastres (Neomeniomorpha), and Polyplacophora (Neoloricata). Two major points of view have been outlined recently (Fig. 1).

Scheltema (1988, 1993, 1996) and Ivanov (1996) consider the Aculifera a monophyletic taxon which is the sister group of the Conchifera. Within the Aculifera, Chaetodermomorpha and Neomeniomorpha constitute the monophyletic Aplacophora. Scheltema (1988, 1993, 1996) considered the latter taxa as partly progenetic (or paedomorphic) and thus derived. Contrary to that view Salvini-Plawen (1972, 1980, 1981, 1985, 1988, 1991; Salvini-Plawen and Steiner, 1996) regarded Aplacophora and Aculifera as paraphyletic assemblages. The recent cladistic analysis of the latter authors revealed a most parsimonious tree with a polytomy of Solenogastres, Caudofoveata, and Testaria (Polyplacophora and Conchifera). Both authors consider many conditions of the aplacophoran taxa as plesiomorphic for Mollusca rather than derived through paedomorphosis.

Recent progress has been made concerning certain relevant molluscan characters as well as concerning cladistic theory with respect to inapplicable characters (see

Salvini-Plawen & Steiner (1996)

Scheltema (1996), Ivanov (1996)

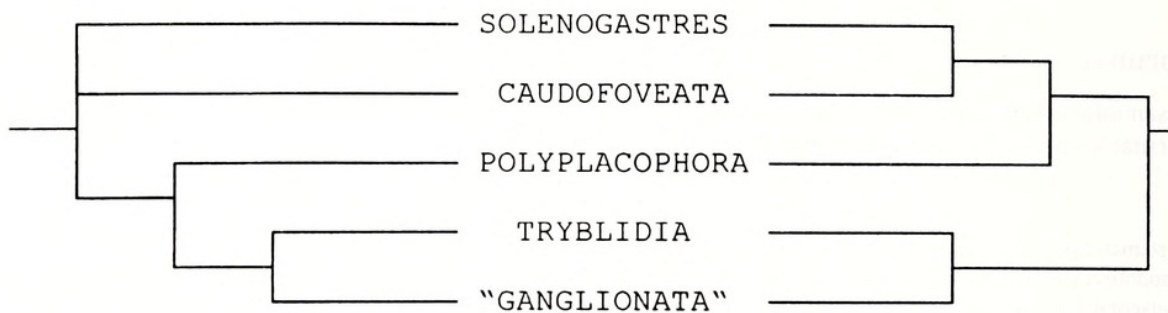


Fig. 1. Current phylogenetic hypothesis on aplacophoran and aculiferan Mollusca. Left: Preferred tree by Salvini-Plawen and Steiner (1996; their most parsimonious tree shows Solenogastres as the first offshoot). The proposed tree by Waller (1998) is similar, but regards Solenogastres and Caudofoveata (Aplacophora) as monophyletic. Right: Tree based on Scheltema (1996) and Ivanov (1996).

below). Accordingly the present cladistic analysis focuses on (1) the still poor knowledge of the aplacophoran taxa and (2) the problem of correct coding of inapplicable characters in molluscan phylogeny.

METHODOLOGY

Outgroups. All current taxa for consideration as molluscan sister-groups have been coded as outgroups: Kamptozoa (= Entoprocta; cf. Bartolomaeus, 1993; Haszprunar, 1996a), Sipuncula (cf. Scheltema, 1993, 1996 in reviving Gerould, 1907), and Annelida (e. g. Götting, 1980a, b).

Ingroups. All traditional, extant molluscan "classes" were taken as ingroups, with both Caudofoveata and Solenogastres separately coded. Although monophyly has been discussed in Bivalvia (e. g. Gustafson, 1987; Adamkewicz *et al.*, 1997; Steiner and Müller, 1996; Giribet

and Carranza, 1999; Steiner, 1999) or Gastropoda (e. g. Ponder and Lindberg, 1997), they are regarded here as monophyletic in the strict sense.

Character selection and weighting. Character selection has been identified as the heaviest way of character weighting (Haszprunar, 1998). Selection of characters mostly follows the recent papers by Salvini-Plawen and Steiner (1996) and Waller (1998), although there are some modifications of the coding, which will be discussed. Reasons are given for those omitted characters that have been discussed with respect to the Aplacophora-problem. All selected characters were weighted with equal weight, because several attempts with unequal weighting did not result in a different tree topology. In general the most plesiomorphic state of a class was taken, but if this is ambiguous, the multistate option has been applied.

Proposed aplacophoran synapomorphies. Apart from the parsimony analysis the synapomorphies proposed by authors in favor of a monophyly of the Aplacophora

Table 1. Proposed synapomorphies of the Aplacophora and their distribution within Mollusca and outgroups. The table shows that none of the shared aplacophoran characters can be reasonably considered as apomorphic *a priori* to a cladistic analysis.

Character	APLACOPHORA	TESTARIA (POLYPLACOPHORA & CONCHIFERA)	KAMPTOZOA, SIPUNCULA, ANNELIDA	CONCLUSION FOR MOLLUSCA
Vermiform body	present (1)	only aberrant species (0->1)	present (1)	plesiomorphic
Body wall musculature	present (1)	absent (0)	present (1)	plesiomorphic
Intercrossing d-v muscles	many (0)	few (1)	lacking (?)	equivocal
Specific circumoral field	present (1)	present (1)	present (1)	uninformative
Foot	reduced (1)	present (0)	lacking (?)	equivocal
Spiculoblasts	unicellular (1)	uni- and multicellular (0)	lacking (?)	equivocal
Shell-field	lacking (0)	present (1)	lacking (0)	plesiomorphic
Coelomoducts	one pair (1)	several or one pair (0/1)	many, one or no pair (0/1)	uninformative
Gametes through pericardium	present (1)	absent (0)	no pericardium (?)	equivocal
Mantle cavity	posterior (1)	circumpedal (0)	no mantle cavity (?)	equivocal
Osphradium	extrapallial (1)	intrapallial (0)	no osphradium (?)	equivocal
Cerebral ganglia	present (1)	present or absent (0/1)	present (1)	uninformative
Radula	basically distichous (1)	basically many teeth (0)	no radula (?)	equivocal

were specifically listed and directly evaluated by means of outgroup comparison (Table 1). Doing this the "red-blue-tail" problem becomes crucial (see below).

Red-blue-tail problem. Concerning the coding of certain characters, the so-called "red-blue-tail" problem, *i. e.*, the problem of coding of inapplicable characters (Maddison, 1993; Nelson and Ladiges, 1993; Wilkinson, 1995; Hawkins *et al.*, 1997, Kitching *et al.*, 1998, Lee, 1999) turned out to be of crucial importance, in particular with respect to the outgroups and thus directly associated with (so far nearly exclusively done) *a priori* estimation of the polarity of characters within the Mollusca.

The problem concerns many significant characters in molluscan evolution, namely the type of body cuticle (#2), presence of the periostracal groove (#6), type of mantle cavity (#9), number of ctenidia (#11), number of intercrossing dorso-ventral muscles (#15), details of the pericardioducts (#25, #26) and gamete release (#34), various aspects of the radular apparatus (#38, #39, #40), pedal ganglia (#49), and position of the osphradium (#56). The specific point concerning the Aplacophora-question is outlined in the following with the example of the various aspects of the radular apparatus (#38, #39, #40).

There is large agreement that the two aplacophoran taxa share a similar radular type, regardless whether it is regarded as a strictly distichous or a monoserial dicuspid radula (see Salvini-Plawen, 1988:355-359 for detailed discussion). In contrast, Polyplacophora and the conchiferan taxa share a polystichous rasping tongue for grazing with several to many teeth per row. None of the outgroups possess a radula, thus it would be indeed nonsense to ask which type of radula would have been present, if there would be a radula at all. Ontogenetic patterns of ingroups also do not solve the problem: there is an early stage in the ontogeny of the chiton radula (Sirenko and Minichev, 1975; Salvini-Plawen, 1988: 365) resembling the aplacophoran type. However, one could interpret this similarity either as a recapitulation of the aplacophoran type in the chiton ontogenesis, or assume with equal *a priori* likelihood a paedomorphic event for the aplacophoran taxa from a chiton-like predecessor.

Thus, in this analysis it remains open which type, the dicuspid/distichous or the rasping type, is the plesiomorphic condition for Mollusca. If the rasping type is plesiomorphic, the dicuspid / distichous one would be a synapomorphy of Aplacophora; in the opposite case the rasping tongue would serve as a synapomorphy for Testaria (Polyplacophora and Conchifera). In the given situation it is impossible to infer character polarity *a priori* to the phylogenetic reconstruction. Nevertheless, the character is not useless for the Aplacophora-problem, because the given distribution makes many possible arrangements of the four-taxa problem such as [(Caudofoveata and Polyplacophora)

(Solenogastres and Conchifera)] being less parsimonious than others such as {Caudofoveata [Solenogastres (Polyplacophora and Conchifera)]} or {Conchifera [Polyplacophora [Caudofoveata and Solenogastres)]}. Moreover, if either Aplacophora or Testaria turn out to be paraphyletic based on other characters, reasonable inference of character polarity is possible *a posteriori* of tree calculation.

The various authors recommend different ways out of the problem of inapplicable characters. One possibility is to calculate trees with all possible character states in all cases of inapplicable characters. In the present analysis this would result in trillions of calculations (15 characters, three outgroups, *i. e.*, $2^{15 \times 3}$ tree calculations) which were far beyond the computer capacity available. To omit such characters from the analysis would strongly influence the most parsimonious tree topology. Herein, inapplicable states are scored with an "x," which is treated by PAUP as equal to "?" (unknown) (cf. Strong and Lipscomb, 1999).

Software and options. The inference of the most parsimonious tree followed the standard procedure: PAUP 4.0 (Beta-Version; Swofford and Begle, 1999) was applied as the parsimony software, input files were done in the NEXUS format. The ACCTRAN option was selected for tree calculation. Tree calculation was followed by a thorough *a posteriori* analysis of characters (see Discussion Part).

CHARACTER ANALYSIS

A summary of character coding and the matrix are presented in Table 2. Taxa are abbreviated as follows: Ann - Annelida; Biv - Bivalvia, Cau - Caudofoveata, Cep - Cephalopoda, Gas - Gastropoda, Kam - Kamptozoa (= Entoprocta), Pol - Polyplacophora, Sca - Scaphopoda, Sip - Sipuncula, Sol - Solenogastres, Try - Tryblidia. Taxon/p means "taxon partim."

#1. Cuticle: (0) = absent: Try, Biv, Sca, Gas, Cep; (1) = present: Ann, Sip, Kam, Sol, Cau, Pol.

The condition of the unspecialized dorsal epidermis of the adult is scored.

#2. Type of cuticle: (0) = chitinous: Kam, Sol, Cau, Pol; (1) = collagenous: Ann, Sip; (x) = cuticle absent: Try, Biv, Sca, Gas, Cep.

Coding of this character has been outlined by Haszprunar (1996a).

#3. Aragonitic scales or spicules: (0) = absent: Ann, Sip, Kam, Try, Biv, Sca, Gas, Cep; (1) = present: Sol, Cau, Pol.

All three aculiferan taxa have solitary scale- or spicule-building cells; in addition, the Polyplacophora also have multicellular spiculoblasts.

#4. Shell: (0) = absent: Ann, Sip, Kam, Sol, Cau;

Table 2. Character coding and data matrix.

#1: Cuticle [0 = absent, 1 = present]	#31: Number of gonads [0 = single "right" (pretorsional left), 1 = single right, 2 = one pair, 3 = two pairs, 4 = more than two pairs]
#2: Cuticle type [0 = chitinous, 1 = collagenous, x = cuticle absent]	#32: Position of gonad [0 = dorsal to gut; 1 = ventral to gut; ? = not clear]
#3: Aculiferan condition [0 = absent, 1 = present]	#33: Urinogenital [0 = absent, 1 = present]
#4: Shell [0 = absent, 1 = shell plates, 2 = shell by shell gland]	#34: Gamete release through pericardium [0 = absent, 1 = present]
#5: Periostracum [0 = absent, 1 = present]	#35: Molluscan Cross [0 = absent, 1 = present]
#6: Periostracal groove [0 = absent, 1 = present, x = no periostracum]	#36: Jaws [0 = absent, 1 = present]
#7: Mantle papillae [0 = absent, 1 = present]	#37: Radula [0 = absent, 1 = present]
#8: Mantle cavity [0 = absent, 1 = present]	#38: Radular membrane [0 = absent, 1 = present, x = radula lacking]
#9: Position of mantle cavity [0 = circumpedal, 1 = posterior, x = no mantle cavity]	#39: Rasping tongue [0 = absent, 1 = present, x = radula lacking]
#10: Ctenidia [0 = absent, 1 = present]	#40: Buccal cartilage [0 = absent, 1 = present, x = no radula]
#11: Number of ctenidia [0 = 1 pair, 1 = 2, 2 = 3 to 6, 3 = > 6, x = no ctenidia]	#41: Oesophageal pouches [0 = absent, 1 = present]
#12: Body wall musculature [0 = ring/diagonal/longitudinal, 1 = otherwise]	#42: Highly glandular midgut [0 = no, 1 = yes]
#13: Longitudinal body muscles [0 = smooth, 1 = striated, x = no longitudinal muscles]	#43: Subdivided midgut for sorting and uptake of food [0 = absent, 1 = present]
#14: Intercrossing dorsoventral muscles (IDVM) [0 = absent, 1 = present]	#44: Bilobed midgut gland [0 = absent, 1 = present, x = no midgut gland]
#15: Number of IDVMs [0 = many, 1 = eight, 2 = less than eight, 3 = less than three, x = no IDVM] ORDERED	#45: Crystalline style [0 = absent, 1 = present]
#16: Hydrostatic muscle system [0 = absent, 1 = present]	#46: Intestinal loops [0 = absent, 1 = longitudinal, 2 = unidirectional, 3 = bidirectional]
#17: Specific head retractor: [0 = absent, 1 = present]	#47: Position of anus [0 = opposite of oral opening, 1 = near mouth opening at dorsal side, 2 = near dorsal opening at ventral side]
#18: Pedal digging by hemolymph pressure [0 = absent, 1 = present]	#48: Tetraneury [0 = absent, 1 = present]
#19: Pedal gland [0 = absent, 1 = present]	#49: Precerebral ganglia [0 = absent, 1 = present]
#20: Pedal cirri [0 = absent, 1 = present]	#50: Pedal ganglia [0 = absent, 1 = present, x = no pedal nervous system]
#21: Coelomatic cavity (histological sense) [0 = absent, 1 = present]	#51: Visceral loop and IDVM [0 = between, 1 = outside, 2 = inside, x = no IDVM]
#22: Eucoelomate condition [0 = absent, 1 = present]	#52: Visceral commissure [0 = suprarectal, 1 = subrectal, x = homology unclear]
#23: Heart with pericardium [0 = absent, 1 = present]	#53: Innervation of the shell(-plate) margin. [0 = also visceral, 1 = only cerebropleural, x = no shell-plate]
#24: Circulatory system [0 = pseudovessels, 1 = endothelial, 2 = sinusial]	#54: Cerebral eyes [0 = absent, 1 = present]
#25: Pericardiodes [0 = absent, 1 = present, x = no pericardium]	#55: Statocysts [0 = absent, 1 = present]
#26: Formation of Coelomoduct [0 = ingrowth, 1 = outgrowth, x = no coelomoduct]	#56: Osphradia [0 = absent, 1 = present]
#27: Number of Coelomoducts [0 = one pair, 1 = two pairs, 2 = more than two pairs, x = no coelomoduct]	#57: Position of osphradia [0 = pallial, 1 = extrapallial, x = no osphradium]
#28: Podocytes [0 = absent, 1 = present]	#58: Subradular organ [0 = absent, 1 = present]
#29: Protonephridia [0 = absent, 1 = present]	
#30: Rhogocytes [0 = absent, 1 = present]	

(1) = shell plates: Pol; (2) = shell by shell gland: Try, Biv, Sca, Gas, Cep.

The homology between the polyplacophoran shell-plates and the conchiferan shell is doubtful (*e. g.* Haas, 1981), therefore both stages are coded.

#5. Periostracum: (0) = absent: Ann, Sip, Kam, Sol, Cau; (1) = present: Pol, Try, Biv, Sca, Gas, Cep.

Periostracum is meant here in a very general way, namely as a purely organic layer covering a shell or shell plate.

#6. Periostracal groove: (0) = absent: Pol; (1) = present: Try, Biv, Sca, Gas, Cep; (x) = no periostracum: Ann, Sip, Kam, Sol, Cau.

Recent fine-structural investigations (Schaefer and Haszprunar, 1997b) revealed significant differences of the organization of the mantle margin between Neopilinidae and other conchiferans. Nevertheless the periostracal groove itself is regarded as homologous throughout the

Conchifera.

#7. Mantle papillae: (0) = absent: Ann, Sip, Kam, Try, Biv, Sca, Gas/p, Cep; (1) = present: Sol, Cau, Pol, Gas/p.

Reindl and Haszprunar (1996a,b; Reindl *et al.*, 1995, 1997) investigated the fine-structure and immunocytochemistry of shell pore contents (so-called papillae and caeca) of various molluscan groups and compared them among each other and with the caeca of articulate Brachiopoda. There is a striking similarity between polyplacophoran aesthetes and brachiopod caeca, whereas the bivalve caeca show entirely different structure and mode of formation.

The available data (Hoffmann 1949, Fischer *et al.* 1980, 1988; Scheltema *et al.* 1994) and personal, unpublished fine-structural (TEM) studies on the mantle papillae of Solenogastres and Caudofoveata cannot exclude a possible homology between these papillae and the polypla-

Table 2. Continued

MATRIX																																								
	1								2								3								4								5							
character	12345	67890	1	23	4	5	6	7	8	90	12345	6	7	8	9	0	1	2	3	4	5	67890	1234	5	678	9	0	12345	678											
Annelida	11000	x00x0	x	01	0	x	0	0	0	00	1100x	0	2	1{0,1}	0	4	?	0	x	0	10xxx	000x	0	000	0	0	xxx10	0x0												
Sipuncula	11000	x00x0	x	01	0	x	0	x	0	00	1100x	0	0	1	0	0	2	?	0	x	1	00xxx	000x	0	110	0	0	xxx10	0x0											
Kamptozoa	10000	x00x0	x	1x	0	x	0	x	0	01	0001x	x	x	0	1	0	2	0	1	x	0	00xxx	010x	0	01?	0	x	xxx10	0x0											
Solenogastres	10100	x1110	x	00	1	0	0	0	0	11	10111	?	0	1	?	1	2	0	0{0,1}	1	01000	010x	0	001{0,1}	0	00x00	110													
Caudofoveata	10100	x1111	0	00{0,1}	0	0	0	0	0	00	10111	?	0	1	?	1	2	0	0	1	?	01100	0110{0,1}	001	1	0	00x00	110												
Polyplacophora	10111	01101	3	1x	1	1	0	0	0	10	10111	1	0	1	1	1	2	0	1	0	1	01111	1111	0	301	0	0	10000	101											
Tryblidia	0x021	10101	2	1x	1	1	0	0	0	00	10110	?	2	1	?	1{2,3}	1	0	0	?	11111	1111	1	201	0	0	11001	0x1												
Bivalvia	0x021	10101	0	1x	1	2	0	0	1	00	10111	1	0	1	1	1	2	0	0	0	1	00xxx	1111	1	301	0	1	11001	100											
Scaphopoda	0x021	10100	x	1x	1	3{0,1}	0{0,1}	00	10011	?	0	1	1	1	1	0	0	0	1	11111	1111	0	321	0	1	11001	0x1													
Gastropoda	0x021	10111	0	1x	1	3	1	1	0	10	10111	1	0	1	1	1	0{0,1}	0	0	1	11111	1111{0,1}	321	0	0	21111	101													
Cephalopoda	0x021	10111{0,1}	1x	?	3	1	1	0	00	10121	1{0,1}	1	0	1{1~3}	0	1	0	0	11111	0111	0	321	0	1	21111	101														

cophoran macroaesthetes, although there are no distinct similarities as in the case of the Brachiopoda. However, if homology is assumed, then the fissurellid (but not bivalvian) caeca need to be included, accordingly the Gastropoda are scored by {0,1}.

#8. Mantle cavity: (0) = absent: Ann, Sip, Kam; (1) = present: Sol, Cau, Pol, Try, Biv, Sca, Gas, Cep.

The reduction and loss of the mantle cavity in various gastropod and certain bivalve taxa is considered as a secondary matter of multiple convergence, therefore both are coded (1).

#9. Position of mantle cavity: (0) = circumpedal: Pol, Try, Biv, Sca; (1) = posterior: Sol, Cau, Gas, Cep; (x) = no mantle cavity: Ann, Sip, Kam.

Hoffmann (1949) and Salvini-Plawen (*e. g.* 1981, 1991) considered the mantle cavity of the Solenogastres as reduced and narrowed, yet of the circumpedal type found in Polyplacophora, Tryblidia, Bivalvia, and Scaphopoda. In all the latter groups the visceral nerve cord surrounds the dorsoventral (shell-) muscle bundles and directly innervates the mantle epithelium and the various organs. In contrast, the visceral cords of Solenogastres run between the two pairs of dorsoventral muscles (see Haszprunar, 1989), and innervation of the peripodal groove has never been shown. Thus, there is no reason to homologize the peripodal groove between the foot-sole and the cuticularized mantle with a mantle cavity. The mantle cavity of Solenogastres is therefore coded as "posterior" (1).

The neural condition of the Caudofoveata is less clear because of the reduction of the dorsoventral muscles.

However, there is no doubt that the caudofoveate mantle cavity is purely posterior.

The anlage of the gastropod mantle cavity is situated posteriorly, therefore gastropods are scored by (1).

Because the character is inapplicable in all outgroups the coding of the circumpedal and posterior stage with (0) or (1) does not imply any decision concerning polarity.

#10. Ctenidia: (0) = absent: Ann, Sip, Kam, Sol, Sca; (1) = present: Cau, Pol, Try, Biv, Gas, Cep.

In recent times Morton (1988), Lindberg (1989), and also Ponder and Lindberg (1997: 112-113) expressed doubts about the homology of the ctenidia between the molluscan classes. Whereas there is high probability that the respiratory surfaces of the ctenidium evolved several times in molluscan evolution, the common ancestry of this originally ventilatory organ (*i. e.*, causing water current; see Haszprunar, 1992) is well supported by shared position, structure, and innervation (see Haszprunar, 1987a: fig. 5).

All authors agree that lack of ctenidia is a secondary phenomenon in the Gastropoda, therefore they are coded by (1).

#11. Number of ctenidial pairs: (0) = 1 pair: Cau, Biv, Gas, Cep/p; (1) = 2 pairs: Cep/p; (2) = 3 to 6 pairs: Try; (3) = more than 6 pairs: Pol; (x) = no ctenidia: Ann, Sip, Kam, Sca.

Recent, unpublished observation on *Micropilina minuta* revealed the presence of four pairs of ctenidia, so that the Tryblidia exhibit a continuous range from 3 to 6 ctenidial pairs.

As outlined by Yonge (1939) the condition of the mantle cavity and ctenidial arrangement differ significantly between the Lepidopleurida and the remaining Polyplacophora (Chitonida). Whereas in the former group the ctenidial number increases with size towards the anal opening, in the Chitonida the ctenidia multiply forwards when becoming larger. Accordingly the multiplication of ctenidia is an independent matter in Lepidopleurida and Chitonida and is not used as a synapomorphy of the Polyplacophora. Because of these circumstances all character states are coded as unordered.

#12. Body wall musculature: (0) = circular/diagonal/longitudinal: Ann, Sip, Sol, Cau; 1 = otherwise: Kam, Pol, Try, Biv, Sca, Gas, Cep.

This character replaces the more obscure "worm-like shape" by an observable character, *i. e.*, the presence of a distinct body wall musculature, which is composed of outer circular, intermediate diagonal, and inner longitudinal muscle fibers. This condition is typical for Sipuncula and Polychaeta; among the Mollusca it exists solely in the aplacophoran taxa. Similar conditions in various groups of opisthobranch or pulmonate slugs are without doubt secondary conditions, because all earlier (5 to 10) gastropod clades lack this condition (Haszprunar, 1988; Ponder and Lindberg, 1997).

#13. Structure of the longitudinal muscles of body wall: (0) = smooth: Sol, Cau; (1) = striated: Ann, Sip; (x) = no longitudinal muscles: Kam, Pol, Try, Biv, Sca, Gas, Cep.

Annelids and sipunculans are known to have obliquely striated longitudinal muscles, whereas those in the aplacophoran taxa are smooth. For all other taxa the character is inapplicable.

Contrary to Salvini-Plawen (1981, 1991) I regard the homology of the longitudinal enrolling muscles in Polyplacophora and Solenogastres as doubtful. The enrolling muscles of Solenogastres and Caudofoveata are a specialized, latero-ventral part of the longitudinal layer of the body wall musculature. Recent studies on the myogenesis of the chiton *Mopalia muscosa* revealed that the enrolling muscle is in principle a ring-system independent of the original body wall muscle grid, and that the enrolling function is provided by the transverse stiffness of the shell-plates (Haszprunar and Wanninger, 2000). Purely pedal position and innervation also exclude homology of both laterally situated and innervated enrolling muscles with the suctorial muscle of extant Monoplacophora.

#14. Intercrossing of the inner dorsoventral musculature (IDVM): (0) = absent: Ann, Sip, Kam; (1) = present: Sol, Cau, Pol, Try, Biv, Sca, Gas, Cep.

In contrast to other "worms" the Mollusca are characterized by a ventral intercrossing of the inner muscle bundles of their dorsoventral (shell-) musculature. Because

of the lack of a pedal sole this character is missing in most Caudofoveata, but the genus *Scutopus* shows the basic condition (Salvini-Plawen, 1972: fig. 16), therefore coding is {0,1}. Contrary to the statement by Voltzow (1988), Patellogastropoda also show intercrossing dorsoventral muscles (pers. obs.). The conditions in the Cephalopoda are unclear (?) because of the major reconstruction of the foot.

#15. Number of dorsoventral muscle pairs: (0) = many: Sol, Cau; (1) = eight: Pol, Try; (2) = less than eight: Biv; (3) = less than three: Sca, Gas, Cep; (x) = no IDVM: Ann, Sip, Kam.

There is a general tendency to reduce the number of dorso-ventral muscles in the Mollusca (Haszprunar and Wanninger, 2000), particularly exemplified in the Bivalvia, in which extant Protobranchia and Pteriomorpha have seven to three pairs, and Heterodonta usually three. Scaphopoda show one or two pairs (Steiner, 1992). The anterior pair of the cephalopod "depressores infundibuli" is the head retractor (see below), so that Cephalopoda have a single pair. Recent ontogenetic data on the myogenesis of Gastropoda confirmed the presence of a single pair of shell muscles even in cases of secondary splittings such as in *Patella* (Wanninger *et al.*, 1999).

Because this is a continuous series of reductions, it makes sense to code this multistate character as "ordered." Indeed, this option is crucial for the resolution of the conchiferan taxa (see discussion).

#16. Hydrostatic muscular system: (0) = absent: Ann, Sip, Kam, Sol, Cau, Pol, Try, Biv, Sac/p; (1) = present: Sca/p, Gas, Cep.

As outlined by Haszprunar (1988: 405) cephalopods and gastropods share a "hydrostatic muscular system" meaning that extension of body parts or tentacles is caused by muscle contraction analogous to the vertebrate tongue rather than by hemolymphatic pressure. According to Shimek and Steiner (1997) the same is true for the foot of dentaliidan scaphopods explaining the ability of rapid extension and burrowing of the latter organ.

#17. Specific head retractor: (0) = absent: Ann, Sol, Cau, Pol, Try, Biv, Sca; (1) = present: Gas, Cep; (x) = no head: Sip, Kam.

Gastropoda and Cephalopoda share a free head, which is separately retractable by a specific head retractor. Limpets in particular show often a distinct insertion scar of this head retractor, in the Cephalopoda these are the anterior pair of the "depressores infundibuli." Contrary to the statement that also Scaphopoda have a free head (*e. g.* Waller, 1998) the latter have a free buccal cone alone, whereas the remaining head (cerebral and buccal mass) is fixed (Shimek and Steiner, 1997).

#18. Pedal digging by hemolymph pressure: (0) = absent: Ann, Sip, Kam, Sol, Cau, Pol, Try, Sca/p, Gas, Cep; (1) = present: Biv, Sca/p.

Bivalves and gadilidan Scaphopoda (Shimek and Steiner, 1997) use their foot for digging by means of hemolymph pressure in a soft sediment. Caudofoveata show a similar feature but use the cerebrally innervated head-region for digging as secondarily achieved by *e. g.* the naticid caenogastropods (head and foot) or bullomorph opisthobranchs. To the contrary many bivalve taxa secondarily settle on hard substrates by means of a byssus.

#19. Pedal gland: (0) = absent: Ann, Sip, Kam, Cau, Biv, Sca, Cep; (1) = present: Sol, Pol, Gas.

A true pedal gland is herein defined as a subepithelial gland at or near the anterior margin of the foot sole. Accordingly the "pedal glands" of Tryblidia and the "funnel gland" of coleoid cephalopods (*Nautilus* lacks a funnel gland) do not fit this definition, since both consist of purely epithelial mucous cells. Polyplacophora are scored by (1), since a true pedal gland occurs in early juveniles.

The so-called "lip gland" of the sipunculid pelagospaera larva is a cerebrally innervated structure (Rice, 1993) and thus is not homologous (Scheltema, 1993) to the pedally innervated molluscan gland (Gerould, 1907).

#20. Pedal cirri: (0) = absent: Ann, Sip, Cau, Pol, Try, Biv, Sca, Gas, Cep; (1) = present: Kam, Sol.

Haszprunar (1986; see also Scheltema *et al.* 1994) described the ultrastructure of pedal cirri in the "pedal pit" of certain Solenogastres. Very similar structures occur at the anterior margin of the gliding sole of kamptozoan larvae (Nielsen, 1971; Haszprunar *et al.*, 1995), although fine-structural studies are still lacking.

#21. Coelomatic cavities: (0) = absent: Kam; (1) = present: Ann, Sip, Sol, Cau, Pol, Try, Biv, Sca, Gas, Cep.

There is no doubt that molluscs are coelomate in the histological and embryological sense, *i. e.*, there are mesodermal epithelial cavities, namely the gonopericardial system, out of the 4d-blastomere.

#22. Eucoelomate condition: (0) = absent: Kam, Sol, Cau, Pol, Try, Biv, Sca, Gas, Cep; (1) = present: Ann, Sip.

Bartolomaeus (1993, 1994, Salvini-Plawen and Bartolomaeus, 1995, Haszprunar, 1996a, b) defined the eucoelomatic condition (#22) by the checkable feature that the inner wall of the coelomic cavity forms the epithelio-muscular layer of the gut. This condition is not present in any mollusc, but is (among many other phyla) found in Sipuncula and Annelida.

#23. Heart in pericardium: (0) = absent: Ann, Sip, Kam, Sca; (1) = present: Sol, Cau, Pol, Try, Biv, Gas, Cep.

The specific structures of the molluscan heart are unique and constitute a synapomorphy for the phylum. One known tryblidian genus (*Micropilina*), the Scaphopoda, and certain opisthobranchs (*e. g.* *Alderia modesta*, *Rhodope* spp.) have lost the heart secondarily. Scaphopoda are unique in retaining at least the pericardial cavity and its

function concerning ultrafiltration (Reynolds, 1990).

#24. Circulatory system: (0) = pseudovessels: Ann, Sip; (1) = mainly sinusal: Kam, Sol, Cau, Pol, Try, Biv, Sca, Gas; (2) = mainly endothelial: Cep.

As outlined by Bartolomaeus (1993) and Haszprunar (1996a), Kamptozoa and Mollusca share a circulatory system of sinuses. Pseudovessels, *i. e.*, a lining by outwards orientated epithelia, are found in most eucoelomates (here Sipuncula and Annelida), whereas true, endothelial vessels occur in certain stylommatophorans (capillaries; *cf.* Luchtel *et al.* 1997) and cephalopods (all except capillaries, *cf.* Budelmann *et al.*, 1997).

#25. Pericardioduct: (0) = absent: Try; (1) = present: Sol, Cau, Pol, Biv, Sca, Gas, Cep; (x) = no pericardium: Ann, Sip, Kam.

With the notable exception of Tryblidia (Haszprunar and Schaefer, 1997a; Schaefer and Haszprunar, 1997a), all molluscs that possess a pericardial cavity also have a pericardioduct releasing the modified primary ultrafiltration product into the mantle cavity. Because a true pericardium is lacking in all outgroups, they are scored by (x).

#26. Formation of coelomoducts: (0) = ingrowth: Ann, Sip; (1) = outgrowth: Pol, Biv, Gas, Cep; (x) = no coelomoduct: Kam; (?) = unknown: Sol, Cau, Try, Sca.

As outlined in detail by Bartolomaeus (1993, 1994) and Salvini-Plawen and Bartolomaeus (1995) the nephridial ducts in molluscs (Polyplacophora, Bivalvia, Gastropoda, and Cephalopoda; no data on the remaining classes) are formed by outgrowth of the coelomic cavity, whereas the (gono-)nephridial ducts in eucoelomates are formed by epidermal ingrowth.

According to Baba (1938), in the solenogastre *Epimenia* "there arise on the neck of proctodaeum a pair of short diverticula which may develop into gonoducts [*i. e.*, pericardial = urinogenital ducts]." However, the proctodaeum itself is an outgrowth of the endodermal mass and not an epidermal infolding. I still code the solenogastre condition as unknown.

#27. Number of coelomoducts: (0) = one: Sip, Sol, Cau, Biv, Sca, Cep/p; (1) = two: Cep/p; (2) = more than two: Ann, Try; (x) = no coelomoduct: Kam.

Among the Mollusca only *Nautilus* shows two pairs of coelomoducts. If (as is done here) the excretory organs are also considered as coelomic cavities (see above), the extant Tryblidia are characterized by several (three to seven) coelomoducts.

#28. Podocytes: (0) = absent: Ann/p, Kam; (1) = present: Ann/p, Sip, Sol, Cau, Pol, Try, Biv, Sca, Gas, Cep.

Podocytes have been described in all molluscan classes. Adults of certain polychaete taxa have solenocytes instead of podocytes (*e. g.* the recent review by Bartolomaeus, 1999).

#29. Protonephridia: (0) = absent: Sip; Cep; (1) =

present: Ann, Kam, Pol, Biv, Sca, Gas; (?) = unknown: Sol, Cau, Try.

Based on the discovery of protonephridial cyrtocytes in the larva of a chiton, Bartolomaeus (1989) postulated larval protonephridia as a character of the molluscan ground pattern. Recent personal investigations on larvae of *Chiton olivaceus* confirmed the presence of prominent protonephridia also for that species. Moreover, the recent discovery of protonephridia in larvae of the primitive limpet *Patella caerulea* (Haszprunar and Ruthensteiner, 2000) and in the larva of the scaphopod *Antalis vulgatum* (Haszprunar *et al.*, 2000), close former significant gaps of occurrence. However, fine-structural data on aplacophoran larvae are badly needed to determine whether protonephridia are also present in Solenogastres and Caudofoveata.

#30. Rhogocytes (pore cells): (0) = absent: Ann, Sip, Kam; (1) = present: Sol, Cau, Pol, Try, Biv, Sca, Gas, Cep.

Haszprunar (1996a,b) has outlined in detail the significance of the diagnostic molluscan rhogocyte (often called pore-cell) for general nephridial evolution. In addition, the presence of rhogocytes has been confirmed for both aplacophoran taxa (pers. obs.) and scaphopods (G. Steiner, pers. comm.).

#31. Number of Gonads: (0) = single "right" (pretorsional left): Gas; (1) = single right: Sca, Cep/p; (2) = one pair: Sip, Kam, Sol, Cau, Pol, Try/p, Biv, Cep/p; (3) = two pairs: Try/p, Cep/p; (4) = more than two pairs: Ann.

The majority of molluscan classes show a single pair of gonads, but there is gonadal asymmetry in Cephalopoda in part (left side), Scaphopoda in general (right side), and Gastropoda in general (posttorsional right = pretorsional left side) show gonadal asymmetry. *Nautilus* and Neopilinidae (*Micropilina arntzi* has a single pair of gonads: Haszprunar and Schaefer, 1997b) have multiple gonads.

#32. Position of Gonad: (0) = dorsal of gut: Kam, Sol, Cau, Pol, Biv, Sca, Gas/p, Cep; (1) = ventral of gut: Try, Gas/p; (?) = equivocal: Ann, Sip.

Both aplacophoran taxa have dorsal gonads. According to Ponder and Lindberg (1997: 128) "the gonad lies dorsally in polyplacophorans, scaphopods, bivalves, cephalopods, and in all gastropods except patellogastropods, in which it is ventral as in monoplacophorans." Sipuncula and Annelida are equivocal in this character, Kamptozoa clearly have a dorsal gonad.

#33. True gonoducts: (0) = absent: Ann, Sip, Sol, Cau, Try, Biv, Sca, Gas; (1) = present: Kam, Pol, Cep.

Among molluscs true gonoducts are restricted to Polyplacophora and Cephalopoda, although this condition also occurs secondarily in the Bivalvia (*e. g.* Mackie, 1984) and Gastropoda (*e. g.* Haszprunar, 1988; Ponder and Lindberg, 1997). In Solenogastres only the genus

Phyllomenia possesses true gonoducts (see below).

#34. Release of gametes through the pericardium: (0) = absent: Sol/p, Pol, Try, Biv, Sca, Gas, Cep; (1) = present: Sol/p, Cau; (x) = no pericardium: Ann, Sip, Kam.

Both Salvini-Plawen (1972, 1981, 1985, but see 1991:17) and Scheltema (1996) agree in regarding the passage of gametes through the pericardium as derived. However, whereas Scheltema regards this character as a synapomorphy of Aplacophora, Salvini-Plawen argued in favour of a convergent evolution of this character because of (secondary) elongation and lateral enrolling of the body. The latter view is based on the exceptional condition of the solenogastre genus *Phyllomenia*, in which true gonoducts do exist as well as true pericardioducts (Salvini-Plawen, 1970).

As outlined in the general character analysis, the lack of a heart in all potential outgroups hinders the direct application of the outgroup-criterion for evaluating the polarity of this character. Concerning ingroup comparison and patterning there are three *a priori* possibilities: (1) The conditions in *Phyllomenia* (and in part *Dorymenia*) represent a secondary atavistic reversal to the ancestral molluscan features. This would be the only explanation in regarding "pericardial release of gametes" as a synapomorphy for Aplacophora. However, because of the highly complex genital system of *Phyllomenia* (Salvini-Plawen, 1970), this assumption is very unlikely. (2) *Phyllomenia* conditions represent a retained primitive feature, implying convergent evolution of heart passage at least once in the remaining Solenogastre (if *Phyllomenia* is the sister taxon of them) and in the Caudofoveata. (3) The general aplacophoran condition is plesiomorphic for Mollusca and *Phyllomenia* represents a parallel, derived condition (see Salvini-Plawen, 1991: 17 for similar ideas). If so, the condition "evolution of true gonoducts" is paralleled in the Polyplacophora as a whole and within several lineages of Bivalvia and Gastropoda (see above). I regard this assumption as the most probable view.

For the cladistic analysis Solenogastres were coded {0,1}, since both conditions occur within the taxon and (contrary to Bivalvia and Gastropoda) the plesiomorphic one is not clear.

#35. Cleavage with "molluscan cross": (0) = absent: Ann, Kam, Cep; (1) = present: Sip, Sol, Pol, Biv, Sca, Gas; (?) = unknown: Cau, Try.

For discussion see Haszprunar (1996a).

#36. Jaws: (0) = absent: Sip, Kam, Sol, Cau, Pol, Biv; (1) = present: Ann, Try, Sca, Gas, Cep.

There is agreement that the presence of jaws is a conchiferan character being secondarily lost in Bivalvia and several gastropod taxa.

#37. Radula: (0) = absent: Ann, Sip, Kam, Biv; (1) = present: Sol, Cau, Pol, Try, Sca, Gas, Cep.

There are no convincing arguments in regarding any buccal structure in any annelidan taxon as a homolog of the molluscan radula.

#38. Radular membrane: (0) = absent: Sol; (1) = present: Cau, Pol, Try, Sca, Gas, Cep; (x) = radula lacking: Ann, Sip, Kam, Biv.

A true radular membrane, i.e., a distinct layer below the radular teeth proper (see Scheltema *et al.*, 1994: fig. 19; Eernisse and Reynolds, 1994: fig. 11A), is present in all molluscan classes with a radula except the Solenogastres, where TEM-studies (Haszprunar in Salvini-Plawen, 1988; Wolter, 1992) suggest a kind of "pre-ribbon" (Wolter, 1992). It should be mentioned that Scheltema (pers. comm.) still insists in the presence of a true radula membrane at least in certain solenogastre species, unfortunately there is no TEM-evidence for this point of view.

#39. Radular type: (0) = basically distichous/bifid: Sol, Cau; (1) = basically rasping: Pol, Try, Sca, Gas, Cep; (x) = radula lacking: Ann, Sip, Kam, Biv.

For discussion see under general methodology.

#40. Buccal cartilages: (0) = absent: Sol, Cau; (1) = present: Pol, Try, Sca, Gas, Cep; (x) = radula lacking: Ann, Sip, Kam, Biv.

There is a long-lasting and continuing equivocal use of the term "radular bolster" which may be formed either by more or less vacuolized muscle cells or by true cartilages. The latter type is restricted to Polyplacophora and Conchifera, whereas the aplacophoran taxa show the muscular type. Heterobranch Gastropoda secondarily show the purely muscular type again (Haszprunar, 1988; Ponder and Lindberg, 1997).

#41. Oesophageal pouches: (0) = absent: Ann, Sip, Kam, Sol, Cau, Cep; (1) = present: Pol, Try, Biv, Sca, Gas.

As outlined in detail by Salvini-Plawen (1988) the presence of broad and glandular oesophageal pouches with a ciliated, dorsal food channel is typical for Polyplacophora and most conchiferan classes at least in their primitive representatives. The only exception is the Cephalopoda.

#42. Highly glandular midgut: (0) = no: Ann, Sip; (1) = yes: Kam, Sol, Cau, Pol, Try, Biv, Sca, Gas, Cep.

Whereas the midgut of Sipuncula and Annelida is a more or less simple tube, those of Kamptozoa and Mollusca have large glandular areas.

#43. Subdivided midgut for sorting and uptake of food: (0) = absent: Ann, Sip, Kam, Sol; (1) = present: Cau, Pol, Try, Biv, Sca, Gas, Cep.

All Mollusca except the Solenogastres show distinct functional subdivisions of the midgut into a sorting area (stomach), digestion area (midgut sac or gland), and transport tube (intestine). Since none of the outgroups shows this subdivision, it is likely a (syn-?) apomorphic condition of Caudofoveata and all remaining Mollusca.

Salvini-Plawen's (1981, 1988) thorough reviews on

the evolution of the molluscan alimentary tract emphasized the differences between the midgut in Caudofoveata and in Testaria. However, having in mind the variability of this region between and within the various conchiferan classes, this seems not a valid argument versus an *a priori* assumption of homology testable by parsimony. To avoid multiple, directly correlated characters, this complex has been taken as a single character, although multiple coding (*e. g.* for intestine, midgut gland, stomach) would be theoretically possible.

#44. Bilobed midgut gland: (0) = absent: Cau; (1) = present: Pol, Try, Biv, Sca, Gas, Cep; (x) = no midgut gland: Ann, Sip, Kam, Sol.

Whereas the midgut sac of the Caudofoveata is a solitary structure, the midgut gland of all other groups is at least bilobed, although secondary asymmetry or multiplication occurs repeatedly among many conchiferan taxa.

#45. Crystalline style: (0) = absent: Ann, Sip, Kam, Sol, Cau/p, Pol, Sca, Gas/p, Cep; (1) = present: Cau/p, Try, Biv, Gas/p.

Chaetodermatid caudofoveates have a gastric shield and a protostyle, whereas the remaining Caudofoveata lack these features. Tryblidia, Bivalvia and many gastropod taxa have so-called crystalline styles or protostyles in their stomach (Salvini-Plawen, 1981, 1988).

#46. Intestinal loops: (0) = absent: Ann, Kam, Sol, Cau; (1) = along longitudinal axis: Sip; (2) unidirectional: Try; (3) true bidirectional looping: Pol, Biv, Sca, Gas, Cep.

Whereas the gut is straight or simply U-shaped in Annelida, Kamptozoa, Solenogastres, and Caudofoveata, intestinal looping is present in the remaining taxa of this study. However, looping is caused by coiling around a longitudinal muscle in Sipuncula, which is not the case in any molluscan taxon. Moreover, the Tryblidia uniquely show unidirectional looping, whereas Polyplacophora, Bivalvia, Scaphopoda, Gastropoda, and Cephalopoda exhibit bidirectional loops.

#47. Position of anus: (0) = opposite of oral opening: Ann, Sol, Cau, Pol, Try, Biv; (1) near mouth opening at dorsal side: Sip, Kam; (2) = near dorsal opening at ventral side: Sca, Gas, Cep.

Ponder and Lindberg (1997) and Waller (1998) have pointed out that Scaphopoda, Gastropoda and Cephalopoda share a so-called "ano-pedal flexure", whereas the remaining molluscan classes the antero-posterior axis is predominate.

#48. Tetraneury: (0) = absent: Ann, Sip; (1) = present: Sol, Cau, Pol, Try, Biv, Sca, Gas, Cep; (?) = unknown: Kam.

Tetraneury is a typical molluscan character, whereas Sipuncula and Annelida show a single pair of longitudinal main cords. The conditions in the adult Kamptozoa are not relevant, and those of the larva are largely unknown, there-

fore Kamptozoa are coded by (?).

Scheltema (1993, 1996, Scheltema *et al.*, 1994) considered "ganglionated tetraneury" as a synapomorphy of Aplacophora. However, according to personal observations on several genera of Caudofoveata and Solenogastres the so-called "ganglia" are in many species (but not all; Salvini-Plawen, pers. comm.) just thickenings in the lateral or pedal cords and do not fit the usual definition of ganglia as being interconnected by axons only.

#49. Precerebral ganglia: (0) = absent: Ann, Sip, Kam, Sol/p, Pol, Try, Biv, Sca, Gas, Cep; (1) = present: Sol/p, Cau.

Precerebral ganglia are generally present in Caudofoveata, whereas they occur only in certain Solenogastres; the latter are therefore coded as {0,1}. Convergent precerebral ganglia are known from a number of interstitial opisthobranchs, but this is clearly a secondary condition in gastropods.

#50. Pedal ganglia: (0) = absent: Ann, Sip, Sol, Cau, Pol, Try, Gas; (1) = present: Biv, Sca, Cep; (x) = no pedal nervous system: Kam.

Among molluscs, true pedal ganglia (versus elongated, pedal cords) are restricted to Bivalvia, Scaphopoda, and Cephalopoda, and they occur as a secondary condition in many gastropod groups.

#51. Position of visceral loop: (0) = between DVM: Sol, Cau; (1) = outwards DVM: Pol, Try, Biv, Sca; (2) = inwards DVM: Gas, Cep; (x) = no DVM: Ann, Sip, Kam.

As outlined earlier (Haszprunar, 1985) the position of the visceral loop (= lateral cord) with respect to the position of the dorsoventral muscles differs significantly between the molluscan classes. In Caudofoveata and Solenogastres the visceral loop runs between the dorsoventral muscle fibers, whereas the visceral loop runs around the shell muscles in the Polyplacophora, Tryblidia, Bivalvia, and Scaphopoda. Gastropoda and Cephalopoda are characterized by a visceral loop lying between the shell muscles enabling these groups to concentrate their nervous system to a great extent. Outgroups lack the specific dorsoventral muscles and are therefore coded as inapplicable (x).

#52. Position of visceral commissure: (0) = suprarectal: Sol, Cau, Pol; (1) = subrectal: Try, Biv, Sca, Gas, Cep; (x) = homology unclear: Ann, Sip, Kam.

The homology of the lateral (visceral) and pedal cord to those of the outgroups is very questionable. Reisinger (1972) regarded the main cords of Sipuncula and Annelida as homologs to the molluscan pedal cord. Considering the suprarectal commissure in aculiferan molluscs and the eucoelomates, it is more likely that the visceral cord is the common one. Because of these uncertainties the outgroups are here coded by (x).

#53. Innervation of the shell(-plate) margin: (0) = cerebropleural and visceral: Pol, Try, Biv, Sca; (1) = only cerebropleural: Gas, Cep; (x) = no shell-plate: Ann, Sip, Kam, Sol, Cau.

This is a new character that has not been considered previously for molluscan relationships. The margin (or growth-zone) of the shell(-plates) of Polyplacophora (Eernisse and Reynolds, 1994), Tryblidia (Lemche and Wingstrand, 1959), Bivalvia (Haas, 1935), and Scaphopoda (Shimek and Steiner, 1997) are innervated by the lateral cords and by the cerebropleural region. In contrast, the shell-margin of Gastropoda (*e. g.* Fretter and Graham, 1962) and Cephalopoda (Young, 1965) are innervated solely by the pleural region or ganglia, but not by the visceral loop. Since the cerebropleural region of gastropods is not involved in the torsion process, the orientation of the adult gastropod shell (teleoconch) is identical to those of the pretorsional ancestor or to the sister group Cephalopoda.

#54. Cerebral (pretrochal) eyes: (0) = absent: Sol, Cau, Pol, Try, Biv, Sca; (1) = present: Ann, Sip, Kam, Gas, Cep.

The homology of metazoan cephalic eyes is still a matter of considerable debate, although there is increasing agreement in favour of multiple convergences despite a common epigenetic "master"-basis (*e. g.* Salvini-Plawen and Mayr, 1977; Salvini-Plawen, 1982; Zuker, 1994; Nilsson, 1996; Gehring and Ikeo, 1999; Meyer-Rochow, 2000). In the Mollusca only Gastropoda and Cephalopoda show cerebrally innervated (*i. e.*, pretrochal) eyes, whereas superficially similar, but pleurally-laterally innervated (*i. e.*, posttrochal) photoreceptive organs in polyplacophoran and bivalve larvae or juveniles do not fulfill the criterion "cerebral".

All outgroups possess cerebral (pretrochal) eyes in the given definition either as adults or at least in the larval stage, although homology is doubtful because of significant differences in their fine-structure (*e. g.* Woollacott and Eakin, 1973; Verger-Bocquet, 1992; Bartolomaeus, 1992; Blumer, 1997).

#55. Paired statocysts: (0) = absent: Ann, Sip, Kam, Sol, Cau, Pol; (1) = present: Try, Biv, Sca, Gas, Cep.

Among molluscs paired statocysts are restricted to the conchiferan classes, although analogous, unpaired gravity receptors have been described in some Solenogastres (Haszprunar, 1986, Scheltema *et al.*, 1994).

#56. Osphradia: (0) = absent: Ann, Sip, Kam, Try, Sca; (1) = present: Sol, Cau, Pol, Biv, Gas, Cep.

Because of the correlation in position and innervation Haszprunar (1987a, b) pointed out the homology of chemoreceptive sensory organs known as "dorsoterminal sense organ", "Geruchsorgan," "Lacaze's Organ," or "osphradium."

#57. Position of osphradia: (0) = pallial: Pol, Biv,

Gas, Cep; (1) = extrapallial: Sol, Cau; (x) = no osphradium: Ann, Sip, Kam, Try, Sca.

Both aplacophoran taxa are characterized by extrapallial osphradia (dorsoterminal sense organs), whereas the osphradium of the remaining classes, if it is present, is pallial.

#58. Subradular Sense Organ: (0) = absent: Ann, Sip, Kam, Sol, Cau, Biv; (1) = present: Pol, Try, Sca, Gas, Cep.

Despite the repeated claim of Heath (1904, 1911) that a subradular organ is present in aplacophorans, it is lacking there (*e. g.* Salvini-Plawen, 1978, 1985; Scheltema *et al.*, 1994). The presence of a subradular organ is restricted to Polyplacophora, Tryblidia, Scaphopoda, Cephalopoda (*Nautilus*), and Gastropoda, where it is lost independently in several subclades.

CHARACTERS BEING EXCLUDED FROM THIS ANALYSIS

Cephalic appendages: Although a general cerebral innervation is present, the probability of homology of cephalic appendages between the molluscan taxa and the selected outgroups is extremely low, because their anlagen are placed anteriorly (gastropod tentacles) versus posteriorly (bivalve oral lappets, scaphopod captaculae) of the prototroch. Therefore the present analysis does not consider this character.

Oral lappets: Waller (1998) proposed the lack of oral lappets as a synapomorphy of Scaphopoda, Gastropoda, and Cephalopoda. However, many gastropods have prominent oral lappets, and cephalopods are equipped with oral tentacles. Therefore this character is not scored herein.

Epipodial projections: Homologization of the scaphopod pedal flaps with the originally posterior epipodial tentacles and the cephalopod funnel (Waller, 1998) is extremely doubtful. Whereas the pedal flaps and the funnel are locomotory organs, gastropod epipodial tentacles are sensory structures. In Patellogastropoda the epipodial tentacles are present already prior to metamorphosis (Wanninger *et al.*, 1999).

Chitinated gill support: Waller (1998) proposed this as a synapomorphy for all Conchifera except Tryblidia. However, basal clades of Gastropoda (Patellogastropoda, Neritimorpha) lack ctenidial skeletal rods. In cephalopods the ctenidial skeleton is situated in the afferent axis, whereas gastropods and bivalves have efferent rods. Therefore homology of the ctenidial skeleton is very improbably and the character is not coded herein.

Position of ctenidia or secondary gills: A posterior (versus lateral and posterior) position of ctenidia or sec-

ondary gills has been considered as a synapomorphy for Scaphopoda, Gastropoda, and Cephalopoda by Waller (1998). However, lepidopleuran Polyplacophora and proto-branch Bivalvia also have purely posteriorly situated ctenidia, and certain Patellogastropoda (*e. g.* *Patella*) exhibit also lateral gills. Therefore this character is not coded in this study.

RESULTS

The parsimony algorithm revealed a single most parsimonious tree with 95 steps, CI (excluding uninformative characters) = 0.701; RI = 0.780 and RC = 0.566 (Fig. 2). Various re-arrangements of outgroups always show (1) that Kamptozoa and Mollusca as well as Annelida and Sipuncula are sister taxa. (2) The *Aplacophora* and *Aculifera* appear as basal and paraphyletic Mollusca, with the Solenogastres, Caudofoveata, and Polyplacophora as subsequent offshoots. (3) Thus, the monophyly of Testaria (Polyplacophora and Conchifera), further of Conchifera and Cyrtosoma (or better Visceroconcha: Gastropoda and Cephalopoda) is confirmed.

Coding of character #15 as unordered results in three most parsimonious trees again with 95 steps. Tree #2 of these is identical to that of Fig. 2, the (majority rule and strict) consensus of all most parsimonious trees shows a polytomy: Tryblidia, Bivalvia, [Scaphopoda (Gastropoda & Cephalopoda)].

DISCUSSION

Solenogastres as the first molluscan offshoot and the Hepagastralia-concept

It was not before the recent cladistic study by Salvini-Plawen and Steiner (1996) that anyone regarded the Solenogastres as the earliest molluscan offshoot and considered the monophyly of the remaining classes. Whereas Ivanov (1996), Scheltema (1993, 1996) and Waller (1998) favoured the Aplacophora-concept, also earlier papers by Salvini-Plawen (mainly 1972, 1981, 1985, 1991) argued for Caudofoveata versus the remaining classes (Adenopoda-concept). Despite some differences in character coding (see above), the present result is in full accordance with that of Salvini-Plawen and Steiner (1996). Herein I name the monophyletic clade consisting of Caudofoveata and Testaria as **Hepagastralia**¹ reflecting the main synapomorphy, the highly distinct and complex subdivision of the midgut. A clade Hepagastralia is additionally supported by

¹I regard it as nonsense to argue about the rank of Hepagastralia as a "sub- or infraphylum" or as a "mega- or gigaclass."

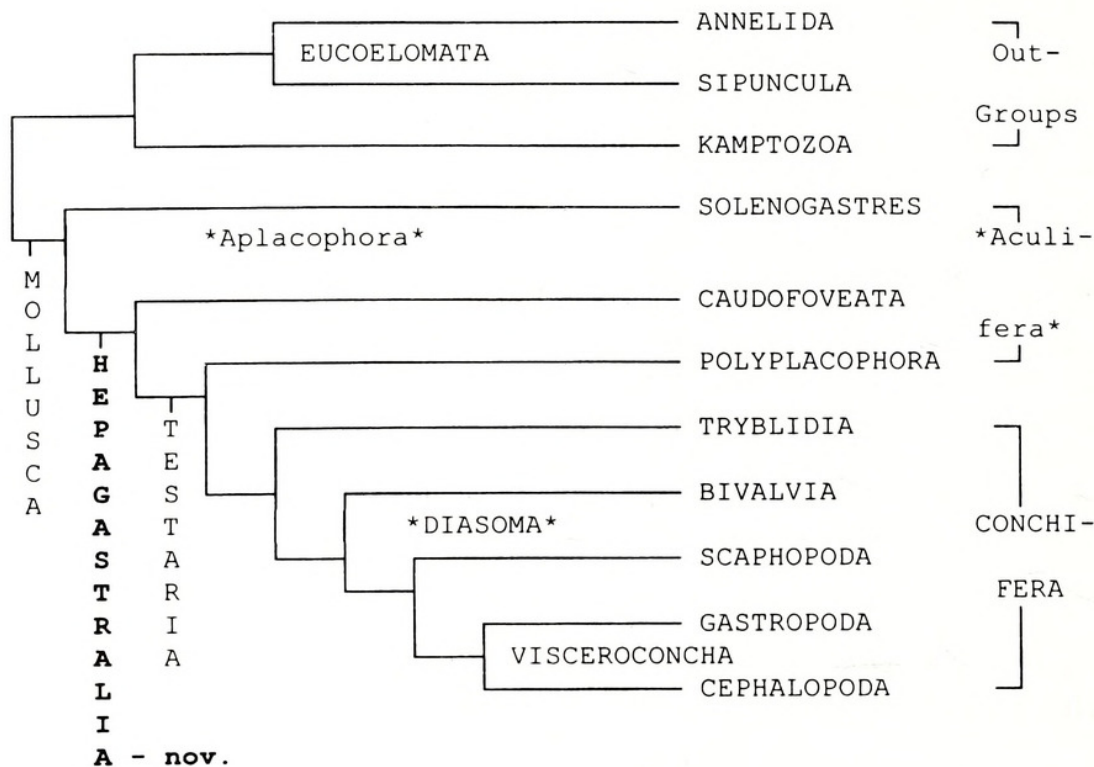


Fig. 2. Single, most parsimonious tree of the current parsimony analysis revealed by coding character #15 as ordered. It is identical to tree #2 (of three), if #15 is coded unordered. *Taxon* means a paraphyletic group.

further characters, the presence of ctenidia, loss of pedal cirri, and presence of a true radular membrane. None of the latter characters is unequivocal, however (see character analysis and below).

Solenogastres show high variability in the principal configuration (anatomy, histology) of the foregut glands and in the number and arrangement of the osphradia (e.g. Salvini-Plawen, 1978). Considering the basal position of the Solenogastres in the molluscan framework, one gets the impression that in the Solenogastres these characters are not yet fully constrained, in contrast to the remaining classes. Moreover, the Solenogastres seem to be the only extant molluscan group in which the original, solely ciliary type of locomotion has been retained. In particular the anteriorly placed ciliary "pit", which consists of compound cilia (Haszprunar, 1986) is strikingly similar to the anterior part of the foot sole of nearly all benthic larvae of Kamptozoa (Nielsen, 1971; see also Haszprunar *et al.*, 1995), although fine-structural details are still lacking in the latter case.

Position of Tryblidia

Recent microanatomical and ultrastructural investigations (Haszprunar and Schaefer, 1997a,b; Schaefer and Haszprunar, 1997a,b) provided evidence that the Tryblidia are not "living fossils" or even "Archi-Mollusca". Herein the Tryblidia appear as an early but not necessarily earliest (see above) conchiferan offshoot.

As outlined above the monophyly of the remaining

Character state distribution in Fig. 2.

h = homoplasy, r = reversal

Eucoelomata: #2:0->1; #13:0->1; #20:1->0(h,r); #22:0->1;
 NN (Sinusoida = Kamptozoa & Mollusca): ?#20:0->1(r); #24:0->1; #42:0->1;
 Mollusca: #3:0->1(r); #7:0->1(r); #8:0->1; #9:x->1; #14:0->1; #23:0->1(r); #25:x->1(r); #26:0->1; #30:0->1; #35:0->1(h); #37:0->1(r); #48:0->1; #51:x->0; #56:0->1(r);
 Hepagastralia: #10:0->1(r); ?#20:1->0; #38:0->1; #43:0->1;
 Testaria: #4:0->1; #5:0->1; #9:1->0; #12:0->1(h); #15:0->1; ?#20:1->0(h,r); #34:1->0; #39:0->1; #40:0->1; #41:0->1(r); #44:0->1; #46:0->3; #51:0->1; #53:x->0; #57:1->0; #58:0->1(r);
 Conchifera: #1:1->0; #3:1->0(r); #4:1->2; #6:0->1; #7:1->0(r); #9:1->0(r); #36:0->1(h,r); #45:0->1(r); #52:0->1; #55:0->1;
 NN (Biv, Sca, Gas, Cep): #15:1->2; #50:0->1(r);
 NN (Sca, Gas, Cep): #15:2->3; ?#16:0->1(r in Sca and Gas); #45:1->0(r); #47:0->2;
 Visceroconcha: #9:0->1(r); #17:0->1; #51:1->2; #53:0->1; #54:0->1(h);
 Annelida (Ann): #27:0->2(h); #31:2->4; #36:0->1(h,r);
 Sipuncula (Sip): #29:1->0(h); #35:0->1(h); #46:0->1; #47:0->1(h);
 Kamptozoa (Kam): #12:0->1(h); #21:1->0; #28:1->0; #33:0->1(h); #47:0->1(h);
 Solenogastres (Sol): #19:0->1(h);
 Caudofoveata (Cau): #34:0->1(h in Sol); #49:0->1(h in Sol);
 Polyplacophora (Pol): #11:0->3; #19:0->1(h); #33:0->1(h);
 Tryblidia (Try): #11:0->2; #25:1->0(r); #27:0->2(h); #32:0->1; #46:3->2; #56:1->0(r);
 Bivalvia (Biv): #18:0->1(h in Sca); #36:1->0(r); #37:1->0(r); #58:1->0(r);
 Scaphopoda (Sca): #10:1->0(r); #15:1->4(h); #23:1->0(r); #31:2->1; #45:1->0(h,r); #56:1->0(r);
 Gastropoda (Gas): #15:3->4; #19:0->1(h); #31:2->0; ?#50:1->0(r);
 Cephalopoda (Cep): #24:1->2; #29:1->0(h); #33:0->1(h); #35:1->0(r); #41:1->0(r);

conchiferan classes depends on the coding of character #15 (number of shell muscles) clade. In any case there is no unequivocal support for this clade, therefore this clade is not named. The proposed term "Ganglioneura" (Lauterbach, 1983) is in any case inappropriate, since primitive gastropods, bivalves, and cephalopods do not show true ganglia.

Position of Scaphopoda

Applying the Hennigian method Waller (1998) has strongly argued against the Diasoma-concept (Rostrochoncha, Scaphopoda and Bivalvia monophyletic). Instead he favoured a clade "Gastropoda (Scaphopoda and Cephalopoda)." As outlined in the character analysis many of his proposed synapomorphies for this arrangement are not accepted herein. Nevertheless, the present analysis again contradicts the Diasoma-concept and argues for monophyly of Scaphopoda, Gastropoda and Cephalopoda. However, contrary to Waller (1998) the sister-group relationship of Gastropoda and Cephalopoda is very well supported by no less than four non-homoplastic synapomorphies. On the other hand, none of the proposed synapomorphies is unequivocal and all show homoplasies within the terminal taxa. Therefore this clade is not named again.

Implications for the groundplan of the Mollusca

The consideration of the *Aplacophora* as the basic molluscan level of organization has major implications for the understanding and reconstruction of the molluscan stem species (HAM = "Hypothetical Ancestral Mollusc"). Many shared aplacophoran features can now reasonably be considered as characters of HAM (see also Salvini-Plawen, 1972, 1981, 1985, 1991; Haszprunar, 1992; Salvini-Plawen and Steiner, 1996): worm-shaped body with chitinous cuticles covered with aragonitic spicules or scales; distinct body wall musculature; posterior mantle cavity with extrapallial osphradium; distichous radula and carnivory; urinogenital ducts and openings.

Up to now all reconstructions of the molluscan archaetype show ctenidia. The lack of ctenidia in the Solenogastres has been regarded as a secondary loss comparable to those in Scaphopoda and many gastropod taxa, and this scenario is still possible. However, Ockham's razor (minimalization of assumptions) favours the assumption of a plesiomorphic lack of ctenidia in the Solenogastres. Indeed, there are many larger species of Solenogastres with respiratory folds in the mantle cavity to increase the respiratory capacity, but none of these gill-leaflets shows the specific ctenidial structure.

Outlook

Is this the final word or the final decision concerning the *Aplacophora*? Of course it is not, since phyloge-

netics never is a dogma, but is a matter of probabilities depending on the current state of data, character selection, and basic assumptions. In particular ontogenetic data on the aplacophoran taxa are badly needed to clear up certain points such as the possible presence of a pedal sole and gland in larval or early juvenile Caudofoveata.

The same is true in particular for the larval characters of the Kamptozoa, which appear again crucial for improving our understanding of molluscan origins and early evolution. Important questions concern presence or absence of locomotory cirri at the anterior end of the foot sole comparable to Solenogastres or the details of the (tetra-neural?) nervous system of the larva.

I do have some personal experience with these highly enigmatic and interesting taxa, but true experts may have a better chance to improve or modify the provided data-matrix based on their long expertise. Nevertheless, it is the argument and the data and not the author who decides the matter. Thus, the rejection of *Aplacophora* as a monophyletic taxon and accordingly the alternative Hepagastralia-concept is the most parsimonious assumption and thus the most probable solution at the present stage of knowledge.

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