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On bivalve phylogeny: a high-level analysis of the Bivalvia (Mollusca) based on combined morphology and DNA sequence data

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Abstract. Bivalve classification has suffered in the past from the crossed-purpose discussions among paleontologists and neontologists, and many have based their proposals on single character systems. More recently, molecular biologists have investigated bivalve relationships by using only gene sequence data, ignoring paleontological and neontological data. In the present study we have compiled morphological and anatomical data with mostly new molecular evidence to provide a more stable and robust phylogenetic estimate for bivalve molluscs. The data here compiled consist of a morphological data set of 183 characters, and a molecular data set from 3 loci: 2 nuclear ribosomal genes (18S rRNA and 28S rRNA), and 1 mitochondrial coding gene (cytochrome *c* oxidase subunit I), totaling ~3 Kb of sequence data for 76 molluscs (62 bivalves and 14 outgroup taxa). The data have been analyzed separately and in combination by using the direct optimization method of Wheeler (1996), and they have been evaluated under 12 analytical schemes. The combined analysis supports the monophyly of bivalves, paraphyly of protobranchiate bivalves, and monophyly of Autolamellibranchiata, Pteriomorphia, Heteroconchia, Palaeoheterodonta, and Heterodonta s.l., which includes the monophyletic taxon Anomalodesmata. These analyses strongly support the conclusion that Anomalodesmata should not receive a class status, and that the heterodont orders Myoida and Veneroida are not monophyletic. Among the most stable results of the analysis are the monophyly of Palaeoheterodonta, grouping the extant trigoniids with the freshwater unionids, and the sister-group relationship of the heterodont families Astartidae and Carditidae, which together constitute the sister taxon to the remaining heterodont bivalves. Internal relationships of the main bivalve groups are discussed on the basis of node support and clade stability.

Additional key words: Mollusca, Bivalvia, Palaeoheterodonta, Heteroconchia, Heterodonta, 18S rRNA, 28S rRNA, cytochrome *c* oxidase I, morphology, direct optimization, sensitivity analysis

Bivalve molluscs are characterized by a laterally compressed body with an external bivalved shell that is hinged dorsally. The valves are connected by a partially calcified elastic ligament and are held together by 1 or 2 adductor muscles. There is no buccal or radular apparatus, and the mantle lobes are either joined or free ventrally. The spacious mantle cavity extends upwards on each side of the visceral mass and contains a pair of ctenidia suspended laterally. The ctenidia may be enlarged, lamellate and plicate. The mouth and anus are located at opposite ends of the body and the gut is typically convoluted. A pair of ciliated labial palps connect the ctenidia to the mouth, and direct food particles into it. The extensible foot is either elongated or laterally compressed.

These modifications from the plesiomorphic molluscan condition have made it difficult to establish a phylogenetic scheme of the group. The problems arise from the difficulty in homologizing certain structures useful for bivalve taxonomy that are not present in the other molluscan classes. Paleontologists and neontologists have disputed the monophyly and phylogenetic position of many groups, such as Anomalodesmata, Protobranchia, and Palaeoheterodonta, while others using molecular sequence data have openly questioned the monophyly of Heterodonta, as well as the orders Veneroida and Myoida.

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There have been several concerted attempts to resolve the contradictory systems of classification of bivalves proposed by paleontologists and neontologists. C.M. Yonge and T.E. Thompson organized the symposium *Evolutionary Systematics of Bivalve Molluscs,* which was published in 1978 (Phil. Trans. R. Soc. Lond. B 284: 199–436). Two decades later, paleontologists, neontologists, and molecular biologists provided additional insights into bivalve phylogeny at the *International Symposium on the Paleobiology and Evolution of the Bivalvia* (Johnston & Haggart 1998) and at a meeting on *The Biology and Evolution of the Bivalvia* (Harper et al. 2000b).These efforts have not yet produced a single combination of morphological and molecular data, and conflicting hypotheses of bivalve evolution remain. It is our aim to investigate previously proposed hypotheses by analyzing morphological and molecular characters of all the extant bivalve orders in a total-evidence framework.

Previous classification systems of bivalves

Comparative anatomical studies of living bivalves have led to several classification schemes. Cox (1960) provided an excellent historical review of early attempts to classify the bivalves. Ridewood (1903) recognized 3 orders of bivalves (Protobranchia, Eleutherorhabda, and Synaptorhabda) based on gill structure. Pelseneer (1906, 1911) developed another system of classification based on 5 grades of gill structure and assigned ordinal status to each grade: Protobranchia, Filibranchia, Pseudolamellibranchia, Eulamellibranchia, and Septibranchia. Iredale (1939) added the order Isofilibranchia to distinguish the mytiloids, which he considered to differ sufficiently in gill structure from the other members of Filibranchia. Atkins (1938) described two types of latero-frontal ciliation on gill filaments and proposed division of the class into 2 groups, the Macrociliobranchia and Microciliobranchia. Later workers proposed that other structures be used in classifying bivalves (stomach: Purchon 1960, 1963, 1968; ctenidial-labial palp associations: Stasek 1963). Scarlato & Starobogatov (1975, 1978, 1979) and Starobogatov (1992) recognized 3 superorders of bivalves, the Nuculiformii (= Protobranchia), Mytiliformii, and Conocardiiformii (= Anomalodesmata). In this new classification, Mytiliformii contained pteriomorphs, palaeoheterodonts, and heterodonts.

Classifications based on single-character systems have been criticized (Cox 1960; Newell 1965, 1969). Newell (1965, 1969) summarized the available evidence on shell structure and anatomy and presented a classification of Bivalvia that is now generally in use. In his scheme, 6 subclasses were recognized: the Palaeotaxodonta (= Nuculoidea and Nuculanoidea), Cryptodonta (= Solemyoida), Pteriomorphia, Palaeoheterodonta, Heterodonta, and Anomalodesmata. Purchon (1978) compiled a data matrix of 9 characters for 40 taxa (superfamilies) of bivalves that was analyzed using a phenetic computer algorithm. Following an expanded analysis (Purchon 1987b), bivalves were divided into 2 subclasses, Protobranchia and Lamellibranchia, the latter containing 4 orders: Pteriomorphia, Mesosyntheta (= Trigonioida and Unionoida [including also Crassatelloidea, Carditoidea, and Leptonoidea]), Anomalodesmata, and Gastropempta (= Heterodonta) (Fig. 1A).

For the purposes of the present study, we follow the classification system of Beesley et al. (1998). Thus, a classification system of 5 subclasses is followed prior to the phylogenetic analyses. This classification is generally corroborated by the morphological analysis of Waller (1998). Taxon names currently in use in the literature are noted where needed. This classification includes the following subclasses; representatives used in this study are listed in Table 2.

Subclass Protobranchia. The classification of the Protobranchia is unstable (Reid 1998). Nuculoidea and Nuculanoidea are considered superfamilies of the order Nuculoida by several authors, although certain phylogenetic studies have suggested non-monophyly of Nuculoida (Waller 1990, 1998; Morton 1996). Therefore, we have used the superfamilies Solemyoidea (2 species of *Solemya*), Nuculoidea (4 species of Nuculidae), and Nuculanoidea (2 species of Nuculanidae, 2 species of Yoldiidae, and 1 of Neilonellidae).

Subclass Pteriomorphia (= Filibranchia). Five orders are recognized in this classification: Mytiloida, Arcoida, Pterioida, Limoida, and Ostreoida. Pojeta (1978) separated mytiloids as a distinct subclass (Isofilibranchia), but Waller (1998) recognized the category Pteriomorphia, regarding Mytiloida as the sister group to the other pteriomorphs. Representatives of the 5 orders have been examined in this study.

Subclass Palaeoheterodonta. This group is composed of 2 orders, Trigonioida and Unionoida. However, some authors do not support the monophyly of the group (e.g., Salvini-Plawen & Steiner 1996). Our study includes representatives of both orders (2 unionids and 2 trigoniids).

Subclass Heterodonta. Classification of Heterodonta has not been resolved, even at the ordinal level (Prezant 1998). Heterodonta (as accepted by Vokes 1968; Cox 1969; Newell 1969; Beesley et al. 1998) consists of 3 orders: the extinct Hippuritoida and the extant Veneroida and Myoida. The large order Veneroida comprises ~18 superfamilies, of which 15 are

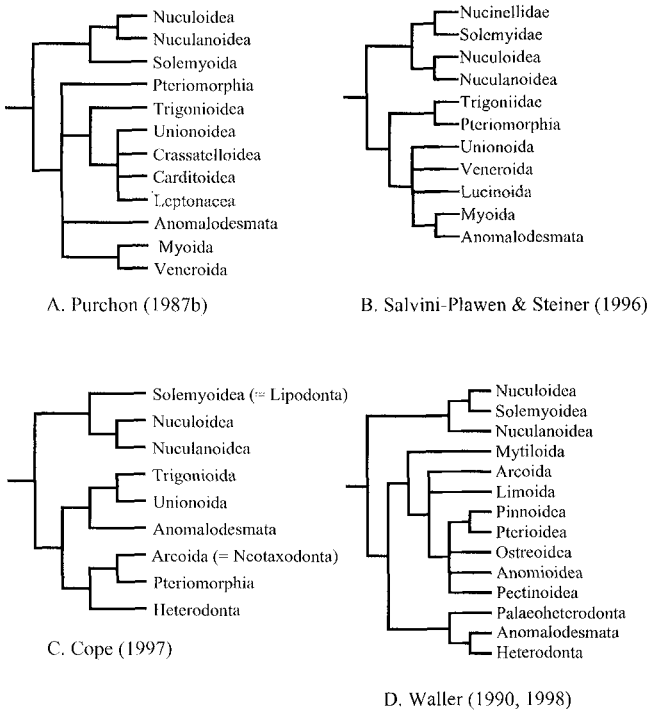

Fig. 1. High-level phylogenetic relationships proposed for the Bivalvia. Leptonacea from Purchon (1987b) comprises Galeommatoidea and Cyamoidea.

included in this study; the 4 superfamilies in the smaller order Myoida are included in this study.

Subclass Anomalodesmata. Beesley et al. (1998) followed the classification outlined by Morton (1982a) in recognizing a single order (Pholadomyoida) with 7 superfamilies. This classification is mainly based on the paleontological work of Runnegar (1974). However, Newell (1965) had divided the subclass into 2 orders, Pholadomyoida and Poromyoida (= Septibranchia or Septibranchida), a classification also followed by Coan et al. (2000). We have included data on 2 species of the superfamily Pandoroidea (1 of Lyonsiidae and 1 of Pandoridae) and 2 species of Cuspidaroidea. The superfamilies Thracioidea, Verticordioidea, and Poromyoidea are not included due to lack of tissues for DNA samples.

Phylogenetic relationships

Although bivalves are well known morphologically, they have been a source of discord both in terms of their relationships to other molluscan classes, and relationships within the class. In the following paragraphs we discuss the most contradictory points.

Morphological studies

Based on anatomical and embryological data, Lacaze-Duthiers (1856, 1857a, 1858) proposed a close relationship between Bivalvia and Scaphopoda, a view shared by Stasek (1972). The Diasoma concept (Runnegar & Pojeta 1974; Pojeta & Runnegar 1976, 1985; Runnegar 1978; Pojeta et al. 1987) united Bivalvia, Scaphopoda, and the extinct group Rostroconchia (= Loboconcha of Salvini-Plawen 1980, 1985). Other authors also suggested monophyly of Scaphopoda and Bivalvia based on the foot structure (Hennig 1979; Lauterbach 1984); Hennig (1979) introduced the name Ancrypoda ("anchor foot") for this clade. Some cladistic analyses also supported this relationship (Götting 1980; Lauterbach 1983; Salvini-Plawen & Steiner 1996), but Waller (1998) excluded Scaphopoda from the Diasoma, considering scaphopods as sister group to Cephalopoda (Grobben 1886), while Haszprunar (2000) placed Bivalvia as the sister group to (Scaphopoda (Gastropoda + Cephalopoda)).

Steiner (1992) listed the putative synapomorphies of the Diasoma/Loboconcha: (1) Development of lateral mantle folds that converge ventrally and enclose the entire body, probably an adaptation to infaunal life; (2) a foot differentiated into a burrowing organ; and (3) an epiathroid nervous system with true pedal ganglia, all of which correspond in position and area of innervation (Haszprunar 1988).

Numerical and parsimony-based analyses of molluscan groups are routinely used to address phylogenetic questions. However, only 2 phenetic analyses (Purchon 1978, 1987b) and 2 parsimony analyses (Salvini-Plawen & Steiner 1996; Carter et al. 2000) assessing higher relationships among bivalves based on morphological data have been published to date. These studies agreed upon 2 main clades of bivalves, Protobranchia (= Palaeotaxodonta) and Autolamellibranchiata[1] (= Lamellibranchia), but differed in other conclusions (Fig. 1). Using a parsimony analysis of 42 characters for 14 terminal taxa, Salvini-Plawen & Steiner (1996) concluded that bivalves are monophyletic and divided into Protobranchia and Autolamellibranchiata. However, Palaeoheterodonta and Heterodonta were not monophyletic (Fig. 1B).

Cope (1997) added numerous fossil taxa to analyses of extant bivalves. This produced a cladistic (but nonnumerical) classification based primarily on shell microstructural data. This unorthodox phylogenetic scheme had Palaeoheterodonta + Anomalodesmata as the sister group to Pteriomorphia + Heterodonta (Fig. 1C). Morton (1996) proposed a superfamilial phylo-

[1] The term Autobranchia has been used in previous publications to refer to Autolamellibranchiata GROBBEN, 1894. We use the correct Latin name, but we prefer to use the term autobranch rather than autolamellibranchiate in the colloquial sense.

genetic system of bivalves including numerous fossil taxa. In his phylogeny, Palaeoheterodonta was nested within Pteriomorphia. Heterodonta s.l. was monophyletic, with Anomalodesmata as a sister group to Myoida. In contrast, Veneroida was not monophyletic. Waller (1990, 1998) proposed a cladistic classification with monophyletic Protobranchia, Autolamellibranchiata, Pteriomorphia, Palaeoheterodonta, Eulamellibranchia, Anomalodesmata, and Heterodonta (Fig. 1D).

Molecular studies

The first high-level phylogenetic analysis of bivalves based on 18S rRNA sequence data included 13 sequences (1 polyplacophoran, 2 gastropods, 8 pteriomorphs, and 2 veneroid heterodonts) and concluded that the 18S rRNA molecule did not recover bivalve monophyly in most of the analyses (Steiner & Müller 1996). Giribet & Carranza (1999) subsequently demonstrated that the polyphyly of Steiner & Müller (1996) was an artifact of taxon sampling. By adding 20 sequences to the data set used by Steiner & Müller (1996), their analysis resulted in bivalve monophyly and recovered the subclasses Pteriomorphia and Heterodonta. However, both studies were based on poor representation of bivalve diversity, and stressed methodology more than the actual phylogeny of the group. In another study of relationships among the molluscan classes, Winnepenninckx et al. (1996) used complete 18S rRNA sequences of 1 aplacophoran (Caudofoveata), 2 polyplacophorans, 7 gastropods, 1 scaphopod, and 13 bivalves (7 pteriomorphs and 6 veneroid heterodonts), with protostome worms and other groups as outgroup taxa. None of the analyses supported bivalve monophyly.

A common problem in molecular phylogenetic analyses is limited taxon sampling, as in the cases of bivalves above. Adamkewicz et al. (1997) alleviated previous taxon sampling deficiencies by analyzing 500 bp from all bivalve subclasses, including all orders except Limoida and Trigonioida (totaling 28 bivalves and 5 outgroup taxa). When all outgroup taxa were included, bivalves were polyphyletic. By removing gastropods and rooting the trees with polyplacophorans, bivalve monophyly was recovered (Adamkewicz et al. 1997, figs. 2, 3), with the 2 anomalodesmatans and 2 protobranchs in a sister clade to the remaining bivalves. The other protobranch (*Nucula*) was sister to a clade that contained 3 pteriomorphs. Pteriomorphs were polyphyletic (distributed in 3 clades). Palaeoheterodonta was the sister clade to the monophyletic Heterodonta.

Campbell et al. (1998) used a combination of partial and complete 18S rRNA sequences of the taxa Protobranchia (their Palaeotaxodonta), Pteriomorphia (their Pteriomorphia and Isofilibranchia), and Heterodonta (including Veneroida and Myoida). Palaeoheterodonta and Anomalodesmata were not sampled, although they placed Myoida within Anomalodesmata in their table 1. The trees resulted in bivalve polyphyly (*Solemya* grouped with Gastropoda), pteriomorph paraphyly, and monophyly of Autolamellibranchiata and Heterodonta.

Hoeh et al. (1998) studied phylogenetic relationships among 14 species of bivalves based on sequences of the mitochondrial cytochrome *c* oxidase subunit I (COI). These analyses, based on 613 bp, supported monophyly of Autolamellibranchiata, Mytiloida, Veneroida, Unionoida, and Palaeoheterodonta, although monophyly of bivalves was not supported; the protobranch fell within the non-bivalve molluscs. The authors concluded that the "molluscan bivalved body plan may have evolved more frequently than traditional phylogenetic hypotheses suggest." Another result suggested the monophyly of Mytiloida + Veneroida, excluding Trigonioida. However, these results were based on limited sequence data of only 5 of the 12 recognized bivalve orders. Their study was the first to include molecular data for the Trigonioida, and supported the morphology-based hypothesis that this marine group is the sister taxon of freshwater unionids, comprising Palaeoheterodonta.

Subsequently, Canapa et al. (1999) studied relationships among some autobranch bivalves based on 18S rRNA sequence data (2 polyplacophorans, 2 gastropods, and 21 bivalves: 10 pteriomorphs, and 11 heterodonts). When using polyplacophorans and gastropods as outgroups, bivalves were not monophyletic. But when only the 2 gastropods were used as outgroups, Bivalvia, Pteriomorphia, and Heterodonta were monophyletic.

Other molecular studies have focused on lower level relationships. Distel (2000) and Distel et al. (2000) used 18S rRNA sequence data to elucidate relationships within Mytilidae, and its position within pteriomorph bivalves. Using 1 solemyid, 1 unionid, and 1 myid as outgroups, pteriomorph monophyly was not obtained in any of the maximum-likelihood, parsimony, or minimum-evolution trees, due to the clustering of *Mya* with the Ostreidae. A recent study of sphaeriid and corbiculid relationships analyzed ~1 Kb of 28S rRNA sequence data for 18 veneroid bivalves (Park & Ó Foighil 2000). They obtained veneroid monophyly with respect to 2 ostreoids, (although no myoid or anomalodesmatan species were sampled). The most important result of this study was to show that Corbiculidae and Sphaeridae were not sister groups, since

Table 1. Outgroup taxa used in the analyses, with GenBank accession numbers.

	18S rDNA	28S rDNA	COI
Class Polyplacophora			
Lepidopleurus cajetanus	AF120502	AF120565	AF120626
Acanthochitona crinita	AF120503	AF120566	AF120627
Class Cephalopoda			
Nautilus pompilius	AF207641	AF411688	AF120628
Loligo pealei	AF120505	AF120568	AF120629
Sepia elegans	AF120506-7	AF120569	
Class Gastropoda			
Haliotis tuberculata	AF120511	AF120570	
Sinezona confusa	AF120512	AF120571	AF120631
Diodora graeca	AF120513	AF120572	AF120632
Viviparus georgianus	AF120516	AF120574	AF120634
Truncatella guerinii	AF120517	AF120575	AF120635
Balcis eburnea	AF120519	AF120576	AF120636
Peltodoris atromaculata	AF120521	AF120577	AF120637
Class Scaphopoda			
Antalis pilsbryi	AF120522	AF120579	AF120639
Rhabdus rectius	AF120523	AF120580	AF120640

the Corbiculidae formed a monophyletic group with veneroids and mactroids (with high nodal support). Thus, the monophyly of Corbiculoidea was not supported.

Steiner & Hammer (2000) addressed pteriomorph and higher bivalvian relationships by using a wide representation of complete 18S rRNA sequences from bivalves and other molluscs as outgroups. This elegant study included nearly complete taxon sampling within the pteriomorphs, along with most bivalve orders. Although Bivalvia appeared diphyletic due to the heterogeneity of substitution rates among lineages, monophyly of Protobranchia, Heteroconchia, and Pteriomorphia was supported. However, Myoida and Veneroida were not monophyletic, and Anomalodesmata was nested within the heterodonts. Resolution within the Pteriomorphia showed conflict with morphological hypotheses in the position of Mytiloidea and Arcoidea (Steiner & Hammer 2000, fig. 8).

Another massive 18S rRNA sequence data analysis was published by Campbell (2000), again with most bivalve orders and superfamilies represented. The results were similar to those of Steiner & Hammer (2000), in supporting polyphyly of bivalves, monophyly of Pteriomorphia and Heteroconchia, and polyphyly of Myoida and Veneroida. The Anomalodesmata nested within the Heterodonta.

In summary, the taxonomic sampling of molecular bivalve studies has improved, although some major lineages such as Trigonioidea are not yet represented in 18S rRNA data sets. It has been suggested that wildly divergent rates of molecular evolution may be responsible for the failure of molecular phylogenetic studies in recovering bivalve monophyly. No analysis has combined data from more than one molecular source or has combined molecular data with morphology in a character-based analytical framework. In the present study, we combine data from morphology and anatomy (183 characters), and molecules (complete 18S rRNA, D3 region of the 28S rRNA and ~660 bp of the COI loci) of 62 bivalves (representing all extant orders and most superfamilies) with 14 outgroup taxa (representing all extant classes of Testaria except Monoplacophora). We hope to resolve inconsistencies of previous studies by providing the first total-evidence investigation of all orders of the class Bivalvia.

Methods

Taxonomic sampling

Molecular and morphological data of 5 classes of testarian molluscs were analyzed (Tables 1, 2): Polyplacophora (2 spp.), Cephalopoda (3 spp.), Gastropoda (7 spp.), Scaphopoda (2 spp.), Bivalvia (62 spp.). Within the bivalves, the 5 subclasses recognized by Beesley et al. (1998) were represented with the following number of terminal taxa: Protobranchia (11), Pteriomorphia (17), Palaeoheterodonta (4), Anomalodesmata (4), Heterodonta (27). All 12 orders of bivalves were represented: 34 superfamilies (representing 74% of bivalve superfamilial diversity according to Beesley et al. 1998) and 43 families (~45% of the familial

Table 2. Systematic list of the bivalve taxa used in the analyses (following Beesley et al. 1998). The list includes 62 species (but 63 exemplars, as *Nucula sulcata* is represented by 2 populations, one Mediterranean and one from the North Atlantic). The asterisk after the ordinal name indicates those orders that do not include all superfamilies. When no superfamilial category is indicated, the order is represented by a single superfamily. Underlined taxon names are categories not supported by the analyses. When the symbols "18S" or "COI" are indicated, these sequences are from GenBank. All other sequences (GenBank accession codes indicated) have been obtained by the authors.

	18S rDNA	28S rDNA	COI
Class Bivalvia			
Subclass Protobranchia			
Order Solemyoida			
Family Solemyidae			
Solemya velum	AF120524	AF120581	COI
Solemya reidi	18S		
Order Nuculoida			
Superfamily Nuculoidea			
Family Nuculidae			
Nucula sulcata MED	AF120525	AF120582	
Nucula sulcata ATL	AF207642	AF207649	AF207654
Nucula proxima	AF120526	AF120583	AF120641
Acila castrensis	AF120527	AF120584	
Superfamily Nuculanoidea			
Family Yoldiidae			
Yoldia limatula	AF120528	AF120585	AF120642
Yoldia myalis	AF207643	AF207650	AF207655
Family Nuculanidae			
Nuculana minuta	AF120529	AF120586	AF120643
Nuculana pernula	AF207644	AF207651	
Family Neilonellidae			
Neilonella subovata	AF207645	AF207652	AF207656
Subclass Pteriomorphia			
Order Mytiloida			
Family Mytilidae			
Geukensia demissa	18S		COI
Mytilus edulis	18S	AF120587	COI
Lithophaga lithophaga	AF120530	AF120588	AF120644
Order Arcoida			
Superfamily Arcoidea			
Family Arcidae			
Arca noae	18S		
Barbatia barbata	AF207646	AF120589	AF120645
Family Noetiidae			
Striarca lactea	AF120531	AF120590	AF120646
Superfamily Limopsoidea			
Family Glycymeridae			
Glycymeris insubrica	AF207647	AF120591	
Order Pteroida			
Superfamily Pterioidea			
Family Pteriidae			
Pteria hirundo	AF120532	AF120592	AF120647
Superfamily Pinnoidea			
Family Pinnidae			
Atrina pectinata	18S	AF120593	AF120648

Table 2. Continued.

	18S rDNA	28S rDNA	COI
Order Limoida			
Family Limidae			
Lima lima	AF120533	AF120594	AF120649
Limaria hians	AF120534	AF120595	AF120650
Order Ostreoida*			
Suborder Ostreina			
Superfamily Ostreoidea			
Family Ostreidae			
Crassostrea virginica	18S		
Ostrea edulis	18S	AF120596	AF120651
Suborder Pectinina			
Superfamily Pectinoidea			
Family Pectinidae			
Pecten maximus	18S		COI
Chlamys varia	18S	AF120597	
Family Spondylidae			
Spondylus sinensis	AF229629		
Superfamily Anomioidea			
Family Anomiidae			
Anomia ephippium	AF120535	AF120598	
Subclass Palaeoheterodonta			
Order Unionoida*			
Superfamily Unionoidea			
Family Unionidae			
Psilunio littoralis	AF120536	AF120599	AF120652
Lampsilis cardium	AF120537	AF120600	AF120653
Order Trigonioida			
Family Trigoniidae			
Neotrigonia bednalli	AF120538		
Neotrigonia margaritacea	AF411690	AF411689	COI
Subclass Anomalodesmata			
Order Pholadomyoida*			
Superfamily Pandoroidea			
Family Pandoridae			
Pandora arenosa	AF120539	AF120601	
Family Lyonsiidae			
Lyonsia hyalina	AF120540	AF120602	AF120654
Superfamily Cuspidarioidea			
Family Cuspidariidae			
Cuspidaria cuspidata	AF120541-2	AF120603	AF120655
Myonera sp.	AF120544	AF120605	
Subclass Heterodonta			
Order Veneroida*			
Superfamily Carditoidea			
Family Carditidae			
Cardita calyculata	AF120549	AF120610	AF120660
Cardites antiquata	AF120550	AF120611	AF120661
Superfamily Crassatelloidea			
Family Astartidae			
Astarte castanea	AF120551	AF120612	AF120662

Table 2. Continued.

	18S rDNA	28S rDNA	COI
Superfamily Chamoidea			
Family Chamidae			
Chama gryphoides	AF120545	AF120606	AF120656
Superfamily Lucinoidea			
Family Lucinidae			
Codakia cfr. *orbiculata*	AF120546	AF120607	AF120657
Superfamily Galeommatoidea			
Family Galeommatidae			
Galeomma turtoni	AF120547	AF120608	AF120658
Family Lasaeidae			
Lasaea sp.	AF120548	AF120609	AF120659
Superfamily Solenoidea			
Family Pharidae			
Ensis ensis	AF120555	AF120616	
Superfamily Tellinoidea			
Family Semelidae			
Abra cfr. *prismatica*	AF120554		
Superfamily Cardioidea			
Family Cardiidae			
Parvicardium exiguum	AF120553	AF120614	AF120664
Fragum unedo	18S		
Superfamily Tridacnoidea			
Family Tridacnidae			
Tridacna gigas	18S		
Hippopus hippopus	18S		
Superfamily Dreissenoidea			
Family Dreissenidae			
Dreissena polymorpha	AF120552	AF120613	AF120663
Superfamily Mactroidea			
Family Mactridae			
Spisula subtruncata	18S	AF120615	AF207657
Tresus nuttalli	18S		
Superfamily Arcticoidea			
Family Arcticidae			
Arctica islandica	18S		
Family Vesicomyidae			
Calyptogena magnifica	AF120556	AF120617	AF120665
Superfamily Corbiculoidea			
Family Corbiculidae			
Corbicula fluminea	AF120557	AF120618	AF120666
Family Sphaeriidae			
Sphaerium striatinum	AF120558	AF120619	AF120667
Superfamily Veneroidea			
Family Veneridae			
Mercenaria mercenaria	AF120559	AF120620	AF120668
Callista chione	18S		
Order Myoida			
Superfamily Myoidea			
Family Myidae			
Mya arenaria	AF120560	AF120621	COI
Family Corbulidae			
Varicorbula disparilis	AF120561	AF120622	AF120669

Table 2. Continued.

	18S rDNA	28S rDNA	COI
Superfamily Gastrochaeonoidea			
Family Gastrochaenidae			
Gastrochaena dubia	AF120562	AF120623	AF120670
Superfamily Hiatelloidea			
Family Hiatellidae			
Hiatella arctica	AF120563	AF120624	
Superfamily Pholadoidea			
Family Teredinidae			
Bankia carinata	AF120564	AF120625	AF120671

diversity). The analysis was limited to extant taxa. For details on collection data, see http://www.mcz.harvard.edu/Departments/InvertZoo/giribet_data.htm.

Data collection

Morphological data. Morphological data were obtained from the literature and from direct observation of specimens as cited in character descriptions, resulting in 183 characters, 182 of which were treated as unordered (non-additive). Besides the many descriptions of characters referred to in the section describing the characters, 3 monographic family-level studies have been crucial (Boss 1982; Beesley et al. 1998; Coan et al. 2000).

The following morphological and anatomical studies were consulted as primary literature sources: *Solemya velum* (Drew 1900; Morse 1913; Gustafson & Lutz 1992); *Solemya reidi* (Gustafson & Reid 1988a); *Yoldia limatula* (Drew 1899a; Kellog 1915); *Nuculana minuta* (Atkins 1936); *Lithophaga lithophaga* (B.R. Wilson 1979); *Anomia ephippium* (Lacaze-Duthiers 1857b; Yonge 1977); *Spondylus sinensis* (*S. americanus* in Yonge 1973); *Neotrigonia margaritacea* (Morton 1987c); *Cardita calyculata* and *Cardites antiquata* (Yonge 1969); *Astarte castanea* (Saleuddin 1965, 1967); *Chama gryphoides* (Yonge 1967); *Galeomma turtoni* (M.L. Popham 1940; Bieler & Mikkelsen 1992); *Lasaea* sp. (M.L. Popham 1940); *Dreissena polymorpha* (Morton 1969; Pathy & Mackie 1993); *Fragum unedo* (*F. erugatum* in Morton 2000a) ; *Tridacna gigas* and *Hippopus hippopus* (Yonge 1980); *Spisula subtruncata* (Yonge 1948, 1982b); *Calyptogena magnifica* (Boss & Turner 1980); *Corbicula fluminea* (Britton & Morton 1982); *Mya arenaria* (Yonge 1982b); *Varicorbula disparilis* (Mikkelsen & Bieler 2001; also *V. gibba* in Yonge 1946); *Gastrochaena dubia* (Carter 1978); *Hiatella arctica* (Yonge 1971); *Bankia carinata* (Turner 1966); *Pandora arenosa* (*P. inaequivalvis* and *P. pinna* in Allen 1954); *Cuspidaria cuspidata* (see Yonge & Morton 1980; Morton 1987b). Additional references are provided in the character description list. The morphological character states were scored for each terminal taxon whenever possible, and if codings were based on other terminal taxa, this has been specified in the character description (Appendix 1). Morphological data (Appendix 2) were entered in the program NDE v. 0.4.6 (Page 2000), and character optimization over trees was conducted with MacClade v. 4.01 (Maddison & Maddison 2000).

Molecular data. Complete 18S rRNA sequences of 74 terminal taxa were analyzed (~1,760–2,500 bases). Of these, 60 terminal taxa were sequenced by the authors. The data set was complemented with 61 new sequences of the D3 region of the 28S rRNA loci (~300–600 bases), and by 53 sequences of the mitochondrial cytochrome *c* oxidase subunit I (COI) (660–672 bases).

Details of DNA isolation, PCR amplification, and DNA sequencing are given in Edgecombe et al. (2002) and Giribet et al. (2002). Primers used for amplification and sequencing can be found in Folmer et al. (1994) and Giribet et al. (1996, 1999, 2002).

Chromatograms obtained from the automated sequencer were read and assembled using the sequence editing software Sequencher™ 3.0. Complete sequences were edited in Genetic Data Environment (GDE) software (Smith et al. 1994). The external primers 1F and 9R (for the 18S rRNA loci), 28Sa and 28Sb (for the 28S fragment), and LCO1490 and HCO2198 (for the COI fragment) were excluded from the analyses. All the new sequences have been deposited in GenBank (accession codes are given in Tables 1 and 2).

Phylogenetic analyses

Homology concept in sequence data. While most molecular analyses use strict base-to-base correspondences (fixed alignments) for primary homology, this may introduce ambiguity and does not accommodate sequences of substantially unequal length. Instead, our

first hypothesis of homology corresponds to secondary structural features (Giribet & Wheeler 2001) followed by a dynamic base-to-base correspondence (direct optimization method; Wheeler 1996). The ribosomal sequences have been divided into unambiguously recognizable homologous regions (see Giribet 2001). The split was initiated by using internal primer regions, and then by identifying secondary structural features. Correspondences among these regions are viewed as primary hypotheses of homology, analogous to the use of morphological features to decide primary homology. The protein-coding COI sequences were not divided because we lacked internal primers or structural predictions.

In total, the 18S rRNA molecule was divided into 30 fragments, and the 28S rRNA region into 5 fragments. Nomenclature of the secondary structural regions of the 18S rRNA loci follows that of Hendriks et al. (1988). Particularly variable regions of the 18S rRNA loci are the following: E10-2 (fragment biv10-2), E21-1 (biv21-1), 41 (biv41), and 47 (biv47-2). These regions present high heterogeneity in sequence length, with large insertions in the cephalopods *Nautilus* and *Loligo* and in the Anomalodesmata, and therefore have been excluded from the analyses. The input files containing the unaligned sequences of all terminal taxa, parameter files, and batch files are available from the website http://www.mcz.harvard.edu/Departments/InvertZoo/giribet_data.htm.

Sequence data analysis: direct optimization. Sequence data were analyzed using the direct optimization method (Wheeler 1996) and implemented in the computer program POY (Gladstein & Wheeler 1997; Wheeler & Gladstein 2000). The method directly assesses the number of DNA sequence transformations (evolutionary events) required by a phylogenetic topology without the use of multiple sequence alignment. This is accomplished through a generalization of existing character optimization procedures to include insertion and deletion events (indels) in addition to base substitutions. The crux of the model is the treatment of indels as processes, as opposed to the patterns implied by multiple sequence alignment. The results of this procedure are directly compatible with parsimony-based tree lengths, and the method appears to generate more efficient (thus simpler) explanations of sequence variation than multiple sequence alignment (Wheeler 1996). Direct optimization, although computationally intense, is much less demanding than parsimony-based multiple sequence alignment algorithms. The method has also been demonstrated to yield more congruent results than multiple sequence alignments when using congruence among data sets as a criterion (Wheeler & Hayashi 1998).

Sensitivity analysis. Character transformations were weighted differentially to observe how they affect phylogenetic conclusions (sensitivity analysis *sensu* Wheeler 1995). Two analytical variables were examined: insertion-deletion cost ratio, and transversion-transition cost ratio. When the transversion-transition ratio was set at a value other than unity, the insertion-deletion cost was set according to the cost of transversions. In total, 12 combinations of parameters were used in the analysis (insertion-deletion ratios of 1, 2, and 4; transversion-transition ratios of 1, 2, 4, and ∞). This strategy allows discerning between stable relationships (those supported throughout the chosen range of parameter values) and unstable relationships (those that appear only under particular parameter sets).

Molecular data analysis. The 3 molecular data sets were analyzed independently and combined directly, with all characters weighted equally without regard to source. These data sets are referred as 18S (18S rRNA data set alone), 28S (28S rRNA data set alone), COI (COI data set alone), and molecular (18S, 28S, and COI). The COI data set, although from a protein-coding gene, was analyzed at the DNA level without specifying reading-frame constraints (because indels were inferred). Moreover, preserving the reading frame may not yield the shortest (most parsimonious) cladograms, and because we are attempting to co-optimize 3 different sources of evidence (morphology, non-coding genes, and protein-coding genes) using a sensitivity analysis framework, this seems the most appropriate way to analyze the data.

Tree search commands executed in POY included random addition sequence followed by a fast parallelized tree-building step and by subtree pruning and regrafting (SPR) and tree bisection and reconnection (TBR) branch swapping. When classical swapping algorithms did not improve tree-length, the data were subjected to several rounds of tree-drifting and tree-fusing (Goloboff 1999) to decrease tree length. The entire search strategy was repeated up to 100 times or until the results converged on the same result at least 3 times in independent replicates, as in previous analyses (Giribet et al. 2001; Edgecombe et al. 2002).

Morphological data analysis. A parsimony analysis of the morphological data set was performed with the computer program NONA v. 1.9 (Goloboff 1998). The tree-search strategy adopted initially involved a heuristic algorithm with random addition-sequence and TBR branch swapping. All characters were treated as unordered (non-additive), except for character 115, and no specific weighting schemes were applied. Since the traditional search combining random addition and TBR found the shortest tree length 1 out of 1000

times, additional analyses were performed with the beta version of TNT (Goloboff et al. 2000) using the driven search (Goloboff & Farris 2001) option. Branch support (Bremer 1988, 1994) up to 4 extra steps was calculated using a heuristic procedure and holding a maximum of 10,000 trees with NONA (command: bs 4).

Combined analysis. Morphological and molecular data (total) were combined directly and analyzed using the direct optimization method (Wheeler 1996) for the same 12 parameters that were applied to each of the molecular data sets and following the same search strategy. The morphological transformations were weighted as equal to the highest of the molecular costs (= indels), to diminish the putative overwhelming effect of molecular data vs. morphology. Bremer support values were estimated using the heuristics procedure implemented in POY (-bremer -constrain "filename" -topology "treetopology").

In total, we analyzed 6 data sets and 12 parameter sets per data set (72 analyses). POY analyses were run in a cluster of 292 Pentium III processors at 1,000 MHz connected in parallel using pvm software and the parallel version of POY (commands -parallel -jobspernode 2 in effect). The morphological analyses were run in an 866 MHz Pentium III processor.

Character congruence. Congruence between data sets (morphological and molecular) was measured by Incongruence Length Difference (ILD) metrics (Mickevich & Farris 1981; Farris et al. 1995) (see Table 3). This value is calculated by dividing the difference between the overall tree length and the sum of its data components:

$$\mathrm{ILD} = \frac{(\mathrm{Length}_{\mathrm{Combined}} - \mathrm{Sum\ Length}_{\mathrm{Individual\ Sets}})}{\mathrm{Length}_{\mathrm{Combined}}} \qquad \text{[Eq. 1]}$$

Character congruence was used as a criterion to choose our optimal tree—the tree that minimized character conflict among all the data. This is understood as an extension of parsimony (or any other minimizing criteria). In the same sense that parsimony tries to minimize the number of overall steps in a tree, the character congruence analysis attempts to find the model that maximizes overall congruence for all the data sources. Obviously, trying to generalize an evolutionary model (viewed as an inferential model we use to make sense of observations) for all taxa and all regions may be too simplistic, especially when evaluating divergences ranging from the Cambrian to the Miocene. However, evaluating for two general parameters (gap/change ratio and transversion/transition ratio) is a start point in evaluating many other parameters when faster computers become available for exploring hypotheses in phylogenetic analysis.

Results

Morphological analyses

The tree-search strategy adopted in NONA (h/10; mult*1000;max*) yielded trees of minimal length in 1 out of 1,000 replications, retaining 1,344 trees of 514 steps (CI = 0.44; RI = 0.83). Since these results were unsatisfactory as to describe the total diversity of trees (a single TBR island was found), we decided to apply more aggressive search algorithms implemented in the program TNT incorporating sectorial searches, tree fusing, and tree drifting (Goloboff 1999). A driven search was conducted and repeated 5 times, finding a consensus of 32 nodes that stabilized already in the first round, hitting minimum tree length 35 times in about 8 minutes (4 hits/min) in an 866 MHz Pentium III (256 Mb of RAM).

The strict consensus of those trees (Fig. 2) shows monophyly of Conchifera, Gastropoda + Cephalopoda, Scaphopoda + Bivalvia, and of the 5 molluscan classes represented. Bivalvia and Autolamellibranchiata are both monophyletic with good Bremer support (bs > 4). However, the protobranchiate bivalves (superfamilies Nuculoidea, Solemyoidea, and Nuculanoidea) are depicted as either monophyletic or paraphyletic, collapsing therefore in the strict consensus tree. None of the fundamental trees supports the current ordinal category Nuculoida (= Nuculoidea + Nuculanoidea) (e.g., Beesley et al. 1998). Autolamellibranchiata splits into 3 lineages: Unionidae, Trigoniidae, and a clade containing Pteriomorphia and Heterodonta, the latter including veneroids, myoids, and anomalodesmatan bivalves. Unionids are resolved either as sister group to trigoniids (making Palaeoheterodonta monophyletic), or as sister to pteriomorphs + heterodonts, thus making Palaeoheterodonta a paraphyletic assemblage. Resolution within the third clade, pteriomorphs + heterodonts, is poor, and only a few suprafamilial relationships are obtained in all the shortest trees (Fig. 2). Heterodonta is paraphyletic, with Pteriomorphia as sister group to *Galeomma turtoni*. Structure within Pteriomorphia shows Arcoida as the sister group to the remaining pteriomorphs. Pteroida, Mytiloida, Arcoida, and Limoida are monophyletic, but not the order Ostreoida, suborder Pectinina, or superfamily Pectinoidea. In addition, the superfamily Arcoidea is paraphyletic since *Glycymeris* (Limopsoidea, Glycymeridae) is placed in between the families Noetiidae and Arcidae.

A few nodes that are supported in the morphological data set are Carditidae, Pandoroidea, Cuspidariidae,

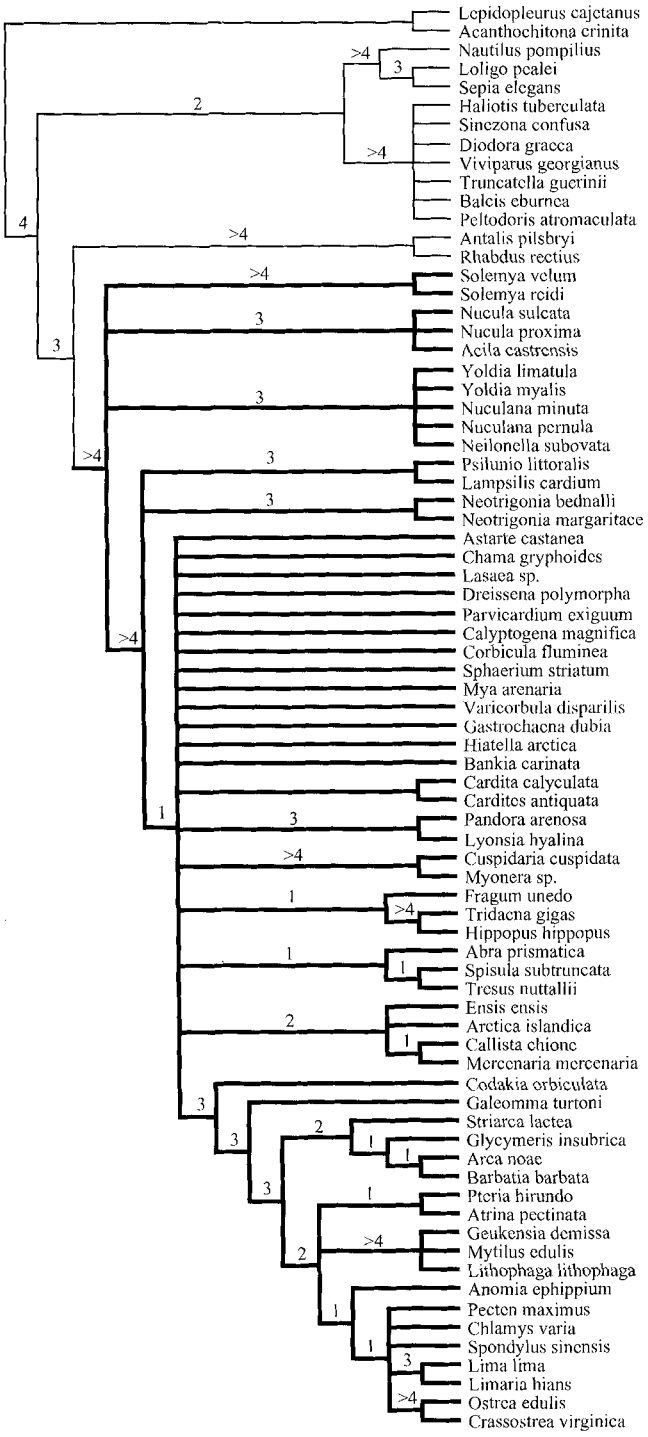

Fig. 2. Strict consensus of 600 trees of 514 steps (CI = 0.44; RI = 0.83) from a parsimony analysis of the morphological data. Numbers on branches indicate Bremer support values as calculated in Nona (up to 4 extra steps, retaining 10,000 trees). Bivalves are represented by bold branches.

Fragum + Tridacninae, Mactridae, *Abra* + Mactridae, *Ensis* + *Arctica* + Veneridae, and (*Codakia* (*Galeomma* + Pteriomorphia)). Some of these nodes are, however, supported by a single extra step (Fig. 2), and monophyly of groups such as Arcticoidea, Cardioidea, Cardiidae, Corbiculoidea, Myoida, Veneroida, and Anomalodesmata is not supported by the morphological data set alone.

Congruence analysis

The parameter set that minimizes incongruence among data sets is the one at gap/change ratio of 1 and transversion/transition ratio of 1, the topmost line of values in Table 3 (gaps are weighted equal to all base transformations). This parameter set—hereafter referred to as the optimal parameter set—reaches a maximum congruence of 0.04028. However, the 2 next suboptimal parameter sets have very similar values, ILD = 0.04049 and 0.04089 (Table 3). Choice of either one of these 3 parameter sets may be conditioned by the aggressiveness of the heuristic search strategy performed. Since the overall topology of the trees obtained under these parameter sets is highly similar, we present the results based on the best parameter set for this particular search.

Partitioned molecular analyses

18S rRNA

The analyses performed for the optimal parameter set yielded 2 trees of minimal tree length (3,979 steps), and found minimum tree length 3 times. Neither tree shows bivalve monophyly, and the strict consensus (Fig. 3) displays a polytomy of 6 clades: Nuculidae, Solemyidae + Nuculanoidea, Arcoida, a clade containing the remaining pteriomorphs, ((Carditidae + Astartidae) Palaeoheterodonta), and a clade containing Gastropoda, Scaphopoda, Cephalopoda, and the remaining bivalves. Gastropoda, Protobranchia, Pteriomorphia, and Heterodonta are each polyphyletic. However, many resolved nodes correspond to conventional taxa: *Solemya,* Nuculanoidea, Nuculoidea, Arcoida, *Astarte* + Carditidae, Palaeoheterodonta, Unionidae, *Neotrigonia,* Mytilidae, Limidae, Pectinoidea, Pectinidae, Ostreidae, Galeommatoidea, Cardioidea, Tridacninae, Veneridae, and Mactridae. Almost all conventional families represented by more than one species are monophyletic, except for Arcidae (but Arcoida is monophyletic).

The strict consensus of all parameters explored supports the following monophyletic groups: Polyplacophora, Conchifera, Coleoidea, Vetigastropoda, Dentaliidae, *Nucula sulcata,* Nuculanoidea, *Nuculana,*

Table 3. Tree lengths, at 12 sets of parameter values, for the 4 individual and 2 combined data sets, and ILD's for the combined analyses of all data. Parameters: gap/change ratio (gap); transversion/transition ratio (tv/ts). Individual data sets: 18S rDNA (18S); 28S rDNA (28S); cytochrome *c* oxidase I (COI); morphology (mor). Combined data sets: molecular (mol = 18S, 28S, and COI); total (18S, 28S, COI, and mor). Values for the parameter set that minimizes incongruence, i.e., has the lowest ILD (0.04028), appear in the topmost line; we refer to this as the "optimal parameter set" (see text).

		Individual				Combined		
gap	tv/ts	18S	28S	COI	mor	mol	total	ILD
1	1	3979	337	7060	514	11788	12389	0.04028
1	2	6094	472	11078	1028	18287	19468	0.04089
1	4	10157	711	18787	2056	30730	33049	0.04049
1	0	1971	113	3765	514	6070	6665	0.04531
2	1	4784	378	7264	1028	12911	14094	0.04541
2	2	7630	549	11417	2056	20353	22729	0.04738
2	4	13109	851	19403	4112	34702	39497	0.05119
2	0	2655	142	3938	1028	7035	8236	0.05743
4	1	6120	439	7392	2208	14595	17031	0.05120
4	2	10183	651	11688	4416	23587	28499	0.05477
4	4	18101	1036	19948	8832	41006	50917	0.05892
4	0	3747	188	4079	2208	8469	10959	0.06725

Mytilidae, *Barbatia* + *Glycymeris,* Limidae, Pectinoidea, Pectinidae, Ostreidae, Palaeoheterodonta, Unionidae, *Neotrigonia, Astarte* + Carditidae, Galeommatoidea, and Mactridae. Despite numerous unresolved nodes in the strict consensus, all the remaining groupings have morphological support.

28S rRNA

The analyses performed for the optimal parameter set yielded 50 trees (until the buffer filled) of minimal tree length (337 steps), and found minimum tree length 4 times. The strict consensus of the 50 trees obtained for the 28S rDNA data is largely unresolved, perhaps because of the small size of the data set (~300 bp used). This tree (not shown) supports polyphyly of Bivalvia, Polyplacophora, and Gastropoda. The monophyletic groups found in all the fundamental trees are Cephalopoda, Coleoidea, Vetigastropoda, *Viviparus* + *Balcis* + *Truncatella, Nucula sulcata, Atrina* + *Lyonsia,* Galeommatoidea, Carditidae, and a clade containing (*Anomia* (*Mytilus* (*Limaria* (*Pandora* + *Myonera*)))). The strict consensus of all the trees found under all parameter sets resolves only 2 clades, Coleoidea and *Atrina* + *Lyonsia.*

COI

The COI tree for the optimal parameter set yielded 1 tree of 7,060 steps (Fig. 4). This tree does not support monophyly of Polyplacophora, Gastropoda, or Cephalopoda. It also does not support bivalve monophyly because Nuculoidea and Solemyoidea nest within a clade containing gastropods and cephalopods. The remaining bivalves are resolved as a monophyletic clade, with Palaeoheterodonta as sister group to the remaining bivalves, but few suprafamilial relationships are congruent with current classifications. Nuculanoidea and *Astarte* + Carditidae are among the results that are congruent with most other data sets and parameter sets. The strict consensus of all the analyses performed with the COI data set alone yields a largely unresolved tree with a few supported nodes: *Loligo* + *Sepia,* Nuculanoidea, *Yoldia,* Arcoidea (Limopsoidea is not represented in the COI data set), Limidae, Unionidae, *Dreissena* + Myoidea, *Galeomma* + *Bankia, Mytilus* + *Geukensia,* Carditidae, and *Astarte* + Carditidae.

COI alignments within bivalves and among molluscs are not trivial, because the gene shows considerable length variation. (A sequence alignment is said to be trivial when it is not parameter dependent, that is, generally does not have insertion/deletion events). The typical length for all non-bivalve taxa studied is 669 bp. This is also true for protobranchs, palaeoheterodonts, anomalodesmatans, and few other pteriomorphs and heterodonts. But the remaining bivalves have sequences varying in length between 660 and 675 bp.

Combined molecular data (18S, 28S, COI)

The analysis of all the molecular data combined, for the optimal parameter set, yielded 2 trees (L=11,788). The strict consensus of the 2 trees (Fig. 5) shows bivalves as polyphyletic, because a clade of Nuculoidea + Solemyoidea is sister to a clade containing Scapho-

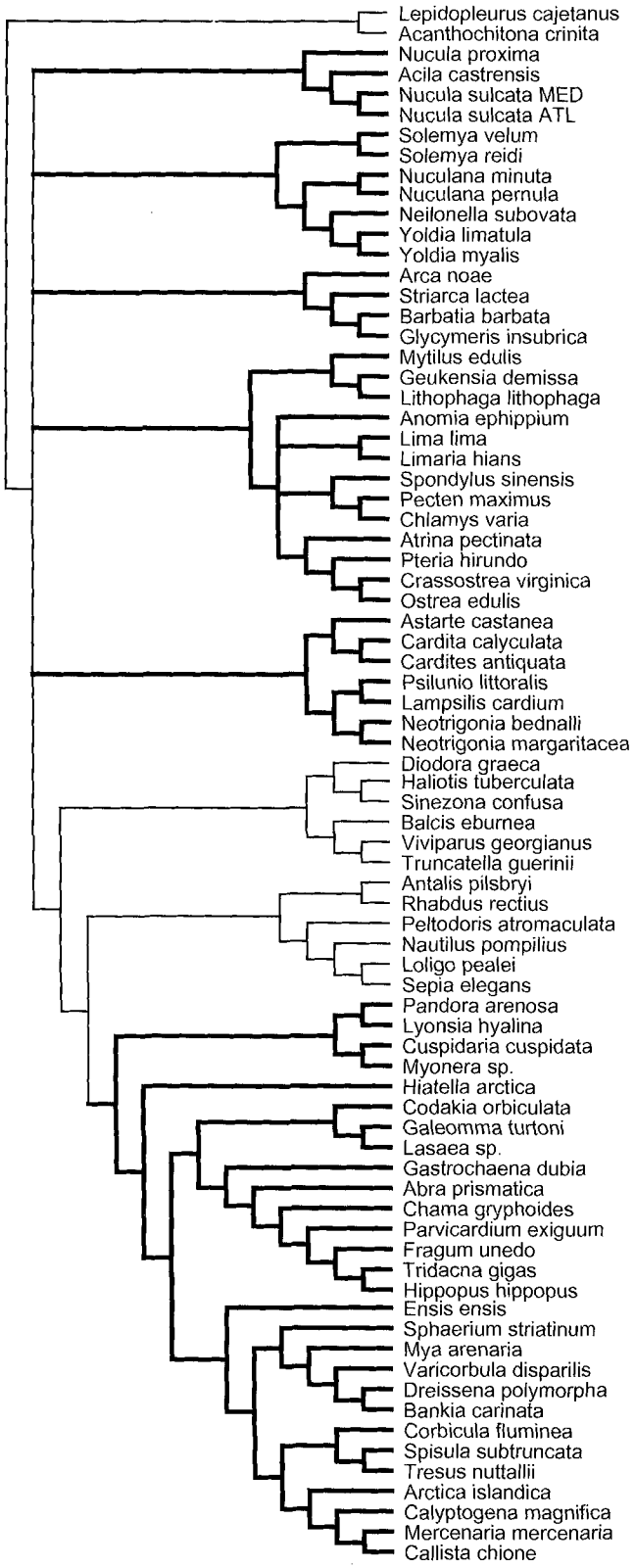

Fig. 3. Strict consensus of 2 trees at 3,979 steps for the 18S rRNA data set yielded by the optimal parameter set. Minimum tree length was found in 3 out of 100 replicates. Bivalves are represented by bold branches.

poda, Cephalopoda, and *Peltodoris*. The non-nuculoid, non-solemyoid bivalves form a clade, with the Palaeoheterodonta as sister to the remaining bivalves, including Nuculanoidea, Pteriomorphia, Heterodonta, and Anomalodesmata. Additional clades obtained are Nuculanoidea, Mytilidae, (Pinnidae (Pteriidae + Ostreidae)), Ostreidae, Arcoida, Nuculanoidea, Spondylidae + Limidae + Pectinidae, Heterodonta, Astartidae + Carditidae, Lucinidae + Anomalodesmata, Anomalodesmata, Chamidae + Cardioidea, Cardioidea, Tridacninae, *Corbicula* + Mactridae, Mactridae, Arcticoidea + Veneridae, and Veneridae (see Fig. 5 for other clades).

The strict consensus of all the parameter sets for all the molecular data analyzed in combination yielded the following monophyletic groups: Polyplacophora, Conchifera, Scaphopoda, Coleoidea, Vetigastropoda, *Nucula sulcata, Solemya,* Nuculanoidea, Mytilidae, Limidae, Ostreidae, Pectinoidea, Pectinidae, Unionidae, *Neotrigonia,* Palaeoheterodonta, Carditidae, *Astarte* + Carditidae, Mactridae, Cardioidea (*sensu* Schneider 1992), and Tridacninae.

Combined analysis (morphological and molecular)

Overall, the most congruent combined analysis of all the data is derived from a gap/change ratio = 1 and a transversion/transition ratio = 1 (ILD = 0.04028; see Table 3). This parameter set yielded a single tree of 12,389 steps (Fig. 6), and found it a single time. When the combined tree is given as a constraint to the morphological matrix, it requires 57 additional steps, a 10% increase in tree length. This indicates some conflict between the morphological and the molecular data sets. Neither the molecular nor the morphological trees drive the final phylogenetic hypothesis; rather each influences different areas of the hypothesis. The cladogram shows monophyly of Polyplacophora, Conchifera (bs = 43), Scaphopoda (bs = 59), Cephalopoda (bs = 109), and Bivalvia (bs = 20), but not Gastropoda, because *Peltodoris* is a sister taxon to Cephalopoda. The strict consensus tree obtained for the 12 parameter sets is also shown (Fig. 6). Figs. 7–10 show a schematic representation of the hypotheses obtained for the 12 parameter sets explored, and Fig. 11 summarizes the hypothesis obtained for the combined analysis.

Outgroup relationships

Scaphopoda was found to be the sister group to *Peltodoris* + Cephalopoda (Fig. 6), not to Bivalvia, as proposed by the morphological data alone (Fig. 2). The clade Scaphopoda + *Peltodoris* + Cephalopoda ap-

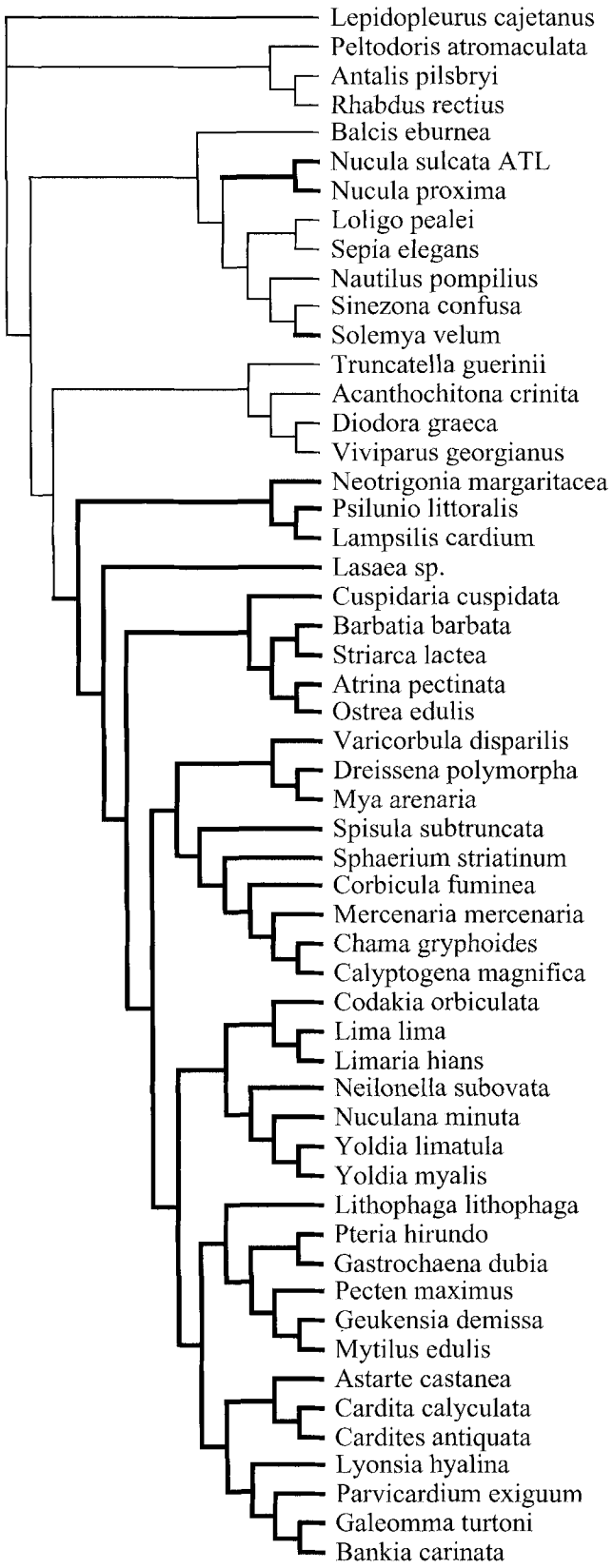

Fig. 4. Single tree at 7,060 steps for the COI data set yielded by the optimal parameter set. Minimum tree length was found in 1 out of 100 replicates. Bivalves are represented by bold branches.

pears as the sister group to the remainder of Gastropoda, and the 3 classes together constitute the sister group to Bivalvia.

Ingroup relationships

Several bivalve groups are stable to parameter change and are monophyletic in all the combined analyses (Fig. 6): *Solemya*, Nuculidae (*Nucula* and *Acila*), Nuculanoidea (*Yoldia, Neilonella,* and *Nuculana*), *Nuculana, Yoldia,* Pteriomorphia, Mytilidae (*Lithophaga, Geukensia,* and *Mytilus*), Arcoida (*Arca, Barbatia, Striarca,* and *Glycymeris*), Ostreidae (*Ostrea* and *Crassostrea*), Pectinoidea (*Spondylus, Pecten,* and *Chlamys*), Pectinidae (*Chlamys* and *Pecten*), Limidae (*Lima* and *Limaria*), Palaeoheterodonta (Unionidae and *Neotrigonia*), Unionidae (*Psilunio* and *Lampsilis*), *Neotrigonia,* Carditidae + Astartidae (*Cardita, Cardites,* and *Astarte*), Carditidae (*Cardita* and *Cardites*), Cardioidea (*Parviocardium, Fragum, Tridacna,* and *Hippopus*), Tridacninae (*Tridacna* and *Hippopus*), Mactridae (*Spisula* and *Tresus*), Veneridae (*Callista* and *Mercenaria*), and *Dreissena* + Myoidea (*Mya* and *Varicorbula*). Monophyly of the groups Bivalvia, Protobranchia, Autolamellibranchiata, Pteriomorphia, Heteroconchia, Anomalodesmata, and Heterodonta is not supported by all the parameters. However, Bivalvia, Autolamellibranchiata, and Anomalodesmata are monophyletic under most parameter sets studied (Figs. 7, 10). The 2 parameters that disrupt their monophyly are the ones showing the highest gap costs, under which the highly autapomorphic Cephalopoda is placed within the Anomalodesmata. Heteroconchia is monophyletic under 7 parameter sets, whereas Heterodonta s.l. is monophyletic under 6 parameter sets.

In the tree yielded by the optimal parameter set (Fig. 6), Bivalvia is monophyletic, with the initial split dividing the non-siphonate protobranchs (Solemyoidea + Nuculoidea) from the rest of bivalves (Nuculanoidea + Autolamellibranchiata). Protobranchia is paraphyletic for all parameter sets explored so far.

Autolamellibranchiata (Fig. 7: node 4) is monophyletic under most parameter sets, including the optimal parameter set and all the nearest suboptimal ones. Autolamellibranchiata is divided into Pteriomorphia and Heteroconchia (= Palaeoheterodonta + Heterodonta s.l.).

Pteriomorphia is monophyletic under all parameter sets (Fig. 8: node 1) with the mytiloids as the sister group to the remaining pteriomorphs (Fig. 8: node 2). Monophyly of Arcoida is supported under all parameter sets (Fig. 8: node 3), although monophyly of the superfamily Arcoidea is not supported, as the limopsoid

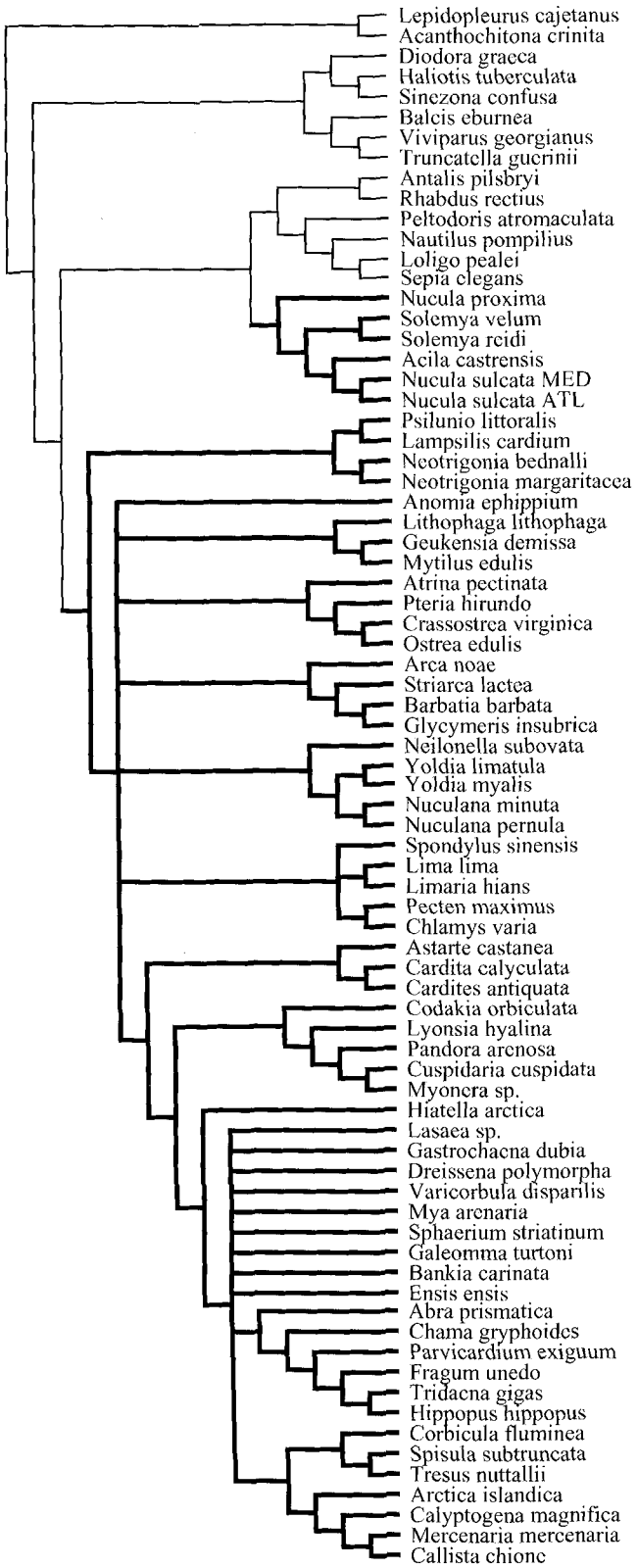

Fig. 5. Strict consensus of 2 trees at 11,788 steps for the combined molecular sequence data (18S, 28S, and COI) yielded by the optimal parameter set. Minimum tree length was found in 2 out of 100 replicates. Bivalves are represented by bold branches.

Glycymeris is generally placed between the families Arcidae and Noetiidae. Monophyly of the remaining pteriomorphs is stable (Fig. 8: node 4), although the internal relationships within the non-mytiloid non-arcoid pteriomorphs are parameter-dependent (Fig. 8). For example, the order Pteroida, composed by the superfamilies Pterioidea (represented by *Pteria*) and Pinnoidea (represented by *Atrina*) is not monophyletic under the optimal parameter set, but is monophyletic under 3 other parameter sets. The position of the family Ostreidae is also unstable; it is the sister group to Pteriidae under the optimal parameter set, but to Pinnidae or to Pectinoidea under other parameter sets (Fig. 8). The order Ostreoida is not monophyletic under any parameter set. The suborder Pectinina (a member of the order Ostreoida) here represented by one member of Anomioidea (*Anomia*) and 2 families of Pectinoidea (the pectinids *Pecten* and *Chlamys*, and the spondylid *Spondylus*) is never monophyletic.

Heteroconchia, a group composed by the monophyletic Palaeoheterodonta and Heterodonta s.l. (heterodonts including Anomalodesmata), is monophyletic under 7 parameter sets, including the optimal and 2 immediate suboptimal ones (Fig. 7: node 5). Palaeoheterodonts are monophyletic for all parameter sets explored, with Unionidae as sister to Trigoniidae.

Some relationships among heterodont groups for the parameter sets explored are shown in Figs. 9 and 10. Heterodont monophyly is obtained under 6 parameter sets (Fig. 9: node 1), including the optimal and some immediate suboptimal ones. The first split within Heterodonta s.l. is between a clade Crassatelloidea + Carditoidea—composed of the 2 carditids (*Cardita* and *Cardites*) + the astartid (*Astarte*)—and the remaining heterodonts, which include the anomalodesmatans. Monophyly of Carditidae + Astartidae is stable to parameter choice (Fig 9: node 2), as is the monophyly of the non-carditid non-astartid heterodonts (Fig 9: node 3). Relationships within the modern (non-crassatelloid, non-carditoid) heterodonts are unstable to parameter choice, and only a few relationships are stable. Among the stable groups are Cardioidea, Tridacninae, Mactridae, Veneridae, and the clade composed by the myoids (*Mya* and *Varicorbula*) + *Dreissena*, of which all are monophyletic for all parameters (Figs. 6, 10). A sister-group relationship between Chamoidea and Cardioidea is also suggested by the data and found under most parameter sets (Fig. 9: node 4), as is the monophyly of Mactroidea + Dreissenoidea + Myoidea + Arcticoidea + Corbiculoidea + Veneroidea, and the monophyly of its subgroups (Mactroidea (*Dreissena* + Myoidea)) and Arcticoidea + Corbuloidea + Veneroidea (Fig. 9: node 5). However, monophyly of Arcticoidea (rep-

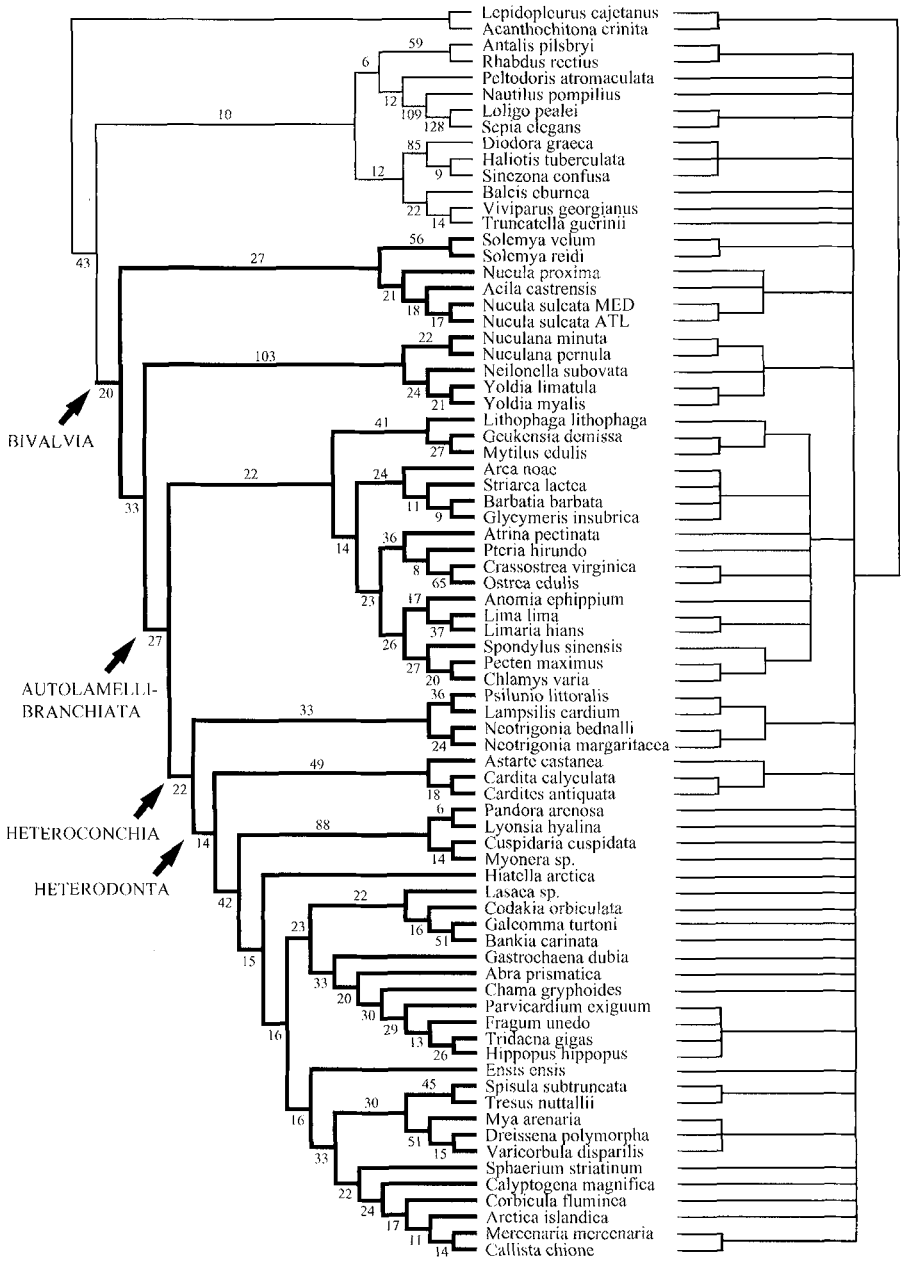

Fig. 6. Analyses of the combined morphological and molecular data.

Left: single tree at 12,389 steps for the optimal parameter set. Minimum tree length was found in 1 out of 100 replicates. Branches in bold represent bivalves. Numbers on nodes represent Bremer support values.

Right: strict consensus of all trees obtained for the 12 parameter sets explored.

resented by the vesicomyid *Calyptogena* and by the arcticid *Arctica*) is doubtful since *Arctica* forms a clade with the veneroids (Fig. 9: node 10). Monophyly of Corbiculoidea (represented by the corbiculid *Corbicula* and by the sphaeriid *Sphaerium*) is not obtained under any parameter sets.

Our data provide no evidence for recognition of the orders Veneroida and Myoida, which are not monophyletic under any analytical circumstance (data sets and parameter sets). Some of the relationships concerning the myoid taxa analyzed here are represented in Fig. 10. The results show monophyly of the superfamily Myoidea (represented by *Mya* and *Varicorbula*) under most parameter sets, and its sister-group relationship with the freshwater zebra mussel *Dreissena*. The wood-boring *Bankia* seems to be related to the galeommatid *Galeomma*. The endolithic *Gastrochaena* appears to be related to *Lasaea* and/or *Galeomma* and *Bankia*, but its exact position is not clear. The position of *Hiatella* is uncertain and highly parameter-dependent.

The data also contain strong support for the inclusion of the subclass Anomalodesmata within Heterodonta s.s. (Fig. 9: node 1, bs = 14), and particularly with the non-crassatelloid non-carditioid heterodonts (Fig. 9: node 3; bs = 42). Although Anomalodesmata

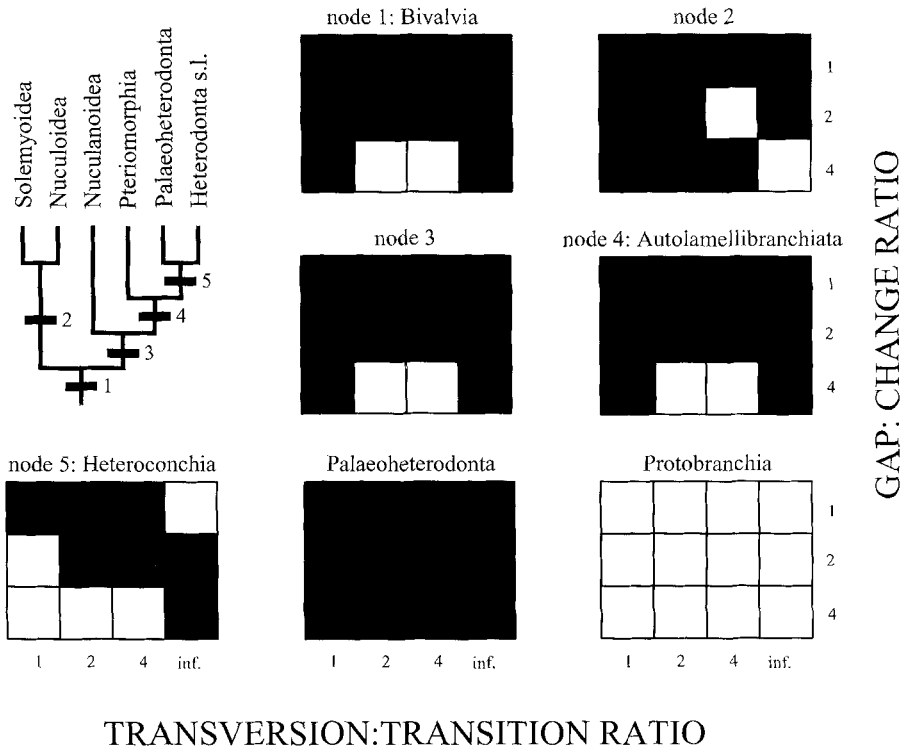

Fig. 7. Summary tree for the basal bivalve relationships and topological congruence plots for the 12 parameter sets explored. ■ = monophyletic; □ = non-monophyletic.

falls within Heterodonta, its phylogenetic position within eulamellibranchs is not clear. Sister-group relationships are suggested for Hiatellidae (2 parameter sets, but not the optimal one). Under the optimal parameter set, Anomalodesmata is sister to all non-crassatelloid, non-carditoid eulamellibranchs. However, when high parameter values are used (421 and 441), anomalodesmatans become paraphyletic with respect to cephalopods. This result may be explained by the high gap costs (of 8 and 16, respectively), which might favor the clustering of species with large insertions.

In summary, the results of the combined analysis for the optimal (most congruent) parameter set strongly suggest paraphyly of protobranchiate bivalves, monophyly of Nuculanoidea + Autolamellibranchiata, Autolamellibranchiata, Pteriomorphia, Palaeoheterodonta, Heterodonta s.l., and Anomalodesmata, as well as paraphyly of Heterodonta s.s. and Veneroida, and polyphyly of Myoida. Subclass-level status of Anomalodesmata is not supported.

Discussion

The analyses presented here are the most extensive study of bivalve phylogeny in terms of morphological characters, molecular characters, molecular loci, and taxon sampling (families, superfamilies, and orders) to date. By using character congruence among data sets as an optimality criterion to choose among multiple hypotheses of relationships, and by exploring data using a sensitivity analysis approach, we can not only generate hypotheses of relationships, but also evaluate their stability without the use of methods that perturb the data. These results should be considered in the light of previous evidence supporting relationships, some stable (which we consider well corroborated), and some not.

Scaphopoda and the sister group of bivalves

Molecular data (Winnepenninckx et al. 1996; Hoeh et al. 1998; Steiner & Hammer 2000; this study) do not support Scaphopoda + Bivalvia. A sister-group relationship between these 2 classes has been proposed by several authors based on morphological evidence (Götting 1980; Lauterbach 1983; Runnegar 1996; Salvini-Plawen & Steiner 1996). In contrast, Waller (1998) and Haszprunar (2000) proposed a closer relationship of Scaphopoda to Cephalopoda and Gastropoda. While the morphological data compiled here do not support Waller's (1998) hypothesis, the molecular data place the Scaphopoda as sister to Cephalopoda + *Peltodoris* (bs = 6), both in a clade with the remaining gastropods. This adds support to the Cyrtosoma hypothesis *sensu* Waller (1998). A clade Scaphopoda + Cephalopoda is found in 3 of the 12 parameter sets explored here, but not a single parameter set supports Scaphopoda + Bivalvia. The close relationship of Scaphopoda to Cephalopoda +

Gastropoda appears to be supported primarily by the molecular data (bs = 10). We thus conclude that Scaphopoda are probably not sister to Bivalvia, although more data are needed. This is clearly indicated by the unexpected behavior in sequence analyses of the gastropod *Peltodoris,* which clusters between Scaphopoda and Cephalopoda under some parameter sets.

Bivalvia

Bivalve monophyly has not generally been supported by molecular studies (Steiner & Müller 1996; Winnepenninckx et al. 1996; Adamkewicz et al. 1997; Campbell et al. 1998; Hoeh et al. 1998; Steiner 1999), even when taxon sampling is improved (Campbell 2000; Steiner & Hammer 2000). Likewise, in the present study, the molecular data alone do not support monophyly of Bivalvia, because a clade of protobranchiate bivalves (Nuculoidea and Solemyoidea) appears nested within some outgroup taxa (Fig. 5). Similarly, the 18S rDNA analyses of Adamkewicz et al. (1997) had *Solemya, Yoldia,* and 2 anomalodesmatans (*Periploma* and *Cuspidaria*) clustering with outgroup taxa, and *Solemya* was also related to the gastropods in the 18S rDNA study of Campbell et al. (1998).

The lack of support for monophyly of bivalves with molecular data has been interpreted to indicate polyphyletic origins of the bivalve body plan (Hoeh et al. 1998). As noted by these authors, their analyses had limited taxon and character sampling (a maximum of 613 bp for 17 taxa: 1 polyplacophoran, 1 scaphopod, 1 gastropod, and 14 bivalves). In our study, the tree obtained from the 54 COI sequences alone (using the same fragment as Hoeh et al. 1998) for the optimal parameter set supported polyphyly of Polyplacophora, Scaphopoda, Cephalopoda, Gastropoda, and Bivalvia (Fig. 4), and did not support monophyly of Protobranchia, Autolamellibranchiata, Pteriomorphia, or Heterodonta. These results suggest that COI sequence data (at least from this COI fragment) lack sufficient phylogenetic signal to reconstruct higher molluscan relationships, instead of indicating a polyphyletic origin of bivalves.

Our combined molecular and morphological data set supports the monophyly of bivalves under most parameter sets (Fig. 6 and Fig. 7: node 1). Bivalves are supported by 10 unambiguous morphological synapomorphies (characters optimized using MacClade 4.0): presence of pallial lines (character 24); body compressed laterally (character 45); absence of a differentiated head (character 46); presence of mantle lobes (character 50) (also present in Scaphopoda); presence of laterofrontal gill cilia (character 75); presence of labial palps (character 79); absence of radula, odontophore, and associated buccal organs (character 85); presence of adductor muscles (character 106); presence of a burrowing foot with anterior enlargement (character 109), also present in Scaphopoda; and presence of an epiathroid nervous system with identical innervation areas (character 123) (also present in Scaphopoda). The large amount of morphological evidence supporting bivalve monophyly, and the Bremer support value (bs = 20), as well as the stability of its monophyly to parameter choice when the morphological and molecular data are combined, strongly suggest that bivalves are monophyletic. We obviously prefer the conclusions based on our more extensive analyses to those based on small subsets of taxa and/or individual fragmentary data sets.

Protobranchiate bivalves

Protobranchiate bivalves have been considered by many authors to be monophyletic and the most primitive group of bivalves because of the presence of a plesiomorphic type of ctenidia and their Cambrian origin. Classification of the Protobranchia has been a matter of contentious debate (Scarlato & Starobogatov 1979; Allen & Hannah 1986; Maxwell 1988). Beesley et al. (1998) adopted a classification system following Maxwell (1988) and recognized 2 orders, Solemyoida and Nuculoida, the latter including the superfamilies Nuculoidea and Nuculanoidea. In contrast, Waller (1998) considered Nuculoida paraphyletic ((Nuculoidea + Solemyoidea) Nuculanoidea). Our morphological tree does not support monophyly of Protobranchia but rather supports Solemyoidea, Nuculoidea, and Nuculanoidea as monophyletic groups. The combined data suggest a close relationship between Solemyoidea and Nuculoidea, as proposed by Waller (1998); this result is stable to parameter change (Fig. 7: node 2). Monophyly of Solemyoidea + Nuculoidea is supported by one unambiguous morphological synapomorphy: the presence of an adoral sense organ (character 141). However, inclusion of more protobranch taxa could change the optimization of this character because adoral sense organs have been observed in some nuculanoids not represented in the present analysis, such as *Nuculana fossa, N. pella,* and *Yoldia amygdalea* (Schaefer 2000).

The clade Solemyoidea + Nuculoidea is not sister to Nuculanoidea, but rather to the clade Nuculanoidea + Autolamellibranchiata, making Protobranchia a paraphyletic group. This result is obtained under 10 of the 12 parameter sets examined (Fig. 7: node 3), including the optimal parameter set. Monophyly of the protobranchiate bivalves is not found under any combination of parameters here explored.

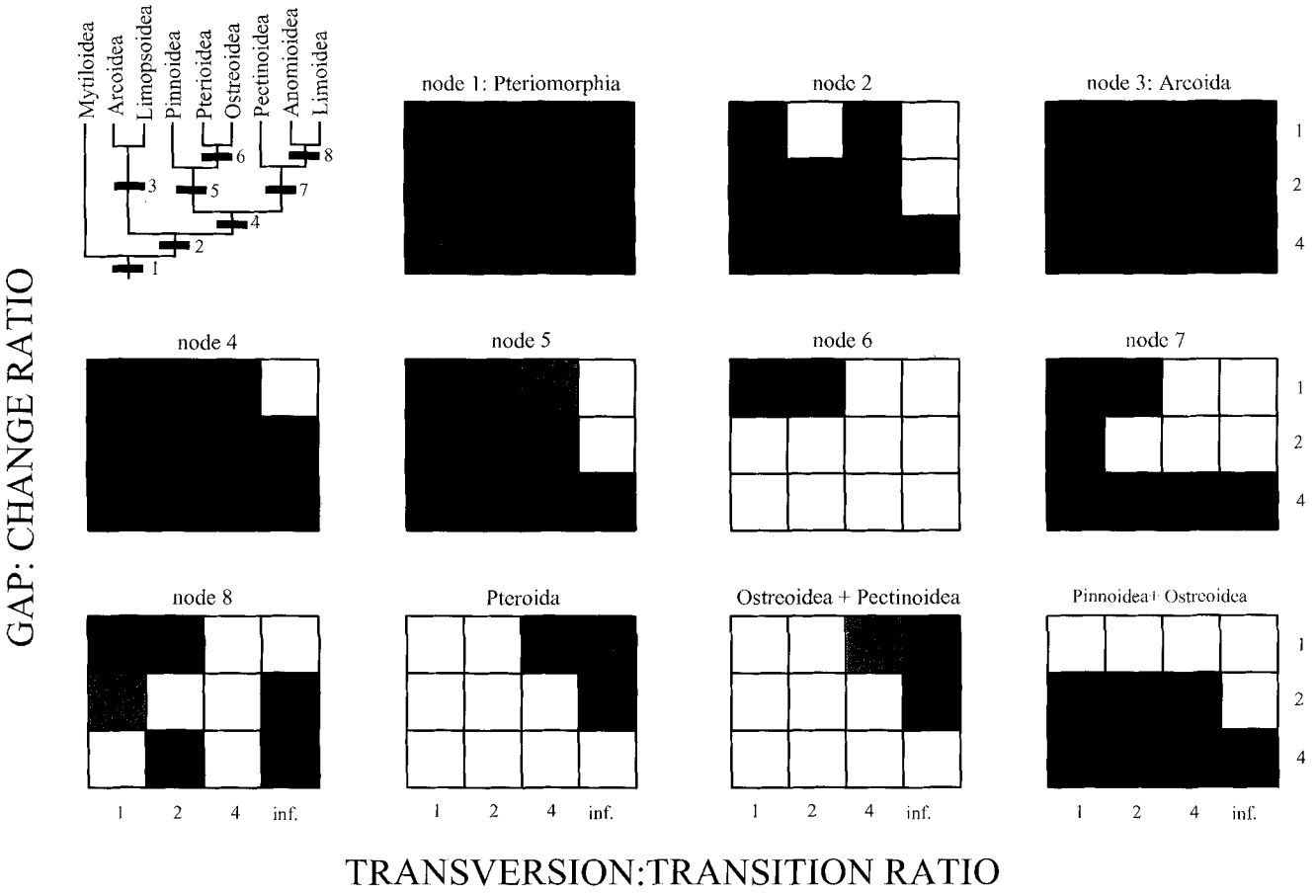

Fig. 8. Summary tree for pteriomorph relationships and topological congruence plots for the 12 parameter sets explored. ■ = monophyletic; ▒ = some of the Most Parsimonious Trees consistent with monophyly; □ = non-monophyletic.

Monophyly of Nuculanoidea + Autolamellibranchiata is supported by 3 unambiguous optimizations: absence of prismatic structure in the shell (character 7), which reverts in several lineages; absence of a hypobranchial gland (character 62); and absence of a molluscan cross during development (character 172). A molluscan cross is absent in all bivalves except solemyoids. A structure similar to a molluscan cross has been observed in *Solemya reidi* (Gustafson & Reid 1986) and *S. velum* (Gustafson & Lutz 1992), but no data are available for Nuculoidea. Optimization of this character might change when new data are added. The alternative hypothesis of protobranch monophyly is supported by 2 unambiguous morphological synapomorphies: occurrence of extra- and intracellular digestion in the midgut gland (character 87), and presence of a pericalymma larva during development (character 174).

Based on our analyses, we tentatively propose that bivalves with gills of the protobranch type are paraphyletic. This conclusion will require further investigation, particularly of developmental characters related to molluscan-cross formation, and of additional data not sampled in this study. Addition of more observations and more taxa could change how several optimizations behave in the relationships presented here.

Autolamellibranchiata

Members of Autolamellibranchiata are characterized as having modified gills that are not of the protobranch type. Autolamellibranchiata constitutes a clearly monophyletic group; this is stable to parameter choice (Fig. 7: node 4), and shows high Bremer support values (bs = 27). The clade is supported by 14 unambiguous morphological optimizations: presence of prosogyrous umbones (character 26), shifting to orthogyrous in a few lineages; having a mantle cavity occupied by gills lateral and posterior to the foot (character 63); presence of reflected ctenidia (character 66); absence of palp appendages (character 81); absence of esoph-

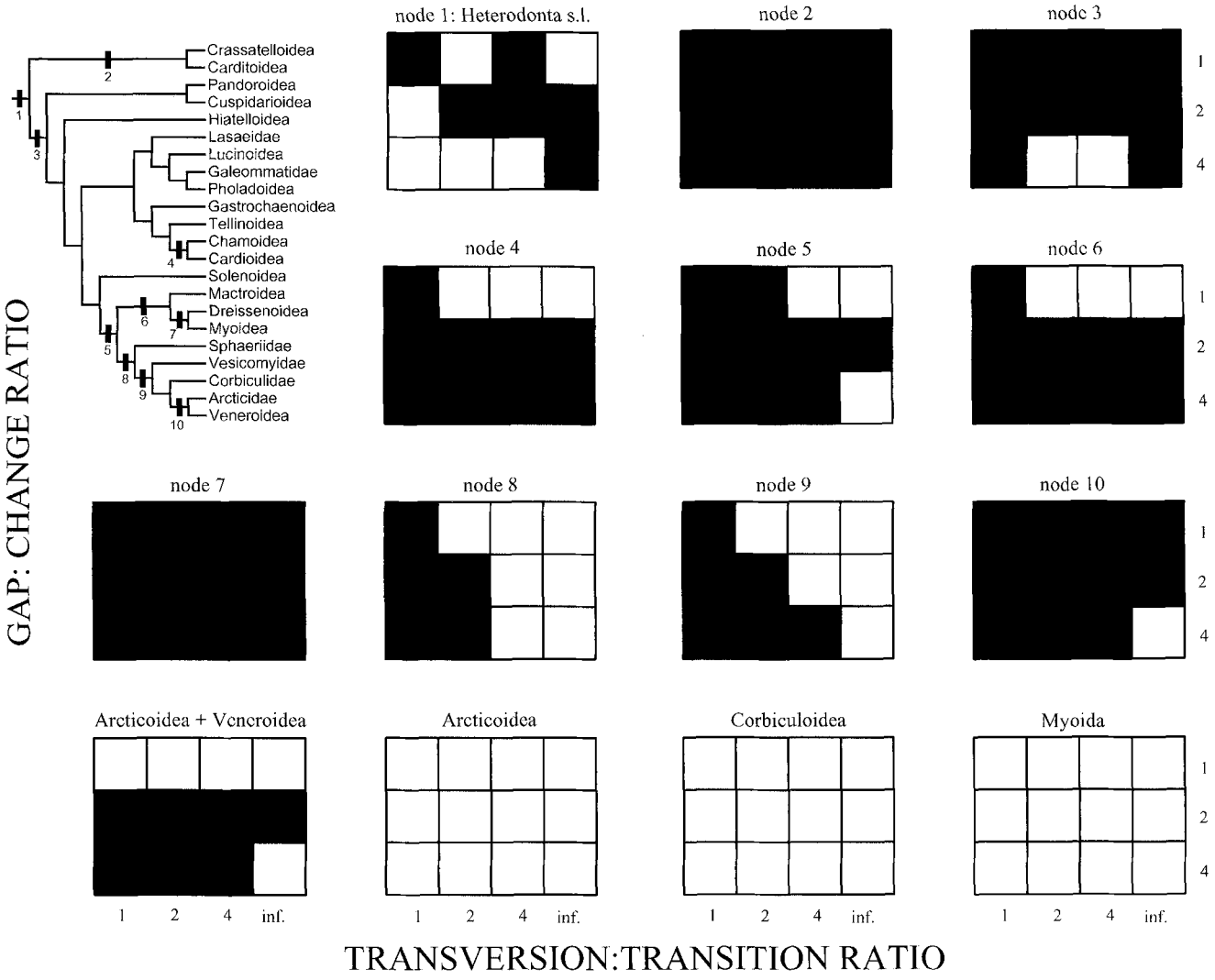

Fig. 9. Summary tree for heterodont relationships and topological congruence plots for the 12 parameter sets explored. ■ = monophyletic; □ = non-monophyletic. Only selected nodes are represented.

ageal ridges (character 86), secondarily originated in lucinids; presence of ciliated midgland ducts (character 88); stomach with a crystalline style (character 89); elongated major typhlosole (character 91); absence of a ventral surface of the foot (character 110); presence of a posterior pedal gland (character 114); presence of byssus (character 115); presence of hemocyanin-like molecules (character 120); visceral ganglia larger than pedal ganglia (126); and presence of nerve-type visceral connectives (character 127).

Autolamellibranch bivalves are also supported as monophyletic in many of the partitioned analyses. Lack of support for monophyly of Autolamellibranchiata in earlier studies may have resulted from limited taxon sampling, problems of alignment, or rooting with uninformative outgroups (see Giribet & Carranza 1999). We propose that Autolamellibranchiata is the sister group to Nuculanoidea, and that it is composed of 2 main clades: Pteriomorphia and Heteroconchia.

Pteriomorphia

Pteriomorph relationships had received little attention in modern phylogenetic studies, until the publication of the morphological analyses of Carter (1990a), Waller (1998), the molecular analysis of Steiner & Hammer (2000), and studies interested in the position of mytilids within bivalves (Distel 2000; Distel et al. 2000). Our analyses clearly suggest that pteriomorph bivalves are monophyletic, agreeing with the study of Steiner & Hammer (2000). This result is stable to parameter choice and has a Bremer support

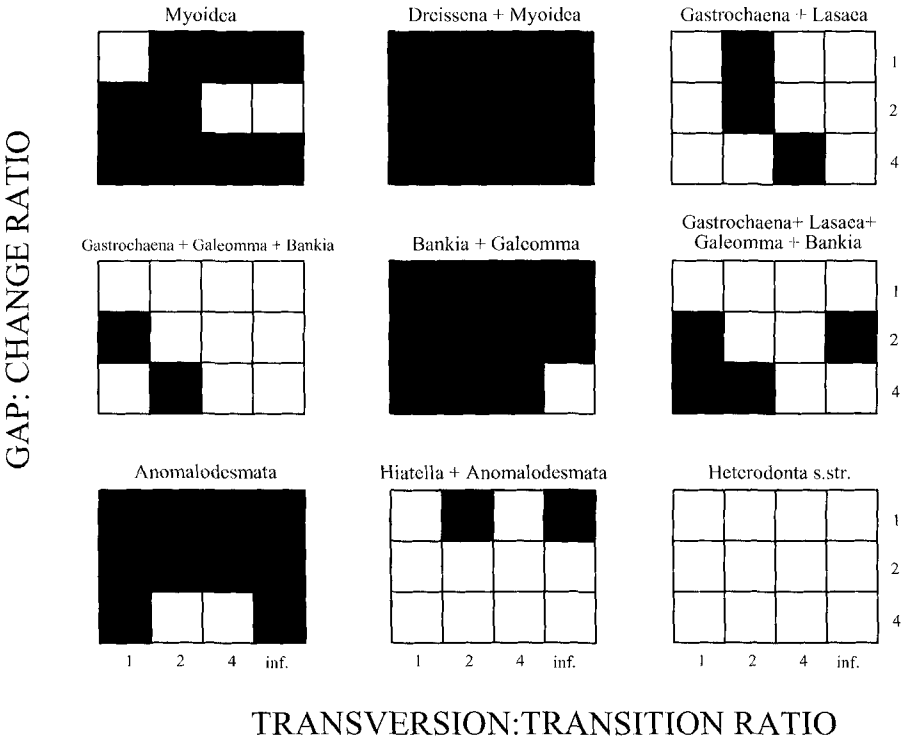

Fig. 10. Topological congruence plots for the 12 parameter sets explored showing relationships for selected myoid and anomalodesmatan heterodonts. ■ = monophyletic; □ = non-monophyletic.

value of 22. Monophyly of Pteriomorphia is supported only by a single unambiguous morphological optimization: presence of egg cleavage with polar lobe formation (character 171). However, the combined molecular and morphological data strongly support this clade.

Mytiloidea constitutes a monophyletic group, sister to the remaining pteriomorphs. This result is stable to parameter changes, and is detected in 8 of the parameter sets explored. The basal position of Mytiloidea within Pteriomorphia has been proposed by other investigators (i.e., Waller 1998; Steiner & Hammer 2000 [combined analysis]), although the molecular analyses published so far do not support the basal position of Mytiloidea (Giribet & Carranza 1999; Steiner 1999; Distel 2000; Steiner & Hammer 2000 [molecular analyses]). The basal position of Mytiloidea is supported by our morphological data (Fig. 2) as well as by most parameter sets for the combined morphological and molecular analyses. However, under certain parameter sets, mytiloids switch positions with arcoids, or appear as the sister group of Heteroconchia, instead of to the remaining pteriomorphs. These results may be due to conflicting data in the molecular data sets, where mytilids show large amounts of change (Distel 2000). Despite uncertainty in their sister-group relationships, our results corroborate the basal position of Mytiloida within Pteriomorphia.

Monophyly of the non-mytiloid pteriomorphs is well corroborated by the data (Fig. 8: node 2; bs = 14), and is supported by 3 unambiguous changes: presence of a byssal gape (character 20); presence of laterofrontal cilia of the microciliobranchiate type (character 76); and a type III ctenidial-palp association (character 78). This result contrasts with the position of Mytiloidea in previous molecular analyses (Steiner & Hammer 2000), but agrees with the most recent morphological analysis of pteriomorph relationships (Waller 1998), and it is stable to parameter changes (Fig. 8: node 2).

Arcoida is sister to the remaining pteriomorphs (non-mytiloids, non-arcoids), which are monophyletic under 11 parameter sets. This result contrasts with the position suggested by the 18S rRNA trees of Steiner & Hammer (2000), but agrees with their combined tree of 18S rRNA and morphology, resolving a basal polytomy presented by Waller (1998). This relationship is not supported by our morphological tree (Fig. 2), which places the arcoids as the sister group to the remaining pteriomorphs (including mytiloids). The monophyly of the arcoidan superfamily Arcoidea (Noetiidae and Arcidae) is not supported by the data because the limopsoid *Glycymeris* disrupts arcoidean monophyly under most parameter sets. Also, the molecular data fail to resolve the relationships among the 4 members of Arcoida. Further examination of the high-level arcoidan relationships is needed. A similar lack of in-

ternal structure of the families was found for a more extensive arcoidean analysis using 18S rRNA sequence data (Steiner & Hammer 2000).

Monophyly of the remaining pteriomorphs is stable (Fig. 8: node 4; bs = 23) but the relationships among these groups (Pterioidea, Pinnoidea, Anomioidea, Limoidea, Ostreoidea, and Pectinoidea) are highly parameter-dependent and need further evaluation. For example, monophyly of the order Pterioida (Pterioidea + Pinnoidea) is obtained under 3 parameter sets (not including the optimal one), but monophyly of Ostreoida (Ostreina + Pectinina) and Pectinina (Pectinoidea + Anomioidea) is not supported. Some other pteriomorph relationships are summarized in Fig. 8. The instability of these results may be ascribed to poor taxon sampling within the group, represented by only 10 of the 22 pteriomorph families. However, the support for monophyly of Pteriomorphia, Mytiloida, Arcoida, the remaining pteriomorphs, Limoidea, Ostreidae, and Pectinoidea constitutes a good basis for further studies of pteriomorph relationships.

Previous molecular studies have failed to obtain pteriomorph monophyly (e.g., Steiner & Müller 1996; Adamkewicz et al. 1997; Campbell et al. 1998; Distel 2000), possibly due to deficiencies in taxon or character sampling, as demonstrated by more inclusive analyses (Campbell 2000; Steiner & Hammer 2000). In conclusion, our analyses indicate that pteriomorph bivalves constitute a monophyletic group, probably with the following internal structure: (Mytiloida (Arcoida ((Pinnoidea (Pterioidea + Ostreoidea)) (Pectinoidea (Anomioidea + Limoidea))))), a topology highly compatible with the combined tree of 18S rRNA and morphology presented by Steiner & Hammer (2000). Ostreoida is polyphyletic, Pteroida and Pectinina are weakly supported by the data, and the relationships among some of their superfamilies are unstable. The position of the superfamilies Plicatuloidea and Dimyioidea has not been addressed in the present analysis.

Heteroconchia

Heteroconchia (*sensu* Cox 1960) includes all bivalves with heterodont hinges. This well corroborated group (bs = 22) includes the Palaeoheterodonta and the Heterodonta s.l. (Heterodonta including Anomalodesmata) although, under some parameter sets, palaeoheterodonts and the oldest heterodonts (Carditoidea + Crassatelloidea) do not form a clade with the remaining heteroconchs. Heteroconchia has been previously proposed as a monophyletic group based on morphological data (Waller 1990, 1998; Starobogatov 1992; Carter et al. 2000) and on 18S rRNA sequence data analyses (Adamkewicz et al. 1997; Campbell 2000; Steiner & Hammer 2000). However, data on Trigonioidea were not available in the molecular studies. In contrast, Heteroconchia was not supported by the cladistic analysis of morphological data of Salvini-Plawen & Steiner (1996), shell structure comparisons (Cope 1996, 1997, 2000), palaeontological comparisons (Morton 1996), or molecular analysis of COI data (Hoeh et al. 1998).

The data presented here support Heteroconchia as a monophyletic group, which is diagnosed by a provinculum with differentiated dentition (character 38) and dorsoventral muscles reduced to 2 pairs (or fewer) (character 105). Heteroconchia is divided into 2 clades: Palaeoheterodonta and Heterodonta s.l.

Palaeoheterodonta

The name Palaeoheterodonta was given by Newell (1965) to group the early Paleozoic actinodonts and the extant unionoids and trigonioids. Palaeoheterodonts were considered to be a monophyletic group (Cope 1996) nested within the Pteriomorphia (Morton 1996), or sister to Anomalodesmata (Cope 1997) (Fig. 1C). A recent suggestion excludes the trigonioids (Cope 2000). Previous morphological character analyses did not support monophyly of Palaeoheterodonta (Purchon 1987b; Salvini-Plawen & Steiner 1996). Purchon (1987b) proposed a relationship among Unionoidea and 3 superfamilies of heterodonts (Crassatelloidea, Carditoidea, and Leptonoidea), with Trigonioidea as their sister group (Fig. 1A). Salvini-Plawen & Steiner (1996) considered trigonioids to be the sister group to Pteriomorphia, while unionoids were related to Heterodonta s.l. (Fig. 1B). The COI sequence of *Neotrigonia margaritacea* (Hoeh et al. 1998) was the first molecular data for a trigonioid and suggested monophyly of Palaeoheterodonta, but did not support Palaeoheterodonta as a sister group of heterodonts. Monophyly of Palaeoheterodonta was corroborated by a broader taxonomic selection of COI sequence data (Graf & Ó Foighil 2000) and is also supported by our molecular data (bs = 33) (with the exception of 28S rRNA) and for the total evidence analyses for all the parameter sets. It is also seen in some of the shortest trees for the morphological data analysis. We conclude that Palaeoheterodonta is a monophyletic group (one of the best corroborated bivalvian clades according to our data), and is sister to Heterodonta s.l. Synapomorphies of Palaeoheterodonta include 3 characters with homoplasy outside the clade: an aragonitic shell of simple prismatic structure (character 7) with 3 shell layers (character 12); and 3 openings of ducts (character 102). Another synapomorphy

without homoplasy is presence of multiple acrosomal vesicles in the sperm (character 155; observed in several unionids and trigoniids; Healy 1989, 1996b; Lynn 1994).

Heterodonta s.l.

Heterodonta s.l. comprises Anomalodesmata and the heterodont orders Myoida and Veneroida. Classically, Anomalodesmata has been considered as the sister group to a monophyletic Heterodonta (Myoida and Veneroida), although other relationships have been proposed. Anomalodesmata has been suggested as a sister group either to Myoida (Morton 1996; Salvini-Plawen & Steiner 1996), to Palaeoheterodonta (Cope 1997), or to Heteroconchia (Cope 2000). Morton (1996) proposed monophyly of Heterodonta s.l., although this was not supported by other morphological analyses (Purchon 1987b; Salvini-Plawen & Steiner 1996). Cope (1997) considered Anomalodesmata and Heterodonta as having independent origins (thus Heterodonta s.l. would not be monophyletic), but later proposed a clade Anomalodesmata + Heteroconchia (including unionoids but not trigonioids) (Cope 2000).

Our analyses suggest that heterodonts including anomalodesmatans form a monophyletic clade Heterodonta s.l., although neither Heterodonta s.s., Myoida, nor Veneroida is monophyletic. This result is consistent with recent molecular analyses (Campbell 2000; Steiner & Hammer 2000). The internal structure of Heterodonta s.l. is not stable, probably because some families were represented by a single taxon, or not represented at all. In Figs. 9 and 10, we have represented the most stable nodes for the heterodont subtree. Heterodonta s.l. can be divided into a clade Crassatelloidea + Carditoidea (Fig. 9: node 2), and a clade containing the rest of the eulamellibranchian taxa, including Anomalodesmata (Fig. 9: node 3). Heterodonts typically have a shell with crossed lamellar structure (character 8), although this is found also in several pteriomorphs, and therefore could be a symplesiomorphy for Autolamellibranchiata. Likewise, ventral mantle fusion (character 51) is also found in *Pteria* and in the mytilids.

Crassatelloidea + Carditoidea. In the present study Crassatelloidea is represented by a single species of the family Astartidae (*Astarte castanea*); the other family, Crassatellidae, is not represented. Carditoidea is represented by 2 species of Carditidae (*Cardita calyculata* and *Cardites antiquata*); the family Condylocardiidae is not represented. Monophyly of Carditidae and of Carditidae + Astartidae is obtained throughout the spectrum of parameters for the combined morphological and molecular data (Fig. 6). Monophyly is also yielded under all parameter sets for the 18S rRNA, COI, and combined molecular analyses, as well as the morphological analysis (Fig. 2). Sperm characters are unambiguous synapomorphies for the group: 8 mitochondria in the midpiece (character 167); a proximal centriole that splits open and unrolls to form a banded rootlet during the transitional phase from spermatid to spermatozoa (character 169). These synapomorphies and the strong molecular signal compel us to propose a sister-group relationship of these 2 superfamilies. The monophyly of this group is also corroborated by certain morphological features not coded in the matrix. For example, in Astartidae, the hinges, especially in *Goodallia* spp., are extremely similar to those of *Cuna* spp. in the Condylocardiidae (P. Middelfart, pers. comm.). Further analyses including members of the families Condylocardiidae and Crassatellidae will be required for a possible systematic rearrangement of the 2 superfamilies. A sister-group relationship of Carditoidea + Crassatelloidea to the remaining heterodonts is found under 6 parameter sets, but under some suboptimal parameters this clade groups with either pteriomorphs or palaeoheterodonts. These results are consistent with a previous hypothesis that Crassatelloidea and Carditoidea are the most primitive eulamellibranchs, and sister group to the remaining heterodonts (Yonge 1969). Other authors also proposed Astartidae as the most basal heterodont taxon represented in a 28S rRNA analysis, although no other crassatelloids or carditoids were sampled (Park & Ó Foighil 2000). Based on 18S rRNA sequence data, Campbell (2000) suggested that Carditoidea was the most basal heterodont taxon, but no crassatelloids were sampled. Purchon (1987b) removed Crassatelloidea, Carditoidea, and Leptonoidea (= Galeommatoidea) from Veneroida, and placed them with Unionoidea in the suborder Unionoida. The basal position of Crassatelloidea and Carditoidea contrasts with the notion that members of Lucinoidea are the earliest diverging heterodonts (Carter et al. 2000). Morton (1996) considered Lucinoidea, Crassatelloidea, and Galeommatoidea to form a clade of the most basal extant heterodont bivalves, whereas members of Carditoidea were regarded as derived heterodonts. However, the data presented here strongly suggest that the clade Carditoidea + Crassatelloidea is monophyletic and is the sister group of the remaining heterodonts, including Anomalodesmata.

Unnamed node 3. This clade includes all heterodonts except for members of the Crassatelloidea + Carditoidea. This node is stable to parameter choice (Fig. 9: node 3), and in all cases includes the former subclass Anomalodesmata, which therefore does not warrant such a taxonomic rank. Few other heterodont relationships are stable

(Fig. 9), and many relationships suggested by the analyses are surprising when compared to classical taxonomy. Some hypotheses are supported. Tridacninae appears nested within Cardiidae (Schneider 1992, 1998; Schneider & Ó Foighil 1999), and therefore the taxon names Tridacnoidea and Tridacnidae should be avoided. Cardioidea (represented by 4 members of Cardiidae) and Chamoidea (represented by *Chama*) are sister taxa under most parameter sets (Fig. 9: node 4). Other stable nodes (Fig. 9) show monophyly of Mactroidea, Dreissenoidea, and Myoidea (node 6) and monophyly of Dreissenoidea and Myoidea (node 7). These relationships, especially the sister-group relationship of *Dreissena* and the 2 myoids (*Mya* and *Varicorbula*), were completely unexpected from a morphological viewpoint. Thus the orders Myoida and Veneroida are both non-monophyletic. This result is further corroborated by many other unexpected sister-group relationships of members of Myoida (see Fig. 10 for several relationships involving myoid taxa). *Gastrochaena* either appears as sister to *Lasaea,* or forms a clade with *Bankia* and *Galeomma,* among other possibilities. *Bankia* is sister to *Galeomma* in most analyses. The relationship of *Galeomma* and *Bankia* is supported by the COI data, while a clade *Galeomma* + *Lasaea,* expected from morphology (but not supported by our morphological analysis) is suggested by the 18S rRNA data (Fig. 3). These groups deserve additional study. Finally, within the myoids, the behavior of *Hiatella* is unexpected, in being highly parameter-dependent.

Other stable relationships within the derived heterodonts are the sister-group relationship of Arcticidae (*Arctica*) and Veneridae (*Callista* and *Mercenaria*), making Arcticoidea (represented by *Calyptogena,* a member of Vesicomyidae, and by *Arctica*) non-monophyletic; Corbiculoidea (represented by *Corbicula* and *Sphaerium*) is not monophyletic under any parameter sets, and generally is related to Arcticoidea and Veneroidea (Fig. 9: node 8). A relationship between Mactroidea, Dreissenoidea, Myoidea, Arcticoidea, Corbuloidea, and Veneroidea is suggested by the data (Fig. 9: node 5). This node of heterodonts is particularly interesting because it includes the 3 families of freshwater heterodont bivalves (Sphaeriidae, Corbiculidae and Dreissenidae). The relative position of these 3 freshwater families was investigated with 28S rRNA data (Park & Ó Foighil 2000). This analysis included several families of Heterodonta s.s. (therefore no anomalodesmatans or myoids were included), and strongly suggested that Corbiculoidea (Corbiculidae and Sphaeriidae) is polyphyletic, with corbiculids closely related to veneroids and mactroids, whereas sphaeriids diverged earlier. No sister-group relationship of *Corbicula* and *Sphaerium* is suggested by either the morphological or molecular data sets, although many parameter sets suggest a convex relationship of both groups (i.e., *Sphaerium* and *Corbicula* nest next to each other but do not form a clade). A character supporting a putative sister-group relationship of *Corbicula* and *Sphaerium* is presence of a hypobranchial gland (character 62). Hypobranchial glands of autolamellibranchs are restricted to a few pteriomorphs (none of which were included in the present data set) and some eulamellibranchs that incubate their larvae (Corbiculidae and Sphaeriidae, the only heterodonts presenting such a structure; Morton 1977).

Anomalodesmata. Anomalodesmata is undersampled in terms of its diversity, with representative members of the families Pandoridae (*Pandora arenosa*), Lyonsidae (*Lyonsia hyalina*), and Cuspidariidae (*Cuspidaria cuspidata* and *Myonera* sp.). Relationships within Anomalodesmata are therefore not extensively discussed in the context of the present study. Anomalodesmatans constitute a clearly monophyletic group (Fig. 10) supported by molecular data alone. The combined morphological and molecular data also recover monophyly (Fig. 6); however, the morphological analysis alone does not (Fig. 2). As mentioned above, anomalodesmatans are nested within heterodont bivalves, and therefore their subclass rank is not justified. However, the sister-group relationship of Anomalodesmata is unstable to parameter-choice, requiring further study. The optimal parameter set places Anomalodesmata as sister to the remaining heterodonts (excluding crassatelloids and carditoids), as suggested by previous molecular analyses (Campbell 2000). Other parameters suggest a sister-group relationship to *Hiatella* (Fig. 10), but alternative possibilities exist. In agreement with recent analyses (Campbell 2000; Steiner & Hammer 2000), Anomalodesmata is monophyletic and derived from heterodont bivalves, unlike previous molecular analyses (Adamkewicz et al. 1997). In fact, the heterodont condition of anomalodesmatans had been reported by earlier authors, who considered Anomalodesmata to be the sister group to Myoida (Morton 1996; Salvini-Plawen & Steiner 1996). Such a relationship makes Heterodonta a paraphyletic group (contra Cope 1997, 2000; Waller 1990, 1998), unless it is rediagnosed to include Anomalodesmata, as we propose.

Phylogenetic conclusions

The taxa analyzed here encompass a large spectrum of bivalve diversity, and offer a large and diverse set of characters (morphological, anatomical, and molecular). Many of the results obtained using character congruence as an optimality criterion are stable to parameter choice, while others will require more data.

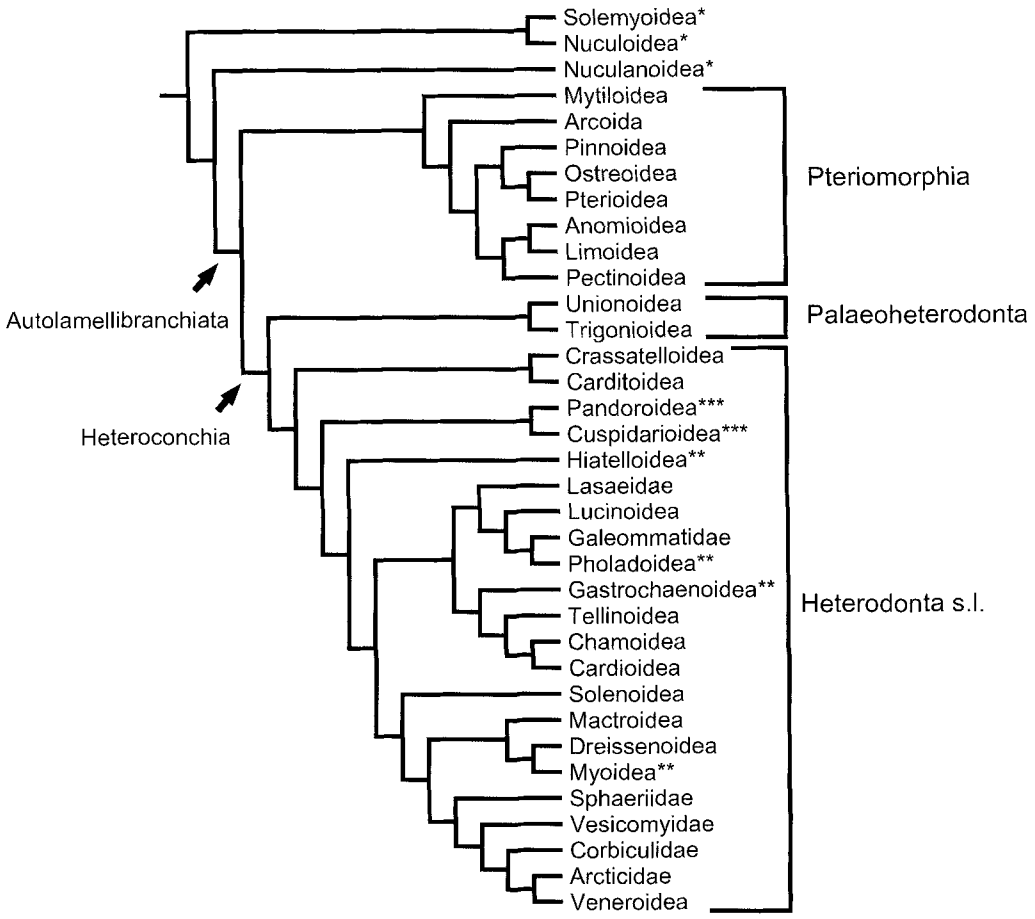

Fig. 11. Summary of bivalve relationships corresponding to the tree obtained for all the data analyzed in combination for the optimal parameter set. Asterisks: * protobranch bivalves; ** myoid heterodont bivalves; *** anomalodesmatans.

The phylogenetic tree proposed here (Fig. 11) largely resembles the system presented by Waller (1990, 1998), albeit with two major differences in basal bivalve relationships, and within Heterodonta s.l. The relationships proposed can be summarized in a cladistic classification as follows:

Bivalvia Linnaeus 1758
- Nuculoidea + Solemyoidea (Node PR-2 of Waller 1998)
  - Nuculoidea Gray 1824
  - Solemyoidea Gray 1840
- Nuculanoidea + Autolamellibranchiata
  - Nuculanoidea Adams & Adams 1858
  - Autolamellibranchiata Grobben 1894 (= Autobranchia)
    - Pteriomorphia Beurlen 1944
      - Mytiloida Rafinesque 1815 (as Mytilacea)
      - Non-mytiloid pteriomorphs
        - Arcoida Stoliczka 1871 (as Arcacea)
        - Non-mytiloid, non-arcoidan pteriomorphs
    - Heteroconchia Cox 1960
      - Palaeoheterodonta Newell 1965
        - Trigonioida Dall 1889 (as Trigoniacea)
        - Unionoida Stoliczka 1871
      - Heterodonta Neumayr 1884 (new definition)
        - Crassatelloidea + Carditoidea
        - Remaining heterodonts (incl. Anomalodesmata)

If this new system withstands further testing, the subclass Protobranchia should be regarded as paraphyletic, as well as the subclass Heterodonta s.s., because it includes Anomalodesmata. At the ordinal level, major differences with previous classifications occur in the Nuculoida (polyphyletic), Ostreoida (polyphyletic), Veneroida (paraphyletic with respect to Anomalodesmata and Myoida), and Myoida (polyphyletic). Suprafamilial classifications are highly congruent with previous classifications, with a few exceptions: Arcoidea includes Limopsoidea, Galeommatoidea is paraphyletic, Cardioidea includes Tridacnoidea (as first suggested by Schneider 1992), and Arcticoidea and Corbiculoidea form a clade that includes Veneroidea. The only families of bivalves for which our hypotheses do not agree with previous ones are Arcidae and Cardiidae. The sister group of bivalves is not yet clarified, but it seems that a sister-group relationship with scaphopods is not supported.

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Appendix 1

Character descriptions. The designation *a/p* indicates the coding: *(0) absent; (1) present.* Matrix of morphological data is in Appendix 2.

1. *Cuticle with spicules: a/p* (Salvini-Plawen & Steiner 1996). The classes Caudofoveata, Solenogastres, and Polyplacophora present a dorsal surface (mantle) with chitinous cuticle and aragonitic scales produced by single or several cells, not present in any other molluscan class.
2. *Discrete shell gland: a/p.* Salvini-Plawen & Steiner (1996) coded for the presence of a shell in conchiferans. Larval conchiferans typically have a discrete shell gland with a pellicle (periostracum) formed at the distal edge of the gland where the outer shell layer is precipitated against the periostracum. In contrast, polyplacophoran shell formation occurs under a thin layer of cuticle across a broad plate field (Eernisse & Reynolds 1994).

Shell microstructure (characters 3–13): data for numerous bivalves have been reviewed by J.D. Taylor et al. (1969, 1973), and Carter (1990b). Generic groundplans have been applied when data for the represented terminal taxa were not available, unless more than one species of the same genus were represented. Codings for Scaphopoda from Reynolds & Okusu (1999).

3. *Mineralogic composition: (0) aragonite; (1) aragonite and calcite.* Aragonite and calcite occur together consistently in Mytiloidea, Pinnoidea, Pterioidea, Pectinoidea, Limoidea, and Ostreoidea, but not in Arcoidea and Limopsoidea. Calcite also appears in shells of 2 heterodont superfamilies, the extant superfamily Chamoidea (reported only in *Chama pellucida,* not in *Chama gryphoides*), and the extinct superfamily Hippuritoidea (J.D. Taylor et al. 1969).
4. *Nacreous structure (sheet nacre): a/p.* This is the best-known and most widely studied shell structure. Present in the Nuculoidea, Mytiloidea, Pinnoidea, Pterioidea, Unionoidea, Trigonioidea, Pandoroidea, and Pholadomyoidea (J.D. Taylor et al. 1969).
5. *Nacreous structure (lenticular nacre): a/p.* Present in Nuculidae, Pteriidae, Mytilidae, Unionidae, Trigoniidae, Pandoridae, and Lyonsiidae.
6. *Foliated structure: a/p.* Calcitic foliated structure that forms the calciostracum (or subnacreous layer) in the Ostreoidea, Pectinoidea, Anomioidea, and Limoidea (J.D. Taylor et al. 1969).
7. *Prismatic structure: (0) absent; (1) simple prismatic structure (aragonite); (2) simple prismatic structure (calcite); (3) composite prismatic structure.*
8. *Crossed lamellar structure: a/p.*
9. *Complex crossed-lamellar structure: a/p.*
10. *Homogeneous structure: a/p.*
11. *Myostracal pillars: a/p.*
12. *Shell layers: (0) three; (1) two.*
13. *Chalky lenses: a/p.* Chalky lenses are present in members of Ostreidae.
14. *Flexible shell margin resulting from extension of periostracum beyond edge of calcified shell and/or presence of secondary prismatic shell microstructure: a/p.* A flexible shell margin resulting from the extension of the periostracum is found in all solemyoids (Beedham & Owen 1965; Waller 1998).
15. *Protoconch shape: (0) cap-like (wider than long); (1) tubular (longer than wide).* According to Ponder & Lindberg (1997), the primitive conchiferan protoconch condition is calcification of a small cap-shaped shell followed by incremental growth, as seen in bivalves, scaphopods, cephalopods (*Nautilus*; Arnold 1987), and monoplacophorans. However, in gastropods, the larval

shell is not cap-shaped but tubular (Ponder & Lindberg 1997). Groundplan coding adopted.

16. *Adult shell type: (0) univalve with one aperture; (1) univalve with two apertures; (2) bivalve.*
17. *Shell coiling: a/p* (Ponder & Lindberg 1997).
18. *Bivalve shell shape: (0) equivalve; (1) inequivalve.* The plesiomorphic state for bivalves seems to be equivalve shells, which have become inequivalve in several groups of pteriomorphs, myoids, and anomalodesmatans, as well as in a few groups of heterodonts (e.g., *Chama*). Coding restricted to bivalves.
19. *Lateral expansions of the shell (auricles): a/p.* Certain pteriomorphs have lateral expansions of the shell (auricles) at each side of the umbo, such as in *Pteria, Pecten, Chlamys, Spondylus, Lima,* and *Limaria.* Coding restricted to bivalves.
20. *Byssal gape: a/p.* An opening remaining for passage of the byssus when the shell is closed: found in most pteriomorphs, but not in Mytiloidea or Ostreoidea. Coding restricted to bivalves.
21. *Anterior adductor muscle (or scar): (0) present; (1) reduced; (2) absent (monomyarian condition).* Presence of 2 muscle scars of similar size (isomyarian condition) seems to be the plesiomorphic state for bivalves. Certain bivalves are anisomyarian, with reduction of anterior muscle (Mytilidae, *Pteria, Atrina,* Limidae, Ostreidae, Pectinidae, Spondylidae, *Dreissena,* and Tridacninae) (Yonge 1953a; Gilmour 1990). The anisomyarian condition of certain pteriomorphs has led to the loss of the anterior adductor in a few cases (*Pteria, Pecten, Chlamys, Spondylus, Lima, Limaria, Anomia, Ostrea,* and *Crassostrea*). The anterior adductor has also been lost in *Tridacna* and *Hippopus.* Coding restricted to bivalves.
22. *Posterior adductor muscle (or scar): (0) present; (1) reduced in size with respect to the anterior adductor.* Certain bivalves are anisomyarian, with reduction of the posterior muscle (*Ensis, Gastrochaena,* and *Bankia*).
23. *Position of posterior pedal retractor scar relative to posterior adductor scar: (0) anterodorsally; (1) inset on the anterior, concave face of a crescentic posterior adductor scar.* The pedal retractor insertions are anterodorsal to the posterior adductor scar in most species of protobranchs and autobranchs, a position assumed to be plesiomorphic (Waller 1998). Within Pteriomorphia, this position appears to be retained in the Mytiloida, Arcoida, Limoida, and Pectinina (Waller 1998), but not in Pinnoidea and Pterioidea. A posterior pedal retractor position that is inset on the anterior concave face of a crescentic posterior adductor scar is apparently restricted to Pinnidae and to the pteroidean families Pteriidae, Malleidae, and Isognomonidae (Yonge 1953a, 1968; Cox 1969). Groundplan coding adopted. Coding restricted to bivalves with pedal retractor muscles.
24. *Pallial line: a/p.* Pallial lines are common throughout Bivalvia but absent in Scaphopoda and Cephalopoda. Among gastropods, pallial muscles attached to the shell are not generally present (J.E. Morton & Yonge 1964) except in limpet-like forms (Waller 1998). Among the represented bivalves, a pallial line is absent in *Atrina, Anomia* and *Sphaerium.*
25. *Pallial sinus: a/p.* Present in the represented nuculanoids, and in the heterodonts *Spisula, Tresus, Abra, Ensis, Callista, Mercenaria, Mya, Varicorbula, Gastrochaena, Hiatella, Lyonsia, Cuspidaria,* and *Myonera.* Coding restricted to bivalves with pallial line.
26. *Umbo: (0) orthogyrous; (1) prosogyrous; (2) opisthogyrous.* In bivalves that obtain food by labial palps at the anterior body end (Nuculidae, Solemyidae, and Nucinellidae) and in those having a well-developed long foot (Pisidiidae, Euglesidae, and Donacidae), the umbones are shifted backward (Starobogatov 1992). The umbones of Ostreidae and *Ensis* are inconspicuous and thus have been coded as "?" Coding restricted to bivalves.
27. *Porphyrin-based pigments: a/p.* Porphyrin-based pigments are soluble in acid (Nuttall 1969), and they are present in some pectinids, *Pteria, Pinctada, Malleus,* and *Pinna.* We have coded its presence for *Pteria, Atrina* (based on *Pinna*), *Pecten,* and *Chlamys.*
28. *Purple pigment in the internal shell layer: a/p.* This pigment cannot be extracted through the use of acids or organic solvents (Morton et al. 1998); it is present in corbiculids and venerids. It has been coded as present in *Lasaea, Corbicula, Callista,* and *Mercenaria.*
29. *Shell tubules: (0) absent or restricted to early shell or to inner shell layers; (1) present throughout the area within the pallial line and penetrating the shell to the inner surface of the periostracum.* Tubules in most bivalve groups are restricted either to early ontogeny, as in Corbiculoidea (Tan-Tiu & Prezant 1989), or are sparsely distributed and do not penetrate the entire shell thickness. It is apparently only in Arcoida that tubules have a dense distribution across the entire area inside the pallial line throughout ontogeny and penetrate the entire shell to the inner surface of the periostracum (Waller 1990, 1998). Tubules with this distribution occur in all extant arcoidean groups so far studied (Morton 1978; Prezant 1990; Waller 1990, 1998; Reindl & Haszprunar 1996), and thus we have coded them as present in *Arca, Barbatia, Striarca,* and *Glycymeris,* adopting a groundplan coding for Arcoida.
30. *External ligament: a/p* (Owen 1959; Yonge 1973, 1978; Yonge & Morton 1980; Waller 1990). The ligament of boring forms (Pholadidae and Teredinidae) is strongly reduced or absent in connection with the necessity of moving the valves in relation to each other (Starobogatov 1992). Noetiid and arcid ligaments have been reviewed (Thomas et al. 2000). Coding restricted to bivalves.
31. *Ligament position: (0) amphidetic; (1) opisthodetic.* Yonge (1978, 1982b) suggested that primitive bivalves were more or less equivalve with an amphidetic external ligament. According to Yonge (1982b), transfer of

the incurrent aperture to the posterior end produced local enlargement of the posteriorly stretched external opisthodetic ligament present in many modern bivalves. The ancestral ligament would have been 2-layered, but covered additionally by an external periostracal layer. However, Waller (1990) concluded that the primitive ligament was opisthodetic.

32. *Ligament type: (0) simple; (1) duplivincular; (2) alivincular; (3) transverse; (4) parivincular.* For definitions of these types of ligaments we follow Carter (1990a).
33. *Larval resilium continues as an adult internal ligament (= resilium): a/p* (Waller 1998). Coding restricted to bivalves.
34. *Non-mineralized, non-fibrous medial core in the resilium, developed mainly ventral to the hinge line: a/p* (Waller 1978, 1998). This type of resilium is present in all species of Pectinoidea and unknown in other pteriomorphs. Coding restricted to bivalves with internal ligament.
35. *Resilifer: (0) absent; (1) present; (2) present as chondrophore.* The ligament may sit in a hollowed out depression in the hinge plate known as the resilifer, located internally just beneath the umbo. A spoon-shaped, projecting resilifer (for example in the mactrids) is termed a chondrophore. Coding restricted to bivalves with internal ligament.
36. *Lithodesma: a/p* (Salvini-Plawen & Steiner 1996). A small calcareous plate or ossicle associated to the ligament is present in shells of Anomalodesmata. A lithodesma effectively divides the ligament into 2 compressive units assuring adequate abductive thrust of an otherwise wide ligament (Yonge & Morton 1980; Prezant & Carriker 1983). A lithodesma has also been reported for some montacutids (Morton 1980a; Allen 2000). Coding restricted to bivalves with internal ligament.
37. *Pseudonymphae: a/p.* The pseudonymphae are modified ostracum secreted in advance of lamellar ligament posteriorly and along the border between fibrous ligament and ostracum (Waller 1990, 1998). Unlike true nymphae, pseudonymphae do not trap lamellar ligament in a groove along dorsal margin. These ligament-support structures appear to be present in all mytiloids except for those, such as *Dacrydium,* that have modified ligament systems consisting only of a resilium, possibly resulting from neoteny (Carter 1990a; see Waller 1990). Coding restricted to bivalves with internal ligament.
38. *Larval hinge apparatus (provinculum): (0) simple row of symmetrical teeth; (1) differentiated dentition; (2) edentate* (Cragg 1996). Provincula of numerous species have been illustrated (Le Pennec 1980; Lutz et al. 1982a,b; Lutz 1985; Webb 1986, 1987; Goodsell et al. 1992; Gustafson & Lutz 1992). Coding restricted to bivalves.
39. *Adult hinge: (0) taxodont; (1) schizodont; (2) heterodont; (3) desmodont; (4) edentate.* The schizodont dentition consists of 2 large diverging, blade-like teeth in the right valve that interlock with 2 deep and narrow sockets in the left valve (Morton 1987c), as characterized in *Neotrigonia.* The dysodont teeth of the Mytilidae are not true cardinal teeth (Le Pennec 1980), and thus we have decided to code mytilids as edentate, and use the dysodont condition as a separate character. Coding restricted to bivalves.
40. *Dysodont condition: a/p.* Coding restricted to bivalves.
41. *Secondary teeth: a/p.* Among the edentate monomyarian bivalves, *Spondylus* and *Plicatula* are characterized by having secondary teeth (Yonge 1973). Coding restricted to bivalves.
42. *Chomata: a/p* (Waller 1998). Chomata are small tubercles on short ridges on the hinge of the right valve of Ostreidae, Gryphaeidae, and Plicatulidae (Harry 1985; Waller 1998), but the members of the genus *Crassostrea* do not develop chomata (Slack-Smith 1998a). Coding restricted to bivalves.
43. *Operculum: a/p.* An operculum is present in all gastropod larvae, although absent (secondarily) in the adults of most euthyneurans (Haszprunar 1988; Ponder & Lindberg 1997).
44. *Principal growth axis: (0) anteroposterior, with mouth and anus at opposite ends of the shell; (1) dorsoventral, with intestinal tract U-shaped, and mouth and anus near the same end of the shell* (Waller 1998).
45. *Body compressed laterally: a/p* (Salvini-Plawen & Steiner 1996). Bivalves are unique among molluscs in having a body compressed laterally.
46. *Differentiated head: (0) present; (1) absent* (Salvini-Plawen & Steiner 1996). A head is absent in bivalves.
47. *Snout: a/p* (Ponder & Lindberg 1997). Coding restricted to molluscs with a differentiated head (character 46, state 0).
48. *Torsion: a/p.* Torsion of the shell and visceral hump in relation to the head-foot axis, followed by asymmetry of the nervous system is present in gastropods. This phenomenon has been discussed at length in the literature (e.g., Spengel 1881; Naef 1913; Wingstrand 1985; Haszprunar 1988; Bieler 1992; Ponder & Lindberg 1997; Waller 1998).
49. *Mantle covering visceral dorsal surface only: a/p* (Salvini-Plawen & Steiner 1996). A mantle covering the visceral dorsal surface only is present in cephalopods and gastropods.
50. *Mantle lobes: a/p* (Salvini-Plawen & Steiner 1996). Mantle lobes are present in scaphopods and bivalves.
51. *Ventral mantle fusion: a/p.* Ventral mantle fusion is present in scaphopods, mytilids, pteriids, and most heterodonts (all those represented here except *Galeomma*).
52. *Part of the mantle epithelium secreting the periostracum: (0) inner surface of the outer fold; (1) outer surface of the middle fold; (2) between the middle and outer folds.* Saleuddin (1965) thoroughly discussed this subject. Field (1922) stated that the periostracum of *Mytilus* comes from the outer surface of the middle

fold as it is always adherent to this surface in sections. Kessel (1944) studied the histology of the mantle edge and the secretion of the periostracum in several bivalves (including *Arctica islandica, Acanthocardia echinata,* and *Ostrea*) and concluded that in all cases the inner surface of the outer fold is responsible for secretion of periostracum. Brown (1952) and Beedham (1958) studied the histology of the mantle edge of *Mytilus edulis, Ostrea edulis,* and *Anodonta cygnea,* reaching the same conclusion. Saleuddin, however, demonstrated that periostracum in *Astarte* is secreted from the middle fold. *Anodonta* is used as a proxy for unionids. Morton (2000a) illustrated mantle margins for *Microfragum erugatum,* suggesting that in this species, the periostracum originates between the middle and the outer folds (proxy used for *Fragum unedo*).

53. *Cementation to substrate by a calcareous secretion of the mantle margins: a/p.* This type of cementation to the substrate (as opposed to attachment by a calcified byssus, typical of the Anomioidea) is found in Ostreoidea, certain of the Pectinidae (*Hinnites*), Spondylidae, Plicatulidae, some species of Etheriidae, Chamoidea, Hippuritoidea, Myochamidae, and Cleidothaeridae (Yonge 1979; Harper 1992; Harper et al. 2000a). For species in our study, this character has been coded as present in *Ostrea, Crassostrea, Spondylus,* and *Chama.*
54. *Adult incurrent: (0) anterior; (1) posterior only; (2) absent* (Yonge 1939a; Salvini-Plawen & Steiner 1996). Yonge (1939a, 1957) proposed that lack of fusion of the mantle lobes ventrally and the presence of an anterior incurrent flow are primitive (plesiomorphic) characters for bivalves. This condition is found in many protobranchs and pteriomorphs (e.g., *Nucula, Arca tetragona, Glycymeris*), whose pallial current enters the cavity anteriorly and leaves posteriorly (Saleuddin 1965). This condition also holds for some eulamellibranchs. Most members of Lucinacea (Allen 1958), *Lasaea rubra* (M.L. Popham 1940), *Galeomma turtoni* (M.L. Popham 1940), and *Kellia suborbicularis* (Yonge 1952a) (and Galeommatoidea in general) have an anterior incurrent flow. In the majority of bivalves, however, the current enters and leaves posteriorly.
55. *Siphons: a/p* (Salvini-Plawen & Steiner 1996). Siphons are present in Nuculanoidea, Unionoidea, Anomalodesmata, and in all heterodont bivalves except Carditoidea. The genus *Lithophaga* exhibits extensive fusion both above and below the excurrent opening that results in an excurrent siphon (Pelseneer 1911; B.R. Wilson 1979; Waller 1990). Other bivalves have functional (but not morphologically defined) siphons delineated by pallial fusions such as in *Neotrigonia* (Gould & Jones 1974; Morton 1987c). In *Galeomma* and *Lasaea,* as in other Galeommatoideans, one of the siphons might not be well developed (M.L. Popham 1940). Coding restricted to bivalves.
56. *Mantle margins and siphonal types: (0) type A; (1) type B; (2) type C* (Yonge 1957, 1982a). Type A: Union of inner folds only; Type B: Union includes middle folds, siphons united with common outer ring of sensory tentacles, incurrent opening fringed with filtering tentacles, excurrent aperture with valvular membrane; Type C: Also involving periostracal groove, often united with very long siphons with a periostracal sheath (Yonge 1982a). Cuspidariids are coded as type B, as Yonge (1982a) found that the siphons are attached for half their length, and lack a periostracal covering. Coding restricted to bivalves with siphons.
57. *Type A siphons with the middle fold greatly reduced and carrying the sensory tentacles and eyes in the inner fold: a/p (type A+)* (Yonge 1957, 1982a). Certain bivalves have a greatly reduced middle fold (ventrally in the Tridacnidae), with sensory tentacles and eyes in the inner mantle folds. The inner folds alone constitute the siphons.
58. *Siphon separation: (0) separated; (1) joined.* Coding restricted to bivalves with siphons.
59. *Pallets: a/p.* Calcareous siphonal pallets that close the burrow when the siphons are retracted are typical of Teredinidae. Coding restricted to bivalves.
60. *Fourth pallial aperture between the incurrent siphon and the pedal gape (or inner-mantle folds forming a waste canal): a/p.* A fourth pallial aperture of unknown function is located between the excurrent siphon and the pedal gape in some members of Solenoidea and Mactroidea (Yonge 1948) and some representatives of Anomalodesmata (Morton 1981, 1985; Prezant 1998; Harper et al. 2000a). From the taxa represented in our study, a fourth pallial aperture has been described for *Spisula subtruncata* (Yonge 1948), Pharidae (Atkins 1937b), and Lyonsiidae (Yonge 1952b; Narchi 1968; Harper et al. 2000a), but it is absent in Pandoridae (Allen 1954) and Cuspidariidae (Harper et al. 2000a). *Tresus nuttallii* has the inner-mantle folds of a waste canal but lacks the fourth aperture (Kellog 1915). Coding restricted to bivalves.
61. *Mantle cavity separated by muscular septum (septibranch condition): a/p.* Present in the septibranch anomalodesmatans.
62. *Hypobranchial gland: (0) present; (1) absent.* In some molluscs, a hypobranchial gland lines the posterior inner wall of the mantle, typically above the ctenidia and below the rectum (Morton 1977). A review of the hypobranchial gland in Mollusca can be found in Yonge (1947). Hypobranchial glands have been described in Nuculidae and Solemyidae but not Nuculanidae (Drew 1901; Yonge 1939a,b; Morton 1977); and in some members of Anomiidae (but absent in *Anomia*) (Atkins 1936; Yonge 1977); Fimbriidae, Corbiculidae and Sphaeriidae (Morton 1977). It is assumed that the hypobranchial glands of autobranchs are restricted to a few pteriomorphs (none of which are included in the present data set) and some eulamellibranchs that incubate their larvae. A familial groundplan coding has been adopted.
63. *Portion of mantle cavity occupied by gills: (0) both lateral and posterior to the foot; (1) posterior to the*

foot. The gills are extended forward along the sides of the body in Bivalvia (Waller 1998); however, the small posterior gills of Protobranchia are posterior to the foot. In Gastropoda and Cephalopoda, the gills are posterior to the foot. Coding restricted to molluscs with one pair of gills.

64. *Ctenidia: (0) present; (1) absent* (Salvini-Plawen & Steiner 1996; Waller 1998). Gills with alternating leaflets or filaments occur in all molluscan classes except Scaphopoda and Solenogastres (Waller 1998; Reynolds & Okusu 1999). Numerous modifications and loss of one or both ctenidia occurred within Gastropoda; heterobranchs do not have ctenidia. Ctenidia are also absent in septibranch anomalodesmatans.
65. *Plicate ctenidia: (0) absent (nonplicate); (1) present* (Atkins 1937a). Coding restricted to autobranch bivalves.
66. *Demibranch: (0) not reflected; (1) reflected* (Salvini-Plawen & Steiner 1996). Coding restricted to molluscs with gills.
67. *Ctenidia: (0) eleutherorhabdic; (1) synaptorhabdic.* Coding restricted to Autolamellibranchiata.
68. *Ctenidial type: (0) protobranch (ctenidiobranch); (1) filibranch; (2) eulamellibranch* (Ridewood 1903; Pelseneer 1911; Atkins 1937a). In protobranch bivalves, the gill consists of 2 rows of leaflets attached to a branchial axis (Atkins 1937a). In filibranch ctenidia (most pteriomorphs and trigoniids), the individual filaments are not united ventrally with their neighbors except by opposing ciliary discs on the lateral bases of the filaments, while the filaments are intimately united in the eulamellibranch ctenidia (Morton et al. 1998). According to Yonge (1977), *Anomia ephippium* (unlike other Anomiidae) exhibits tissue fusion, and therefore has been coded as eulamellibranch type. Similarly, ostreids have some degree of inter-lamellar fusion and development of inter-filamental junctions, and therefore have been coded as having the eulamellibranch ctenidial type.
69. *Outer demibranch: (0) present and consisting of ascending and descending lamellae; (1) upturned* (*type E gill* of Atkins 1937a); *(2) outer demibranch consisting of the descending lamella only* (*type F gill* of Atkins 1937a); *(3) absent* (*type G gill* of Atkins 1937a). Coding restricted to bivalves with reflected demibranchs.
70. *Eulamellibranch ciliary currents (gill type): (0) Type C; (1) Type D.* This character reflects the ciliary types of Atkins (1937b) found in eulamellibranch bivalves with well-developed outer demibranch (types C and D). Since types E, F, and G are considered in character 69, we do not account for them in this character. Also, we have excluded from this character types A and B, which are included in character 68 (coding for protobranch and filibranch type of ctenidia). Yonge (1969) reported the ciliary currents of the Carditoidea as being a modified type D (here considered as type D), similar to that of *Astarte sulcata,* although Saleuddin (1965) reported *A. sulcata* as being type C(1). Tevesz (1975) considered the ctenidial ciliation of *Neotrigonia* to be of type D, as in the Unionoidea (Atkins 1937a), but Morton (1987c) showed them to be Type B(1b) (ordinary filaments) as in many pteriomorphs.
71. *Type C gill with a groove at the free edge of the outer demibranch (Type C(2): a/p* (Atkins 1937a). This condition has been observed in several Mactridae (but not *Spisula subtruncata* [Atkins 1937a]), Veneridae (including *Mercenaria mercenaria* [Kellog 1915]), Myidae (including *Mya arenaria* [Kellog 1915; Yonge 1923]), Pholadidae, Solenidae, and Pharidae (Atkins 1936, 1937a). Coding restricted to bivalves with ciliary currents of type C1.
72. *Chitinous rods of the gill filament with a major structural enlargement in the base of the filament: a/p.* Morton (1987c) reported a similarity between the gill filaments of *Neotrigonia margaritacea* and certain pteriomorphs, in having the major structural enlargement of the chitinous rods at the base (*Mytilus edulis* and *Barbatia virescens* were shown as having a similar structure). On the contrary, the eulamellibranchs (he illustrated *Anodonta woodiana*) have the major structural enlargement in a more distal position, and thus the central stalk and apical components of each filament are only flexibly supported.
73. *Calcification of of the chitinous rods of the gill filaments (gill spicules): a/p.* According to Atkins (1938) the Trigonioidea have calcareous gill spicules as seen in the Unionoidea (Ridewood 1903). J.D. Taylor et al. (1973) discussed that Trigonioidea and Unionoidea may be the only bivalve groups to possess such spicules, which in fact should be calcified chitinous rods of the gill filament, but Morton could not differentiate between the calcified chitinous rods of *Neotrigonia* and other bivalves (Morton 1987c). We have adopted here Morton's coding.
74. *Ctenidial filament morphology: (0) homorhabdic; (1) heterorhabdic* (Atkins 1937a; Beninger & Dufour 2000; Graf 2000). Coding restricted to Autobranchia.
75. *Laterofrontal gill cilia: a/p* (Waller 1998). Laterofrontal gill cilia or cirri are unique to Bivalvia (Owen 1966, 1978; Waller 1998). Coding restricted to molluscs with gills.
76. *Laterofrontal cilia: (0) eulaterofrontal cilia, together with prolaterofrontal cilia (macrociliobranchiate); (1) microlaterofrontal cilia (microciliobranchiate); (2) anomalous, together with paralaterofrontal cilia* (Atkins 1938; Salvini-Plawen & Steiner 1996; Waller 1998). Coding restricted to bivalves with laterofrontal gill cilia (gilled bivalves).
77. *Abfrontal cilia: (0) present; (1) absent* (Salvini-Plawen & Steiner 1996). According to Salvini-Plawen & Steiner (1996), ctenidiobranch gills with abfontal cilia are plesiomorphic for bivalves.
78. *Type of ctenidial-palp association: (0) type I; (1) type II; (2) type III.* Stasek (1963) defined three main anatomical categories of associations between the ctenidia

and the labial palps in bivalves. The categories were (I) in which the ventral tips of at least the first few or, usually, of many anterior filaments of the inner demibranch are inserted unfused into a distal oral groove (a designation originated by Kellog 1915); (II) in which the ventral tips of the anteriormost filaments of the inner demibranch are inserted into and fused to a distal oral groove; (III) in which the ventral tips of the anterior filaments of the inner demibranch are not inserted into a distal oral groove, although the antero-ventral margin of the inner demibranch may be fused to the inner palp lamella. Coding restricted to bivalves.

79. *Labial palp: a/p* (Salvini-Plawen & Steiner 1996; Waller 1998). Labial palps are present in all bivalves.
80. *Hypertrophied labial palps: a/p.* Hypertrophied labial palps are found in members of Nuculoidea and Nuculanoidea. Coding restricted to bivalves.
81. *Palp appendages: a/p* (Salvini-Plawen & Steiner 1996; Waller 1998). Palp appendages are known only in Protobranchia (Stasek 1961). Coding restricted to bivalves.
82. *Palp pouch: a/p* (Waller 1998). The palp pouch is a non-extensible prolongation of the posterior edge of each outer palp lamella that develops on the posterior side of the palp appendage (Stasek 1965) of Nuculidae. Some solemyids, such as *Solemya reidi,* have what appears to be the homolog of a palp pouch (Reid 1980); other species have only the palp appendage remaining with no trace of a palp pouch. Coding restricted to bivalves with palp appendages.
83. *Adult with pedal retractor muscles: (0) present; (1) absent.* Post-settlement oysters and members of Spondylidae lack pedal retractor muscles. Coding restricted to bivalves. This character, thought to be convergent between Ostreidae and Spondylidae, is included because it is informative below the family level (i.e., it is not homoplastic between *Ostrea* and *Crassostrea*).
84. *Position of mouth relative to anterior adductor: (0) adjacent to posterior edge of adductor; (1) mouth located more posteriorly and not adjacent to posterior edge of adductor* (Allen & Hannah 1986; Salvini-Plawen & Steiner 1996; Waller 1998). Coding restricted to bivalves. This character is regarded as a synapomorphy of Nuculanidae.
85. *Radula, odontophore, and associated buccal organs: (0) present; (1) absent* (Waller 1998). Loss of the buccopharyngeal region with jaw, radular apparatus, subradular organ, buccopharyngeal glands, and buccal ganglia is a bivalve synapomorphy (Salvini-Plawen 1988).
86. *Esophageal ridges: (0) present; (1) absent* (Salvini-Plawen & Steiner 1996).
87. *Digestion in midgut gland: (0) extracellular; (1) extra- and intracellular* (J.E. Morton 1953; B.S. Morton 1983).
88. *Midgut gland ducts: (0) not ciliated; (1) ciliated* (Salvini-Plawen & Steiner 1996).
89. *Stomach with: (0) protostyle; (1) crystalline style* (Salvini-Plawen & Steiner 1996).
90. *Stomach coating/lining: (0) gastric shield; (1) largely cuticular* (Salvini-Plawen & Steiner 1996).
91. *Major typhlosole: (0) short; (1) elongated* (Salvini-Plawen & Steiner 1996). Coding restricted to bivalves.
92. *Destination of the major typhlosole and intestinal groove inside the stomach in filter feeders: (0) in association with the left pouch; (1) on the left posterior stomach floor; (2) external to the left caecum; (3) enters the left caecum* (Purchon 1987a). Coding restricted to bivalves with major typhlosole.
93. *Origin of major typhlosole and intestinal groove within the stomach that enters the left caecum and: (0) enters within the left caecum; (1) forms a spiral coil within the left caecum; (2) emerges and ends just outside the left caecum* (Purchon 1987a). Coding restricted to taxa showing state "3" in character 92.
94. *Stomach type: (0) type I; (1) type II; (2) type III; (3) type IV; (4) type V* (Purchon 1987a). Data on stomach structure were obtained by several authors (Purchon 1956, 1957, 1958, 1960, 1987a; Reid 1965; Dinamani 1967; Starobogatov 1992). Purchon (1987a) reviewed 261 species of bivalves assigned to 68 families. A stomach of type I has been described for members of Nuculidae, Malletidae, Nuculanidae; type II has been described for Cuspidariidae; type III is present in members of Pteroidea and Mytiloidea; type V is present in certain members of Veneroida; a type IV stomach is found in several groups of autobranchs. Coding restricted to bivalves.
95. *Type I stomach multiple looped: a/p.* All protobranchs except for of the Solemyoidea have a lengthened hindgut. A single loop of hindgut on the right side of the stomach is likely the primitive condition in Protobranchia (Allen 1978; Allen & Hannah 1989; Waller 1998), with multiple looping condition derived in several groups: Nuculidae, Pristiglomidae, Neilonellidae, Spinulinae, and Ledellinae. Coding restricted to taxa with type I stomach.
96. *Type III stomach with regularly folded sorting area: (0) present; (1) absent* (Purchon 1987a). Coding restricted to taxa with type III stomach.
97. *Type III stomach with duct orifices: (0) scattered; (1) clustered* (Purchon 1987a). Coding restricted to taxa with type III stomach.
98. *Type IV stomach with a conspicuous sorting area on the anterior floor of the stomach, emptying into the intestinal groove: (0) present; (1) absent* (Purchon 1987a). Coding restricted to taxa with type IV stomach.
99. *Type IV stomach with: (0) many duct orifices scattered or clustered; (1) duct orifices concentrated into a few embayments* (Purchon 1987a). Coding restricted to taxa with type IV stomach.
100. *Type IV stomach with the major typhlosole that passes: (0) to the left pouch; (1) towards left caecum; (2) short, posterior in position, not passing to either* (Purchon 1987a). Coding restricted to taxa with type IV stomach.
101. *Opening of ducts: (0) not in caeca; (1) in caeca* (Salvini-Plawen & Steiner 1996).

102. *Number of openings: (0) two; (1) three; (2) many* (Salvini-Plawen & Steiner 1996).
103. *Intestine: (0) normal; (1) reduced* (Salvini-Plawen & Steiner 1996). A reduced intestine consists of an alimentary canal reduced to a simple tube with 2 ducts to the small digestive diverticula and a narrow intestine passing through the ventricle of the heart. In some representatives, the entire alimentary system is absent. This condition is found in Solemyidae.
104. *Dorsal hood: a/p* (Salvini-Plawen & Steiner 1996).
105. *Dorsoventral muscles reduced to two pairs or fewer: (0) absent (more than two pairs); (1) present.* Salvini-Plawen & Steiner (1996) used a similar character to characterize the Heterodonta s.l., which have reduced the number of dorsoventral muscles to 2 pairs or fewer in a few cases, vs. the plesiomorphic state of having several dorsoventral muscle pairs.
106. *Adductor muscles: a/p* (Salvini-Plawen & Steiner 1996; Waller 1998). Adductor muscles are present in all the representatives of Bivalvia.
107. *Siphuncular tube: a/p.*
108. *Heart: (0) present; (1) absent* (Waller 1998). A heart consisting of a medial ventricle, at least one pair of auricles, and an anterior aorta connecting with an open haemocoelic blood circulation system is known only in Mollusca and occurs in all molluscan classes except Scaphopoda (Waller 1998; see Reynolds 1990). Groundplan coding adopted.
109. *Burrowing foot with anterior enlargement: a/p* (Salvini-Plawen & Steiner 1996). This type of foot is present in scaphopods and bivalves, and is a modification for burrowing. Similarities in the longitudinal and transverse muscle fibers of the foot of protobranchian bivalves and scaphopods, regarded by Steiner (1996) as a synapomorphy for the 2 groups, are considered to be convergent by Waller (1998).
110. *Ventral surface of the foot (sole): (0) present; (1) absent* (Salvini-Plawen & Steiner 1996). Most autobranch bivalves have a foot without a ventral surface. The typical foot has been modified in Cephalopoda, and therefore we have coded this character as inapplicable. This character has been discussed by Waller (1998: 21).
111. *Foot modified to form an efficient creeping organ: a/p.* Members of the Galeommatoidea (*Galeomma* and *Lasaea* here) have developed a creeping habit with a modified foot (M.L. Popham 1940).
112. *Anchor-like foot with "toe" and "heel": a/p.* This type of foot is present in the members of the genus *Neotrigonia* (Morton 1987c).
113. *Heel of foot: (0) absent or weakly developed as a posteriorly directed triangular projection of margin of sole, but not separated from sole; (1) distinct and sharply separated from sole* (Waller 1998). The members of Nuculidae here represented have a distinct heel sharply separated from the sole (Sanders & Allen 1973).
114. *Posterior pedal gland: a/p* (Salvini-Plawen & Steiner 1996). In Bivalvia, the main pedal gland or glandular complex is near the posterior end of the sole of the foot. It is consistently present in juveniles but commonly absent in adult bivalves that do not retain the juvenile ability to secrete a byssus (Waller 1998).
115. *Byssus: (0) absent; (1) present in larvae and adults; (2) lost in adults.* In animals that produce a larval but not an adult byssus, we assume that the adult has lost the byssus secondarily, and therefore the character has been treated as ORDERED. For *Neotrigonia,* we follow Gould (1969); for *Gastrochaena* we follow Carter (1978).
116. *Ontogenetic loss of foot inmediately after settlement: a/p* (Waller 1998). Ontogenetic loss of the foot after settlement is found in Ostreoidea (Harry 1985), and thus we have coded it as present in *Ostrea* and *Crassostrea.*
117. *Circumoral arms (= tentacles): a/p.* Presence of arms is a synapomorphy for Cephalopoda (Salvini-Plawen 1980; Boletzky 1988; Waller 1998).
118. *Kidneys: (0) tubular; (1) sac-shaped; (2) U-shaped* (Brusca & Brusca 1990; Waller 1998). The basic molluscan kidney plan consists of a pair of tubular structures, as in the Polyplacophora (Andrews 1988). This is also true in the early ontogeny of bivalves, the kidneys becoming U-shaped in adult bivalves as kidney length increases (Raven 1966). Typically the 2 limbs are structurally and functionally different, the proximal limb being resorptive and the distal one excretory. U-shaped tubular kidneys occur throughout Bivalvia, whereas Scaphopoda, Gastropoda, Cephalopoda, and Monoplacophora have sac-shaped kidneys (Pelseneer 1906; Andrews 1988; Waller 1998).
119. *Intracellular hemoglobin: a/p* (Booth & Mangum 1978). Hemoglobin is present in erythrocytes of members of the families Arcidae and Glycymeridae (Boyd 1998; Morton et al. 1998), Carditidae (citations in Slack-Smith 1998b), and *Calyptogena magnifica* (R.C. Terwilliger et al. 1983). A familial groundplan coding has been adopted.
120. *Hemocyanin-like molecules: (0) present; (1) absent.* Hemocyanin-like molecules have been described for Polyplacophora, Gastropoda, and Cephalopoda (Morse et al. 1986; Mangum et al. 1987). Hemocyanin molecules have also been found in the protobranchs *Solemya velum, Nucula proxima, N. sulcata, N. hanleyi, Acila castrensis, Yoldia limatula,* and *Y. thraciaeformis* (Morse et al. 1986; Mangum et al. 1987; N.B. Terwilliger et al. 1988; Herskovits et al. 1990; Lambert et al. 1995; A.C. Taylor et al. 1995). The absence of such a pigment in the pteriomorph *Noetia ponderosa* (proxy used for *Striarca lactea*) and in the heterodont *Cyclocardia ventricosa* (proxy used for *Cardita* and *Cardites*) (Mangum et al. 1987) may suggest that hemocyanins are found only in protobranchiate bivalves.
121. *Captacula: a/p* (Reynolds & Okusu 1999). Captacula are small, elongate, retractile feeding tentacles with bulbous ends, characteristic of the Scaphopoda (see Shimek 1988).

122. *Cartilaginous cranium: a/p.* A cartilaginous cranium housing a brain formed by extensive fusion of ganglia is found in Cephalopoda (Waller 1998).
123. *Epiathroid nervous system with identical innervation areas (but convergent elaboration of respective ganglia): a/p* (Salvini-Plawen 1985; Haszprunar 1988; Steiner 1992; Salvini-Plawen & Steiner 1996). This character is a putative synapomorphy for Loboconcha (= Diasoma), although Waller (1998) regards it as convergence because it is also present in Monoplacophora.
124. *Lateral (pleural, visceral) nerve cords: (0) lateral or visceral nerve a major nerve encircling body, outside shell muscles; (1) visceral nerve cord, inside shell muscles* (Ponder & Lindberg 1997). Groundplan coding adopted.
125. *Visceral and pedal ganglia: a/p* (Waller 1998). Distinct visceral and pedal ganglia occur in Bivalvia, Gastropoda, and Scaphopoda. In cephalopods, the specialized nervous system is highly concentrated in the head region, but homologs of the pedal ganglia have been recognized (Haszprunar 1988). The presence of discrete ganglia in the higher Conchifera but not in the Monoplacophora led Hennig (1979) to recognize this group as the clade Ganglioneura (see also Lauterbach 1983).
126. *Visceral ganglia vs. cerebral ganglia: (0) smaller or equal; (1) larger* (Salvini-Plawen & Steiner 1996). Groundplan coding adopted following Salvini-Plawen & Steiner (1996).
127. *Visceral connectives: (0) "(partly) chord-like;" (1) nerves* (Salvini-Plawen & Steiner 1996). Groundplan coding adopted following Salvini-Plawen & Steiner (1996).
128. *Cephalic tentacles: a/p* (Haszprunar 1988; Ponder & Lindberg 1997). Presence of cephalic tentacles is regarded as a putative synapomorphy for Gastropoda. We follow Ponder & Lindberg (1997) in not considering other cerebrally innervated structures of bivalves, scaphopods, or cephalopods as true cephalic tentacles.
129. *Cephalic (or cerebral) eyes: (0) absent; (1) open pit; (2) closed eye; (3) coleoid eye.* Paired cerebral eyes are found in gastropods and cephalopods, as well as in veligers of bivalves. Similar paired cerebral eyes (also referred to as cephalic eyes or cerebral ocelli) were noticed in adults of *Mytilus edulis* (Rosen et al. 1978). They are small pigment-lined cups filled with a crystalline material, located on the axial face of the first gill filament at the base, innervated from the cerebral ganglia, and comprising pigment and ciliated sensory cells. They are restricted to some members of Pteriomorphia (Pelseneer 1899; Rosen et al. 1978; Morton et al. 1998). Coded as absent in all non-pteriomorphs. Among the pteriomorphs, present in *Mytilus, Arca, Barbatia, Pteria,* and *Anomia*; coded as "?" in *Geukensia, Lithophaga, Striarca,* and *Glycymeris.* We follow Ponder & Lindberg (1997) in coding the eyes of *Nautilus* as putative homologs to the open pit of basal gastropods. We have added a fourth state for the very special eye of coleoid cephalopods.
130. *Pallial eyes: (0) absent; (1) develop from the outer mantle folds; (2) develop from the middle mantle folds; (3) develop from the inner mantle folds.* Pallial eyes are ectopic eyes with nervous links to the visceral ganglia via the pallial nerves seen in species of Arcoidea, Limopsoidea, Pterioidea, Limoidea, Pectinoidea, Cardioidea, and Laternulidae (Dakin 1928; Morton 2000b,c). Such eyes develop on either the outer, middle, or inner mantle folds (Morton 2000b). Since their positional homology is uncertain, we have chosen to code this character as multistate.

    All the examined representatives of Arcoidea (*Arca, Barbatia*; coded as "?" in *Striarca*) and Limopsoidea (*Glycymeris*) have ommatidium-like eyes developing on a sub-fold of the outer mantle fold—beneath the periostracum (Waller 1980; Morton 1987a, 2000c). Eyes of this type are also apparently present in *Lima lima* but not in *Ctenoides floridanus,* where they occur on the middle folds as in Pectinoidea (Morton 2000b).

    Complex pallial eyes developing on the middle mantle folds (see reviews in (Morse & Zardus 1997; Morton et al. 1998) are present in virtually all shallow-genera of Spondylidae and Pectinidae (Morton et al. 1998; Morton 2000c). A thin cornea overlies a multicellular lens. Beneath this is a double retina composed of sensory and interstitial cells. Both retinas are of the inverse type, the optic fibers passing between lens and retina. Below the retina is a light-reflecting layer or tapetum derived from the underlying cellular pigment layer (Morton et al. 1998; see Barber et al. 1967 for *Pecten maximus*; Morse & Zardus 1997 for *Chlamys varia*).

    Simple pallial eyes (with an inverse type retina) developing on the inner mantle folds are found in heterodonts and anomalodesmatans (Morse & Zardus 1997; Morton et al. 1998; Morton 2000c). The 2 siphons of *Cerastoderma edule* have about 100 eye-bearing tentacles (Barber & Wright 1969), each eye consisting of a cup of reflecting cells that enclose some 12–20 receptor cells. Each eye has a thin cornea, a large oval multicellular lens with its long axis parallel to the optic axis, and a single layer of columnar cells constituting the retina. The retina is of inverse type, the nervous supply from the tentacular nerve to the sensory cells passing between lens and retina (Stasek 1966; Barber & Wright 1969; Schneider 1992). This type of simple eye has been observed on the ends of the tentacles of *Parvicardium exiguum* (J. Schneider, pers. comm.) and *P. pinnulatum* (Meyer & Möbius 1872), and in *Tridacna* sp. (Morton et al. 1998). It is coded absent for *Fragum unedo* based on a member of the same subfamily, *Microfragum erugatum* (Morton 2000a). An eye of similar structure has been described for the anomalodesmatan *Laternula truncata* (Adal & Morton 1973).
131. *Bivalve pallial tentacles in the mantle edge: a/p* (Waller 1978). Pallial tentacles are present in numerous bivalve groups, including Limidae, Ostreidae, Pectinidae,

Spondylidae, Anomiidae, Trigoniidae, Chamidae, Galeommatidae, Tridacnidae, and Corbulidae. Coding restricted to bivalves.

132. *Type of pallial tentacles: (0) simple lobate extensions of mantle edge, poorly extensible; (1) complex autotomizing tentacles with bands of cells secreting predator repellants* (Waller 1998). Limoid tentacles present certain complex features not occurring in the tentacles of any other bivalves: (i) internal septa that subdivide the tentacle into a number of independent hydrostatic units for complex movements; (ii) rings of gland cells that secrete sticky, predator-repelling mucus; and (iii) autotomy, occurring either at the base of the tentacle or at any of the septa (Gilmour 1963, 1967; Waller 1998). Coding restricted to bivalves with pallial tentacles.
133. *Sensory mantle tentacle: a/p* (Salvini-Plawen & Steiner 1996; Waller 1998). According to Waller (1998), a single retractile tentacle developed from the middle fold of the mantle in the region of the siphonal embayment is a unique feature of Nuculanoidea. It is apparently absent only in Nuculanidae and in some members of Tindariidae but is consistently present in all other nuculanoidean taxa (Brooks 1875; Yonge 1939a; Allen & Sanders 1982, 1996; Boss 1982; Allen & Hannah 1989).
134. *"Palp siphon:" a/p* (Salvini-Plawen & Steiner 1996). We assume that the palp siphon of Salvini-Plawen & Steiner (1996) corresponds to the unique feeding aperture of Nuculanoidea (Allen 1985), which marks the place where the palp proboscides emerge from the shell. This character was also used by Waller (1998: aperture for palp appendages).
135. *Dorsal pallial organ: a/p.* A pre-oral, unpaired pallial gland is a unique organ of Pinnidae (Yonge 1953b).
136. *Stempell's organ: (0) absent; (1) present.* This tube-shaped organ is situated immediately dorsal to the anterior adductor muscle of some protobranchs (*Nucula nucleus, N. delphinodonta,* and *N. sulcata* [Drew 1901; Stempell 1898; Haszprunar 1985c]). Stempell's organ has also been observed in *Acila castrensis* (Kurt Schaefer, pers. comm.). It has been coded as "?" in *N. proxima.* It is absent in *Malletia inequalis* and *Nuculana pernula* (Israelson, pers. obs. 1999), and thus we assume that it is absent in all nuculanoids.
137. *Abdominal sense organ (ASO): a/p* (Salvini-Plawen & Steiner 1996). An abdominal sense organ in the form of paired ectodermal thickenings on the posterior side of the posterior adductor near the anus is present throughout Pteriomorphia (Thiele 1887, 1889; List 1902; Clasing 1923; Studnitz 1931; Moir 1977; Yonge 1977; Haszprunar 1983, 1985c, 1985d; Morse & Zardus 1997; Waller 1998), Trigonioidea (Pelseneer 1891; Haszprunar 1983, 1985d), and Unionoidea (Herbers 1914 [cited in Waller 1998]). Consequently, it has been coded as present in all pteriomorphs and palaeoheterodonts.
138. *Position of the ASO: (0) outside gill axes; (1) inside gill axes* (Haszprunar 1983, 1985d). The coding of this character follows a groundplan as summarized by Haszprunar (1983), with Mytiloidea (5 genera and 11 families investigated) having the ASO outside of gill axes. Coding restricted to bivalves with ASO.
139. *Symmetry of paired ASO: (0) symmetrical; (1) asymmetrical, with the left small or vestigial relative to the right; (2) asymmetrical, with the left absent; (3) both reduced* (Haszprunar 1983, 1985d; Waller 1998). Haszprunar (1983, 1985d) summarized data on symmetry of the ASO in Pteriomorphia, showing their symmetrical development in Mytilidae, Arcoidea, Limopsoidea (except Glycymerididae), Limidae, and Trigoniidae and greater development of the right abdominal sense organ in Pinnidae, Pterioidea, Pectinoidea, Dimyidae, Plicatulidae, Spondylidae, Ostreidae, and Anomiidae. *Anomia ephippium* has lost both ASOs (Haszprunar 1983). Coding restricted to bivalves with ASO.
140. *Stenta's (marginal) organ: a/p.* A ciliated sense organ in the middle fold of the mantle edge near the anterior end is universally present in Nuculanidae (Yonge 1939a). It has been described for *Nuculana commutata* (Stenta 1909); *N. pernula, N. pella, Yoldia limatula, Portlandia isonota,* and *Malletia gigantea* (Stoll 1939), *N. minuta, N. pella, Yoldiella lucida, Malletia obtusata,* and *Yoldia limatula* (Yonge 1939a); and several species of *Spinula, Neilonella, Ledella, Propeleda, Silicula, Lametila, Nuculana, Malletia, Tindaria,* and *Yoldiella* (Allen & Sanders 1973, 1982, 1996; Sanders & Allen 1977; Allen & Hannah 1989; Allen 1993; Allen et al. 1995). This has been termed "anterior sense organ" (Allen 1985; Allen & Hannah 1986; Salvini-Plawen & Steiner 1996) or "anterior mantle sense organ" (Waller 1998). Salvini-Plawen & Steiner coded the presence of the anterior sense organ in Nuculoidea and Nuculanoidea (their character 38), but we follow Yonge (1939a) and Allen (1985) in considering that this character is a putative synapomorphy for Nuculanoidea.
141. *Adoral (or cephalic) sense organ: a/p* (Yonge 1939a,b; Haszprunar 1985c; Salvini-Plawen & Steiner 1996; Waller 1998; Schaefer 2000). An adoral sense organ has been described in several species of Solemyidae (*Solemya togata* and *S. reidi*), Nuculidae (*Acila* and *Nucula*), Nuculanidae (*Nuculana*), and Yoldiidae (*Yoldia*) (see Schaefer 2000 for references). Absence of the adoral sense organ outside the protobranch bivalves has been coded as a groundplan assumption. For the protobranch species studied here, we follow the interpretations of Schaefer (2000).
142. *Pedal reversal: a/p* (Waller 1998). All known extant limoids have a unique foot that is rotated 180 degrees, affecting the pedal nerves (Seydel 1909; Stuardo 1968; Gilmour 1990).
143. *Osphradia: (0) present; (1) absent.* Osphradia are epithelial sense organs innervated by the visceral ganglia and functioning as chemoreceptors to test incoming water (or outgoing water in some gastropods) (Krae-

mer 1979; Haszprunar 1985a,b, 1987; Waller 1998). They are present in all molluscan classes except Scaphopoda and probably Monoplacophora (see Stork 1934; Charles 1966; Harry 1969; Haszprunar 1987). Osphradia are present in *Nautilus* where they are called "interbranchial papillae," but are absent in coleoid cephalopods (Naef 1923). Among bivalves, osphradia have been described for *Nucula sulcata* (Yonge 1939a, 1947; Haszprunar 1987); *Leda sulculata* and *Malletia chilensis* (Stempell 1898); *Malletia gigantea* (Stoll 1939); *Yoldiella lucida* (Haszprunar 1987); Mytilidae (List 1902; Clasing 1923; Haszprunar 1987); *Arca noae* (Spengel 1881; Dakin 1910; Haszprunar 1987); *Pecten* (Dakin 1910); Anomiidae (Atkins 1936); Spondylidae (Dakin 1928); Unionidae (Freidenfelt 1897, 1904; Kraemer 1981; Zaitseva & Sokolov 1981; Sokolov & Zaitseva 1982; Haszprunar 1987); *Dreissena polymorpha* and *Venus verrucosa* (Haszprunar 1987); *Venus casina* (Dakin 1910); *Corbicula fluminea* (Dakin 1910); *Pholas dactylus* (Förster 1914; Haszprunar 1987); *Cerastoderma edule, Spisula subtruncata, Sphaerium corneum,* and *Pisidium henslowanum* (Stork 1934). We have adopted a familial groundplan coding.

144. *Storage vesicles in connective tissue: a/p.* Scattered vesicles lined by large conical cells and surrounded by fine strands of connective tissue may bind together the various organs of the visceral mass and spread into the mantle (Dakin 1910). These occur in several species of *Astarte,* including *A. castanea* (Saleuddin 1967). This character, although uninformative in the present matrix, is a putative synapomorphy for the genus *Astarte,* and it is included here for descriptive purposes.

145. *Luminescent acinous glands: a/p.* A special type of acinous glands has been shown to be luminescent in *Astarte sulcata* (Saleuddin 1965). Glands of similar histological appearance and position are found in *A. castanea* (Saleuddin 1967). Photogenic cells (of different type) are also found in other few bivalves such as in the pectinid genera *Parvamussium* and *Propeamussium* (Hicks & Marshall 1985), in *Pholas dactylus, Gastrochaena grandis,* and *Barnea candida* (Harvey 1952).

146. *Intracellular ctenidial bacteria involved in sulphide-oxidizing symbiosis: a/p.* Symbiotic, chemoautotrophic bacteria within bacteriocytes which play a role in nutrition through the oxidation of sulphur are found in the gills of several bivalve families: Solemyidae, Nucinellidae, Mytilidae, Lucinidae, Fimbriidae, Thyasiridae, and Vesicomyidae (Reid & Brand 1986; Reid 1990; Distel 1998). Among the species represented here, this symbiosis occurs in *Solemya velum* (Cavanaugh 1983), *S. reidi* (Felbeck et al. 1981; Felbeck 1983), *Calyptogena magnifica* (Boss & Turner 1980; Felbeck et al. 1981; Cavanaugh 1983), and *Codakia orbiculata* (Berg et al. 1982). The remaining species have been coded as absent, although the absence has been documented only in *Acila castrensis, Yoldia* sp., *Geukensia demissa, Arctica islandica,* and other members of the families Ungulinidae, Veneridae, Corbulidae, Solenidae, Kelliidae, Tellinidae, and Thyasiridae (see references in Reid 1990).

147. *Symbiotic zooxanthellae: a/p.* Symbiotic zooxanthellae have been found in all members of Tridacninae (Yonge 1980), other members of Cardiidae: *Corculum cardissa* (Kawaguti 1950) and *Fragum* spp. (Ohno et al. 1995; Morton 2000a); proxy used for *Fragum unedo*), and in one species of the family Trapeziidae (Morton 1982b).

148. *Symbiotic zooxanthellae in the siphons and other regions of the mantle exposed to light: a/p.* A major adaptation in Tridacnidae is the enlargement of the siphons for housing and exposure to light of the symbiotic zooxanthellae. This involves hypertrophy of the inner mantle fold on the upper surface, as well as in the *under* surface of the middle mantle folds of attached species (Yonge 1980).

149. *Zooxanthella tube system: a/p.* A tube system (Mansour's ducts) that contains zooxanthellae and connects the digestive diverticula with the kidney (*Microfragum erugatum*; Morton 2000a), or with the kidney and the haemocoelic spaces of the siphonal tissues (*Tridacna gigas*; Norton & Jones 1992) is a putative synapomorphy of Fragiinae + Tridacninae as proposed by Schneider (1992; see also Morton 2000a [but see Schneider 1998]). A genus-level coding has been adopted for this character.

150. *Gland of Deshayes containing cellulolytic nitrogen-fixing bacteria: a/p.* Cellulolytic nitrogen-fixing bacteria have been isolated from the gland of Deshayes in numerous teredinids (Popham & Dickson 1973; Waterbury et al. 1983).

Reproduction (characters 151–153): Sexual strategies vary enormously among bivalves. Hermaphroditism occurs in many bivalves species (Sastry 1979). It has been adopted as a reproductive strategy in virtually all representatives of Anomalodesmata, Galeommatoidea, Pectinoidea, Teredinidae, Ostreidae, and Sphaeriidae (Morton et al. 1998). Hermaphroditism may be (1) simultaneous (functioning as male and female at the same time), (2) consecutive (either protandric or protogynic), or (3) alternating (functioning as male or female in regularly or irregularly alternating periods). In the case of *Mercenaria mercenaria,* in which consecutive sexuality is observed, a small proportion of individuals are gonochoristic. Coding restricted to documented cases; coding for *Lasaea* sp. follows Ó Foighil (pers. comm.), who provided the specimens of this unidentified species and the reproductive observations.

151. *Number of gonoducts: (0) paired; (1) single, from pretorsional left gonad; (2) single, from pretorsional right gonad* (Ponder & Lindberg 1997).

152. *Reproductive method: (0) free-spawning; (1) brooding to larvae; (2) brooding to juveniles; (3) ovoviviparous* (Mackie 1984; Kabat & Ó Foighil 1987; Kasyanov et al. 1998; Ó Foighil & Taylor 2000). Coding of characters 152 and 153 for *Codakia orbiculata* based on

the congener *C. orbicularis* (Alatalo et al. 1984). Codings restricted to documented cases.

153. *Reproductive strategy: (0) planktotrophy; (1) strict lecitotrophy; (2) direct development* (Sastry 1979; Lutz et al. 1982a,b. Coding for *Neotrigonia margaritacea* follows Ó Foighil & Graf (2000); coding for *Varicorbula disparilis* follows Mikkelsen & Bieler (2001), who showed prodissoconch I to be separated from prodissoconch II by a distinct growth line, indicative of planktic development. Codings restricted to documented cases.

Sperm (characters 154–169): A bivalve sperm consists typically of an ellipsoid or conical nucleus, an acrosome of variable complexity, a middle piece consisting of usually 4–5 mitochondria surrounding a pair of centrioles, and a flagellum. This is seen in many other molluscs, but several modifications occur in different groups. Detailed studies of sperm ultrastructure are available for many bivalve species, and a few broader comparative studies are available for bivalves in general (Popham 1979), Veneroida (Healy 1995a), and Pteriomorphia (Healy et al. 2000).

Codings used here are based on the following sources: *Nucula sulcata* (Franzén 1983); *N. proxima* based on *N. hartvigiana* (Popham & Marshall 1977); *Mytilus edulis* (Hodgson & Bernard 1986; Sousa & Azevedo 1988; Sousa et al. 1995); *Lithophaga lithophaga* based on *L. curta* (Dan & Wada 1955); *Barbatia barbata* based on *B. obliquata* and *B. foliata* (Reunov & Hodgson 1994); *Glycymeris insubrica* based on *G. holosericus* (Healy 1996a; Healy et al. 2000); *Striarca lactea* (Healy et al. 2000); *Pteria hirundo* based on *Pinctada* sp. (Healy et al. 2000); *Anomia ephippium* based on *A. trigonopsis* (Popham 1979); *Ostrea edulis* (Popham 1979; Sousa & Oliveira 1994; Sousa et al. 1995); *Crassostrea virginica* (Eckelbarger & Davis 1996); *Pecten maximus* (Dorange & Le Pennec 1989); *Chlamys varia* based on *C. hastata* (C.A. Hodgson & Burke 1988); *Spondylus sinensis* based on *S. nicobaricus* (Healy et al. 2000); *Limaria hians* based on *L. fragilis* (Healy et al. 2000); *Atrina pectinata* based on *A. vexillum* (Healy et al. 2000); *Neotrigonia bednalli* (Healy 1989); *Neotrigonia margaritacea* (Healy 1996b); *Psilunio littoralis* based on *Velesunio ambiguus* (Healy 1989); *Cardita calyculata* based on *Cardita muricata* (Healy 1995b); *Astarte castanea* coded based on crassatellids[2] *Eucrassatella cumingii, E. kingicola,* and *Talabrica aurora* (Healy 1995b); *Galeomma turtoni* based on *Divariscintilla yoyo, D. troglodytes,* and *Cintilla* sp. (Eckelbarger et al. 1990); *Lasaea* sp. based on *L. subviridis* (Ó Foighil 1985a); *Codakia orbicularis* based on *C. punctata* (Healy 1995a); *Chama gryphoides* based on *C. macerophylla* (Hylander & Summers 1977); *Ensis ensis* (Casas & Subirana 1994); *Fragum unedo* (Healy 1995a; Keys & Healy 1999); *Tridacna gigas* and *Hippopus hippopus* (Keys & Healy 2000); *Spisula subtruncata* based on *S. trigonella* (Healy 1995a) and *S. solidissima* (Hylander & Summers 1977; Sousa et al. 1995); *Arctica islandica* based on *Trapezium sublaevigatum* (Healy 1995a); *Corbicula fluminea* (Kraemer 1983); *Callista chione* (Nicotra & Zappata 1991); *Dreissena polymorpha* (Franzén 1983); *Varicorbula disparilis* based on *Notocorbula vicaria* (Popham 1979); *Bankia carinata* (Popham et al. 1974); *Lyonsia hyalina* based on *L. ventricosa* (Kubo & Ishikawa 1978); *Cuspidaria cuspidata* based on *Cuspidaria* sp. (Healy 1996a).

Codings for the outgroups are based on the following sources: *Acanthochitona crinita* based on *A. garnoti* and *Lepidopleurus cajetanus* based on the Lepidopleurinae *Leptochiton asellus* (Hodgson et al. 1988); *Haliotis tuberculata* based on *H. midae* (Hodgson & Foster 1992) and *H. laevigata* (Healy et al. 1998); *Diodora graeca* based on *D. aspera* (Hodgson & Chia 1993); *Sinezona confusa* based on *Sinezona* sp. (Healy 1990); *Viviparus georgianus* based on *V. viviparus* (Griffond 1980); *Peltodoris atromaculata* based on several members of Doridiidae (Healy & Willan 1991); *Nautilus pompilius* (Arnold & Williams-Arnold 1978); *Sepia elegans* based on *S. officinalis* (Maxwell 1975); *Loligo pealei* based on *Loligo forbesi* (Maxwell 1975); *Antalis pilsbryi* based on *A. entails* (Hou & Maxwell 1991).

154. *Acrosomal vesicle: (0) present; (1) absent.* An acrosomal vesicle is absent in several Polyplacophora, but not in Lepidopleurinae (Hodgson et al. 1988).

155. *Multiple acrosomal vesicles: (0) present; (1) absent.* The presence of multiple acrosomal vesicles in *Velusunio ambiguus* (Healy 1989), *Anodonta grandis* (Lynn 1994), and 3 species of *Neotrigonia* (Healy 1989, 1996b) has been interpreted as a putative synapomorphy for the Palaeoheterodonta (but see Peredo et al. 1990; Rocha & Azevedo 1990). We have followed the codings of Healy, assigning a groundplan coding for Unionidae in order to be able to make use of this potentially informative phylogenetic information.

156. *Shape of the acrosomal vesicle: acrosomal vesicle with undifferentiated acrosomal contents (0); acrosomal vesicle with a thick posterolateral, highly electron-dense basal ring (1); acrosomal vesicle with its contents differentiated into a highly electron-dense anterior layer and a less dense posterior layer (2); broad acrosomal vesicle with a differentiated, apical wedge-zone (3); acrosomal vesicle with a highly electron-dense internal layer which recurves posteriorly, giving a double-layered effect through most of its length (4); acrosomal vesicle with contents differentiated into a very dense inner layer surrounded by less dense material (5); acrosomal vesicle with contents differentiated into a very dense outer layer surrounding a less dense material (6); acrosomal vesicle with anteriorly truncate profile ("Pandoroidea type") (7).*

Healy (1995a) differentiates among the acrosomal vesicle of his types A and B vs. C in that the members

[2] This coding assumes monophyly of Crassatellidae + Astartidae, and that the sperm anatomy described for 3 crassatellids is the groundplan for the common ancestor of *Astarte* and the crassatellids. *Astarte sulcata* was investigated by means of light-microscopy by Franzén (1955), who found that the midpiece contained only 4 mitochondria and that the nucleus, although elongate was not capped by an obvious acrosome.

of type C have the electron-dense basal ring developed longitudinally. Here we code these three types within the same category (short conical acrosomal vesicle with an electron-dense basal ring). Differences within this state could be considered as an additional character. Several other autapomorphic types of acrosomal vesicles occur in molluscs.

157. *Acrosomal contents with a highly electron-opaque layer associated with long radiating plates: (0) present; (1) absent.* In their review of pteriomorph spermatozoa, Healy et al. (2000) proposed a putative synapomorphy for Pterioidea, Pinnoidea, and Pectinoidea, the presence of acrosomal contents with a highly electron-opaque layer associated with long radiating plates, sometimes with additional differentiation zones. In Ostreidae, radiating plates are associated with the basal region of the acrosomal vesicle of *Dendrostrea folium* but have not been detected in other ostreids examined. Lacking data on transverse sections of the acrosome in other ostreids, we have coded them as "?." This character has been investigated mostly for Pteriomorphia (Healy et al. 2000) and cannot be coded for most other terminal taxa.

158. *Position of the acrosomal vesicle: (0) anterior; (1) posterior, at the side of the midpiece.* A posteriorly positioned acrosome (the "temporary acrosome" of Kubo 1977) has been found in the families Lyonsiidae, Laternulidae, and Myochamidae (Kubo 1977, 1979; Kubo & Ishikawa 1978; Popham 1979; Healy 1996a). Here we have coded *Lyonsia hyalina* based on the coding of *L. ventricosa* (Kubo & Ishikawa 1978). On the contrary, *Cuspidaria* sp. (proxy used for *C. cuspidata*) possesses an anteriorly positioned acrosomal vesicle (Healy 1996a) resembling the one of *Notocorbula vicaria* (Popham 1979). The temporary acrosome has not been observed in any non-anomalodesmatan bivalve.

159. *Anterior acrosomal vesicle: (0) oriented following the longitudinal axis of the sperm; (1) arranged at a considerable angle to the longitudinal axis of the sperm.* An acrosomal vesicle arranged at a considerable angle to the longitudinal axis of the sperm (sperm type of group B of Healy 1995a) is found in *Lasaea subviridis, Pseudophytina rugifera, Scintilla* sp., *Divariscintilla yoyo,* and *D. troglodytes* (Ó Foighil 1985a,b; Eckelbarger et al. 1990).

160. *Anterior nuclear fossa: a/p* (Healy 1990).

161. *Subacrosomal space contains granular material forming an axial rod (perforatorium): a/p.* The subacrosomal material polymerizes at the time of the acrosome reaction. However, in several species, the subacrosomal substance is organized into a more or less completely preformed acrosomal filament or axial rod (Popham 1979; Dohmen 1983).

162. *Nucleus with eccentrically positioned flagellum: a/p* (Healy 1996a).

163. *Nuclear peg penetrating deep into the invagination of the acrosomal vesicle: a/p.* The nucleus of *Tridacna maxima* (Keys & Healy 1999) and *Cerastoderma edule* (Sousa & Azevedo 1988; Sousa et al. 1995) is elongate and refined apically into a peg-shaped structure penetrating deep into the invagination of the acrosomal vesicle.

164. *Mitochondrial midpiece: (0) present; (1) absent.* A mitochondrial midpiece forms part of the typical molluscan sperm, but those of several cephalopods lack a midpiece (Healy 1996a).

165. *Location of mitochondria: (0) in midpiece; (1) enclosed within a membrane sac; (2) two mitochondria running along lateral furrows in the nucleus* (Maxwell 1975; Arnold & Williams-Arnold 1978; Healy 1996a).

166. *Distribution of mitochondria in midpiece: (0) regularly distributed around centrioles; (1) excentrically distributed* (C.A. Hodgson & Burke 1988; Healy 1996a). Coding restricted to molluscs with mitochondrial midpiece.

167. *Eight mitochondria in midpiece: a/p.* Bivalve sperm typically have a midpiece consisting of (usually) 4–5 mitochondria surrounding a pair of centrioles, although other configurations exist. This character recognizes the presence of typically 8 mitochondria in members of Carditidae and Crassatellidae, a configuration not found in any other bivalve studied so far (Healy 1995b). Coding restricted to molluscs with mitochondrial midpiece.

168. *Membrane skirt: a/p* (Maxwell 1975; Arnold & Williams-Arnold 1978; Healy 1996a).

169. *Proximal centriole splits open and unrolls to form a banded rootlet during the transitional phase from spermatid to spermatozoa: (0) absent (two centrioles present); (1) present.* At the beginning of spermiogenesis, 2 centrioles are present. In typical molluscan sperm, both centrioles are conserved and are positioned at right angles to each other. The proximal centriole is oriented perpendicular to the axoneme, and the distal one in line with the axoneme; the distal one forms the basal body of the flagellum (Dohmen 1983). In some cases, such in *Laternula limicola,* the proximal centriole moves to the lateral side of the distal centriole, so that the 2 centrioles are parallel (Kubo & Ishikawa 1978). The reduction of one of the 2 centrioles during spermiogenesis maturation has been observed in Carditidae and Crassatellidae (Healy 1995b).

Developmental data (characters 170–181): Data on cleavage and germ layer formation are scarce and we have adopted different groundplans. We have used the developmental data of Heath (1899) on *Stenoplax heathiana* (Ischnochitonina) as a proxy for *Lepidopleurus* and *Acanthochitona* (Lepidopleurina and Acanthochitonina, respectively) (see Pearse 1979). Data from *Antalis* sp. (Lacaze-Duthiers 1856, 1857a, 1858) are used as a proxy for *A. pilsbryi.* Detailed studies on cell lineage for bivalves are available for the following species: *Ostrea edulis* (Fujita 1929), *Lasmigona complanata* (Lillie 1895) (proxy used for *Psilunio* and *Lampsilis*), *Dreissena polymorpha* (Meisenheimer 1901), and *Sphaerium striatinum* (Woods 1931) (proxy used for *Sphaerium striatum*). Embryological data for *Nucula* spp. based on *Nucula*

delphinodonta (Drew 1901); *Pecten maximus* based on *P. tenuicostatus* (Drew 1906); *Chlamys varia* based on *C. hastata* (C.A. Hodgson & Burke 1988); *Codakia orbiculata* based on *C. orbicularis* (Gros et al. 1997).

170. *Mode of development: (0) unequal cleavage; (1) equal cleavage; (2) yolky meroblastic egg, with non-spiral cleavage, and direct development.* The typical cleavage in molluscan eggs is a modification of holoblastic radial cleavage (Verdonk & Van den Biggelaar 1983), and has been called spiral cleavage by E.B. Wilson (1892). All cephalopods seem to have development that involves a yolky meroblastic egg, non-spiral cleavage, and direct development (Bandel & Boletzky 1979; Waller 1998).
171. *Cleavage with polar lobe formation: a/p.* Polar lobe formation during cleavage has been found in numerous molluscs with spiral development (see Sastry 1979; Verdonk & Van den Biggelaar 1983; Freeman & Lundelius 1992; Ponder & Lindberg 1997; and references therein).
172. *Molluscan cross during development: (0) present; (1) absent.* In molluscs, the ectoderm is divided into a pretrochal and a post-trochal region by a band of ciliated cells, the so-called prototroch cells. The pre-trochal region (the future head region) originates from the first quartet of micromeres (1a–d), formed at third cleavage. In all molluscs except bivalves, this first quartet forms a typical structure, known as the molluscan cross (Verdonk & Van den Biggelaar 1983). Within the bivalves, a structure similar to a molluscan cross has been observed in *Solemya reidi* (Gustafson & Reid 1986) and *S. velum* (Gustafson & Lutz 1992).
173. *Apical tuft on the larva: (0) present; (1) absent.* An apical tuft is common in the free-swimming larvae of the Bivalvia and in outgroups (Cragg 1996; Waller 1998), although it is absent in some members of Ostreidae, including *Ostrea edulis* (Waller 1981) and *Crassostrea virginica.*
174. *Pericalymma larvae: a/p.* Pericalymma larvae have been described for only a few species of protobranch bivalves: 4 nuculids, *Nucula proxima, N. turgida, N. delphinodonta,* and *Acila castrensis*; 2 nuculanids, *Nuculana pernula* and *N. fossa*; a yoldiid, *Yoldia limatula*; and 2 solemyids, *Solemya reidi* and *S. velum* (Drew 1897, 1899a,b, 1901; Trevallion 1965; Gustafson & Reid 1986, 1988a,b; Gustafson & Lutz 1992; Zardus & Morse 1998). Larvae of 2 other species, *Nucula nucleus* and *N. nitida,* were raised by Lebour (1938), but aside from mentioning their barrel-shaped form, he provided no description (Zardus & Morse 1998). A groundplan coding of absent has been adopted for the non-protobranch molluscs.
175. *Ciliation of test-cell larva: (0) in distinct bands; (1) entire test uniformly ciliated* (Drew 1901; Gustafson & Reid 1986; Waller 1998). Coding restricted to taxa with pericalymma larva.
176. *Trochophora larvae: (0) present; (1) absent.*
177. *Veliger larvae: a/p.* The molluscan veliger larval stage is a link between the trochophore and the pediveliger stage, and is represented in some members of Bivalvia and Gastropoda (Carriker 1990; see Cragg 1996 for references).
178. *Pediveliger stage: a/p.* The swimming-crawling, bivalve-shelled pediveliger is a critical stage between planktonic and benthic existence in most bivalves. A review of the literature by Carriker (1990) confirmed the presence of a pediveliger in 31 families and 66 genera of bivalves. The pediveliger larva possesses a 2-valved, hinged, mineralized shell; a strongly ciliated velum; and a densely ciliated, powerful foot (Carriker 1990). Detailed descriptions of pediveligers are those of *Ostrea edulis* (Yonge 1926; Cole 1938), *Crassostrea virginica* (Galtsoff 1964), *Mytilus edulis* (Bayne 1971), *Chlamys hastata* (C.A. Hodgson & Burke 1988), and *Codakia orbicularis* (Gros et al. 1997). For a revision on the subject and citations for the species here coded, see Carriker (1990).
179. *Statocysts in pediveliger stage: (0) single statolith in each statocyst; (1) several statoconia in each statocyst.* Larvae of many species of gastropod and bivalve molluscs develop statocysts in the swimming/crawling stage prior to metamorphosis. In bivalve pediveligers, these statocysts may contain either a single statolith or several small statoconia (Cragg & Nott 1977; Carriker 1990; Cragg 1996). Coding restricted to bivalves with pediveliger.
180. *Pallial eyes in pediveliger stage: (0) present; (1) absent* (Cragg 1996). Eyes of bivalve pediveligers lie roughly at the center of each valve just beneath the larval shell, each consisting of a pigmented epithelial cup surrounding a central amorphous lens, the open end toward the exterior of the larva, and a nerve leading inwards from each (Carriker 1990).
181. *Glochidium: a/p.* Glochidia have been described only for Unionoidea (see Hoggarth 1999), and thus all non-unionoids have been coded as absent, even though for some of them the larval development is unknown. For the species used in this study, the glochidium of *Psilunio littoralis* has been illustrated by Altaba (1992), and the glochidium of *Lampsilis cardium* was observed by the authors.
182. *Swimming capacity through valval movement: a/p.* This type of valval movement has been described for a few pectinids (Morton 1980b), and we have observed it in *Limaria hians* and in *Pecten maximus.*
183. *Animal secreting a calcareous tube: a/p.* Calcareous tubes are secreted by certain myoids and certain anomalodesmatans. From the taxa here represented, calcareous tubes are built by *Gastrochaena* (Carter 1978) and *Bankia* (Turner 1966).

Appendix 2. Morphological data matrix of 183 characters.

Lepidopleurus cajetanus	100???????	???---0---	---0--000-	----------	--00000000	0?0-------	-0-0-0-0--	-??-0-0-0-	----000?00	----------
	0?0?000000	-000000000	0000000000	--0-000---	0000000000	0010002000	0000000001	0000-000--	000	
Acanthochitona crinita	100???????	???---0---	---0--000-	----------	--00000000	0?0-------	-0-0-0-0--	-??-0-0-0-	----000?00	----------
	0?0?000000	-000000000	0000000000	--0-000---	0000000000	0011------	-1-0010001	0000-000--	000	
Nautilus pompilius	0101101000	?000001---	---0--000-	----------	--01000010	??0-------	-010-0-0--	-??-0-0-0-	----000?00	----------
	0?0?00100-	-000001100	0101100010	--0-000---	0000000000	02200??000	00012--102	0?--------	000	
Loligo pealei	01--------	---0-?0---	---0--000-	----------	--01000010	??0-------	-110-0-0--	-??-0-0-0-	----000?00	----------
	0?0?0000-	-000001100	0101100030	--0-000---	0010000000	22200??000	01011--102	??--------	000	
Sepia elegans	01--------	---0-?0---	---0--000-	----------	--01000010	??0-------	-110-0-0--	-??-0-0-0-	----000?00	----------
	0?0?00100-	-000001100	0101100030	--0-000---	0010000000	22200??000	01011--102	??--------	000	
Haliotis tuberculata	0101101000	?000101---	---?--000-	----------	--11001110	0?0-------	-010-0-0--	-??-0-0-0-	----000?00	----------
	0?0?000000	-000000100	0001100110	--0-000---	0000000000	10?0000001	100000000?	1??0-010--	000	
Sinezona confusa	0101101000	?000101---	---?--000-	----------	--11001110	0?0-------	-?10-0-0--	-??-0-0-0-	----000?00	----------
	0?0?000000	-000000100	0001100120	--0-000---	0000000000	1??000?001	10000??00?	????????--	000	
Diodora graeca	0101101000	?000101---	---1--000-	----------	--11001110	0?0-------	-010-0-0--	-??-0-0-0-	----000?00	----------
	0?0?000000	-000000100	0001100120	--0-000---	0000000000	10?000?000	0010000001	1000-010--	000	
Viviparus georgianus	010???????	??00101---	---0--000-	----------	--11001110	0?0-------	-?10-0-0--	-??-0-0-0-	----000?00	----------
	0?0?000000	-000000100	0001100120	--0-000---	0000000000	1??00??00?	????0??0?0	???0-??0--	000	
Truncatella guerinii	01????????	??00101---	---0--000-	----------	--11001110	0?0-------	-?10-0-0--	-??-0-0-0-	----000?00	----------
	0?0?000000	-000000100	0001100120	--0-000---	0000000000	1?????????	??????????	???0-??0--	000	
Balcis eburnea	01????????	??00101---	---0--000-	----------	--11001110	0?0-------	-?10-0-0--	-??-0-0-0-	----000?00	----------
	0?0?000000	-000000100	0001100120	--0-000---	0000000000	1?????????	??????????	???0-??0--	000	
Peltodoris atromaculata	01--------	----1-----	------000-	----------	--11001110	0?0-------	-111------	-??-0-0-0-	----000?00	----------
	0?0?000000	-000000100	0001100120	--0-000---	0000000000	10?00??000	?0?00????0	00?0-??0--	000	
Antalis pilsbryi	0100001???	?000010---	---0--000-	----------	--01000001	1?0-------	-?-1------	--------0-	----000000	----------
	0200100110	-00000010?	1010100000	--0-000---	0010000000	20100??000	0010000000	1?00-100-?	000	
Rhabdus rectius	0100001???	?000010---	---0--000-	----------	--01000001	1?0-------	-?-1------	--------0-	----000000	----------
	0200100110	-00000010?	1010100000	--0-000---	0010000000	2?????????	??????????	??0???00-?	000	
Solemya velum	0100001001	0101020000	0001020001	1410100240	000011-001	0?000---00	-010-0-0--	-??-101010	1000101000	0---------
	0011010010	0000000200	0010100000	0-00000--0	?0?0010000	001???????	?????????1	00111100-?	000	
Solemya reidi	0100001001	0101020000	0001020001	1410100?40	000011-001	0?000---00	-010-0-0--	-??-101010	11001???--	----------
	0011010010	000000020?	0010100000	0-00000--0	10?0010000	001???????	?????????1	00111100-?	000	
Nucula sulcata	0101103000	0000020000	0001020000	-010100000	000011-001	0?000---00	-010-0-0--	-??-100011	1100101000	0--01-----
	0101010010	0010000200	0010100000	0-00010--0	1000000000	0??000?000	0000000000	1?????????	000	
Nucula proxima	0101102000	0000020000	0001020000	-010100000	000011-001	0?000---00	-010-0-0--	-??-100011	1100101000	0--01-----
	0101010010	0010000200	0010100000	0-00010--0	1000000000	0010002000	0000000000	1?010100-?	000	
Acila castrensis	0101103000	0000020000	0001020000	-010100000	000011-001	0?000---00	-010-0-0--	-??-100011	1100101000	0--01-----
	0101010010	0010000200	0010100000	0-00010--0	1000000000	001???????	??????????	??010100--	000	

Appendix 2. Continued.

Yoldia limatula	0100000001	0100020000	0001120001	0010100000	000011-001	0?011??100	-110-0-0--	-??-101011	1001101000	0--00-----
	0?01010010	0000000200	0010100000	0-11000--1	0000000000	001???????	??????????0	01010100--	000	
Yoldia myalis	0100000001	0100020000	0001120001	0010100000	000011-001	0?011??100	-110-0-0--	-??-101011	1001101000	0--00-----
	0?01010010	000000020?	0010100000	0-11000--?	?000000000	0?????????	??????????	??????????	000	
Nuculana minuta	0100000001	0100020000	0001120001	0010100000	000011-001	0?011??100	-110-0-0--	-??-101011	1001101000	0--00-----
	0?01010010	000000020?	0010100000	0-01000--1	?000000000	0?????????	??????????	??????????	000	
Nuculana pernula	0100000001	0100020000	0001120001	0010100000	000011-001	0?011??100	-110-0-0--	-??-101011	1001101000	0--00-----
	0?01010010	000000020?	0010100000	0-01000--1	0000000000	001???????	??????????	??010100--	000	
Neilonella subovata	010???????1	?000020000	0001120001	1010100000	000011-001	0?011??100	-110-0-0--	-??-101011	1001101000	0--00-----
	0?01010010	000000020?	0010100000	0-11000--?	?0?0000000	0?????????	??????????	??????????	000	
Geukensia demissa	011110?001	?100020000	1001010001	1210001041	000011-001	1?010---00	010001010-	-??0100010	0-00110110	10-2-10---
	0201010011	000110020?	0010111?10	0-00001000	0000000000	0?0????????	??????????	????0-01???	000	
Mytilus edulis	0111102000	1100020000	1001010001	1210001041	000011-001	10010---00	010001010-	-100100010	0-00110110	10-2-10---
	0201010011	000110020?	0010111010	0-00001000	0000000000	0000060001	1000000000	1100-01110	000	
Lithophaga lithophaga	0111102000	1000020000	1001010001	1210001041	000011-001	1?011??-00	010001010-	-??0100010	0-00110110	10-2-10---
	0201010011	000120020?	0010111?10	0-00001000	0000000000	0?000??00?	?0?0000?0?	????0-01???	000	
Arca noae	0100000110	1100020001	0001010011	0110000000	000011-001	0?000---00	010001010-	-??0110210	0-00110110	10-2-00---
	0201010011	000110021?	0010111011	0-00001100	0000000000	000???????	??????????	????0-011?0	000	
Barbatia barbata	0100000110	1100020001	0001010011	0110000000	000011-001	0?000---00	0100?1010-	-10?110210	0-00110110	10-2-00---
	0201010011	000110021?	0010111011	0-00001100	0000000000	00?0000000	0000000002	????-?????	000	
Striarca lactea	0100000110	?100020001	0001000011	0110000000	000011-001	0?000---00	010001010-	-??0110210	0-00110110	10-2-00---
	0201010011	0001100201	0010111???	0-00001100	00?0000000	0??0000000	0000000002	????-?????	000	
Glycymeris insubrica	0100000110	1100020001	0001000011	0110000000	000011-001	0?000---00	010001010-	-0-0110210	0-00110110	10-2-00---
	0201010011	000120021?	0010111??1	0-00001110	00?0000000	00?0070000	0000000002	????-?????	000	
Pteria hirundo	0111102000	1000020111	2011001001	120--00040	000011-001	1?010---00	010011010-	-??1110210	0-00110110	10-2-10---
	0201010011	000110020?	0010111010	0-00001110	00?0000000	0?00021001	0000000000	1???0-01???	000	
Atrina pectinata	0111002000	0100020101	1010-01001	130--00040	000011-001	0?010---00	010011110-	-??1110210	0-00110110	10-2-01---
	0201010011	000110020?	0010111000	0-00101110	00?0000000	0?00021001	0000000?0?	????0-01???	000	
Lima lima	0110012010	0100020011	2001000001	0210100040	000011-001	0?010---00	010011110-	-??1110210	0-00110110	10-3---000
	0201010011	000110020?	0010111001	1100001100	01?0000000	0?0???????	??????????	????0-01???	000	
Limaria hians	0110010010	0100020011	2001000001	0210100040	000011-001	0?010---00	010011110-	-??1110210	0-00110110	10-3---000
	0201010011	000110020?	0010111002	1100001100	01?0000000	0?00031001	0000000002	????0-01???	010	
Ostrea edulis	0110012000	0110020100	20-10?0001	0210100040	010011-001	00110---00	0100111202	????120210	0-10110110	10-2-11---
	020101000-	----21020?	0010111000	1000001120	00?0000000	0100032001	1000000000	1110-01110	000	
Crassostrea virginica	0110010000	0110020100	20-10?0001	0210100040	000011-001	0?110---00	0100111202	????1?0210	0-10110110	10-2-11---
	020101000-	----21020?	0010111000	1000001120	00?0000000	0000032001	1000000000	1110-01110	000	
Pecten maximus	0110010000	0100020111	2001001001	0211100040	000011-001	0?010---00	0100111010-	-??1110210	0-00110110	10-3---000
	0201010011	000120020?	0010111002	1000001120	0000000000	0000041001	0000000000	1?00-01111	010	

Appendix 2. Continued.

Chlamys varia	0110010100	0000020111	2001001001	0211100040	000011-001	0?010---00	010011010-	-??1110210	0-00110110	10-3---000
	0201010011	000110020?	0010111002	1000001120	0000000000	00000??00?	?0?00000?0	1100-011?0	000	
Spondylus sinensis	0110010?00	0?00020110	20-1000001	0211100040	100011-001	0?1?0---00	010011010-	-??1110210	0-10110110	10-3---000
	0201010011	0000?0020?	0010111002	1000001120	0000000000	0??0041001	0000000000	???0-0????	000	
Anomia ephippium	0110010010	0100020101	20?0-00001	0210100040	000011-001	0?010---00	0100?1020?	?0-0110210	0-00110110	10-3---000
	0201010011	000110020?	0010111010	1000001130	0000000000	0??000?001	0000000000	???0-01110	000	
Psilunio littoralis	0101101000	0000020000	0001010001	140--00?20	000011-001	00011??-00	0100011201	-110101010	0-00110110	1303---111
	0101110011	000120020?	0010111000	0-00001??0	0000000000	02201--000	?000000000	01?0-100--	100	
Lampsilis cardium	010???????	??00020000	0001010001	140--00?20	000011-001	00011??-00	0100011201	-110101010	0-00110110	1303---111
	0101110011	000120020?	0010111000	0-00001??0	0000000000	02201--000	?000000000	01?0-100--	100	
Neotrigonia bednalli	0101101000	1000020000	0001000001	140--00110	000011-001	0?010---00	010001010-	-100100010	0-00110110	12-3---111
	0101110011	010120020?	0010111000	1000001100	00?0000000	0??01--000	?000000000	??????????	000	
Neotrigonia margaritacea	0101101000	1000020000	0001000001	140--00110	000011-001	00010---00	010001010-	-100100010	0-00110110	12-3---111
	0101110011	010120020?	0010111000	1000001100	00?0000000	00101--000	?000000000	??????????	000	
Cardita calyculata	0100000110	1100020000	0001010001	1410100120	000011-001	1?010---00	0100011201	-??0101110	0-00110110	12-3---111
	1201110011	0001100211	0010111000	0-00000--0	00?0000000	0220050001	1000000101	???0-10?-?	000	
Cardites antiquata	0100000110	1100020000	0001010001	1410100120	000011-001	1?010---00	0100011201	-??0101110	0-00110110	12-3---111
	1201110011	0001100211	0010111000	0-00000--0	00?0000000	022????????	??????????	???0-10?-?	000	
Astarte castanea	010000001??	?100020000	0001010001	140--00120	000011-001	1100100-00	0100011200	00-0101010	0-00110110	12-3---111
	1201110011	000120020?	0010111000	0-00000--0	0011100000	0???050001	1000000101	???0-?????	000	
Codakia orbiculata	0100003110	1000020000	0001010001	1410200120	000011-001	1?00100000	0100?1123-	-??0101210	0-00100111	0303---???
	0201110011	000100020?	0010111000	0-00000--0	00?0010000	001001?000	0000000000	1100-111??	000	
Chama gryphoides	0100000110	1100020100	0001010001	1410200120	000011-001	1?11100000	0100111200	1???101110	0-00110110	1304------
	?201110011	000110020?	0010111000	1000000--0	00?0000000	0?0001?00?	?0?00?????	???0-01???	000	
Galeomma turtoni	010???????	??00020000	0001000000	--10200140	000011-001	0?001??000	0100011200	00-0101210	0-00110110	1??3---???
	?201110011	100110020?	0010111000	1000000--0	00?0000000	010001?01?	?100000???	???0-01???	000	
Lasaea sp.	010???????	??00020000	0001010100	--10100120	000011-001	1?001??000	0100?1122-	-??0101?10	0-00110110	1??3---111
	?201110011	100110020?	0010111000	0-00000--0	00?0000000	022001?01?	1100000000	???0-00?-?	000	
Dreissena polymorpha	0100000110	0100020001	1001010001	1?10000140	000011-001	1?01100000	010001?200	00-0101110	0-00110110	1324------
	1201110011	000110020?	0010111000	0-00000--0	0000000000	0?0001????	1????????0	0100-0110?	000	
Parvicardium exiguum	0100000110	0100020000	0001010001	1410200120	000011-001	1?01101000	0100111200	0??1101110	0-00110110	1314------
	1201110011	000110020?	0010111003	0-00000--0	0000000000	010???????	??????????	???0-111?1	000	
Fragum unedo	0100000110	0100020000	000101001	1410200120	000011-001	1201101000	0100111200	00-0101110	0-00110110	1314------
	1201110011	000110020?	0010111000	0-00000--0	0000001010	0?0001?000	0000000000	???0-?1???	000	
Tridacna gigas	0100000110	0100020001	2001010001	140--00120	000011-001	1001101000	0100?1120?	????101110	0-00110111	1314------
	1201110011	000110020?	0010111003	1000000--0	00?0001110	000001?000	0010000000	??00-011?1	000	
Hippopus hippopus	0100000110	0100020000	2001010001	140--00120	000011-001	1201101000	0100?1120?	????101110	0-00110111	1314------
	1201110011	000110020?	0010111003	1000000--0	00?0001110	000001?000	0000000000	???0-011??	000	

Appendix 2. Continued.

Spisula subtruncata	0100000110	0100020000	0001110001	1410200120	000011-001	1?0112-001	0100011200	00-0101?10	0-00110110	1324------
	1201110011	000100020?	0010111000	0-00000--0	0000000000	000001?000	1000000000	01?0-011?1	000	
Tresus nuttallii	0100000110	0100020000	0001110001	1410200120	000011-001	1?0112-000	0100?112??	????101?10	0-00110110	1324------
	1201110011	000100020?	0010111000	0-00000--0	0000000000	000???????	??????????	???0-01???	000	
Abra prismatica	0100003110	0000020000	0001120001	1410200120	000011-001	1?01100100	010001121-	-0-0101110	0-00110110	1314------
	1201110011	000100020?	0010111000	0-00000--0	00?0000000	000???????	??????????	???0-10?-?	000	
Ensis ensis	0100000101	0100020000	01011?0001	140--00120	000011-001	1?011??001	0100111200	10-1101210	0-00110110	1324------
	1201110011	000100020?	0010111000	0-00000--0	00?0000000	0??006?000	0000000000	11?0-?11?0	000	
Arctica islandica	0100000001	0100020000	0001010001	140--00120	000011-001	10011??000	0100?112??	???1101110	0-00110110	1314------
	1201110011	000100020?	0010111000	0-00000--0	00?0000000	000001?000	000000000?	???0-011?1	000	
Calyptogena magnifica	0100000001	0100020000	0001010001	140--00120	000011-001	1?01100000	0100011200	00-0101210	0-00110110	1??4------
	1201110011	000120021?	0010111000	0-00000--0	00?0010000	0?1???????	??????????	???0-01???	000	
Corbicula fluminea	0100000110	0100020000	0001010101	140--00120	000011-001	1?011??100	0000011200	00-0101?10	0-00110110	1324------
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Varicorbula disparilis	0100000110	0100020100	1101110001	1410200130	000011-001	1?0112-100	0100011200	00-0101210	0-00110110	1304------
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Hiatella arctica	0100000001	0100020100	0001110001	140--00140	000011-001	1?0112-100	0100011200	00-0101210	0-00110110	12-3---111
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Pandora arenosa	0101101000	?000020100	0001000001	0410210120	000011-001	1?0111-100	0100?1?21-	-0-1101210	0-00110110	11-3---012
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Lyonsia hyalina	0101101000	?000020100	0001110001	1410210120	000011-001	1?0111-001	0100?1?21-	-0-1101110	0-00110110	11-3---012
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