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Phylogeny of the gastropod superfamily Cerithioidea using morphology and molecules

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The Cerithioidea is an ecologically important superfamily of basal Caenogastropoda with speciose marine, brackish water, and freshwater lineages primarily in tropical, subtropical, and warm temperate regions of the world. They often represent significant components of the communities where they occur and have given rise to several spectacular endemic radiations in rivers and ancient lakes. Earlier attempts to resolve the phylogenetic history of the group have been based on smaller taxon and character subsets with incongruent results. Here the monophyly and phylogeny of the group is evaluated with expanded morphological and molecular (16S, 28S rRNA) data sets. For morphological analyses, 151 characters (shell, operculum, radula, alimentary tract, kidney, nervous system, reproductive anatomy, and sperm ultrastructure) were scored for 47 cerithioideans (representing 17 families) and nine outgroup taxa. To test monophyly of the Cerithioidea, extended molecular data sets of 16S and 28S sequences for 57 and 44 taxa, respectively, were compiled using new and previously published sources. For combined analyses, a pruned molecular data set was combined with the morphological partition. The morphological data were analysed alone using only parsimony; molecular and simultaneous analyses were performed using both parsimony and Bayesian inference. The effect of excluding unconserved regions of the alignments was also explored. All analyses, with the exception of the individual 16S and 28S data sets, support monophyly of the Cerithioidea as currently formulated. Of the 12 families represented by more than one terminal, only two (Planaxidae, Potamididae) are always supported as monophyletic; Batillariidae, Cerithiidae, Pachychilidae, Pleuroceridae, Semisulcospiridae, Thiaridae, and Turritellidae are monophyletic in most but not all topologies. The combination of diverse data sources (morphology, 16S and 28S sequences) and inclusion of unconserved regions of the alignments improved the recovery of monophyletic families. At deeper levels, a consensus is beginning to emerge in the recognition of three main assemblages, but whether these represent clades or grades is still unclear; the resolution of these assemblages and the branching order within them are sensitive to exclusion of unconserved regions and choice of optimality criterion. No clear conclusion is reached with respect to the number of freshwater invasions, with two invasions supported on some topologies and three supported on others. Progress toward a robust and stable resolution of cerithioidean relationships will require (1) strategically coordinated sampling for additional morphological and molecular data; (2) comprehensive anatomical treatments for several poorly documented limnic lineages (e.g. Melanopsidae, Thiaridae) and comparative data for poorly understood organ systems (e.g. renal system); (3) the addition of poorly known, minute, and/or rare marine taxa, to provide novel character combinations, insight into putative homologies, and to help anchor basal nodes and break up long branches.

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ADDITIONAL KEYWORDS: anatomy – freshwater – Mollusca – simultaneous analysis.

Dedicated to Richard S. 'Joe' Houbrick (1937–1993), who has inspired systematic work on cerithioidean phylogeny and has laid the foundation on which this analysis rests.

INTRODUCTION

The Cerithioidea Férussac, 1819 is a large superfamily of caenogastropods that currently includes 17 Recent families, approximately 200 extant genera, and roughly 1100 extant species considered valid (Table 1). Cerithioideans are distributed worldwide with the vast majority of taxa in tropical, subtropical, and warm temperate regions, and inhabit a variety of marine, brackish water, and freshwater biotopes, including coral reefs and seagrass beds (e.g. cerithiids, modulids, scaliolids), rocky intertidal shores (e.g. cerithiids, planaxids), algal and seagrass fronds (e.g. bittiines, dialids, litiopids), estuarine mudflats (e.g. batillariids), mangrove forests (e.g. potamidids), and fast-flowing rivers and streams and lakes (e.g. melanopsids, pachychilids, paludomids, pleurocerids, semisulcospirids, thiarids). Cerithioideans are often significant, sometimes dominant, members in the communities where they occur, including many coastal littoral and limnic environments and freshwater ecosystems in parts of Asia and the Indo-Pacific, Africa, the Mediterranean, South America, and the south-eastern USA (Houbrick, 1988;

Table 1. Family-level classification of the Cerithioidea and estimated number of described Recent species currently considered valid

Family	Estimated valid species	Source(s)
Batillariidae	14	Ozawa *et al*. (2009)
Cerithiidae		Keen (1971); Houbrick (1978, 1992, 1993a, b); Spencer, Marshall & Willan (2009);
Bittiinae	71	CLEMAM (2010); IPMD (2006); Malacolog (Rosenberg, 2009)
Cerithiinae	114	
Dialidae	8	Ponder & de Keyzer (1992)
Diastomatidae	1	Houbrick (1981b)
Litiopidae	16–18	Keen (1971); W. F. Ponder (unpubl. data); CLEMAM (2010); IPMD (2006); Malacolog (Rosenberg, 2009)
Melanopsidae	25–50	Strong *et al*. (2008)
Modulidae	~6	Houbrick (1980)
Pachychilidae	191–226	Strong *et al*. (2008); F. Köhler (AM; pers. comm.); T. von Rintelen (ZMB; pers. comm.)
Paludomidae	100	Strong *et al*. (2008)
Planaxidae	~30–40	Houbrick (1987a); P. Lozouet (MNHN; pers. comm.)
Pleuroceridae	~150	Johnson *et al*. (2005); Strong *et al*. (2008)
Potamididae	29	Reid *et al*. (2008)
Scaliolidae	~12	Ponder (1994; W. F. Ponder, unpubl. data); Hasegawa (1998)
Semisulcospiridae	~50	Johnson *et al*. (2005); Strong & Frest (2007); Strong *et al*. (2008)
Siliquariidae	~40	R. Bieler (FMNH; pers. comm.)
Thiaridae	~110	Strong *et al*. (2008); Glaubrecht *et al*. (2009)
Turritellidae	125	WoRMS (2010)
Total	1092–1164	

Note: query results from online biodiversity databases were refined as necessary to remove duplicate records and occasional synonyms.
AM, Australian Museum, Sydney; CLEMAM, Check List of European Marine Mollusca; FMNH, Field Museum of Natural History; IPMD, OBIS Indo-Pacific Molluscan Database; Malacolog, Database of Western Atlantic Marine Mollusca; MNHN, Museum National d'Histoire Naturelle, Paris; WoRMS, World Register of Marine Species; ZMB, Berlin Museum of Natural History.

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Glaubrecht, 1996; Healy & Wells, 1998a; Strong *et al*., 2008).

Several taxa have undergone impressive radiations, concentrating a significant proportion of the diversity amongst just a few lineages. For example, in marine habitats, cerithiids are highly speciose (e.g. Houbrick, 1974, 1985, 1992, 1993a), although, as presently understood, most other marine groups are not particularly diverse (see Table 1). Amongst limnic taxa, several families have radiated in ancient lakes (e.g. Semisulcospiridae, Lake Biwa: Nishino & Watanabe, 2000; Paludomidae, Lake Tanganyika: Michel, 1994; Glaubrecht, 1996; Pachychilidae, central lakes on Sulawesi: von Rintelen *et al*., 2004; von Rintelen, Bouchet & Glaubrecht, 2007; Glaubrecht & von Rintelen, 2008) as well as fluviatile systems in North America (Pleuroceridae: Lydeard & Mayden, 1995; Lydeard *et al*., 2004; Strong *et al*., 2008), and various freshwater systems in the Mediterranean (Melanopsidae: Glaubrecht, 1993, 1996), South-East Asia (Pachychilidae: Glaubrecht & Köhler, 2004; Köhler & Glaubrecht, 2006), and on Madagascar (Köhler & Glaubrecht, 2010).

In addition to their ecological diversity and species richness, cerithioideans have evolved an impressive array of shell shapes [typical coiled shells vs. uncoiled, irregular shells (Turritellidae, Siliquariidae)] (Fig. 1), adult body sizes [(e.g. *Cerithidium*, *Scaliola* – maximum adult shell length < 5.0 mm (Houbrick, 1993a), to *Terebralia palustris* (Linné, 1767) – maximum adult shell length ~190 mm (Houbrick, 1991a)], life habits [mobile benthic crawlers vs. sessile forms cemented to firm substrates (*Vermicularia* in the Turritellidae) or embedded within sponges (Siliquariidae)], feeding modes [herbivorous grazers or detritus feeders vs. ctenidial suspension feeders (Siliquariidae, Turritellidae)], and reproductive and life history strategies [ovipary vs. vivipary (Thiaridae) or ovovivipary (Pachychilidae, Paludomidae, Planaxidae, Siliquariidae, Semisulcospiridae, Turritellidae); gonochorism vs. parthenogenesis (Thiaridae) or protandrous hermaphroditism (Planaxidae)].

Cerithioidean species are often highly polymorphic, particularly fluviatile members of the group, contributing to such a proliferation of names during the 18th and 19th centuries that the estimated ratio of available names to valid species is as high as 10:1 in a few groups (e.g. Melanopsidae: Glaubrecht, 2004, 2009; Pleuroceridae: Graf, 2001; Thiaridae: Glaubrecht, Brinkmann & Pöppe, 2009). However, protoconch morphology and modern molecular tools are revealing cryptic complexes within some polymorphic marine species (e.g. *Cerithium*: Boisselier-Dubayle & Gofas, 1999; Bittiinae: E. E. Strong, unpubl. data) indicating that some groups have been over-synonymized. Many of the marine and estuarine families have been treated in recent reviews, including Batillariidae (Ozawa *et al*., 2009), Cerithiidae (Houbrick, 1974, 1975, 1978, 1992, 1993a), Dialidae (Ponder, 1991; Ponder & de Keyzer, 1992), Litiopidae (Houbrick, 1987b), Modulidae (Houbrick, 1980), Planaxidae (Houbrick, 1987a, 1990a), Potamididae (Houbrick, 1984, 1991a; Reid *et al*., 2008), and Scaliolidae (Ponder, 1994); several freshwater families have come under intense scrutiny in recent morphological and molecular analyses, including Pachychilidae (e.g. von Rintelen & Glaubrecht, 1999, 2003, 2005, 2008; Köhler & Glaubrecht, 2001, 2003, 2006, 2010; Glaubrecht & Köhler, 2004; Köhler *et al*., 2004; von Rintelen *et al*., 2004, 2007), Paludomidae (e.g. West & Michel, 2000; Strong & Glaubrecht, 2002, 2003, 2007, 2008, 2010; Glaubrecht & Strong, 2004, 2007; Michel, 2004; Wilson, Glaubrecht & Meyer, 2004; Glaubrecht, 2008), Pleuroceridae (e.g. Lydeard *et al*., 1997; Holznagel & Lydeard, 2000; Strong, 2005) and Semisulcospiridae (e.g. Strong & Frest, 2007; Strong & Köhler, 2009). Detailed species-level revisions are lacking at the family level except for Dialidae (Ponder & de Keyzer, 1992) and Diastomatidae where only one living species remains (Houbrick, 1981b).

Despite their abundance and often large size, there are relatively few modern studies on cerithioidean species comparative anatomy with the notable exception of a rather comprehensive study of Simone (2001) and a study of cerithioidean midgut anatomy (Strong, in press) both of which generated much new data. Previous comparative investigations include those going back to the end of the 19th century, for example, on the nervous system by Bouvier (1887) or reproductive anatomy (e.g. Sunderbrinck, 1929; Risbec, 1935, 1943) and were supplemented by a few later studies (e.g. Starmühlner & Edlauer, 1957; Starmühlner, 1969, 1984a, b). However, many of the more detailed anatomical studies are relatively recent and focus on a limited subset of constituent taxa (e.g. Marcus & Marcus, 1963, 1964; Dazo, 1965; Glaubrecht, 1996; Bieler & Simone, 2005; and references above) (see also Table 2).

Phylogeny and systematics of Cerithioidea

The Cerithioidea is a pivotal group owing to its basal position within the Caenogastropoda, a large higher grouping of gastropods that comprises one of the five main clades and ~60% of living gastropod species (Ponder & Lindberg, 1997; Ponder *et al*., 2008). Consequently, cerithioideans are vital for understanding homology and polarity of character transformations in higher-order phylogenetic studies. Cerithioideans are characterized by aphallate males, open gonoducts, and reproduction via spermatophores, which are

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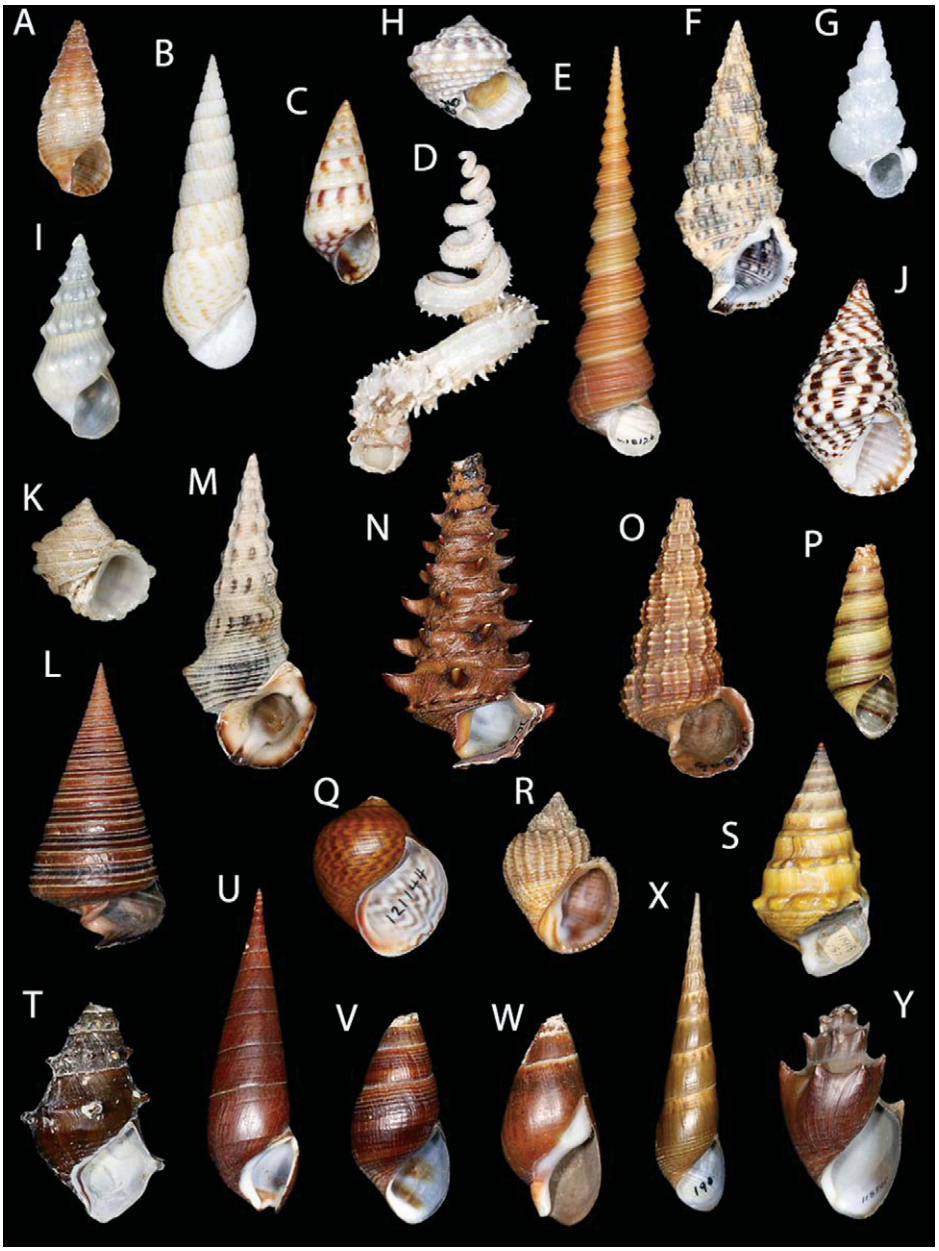

Figure 1. Shell diversity of representative marine (m), brackish (b), and freshwater (f) Cerithioidea. Not to scale; shell lengths given in parentheses. A, *Ittibittium parcum* (Gould, 1861) (Cerithiidae) (m) (2.8 mm); B, *Diastoma melanioides* (Reeve, 1849) (Diastomatidae) (m) (49.7 mm); C, *Diala semistriata* (Philippi, 1849) (Dialidae) (m) (4.7 mm); D, *Tenagodus anguinus* (Linné, 1758) (Siliquariidae) (m) (44.6 mm); E, *Turritella terebra* (Linné, 1758) (Turritellidae) (m) (91.8 mm); F, *Cerithium atratum* (Born, 1778) (Cerithiidae) (m) (28.3 mm); G, *Scaliola bella* Adams, 1860 (Scaliolidae) (m) (3.5 mm); H, *Modulus modulus* (Linné, 1758) (Modulidae) (m) (10.6 mm); I, *Alaba monile* Adams, 1862 (Litiopidae) (m) (5.8 mm); J, *Planaxis sulcatus* (Born, 1780)) (Planaxidae) (m) (23.8 mm; K, *Fossarus garrettii* Pease, 1868 (Planaxidae) (m) (5.5 mm); L, *Telescopium telescopium* (Linné, 1758) (Potamididae) (b) (81.5 mm); M, *Pyrazus ebeninus* (Bruguière, 1792) (Batillariidae) (m/b) (91.7 mm); N, *Tympanotonus fuscatus* (Linné, 1758) (Potamididae) (b) (41.9 mm); O, *Cerithidea anticipata* Iredale, 1929 (Potamididae) (b) (36.6 mm); P, *Elimia virginica* (Gmelin, 1791) (Pleuroceridae) (f) (20.0 mm); Q, *Paludomus pictus* Reeve, 1847 (Paludomidae) (f) (23.1 mm); R, *Lavigeria grandis* Smith, 1881 (Paludomidae) (f) (30.9 mm); S, *Pleurocera canaliculata* (Say, 1821) (Pleuroceridae) (f) (35.2 mm); T, *Brotia pagodula* (Gould, 1847) (Pachychilidae) (f) (29.8 mm); U, *Faunus ater* (Linné, 1758) (Pachychilidae) (b/f) (62.6 mm); V, *Semisulcospira libertina* (Gould, 1859) (Semisulcospiridae) (f) (32.9 mm); W, *Melanopsis praemorsa* (Linné, 1758) (Melanopsidae) (f) (22.2 mm); X, *Stenomelania plicaria* (Born, 1780) (Thiaridae) (f) (58.4 mm); Y, *Thiara amarula* (Linné, 1758) (Thiaridae) (f) (42.5 mm).

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Table 2. Sources of morphological and molecular data

Taxon	16S	28S	Sources
Architaenioglossa			
Cyclophoridae			
Neocyclotus dysoni ambiguum (Martens, 1890)			Thompson (1969), Strong (2003). Supplemented by Simone (2004) for *Neocyclotus prominulus* (d'Orbigny, 1840). Sperm ultrastructure combined for *Cochlostoma montanum* (Issel, 1866) (Giusti & Selmi, 1982, 1985; Selmi & Giusti, 1980), *Cyclophorus herklotsi* von Martens, 1861 (Koike, 1985) and *Liarea ornata* Powell, 1954 (Healy, 1984). Chromosome number for *Cyclophorus jerdoni* (Benson, 1851) (Thiriot-Quiévreux, 2003). Simultaneous analyses: *Neocyclotus dysoni ambiguum* (morphological) + *Cyclophorus hirasei* (molecular).
Cyclophorus hirasei Pilsbry, 1901	AY010505*	HM003647*	
Ampullariidae			
Marisa cornuarietis (Linné, 1758)	AY449498		Demian (1964, 1965), Lutfy & Demian (1965, 1967), Berthold (1991), Strong (2003). Sperm ultrastructure combined for *Lanistes*, *Pila*, and *Ampullaria*/*Pomacea* spp. (Anderson & Personne, 1970, 1976; Kohnert & Storch, 1984a, b; Catalán, Schlick de Santolaya & Winik, 1997; Winik, Catalán & Schlick, 2001) and J. M. Healy (unpubl. data). Chromosome number for *Pomacea canaliculata* (Lamarck, 1822) (Thiriot-Quiévreux, 2003). 16S data for *Marisa cornuarietis*, extended analysis only. Simultaneous analyses: *Marisa cornuarietis* (morph) + *Pomacea paludosa* (mol).
Pomacea paludosa (Say, 1829)	AY010506*	HM003648*	
Viviparidae			
Viviparus viviparus (Linné, 1758)		U75863	Krull (1935), Rohrbach (1937), Griffond (1980, 1981), Falniowski (1989), Falniowski, Mazan & Szarowska (1996a, b), J. M. Healy (unpubl. data) and E. E. Strong (unpubl. data). Supplemented by Simone (2004) for *Viviparus contectus* (Millett, 1813). Sperm ultrastructure supplemented from *Cipangopaludina chinensis* (Gray, 1834) (as *Cipangopaludina malleata, Cipangopaludina chinensis malleata*, or *Viviparus malleatus*) (Ishizaki & Kato, 1958; Tanaka, 1958; Yasuzumi & Tanaka, 1958; Gall, 1961; Koike, 1985; Kim & Choi, 1986), and *Sinotaia histrica* (Gould, 1859) and *Heterogen longispira* (Smith, 1886) (Hachiri & Higashi, 1972, 1974). Simultaneous analyses: *Viviparus viviparus* (morphological, 28S) + *Viviparus georgianus* (16S).
Viviparus georgianus (Lea, 1834)	AY377626		
Campaniloidea			
Campanilidae			
Campanile symbolicum Iredale, 1917	AY010507*	HM003649*	Bouvier (1887), Houbrick (1981a, 1989), Healy (1986a, b, 1988a, 2000).

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Table 2. *Continued*

Taxon	16S	28S	Sources
Plesiotrochidae			
Plesiotrochus crinitus Thiele, 1930			Houbrick (1990b) [as *Plesiotrochus* cf. *penitricinctus* (Cotton, 1932)], Healy (1993a). Supplemented by Houbrick (1990b) for *Plesiotrochus unicinctus* (A. Adams, 1853) (as *Plesiotrochus souverbianus* Fischer, 1878) and *Plesiotrochus monachus* (Crosse & Fischer, 1864). Midgut for *Plesiotrochus unicinctus* (Strong, in press).
Littorinoidea			
Littorinidae			
Littorina littorea (Linné, 1758)	DQ093481		Fretter & Pilkington (1970), Fretter & Graham (1994), Reid (1996) and Strong (2003). Sperm ultrastructure combined for *Littorina sitkana* Philippi, 1846 (Buckland-Nicks, 1973), *Littorina scutulata* Gould, 1849 (Buckland-Nicks & Chia, 1977), *Littorina saxatilis* (Olivi, 1792), *Littorina obtusata* (Linné, 1758), *Littorina neritoides* (Linné, 1758) (Kohnert & Storch, 1984a, b), *Littorina neritoides* (Giusti & Selmi, 1982), and *Littorinopsis scabra* (Linné, 1758) (Koike, 1985). Chromosome number for *Melaraphe neritoides* (Linné, 1758) (Thiriot-Quiévreux, 2003). 16S data for *Littorina littorea*, extended analysis only. Simultaneous analyses: *Littorina littorea* (morphological) + *Austrolittorina unifasciata* (molecular).
Austrolittorina unifasciata (Gray, 1826)	AY010326*	HM003650*	
Stromboidea			
Strombidae			
Strombus mutabilis (Swainson, 1821)			Strong (2003). Supplemented by Simone (2005) for *Canarium urceus* (Linné, 1758), by Robertson (1959) for spawn of *Eustrombus gigas* (Linné, 1758). Sperm ultrastructure combined for *Lambis lambis* Linné, 1758 and *Strombus luhuanus* Linné, 1758 (Koike & Nishiwaki, 1980; Healy, 1984; Koike, 1985), *Eustrombus gigas* (Casse *et al*. 1994) and *Strombus gibberulus* Linné, 1758 (Buckland-Nicks, 1998). Chromosome number for *Strombus gibberulus albus* Mørch, 1850 (Thiriot-Quiévreux, 2003). Simultaneous analyses: *Strombus mutabilis* (morphological) + *Strombus luhuanus* (molecular)
Strombus luhuanus Linné, 1758	AF174212	AY296891	
Calyptraeoidea			
Calyptraeidae			
Crepidula philippiana Gallardo, 1977	AF545952	AF545875	Extended analysis only
Xenophoridae			
Xenophora pallidula (Reeve, 1842)	AF550469	AF550441	Extended analysis only

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Table 2. *Continued*

Taxon	16S	28S	Sources
Rissooidea			
Hydrobiidae *s.l.*			
Oncomelania hupensis robertsoni (Bartsch, 1946)	DQ212870	AY207042	Extended analysis only
Potamopyrgus antipodarum (Gray, 1843)	AY634109	EF417135	Extended analysis only
Vermetoidea			
Vermetidae			
Serpulorbis zelandicus (Quoy & Gaimard, 1834)			Morton (1951a, 1955, 1965). Supplemented by Hadfield (1970) for *Serpulorbis squamigerus* (Carpenter, 1857), by Hadfield & Hopper (1980) for spermatophores of *Serpulorbis variabilis* Hadfield & Kay, 1972, and by Simone (2001) for midgut of *Serpulorbis decussatus* (Gmelin, 1791). Sperm ultrastructure combined for *Serpulorbis* sp. (Healy, 1988b), *Serpulorbis variabilis* and *Serpulorbis squamigerus* (Buckland-Nicks, 1998; Buckland-Nicks & Hadfield, 2005). Simultaneous analyses: *Serpulorbis zelandicus* (morphological) + *Serpulorbis squamigerus* + *Serpulorbis* sp. (molecular)
Serpulorbis squamigerus (Carpenter, 1857)	AY010325*		
Serpulorbis sp.		AY296890	
Dendropoma lamellosa (Hutton, 1873)			Morton (1951c, 1955, 1965), Hadfield & Hopper (1980). Supplemented by Ponder (1967) for *Dendropoma squamifera* Ponder, 1967, by Calvo, Templado & Penchaszadeh (1998) for *Dendropoma petraeum* (Monterosato, 1884). Gut, nerve, and details of gonoduct for *Petaloconchus varians* (d'Orbigny, 1841) (Strong, 2003). Sperm ultrastructure combined for *Dendropoma* sp. (Healy, 1988b) and *Lemintina arenaria* (Linné, 1758) (Melone, Donin & Cotelli, 1980). Chromosome number for *Dendropoma petraeum* (Monterosato, 1884) (Thiriot-Quiévreux, 2003). Simultaneous analyses: *Dendropoma lamellosa* (morphological) + *Dendropoma corrodens* (d'Orbigny, 1842) (molecular).
Dendropoma corrodens (d'Orbigny, 1842)	AF338144		
Cerithioidea			
Marine and brackish			
Batillariidae			
Batillaria australis (Quoy & Gaimard, 1834)	AY010325*	HM003651*	Bishop (1979), Healy (1983, 1986a), M. Glaubrecht, R. S. Houbrick & W. F. Ponder (unpubl. data). Chromosome number (Patterson, 1969) for *Batillaria zonalis* (Bruguière, 1792). Sperm ultrastructure supplemented by Koike (1985) for *Batillaria multiformis* (Lischke, 1869).
Pyrazus ebeninus (Bruguière, 1792)	AY010512*		Bishop (1979), Healy & Jamieson (1981), Healy (1982), M. Glaubrecht, R. S. Houbrick & W. F. Ponder (unpubl. data).

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Table 2. *Continued*

Taxon	16S	28S	Sources
Cerithiidae			
Alabina cerithidioides (Dall, 1889)			W. F. Ponder (unpubl. data). Supplemented by Simone (2001) for *Alabina* sp. [as *Finella dubia* (d'Orbigny, 1842)].
Bittium reticulatum (Da Costa, 1778)			Houbrick (1993a), Johansson (1947). Sperm ultrastructure for *Bittium* cf. *impendens* (Hedley, 1899) (Healy, 1986c).
Cacozeliana granaria (Kiener, 1842)	AF101007*		Houbrick (1993a)
Cerithidium fuscum (Adams, 1860)			W. F. Ponder (unpubl. data)
Cerithium atratum (Born, 1778)		HM003654	Houbrick (1974), Bandel (1984). Supplemented by Marcus & Marcus (1964) and Simone (2001) for midgut; given radular differences, this is unlikely to be same species studied by Houbrick. Sperm ultrastructure combined for *Cerithium vulgatum* Bruguière, 1792 (Giusti, 1971; Giusti & Selmi, 1982; Afzelius, Giusti & Dallai, 1986), *Cerithium rupestre* Risso, 1826 (Minniti, 1993), and *Cerithium columna* (Sowerby, 1834) (Buckland-Nicks, 1998; Buckland-Nicks & Hodgson, 2005). Chromosome number for *Cerithium vulgatum* (Thiriot-Quiévreux, 2003). 28S data for *Cerithium atratum*, extended analysis only. Simultaneous analyses: *Cerithium* 1 = *Cerithium atratum* (morphological) + *Cerithium eburneum* (molecular). Sequenced specimens from Missouri Key, Florida, USA (ZMB 106.122, 106.319).
Cerithium coralium Kiener, 1841	AY010514*	HM003653*	
Cerithium eburneum Bruguière, 1792	AY010513*	HM003652*	
Cerithium litteratum (Born, 1778)		HM003655	Extended analysis only. Sequenced specimens from Missouri Key, Florida, USA (ZMB 106.123, 106.318).
Cerithium nodulosum Bruguière, 1792			Risbec (1943), Houbrick (1971, 1974, 1992), Koike (1985). Supplemented by Bouvier (1887) for nerves of *Cerithium vulgatum*. Simultaneous analyses: *Cerithium* 2 = *Cerithium nodulosum* (morphological) + *Cerithium coralium* (molecular).
Clypeomorus bifasciata (Sowerby, 1855)			Houbrick (1985), Attiga & Al-Hajj (1996). Sperm ultrastructure supplemented by Healy (1983, 1986b) for *Clypeomorus batillariaeformis* Habe & Kosuge, 1966 [as *Clypeomorus moniliferus* (Kiener, 1841)], and Attiga & Al-Hajj (1996) possibly for *Clypeomorus petrosa petrosa* (Wood, 1925) [as *Clypeomorus tuberculatus* (Linné, 1758)]. Simultaneous analyses: *Clypeomorus bifasciata* (morph) + *Clypeomorus* sp. (mol).
Clypeomorus sp.	AY010515*	HM003656*	
Ittibittium parcum (Gould, 1861)			Houbrick (1993a). Sperm ultrastructure for *Ittibittium houbricki* (Ponder, 1993) (J. M. Healy, unpubl. data)

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Table 2. *Continued*

Taxon	16S	28S	Sources
Diastomatidae			
Diastoma melanioides (Reeve, 1849)			Houbrick (1981b)
Dialidae			
Diala suturalis (Adams, 1853)			Ponder (1991), Ponder & de Keyzer (1992). Midgut for *Diala sulcifera scobina* (Laseron, 1950) (Strong, in press). Sperm ultrastructure for *Diala semistriata* (Philippi, 1849) (Healy, 1984, 1986a)
Litiopidae			
Alaba incerta (d'Orbigny, 1842)			Houbrick (1987b), Simone (2001). Midgut for *Alaba opiniosa* (Iredale, 1936) (Strong, in press). Sperm ultrastructure for *Alaba* cf. *difformis* (Laseron, 1956) (as *Australaba* sp.) (Healy, 1983, 1986a). Simultaneous analyses: *Alaba incerta* (morphological) + *Alaba opiniosa* (molecular)
Alaba opiniosa (Iredale, 1936)	AY010510*	HM003657*	
Modulidae			
Modulus modulus (Linné, 1758)	AY010321*	HM003658*	Houbrick (1980), Simone (2001). Sperm ultrastructure for *Modulus tectum* (Gmelin, 1791) (Healy, 1984)
Planaxidae			
Fossarus ambiguus (Linné, 1758)			Houbrick (1990a). Supplemented by W. F. Ponder (unpubl. data) for *Fossarus* sp.
Planaxis sulcatus (Born, 1780)	AY010320*		Risbec (1935), Healy (1983, 1986a), Koike (1985), Houbrick (1987a)
Potamididae			
Cerithidea anticipata Iredale, 1929	AY010316*	HM003660*	
Cerithidea morchii Sowerby II, 1855	AY010319*		Extended analysis only
Cerithidea scalariformis (Say, 1825)			Houbrick (1984). Nerves for *Cerithidea obtusa* (Lamarck, 1822) (Bouvier, 1887). Sperm ultrastructure combined for *Cerithidea anticipata* (as *Cerithidea obtusa*) and *Cerithidea largillierti* (Philippi, 1849) (Healy, 1983, 1986a), *Cerithidea obtusa* (Suwanjarat & Klepal, 2001), *Cerithidea cingulata* (Gmelin, 1791) (Suwanjarat & Suwaluk, 2003), and *Cerithidea decollata* (Linné, 1758) (Buckland-Nicks & Hodgson, 2005). Chromosome number for *Cerithidea rhizophorarum* A. Adams, 1855 (Thiriot-Quiévreux, 2003). Simultaneous analyses: *Cerithidea scalariformis* (morphological) + *Cerithidea anticipata* (molecular)
Telescopium telescopium (Linné, 1758)	AY010318*	HM003662*	Bouvier (1887), Ramamoorthi & Natarajan (1973), Healy (1983, 1986a), Houbrick (1991a).
Terebralia sulcata (Born, 1778)			Bouvier (1887), Houbrick (1991a), Kowalke & Bandel (1996). Midgut for *Terebralia semistriata* (Mörch, 1852) (Strong, in press). Sperm ultrastructure for *Terebralia palustris* (Linné, 1767) (Healy, 1983, 1986a; Koike, 1985). Simultaneous analyses: *Terebralia sulcata* (morphological) + *Terebralia palustris* (molecular)
Terebralia palustris (Linné, 1767)	AY010319*	HM003661*	

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Table 2. *Continued*

Taxon	16S	28S	Sources
Tympanotonus fuscatus (Linné, 1758)			Johansson (1956), Bandel & Kowalke (1999); see also discussion in Houbrick (1984, 1991a).
Scaliolidae			
Finella pupoides Adams, 1860			Ponder (1994). Sperm ultrastructure for *Finella fabrica* (Laseron, 1956) [as *Obtortio* cf. *fulva* (Watson, 1886)] (Healy, 1982). Radular characters for *Finella purpureoapicata* Preston, 1905 (Ponder, 1994). Simultaneous analyses: *Finella pupoides* (morphological) + *Finella* sp. (molecular).
Finella sp.	AY010509*	HM003659*	
Scaliola sp.	AY010508*		Ponder (1994), J. M. Healy (unpubl. data).
Siliquariidae			
Stephophoma nucleogranosum Verco, 1904			Morton (1951b), Bieler & Simone (2005). Supplemented by Bieler (2004) and Strong (in press) for *Tenagodus squamatus* (Blainville, 1827). Sperm ultrastructure for *Siliquaria ponderosa* (Mörch, 1860) (J. M. Healy, unpubl. data).
Turritellidae			
Maoricolpus roseus (Quoy & Gaimard, 1834)	AY010322*	HM003663*	
Protoma capensis (Krauss, 1848)	AY010323*	HM003664*	
Turritella communis (Risso, 1826)			Randles (1902), Lebour (1933), Graham (1938), Johansson (1946), Morton (1953), Melone *et al*. (1980), Afzelius & Dallai (1983), Kennedy & Keegan (1992), Kennedy (1995). Chromosome number for *Turritella attenuata* Reeve, 1849 (Patterson, 1969). Simultaneous analyses: Turritellidae 1 = *Turritella communis* (morphological) + *Maoricolpus roseus* (molecular)
Turritella terebra (Linné, 1758)			W. F. Ponder (unpubl. data). Sperm ultrastructure combined for *Turritella* sp. (J. M. Healy, unpubl. data) and *'Haustator cingulata'* [?*Haustator cingulifera* (Sowerby, 1825)] (Koike, 1985). Chromosome number for *Turritella attenuata* Reeve, 1849 (Patterson, 1969). Simultaneous analyses: Turritellidae 2 = *Turritella terebra* (morphological) + *Protoma capensis* (molecular)
Freshwater			
Melanopsidae			
Holandriana holandri (Pfeiffer, 1828)	AY010314*	HM003675*	Glaubrecht (1996).
Melanopsis praemorsa (Linné, 1758)	AY010315*	HM003674*	Bilgin (1973), Glaubrecht (1996), Mouahid *et al*. (1996). Supplemented by Starmühlner & Edlauer (1957) for *Melanopsis doriae* Issel, 1866. Sperm ultrastructure combined for *Melanopsis dufouri etrusca* (Villa, 1862) (Afzelius, Dallai & Callaini, 1989), and for *Melanopsis buccinoidea* Olivier, 1801, *Melanopsis saulcyi* Bourguignat, 1853, *Melanopsis costata* Olivier, 1804, *Melanopsis meiostoma* Heller & Sivan 2000 (Hodgson & Heller, 2000). Chromosome number for *Melanopsis dufouri* Férussac, 1823 (Thiriot-Quiévreux, 2003).

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Table 2. *Continued*

Taxon	16S	28S	Sources
Pachychilidae			
Doryssa atra (Bruguière, 1792)			Abbott (1955), Simone (2001).
Brotia pagodula (Gould, 1847)			Köhler & Glaubrecht (2001). Simultaneous analyses: *Brotia pagodula* (morphological) + *Brotia* sp. (molecular)
Brotia sp.	AF101008*		As *Paracrostoma paludiformis* (Yen, 1939)
Faunus ater (Linné, 1758)	AY010526*	HM003672*	Houbrick (1991b).
Madagasikara spinosa (Lamarck, 1822)		HM003673	Extended analysis only. Sequenced specimen from Madagascar (ZMB 200.287); see also Köhler *et al*. (2004) [as *Melanatria fluminea* (Gmelin, 1791)]
Pachychilus sp.	AY010524*	HM003671*	Simone (2001). Midgut for *Pachychilus indiorum* (Morelet, 1849) (Strong, in press)
Paludomidae			
Cleopatra johnstoni (Smith, 1893)	AY456590		Kohnert & Storch (1984a, b), E. E. Strong (unpubl. data). Chromosome number for *Cleopatra bulimoides* (Olivier, 1804) (Thiriot-Quiévreux, 2003)
Lavigeria grandis (Smith, 1881)	AY958771		Extended analysis only
Lavigeria sp. A	AY958773		Strong & Glaubrecht (2007). Male reproductive anatomy for *Lavigeria* sp. B (Michel, 2004). Sperm ultrastructure for *Lavigeria* sp. (J. M. Healy & M. Glaubrecht, unpubl. data).
Paludomus siamensis Blanford, 1903	AY456614	HM003670	E. E. Strong (unpubl. data). Chromosome number for *Paludomus tanschaurica* Gmelin, 1791 (Patterson, 1969). Sequenced specimen from Thailand (ZMB 200.234); see also Wilson *et al*. (2004).
Tanganyicia rufofilosa (Smith, 1880)	AY456634		Strong & Glaubrecht (2002).
Tiphobia horei Smith, 1880	AY456636		Glaubrecht & Strong (2004), Strong & Glaubrecht (2007).
Pleuroceridae			
Elimia livescens (Menke, 1830)	DQ311116	DQ311127	Jewell (1931), Dazo (1965), Strong (2005). Sperm ultrastructure for *Elimia proxima* (Say, 1825) (Bergstrom, Henley & Costello, 1973; Henley, 1973).
Elimia interrupta (Haldeman, 1840)	AY010521*	HM003677*	
Pleurocera acuta Rafinesque, 1831	AF100994		Dazo (1965), Strong (2005). Radular morphology for *Pleurocera* spp. (Sides, 2005).
Pleurocera vestita (Conrad, 1834)		HM003678	Sequenced specimen from Alabama, USA (NCSM-P-4691); see also Holznagel & Lydeard (2000).
Pleurocera canaliculata (Say, 1821)	AF100991*	DQ256747	
Semisulcospiridae			
Hua jacqueti (Dautzenberg & Fischer, 1906)	FJ471494	HM003679	Strong & Köhler (2009). 28S sequence from F. Köhler (AM). Sequenced specimen from Vietnam (ZMB 114.163); see also Strong & Köhler (2009).
Juga nigrina (Lea, 1856)	AY010523*		
Juga silicula (Gould, 1847)	DQ311121	DQ311135	Strong & Frest (2007), T. J. Frest (unpubl. data). Chromosome number for *Juga hemphilli* (Henderson, 1935) (Thiriot-Quiévreux, 2003)

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Table 2. *Continued*

Taxon	16S	28S	Sources
Koreanomelania nodifila (von Martens, 1894)	DQ319907	DQ319948	
'Parajuga' sp.			Prozorova (1990), Prozorova & Rasshepkina (2003). Simultaneous analyses: *'Parajuga'* sp. (morphological) + *'Parajuga' 'calculus'* (molecular)
'Parajuga' 'calculus' (Reeve, 1859)	AY010522*		As *Hua calculus*; see Strong & Köhler (2009) for comments on identification of the sequenced specimen
Semisulcospira libertina (Gould, 1859)	AY010525*	HM003676*	Itagaki (1960) [as *Semisulcospira bensoni* (Philippi, 1851)], Yasuzumi, Nakano & Matsuzaki (1962), Davis (1969), Koike (1985), Kohata, Okura & Yasuzumi (1986), Nakano & Nishiwaki (1989), Ko, Lee & Kwon (2001), Prozorova & Rasshepkina (2005). Sperm ultrastructure supplemented by *Semisulcospira decipiens* (Westerlund, 1883) and *Semisulcospira niponica* (Smith, 1876) (Hachiri & Higashi, 1971).
Thiaridae			
Hemisinus lineolatus (Wood, 1828)			Glaubrecht (1996). Simultaneous analyses: *Hemisinus lineolatus* (morphological) + *Hemisinus cubanianus* (molecular)
Hemisinus cubanianus (d'Orbigny, 1860)	AY010516*	HM003669*	
Melanoides tuberculata (Müller, 1774)	AY010517*	HM003666*	Starmühlner (1969), Kohnert & Storch (1984a, b), Hodgson & Heller (1990), Glaubrecht (1996), Hodgson (1997), Simone (2001).
Stenomelania cf. *plicaria* (Born, 1780)			Pace (1973), Starmühlner (1976, 1984a, b), Glaubrecht (1996), Bandel, Glaubrecht & Riedel (1997). Chromosome number for *Stenomelania* cf. *arthuri* (Brot, 1871) (as *Melania (Radina) crenulata* Deshayes, 1838) (Patterson, 1969). Midgut for *Stenomelania denisoniensis* (Brot, 1877) (Strong, in press). Simultaneous analyses: *Stenomelania* cf. *plicaria* (morphological) + *Stenomelania* sp. (molecular)
Stenomelania sp.	AY010518*	HM003667*	
Tarebia granifera (Lamarck, 1816)	AY010519*	HM003668*	Abbott (1952), Starmühlner (1976), Glaubrecht (1996). Chromosome number for *Tarebia lineata* (Wood, 1828) (Patterson, 1969).
Thiara amarula (Linné, 1758)	AY010520*	HM003665*	Starmühlner (1969), Glaubrecht (1996), Schütt & Glaubrecht (1999), J. M. Healy & M. Glaubrecht (unpubl. data). Midgut for *Thiara cancellata* (Röding, 1798) (Strong, in press). Chromosome number for *Thiara scabra* (Müller, 1774) (Patterson, 1969).

The primary terminal is indicated in the far left column; supplementary sources of anatomical information and strategies for merging morphological and molecular terminals are detailed under Sources. Unless otherwise indicated, stomach data are based on Strong (in press); chromosome numbers are from Nishikawa (1962), Patterson (1969), Thiriot-Quiévreux (2003), and references therein. Polymorphic coding was used when morphological variation was evident within concatenated terminals. Entries in the 16S and 28S columns are GenBank accession numbers. For 16S sequences, * indicates data originally included in the analysis of Lydeard *et al*. (2002); newly generated 28S sequences (GenBank accession numbers HM003647-HM003679) also indicated with * are for the same specimen (see Lydeard *et al*., 2002, for details). Voucher and locality information for other newly generated sequences are provided under Sources.
AM, Australian Museum, Sydney; NSCM, North Carolina State Museum of Natural Sciences; ZMB, Berlin Museum of Natural History.

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generally regarded as plesiomorphic traits, and are not unique in these regards amongst caenogastropods (e.g. Vermetidae, Campanilidae). However, they are unique in the range of midgut morphologies evident (Strong, 2003 and in press) and in the complexity of the female pallial reproductive tract, which bears specialized sperm storage pouches of uncertain homology to those of other caenogastropods.

Although the current concept of Cerithioidea includes 17 Recent families, several additional families that were included in earlier classifications (Thiele, 1929; Wenz, 1939; Taylor & Sohl, 1962) are now excluded. These are the caenogastropods Campanilidae and Plesiotrochidae (Campaniloidea), Vermetidae (Vermetoidea), Caecidae (Rissooidea), Triphoridae and Cerithiopsidae (Triphoroidea), Abyssochrysidae (Abyssochrysoidea), and the lower heterobranchs Architectonicidae (Architectonoidea) and Mathildidae (Mathildoidea). This heterogeneous assemblage was united by features of the shell (mostly tall, conical with numerous whorls, with or without a small siphonal canal) and operculum (corneous, pauci- to multi- spiral) and absence of the male copulatory organ (Thiele, 1929).

A major restructuring of 'prosobranch' relationships brought about in part through new ultrastructural data of the osphradium, led to the removal of several 'mesogastropods' to the basal Heterobranchia (Haszprunar, 1985, 1988), including Valvatidae, Architectonicidae, and Mathildidae. Ultrastructural studies of the eusperm and parasperm have also been highly influential in structuring our current understanding of the composition of the superfamily and have confirmed the affinities of the basal heterobranch taxa (Healy, 1988a, 1991, 1993b, 1995). In addition, comparative studies revealed that basal caenogastropods in the Viviparoidea, Cyclophoroidea, Campaniloidea, and Cerithioidea possess similarities in sperm morphology that set them apart from all other caenogastropods, including distinctive features of the eusperm acrosome (conical to flattened, lacking an apical bleb and usually lacking an accessory membrane), eusperm midpiece (often with parallel cristal plates), and parasperm (with head and tail tuft) (see Healy, 1983, 1988a and references therein). Recognition of this common organization supported removal of the Vermetidae, Cerithiopsidae, and Triphoridae (Healy, 1984, 1988a, 1990; see also Buckland-Nicks & Hadfield, 2005), all of which possess sperm characteristics typical of more derived caenogastropods. Houbrick (1979) removed the Abyssochrysidae based on unique anatomical features including a distinctive radula and pallial penis (later demonstrated to be a pallial tentacle; Ponder & Warén, 1988; Warén & Ponder, 1991) and placed the family in the vicinity of the Zygopleuridae and Pseudozygopleuridae (formerly in the Loxonematoidea, but currently in the 'zygopleuroid group'; Bouchet & Rocroi, 2005) given the great similarity in shell morphology to these Palaeozoic fossils. Eusperm morphology and the presence of distinctive spermatozeugmata later confirmed that the Abyssochrysidae lies outside the Cerithioidea, but indicated that their affinities lie rather with the Littorinimorpha (Littorinoidea and Rissooidea, in particular; Healy, 1989); new molecular data demonstrate that abyssochrysids are in fact nested within Provannidae (Johnson *et al*., 2010).

Campanilidae and Plesiotrochidae are the taxa most recently removed from the superfamily. Campanilidae contains only one Recent species, *Campanile symbolicum* Iredale, 1917 of Western Australia. Although included in the Cerithioidea by Houbrick (1981a, 1988) and Ponder & Warén (1988), it is now considered to represent a distinct group supported by anatomical data (Houbrick, 1981a, 1989) and sperm (Healy, 1986b, 2000) and osphradial fine structure (Haszprunar, 1988, 1992). *Plesiotrochus* was formerly classified in the Cerithiidae (e.g. Thiele, 1929) and Houbrick (1980) retained the Plesiotrochidae within the Cerithioidea when he erected the family. However, eusperm and parasperm of *Plesiotrochus* are similar to those of *Campanile* and the two are currently united in the Campaniloidea (Healy, 1993a; Healy & Wells, 1998b).

Historically, little attention has been paid to the relationships amongst cerithioidean families and broad family concepts have dominated. For example, the Cerithiidae was used to encompass many diverse taxa ranging from *Ataxocerithium* (Triphoroidea), *Campanile* and *Plesiotrochus* (Campaniloidea) to *Diala* (Dialidae), and *Litiopa* (Litiopidae) albeit often in several subfamilies. Similarly all limnic cerithioideans were previously included within the Thiaridae (often under the invalid name 'Melaniidae'; e.g. Brot, 1874; Thiele, 1925, 1928, 1929; Sunderbrinck, 1929; Wenz, 1939) despite being acknowledged as a heterogeneous assemblage of unrelated taxa (e.g. Moore, 1897, 1898; Smith, 1904; Pilsbry & Bequaert, 1927). Apart from Thiele (1929), whose classification recognized six distinct freshwater subfamilies that conform broadly to current family-level concepts, the only other attempt to formalize such hypotheses was the classification of Morrison (1954), which supported three freshwater lineages (Pleuroceridae, Melanopsidae, Thiaridae) each with independent marine origins. Regrettably, Morrison's influential classification advanced family concepts that were highly polyphyletic based on the assumed homology of brood structures (see Glaubrecht, 1996). Since that time, the significant new morphological and molecular data produced for freshwater taxa (see above) have largely confirmed Thiele's view, but these data have not been

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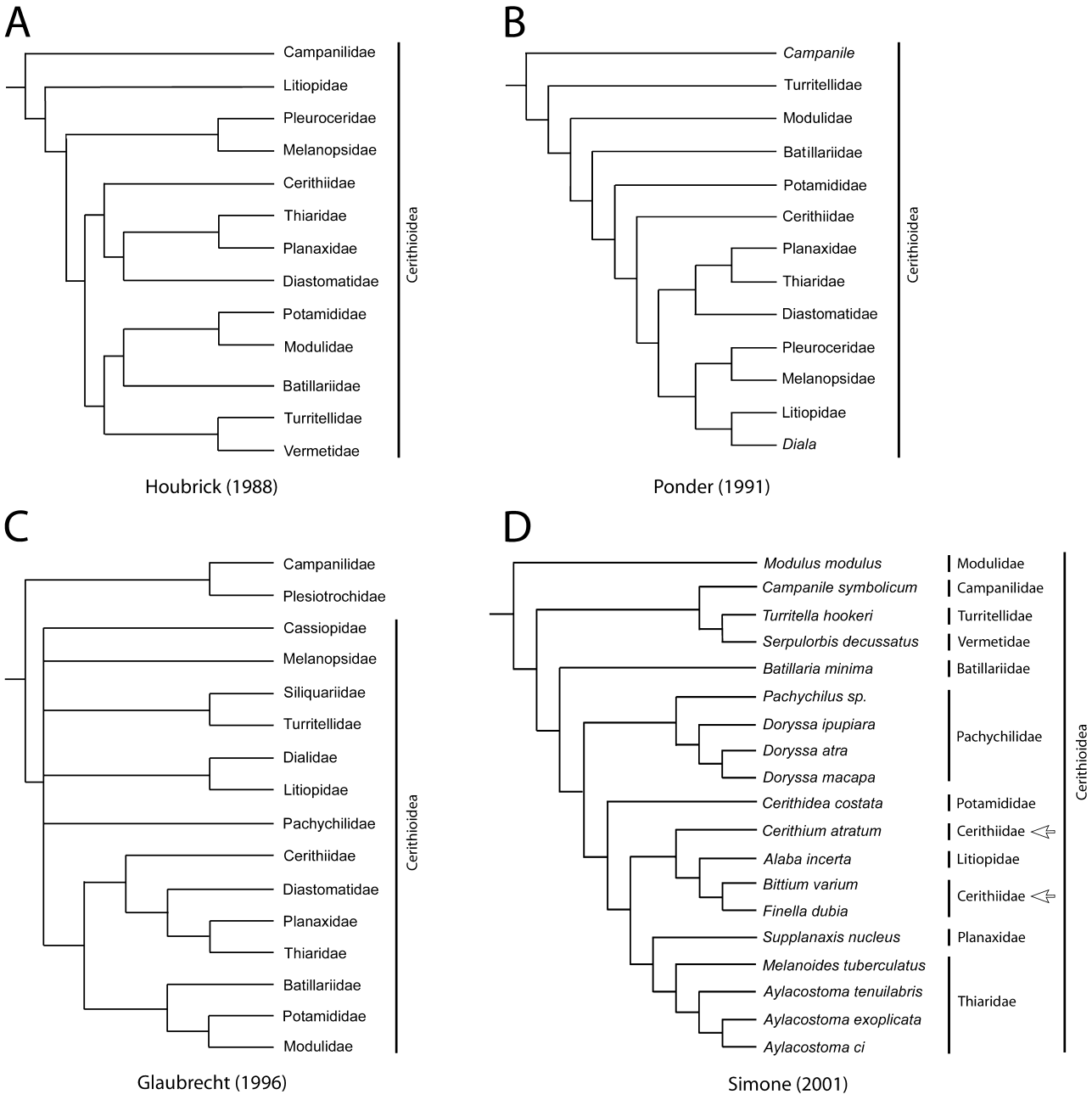

Figure 2. Hypotheses of cerithioidean relationships based on morphological data. A, modified from Houbrick (1988: fig. 2); B, modified from Ponder (1991: fig. 12); C, modified from Glaubrecht (1996: fig. 5); D, modified from Simone (2001: fig. 441). Open arrows indicate families resolved as nonmonophyletic.

assessed in a comprehensive cladistic framework and the relationship amongst freshwater lineages is still unclear.

Family-group members of the current concept of Cerithioidea were first formally listed by Ponder & Warén (1988), with the exception of the inclusion of Campanilidae, and most recently by Bouchet & Rocroi (2005). However, phylogenetic analyses of Cerithioidea to date have produced conflicting topologies and have not always supported composition of the ingroup as currently recognized (Houbrick, 1988; Ponder, 1991; Glaubrecht, 1996; Simone, 2001; Lydeard *et al*., 2002) (see Figs 2, 3). In the first morphology-based phylogenetic analysis of the group, Houbrick (1988) included 14 family-level ingroup terminals, 11 of which are counted amongst the 17 currently recog-

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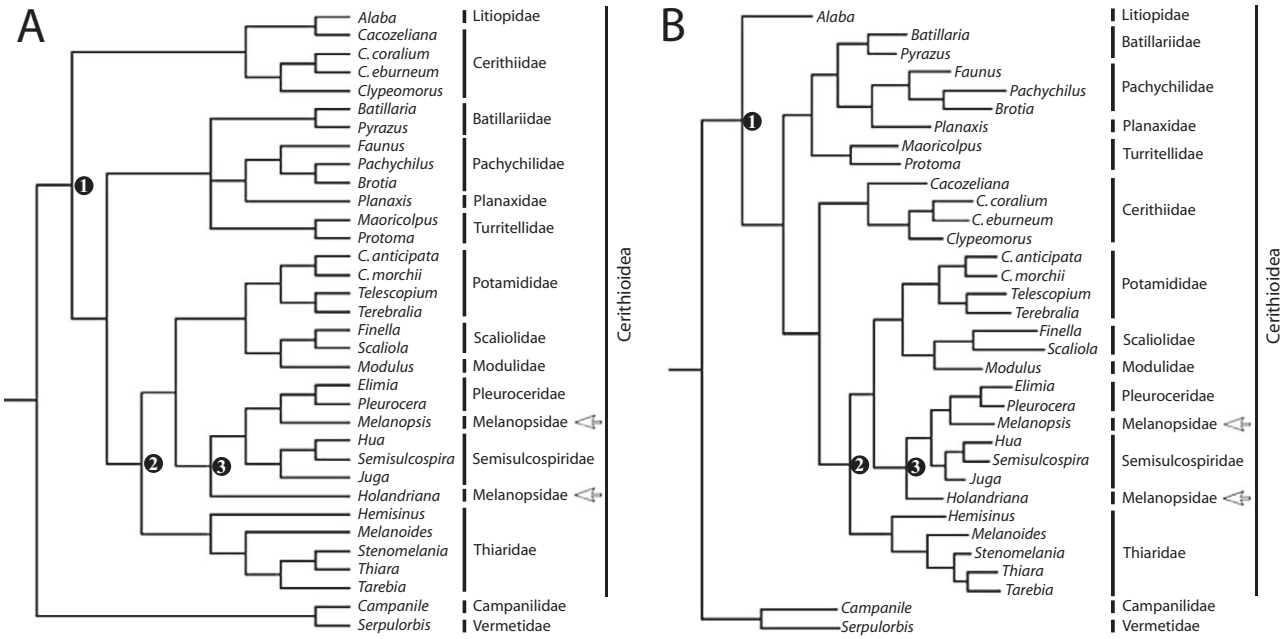

Figure 3. Hypotheses of cerithioidean relationships based on molecular data, modified from Lydeard *et al*. (2002: figs 1, 2). A, strict consensus tree of four equally parsimonious trees based on parsimony analysis of mtLSU rDNA and flanking tRNA gene sequences, all characters unordered and equally weighted; B, single most parsimonious tree based on weighted parsimony analysis (transversions 2 × transitions). Three main assemblages are numbered; see text for details. Open arrows indicate families resolved as nonmonophyletic.

nized, with *Rissoa* and *Strombus* as outgroups; 58 morphological characters were coded, including features of the teleoconch, operculum, external anatomy, radula, alimentary, reproductive and nervous systems, and sperm ultrastructure. Houbrick's view of the classification of cerithioideans at that time was rooted in that of Thiele (1929), with campanilids and vermetids as part of the ingroup, but he acknowledged that some families were likely to be polyphyletic. Houbrick (1988) attempted to mitigate the impact of this, as well as that of high intrafamilial variability, by coding only the nominal taxon for which each family-group name was derived. Consequently, his analysis did not assess monophyly of individual families, but only attempted to establish the relationships amongst them. Houbrick's results supported Campanilidae as the most basal offshoot, and Pleuroceridae plus Melanopsidae as the third most basal offshoot after Litiopidae. The remaining taxa clustered in two main clades: one with Cerithiidae, Diastomatidae, and Thiaridae and Planaxidae as sister taxa, and a second clade with Vermetidae as sister to Turritellidae, and with Batillariidae, Modulidae, and Potamididae (Fig. 2A). Houbrick (1989) later modified his views and supported placement of Campanilidae in a separate superfamily given a reinterpretation of new and existing characters. The placement of Campanilidae at the base of the tree is consistent with this view, but Vermetidae is placed firmly within the ingroup, which conflicts with current concepts.

Ponder (1991) reanalysed Houbrick's (1988) data but excluded vermetids and added new morphological information for *Diala*. Ponder argued that Houbrick's use of Rissoidae as an outgroup was inadequate to polarize characters given their distant relationship; excluding Rissoidae and using *Campanile* as the sole outgroup resulted in a reversal of the polarity of the tree in one of the two most parsimonious trees (Fig. 2B) with Turritellidae at the base, demonstrating sensitivity of the results to placement of the root.

Glaubrecht (1996) produced an hypothesis of cerithioidean relationships using Hennigian argumentation involving the weighting and polarizing of 48 anatomical characters by hand (teleoconch, external anatomy, operculum, radula, alimentary and reproductive systems, and sperm ultrastructure) for 13 cerithioidean families; 'Eucaenogastropoda', Ampullarioidea, and Cyclophoroidea served as outgroups, and Campanilidae plus Plesiotrochidae were also included (Fig. 2C). In the resulting topology, the Campaniloidea was monophyletic and sister to the Cerithioidea. Within the Cerithioidea, Melanopsidae, Pachychilidae (= Pleuroceridae plus Pachychilidae in part, as currently conceived), Siliquariidae plus Turritellidae and Dialidae plus Litiopidae all form

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an unresolved polytomy at the base of the tree; the remaining taxa clustered in two clades, one with Cerithiidae, Diastomatidae, Planaxidae plus Thiaridae (= Thiaridae *s.s.* plus Paludomidae and Pachychilidae in part, as currently conceived), and the other with Batillariidae and Potamididae plus Modulidae.

Simone's (2001) morphological phylogeny of the superfamily incorporated 19 primarily western Atlantic/neotropical species-level terminals distributed amongst 12 families; Campanilidae and Vermetidae were amongst these to test their exclusion from the superfamily. The morphological data set comprised 122 characters for teleoconch, external anatomy, operculum, renal, alimentary ,and reproductive systems, and 22 characters new to cerithioidean systematics relating to buccal musculature; sperm ultrastructure characters were not included. Given Simone's view of the Cerithioidea as stem-group caenogastropods, a pooled 'archaeogastropod' served as the primary outgroup, with the caenogastropod families Viviparidae, Hydrobiidae, and Littorinidae as secondary outgroups. The consensus of three most parsimonious trees placed Modulidae as the most basal offshoot, followed by a clade with Campanilidae as sister to Vermetidae plus Turritellidae; two freshwater clades were obtained, one with Pachychilidae, and one with Planaxidae as sister to Thiaridae *s.s.* (Fig. 2D). However, the choice of taxon sampling did not allow rigorous assessment of familial monophyly. Simone also reanalysed Houbrick's (1988) data using the pooled 'archeogastropod' as the outgroup, and similarly recovered a tree with essentially reversed polarity, placing Turritellidae plus Vermetidae at the base and Campanilidae as the second offshoot, recapitulating Ponder's (1991) findings with regards to rooting sensitivity.

In the only molecular phylogenetic analysis of the superfamily, Lydeard *et al*. (2002) analysed DNA sequences from mitochondrial large subunit rRNA and flanking tRNA genes. The data set comprised 40 nearly full-length sequences (32 cerithioideans, eight outgroups) with a total aligned length of 1873 bp. This analysis is the most comprehensive to date, allowing evaluation of monophyly of a number of cerithioidean families for the first time. Parsimony analysis resulted in four equally parsimonious trees with the strict consensus tree shown in Figure 3A; a slightly different topology was recovered with transversion weighting (Fig. 3B). Monophyly of the Cerithioidea as currently conceived was supported with *Campanile* plus *Serpulorbis* as the sister group to the Cerithioidea. The exclusion of Campanilidae and Vermetidae was supported by a unique tRNA gene order arrangement, with mitochondrial small subunit (mtSSU)-thr-gly-val-mitochondrial large subunit (mtLSU) in all cerithioideans versus mtSSU-val-mtLSU in other caenogastropods. Amongst families with more than a single representative in the analysis, both equally weighted and differentially weighted topologies supported monophyly of the Batillariidae, Pachychilidae, Pleuroceridae, Potamididae, Scaliolidae, Semisulcospiridae, Thiaridae, and Turritellidae. Cerithiidae was monophyletic in the differentially weighted but not the equally weighted analysis, whereas Melanopsidae was polyphyletic in both analyses.

In summary, existing morphological phylogenies have had limited capacity to assess familial monophyly and do not reflect significant new data generated in recent years (see above). In addition, there is considerable disagreement amongst the analyses produced thus far and no analysis has explored simultaneous analysis of morphological and molecular information. The goal of the present analysis is to generate an updated morphological data set for an expanded selection of taxa in the most inclusive morphological analysis of the superfamily to date. The molecular data of Lydeard *et al*. (2002), pertinent sequences that have become available since, and newly generated 28S sequences are synthesized and analysed separately and together with the morphological data, to provide the best estimate of phylogenetic relationships within the group possible with current information.

MATERIAL AND METHODS

Morphological analysis

The approach taken here emphasizes as much as possible species and genus level terminals. The fragmentary and uncoordinated sampling for morphological, physiological, ecological, and molecular systematic studies has necessitated that in many cases data for the principal terminal have been supplemented using congeneric or, rarely, confamilial species. We have attempted to minimize data concatenation from nonconspecific sources as much as possible but have chosen to do so in order to maximize information and minimize ambiguity. Polymorphic coding was used when the features of interest varied at the focal taxonomic level. The resulting data matrix comprises 151 characters for 56 taxa (47 ingroup, nine outgroup taxa) with representatives from all 17 Recent families, and multiple representatives from 12 of them. Included taxa and sources of anatomical data are provided in Table 2; the data matrix is shown in Table 3.

Ingroup taxon selection reflects the dual interests of taxonomic inclusivity and availability of comparative data; the high number of freshwater taxa in

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Table 3. Morphological data matrix for 56 taxa and 151 characters

Taxon	Characters
	1 2 3 4 5 6 7 8 .....0.....0.....0.....0.....0.....0.....0.....0
Neocyclotus dysoni ambiguum	2001001010101010000-000-00001------0010-0100-10*1000000?210-------0--0--310-----
Marisa cornuarietis	2000001010002110000-010-001011023002220-0100-00010022000210-------0--0--210-----
Viviparus viviparus	1001011000002100000-0?0-001110003102030-0000-10010110000200-------0--0--210-----
Campanile symbolicum	0100130000000210300-021000000120301020101100-0201002202121001-----00-50-120----0
Plesiotrochus crinitus	0100130000000101011?0?000000120?0?221101100-02010012010200-------0--0--120-----
Littorina littorea	1001000010000110000-010-000000001001110-0001002*111100-02111------00-0--210-----
Strombus mutabilis	1111000010200211000-020-000000204002220-0000000000220302001--010000-10-12100120
Serpulorbis zelandicus	300000100-----101000120-001000001012230-0000-00010033O3?20001?0?0000-10-120----0
Dendropoma lamellosa	3000001000111010100-110-001000002012220-0100-00010033031200012010000-10-000----0
Batillaria australis	0111100010101011000-011000000000101223111100-1101002223020100310100115O-00111000
Pyrazus ebeninus	0111100010101011000-011000000000121223111100-1101002223020100310100115O-00111000
Alabina cerithidioides	0000000020000300011001100000020012020l0-0000-00010010?30?00?????000??20-00100220
Bittium reticulatum	0101000020100000001100100000021020022l0-1100-0101001213000101211000O-20-00100220
Cacozeliana granaria	0101000020000000000100?100000022000?2210-1100-0101001213100101211000O-60-00100220
Cerithidium fuscum	0100000020000000001001100000020010?2110-0100-00010020130O0?012110000-20-000----0
Cerithium atratum	0111100020000110000-011000000020000222O-1001101010011030001000110000-60-00100220
Cerithium nodulosum	0111100020000100000-0?100000002000022O-1001101010012030001000110000-60-00100220
Clypeomorus bifasciata	0101000020000110000-0?100000002010O?220-1001101010012?30?01??????????????????????
Ittibittium parcum	0100000020000100011111100000022010022l0-1100-0101001213000101211000O-20-00100220
Diastoma melanioides	0000001011000011000O-0?100000020101221O-110100?0100120300000002100000-60-00100220
Diala suturalis	0000000000000010000100?0-000002001002110-1100-0001001203200101211000O-20-00100220
Alaba incerta	0000000020000100011110O-000002101002210-1100-0201001203000101211000O-20-00100220
Modulus modulus	2000001110101011000-011000000000100212O-000101101110043010100110000102O-10101100
Fossarus ambiguus	2010001010000200000-000-000000002002131001O0-1001001103000101200000102O-00100220
Planaxis sulcatus	1101000010000200000-010-000000001000131001010000111002300010021000010400-000----0
Cerithidea scalariformis	0110101010101011200-010-010010012202130-000101001011023000000110010104O-10101101
Telescopium telescopium	0100100100101010200-011001000012202040-000112101001223000000000000010410101011O1
Terebralia sulcata	0111100120101011200-011001000001120023O-0000-110100102300000001001010410101011O1
Tympanotonus fuscatus	0111100020101011200-011001001001321212O-0001000????002300000000101101430-10101101
Finella pupoides	0000000010101010000-001000000200100200O-0000-1001*0$0030010??21??00??20-00?????0
Scaliola sp.	0000020000101010000-000-000002002002000-0000-000100230300l1??21??00??20-00?????0
Stephopoma nucleogranosum	3000001001111010-00-011000110000010201O-0000-0000001003110O1-2010000-50-00112000
Turritella communis	0000100001111010011001101011000001022l0-0000-0000001103?000002110000-50-00112000
Turritella terebra	0000100000111010301001101011000001020?0-0000-00010000?3??00???????00-50-00112100
Holandriana holandri	1000000000000310000-010-0000?00120?223100101011011100?3000000300100143O-00101011
Melanopsis praemorsa	1100000000000110000-010-000010012001201010110010100021300000030010014310001010l1
Doryssa atra	0000000000101010000-010-000010002001210-101100011100013120O??4000011050-00102020
Brotia pagodula	1000000000101010000-0?0-000010012001100-101100011002213120000400001105O-00102020
Faunus ater	0101000010000110000-011000001002011230-001101001002213110100400001105O-00102020
Pachychilus sp.	0000000000000110000-010-000010002001220-101100011002213120200400001105O-00102020
Cleopatra johnstoni	1001001000002010000-010-000010012002120-000111101110033000000010100133101010l1
Lavigeria sp. A	1001000010000210000-010-000010012002O?0-000110101011033011000200000123101010l1
Paludomus siamensis	1001000010002010000-011100001001200212O-000112101110033000000110100133101010l1
Tanganyicia rufofilosa	10*1001010002010000-010-000010013002030-000112101110033000000200100133101010l1
Tiphobia horei	2100000000002001000-010-000010012002020-000112100001O?3000000000100133101010l1
Elimia livescens	0000000000000210000-010-000010002002231000010110111004300000030010014310101011
Pleurocera acuta	0000100000000110000-010-000010002002232?0001111101110043000000300100123O-10101101
Hua jacqueti	1001100010000110000-010-000010002000231000012010111004300010030010012300-10101101
Juga silicula	0000100000000110000-010-000010002002231000011010111004300000030010014300-00102001
'Parajuga' 'calculus'	000000000000l??????????????????????????2310000100l??????????????????????????????
Semisulcospira libertina	0000000000000110?00-000-000010002002231000010110111004300000030010010300-10101101
Hemisinus lineolatus	0100000000000210??0-0?110?00?000?0??2310000112101111003???????????????????????????
Melanoides tuberculata	0000100000000210000-011100001000%2022210000102001110033000000010100143111010110l
Stenomelania cf. *plicaria*	0000*00000000210000-011100001000100223100000-210111003300000001010014311101011O1
Tarebia granifera	0000100000000210000-011100001000$0022010000102101110033100000010100143111010111l
Thiara amarula	1000000000000210000-011100001000100223100001020011100330000000101001431110101111

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Table 3. *Continued*

Taxon	Characters
	1 1 1 1 1 1 9 0 1 2 3 4 5 .....0.....0.....0.....0.....0.....0.....0.
Neocyclotus dysoni ambiguum	0-0000000111000-0-000--310001000000-1100000020000000101000l-10002000121
Marisa cornuarietis	0-0000010111000-0-000--310000000000-0100000201010*10010001-10*02000121
Viviparus viviparus	0-0000011011000---100--30?000000000-0100000000001001100?011-1*202000-20
Campanile symbolicum	0-1000012101-0110-000--000000000011100011100?1100100011011000*0#$00?02?
Plesiotrochus crinitus	0-0000012011??110-000--000000100011000l?1??0111001000101?0201-32001?0?
Littorina littorea	0-000000201101100-000--300000001000-1000100011110221001000l-41---1*0102
Strombus mutabilis	0-1?2110201101110-000--?000000011010100010000111001100l0001-31-22110100
Serpulorbis zelandicus	0-1000102001-?0---010--000000000101000l?000011100110010001-31-2211012?
Dendropoma lamellosa	0-1000102001-10---010--000000000101000011000011100110010001-31-22110123
Batillaria australis	0-0100102101-01110000--000101000111000011000000000001100000010000000?4
Pyrazus ebeninus	0-0100102101-01110000--000201000101000011000000000001100000010000000??
Alabina cerithidioides	??0?00102100-1100-000--00010100000--000?1000??????????????????????000?
Bittium reticulatum	0-0000102000-?1110000--000101100101000011000200000012000??10000000000?
Cacozeliana granaria	0-010010200?-?1110000--00010110010100000?????????????????????????????000?
Cerithidium fuscum	0-010010210?-1100-000--300010100101000?1?00?????????????????????????0?0?
Cerithium atratum	0-0100102001-01110000--000101000111000011000201000001200000010000000004
Cerithium nodulosum	0-0100102001-01110000--00010100011100001100021?10000012000??????????0000
Clypeomorus bifasciata	????00102001-?110-000--000101000101000????02010000012000000l0000000004
Ittibittium parcum	0-0100102000-?110-000--010101000001000??0??201000001202000010000000002?
Diastoma melanioides	0-0100102001-01111000--000101000101000l?000??????????????????????????0???
Diala suturalis	0-0100102?00-1100-000--110101000101000011000200000001200001-21-22110002
Alaba incerta	0-0100102000-?1110000--000101000011000l?000201000001202002?10000000000?
Modulus modulus	0-0110102??1??1110000--000111000011000011000??000000100100??1??????002?
Fossarus ambiguus	0-0100102000-110--00111000101000101000??000?????????????????????????2-0?
Planaxis sulcatus	0-0000102001-111--00111000101000101000l?000000000001100002?10000000-0?
Cerithidea scalariformis	120111102101-01110000--000201000111000011000100000001001000110011000023
Telescopium telescopium	120121102101-01110000--00020100010100??1?000000000001001000110011000002?
Terebralia sulcata	120121102101-01111000--200101000101000l?000100000001001000110011000002?
Tympanotonus fuscatus	100111102101-01110000--000201000101000??000?????????????????????????0?0?
Finella pupoides	??0?00102100-10-11000--110111100201100011000001000001001001-11-22000?0?
Scaliola sp.	??0?00102100-10-11000--110101000201100l?100020100000100l001-11-22000?0?
Stephopoma nucleogranosum	0-0000102100-?11--010--000000000000--0--?1000???????0120?????????????0-2?
Turritella communis	0-0100102101-11?0-000--000101000011000011000000000001200000010000000102
Turritella terebra	??0?00102101-0110-000--00010100001100001?000000000001200000010000000??2
Holandriana holandri	1001001121?1?01111000--000101000101000?????????????????????????????0?2?
Melanopsis praemorsa	1001001121111101111000--000101000101000011010200000001000001-10102020124
Doryssa atra	0-0?00112??1?01110000--00010100000--002?1001?????????????????????????0???
Brotia pagodula	0-0120112001-011--0010100010100000--000??001?????????????????????????0-2?
Faunus ater	0-0100102001-01111000--010101000101000???00?????????????????????????0???
Pachychilus sp.	0-0100112001-01110000--00010100000--002?1001?????????????????????????0???
Cleopatra johnstoni	110110102001-01011000--1001010002010011110202000?????????????????0?21
Lavigeria sp. A	110110102100-00---100--1001010002010011110202010000010010001?0000000-2?
Paludomus siamensis	110110102001-01011000--100101000201001111020?????????????????????0?25
Tanganyicia rufofilosa	1?0110102001-00-1100121100101000201001111020?????????????????????0-2?
Tiphobia horei	110110102001-00---100--10010100000--01111020?????????????????????0-2?
Elimia livescens	1001001021111101111000--00010100000--000110102000000010000??11-?1000124
Pleurocera acuta	1001001021111101111000--00010100000--00011010?????????????????????????0123
Hua jacqueti	1001001021111101011000--000101000101000?1010?????????????????????????0???
Juga silicula	1001001021111101111000--0001010001010000011010?????????????????????0124
'Parajuga' 'calculus'	????????????????11??000--000101000101000011010?????????????????????012?
Semisulcospira libertina	100100102111?00---100--000101000101000?101020000000100000??10000020-24
Hemisinus lineolatus	???????02001-00---0010010?????10????000?????????????????????????????-1?
Melanoides tuberculata	110120102001-10---0010030100001000--0???10102000012010O?00??10-3100#-10
Stenomelania cf. *plicaria*	110120102001-10---0010030100001000--0?????10?????????????????????????#-04
Tarebia granifera	110120102001-10---0010030100001000--0????010?????????????????????????3-16
Thiara amarula	110120102001-10---0010030100001000--000110102010022010010O1-11-2202#-06

? indicates missing data; - indicates inapplicable characters. Polymorphic codes: '0/1' = *; '0/2' = $; '0/3' = #; '2/3' = %.

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particular reflects the wealth of data that is now available for these taxa (see above) and the ongoing uncertainty about familial monophyly and relationships amongst currently recognized families. A diverse range of outgroup taxa was selected based on recent higher-order morphological and molecular analyses (Colgan, Ponder & Eggler, 2000; Colgan *et al*., 2007; Ponder *et al*., 2008) to evaluate monophyly of the superfamily as currently conceived. Morphological data were coded partly from the literature and supplemented by our own unpublished observations. Some pertinent characters used by Simone (2001) were not included (i.e. buccal musculature) as there is little overlap in taxon sampling with the present study even at genus level and these characters remain unexplored amongst other cerithioideans. Several character sets, including protoconch and teleoconch sculpture and radular cusp counts, were explored but ultimately not included in the analysis because of high levels of intraspecific and intrageneric variation; protoconch characters were also omitted as they are highly correlated and sometimes completely redundant with characters relating to developmental mode.

Parsimony analyses were performed using the Ratchet as implemented in WinClada v. 1.00.08 (Nixon, 2002), with 1000 iterations, ten trees held at each iteration. All characters were unordered and equally weighted. Jackknife analyses (1000 replicates) were also conducted using WinClada. Character optimizations were examined on the strict consensus tree. Unambiguous character changes (i.e. unequivocal transformations) were verified on all equally parsimonious trees; ambiguous character changes were examined using accelerated transformation (ACCTRAN) optimization.

Molecular and simultaneous analyses

As discussed above, Lydeard *et al*. (2002) generated a mtLSU rRNA and tRNA gene data set comprising 40 nearly full-length 16S sequences for 32 cerithioidean and eight outgroup taxa. Although most 16S sequences available in GenBank are only partial, we diversified taxon selection amongst several basal caenogastropod outgroups [*Littorina littorea* (Linné, 1758), *Viviparus georgianus* (Lea, 1834), *Marisa cornuarietis* (Linné, 1758), *Dendropoma corrodens* (d'Orbigny, 1842), *Strombus luhuanus* Linné, 1758)] and for several ingroup taxa that have become available since 2002 to maximize congruence with the morphological partition [(*Paludomus siamensis* Blanford, 1903, *Cleopatra johnstoni* (Smith, 1893), *Lavigeria grandis* (Smith, 1881), *Lavigeria* sp. A, *Tanganyicia rufofilosa* (Smith, 1880), *Tiphobia horei* Smith, 1880, *Elimia livescens* (Menke, 1830), *Pleurocera acuta* Rafinesque, 1831, *Hua jacqueti* (Dautzenberg & Fischer, 1906) and *Juga silicula* (Gould, 1847)] (see Table 2). Several outgroups from the molecular analysis of Lydeard *et al*. (2002) [i.e. *Busycotypus spiratus* (Lamarck, 1816), *Hydrobia* sp., *Littorina saxatilis* (Olivi, 1792)] were omitted to maximize congruence with available morphological and molecular sources.

In addition, a data set was generated for a substantial portion of the nuclear 28S cytoplasmic nuclear rRNA gene. Primers were modified from Medina *et al*. (2001) (28S DK-F: 5′-gat cgg ac gaga tta ccc gct gaa-3′ and 28S DK-R 5′-cag atg tac cgc ccc agt caa act-3′) to yield a 1284 bp fragment using Long PCR (94 °C, 30 s; 55 °C, 30 s; 72 °C, 2.5 s, ×30 cycles; 72 °C, 5 min) for 33 taxa, including 29 cerithioideans and four outgroups; these were supplemented with partial 28S sequences from GenBank for four cerithioideans and six outgroups (see Table 2 for details).

The restructured molecular data matrix comprises 37 nearly full-length 16S sequences for 32 cerithioidean and five outgroup taxa (Lydeard *et al*., 2002), 20 partial 16S sequences (lacking the 5′ segment) for 11 cerithioidean and nine outgroup taxa, and 44 28S sequences. Sequences were aligned with CLUSTALX (Thompson *et al*., 1997) using default parameter values. Alignments were conducted separately for each gene partition and were performed separately for the extended and pruned data sets (see below) to accommodate changes in taxonomic composition. Attempts were made to obtain a better alignment using MUSCLE (Edgar, 2004) (default settings and *–refine* option), T-Coffee (Notredame, Higgins & Heringa, 2000), or the M-Coffee method of combining and refining alignments produced by a variety of other programs (Wallace *et al*., 2006). All of these approaches produced alignments that were longer in aligned length than that produced by the CLUSTAL 'slow-accurate' algorithm and all produced trees that required more steps using the same search strategy. To explore the effect of unconserved regions, divergent regions were selected and removed with GBLOCKS v. 0.91b (Castresana, 2000) using all three options for a less-stringent selection (allowing 'smaller final blocks', 'gap positions within the final blocks' and 'less strict flanking positions').

To test monophyly of the Cerithioidea and to assess concatenation strategies for the combined morphological + molecular analyses, a taxonomically extended molecular data set with denser sampling particularly amongst outgroup taxa was analysed for 61 terminals (47 cerithioideans and 14 outgroups); for combined morphological + molecular analyses, a pruned molecular data set that maximizes taxonomic congruence with the morphological partition was re-aligned and combined with the morphological data

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(see Table 2 for details). The alignment for the extended 16S rRNA data set was 1454 bp in length; of these, 319 were invariable, 154 variable but not parsimony informative, and 981 parsimony informative. With unconserved regions removed, the data set was 923 bp in length, with 293 invariable, 119 variable but not parsimony informative, and 511 parsimony informative. The alignment for the extended 28S rRNA data set was 1146 bp in length; of these, 666 were invariable, 177 variable but not parsimony informative, and 303 parsimony informative. With unconserved regions removed, the data set was 969 bp in length, with 592 invariable, 147 variable but not parsimony informative, and 230 parsimony informative. The alignment for the pruned 16S rRNA data set was 1460 bp in length; of these, 332 were invariable, 177 variable but not parsimony informative, and 951 parsimony informative. With unconserved regions removed, the data set was 1039 bp in length, with 305 invariable, 140 variable but not parsimony informative, and 594 parsimony informative. The alignment for the pruned 28S rRNA data set was 1141 bp in length; of these, 687 were invariable, 178 variable but not parsimony informative, and 276 parsimony informative. With unconserved regions removed, the data set was 986 bp in length, with 624 invariable, 149 variable but not parsimony informative, and 213 parsimony informative. Gaps were coded as missing.

The 16S and 28S molecular partitions were analysed separately and together for the extended data set using parsimony and Bayesian methods of inference. Parsimony analyses used WinClada with the same search routine as for the morphological partition; more rigorous search routines did not recover shorter trees or discover additional islands of trees. The substitution model for Bayesian analyses was selected using the Akaike information criterion (Akaike, 1974) implemented in MrModelTest 2.3 (Nylander, 2004), which favoured the general time-reversible + proportion invariant + gamma (GTR + I + G) model for both the 16S and 28S partitions, including extended and pruned data sets, and with unconserved regions removed. Bayesian analyses were conducted using MrBayes v. 3.1.2 (Huelsenbeck & Ronquist, 2001). Metropolis-Coupled Markov chain Monte Carlo (eight chains) were run for 2 000 000 generations using the model specified by MrModelTest. The overall substitution rate was allowed to vary independently for each partition ('ratepr = variable'). Other parameters (base frequencies, substitution matrix, the alpha parameter of the gamma distribution, and the proportion of invariable sites) were independently estimated, using the 'unlink' command. Topologies were sampled every 1000 generations; the first 250 000 generations were discarded to allow for convergence.

Simultaneous analyses (morphological + molecular) were also performed using parsimony and Bayesian inference. Identical settings as for the separate analyses were used for the molecular partitions, and the default (standard discrete) model with gamma-distributed rate variation was used for the morphology partition. All trees were rooted with Cyclophoridae as the primary outgroup. Unambiguous and ambiguous (ACCTRAN) morphological character changes were examined on all topologies obtained for the combined morphological + molecular data sets (parsimony and Bayesian, unconserved regions included or excluded). The Bayesian analysis of the combined data set with unconserved regions included was selected to illustrate morphological evolution as this topology is the most resolved and maximizes the number of monophyletic families (see Fig. 10).

CHARACTERS

A character matrix of 151 characters (teleoconch, operculum, radula, alimentary, reno-pericardial, nervous and reproductive systems, sperm ultrastructure) was compiled and coded for all 56 morphological terminals (Table 3). Character descriptions are provided below; any pertinent information relating to character state delineation or homology assessment is discussed in more detail as necessary.

TELEOCONCH

1. Spire angle: 0 – long spire (narrow to elongately conical, < 20°); 1 – medium spire (moderately wide, 40–110°); 2 – short, wide spire (> 120°); 3 – irregular, uncoiling growth form.
2. Condition of anterior aperture: 0 – continuous (entire); 1 – discontinuous (siphon, notch or truncated columella).
3. Outer lip of aperture: 0 – simple; 1 – flaring.
4. Anal canal: 0 – absent; 1 – present.

Although there is considerable variation in development of the anal canal, from a small notch to a large sinus, it was not possible to capture this variation in discrete character states.

5. Posterior to medial outer lip sinus: 0 – absent; 1 – present.
6. Periostracum: 0 – smooth; 1 – hispid; 2 – agglutination; 3 – intracalyx (secondarily calcified).

Scaliolidae cement sand grains to the surface of their shell, presumably through adhesion by periostracal fluid (Ponder, 1994). A periostracum that is

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secondarily externally calcified ('intracalyx') is unique in the Campanilidae and Plesiotrochidae amongst the taxa sampled here.

7. Umbilicus (adult): 0 – closed; 1 – open.
8. Columellar fold or plait: 0 – absent; 1 – present.
9. Mode of growth: 0 – indeterminate; 1 – determinate, with terminal varix or thickening of apertural lip; 2 – determinate, periodic with numerous varices.

Adult operculum

10. Setae on outer surface: 0 – absent, 1 – present.
11. Shape (outline): 0 – ovate; 1 – circular; 2 – spatulate.
12. Shape (profile): 0 – flat; 1 – concave.
13. Coiling: 0 – paucispiral; 1 – multispiral; 2 – concentric.
14. Nucleus placement: 0 – central; 1 – eccentric (= lateral); 2 – terminal (= basal); 3 – subcentral.

External anatomy

15. Cephalic tentacles: 0 – long; 1 – short.

Although some taxa clearly have extremely short tentacles (e.g. *Scaliola*), there is a continuum between very short and intermediate length (approximately equal to snout length); these are all coded as 'short'. Taxa with tentacles much longer than the snout are coded as 'long'.

16. Position of eyes relative to base of cephalic tentacles: 0 – at base; 1 – above base.

Several taxa have elongated the basal portion of the cephalic tentacles such that the eyes are elevated above the base (e.g. *Modulus*, potamidid taxa).

17. Propodial pedal gland: 0 – anterior sole margin only; 1 – restricted to central part of anterior sole margin; 2 – anterior half of sole margin; 3 – entire sole margin.

Typically, the propodial pedal gland opens to a shallow groove along the anterior edge of the foot sole. In Campanilidae and some turritellids, the entire foot sole is rimmed by a shallow mucus-secreting groove. In potamidids, the propodium comprises a larger proportion of the foot with the anterior pedal gland extending approximately half way down the side of the foot.

18. Mesopodial mucous gland: 0 – absent; 1 – present.

This character relates to the formation of a discrete internal gland with an opening in the middle of the mesopodium. It typically secretes a fine mucus thread that is used to anchor the individual to its substrate.

19. Epipodial skirt: 0 – absent; 1 – present.

The epipodium and associated tentacles and papillae are characters usually considered typical of Vetigastropoda (e.g. Ponder & Lindberg, 1997). Whether these cerithioidean structures are homologous or not has yet to be properly tested.

20. Epipodial papillae or tentacles: 0 – absent; 1 – present.
21. Propodial projections: 0 – absent; 1 – present.

These structures are narrow projections at the anterolateral corners of the foot.

22. Columellar muscle: 0 – short (up to one half of the mantle length); 1 – moderately long (~equal to mantle cavity in length); 2 – long, strap-like.
23. Mantle edge papillae or tentacles: 0 – papillae and tentacles absent (mantle edge smooth); 1 – papillae or tentacles present.
24. Papillae/tentacles: 0 – thin; 1 – thick.

Thick, broad mantle papillae are found only in the freshwater Thiaridae and some Paludomidae.

25. Branched tentacles ventrally behind mantle edge: 0 – absent; 1 – present.

These structures are confined to Turritellidae.

26. Pallial sensory structures: 0 – absent; 1 – present.

All potamidids (Houbrick, 1984, 1991a) possess pallial sensory structures at the mantle edge in the inhalant siphon. Well-developed pallial eyes, complete with lens and cornea, are found in *Tympanotonus* and *Cerithidea*, although some members of *Cerithidea* possess only a simple pit. *Telescopium* possesses a pit-like light sensitive organ with a lens, but it is less well organized. A light sensitive pigment cup is found in the same position in *Terebralia* (Johansson, 1956; Houbrick, 1984, 1991a). Siphonal sensory structures are also present in the cerithiids *Gourmya* and *Rhinoclavis* (not included here), but are not considered homologous to those of potamidids (see Houbrick, 1984). Alternative codings of this character, for example coding only the presence of complex eyes in *Tympanotonus* and *Cerithidea*, does not change the outcome of the analysis.

Mantle cavity

27. Food groove on pallial floor: 0 – absent; 1 – present.

This structure is found only in filter-feeding taxa and has been independently derived in several caenogastropod clades (Ponder *et al*., 2008).

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28. Endostyle: 0 – absent; 1 – present.

This glandular structure is developed along the base of the ctenidium. Like the food groove, it has been independently derived in several filter-feeding caenogastropod clades (Ponder *et al*., 2008).

29. Hypobranchial gland: 0 – well developed, with thick pendulous folds; 1 – thin, simple.
30. Osphradium shape: 0 – narrow (thin, ridge-like); 1 – broadly oval; 2 – elongately oval.
31. Osphradium surface: 0 – simple, smooth; 1 – monopectinate; 2 – bipectinate.

Taylor & Miller's (1989) preliminary work on the surface morphology of the osphradium showed considerable differentiation in the structure of osphradial leaflets in various groups of higher caenogastropods. It is likely that the codings here represent an oversimplification of these structures and warrant more detailed study.

32. Osphradium position: 0 – on surface; 1 – in shallow depression; 2 – elevated on stalk.
33. Osphradium length relative to ctenidium: 0 – equal to ctenidium; 1 – slightly less than ctenidium; 2 – roughly half of ctenidium; 3 – very short; 4 – extending far anterior to ctenidium.
34. Ctenidial filament shape: 0 – triangular; 1 – elongate (base shorter than height); 2 – broad (base longer than height).
35. Length of efferent ctenidial vein between the gill and the pericardium: 0 – short; 1 – long.

Taxa that possess a gill extending to the pericardium are coded as 'short'; taxa possessing a gill that does not extend to the base of the mantle cavity are coded as 'long'.

Radula

36. Radular sac: 0 – moderately long; 1 – very long, posteriorly coiled; 2 – short.

The radular sac may extend just beyond the buccal mass, or perhaps curve slightly behind it under the oesophagus (i.e. 'short' radular sac). Some taxa (e.g. pachychilids) possess a radular sac that is very long and highly coiled within the cephalic haemocoel (i.e. 'long' radular sac). All taxa possessing a radular sac of intermediate length, roughly the length of the buccal mass, are coded as possessing a 'moderately long radular sac'.

37. Overall shape of central tooth basal plate: 0 – higher than wide; 1 – squarish; 2 – wider than high.

Proportions are calculated including the basal extension (characters 44, 45).

38. Lateral sides of central tooth: 0 – straight and vertical; 1 – concave; 2 – convex; 3 – straight and at a positive angle; 4 – straight and at a negative angle.
39. Central tooth basal denticles: 0 – absent; 1 – present.
40. Central tooth basal denticles number: 0 – one; 1 – two.
41. Central tooth with basal plate extending beyond cutting edge; 0 – absent; 1 – present.

Cusps of the central tooth may emerge from the leading edge of the tooth ('absent'), or the basal plate may extend (anteriorly and/or laterally) beyond the base of the cusps ('present').

42. Face of central tooth with basal, lateral extensions at ~45°: 0 – absent; 1 – present.
43. Central tooth glabella: 0 – absent; 1 – present.
44. Central tooth basal extension: 0 – absent; 1 – present.
45. Central tooth basal extension shape: 0 – rounded; 1 – v-shaped; 2 – w-shaped.
46. Lateral tooth lateral extension: 0 – short (approximately equal to cutting edge in length); 1 –long (approximately twice as long as cutting edge); 2 – very long (more than twice as long as cutting edge).
47. Inner basal extension of lateral tooth: 0 – absent; 1 – vertical; 2 – oblique thickened area.
48. Shape of marginal teeth: 0 – straight to gently curving, scythe-like; 1 – distinctly bowed.
49. Distal tips of marginal teeth: 0 – simple, straight; 1 – hooked.
50. Shape of distal tip of inner marginal tooth: 0 – tapering; 1 – flaring.
51. Shape of distal tip of outer marginal tooth: 0 – tapering; 1 – flaring.
52. Cusps of inner marginal tooth: 0 – cusps confined to distal tip; 1 – cusps extending from tip along both edges; 2 – cusps along inner edge only; 3 – cusps on outer edge only.
53. Cusps of outer marginal tooth: 0 – cusps confined to distal tip; 1 – cusps extending from tip along both edges; 2 – cusps along inner edge only; 3 – cusps on outer edge only.
54. Outer marginal tooth flange: 0 – without outer flange; 1 – flange at outer base; 2 – flange along most of outer edge with sharp, distal corner; 3 – narrow flange along both edges; 4 – distal flange only along both edges.

Alimentary system: foregut

55. Jaws: 0 – paired, small, bilayered, anterior to dorsal folds; 1 – paired, peg-like; 2 – paired, thick, heavy, complexly layered; 3 – paired, small, partially bilayered, at anterior end of dorsal folds.

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Most sorbeoconchans (all caenogastropods excluding architaenioglossans) possess a small paired jaw situated at the anterior end of the dorsal folds within the buccal cavity; the jaws are chitinous and composed of rod-like elements with a laterally overlapping homogeneous layer; in contrast, architaenioglossans possess a wholly bilayered jaw that occurs far forward of the initiation of the dorsal folds; littorinids possess a cuticular lining of the buccal cavity, but it is not elaborated into discrete jaw plates (Strong, 2003). Campanilidae possess a thick, multi-layered jaw that is unique amongst caenogastropods; plesiotrochid jaws are highly modified into peg-like blades probably for macroherbivory.

56. Salivary gland position: 0 – passing through circum-oesophageal nerve ring; 1 – anterior to nerve ring (too short to pass through nerve ring); 2 – long, bypassing nerve ring.
57. Salivary gland morphology: 0 – simple tube; 1 – lobate/branched tube (with common lumen); 2 – complex, massive (without common lumen).
58. Buccal pouches: 0 – absent; 1 – present.

Glandular elaborations of the posterior buccal cavity and anterior oesophagus occur rarely amongst cerithioideans and are present only in *Finella*, *Scaliola*, and *Lavigeria* amongst the taxa included in this analysis. Whereas this feature probably represents an anterior extension of the oesophageal gland in *Finella* and *Scaliola*, the pouches are clearly restricted to the buccal cavity in *Lavigeria* and an oesophageal gland is lacking; thus, they are unlikely to be homologous in the two groups.

59. Oesophageal gland: 0 – absent; 1 – present; 2 – papillate.

In non-neogastropod caenogastropods, the oesophageal gland typically comprises transverse, glandular septae that are modifications of the morphologically ventral aspect of the mid-oesophagus. Amongst cerithioideans, although details of the mid-oesophageal glands are not usually included in morphological descriptions, at least two types of gland are present: bilaterally symmetrical, transverse septae (e.g. some batillariids; Strong, 2003) or papillae (e.g. some pachychilids; Simone, 2001).

Alimentary system: midgut

For comprehensive descriptions and discussion of midgut characters, see Strong (in press).

60. Shape of marginal fold: 0 – s-shaped; 1 – straight.
61. Position of oesophageal aperture with respect to recurved segment of marginal fold: 0 – at or near tip of recurved segment of marginal fold; 1 – at apex of marginal fold.
62. Sorting area shape: 0 – rectangular, rounded posteriorly; 1 – elongately triangular, rounded posteriorly; 2 – elongately triangular, pointed posteriorly; 3 – rectangular, tapering, with pointed, slightly curving posterior tip; 4 – pointed, crescent shaped.
63. Sorting area left margin: 0 – even and/or straight; 1 – with conspicuous bulge.
64. Sorting area and marginal fold: 0 – fold terminates at tip of sorting area; 1 – fold extends past sorting area tip.
65. Sorting area pad: 0 – absent; 1 – present.
66. Anterior sorting area flap: 0 – absent; 1 – present.
67. Crescentic pads: 0 – absent; 1 – present.
68. Accessory marginal fold: 0 – absent; 1 – present.
69. Accessory marginal fold: 0 – straight segment along left side of sorting area only, with curving and often flaring or bifurcate posterior tip; 1 – segment along left side of sorting area only, forming deep pocket overhanging posterior tip of sorting area; 2 – curving from oesophagus around posterior end of sorting area, narrowly bifurcate posteriorly; 3 – curving from oesophagus around posterior end of sorting area, often narrowly bifurcate, intersecting broadly curving fold at left, posterior tip of sorting area; 4 – curving from oesophagus around posterior end of sorting area, often narrowly bifurcate, intersecting short, slightly curving fold at left, posterior tip of sorting area.
70. Glandular pad: 0 – low, indistinct, ciliated strip; 1 – small collar, barely projecting past posterior end of gastric shield; 2 – small rounded mound, projecting short distance posteriorly behind gastric shield; 3 – broadly rounded, flaring posteriorly, with narrow stalk; 4 – large, elongate, with narrow stalk; 5 – large, long, and narrow mound; 6 – rectangular with rounded posterior tip and lateral flap.
71. Accessory pads: 0 – absent; 1 – present.
72. Accessory pads: 0 – small and smooth; 1 – large and textured.
73. Digestive gland duct number: 0 – one; 1 – two; 2 – three; 3 – four or more.
74. Digestive gland duct position: 0 – open to left side of glandular pad; 1 – open to crystalline style pocket; 2 – open to both.
75. Crescentic ridge: 0 – absent; 1 – present.
76. Crescentic ridge form: 0 – single; 1 – double.
77. Crescentic ridge morphology: 0 – short diverticulum; 1 – long, curved, closely adhering to glandular pad; 2 – long, not closely adhering to glandular pad.
78. Crescentic ridge proximal end: 0 – begins at digestive gland duct; 1 – begins anterior to digestive

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gland duct; 2 – begins posterior to digestive gland duct.
79. Crescentic ridge distal end: 0 – attaches to right side of glandular pad behind gastric shield, and may curve slightly into caecum; 1 – attaches to right side of glandular pad and coils deeply into caecum; 2 – attaches to posterior end of glandular pad.
80. Caecum: 0 – absent; 1 – present.
81. Caecal folds: 0 – absent; 1 – present.
82. Caecal fold number: 0 – one; 1 – two; 2 – three.
83. Intestinal groove flap: 0 – absent; 1 – present.
84. U-shaped fold: 0 – absent; 1 – present.
85. Fusion of style sac typhlosoles: 0 – unfused; 1 – partially fused (two thirds/to three quarters); 2 – completely fused.
86. Style sac: 0 – short (limited to viscera); 1 – long (extending into pallial roof).
87. Crystalline style: 0 – absent; 1 – present.

Nervous system

88. Cerebral ganglia: 0 – short commissure; 1 – long commissure.

Taxa possessing a short commissure are those with the cerebral ganglia in direct contact, or separated by a slight constriction that is less than half as long as an individual cerebral ganglion; all other taxa with cerebral ganglia separated by a distance greater than one half of the length of a cerebral ganglion are coded as possessing a long commissure.

89. Type of nervous system: 0 – hypoathroid; 1 – dystenoid; 2 – epiathroid.
90. Zygoneury: 0 – absent; 1 – zygosis between right pleural and sub-oesophageal ganglia.
91. Sub-oesophageal ganglion: 0 – close to left pleural ganglion; 1 – widely separate from left pleural ganglion.
92. Supra-oesophageal ganglion: 0 – close to right pleural ganglion; 1 – widely separate from right pleural.
93. Accessory ganglion: 0 – absent; 1 – present.
94. Statocysts: 0 – numerous statoconia; 1 – single statolith.

Reproductive system

95. Ciliated egg groove on right side of female foot: 0 – absent; 1 – present.
96. Egg groove: 0 – shallow; 1 – deep.
97. Ovipositor: 0 – absent; 1 – present.

This character corresponds to the deep pore or warty, glandular elaborations on the side of the foot present in many cerithioideans. Although *Littorina littorea* possesses a simple, ciliated tract on the side of the foot that plays an analogous function in oviposition (Fretter & Graham, 1994), given the lack of elaboration of the structure, *Littorina* is coded as 'absent'.

98. Ovipositor: 0 – external pad; 1 – internal pore.

Available evidence supports numerous independent origins of brooding (e.g. Glaubrecht, 2006; Strong & Glaubrecht, 2007) and it is not always clear if brooding in homologous structures is even functionally homologous. Consequently, each type of brood pouch is coded with a separate character. A separate character (character 102) is included specifying the location of embryos in the subhaemocoelic brood pouch, distinguishing between the brood pouches of planaxids and thiarids. These have been considered to be homologous (Houbrick, 1988; Glaubrecht, 1996).

99. Brood pouch in pallial oviduct: 0 – absent; 1 – present.
100. Embryos brooded in mantle cavity: 0 – absent; 1 – present.
101. Subhaemocoelic brood pouch: 0 – absent; 1 – present.
102. Location of subhaemocoelic pouch: 0 – neck only to about posterior end of mantle cavity; 1 – neck and right head foot; 2 – foot.
103. Brood pore in female: 0 – in neck on right side; 1 – anterior in right foot.
104. Pallial oviduct: 0 – almost or completely open; 1 – open anterior third; 2 – medially fused; 3 – closed.
105. Location of pallial oviduct: 0 – pallial only; 1 – extending into visceral mass.
106. Pallial oviduct morphology: 0 – glandular; 1 – nonglandular tube.
107. Sperm gutters in pallial oviduct medial lamina: 0 – none; 1 – one; 2 – two.
108. Sperm gutter in pallial oviduct lateral lamina: 0 – none; 1 – one.

Houbrick indicated a sperm gutter is present in the lateral lamina of *Faunus* (Houbrick, 1991b) and some potamidids (Houbrick, 1991a). However, the features described within the lateral laminae of *Tympanotonus* and *Cerithidea* are glandular ridges that probably interact with the free edge of the medial lamina to produce a functionally closed tube. The feature described within the lateral lamina of *Faunus* is a short, bifurcate fold that is not associated with any sperm storage pockets or sacs; its function is unclear (E. E. Strong, pers. observ.).

109. Spermatophore bursa in medial lamina: 0 – absent; 1 – present.
110. Spermatophore bursa in lateral lamina: 0 – absent; 1 – present.
111. Thiarid bursa: 0 – absent; 1 – present.

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The thiarid bursa is large, comprising much of the pallial portion of the oviduct; the derivation of this structure is unclear.

112. Anterior bursa: 0 – absent; 1 – present.
113. Seminal receptacle in medial lamina: 0 – absent; 1 – present; 2 – ventral channel.

Several taxa possess a seminal receptacle that opens to the ventral channel (*Finella*, *Scaliola*, *Paludomus*, *Lavigeria*). Based on their slightly asymmetrical position, these are hypothesized to represent modifications of the medial lamina seminal receptacle – an interpretation supported by the resulting topology.

114. Seminal receptacle in lateral lamina: 0 – absent; 1 – present.
115. Seminal receptacle derivation: 0 – from renal oviduct; 1 – from pallial oviduct.
116. Seminal receptacle (derived from pallial oviduct) extension: 0 – pallial (more or less contained within laminae); 1 – extending into viscera (posterior to pallial cavity).

The seminal receptacle in *Finella*, *Scaliola*, and *Campanile* is derived from the lateral lamina and extends well posterior to the glandular portion of the oviduct, lying embedded within the viscera.

117. Cephalic penis: 0 – absent; 1 – present.
118. Male pallial gonoduct (prostate): 0 – open; 1 – closed.
119. Spermatophore forming organ in prostate: 0 – absent; 1 – present, anterior; 2 – present, in posterior medial lamina.

Paludomids possess an anterior spermatophore forming organ that is a hollow glandular tube extending dorsally from the gonoductal groove. Neotropical pachychilids possess an analogous structure posteriorly within the medial lamina; Simone (2001) misidentified this feature as a spermatophore bursa.

120. Spermatophores: 0 – absent; 1 – present.
121. Proximal (visceral) vas deferens forming seminal vesicle: 0 – absent; 1 – present.
122. Position of gonad: 0 – mainly dorsal to digestive gland; 1 – interspersed amongst digestive gland.

In all cerithioideans examined thus far the gonad dorsally overlies the digestive gland, sometimes completely occupying the apical whorls; this condition is present in most other caenogastropods as well. However, in campaniloideans, the gonad is dispersed amongst the tubules of the digestive gland.

Renal system

123. Kidney bladder: 0 – absent; 1 – present, chamber undivided; 2 – present, chamber divided.

In most marine cerithioideans, the kidney forms a simple, undivided chamber extending into the mantle roof. Many freshwater taxa have modified the kidney and separated the dorsal concentration of excretory tissue from a more ventral 'bladder' via a septum, perforated by a small aperture allowing communication between the two. The bladder contains variable amounts of excretory tissue as well and communicates with the mantle cavity via the nephropore. The bladder may be simple or subdivided by an incomplete septum.

124. Kidney opening: 0 – simple; 1 – covered with flap from gonoduct.

Gametes

Euspermatozoal characters

125. Acrosomal vesicle shape: 0 – conical throughout length; 1 – conical basally, flattened anteriorly; 2 – flattened throughout length.
126. Acrosomal vesicle apical bleb: 0 – absent; 1 – present.
127. Acrosomal vesicle basal invagination: 0 – approximately half of vesicle length or less; 1 – two thirds of vesicle length or more.
128. Accessory membrane associated with acrosomal vesicle: 0 – absent; 1 – present.
129. Nuclear shape: 0 – straight; 1 – helically twisted.
130. Nuclear basal invagination length (centriolar fossa): 0 – short; 1 – long but well short of apex; 2 – long, almost to nuclear apex.
131. Nuclear length: 0 – short (< 6 μm); 1 – intermediate (9–12 μm); 2 – long (> 15 μm).
132. Mitochondria of midpiece: 0 – straight; 1 – helical.
133. Mitochondrial cristae: 0 – unmodified, irregular; 1 – highly modified and organized as parallel plates.
134. Mitochondrial size: 0 – equal size; 1 – two large + two small, block-shaped in transverse section profile; 2 – two large + two small, arrow-head shaped in transverse section profile.
135. Mitochondrial number: 0 – four; 1 – > four (usually six to ten).
136. Mitochondrial neck: 0 – simple; 1 – with thin flanges; 2 – associated with dense body.
137. Mitochondria associated with segmented dense sheath: 0 – sheath absent; 1 – sheath present.

Paraspermatozoal characters

138. Number of parasperm types present: 0 – one; 1 – two.
139. Acrosome-like structure: 0 – present; 1 – absent.

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140. Basal invagination of acrosome-like structure: 0 – filled by membrane-bound vesicle of dense material; 1 – filled by apical tip of nucleus; 2 – empty.
141. Axonemal number and disposition: 0 – two to three, emergent as posterior tail tuft; 1 – five to 40, emergent as posterior tail tuft; 2 – 80–90, emergent along posterior half of parasperm body; 3 – 3–120, completely contained within parasperm body; 4 – axonemes absent.
142. Nucleus: 0 – present; 1 – absent (completely obliterated during paraspermiogenesis).
143. Nuclear shape and content: 0 – condensed, elongate, central rod; 1 – condensed apical fragment; 2 – hollow apical cap or membranes, devoid or virtually devoid of DNA.
144. Axoneme attachment: 0 – attached to nucleus only; 1 – attached to nucleus and dense vesicles; 2 – attached to dense material at cell apex; 3 – attached to dense vesicles only.
145. Axoneme penetration (maximum) of head region: 0 – base only; 1 – deep; 2 – virtually full length of head.
146. Dense vesicles: 0 – small; 1 – large.
147. Dense vesicles: 0 – homogeneous; 1 – heterogeneous, showing spherical zonation internally; 2 – heterogeneous, showing internal cavities.

Reproduction and development

148. Reproductive mode: 0 – gonochorism; 1 – simultaneous hermaphroditism; 2 – protandrous hermaphroditism; 3 – parthenogenesis.

All thiarids for which males have been documented, are coded as both gonochoristic and parthenogenetic. *Tarebia* is the only thiarid for which no males have been documented and thus may reproduce exclusively parthenogenetically.

149. Type of spawn: 0 – capsules surrounded in jelly; 1 – capsules not surrounded in jelly.
150. Embryonic development: 0 – free-swimming veliger larva; 1 – extra-apsular (but within parental body); 2 – intracapsular.
151. Chromosome number (haploid): 0 – $n = 7$–13; 1 – $n = 14$; 2 – $n = 16$; 3 – $n = 17$; 4 – $n = 18$; 5 – $n = 19$; 6 – $n > 20$.

There are some discrepancies in chromosome number reported for ostensibly the same species [e.g. *Cerithium vulgatum* Bruguière, 1792, $n = 16$ (see Nishikawa, 1962) vs. $n = 18$ (see Thiriot-Quiévreux, 2003); *Elimia livescens* $n = 20$ (see Patterson, 1969) vs. $n = 18$ (see Thiriot-Quiévreux, 2003)]; in these cases, we have taken the most recently published estimate.

In Thiaridae *s.s.*, chromosome numbers are highly variable because of the presence of numerous parthenogenetically reproducing diploid and polyploid clonal lineages within species. For example, haploid chromosome numbers for *Melanoides tuberculata* (Müller, 1774) have been reported as $n = 11$ or $n = 16$ for diploid lineages, and $n = 45$–47 for one polyploid lineage (see Patterson, 1969; Yaseen, 1996). In this case, we used the chromosome number ($n = 16$) for the diploid lineage that was sampled from India, geographically close to the type locality (Coromandel coast).

RESULTS

Morphological analysis

Parsimony analysis of 151 morphological characters produced 122 equally parsimonious trees, length (L) = 766, consistency index (CI) = 0.31, retention index (RI) = 0.65; six nodes collapsed in the strict consensus (Fig. 4). Monophyly of the Cerithioidea as currently formulated (excluding Campaniloidea and Vermetoidea) is supported. This restricted concept of the ingroup is supported by 16 synapomorphies under ACCTRAN optimization; seven unambiguous synapomorphies at this node include features of the anterior alimentary system [salivary glands forming simple tubes – 57(0)], midgut [small, rounded glandular pad – 70(2)], nervous system [zygoneury present – 90(1); supra-oesophageal and right pleural ganglia in close proximity – 92(0)], reproductive system [single sperm gutter in medial lamina – 107(1); spermatophore bursa in medial lamina present – 109(1)] and sperm ultrastructure [four mitochondria in eusperm midpiece – 135(0)]. Most family-level taxa represented by more than a single terminal are monophyletic, with the exception of a polyphyletic Cerithiidae and unresolved relationships amongst Pleuroceridae and Semisulcospiridae. Scaliolidae is the most basal cerithioidean offshoot, followed by Turritellidae and Siliquariidae as sister taxa. A polyphyletic Cerithiidae, monophyletic Planaxidae, *Diala* (Dialidae), *Alaba* (Litiopidae), *Diastoma* (Diastomatidae), and monophyletic Pachychilidae and Batillariidae collectively form a paraphyletic grade (Fig. 4, Group 1) basal to a large clade (Fig. 4, Groups 2, 3) uniting all remaining cerithioideans. *Modulus* (Modulidae) is the first offshoot at the base of this clade, with the brackish water potamidids as the sister group to a large freshwater clade including Paludomidae, Thiaridae, and the unresolved Pleuroceridae plus Semisulcospiridae, within which is nested a monophyletic Melanopsidae. Jackknife values are generally robust for family level groupings, but drop below 50 for most basal nodes.

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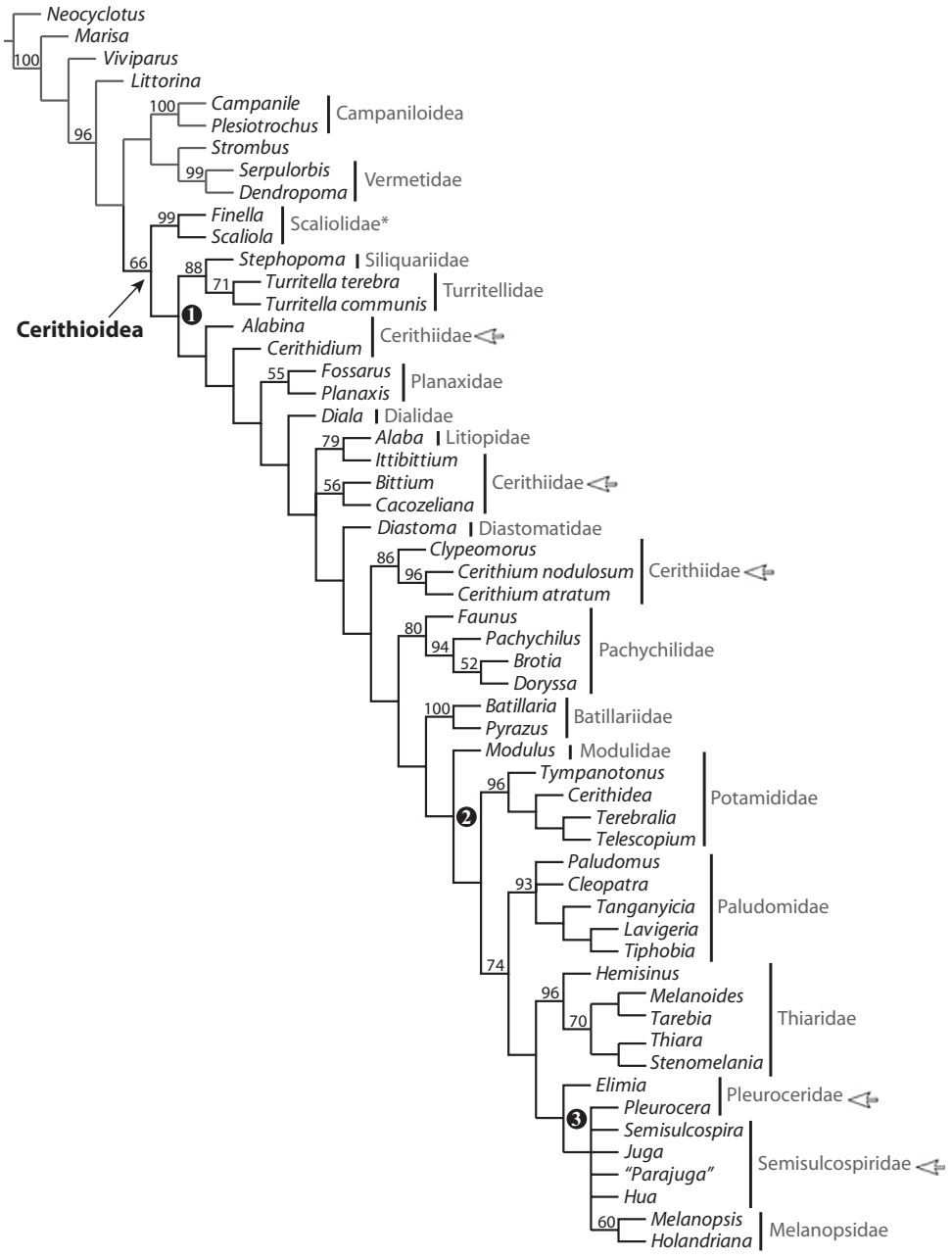

Figure 4. Analysis of morphological data set. Strict consensus of 122 equally parsimonious trees, length = 766, consistency index = 0.31, retention index = 0.65, resulting from parsimony analysis of 151 characters for 56 taxa (47 ingroup, nine outgroup taxa). All characters unordered and equally weighted. Jackknife values (1000 replicates) greater than 50 are indicated at the node. Three main assemblages are numbered; see text for details. *, Scaliolidae occurs in assemblage 2 in all other topologies. Open arrows indicate families resolved as nonmonophyletic.

Molecular analyses

Parsimony and Bayesian analyses of the extended 16S and 28S data sets combined produced similar topologies (Fig. 5). Heuristic searches of the combined molecular data set resulted in two equally parsimonious trees (L = 10 002, CI = 0.31, RI = 0.44); one node collapsed in the strict consensus (Fig. 5A). Both the parsimony and Bayesian analyses (Fig. 5B) recovered a monophyletic Cerithioidea, as well as monophyletic Cerithiidae, Pleuroceridae, Potamididae, Semisulcospiridae, Thiaridae, and Turritellidae; Scaliolidae, Melanopsidae and Paludomidae are para- or polyphyletic. Batillariidae and Pachychilidae are monophyletic in the parsimony but not the Bayesian

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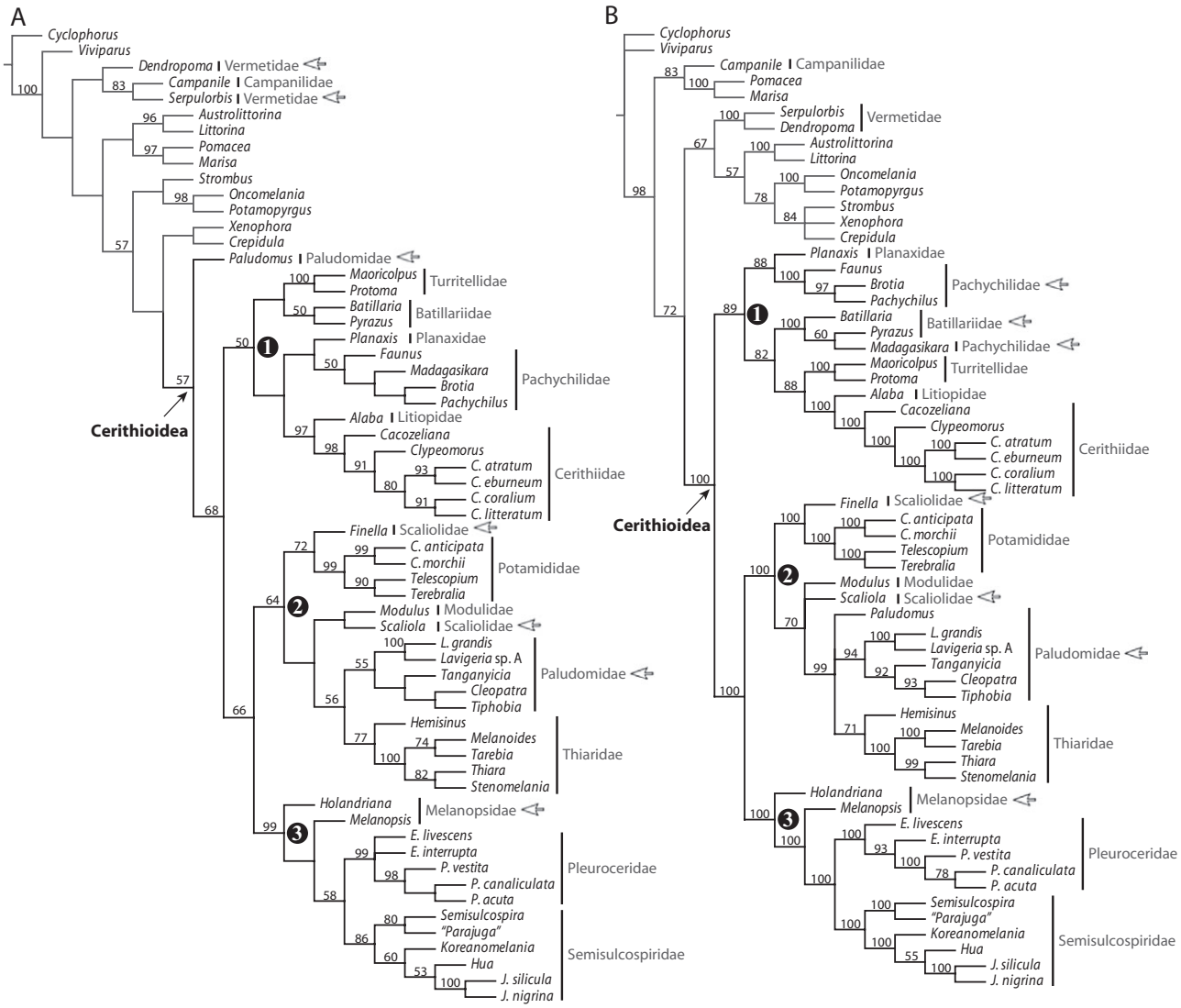

Figure 5. Analysis of extended molecular data set (16S, 28S). A, parsimony analysis; strict consensus of two equally parsimonious trees, length = 10 002, consistency index = 0.31, retention index = 0.44. Jackknife values (1000 replicates) greater than 50 are indicated at the node. B, Bayesian analysis; posterior probabilities are indicated at the node. Three main assemblages are numbered; see text for details. Open arrows indicate families resolved as nonmonophyletic.

analysis. Both analyses support three main monophyletic clades of cerithioideans with identical composition: Group 1 with the marine and brackish Batillariidae, Cerithiidae, Litiopidae, and Turritellidae and with the Planaxidae as the sister group to the freshwater Pachychilidae; Group 2 with *Finella* (Scaliolidae) as sister taxon to a monophyletic Potamididae, and *Scaliola* (Scaliolidae) and *Modulus* at the base of a clade uniting the Paludomidae and Thiaridae; Group 3 an exclusively freshwater clade with a paraphyletic Melanopsidae at the base and with monophyletic Pleuroceridae and Semisulcospiridae as sister taxa (see Fig. 9).

The branching order within these groups is also similar between the parsimony and Bayesian topologies, with several noteworthy exceptions: in Group 1, the branching order amongst the basal taxa (Planaxidae, Pachychilidae, Turritellidae, and Batillariidae) differs between the two analyses; *Madagasikara spinosa* (Lamarck, 1822) (Pachychilidae) is supported within the Batillariidae in the Bayesian analysis, but as the second offshoot of the Pachychilidae in the parsimony analysis; *Paludomus* falls to the base of the Cerithioidea in the parsimony tree but is supported in an unresolved polytomy with the remaining Paludomidae and Thiaridae in the Bayesian analysis.

Separate analyses of the extended 16S and 28S data sets also return three main assemblages of cerithioideans with essentially the same composition as

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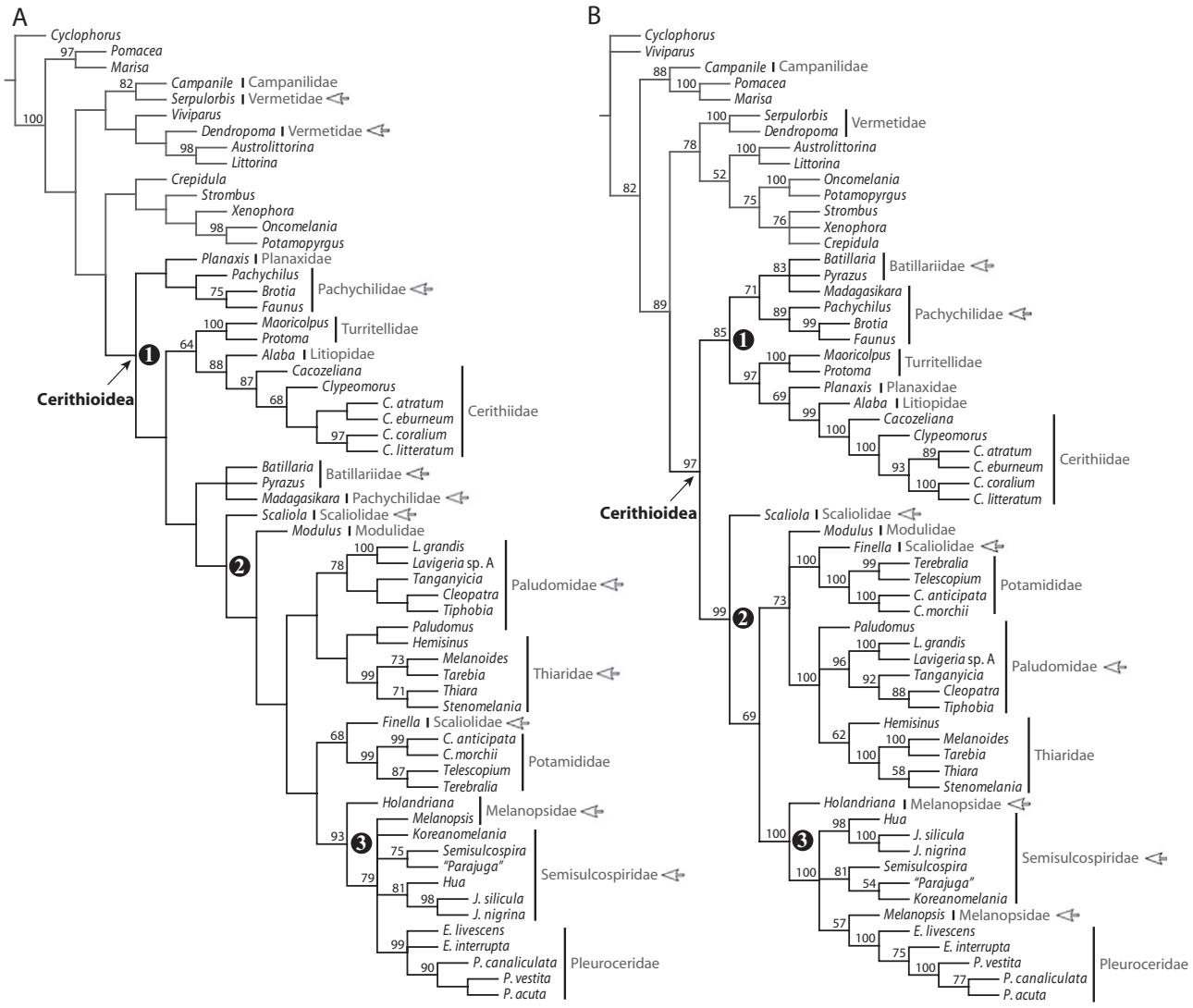

Figure 6. Analysis of extended molecular data set (16S, 28S) with unconserved regions removed. A, parsimony analysis; strict consensus of 14 equally parsimonious trees, length = 4870, consistency index = 0.34, retention index = 0.46. Jackknife values (1000 replicates) greater than 50 are indicated at the node. B, Bayesian analysis; posterior probabilities are indicated at the node. Three main assemblages are numbered; see text for details. Open arrows indicate families resolved as nonmonophyletic.

in the combined analyses, but terminal mismatch makes the branching order somewhat difficult to compare. Results of the 16S analyses are most similar to those of the combined analyses, with comparable branching order amongst and within the three main groups. However, cerithioidean monophyly is supported only in the 16S Bayesian analysis. In the 16S parsimony analysis (*Campanile* + *Serpulorbis*) is nested within a monophyletic Group 1, and *Paludomus* falls to the base of Group 2, which forms a paraphyletic grade. For the 28S data set, *Paludomus* falls out of the ingroup in both analyses, Group 2 is monophyletic and the most basal offshoot in the parsimony analysis but Group 1 is a paraphyletic grade at the base of the tree in the Bayesian analysis, and (*Crepidula* + *Xenophora*) is supported as the most basal offshoot of Group 2 (see Fig. 9, and Figs. S1, S2 in Supporting Information).

Parsimony analysis of the extended molecular data sets but with unconserved regions excluded resulted in 14 equally parsimonious trees (L = 4870, CI = 0.34, RI = 0.46); five nodes collapsed in the strict consensus (Fig. 6A). The result of the Bayesian analysis is shown in Figure 6B. Again, three main assemblages were recovered, but only Group 3 is supported as monophyletic in both analyses; Group 1 is monophyl-

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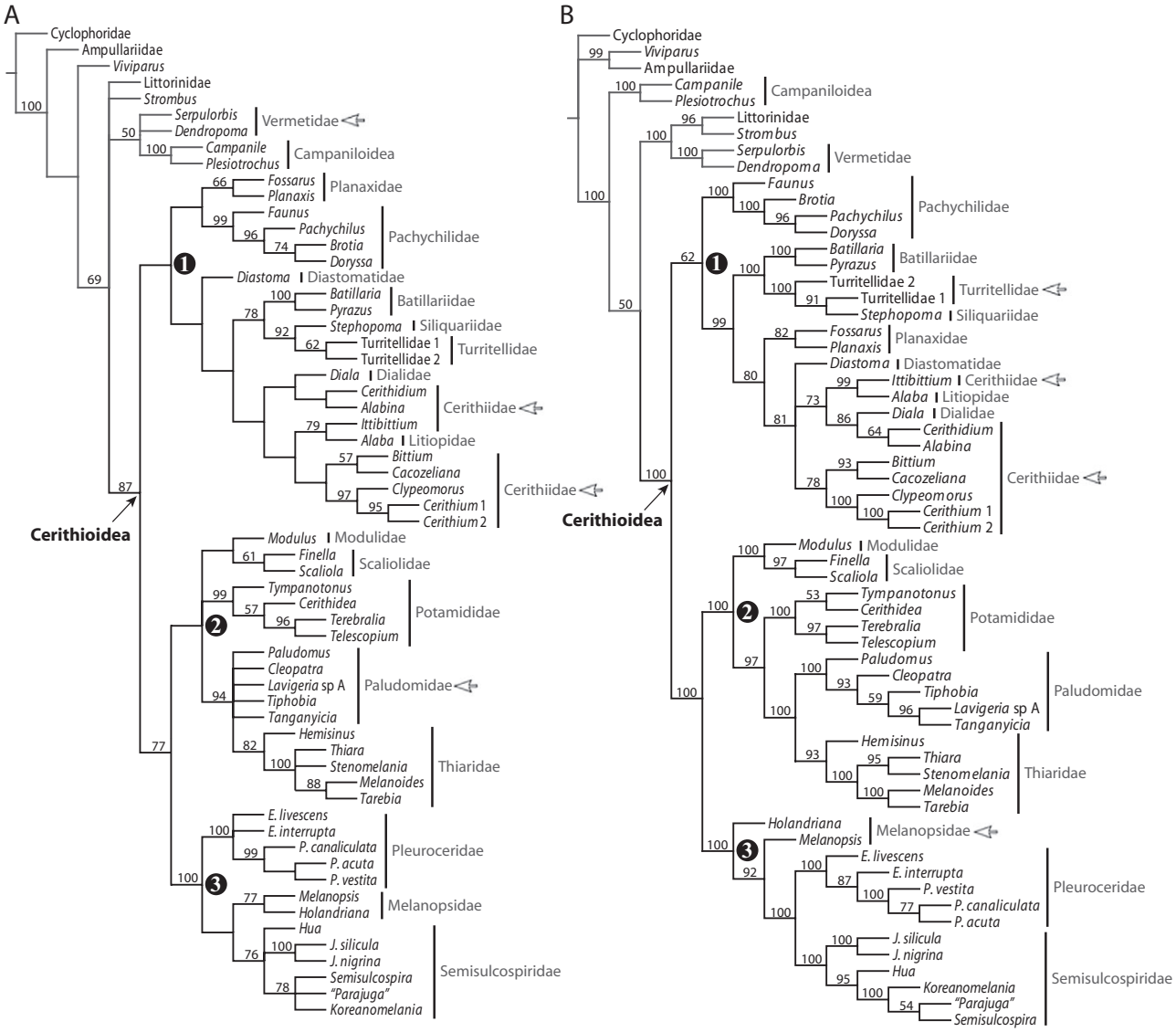

Figure 7. Simultaneous analysis of morphological and pruned molecular data sets (16S, 28S). A, parsimony analysis; strict consensus of ten equally parsimonious trees, length = 10067, consistency index = 0.32, retention index = 0.45. Jackknife values (1000 replicates) greater than 50 are indicated at the node. B, Bayesian analysis; posterior probabilities are indicated at the node. Three main assemblages are numbered; see text for details. Open arrows indicate families resolved as nonmonophyletic.

etic only in the Bayesian analysis and Group 2 is a paraphyletic grade in both the parsimony and Bayesian analyses. Several families recovered as monophyletic when unconserved regions were included are para- or polyphyletic with unconserved regions excluded, including Semisulcospiridae in both analyses, and Batillariidae, Pachychilidae, and Thiaridae in the parsimony analysis. Although removal of unconserved regions caused the retention index to improve somewhat, posterior probabilities declined slightly, fewer families were recovered as monophyletic, several more basal nodes collapsed, and the resulting topologies exhibit greater sensitivity to choice of optimality criterion.

SIMULTANEOUS ANALYSES

Parsimony analysis of the combined morphological and pruned molecular data sets resulted in ten equally parsimonious trees (L = 10067, CI = 0.32, RI = 0.45); 12 nodes collapsed in the strict consensus (Fig. 7A). The result of the Bayesian analysis is shown in Figure 7B. Monophyly of the Cerithioidea is supported in both analyses, as well as the tripartite

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division of the ingroup into three monophyletic clades: Group 1 with the freshwater Pachychilidae and the marine and brackish Batillariidae, a paraphyletic Cerithiidae, Dialidae, Diastomatidae, Litiopidae, Planaxidae, Siliquariidae, and Turritellidae; Pachychilidae is again supported as the sister group to the Planaxidae in the parsimony analysis, but forms the most basal offshoot in the Bayesian analysis; Group 2 with (*Modulus* + Scaliolidae), a monophyletic Potamididae, and (Thiaridae + Paludomidae); Paludomidae collapsed in an unresolved polytomy in the parsimony analysis because of instability of *Paludomus*; Group 3, a freshwater clade with monophyletic Pleuroceridae and Semisulcospiridae; in the Bayesian analysis, these two families are sister taxa with a paraphyletic Melanopsidae at the base, and in the parsimony analysis a monophyletic Melanopsidae is sister to the Semisulcospiridae (see Fig. 9). The Bayesian topology differs most significantly from the parsimony tree in the branching order of family-level taxa in Group 1, paraphyly of Turritellidae, enhanced resolution of Paludomidae and Semisulcospiridae, and paraphyly and placement of the melanopsids.

Parsimony analysis of the combined morphological + pruned molecular data sets with unconserved regions excluded resulted in four equally parsimonious trees ($L = 6255$, $CI = 0.33$, $RI = 0.47$); six nodes collapsed in the strict consensus (Fig. 8A). The result of the Bayesian analysis is shown in Figure 8B. The tripartite division of the ingroup is maintained, but only Groups 1 and 3 are monphyletic, with Group 2 forming a paraphyletic grade. Removal of unconserved regions again caused the retention index to improve and posterior probabilities to decline slightly, but the combination of morphology with the molecular data seems to buffer the results somewhat against the removal of the unconserved regions. Some resolution is lost (Group 3, Semisulcospiridae) compared to the analyses with unconserved regions included, but the effect is not as severe as in the analyses of the molecular data sets alone. In this case, removal of unconserved regions does not seem to increase sensitivity unduly to choice of optimality criterion.

DISCUSSION

Although there is still considerable disagreement between the morphological and molecular/combined analyses, a consensus on the phylogenetic relationships within the Cerithioidea is beginning to emerge (Fig. 9). All the present analyses produced topologies with three main assemblages of cerithioideans; the main disagreements being whether these represent monophyletic clades or paraphyletic grades and the branching order within them. Group 3 is consistently supported as monophyletic in all analyses, whereas monophyly of Groups 1 and 2 is most sensitive to the exclusion of unconserved regions and less so to choice of optimality criterion. Branching order of family-level taxa is most unstable in Group 1, with comparable topologies found within Groups 2 and 3 across all analyses. Group 1 includes numerous poorly known, minute marine taxa, many known only from morphology, which undoubtedly contributes to this instability. Group 2 includes Potamididae usually as a basal member, with Paludomidae and Thiaridae as sister taxa except in the morphology tree; *Modulus*, *Finella*, and *Scaliola* are the main sources of instability in this group, with the latter two again comprising poorly known, minute marine taxa. Group 3 includes Pleuroceridae and Semisulcospiridae, usually as sister taxa, with the poorly known melanopsid taxa comprising the main source of instability.

The framework of the morphology tree is predominantly pectinate and is a clear outlier amongst the results presented here. Group 3 is the only one of the three assemblages supported as monophyletic; Groups 1 and 2 are paraphyletic grades with the exception that Scaliolidae is the most basal cerithioidean offshoot, but is usually a basal member of Group 2 in other analyses. Other significant points of disagreement of the morphological analysis with the other analyses include: (1) Pleuroceridae and Semisulcospiridae are not supported as monophyletic by morphological data; (2) Pachychilidae and Batillariidae are supported in a distinctly more derived position; (3) Thiaridae and Paludomidae are not supported as sister taxa by morphological data, although this is obtained in all other analyses except the 28S analysis.

The topologies obtained here are generally consistent with those obtained by Lydeard *et al*. (2002) for a smaller subset of cerithioideans, but Groups 1 and 2 are paraphyletic in both reported topologies. As in the molecular/combined analyses, batillariids and pachychilids are supported in a more basal position, with Litiopidae, Cerithiidae, Batillariidae, Pachychilidae, Planaxidae, and Turritellidae emerging near the base. Thiaridae is basal to a clade containing all remaining cerithioideans, rather than derived within Group 2.

As a consequence of low support values and sensitivity of the topology to weighting, Lydeard *et al*. (2002) concluded that mtLSU rDNA sequences are of limited utility at deeper hierarchical levels. In contrast, more slowly evolving nuclear markers have demonstrated utility at deeper hierarchical levels with the nuclear 28S ribosomal RNA gene being used in a number of studies to infer relationships within gastropods or bivalves (e.g. McArthur & Koop, 1999; Colgan *et al*., 2000, 2003; Giribet & Distel, 2003; Klussmann-Kolb *et al*., 2008). When the 28S partition

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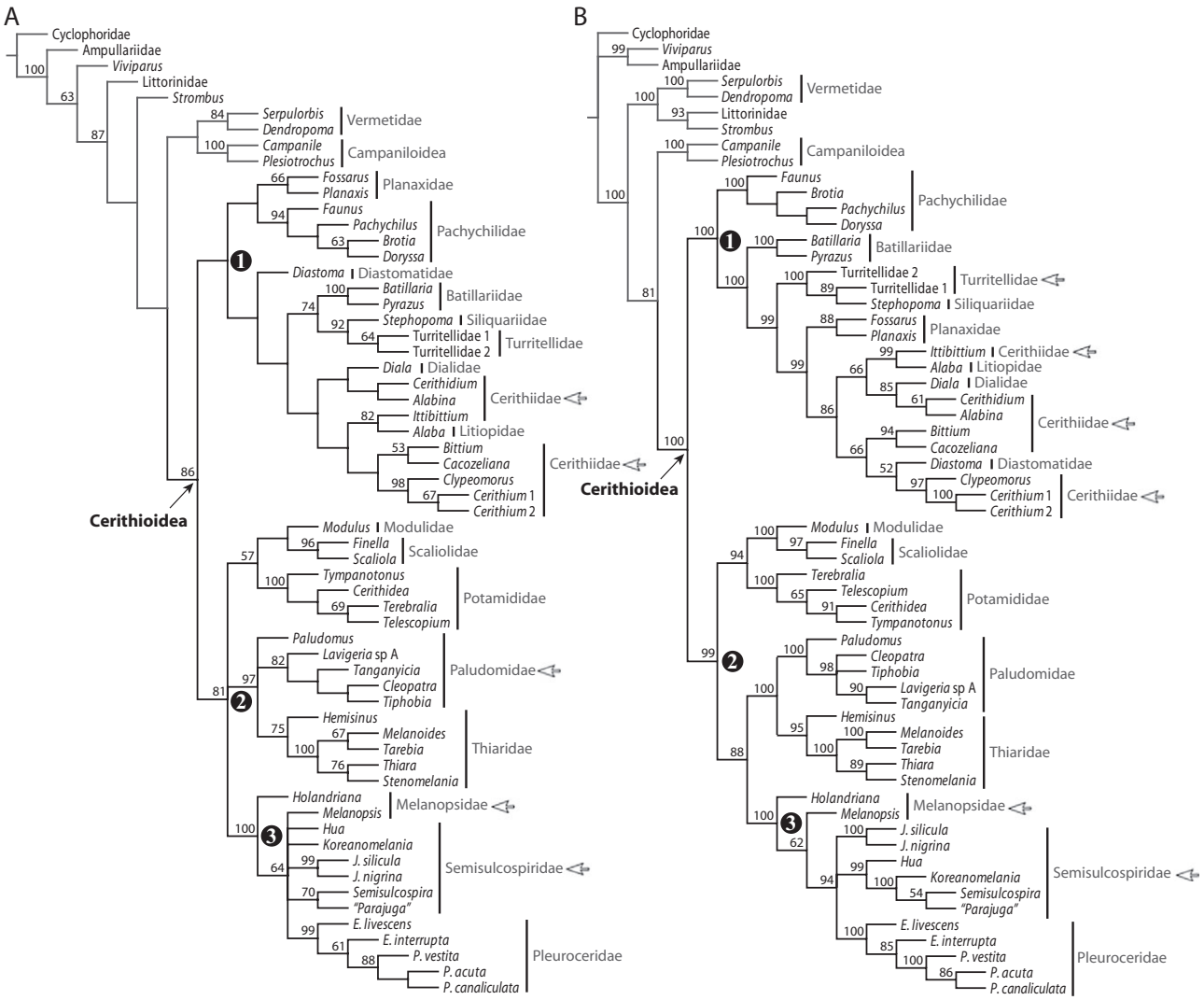

Figure 8. Simultaneous analysis of morphological and pruned molecular data sets (16S, 28S) with unconserved regions removed. A, parsimony analysis; strict consensus of four equally parsimonious trees, length = 6255, consistency index = 0.33, retention index = 0.47. Jackknife values (1000 replicates) greater than 50 are indicated at the node. B, Bayesian analysis; posterior probabilities are indicated at the node. Three main assemblages are numbered; see text for details. Open arrows indicate families resolved as nonmonophyletic.

is analysed alone, short internodal differences in deeper levels of the phylogram (relative to those obtained for the 16S partition) confirm that the gene provides more conservative variation for resolving deeper phylogenetic relationships. Yet it is clear from the results described above that both of the individual molecular data sets have limited capacity to resolve robustly cerithioidean relationships when analysed separately. Analysis of the molecular data sets together, and especially in combination with the morphological data, results in a greater proportion of monophyletic taxa (including Cerithioidea itself) and higher nodal support values and posterior probabilities at many nodes. Removal of unconserved regions of the alignments does not improve nodal support or posterior probabilities, does not enhance recovery of monophyletic family-level taxa, and in several instances has the reverse effect and decreases resolution; whereas all analyses show some sensitivity to choice of optimality criterion, removing these regions increases sensitivity, especially for the molecular data alone.

Although the molecular and simultaneous analyses are beginning to converge on a similar pattern, the same cannot be said of the morphological phylogenies. To the extent that comparisons are possible, no previous morphological analysis returned the three main groupings obtained here either as clades or grades,

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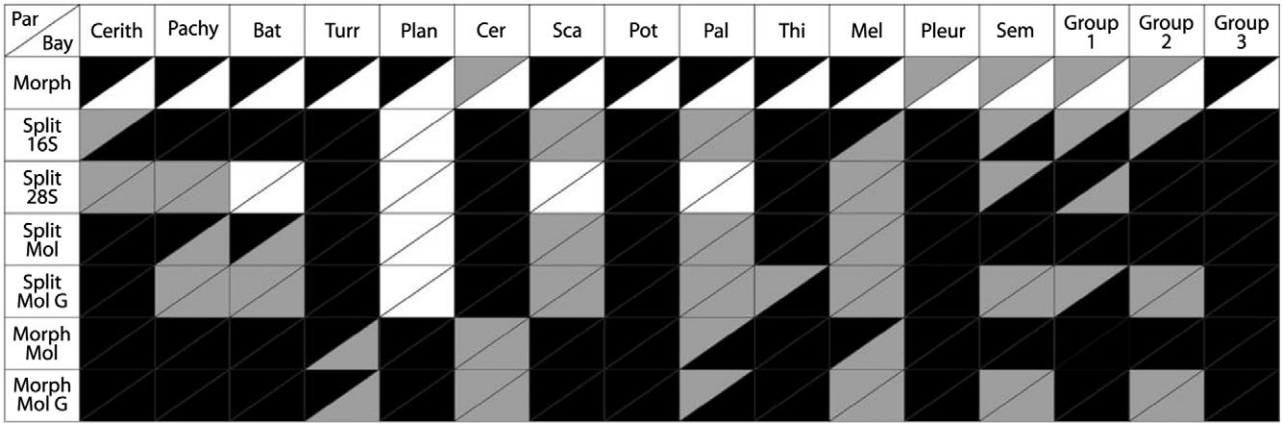

Figure 9. Comparative performance of parsimony (Par) and Bayesian (Bay) methods of inference in returning monophyletic clades of cerithioideans in analyses of the morphological partition (Morph), the extended 16S data set (Split 16S), the extended 28S data set (Split 28S), the extended 16S + 28S data sets combined (Split Mol) and with unconserved regions removed (Split Mol G), and the combined morphological and pruned molecular data sets (Morph Mol) and with unconserved regions removed (Morph Mol G). Black indicates monophyly, grey indicates nonmonophyly, white indicates not applicable. Abbreviations: Cerith, Cerithioidea; Pachy, Pachychilidae; Bat, Batillariidae; Turr, Turritellidae; Plan, Planaxidae; Cer, Cerithiidae; Sca, Scaliolidae; Pot, Potamididae; Pal, Paludomidae; Thi, Thiaridae; Mel, Melanopsidae; Pleur, Pleuroceridae; Sem, Semisulcospiridae; Group 1, Batillariidae, Cerithiidae, Dialidae, Diastomatidae, Litiopidae, Planaxidae, Siliquariidae, Turritellidae; Group 2, Modulidae, Paludomidae, Potamididae, Scaliolidae, Thiaridae; Group 3, Melanopsidae, Pleuroceridae, Semisulcospiridae. Note that taxon sampling is not identical, so that the composition of Groups 1, 2, and 3 may differ slightly.

with the exception of Houbrick (1988) and Ponder (1991) whose results supported Pleuroceridae and Melanopsidae as sister taxa (Group 3, in part). Planaxidae and Thiaridae are sister taxa in all previous morphological topologies but are only distantly related here (Groups 1 and 2, respectively), with Planaxidae supported as the sister taxon to Pachychilidae in all analyses excluding morphological data. The derived placement of Modulidae is very different from its basal position in the analyses of Ponder (1991) and Simone (2001); the basal placement of Litiopidae is comparable to the results of Houbrick (1988), but Simone's (2001) analysis recovered it in a clade with Cerithiidae and Scaliolidae. However, the present results confirm the rooting obtained in the analyses of Ponder (1991) and Simone (2001) with Turritellidae and Batillariidae near the base.

Evaluation of morphological characters

Houbrick (1988) noted the difficulty of identifying synapomorphic features that separate the Cerithioidea from other caenogastropods and emphasized that what sets them apart is their unique combination of characters, including a complex midgut, open pallial gonoducts, aphallate males, reproduction via spermatophores, glandular ovipositors, brooding (in many taxa), epiathroid/dialyneurous nervous systems with occasional zygoneury and unusual eusperm. A number of caenogastropods possess some of these attributes. For example, Campaniloidea, Vermetoidea, Littorinidae, Epitoniidae, and Cerithiopsoidea have open pallial gonoducts; Campaniloidea, Vermetoidea, Epitoniidae, Cerithiopsoidea, and Cingulopsoidea are aphallate (see e.g. Reid, 1989); Campaniloidea and Vermetoidea transfer sperm via spermatophores (see e.g. Hadfield & Hopper, 1980). As mentioned above, however, these are considered to represent plesiomorphies and cannot be considered as evidence of close phylogenetic affinity. However, no other caenogastropod superfamily is known to possess the unusual pallial female gonoduct and diversity or complexity of midgut morphologies evident within the Cerithioidea.

Houbrick's (1988) expanded concept of Cerithioidea was supported by ten synapomorphies, including features of the shell (anterior canal), ovipositor, oesophageal gland, reproductive anatomy (aphallate, open pallial gonoducts), and sperm ultrastructure; the first ingroup node, which excludes Campaniloidea (but includes Vermetidae), is supported by four synapomorphies, including features of the ovipositor, mantle edge papillae, salivary glands and parasperm. In Glaubrecht's (1996) analysis, monophyly of a restricted concept of Cerithioidea was supported by a single eusperm ultrastructure character (four, straight mitochondria in eusperm midpiece; characters 132 and 135 herein) (Healy, 1988a). Simone's

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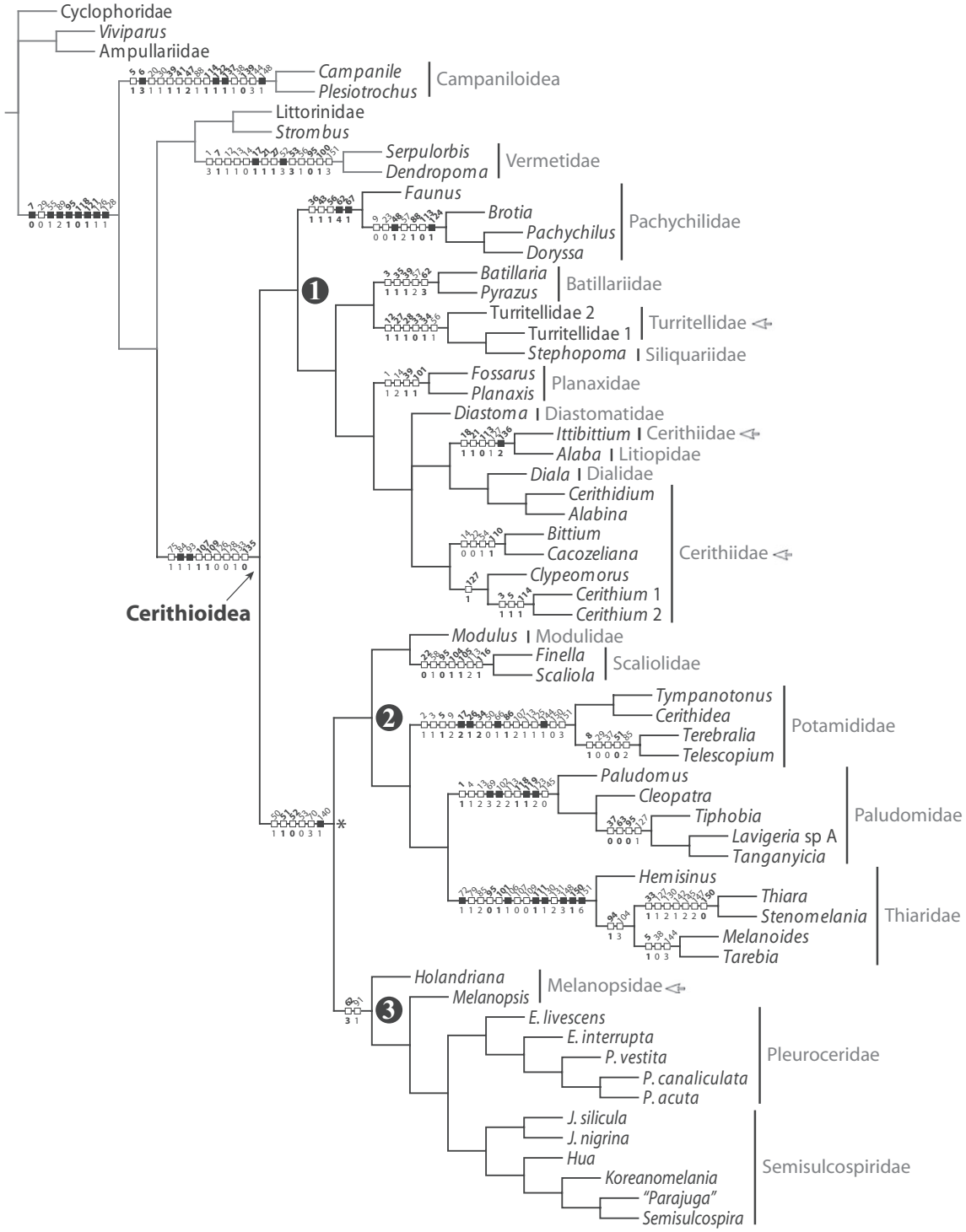

Figure 10. Morphological evolution of cerithioideans. Morphological characters mapped with accelerated transformation (ACCTRAN) optimization on Bayesian topology for the combined morphological and pruned molecular data sets. Only changes and nodes shared with the topology obtained for morphological data alone are highlighted; for simplicity, autapomorphies along terminal branches are not shown. Characters in bold represent unambiguous character changes. * indicates a node that appears in the morphological phylogeny, with the exception of Scaliolidae. Black hashmarks indicate forward changes; white hashmarks indicate homoplasies. Three main assemblages are numbered. Open arrows indicate families resolved as nonmonophyletic.

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(2001) broader concept of Cerithioidea was supported by 23 synapomorphies; the ones he considered the most significant included aspects of buccal musculature, but also a papillate mantle border, the presence of a large glandular pad in the midgut, and the presence of an ovipositor.

Assessing the pattern of synapomorphies in the present analysis is complicated by the different topologies obtained; of the 16 synapomorphies that optimize to the ingroup node under ACCTRAN on the morphology tree (Fig. 4), only nine of these also optimize to the ingroup node on the Bayesian combined topology (Figs 7B, 10). However, the majority of these nine characters represent systems that have been noted to set cerithioideans apart, specifically midgut and reproductive morphology and sperm ultrastructure: presence of a crescentic ridge [75(1)] and u-shaped fold [84(1)] in the midgut, a single sperm gutter in the medial lamina [107(1)], the presence of a spermatophore bursa in the medial lamina [109(1)], absence of the acrosomal vesicle apical bleb [126(0)], absence of the acrosomal vesicle accessory membrane [128(0)], parallel mitochondrial cristae [133(1)] and four mitochondria in the eusperm midpiece [135(0)]. Three of these characters (107, 109, 135) optimize to the ingroup node unambiguously on the morphology tree, and on all topologies obtained with combined morphological and molecular data (Figs 7, 8) (see Fig. 10, characters in bold).

Comparisons to previous morphological analyses are of limited value given differences in taxon sampling, errors in character coding, and the polyphyletic concept of Cerithioidea of some. Essentially only sperm characters are consistently cited as supporting the ingroup node in almost all morphological analyses. In the present study, the importance of sperm ultrastructure data in defining current concepts of the superfamily and relationships within it is again confirmed. Even with sperm characters lacking for 21 of 56 terminals, their importance is underscored by the fact that four sperm characters support the ingroup node, one of them unambiguously. If sperm characters are excluded from the morphological analysis, a topology is obtained with vermetids nested in the ingroup and with Campaniloidea as sister group to the Cerithioidea. Indeed, the exclusion of sperm characters may have contributed to the expanded concept of Cerithioidea of Simone (2001). Inclusion of three sperm characters in the analysis of Houbrick (1988) (essentially characters 134, 135, and 138, herein) also resulted in a topology uniting vermetids within the ingroup; however, his scoring for two of these sperm characters for *Campanile symbolicum* was incorrect.

The presence of an ovipositor [97(1)], cited as a synapomorphy by Houbrick (1988) and Simone (2001), is supported here as an unambiguous synapomorphy only in the combined morphological + molecular analyses (with unconserved regions included or excluded) but as derived in the ingroup on the morphology topology. Despite the fact that one of the distinguishing features of the midgut of many cerithioideans is a hypertrophied glandular pad [70] (e.g. Simone, 2001; Strong, in press), this is also shown to be a derived feature within the ingroup on all topologies. The presence of zygoneury [90(1)] optimizes unambiguously to the ingroup node only on the morphological tree, with several gains and reversals within the ingroup. Of the additional features highlighted by Houbrick (1988), open pallial gonoducts [104(0); 118(0)], absence of a cephalic penis [117(0)], and the presence of spermatophores [120(1)] are indeed supported as plesiomorphic within the ingroup on all trees.

Within the superfamily, most family-level taxa are well supported with large numbers of synapomorphies, a higher proportion of forward changes and correspondingly high support measures. Several clades are noteworthy for the many apomorphies derived within them; for example, the unique mantle cavity modifications for ctenidial suspension feeding including the food groove [27(1)], endostyle [28(1)], and long gill filaments [34(1)] in Turritellidae plus Siliquariidae; the unique foot [17(2)], pallial sensory structures [26(1)], accessory flap in the midgut [66(1)], and parasperm [144(1)] of Potamididae; the accessory marginal fold in the midgut [69(3)], spermatophore forming organ [119(1)], and kidney [123(2)] of Paludomidae (characters 69 and 123 optimize ambiguously at this node owing to missing data in *Hemisinus*); the accessory pad in the midgut [72(1)], atypical nonglandular oviduct [106(1)], and spermatophore bursa [111(1)] of Thiaridae (although missing data, again for *Hemisinus*, make it uncertain if these are synapomorphies of the entire family).

However, basal nodes and relationships amongst large clades are relatively weakly supported by only a few characters and a higher proportion of homoplasies. This pattern is not unusual in higher-order analyses using morphological data, and speaks to the antiquity of these lineages with morphological specialization, both homologous and homoplastic, outweighing and to some extent overriding the pattern of shared derived characters uniting larger clades. Not surprisingly, when comparing the optimization of characters on the different topologies, there is little consistency in the synapomorphies at basal nodes, reflecting the difficulty in discovering uniquely derived characters that support them. This undoubtedly could be ameliorated to some extent with targeted surveys of understudied taxa and organ systems (see below).

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Implications for cerithioidean systematics

This analysis confirms the monophyly of the Cerithioidea as currently conceived; the distinctiveness of cerithioideans, campaniloideans, and vermetoideans has also been supported in several higher-order analyses of the Caenogastropoda with more limited taxon sampling (e.g. Harasewych *et al*., 1998; Colgan *et al*., 2007; Ponder *et al*., 2008). Several additional points of cerithioidean systematics are also now well established. This study upholds the transfer of *Faunus* from Melanopsidae to the Pachychilidae – a placement that was first supported decisively with midgut data (Strong & Glaubrecht, 2000; see also Lydeard *et al*., 2002; Strong, in press). In contrast to all previous morphological analyses, the limnic Thiaridae and marine Planaxidae are not sister taxa – an affinity often assumed owing to presumed homology of their subhaemocoelic brood pouches (e.g. Morrison, 1954; Glaubrecht, 1996). Consequently, the brood pouches present in these two families are analogous structures – a fact corroborated by their non-identical positions within the head-foot (e.g. Houbrick, 1987a, 1990a; Glaubrecht, 2006).

Less robustly supported but still corroborated in many topologies is the monophyly of the freshwater taxa formerly united in the Thiaridae *s.l.* (or 'Melaniidae'): Melanopsidae, Pachychilidae, Paludomidae, Pleuroceridae, Semisulcospiridae, and Thiaridae *s.s.* There has been a great deal of confusion about the independence and composition of these lineages (see reviews in Glaubrecht, 1996, 1999, 2006) and the names that should be applied to them. This is the first phylogenetic analysis to include representatives of all of them and the results largely confirm the classification of Thiele (1929) with regards to composition, although relationships amongst these clades are still highly unstable.

Thiaridae *s.s.* is monophyletic in almost all analyses (see Fig. 9), with *Hemisinus* consistently emerging at its base. As highlighted above, several unusual aspects of thiarid anatomy have been well documented (primarily of the oviduct), demonstrating their distinctiveness from other lineages. They have been intensely studied as a consequence of their viviparous reproductive mode and capacity for successful colonization with several species introduced worldwide. However, anatomical studies of thiarids are highly dispersed, typically focus on only a narrow aspect (e.g. reproductive anatomy), and perpetuate several inaccuracies (e.g. the 'ureter', which is an anterior branch of the renal oviduct; see e.g. Starmühlner, 1969; Schütt & Glaubrecht, 1999). Despite their visibility, modern comprehensive anatomical studies are conspicuously lacking.

Paludomidae is monophyletic only in the morphological analysis and the Bayesian analyses of the combined morphological + molecular data (unconserved regions included or excluded) owing to instability in the position of *Paludomus*. *Paludomus* shares several uniquely derived complex characters with other paludomids, including the bladder septum and the spermatophore-forming organ (see e.g. Strong & Glaubrecht, 2010), so its affinities based on morphological data seem secure. The instability in analyses including molecular data is probably a consequence of missing data as *Paludomus* is the only paludomid with 28S data and the first half of the 16S data set is missing for all paludomids.

The taxa currently placed in the Semisulcospiridae were previously united in the Pleuroceridae *s.l.*, but recent studies have demonstrated that Asian and western North American semisulcospirids form a clade that is morphologically distinct from eastern North American forms (i.e. Pleuroceridae *s.s.*) and the two are supported as reciprocally monophyletic in analyses of 16S mtDNA sequences (Lydeard *et al*., 2002; Strong & Frest, 2007; Strong & Köhler, 2009). Herein, pleurocerids are monophyletic in all but the morphological analysis and semisulcospirids are monophyletic in many but not all topologies with monophyly especially sensitive to exclusion of unconserved regions (see Fig. 9). However, the analysis of Strong & Köhler (2009) is based on a more comprehensive taxonomic subset within the ingroup and produced topologies that have high nodal support values and are robust to choice of optimality criterion. Consequently, the instability here is likely to be an issue of taxon sampling, at least in part. The interpolation of Melanopsidae in several analyses herein indicates that the splitting of Pleuroceridae *s.l.* into multiple families may have more than a question of family definition as a basis. Melanopsids are monophyletic in only some of the topologies but this family is the most poorly represented of all the freshwater lineages, and no comprehensive morphological study has been published for any species in the family. Again, this instability is likely to be a consequence of taxon sampling and incomplete or missing data.

Apart from these rather minor sources of ambiguity, key points of instability remain for several marine groups, highlighting taxa in critical need of study. These include some lineages that are underrepresented here relative to their diversity (e.g. Bittiinae), as well as several minute, rare, and/or deep water cerithioideans for which scant anatomical or molecular data are available [e.g. *Alabina* and *Cerithidium* (Cerithiidae), Litiopidae, Scaliolidae]. Given the position of these taxa in Groups 1 and 2, they have a disproportionate impact in determining the overall shape of the tree (i.e. pectinate vs. balanced),

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so resolving their affinities is of critical importance for understanding the pattern of cerithioidean phylogeny as a whole.

Cerithiinae (*Cerithium*, *Clypeomorus*) is monophyletic in all analyses, but monophyly of Cerithiidae collapses upon the addition of several minute species known only from morphology (*Alabina*, *Bittium*, *Cerithidium*, *Ittibittium*). Bittiinae (*Bittium*, *Cacozeliana*, *Ittibittium*) is not supported as monophyletic in any analysis with more than a single representative, but all bittiine terminals except *Cacozeliana* are known only from morphology. Unsurprisingly, the enigmatic *Cerithidium* with its unique reproductive anatomy (W. F. Ponder, unpubl. data) does not cluster with most other cerithiids even in the morphology tree, and is supported as the sister taxon to *Alabina* in the combined morphological + molecular analyses (unconserved regions included or excluded). *Alaba* (Litiopidae) is supported as the sister taxon to Cerithiidae in molecular analyses (unconserved regions included or excluded), but is sister to *Ittibittium* in the morphology and combined morphological + molecular trees (unconserved regions included or excluded). Scaliolids are the most unstable of all and are resolved in Group 2 in all analyses except the morphology tree where they emerge at the base of the ingroup.

As demonstrated by *Stephopoma* (Siliquariidae), *Fossarus* (Planaxidae), and *Tympanotonus* (Potamididae), the absence of molecular data need not be an insurmountable obstacle to unambiguous placement in the phylogeny. However, for the minute cerithiids, litiopids, and scaliolids, available morphological data alone are not adequately decisive and in some cases (Scaliolidae) appear to be misleading. This could be because of any number of reasons including erroneous or missing data, but given their small size, inaccurate homology assessment, and/or simplification because of size reduction may be at least partly to blame. Although increased taxon sampling may help, this situation is probably best confronted by combining diverse data sources (e.g. morphology, molecules). Clearly molecular data are needed to assess the affinities of these taxa with confidence.

Virtually nothing is currently known of some cerithioidean taxa (e.g. *Argyropeza*, *Microstylifer*, *Paradiala*, *Royella*, etc.) leaving entire clades unsampled in this analysis. Such understudied taxa can be expected to provide novel combinations of characters and insight into character transformations and putative homologies. Although taxon sampling will always be an issue in phylogenetic studies, for a group such as the Cerithioidea where the major evolutionary patterns are just emerging, such insights will probably have a significant impact. For the moment, however, the classification of these forms can be considered far from conclusive.

Despite these caveats, it is pertinent to examine the dramatic restructuring of cerithioidean classification based on a comparative survey of protoconch morphology and sculpture advanced by Bandel (2006), representing a vast departure from current concepts of superfamily membership and family-level relationships. As we were unable to include exclusively fossil lineages as well as several Recent taxa dealt with by Bandel (e.g. *Argyropeza*, *Styliferina*, *Pachymelania*), it is not possible to evaluate all of his recommendations. The present results are unanimous in contradicting many of the changes recommended by Bandel, chief amongst these being: (1) separation of the Turritellidae, Vermiculariidae, and *Styliferina* in a separate superfamily (Turritelloidea); (2) unification of the Vermetidae and Siliquariidae, amongst others, in the Vermetoidea; (3) unification of Alabininae, Dialinae, Diastomatinae, and Finellinae as subfamilies within the Bittiidae, which was elevated to family rank. Placement of the brooding paludomid *Tanganyicia* in the Thiaridae (see also Strong & Glaubrecht, 2002; Wilson *et al*., 2004) and *Cerithidium* in the Bittiidae are amongst the more minor rearrangements made by Bandel (2006) that are also unsupported here.

Invasion of freshwater

A consistent theme in the evolution of the Gastropoda has been the invasion of freshwater (see e.g. Glaubrecht, 1996), with an estimated minimum of 33–38 independent lineages that have diversified in continental waters (Strong *et al*., 2008). Recent phylogenetic hypotheses have not been able to assess unambiguously the number of independent freshwater cerithioidean lineages. Morphological phylogenies have been hampered by insufficient taxon sampling, polyphyletic terminals, and/or poor resolution (see Introduction) and have supported two (Houbrick, 1988; Ponder, 1991; Simone, 2001) or two to three (Glaubrecht, 1996) invasions. The optimization of freshwater lineages in Lydeard *et al*. (2002) is ambiguous and could be interpreted as three independent freshwater invasions or – much less likely but equally parsimonious – two invasions with a return to brackish and marine waters in the Potamididae, Modulidae, and Scaliolidae.

Given the discrepancies amongst the topologies obtained here, there is still uncertainty about the number of freshwater invasions. The morphological analysis supports two, one in Pachychilidae and one in Paludomidae, Thiaridae, Pleuroceridae, Semisulcospiridae, and Melanopsidae (Group 2, in part + Group 3). Most analyses of the molecular and combined data sets, including and excluding unconserved regions, support three (one in Pachychilidae, one in Paludomidae, Thiaridae, and one in Melanopsidae,

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Pleuroceridae, Semisulcospiridae). However, in the Bayesian combined morphological + molecular analysis with unconserved regions excluded, a result similar to the morphology tree is obtained, with two invasions of freshwater.

The morphological distinctiveness of Pachychilidae, not only from other freshwater taxa but in the context of Cerithioidea as a whole, attests to the independent modification of this clade for a freshwater existence (Glaubrecht, 1999, 2006; Köhler *et al*., 2004). In addition, kidney morphology of pachychilids is very different from other freshwater taxa; like marine forms, the organ is not internally subdivided and in most members of the family the nephropore is concealed beneath a unique flap extending from the gonoduct (character 124). In contrast, the kidney of all other freshwater taxa (Melanopsidae, Paludomidae, Pleuroceridae, Semisulcospiridae, Thiaridae) is internally subdivided, with a bladder communicating externally via the nephrophore; in paludomids, the bladder itself is partially subdivided by a transverse septum of excretory tissue (character 123) (see e.g. Strong, 2005; Strong & Frest, 2007; Strong & Glaubrecht, 2010; E. E. Strong, unpubl. data). Presence of a bladder is one of the key characters uniting the latter taxa in the morphology tree; no other synapomorphy at this node in the morphology tree, with the possible exception of spawn type (character 149), can be considered functionally linked to a freshwater existence. With life in freshwater requiring the production of copious amounts of hypo-osmotic urine, subdivision of the kidney and possession of the bladder undoubtedly facilitate resorption of critical organic solutes prior to excretion. If we conclude that this feature has arisen in parallel, as supported by topologies indicating three freshwater invasions, having a bladder presumably provides a strong selective advantage and suggests that there must be some compensatory mechanism in pachychilids. Transmission electron microscopy of kidney structure may bring interesting insight into the homology of the bladder in the lineages that possess it, and its functional equivalent in pachychilids. Alternatively, this key character could be an indication that the definitive resolution of cerithioidean relationships will support only two freshwater invasions.

A robust and stable framework to address these and other critical evolutionary questions will require (1) strategically coordinated sampling for morphological data and additional molecular markers; (2) comprehensive anatomical treatments for several poorly documented limnic lineages (especially Melanopsidae and Thiaridae) and comparative data for poorly understood organ systems, such as the renal system, to satisfy gaps in our knowledge that will help stabilize relationships amongst and within freshwater clades and provide insight, for example, into the morphological basis for the conquest of freshwater; (3) the addition of poorly known, minute and/or rare marine taxa, some from deep-water, to provide novel character combinations and insight into putative homologies, to help anchor basal nodes, and break up long branches.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Analysis of extended 16S data set with all base positions included. A, parsimony analysis; strict consensus of eight equally parsimonious trees, length = 8369, consistency index = 0.28, retention index = 0.43; five nodes collapse in the strict consensus. Jackknife values (1000 replicates) greater than 50 are indicated at the node. B, Bayesian analysis; posterior probabilities are indicated at the node.

Figure S2. Analysis of extended 28S data set with all base positions included. A, parsimony analysis; strict consensus of 18 equally parsimonious trees, length = 1550, consistency index = 0.48, retention index = 0.55; six nodes collapse in the strict consensus. Jackknife values (1000 replicates) greater than 50 are indicated at the node. B, Bayesian analysis; posterior probabilities are indicated at the node.

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