Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia)

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A new molecular phylogeny of the chemosymbiotic bivalve family Lucinidae is presented. Using sequences from the nuclear 18S and 28S rRNA genes and the mitochondrial gene cytochrome *b*, 105 specimens were analysed representing 87 separate species classified into 47 genera. Samples were collected from a wide range of habitats including mangroves, seagrass beds, shallow sands, offshore muds, and hydrocarbon seeps at depths ranging from the intertidal to over 2000 m. A chronogram, derived from the combined molecular tree, was calibrated using ten lucinid fossils. The trees show five well-supported clades and two single branches of *Fimbria fimbriata* (Linnaeus, 1758) and *Monitilora ramsayi* (Smith, 1885). A new classification of Lucinidae is proposed with seven subfamilial divisions: three new subfamilies – Pegophyseminae, Leucosphaerinae, and Monitilorinae – are introduced and Codakiinae, usually treated as a synonym of Lucininae, is revived to include the *Lucinoma*, *Codakia*, and *Ctena* subclades. Membership of the Lucininae and Myrteinae is considerably revised compared with Chavan's commonly employed 'Treatise' classification. Previously considered as a separate family, Fimbriinae is now regarded as a subfamily within Lucinidae. The status of Milthinae is presently equivocal pending further analysis and Divaricellinae is recognized as polyphyletic, and is therefore abandoned, with species and genera now grouped in various places within the Lucininae. Deeper water Lucinidae mainly belong to Leucosphaerinae, Codakiinae (*Lucinoma* clade), and Myrteinae, with *Lucinoma* species being most frequently associated with hydrocarbon seeps. Species occurring in seagrass habitats derive largely from Pegophyseminae, Codakiinae, and Lucininae, and species from mangrove habitats derive from the Pegophyseminae and Lucininae.

INTRODUCTION

Bivalves of the family Lucinidae are remarkable for their obligate symbiosis with sulphide-oxidising Proteobacteria, housed in the ctenidia, from which they gain much of their nutrition (e.g. Distel & Felbeck, 1987; Distel, 1998; Gros, Liberge & Felbeck, 2003; Ball *et al*., 2009). Morphological and palaeoecological evidence from fossils suggests that the chemosymbiosis is ancient (Liljedahl, 1991a, b; Taylor & Glover, 2000), with the implication that the course of lucinid

evolution and their habitat occupation patterns have been strongly constrained by the association. Although chemosymbiosis has been recorded in six bivalve families, Lucinidae are by far the most diverse (Taylor & Glover, 2010). They are particularly varied and abundant in the tropics, with a depth range from the intertidal zone to around 2500 m, and occupying a wide range of habitats, including mangrove muds, intertidal sands, seagrass beds, subtidal sites of organic enrichment, oxygen minimum zones, cold seeps, mud volcanoes, and hydrothermal vents.

There are estimated to be 330 documented living species of Lucinidae classified into 88 genera (J.

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Taylor & E. Glover, pers. database), but we are aware of many undescribed species, especially from tropical offshore habitats. Burgeoning interest in chemosymbiosis and deep-sea exploration, particularly around hydrocarbon seeps and vents, has stimulated much taxonomic research. Continuing systematic studies of Lucinidae from both shallow and deep-water habitats have demonstrated that diversity has been grossly underestimated, with a plethora of new species and genera described within the last 10 years. For example, Cosel & Bouchet (2008) described 32 new species and nine new genera from bathyal depths of the Indo-West Pacific, Glover & Taylor (2007) reported 18 new species and nine new genera from around New Caledonia, Cosel (2006) introduced eight new species and six new genera from waters off West Africa, and Taylor & Glover (2009a) described four new species and a new genus from hydrocarbon seeps in the western Atlantic.

In addition to the diversity of living lucinids the family has a long fossil history dating back at least to the Silurian (Ludlovian, *c*. 420 Ma; Liljedahl, 1991a, b). There are surprisingly few records from the late Palaeozoic, but diversity increased significantly throughout the Mesozoic, followed by a major radiation in the early Cenozoic, and with many living genera making first appearances in the Neogene.

Our aim in this study is to provide a new molecular phylogeny for the Lucinidae. As well as reconstructing the evolutionary history of the modern Lucinidae, a robust molecular phylogeny from a wide range of taxa will form the basis of a new classification, providing a framework for the study of chemosymbiosis in the family, including the distribution of bacterial symbionts and the recognition of possible co-evolutionary pathways, and additionally, tracking morphological characters associated with symbiosis. Patterns of habitat occupation and the association of distinct clades of lucinids with, for example, mangroves, seagrass beds, cold water, deep water, hydrocarbon seeps, and hydrothermal vents can also be examined. Finally, a strong molecular phylogeny should allow us to evaluate the phylogenetic signal of shell characters, such as the presence of divaricate ribbing, ligamental structure, patterns of hinge teeth, shape of the anterior adductor muscle scar, and form of lunule, which might aid the study and reinterpretation of the rich fossil record of Lucinidae.

Prior to 2004, the superfamily Lucinoidea was generally considered to comprise the families Lucinidae, Fimbriidae, Thyasiridae, Ungulinidae, Cyrenoididae, and Mactromyidae (Chavan, 1969). Molecular analyses have revised this concept, demonstrating that three families, Ungulinidae, Thyasiridae, and Cyrenoididae, are not closely related to Lucinidae, and should be removed from the Lucinoidea and clas-

sified elsewhere within euheterodont bivalves (Williams, Taylor & Glover, 2004; Taylor & Glover, 2006; Taylor *et al*., 2007; Taylor, Glover & Williams, 2009). As for the Fimbriidae, *Fimbria fimbriata* (Linnaeus, 1758) nested amongst a range of Lucinidae species, with no support for separate familial status (Williams *et al*., 2004), although *Fimbria*-like bivalves have a long fossil history into the Mesozoic. Thus, for living taxa, Lucinoidea now comprises only Lucinidae, with the positions of the extinct Mactromyidae and Paracyclidae remaining equivocal. The monophyly of the Lucinidae was established by previous molecular analyses using species from a wide variety of heterodont families as out-groups, and using independent lucinid data sets (Williams *et al*., 2004; Taylor, Glover & Williams, 2005; Taylor, Williams & Glover, 2007).

The first comprehensive study of Recent and fossil Lucinidae to develop ideas of relationship and phylogeny was that of Chavan (1937–1938), which, as well as including an extensive discussion of the affinities of genera, included a geological range chart of recent and fossil genera that outlined his ideas. Later, Chavan (1951) reviewed the lucinids possessing divaricate shell ribbing, and these were subsequently classified by Glibert & Van de Poel (1967) into a separate new subfamily: Divaricellinae. Thirty years later Chavan's ideas had changed significantly (Chavan, 1969), and he divided the Lucinidae into four subfamilies, Lucininae, Myrteinae, Milthinae, and Divaricellinae, but with Fimbriidae as a separate family. Bretsky (1976), working with mostly North American taxa, combined results from a phenetic analysis (Bretsky, 1970) with data from fossils to produce a series of phylogenetic trees for different lucinid lineages. The classification based on these studies used no supragerneric categories, but divided lucinids into seven broad genera with numerous subgenera. There are major conflicts between the shell-based phylogenies and classifications of Chavan and Bretsky, probably resulting from the homoplasy of shell characters (for a more detailed review, see Taylor & Glover, 2006). Despite these problems, further compounded by poor illustrations, Chavan's (1969) classification of lucinid genera remains the most widely used. However, an initial molecular analysis using 31 species from 21 genera of Lucinidae (Williams *et al*., 2004) revealed major incongruence with the morphology-based phylogenies and classifications, suggesting that a major revision of ideas concerning lucinid relationships was needed. Notable results from this preliminary molecular analysis were the identification of a distinct clade of *Anodontia* species [excepting *Anodontia alba* (Link, 1807)], two major clades of shallow-water lucinids, and the basal position of *Myrtea* and *NotoMyrtea*. Since then, further molecular analyses of lucinids have investi-

gated the status and relationships of some individual species (Glover, Taylor & Rowden, 2004) and genera (Glover, Taylor & Williams, 2008). Where appropriately preserved material was available, taxonomic decisions based on shell morphology have been corroborated by molecular results (Taylor & Glover, 2005; Glover *et al.*, 2008). Additionally, it has been recognized that some living species have been 'shoehorned' into inappropriate genera, for instance the abundant western Atlantic species '*Lucina*' *costata* (d'Orbigny, 1846), has been variously classified as *Codakia*, *Ctena*, or *Parvilucina*. Molecular data should clarify the positions of such taxa.

This new molecular analysis using the nuclear 18S and 28S rRNA genes, and the mitochondrial gene cytochrome *b*, is based on 105 samples, including 87 recognized species from 47 genera (53% of living genera 47/88), and encompassing most of the major groups of living Lucinidae from around the world collected from a wide range of habitats at depths from 0 to 2050 m. The analysis includes longer sequences for 18S and 28S genes, and new cytochrome *b* data for many of the taxa previously analysed by Williams *et al.* (2004). Despite the sampling effort, important taxa such as *Miltha* and *Eomiltha*, which represent living but rare survivors of once diverse groups of lucinids from the Cenozoic, are unfortunately missing from the analysis.

MATERIAL AND METHODS

Species analysed, with collection localities, genes sequenced, and GenBank numbers, are listed in Table 1. Taxa previously referred to as '*Lucina*' new genus and species and '*Lucina*' *dalli* Lynge, 1909 in our previous molecular analysis (Williams *et al.*, 2004) are now classified as *Bathyaustriella thionipta* Glover *et al.*, 2004 and *Indoaustriella scarlatoi* (Zorina, 1974), respectively (Glover *et al.*, 2004, 2008).

The DNA extraction and amplification protocols described by Williams & Ozawa (2006) and Taylor, Glover & Williams (2008) were used to amplify portions of three genes: the nuclear 18S and 28S rRNA genes, and the mitochondrial gene cytochrome *b* (cyt*b*). Sequence reactions were performed directly on purified PCR products using a BigDye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems, Carlsbad, CA, USA), run on an Applied Biosystems 3730 DNA Analyser automated capillary sequencer. Sequencing and PCR primers are listed in Table 2.

Complete double-stranded forward and reverse sequences for each gene fragment were assembled and edited using SEQUENCHER v4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). The alignment of cyt*b* sequences was unambiguous and no stop codons were observed. Sequences of ribosomal genes were aligned using ClustalX v2.0.9 (Thompson, Higgins & Gibson, 1994; Thompson *et al.*, 1997) (delay divergent sequence = 95%, gap-opening penalty = 15, gap-extension penalty = 7, and with iterations at the end of the alignment), with minor adjustments made by eye in MACCLADE v4.08 OSX (Maddison & Maddison, 2003). Poorly aligned sites in the ribosomal gene alignments were identified using GBLOCKS v0.91b (Castresana, 2000) and removed from the analyses. The parameters for GBLOCKS were set as: minimum number of sequences for a conserved position, 70% of total number of sequences; minimum number of sequences for a flanking position, 90% of the total number of sequences; maximum number of contiguous non-conserved positions, 3; minimum length of a block, 10; and all gap positions allowed. After the removal of ambiguous blocks of data, selected using GBLOCKS, a total of 980 bp of 18S rRNA (84% of 1156 bp in the original alignment) and 1351 bp of 28S rRNA (75% of 1796 bp in the original alignment) remained to be used in the phylogenetic analyses. Alignments are available on request from the authors.

Phylogenies (Figs 1–4) were constructed using Bayesian methods (MRBAYES v3.1.2; Huelsenbeck & Ronquist, 2001). Models used in the Bayesian analyses were determined by MRMODELTEST v2.1 (J. A. A. Nylander, 2004. Program distributed by the author. Evolutionary Biology Centre, Uppsala University). The cyt*b* data set was further tested to see whether variation across codon positions would result in an improved likelihood. The best model for all data sets was determined to be GTR + G + I using the hierarchical likelihood-ratio tests. In the Bayesian analysis the GTR + G + I model was used for each gene partition, four chains were used, and the starting tree was random. As suggested by the model, base frequencies were estimated, rate variation was gamma-distributed among sites and approximated with four categories (α shape estimated) and an allowance was made for invariant sites. In the combined analyses variation was partitioned among genes, and gene-specific model parameters were used (with all parameters free to vary independently within each partition). In addition, each gene was allowed to evolve at a different rate. The analysis for each data set was run for 3 500 000 generations (7 500 000 for combined gene analyses), with a sample frequency of 100. Each analysis was run twice. The first 15 000 trees from each run were discarded so that the final consensus tree was based on the combination of accepted trees from each run (a total of 40 000 trees; 80 000 for the combined gene tree). Convergence between the two runs was tested by examining the potential scale reduction factors (PSRFs) produced by the 'sump' command in MRBAYES. Support for nodes

Table 1. Species included in the analysis classified in new subfamily classification (Table 2), collection localities, museum registration numbers for vouchers and GenBank accession numbers for the genes sequenced for each taxon

Species	Locality	Locality code	Museum number	18S rRNA	28S rRNA	Cyt*b*
Pegophyseminae						
Pegophysema philippiana (Reeve, 1850)	King Bay, Dampier, Western Australia		BMNH 20070286	AJ581846	AM779673	
Cavatidens bullula (Reeve, 1850)	Roebuck Bay, Broome, Western Australia	BR	BMNH 20100264	FR686688	FR686769	FR688599
Cavatidens bullula (Reeve, 1850)	Kungkraben Bay, Thailand	KK	BMNH 20070284	AM774495	AM779668	FR688598
Cavatidens omissa (Iredale, 1930)	Moreton Bay, Queensland, Australia	MB	BMNH 20100278	AJ581847	AJ581881	FR688601
Cavatidens omissa (Iredale, 1930)	Gunnamatta Bay, New South Wales, Australia	SYD	BMNH 20100285	AJ581843	AJ581878	FR688626
Cryptophysema vesicula (Gould, 1850)	Dili, East Timor	TM	BMNH 20100288		FR686768	FR688603
Cryptophysema vesicula (Gould, 1850)	Onna, Okinawa, Japan	OK	BMNH 20100289		FR686767	FR688604
Euanaodontia ovum (Reeve, 1850)	Lizard Island, Queensland, Australia	LI	BMNH 20100290	AJ581844	AJ581879	FR688600
Euanodontia ovum (Reeve, 1850)	Rodrigues, Indian Ocean	ROD	BMNH 20100295	AJ581845	FR687321	FR688602
Loripinus fragilis (Philippi, 1836)	Embiez Island, France		BMNH 20100270	AJ581842	AJ581877	
Leucosphaerinae						
Leucosphaera cf. *diaphana* Glover & Taylor, 2007	Ubajan, Bohol Island, Philippines. PANGLAO 2004, st. S27, 9°41.5′N, 123°51.0′E. 12 m		MNHN IM-2009-10359	FR686699	FR686781	FR686683
Anodontia alba Link, 1804	Lower Matecumbe Key, Florida, USA		BMNH 20070286	AJ581840	AM779672	FR686597
Pseudolucinisca lacteola (Tate, 1897)	Esperance, Western Australia		BMNH 20100248	AJ581867	AJ581900	FR688624
Dulcina sp.	Bohol Sea, Philippines. PANGLAO 2005, St. CP 2335, 9°34.3′N, 123°37.8′E. 729–733 m		MNHN IM-2009-10371	FR686695	FR686777	FR688615
Dulcina karubari Cosel & Bouchet (2008)	Maribojoc Bay, Bohol Sea, Philippines. PANGLAO 2005, st CP 2331, 9°39.2′N, 123°47.5′E. 255–268 m		MNHN IM-2009-10372	FR686697	FR686776	FR686608
Undescribed genus/species (UGS-1)	Maribojoc Bay, Bohol Sea, Philippines. PANGLAO 2005, st CP 2397, 9°34.9′N, 123°41.7′E. 642–669 m		MNHN IM-2009-10373	FR686696	FR686778	FR686611
Undescribed genus/species (UGS-2)	Manga, Bohol Island, Philippines. PANGLAO 2004, st S20, 9°41.8′N, 123°51.1′E. 10 m		MNHN IM-2009-10360	FR686698	FR686780	FR686681
Undescribed genus/species (UGS-3)	Chesterfield Bank, New Caledonia. EBISCO 2005, st CP 2614, 19°39′S, 158°47′E. 608–642 m		MNHN IM-2009-10376	FR686701	FR686779	FR686606

Myrteinae

Taxon	Locality	Code	Voucher			
Myrtea spinifera (Montagu, 1803)	Shetland Islands, UK 60.1956°N, 1.1253°W. 48 m.		BMNH 20100296	FR688690	FR688774	FR688668
Notomyrtea botanica (Hedley, 1918)	Victor Harbour, South Australia		BMNH 20100265	AJ581862	AJ581896	FR688666
Myrtea flabelliformis (Prashad, 1932)	Bohol Sea, Philippines. PANGLAO 2005, st CP 2388, 9°26.9'N, 123°34.5'E. 762–786 m		MNHN IM-2009-10375	FR688694	FR688775	FR688614
Myrtea sp.	off Pamilacan Island Philippines. PANGLAO 2005, st CP 2348, 9°29.6'N, 123°52.5'E, 196–216 m		MNHN IM-2009-10369	FR688693	FR688770	FR688613
Myrtea sp.	Safaga, Egypt, Red Sea	SAF	BMNH 20100300	FR688689	FR688773	
Gloverina rectangularis Cosel & Bouchet (2008)	Bohol Sea, Philippines. PANGLAO 2005, st CP 2389, 9°27.9'N, 123°38.4'E, 784–786 m		MNHN IM-2009-11084	FR688692	FR688771	FR688612
Gloverina cf. *rectangularis* Cosel & Bouchet (2008)	Bohol Sea, Philippines. PANGLAO 2005, st CP 2388, 9°26.9'N, 123°34.5'E, 762–786 m		MNHN IM-2009-10368	FR688691	FR688772	FR688607

Codakiinae

Taxon	Locality	Code	Voucher			
Codakia orbicularis (Linnaeus, 1758)	Little Duck Key, Florida, USA		BMNH 20100281	AM774500	AM779674	FR688625
Codakia paytenorum (Iredale, 1937)	Miyako Island, Okinawa, Japan	OK	BMNH 20100283	FR686709	FR688816	FR688630
Codakia paytenorum (Iredale, 1937)	Lord Howe Island, Australia	LH	BMNH 20100279	FR686708	FR688815	FR688629
Codakia rugifera (Reeve, 1850)	Ulladulla, New South Wales, Australia		BMNH 20100291	AJ581851	AJ581885	FR688632
Codakia tigerina (Linnaeus, 1758)	Lizard Island, Queensland, Australia		BMNH 20100286	AJ581852	AJ581886	FR688641
Codakia interrupta (Lamarck, 1816)	Alona Beach, Panglao Island, Philippines. PANGLAO 2004, st M1, 9°32.9'N, 123°46.6'E. 0–1 m		MNHN IM-200910357	FR686702	FR688817	FR688664
Ctena bella (Conrad, 1837)	Moreton Bay, Queensland, Australia	MB	BMNH 20100274	FR688711	FR688823	FR688639
Ctena bella (Conrad, 1837)	Yonahisamatsu Ryuku Islands, Japan	OK	BMNH 20100297	FR686704	FR688824	FR688618
Ctena decussata (da Costa, 1829)	Embiez Islands, France	FR	BMNH 20100271	FR686706	FR688826	FR688621
Ctena decussata (da Costa, 1829)	Mali Ston Bay, Croatia	CR	BMNH 20100261	FR686705	FR688825	FR688620
Ctena delicatula (Pilsbry, 1904)	Hong Kong	HK		FR686710		FR688647
Ctena delicatula (Pilsbry, 1904)	Kungkrabaen Bay, Thailand	KK	BMNH 20070283	AM774494	AM779667	FR688638
Ctena eburnea (Gmelin, 1791)	Maio Island, Cape Verde Islands		BMNH 20100287	FR686707	FR686827	FR688622
Ctena mexicana (Dall, 1901)	Bahias de Punta, Soliman, Mexico		BMNH 20070285	AM774496	AM779669	FR688640
Ctena orbiculata (Montagu, 1808)	Long Key, Florida, USA	FK	BMNH 20100254	AJ581853	AJ581887	FR688627
Ctena orbiculata (Montagu, 1808)	Bermuda	BD	BMNH 20100249	FR686714	FR688822	FR688635
Ctena imbricatula (C. B. Adams 1845)	Bocas, Panama	BOC	BMNH 20100263	FR686715	FR688829	FR688636

Table 1. *Continued*

Species	Locality code	Locality	Museum number	18S rRNA	28S rRNA	Cytb
Ctena chiquita (Dall, 1901)	COS	Cabo Blanco, Costa Rica	BMNH 20100256	FR686716	FR688830	FR686637
Ctena sp.	PAN	Pamilacan Island, Philippines. PANGLAO 2004, st S12, 9°29.4'N, 123°56.0'E. 6–8 m	MNHN IM-2009-10365	FR686703	FR688821	FR686679
Epicodakia tatei (Angas, 1879)		Victor Harbor, South Australia	BMNH 20100275	FR686712	FR688828	FR686645
Lucinoma annulata (Reeve, 1850)		Southern California, USA	BMNH 20100251	FR686717		
Lucinoma aequizonata (Stearns, 1890)		500m, Santa Barbara Basin, California, USA	BMNH 20070307	FR686719	FR688820	FR686649
Lucinoma borealis (Linnaeus, 1767)		Salcombe, Devon, UK	BMNH 20070289	AM774501	AM779675	FR686662
Lucinoma myriamae Cosel, 2006	NIG	cold seep, 1700 m, off Nigeria	BMNH 20100293	FR686718	FR688818	FR686656
Lucinoma myriamae Cosel, 2006	ANG	off Angola, 6°34.15'S 7°8.48'E. 2050 m	BMNH 20100292	FR686713	FR688819	FR686661
Fimbriinae						
Fimbria fimbriata (Linnaeus, 1758)		Lizard Island, Queensland, Australia	BMNH 20070293	AM774505	AM779679	FR686646
Monitilorinae						
Monitilora ramsayi (Smith, 1885)		Moreton Bay, Queensland, Australia	BMNH 20070292	AM774504	AM779678	FR686667
Lucininae						
Austriella corrugata (Deshayes, 1843)	DMP	King Bay, Dampier, Western Australia	BMNH 20070306	AJ581848	AJ581882	AM774139
Austriella corrugata (Deshayes, 1843)	SIN	Sungai Buloh, Singapore	BMNH 20070290	AM774128	AM779676	AM774140
Bathyaustriella thionipta Glover *et al.*, 2004		480 m, Kermadec Ridge, New Zealand	BMNH 20070337	AJ581858	AJ581892	AM774147
Bretskya scapula Glover & Taylor, 2007		Cortes, Bohol Island, Philippines. PANGLAO 2004, st T19, 9°42.2'N, 123°50.8'E. 10–26 m	IM-2009-10825	FR686722		FR686616
Cardiolucina australopilula Taylor & Glover, 1997		Rat Island, Houtman Abrolhos Islands, Western Australia	BMNH 20100262	FR686723	FR686785	FR686617
Cardiolucina pisiformis (Thiele, 1930)		Withnell Bay, Dampier, Western Australia	BMNH 20100269	AJ581849	AJ581883	FR686631
Cardiolucina quadrata (Prashad, 1932)		Off Balicasag Island, Bohol Sea, Philippines. PANGLAO 2005, st CP 2340, 9°29.4'N, 123°44.4'E. 271–318 m	MNHN IM-2009-10374	FR686721	FR686787	FR686610
Cardiolucina semperiana (Issel, 1869)		Safaga, Egypt	BMNH 20100301	FR686728	FR686786	FR686633
Cardiolucina siquijorensis Taylor & Glover, 1997		Taloto, Bohol Island, Philippines. PANGLAO 2004, st. M26, 9°40.9'N, 123°51.1'E. 0–2 m	MNHN IM-2009-10366	FR686740	FR686789	FR686665
Cardiolucina undescribed species		Manga, Bohol Island, Philippines. PANGLAO 2004, st. S20, 9°41.8'N, 123°51.1'E. 10 m	MNHN IM-2009-10361	FR686748	FR686788	FR686682

Species	Locality	Code	Voucher			
Cavilinga blanda (Dall & Simpson, 1901)	Lower Matecumbe Key, Florida, USA		BMNH 20100246	FR686724	FR686802	
Chavania sp.	Moreton Bay, Queensland, Australia	MB	BMNH 20100255	FR686726	FR686790	FR686623
Chavania striata (Tokunaga, 1906)	Lizard Island, Queensland, Australia		BMNH 20100302	AJ581850	AJ581884	FR686634
Discolucina virginea (Deshayes, 1832)	Tagbilaran, PANGLAO channel, Philippines. PANGLAO 2004, st. D13, 9°38.0'N, 123°51.4'E. 2–3 m		MNHN IM-2009-10363	AM774497	AM779671	FR686660
Divalinga bardwelli (Iredale, 1936)	Denham, Shark Bay, Western Australia		BMNH 20100253	FR686729	FR686793	FR686642
Divalinga quadrisulcata (d'Orbigny, 1842)	Guadeloupe, French West Indies		tissue sample	AJ581854	AJ581888	FR686644
Divaricella irpex (Smith, 1885)	Roebuck Bay, Broome, Western Australia	BR	BMNH 20100259	FR686730	FR686784	FR686643
Divaricella irpex (Smith, 1885)	Lizard Island, Queensland, Australia	LI	BMNH 20100244	AJ581855	AJ581889	
Funafutia levukana (Smith, 1885)	Pamilacan Island, Philippines. PANGLAO 2004, st. B30, 9°29.4'N, 123°56.1'E. 25 m		MNHN IM-2009-10358	FR686700	FR686782	FR686605
Indoaustriella dalli (Lynge, 1909)	Kungkraben Bay, Thailand		BMNH 20070308	AM774130	AM774135	AM774143
Indoaustriella lamprelli Glover et al., 2008	Brisbane, Queensland, Australia		BMNH 20070304	AM774131	AM774136	AM774144
Indoaustriella plicifera (Adams, 1855)	Tajong Laboh, Malaysia		BMNH 20070309	AM774132	AM774137	AM774145
Indoaustriella scarlatoi (Zorina, 1974)	Tai Tam, Hong Kong		BMNH 20070310	AJ581859	AJ581893	AM774146
Lepidolucina venusta (Philippi, 1847)	Port Dickson, Malaysia		BMNH 20100258	FR686739	FR686806	FR686663
Loripes clausus (Philippi, 1848)	Ibo Island, Mozambique		BMNH 20100277	FR686737	FR686792	FR686658
Loripes lucinalis (Lamarck, 1818)	Embiez Islands, France	FR	BMNH 20100276	FR686735	FR686794	FR686655
Loripes lucinalis (Lamarck, 1818)	Weymouth, UK	UK	BMNH 20100272	AJ581857	AJ581891	FR686654
Lucina adansoni d'Orbigny, 1839	Boavista Island, Cape Verde Islands		BMNH 20080839	FR686731	FR686803	FR686648
Lucina pensylvanica (Linnaeus, 1758)	Lower Matecumbe Key, Florida	FK	BMNH 20070311	AM774127	AM774138	AM774148
Lucina pensylvanica (Linnaeus, 1758)	Guadeloupe, French West Indies	GDL	tissue sample	AJ581856	AJ581890	FR686653
Lucina pensylvanica (Linnaeus, 1758)	Los Roquas, Venezuela	VEN	BMNH 20100282	FR686738	FR686805	FR686659
Lucina pensylvanica (Linnaeus, 1758)	Bocas, Panama	BOC	BMNH 20100266	FR686744	FR686804	FR686672
'*Lucina*' *desiderata* Smith, 1885	Cortes, Bohol Island, Philippines. PANGLAO 2004, st T19, 9°42.2'N, 123°50.8'E. 10–26 m		MNHN IM-2009-10364	FR686750	FR686783	
Lucinella divaricata (Linnaeus 1758)	Embiez Islands, France		BMNH 20100280	FR686733	FR686801	FR686651
Lucinisca centrifuga (Dall, 1901)	Islas Perlas, Panama, Eastern Pacific		BMNH 20100299	FR686732	FR686810	FR686650
Lucinisca fenestrata (Hinds, 1845)	Islas Perlas, Panama, Eastern Pacific		BMNH 20100298	FR686734	FR686811	FR686652
Lucinisca nassula (Conrad, 1846)	Little Duck Key, Florida, USA		BMNH 20100245	FR686736	FR686812	FR686657
Parvilucina crenella (Dall, 1901)	Ramrod Key, Florida, USA		BMNH 20100273	FR686741	FR686799	FR686669

Table 1. *Continued*

Species	Locality	Locality code	Museum number	18S rRNA	28S rRNA	*Cytb*
Parvilucina pectinella (Adams, 1852)	Bocas, Panama	BOC	BMNH 20100257	FR686742	FR686798	FR686670
'Parvilucina' costata (d'Orbigny, 1842)	Bocas, Panama		BMNH 20100252	FR686727	FR686809	FR686628
'Parvilucna' costata (d'Orbigny, 1842)	Ile Cochon, Guadeloupe, French West Indies	GDL	BMNH 20100267	FR686725	FR686808	FR686619
Phacoides pectinatus (Gmelin, 1792)	Fort Pierce, Florida, USA		BMNH 20070291	AM774503	AM779677	FR686674
Pillucina australis Glover & Taylor, 2001	Rat Island, Houtman Abrolhos Islands, Western Australia		BMNH 20100294	FR686743	FR686800	FR686671
Pillucina pisidium (Dunker, 1860)	Gunnamatta Bay, New South Wales Australia		BMNH 20100284	AJ581865	AJ581898	
Pillucina vietnamica Zorina, 1978	Abu Dhabi, Arabian Gulf		BMNH 20080847		FR686796	FR686675
Pillucina vietnamica Zorina, 1978	Kungkraben Bay, Thailand		BMNH 20070282	AM774493	AM779666	FR686673
Pillucina sp.	Manga, Bohol Island, Philippines, PANGLAO 2004, st S19, 9°42.1'N, 123°51.4'E. 3–4 m	PAN	MNHN IM-2009-10362	FR686747	FR686795	FR686680
Rasta lamyi (Abrard, 1942)	Aqaba, Jordan		BMNH 20070294	AJ581868	AM779680	FR686678
Radiolucina amianta (Dall, 1901)	Ramrod Key, Florida, USA		BMNH 20100247	FR686745	FR686813	FR686676
Radiolucina cancellaris (Philippi, 1846)	Islas Perlas, Panama, Eatern Pacific		BMNH 20100268	FR686746	FR686814	FR686677
Stewartia floridana (Conrad, 1833)	Cedar Key, West Florida, USA		BMNH 20100260	FR686749	FR686797	FR686684
Troendleina cf. *musculator* Cosel & Bouchet, 2008	Bohol/Sulu Seas sill, Philippines. PANGLAO 2005, st CP 2362, 8°56.5'N, 123°32.7'E. 679–740 m		MNHN IM-2009-10367	FR686720	FR686807	FR686609
Wallucina assimilis (Angas, 1867)	Jervis Bay, New South Wales, Australia		BMNH 20100260	AJ581869	FR686791	FR686687
Out-groups						
Eucrassatella cumingi (Adams, 1852)	Moreton Bay, Queensland, Australia		BMNH20070212	AM774479	AM779653	
Parathyasira equalis (Verrill & Bush, 1898)	Gullmarsfjorden, Sweden		BMNH20070296	AM392453	AM392437	FR686685
Thyasira polygona (Jeffreys, 1864)	Northern North Saa		BMNH20070298	AM774484	AM392433	FR686686

Locality codes for Figures 1–5.

Table 2. Forward (F) and reverse (R) PCR primers (also used in sequencing), and forward (FS) and reverse (RS) internal sequencing primers

Gene/Primer	Sequence 5′ → 3′	Annealing temp	[MgCl₂]	Primer reference
18S rRNA		54 °C	3.0 mM	
18S-5′ (F)	CTGGTTGATYCTGCCAGT			Winnepenninckx, Reid & Backeljau, 1998
18S1100R (RS)	CTTCGAACCTCTGACTTTCG			Williams, Reid & Littlewood, 2003
18S600F (FS)	GGTGCCAGCAGCCGCGGT			Williams & Ozawa, 2006
18S600R (RS)	ACCGCGGCTGCTGGCACC			Modified from Littlewood, Curini-Galletti & Herniou, 2000
28S rRNA		52 °C	2.5 mM	
LSU5 (F)	TAGGTCGACCCGCTGAAYTTAAGCA			Littlewood *et al.*, 2000
LSU1600R (R)	AGCGCCATCCATTTTCAGG			Williams *et al.*, 2003
900F (FS)	CCGTCTTGAAACACGGACCAAG			Lockyer *et al.*, 2003
ECD2S (RS)	CTTGGTCCGTGTTTCAAGACGG			Modified from Littlewood *et al.*, 2000
LSU330F (FS)	CAAGTACCGTGAGGGAAAGTTG			Littlewood *et al.*, 2000
cytochrome *b*		45 °C	3.0 mM	
cytB-F (F)	GRGGKGCTACKGTAATTACTAA			Taylor *et al.*, 2008
cytB-R (R)	AAATAYCAYTCNGGCTGRATATG			Taylor *et al.*, 2008
cytbR_new (R)	AAATAYCACTCGGGCTGGATATG			This study

Annealing temperatures and concentration of magnesium chloride [MgCl₂] used in polymerase chain reactions.

was determined using posterior probabilities (PP, calculated by MRBAYES).

We also analysed the combined data set (N = 80 taxa) using BEAST v1.5.1 (Drummond & Rambaut, 2007) to produce a phylogenetic hypothesis based on three genes (concatenated sequences from 18S, 28S and cyt*b* genes) using Bayesian inference with an uncorrelated relaxed, lognormal clock. This method allows for the co-estimation of both phylogeny and divergence times, and is thought to result in better trees than Bayesian analysis alone (Drummond *et al.*, 2006). It also calculates the 95% highest posterior density (HPD) interval for node heights (ages). The 95% HPD is the shortest interval that contains 95% of the sampled values. Only one exemplar of each species was included, although in some cases it was necessary to concatenate sequences from different individuals of the same species. The Yule tree prior was used, which assumes a constant speciation rate among lineages, with a lognormal prior for the birth rate. Sequence variation was partitioned among genes, and gene-specific model parameters were used with each gene allowed to evolve at a different rate. Models were chosen after several preliminary analyses (GTR + G + I for 18S and 28S, and SRD06 for cyt*b*). Based on MRBAYES analyses, we set the in-group to be monophyletic to ensure the correct placement of the root.

The starting trees for the BEAST analyses were neighbour-joining trees with branches transformed using nonparametric rate smoothing (NPRS) and node heights scaled so that all calibration points fell within the limits defined by the priors (NPRS transformed and scaled using TREEEDIT v1.0a10; A. Rambaut & M. Charleston, http://evolve.zoo.ox.ac.uk). The analysis ran for 125 000 000 generations with a sample frequency of 10 000. All effective sample size (ESS) values were greater than 100 (some were orders of magnitude greater). The final tree (Fig. 5) is a maximum clade credibility tree with node heights based on median values of 12 400 trees (after a burn-in of 100 generations), and support for nodes was determined using posterior probability (PP; calculated by BEAST).

MOLECULAR CLOCK CALIBRATION

The chronogram was calibrated using ten fossil records. Details for each calibration are listed below and positions are indicated on Figure 5. Calibrations with fossils using lognormal priors:

1. Date 1: '*Loripinus*' *conili* (de Raincourt, 1877), early Eocene, late Ypresian (55.8–48.6 Ma), Herouval, Paris Basin, France (Cossmann & Pissarro, 1904–06: fig. 82iv–3). To date crown Pegophyseminae (median, 48.6 Ma; SD 0.089 Myr;

zero offset, 7.78 Myr; 95% interval, 65.6–48.6 Ma).

2. Date 2: '*Lucina*' *blanckenhorni* Chavan, 1947, late Cretaceous, Campanian (83.5–70.6 Ma), Mount of Olives, Jerusalem, Israel (Fig. 6D). To date Myrteinae stem group (median, 55.8 Ma; SD 0.125 Myr; zero offset, 12.13 Myr; 95% interval, 83.4–55.8 Ma).

3. Date 3: *Lucinoma* sp., undescribed species (BMNH L64868–70), Palaeocene, Selandian–Thanetian, 62–59 Ma; Aquia Formation, Aquia Creek, Potomac River, Virginia, USA (Fig. 6H, I). To date first appearance of *Lucinoma* (median, 59 Ma; SD 0.105 Myr; zero offset, 10.98 Myr; 95% interval, 83.5–59 Ma).

4. Date 4 : '*Phacoides*' *dejaeri* (Vincent, 1930), Palaeocene (Danian 65–61 Ma), Calcaire de Mons, Belgium (Fig. 6K). Considered as possible *Codakia* stem group (median, 61 Ma; SD 0.0915 Myr; zero offset, 10.02 Myr; 95% interval, 83–61 Ma).

5. Date 5: *Codakia leonina* (Basterot, 1825), early Miocene, Aquitanian (23–20.4 Ma) Saucats, Aquitaine Basin, France (Fig. 6L). To date crown group *Codakia* (median, 23 Ma; SD 0.06 Myr; zero offset, 2.55 Myr; 95% interval, 28.4–23 Ma).

6. Date 6: *Epicodakia* sp., middle to late Eocene (Bartonian–Priabondian 40.4–33.9 Ma), Kalbarri, Western Australia (Fig. 6N) (Darragh & Kendrick, 2008). To date crown group *Ctena/Epicodakia* (median, 33.9 Ma; SD 0.11 Myr; zero offset, 6.57 Myr; 95% interval, 48.6–33.9 Ma).

7. Date 7: *Lucinisca plesiolopha* Dall, 1900, middle Miocene (16–11.6 Ma), Alum Bluff Group, Florida (Gardner, 1926: pl. 19, figs 1, 2). To date crown group *Lucinisca* (median, 11.6 Ma; SD 0.345 Myr; zero offset, 5.701 Myr; 95% interval, 28.7–11.6 Ma).

8. Date 8: *Loripes dujardini* (Deshayes, 1850), early Miocene, Aquitanian (23–20 Ma), Saucats, Aquitaine Basin, France (Fig. 6P). To date the stem of the *Loripes* clade (median, 20 Ma; SD 0.175 Myr; zero offset, 5.81 Myr; 95% interval, 34–20 Ma).

9. Date 9: *Parvilucina sphaeriola* (Dall, 1903), middle Miocene (16–11.6 Ma), Alum Bluff Group, Florida, USA (Gardner, 1926: pl. 20, fig. 6). Date for the stem for North American *Parvilucina* (median, 11.6 Ma; SD 0.436 Myr; zero offset, 6.664 Myr; 95% interval, 33.9–11.6 Ma).

10. Date 10: *Cardiolucina agassizi* (Michelotti, 1839), late Miocene (Tortonian 11.6–7.2 Ma), Southern Europe (Taylor & Glover, 1997: fig. 1). To date crown group *Cardiolucina* (median, 7.5 Ma; SD 0.275 Myr; zero offset, 3.125 Myr; 95% interval, 16–7.5 Ma).

RESULTS

Phylogenetic trees constructed from the separate gene data sets are shown in Figures 1–3. Not all taxa are represented in all three trees: for example, we failed to obtain 18S sequences for *Cryptophysema vesicula* (Gould, 1850) or cyt*b* for *Pegophysema philippiana* (Reeve, 1850).

The tree derived from 18S rRNA data (Fig. 1) shows a clade of *Myrtea*, *Notomyrtea*, and *Gloverina* species. A clade containing species usually classified in the *Anodontia* group form a highly supported long branch, but within the clade species are also separated from each other on long branches. Notably, *Anodontia alba* does not group in this clade, but falls within a sister clade of morphologically heterogeneous taxa, including *Pseudolucinisca lacteola* (Tate, 1897), *Leucosphaera*, *Dulcina* species, and three separate undescribed taxa (UGS-1, UGS-2, and UGS-3).

Fimbriata fimbriata and *Monitilora ramsayi* (Smith, 1885) form separate branches sister to the rest of the lucinid species that are resolved into two large clades. One of these clades comprises species of *Ctena*, *Codakia*, and *Lucinoma*, and the second consists of a wide range of mainly shallow water lucinids. Sequences for species within this latter clade were highly conserved and there was little resolution of subclades. The position of *Phacoides pectinatus* (Gmelin, 1792) is notable on a long branch within this large clade.

The 28S rRNA tree (Fig. 2) showed a similar topology, but with higher resolution of the major clades and their internal structure. Ten '*Anodontia*' exemplars, representing five subgenera, are separated as a highly supported clade, with long internal branches, especially that of *Cryptophysema vesicula*. Again, *Anodontia alba* lies outside this clade. *Monitilora* and *Fimbria* form isolated branches. As in the 18S tree there are two major clades of lucinids, but subclade and generic divisions are much better resolved, as are the *Codakia*, *Ctena*, and *Lucinoma* subclades, for example. Again, *Phacoides pectinatus* occupies a long branch within the larger clade.

The tree derived from cyt*b* data (Fig. 3) had essentially the same topography as the 18S and 28S trees, but provides finer detail at shallower nodes and clearer resolution of genera. The position of the long branch of *Euanodontia ovum* (Reeve, 1850), separate from the *Cavatidens/Cryptophysema* clade, is anomalous, but there is poor support for this topography. Notable within the largest lucinid clade is the well-supported subclade consisting of the genera *Loripes*, *Lucinella*, *Wallucina*, *Pillucina*, and *Chavania*, the subclade comprising species of *Austriella* and *Indoaustriella*, and another with six species of *Cardiolucina*.

Figure 1. Molecular phylogeny of the Lucinidae based on the single gene analysis of 18S rRNA produced by Bayesian analysis using MRBAYES. Support values are Bayesian posterior probabilities (%). Details of the taxa are given in Table 1.

Figure 2. Molecular phylogeny of the Lucinidae based on the single gene analysis of 28S rRNA produced by Bayesian analysis using MRBAYES. Support values are Bayesian posterior probabilities (%). Details of taxa are given in Table 1.

Figure 3. Molecular phylogeny of the Lucinidae based on the single gene analysis of cytochrome *b* produced by Bayesian analysis using MRBAYES. Support values are Bayesian posterior probabilities (%). Details of taxa are given in Table 1.

In the tree derived from the combined data set of the three genes (Fig. 4), the topology was similar to the individual gene trees, but support values were in most cases higher. The species analysed group into five highly supported clades (PP > 98%): the *Euanodontia*/*Cavatidens* group; the *Anodontia*/*Dulcina*/*Pseudoluciniscia* group; the *Myrtea*/*Gloverina* group; the *Ctena*/*Lucinoma*/*Codakia* group; and the very large clade of other lucinids, with *Funafutia levukana* (Smith, 1885) as the sister group. Additional to these are *Monitilora ramsayi* and *Fimbria fimbriata*, which form separate unstable branches in the basal part of the tree. Within the two major clades generic divisions are well supported. Further discussion of the positions of genera within the major clades follows below.

With a smaller taxon set used in the BEAST chronogram analysis (Fig. 5), the five highly supported clades are very similar in topography to those in the combined tree.

DISCUSSION

Preliminary molecular results (Williams *et al.*, 2004; Taylor & Glover, 2006) showed major incongruence with previous classifications of Lucinidae based on shell characters (Chavan, 1969; Bretsky, 1976). Although traditional shell characters have long been and continue to be universally used for the recognition of genera and species, they have proven to be a poor guide to suprageneric relationships. Using the molecular results from the larger data set outlined in Figures 3 and 4, we propose a new hypothesis of relationships and classification of the Lucinidae (Table 3). Although we have sampled only 53% of living genera, the major groups identified are robust and well supported in our analysis. We classify the major clades recognized as subfamilies of Lucinidae. Family group names are already available for five of these clades, and we introduce three new names. Additionally, included in the classification are living genera for which no molecular data is yet available (Table 3). The placement of these is provisional but testable by future molecular analysis.

PEGOPHYSEMINAE – NEW SUBFAMILY

Except for *Anodontia alba* (type species of *Anodontia*), all other species analysed that have been previously classified as *Anodontia* are separate on a highly supported long branch. Within this clade, the species previously classified into various subgenera of *Anodontia*, namely *Loripinus*, *Pegophysema*, *Euanodontia*, *Cryptophysema*, and *Cavatidens* also lie on long internal branches (most taxa included in 28S tree; Fig. 2). Because of their phylogenetic distinctiveness we propose a new subfamily Pegophyseminae, and in consideration of the differences from *Anodontia alba* we elevate the subgenera listed above, together with *Afrophysema* and *Bythosphaera* (Taylor & Glover, 2005), to full generic status. The type species of *Pegophysema* is *Pegophysema schrammi* (Crosse, 1876), and an 18S sequence from this species (donated by D. Distel, specimen from Bermuda) grouped with other pegophysemine species in the analysis of Williams *et al.* (2004). A closely similar species from the Indo-West Pacific, *Pegophysema philippiana*, is included in the 28S and 18S trees herein.

Pegophyseminae are united by some unusual morphological characters, including thin, globular, smooth shells, a narrow edentulous hinge with an internal and laterally extended ligament in most species, and, anatomically, the presence of a mantle septum, digitate mantle gills, and extensive posterior mantle fusion (Taylor & Glover, 2005).

Although the chronogram (Fig. 5) suggests a late Cretaceous origin, there are no convincing records of Pegophyseminae-like bivalves in pre-Cenozoic rocks. Records for the Cenozoic are frequent, and contemporaneously in the Eocene of the Paris Basin and southern USA (Cossmann & Pissarro, 1904–06; Gardner, 1951), there were lucinids with characters of living Pegophyseminae such as *Anodontia augustana* Gardner, 1951, '*Lucina*' *conili* de Raincourt, 1877, and '*Lucina*' *parnensis* Deshayes, 1857. Pre-Cenozoic species with a superficial resemblance to pegophysemines include the hydrocarbon seep-associated '*Cryptolucina*' *kuhnpassetensis* Kelly, 2000 from the Cretaceous of Greenland, which is inflated and edentulous (Kelly *et al.*, 2000). From the Palaeozoic, Boyd & Newell (1979) compared the Permian *Gigantocyclus zidensis* Termier & Termier, 1977, from the Permian of Tunisia with *Anodontia*, and the Devonian *Paracyclas* species, placed by Johnston (1993) into the family Paracyclidae, are similar in general shape to living taxa. There is insufficient evidence to include any of these genera in the Pegophyseminae.

LEUCOSPHAERINAE NEW SUBFAMILY

This group of species forms a distinct, well-supported clade in the molecular analysis, but there are no clear and consistent morphological characters that unite the group. We propose a new subfamily name Leucosphaerinae for this clade, based on the genus *Leucosphaera*. Unfortunately, an obvious subfamily name based on *Anodontia* could not be used because of the prior use for the freshwater mussel *Anodonta*.

Lucinids in this clade have no radial shell sculpture, cardinal teeth are usually small or absent, lateral teeth are lacking, whereas the lunule is prominent and highly asymmetrical in *Pseudoluciniscia*,
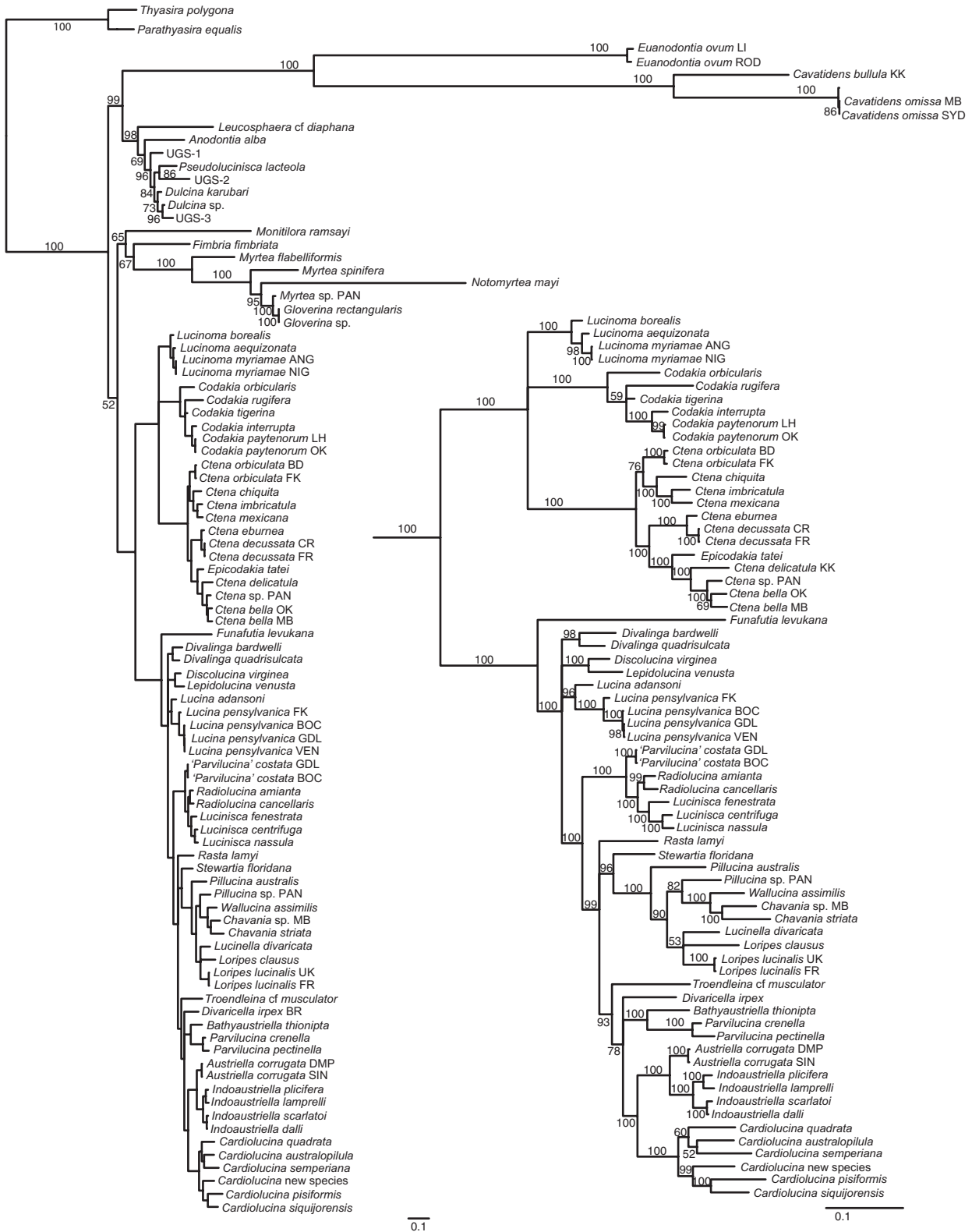
Figure 4. Molecular phyogeny of Lucinidae produced by Bayesian analysis of the combined data set from concatenated sequences of the nuclear 18S rRNA and 28S rRNA, and mitochondrial cytochrome *b* genes, using Thyasiridae species as out-groups. *Phacoides pectinatus* is excluded from this tree because of its unstable position within the large clade. The inset to the right shows details of the larger clades. Support values are Bayesian posterior probabilities (%). Details of taxa in Table 1.

Figure 5. Chronogram generated by BEAST for species of Lucinidae, and calibrated using ten fossil records. The position of each calibration point is indicated by the numbers in circles (see the Material and methods and Discussion sections for details about the fossils). Error bars for node ages are the 95% highest posterior density intervals; clades with less than 50% support have no error bars; the root node has node bar trimmed by 50% for clarity. New subfamily divisions are shown on the right-hand side, with details presented in Table 3.

Table 3. Proposed classification of Lucinidae based on the molecular analyses and including those genera with living representatives only

Lucinidae Fleming, 1828
PEGOPHYSEMINAE new subfamily Taylor & Glover herein
   Pegophysema Stewart, 1930 (*Lucina schrammi* Crosse, 1876)
   Cavatidens Iredale, 1930 (*Cavatidens omissa* Iredale, 1830)
   Cryptophysema Taylor & Glover, 2005 (*Lucina vesicula* Gould, 1850)
   Euanodontia Taylor & Glover, 2005 (*Lucina ovum* Reeve, 1850)
   Loripinus Monterosato, 1883 (*Lucina fragilis* Philippi, 1836)
   Unconfirmed:
      Afrophysema Taylor & Glover, 2005 (*Cryptodon eutornus* Tomlin, 1921)
      Bythosphaera Taylor & Glover, 2005 (*Cryptodon watsoni* Smith, 1885)
      Meganodontia Bouchet & Cosel 2004 (*Meganodontia acetabulum* Bouchet & Cosel, 2004)
LEUCOSPHAERINAE new subfamily Taylor & Glover herein
   Leucosphaera Taylor & Glover, 2005 (*Lucina* (*Loripinus*) *salamanensis* Thiele & Jaeckel, 1931)
   Anodontia Link, 1807 (*Anodonta alba* Link, 1807)
   Dulcina Cosel & Bouchet, 2008 (*Dulcina guidoi* Cosel & Bouchet, 2008)
   Pseudolucinisca Chavan, 1959 (*Lucina lacteola* Tate, 1897)
   Undescribed genera – UGS-1, UGS-2. UGS-3
   Unconfirmed:
      Afrolucina Cosel, 2006 (*Afrolucina discontinua* Cosel, 2006)
      Alucinoma Habe, 1958 (*Alucinoma soyae* Habe, 1958)
      Callucina Dall, 1901(*Lucina radians* Conrad, 1841)
      Epidulcina, Cosel & Bouchet, 2008 (*Epilucina delphinae* Cosel & Bouchet, 2008)
      Minilucina, Cosel & Bouchet, 2008 (*Minilucina coriolis* Cosel & Bouchet, 2008)
      Neophysema Taylor & Glover, 2005 (*Neophysema aphanes* Taylor & Glover, 2005)
      Semelilucina Cosel & Bouchet, 2008 (*Semelilucina semeliformis* Cosel & Bouchet, 2008)
      Tinalucina Cosel, 2006 (*Tinalucina aequatorialis* Cosel, 2006)
MYRTEINAE Chavan, 1969
   Myrtea Turton, 1822 (*Venus spinifera* Montagu, 1803)
   Gloverina Cosel & Bouchet, 2008 (*Gloverina vestifex* Cosel & Bouchet, 2008)
   Notomyrtea Iredale, 1924 (*Myrtea botanica* Hedley, 1918)
   Unconfirmed:
      Elliptiolucina Cosel & Bouchet, 2008 (*Elliptiolucina magnifica* Cosel & Bouchet, 2008)
      Eulopia Dall, 1901 (*Lucina sagrinata* Dall, 1886)
      Gonimyrtea Marwick, 1929 (*Loripes concinna* Hutton, 1885)
      Graecina Cosel, 2006 (*Graecina karinae* Cosel, 2006)
      Jorgenia Taylor & Glover, 2009a (*Jorgenia louisiana* Taylor & Glover, 2009a)
      Myrtina, Glover & Taylor, 2007 (*Myrtina porcata* Glover & Taylor, 2007)
      Poumea Glover & Taylor, 2007 (*Poumea coselia* Glover & Taylor, 2007)
      Rostrilucina, Cosel & Bouchet, 2008 (*Rostrilucina garuda* Cosel & Bouchet, 2008)
      Solelucina Glover & Taylor, 2007 (*Solelucina koumacia* Glover & Taylor, 2007)
      Taylorina, Cosel & Bouchet, 2008 (*Taylorina alata* Cosel & Bouchet, 2008)
MONITILORINAE new subfamily Taylor & Glover herein
   Monitilora Iredale, 1930 (*Lucina ramsayi* Smith, 1885)
   Unconfirmed:
      Prophetilora Iredale, 1930 (*Prophetilora arizela* Iredale, 1930)
FIMBRIINAE Nicol, 1950
   Fimbria Mühlfeld, 1811 (*Fimbria magna* Mühlfeld, 1811)
CODAKIINAE Korobokov, 1954
   Codakia Scopoli 1777 (*Venus orbicularis* Linnaeus, 1758)
   Ctena Mörch, 1861 (*Codakia mexicana* Dall, 1901)
   Epicodakia Iredale, 1930 (*Epicodakia consettiana* Iredale, 1930)
   Epilucina Dall, 1901 (*Lucina californica* Conrad, 1887)
   Lucinoma Dall, 1901 (*Lucina filosa* Stimpson, 1851)
   Unconfirmed:
      Epilucina Dall, 1901 (*Lucina californica* Conrad, 1887)

Table 3. *Continued*

LUCININAE Fleming, 1828
  Austriella Tenison-Woods, 1881 (*Austriella sordida* Tenison-Woods, 1881)
  Bathyaustriella Glover, Glover *et al*. 2004 (*Bathyaustriella thionipta* Glover *et al*., 2004)
  Bretskya Glover & Taylor, 2007 (*Bretskya scapula* Glover & Taylor, 2007)
  Cardiolucina Sacco, 1901 (*Cardium agassizi* Michelotti, 1839)
  Cavilinga Chavan, 1937 (*Lucina trisulcata* Conrad, 1841)
  Chavania Glover & Taylor, 2001 (*Lucina erythraea* Issel, 1869)
  Discolucina Glover & Taylor, 2007 (*Lucina virginae* Deshayes, 1832)
  Divalinga Chavan, 1951 (*Lucina quadrisulcata* d'Orbigny, 1846)
  Divaricella Martens, 1880 (*Lucina (Divaricella) angulifera* Martens, 1880
  Funafutia Glover & Taylor, 2001 (*Lucina levukana* Smith, 1885)
  Indoaustriella Glover *et al*., 2008 (*Lucina plicifera* Adams, 1855)
  Lepidolucina Glover & Taylor, 2007 (*Lucina venusta* Philippi, 1847)
  Loripes Poli, 1791 (*Loripes lacteus* Poli, 1791)
  Lucina Bruguière, 1797 (*Venus pensylvanica* Linnaeus, 1758)
  Lucinella Monterosato, 1883 (*Lucina commutata* Philippi, 1836)
  Lucinisca Dall, 1901 (*Lucina nassula* Conrad, 1846)
  Parvilucina Dall, 1901 (*Lucina tenuisculpta* Carpenter, 1864)
  Phacoides Gray, 1847 (*Tellina pectinata* Gmelin, 1791)
  Pillucina Pilsbry, 1921 (*Pillucina spaldingi* Pilsbry, 1921)
  Radiolucina Britton, 1972 (*Phacoides amiantis* Dall, 1901)
  Rasta Taylor & Glover, 2000 (*Rastafaria thiophila* Taylor & Glover, 1997)
  Stewartia Olsson & Harbison, 1953 (*Lucina anodonta* Say, 1824)
  Troendleina Cosel & Bouchet, 2008 (*T. marquesana* Cosel & Bouchet, 2008)
  Wallucina Iredale, 1930 (*Lucina jacksoniensis* Smith, 1885)
  Unconfirmed:
    Barbierella Chavan, 1938 (*Lucina barbieri* Deshayes, 1857)
    Bourdotia Dall, 1901 (*Lucina bourdoti* Cossmann, 1882)
    Cavilucina Fischer, 1887 (*Lucina sulcata* Lamarck, 1806)
    Divalucina Iredale, 1936 (*Cyclas cumingi* A. Adams, 1864)
    Falsolucinoma Cosel, 2006 (*Lucina leloeuffi* Cosel, 1989)
    Ferrocina Glover & Taylor 2007 (*Ferrocina multiradiata* Glover & Taylor, 2007)
    Gibbolucina Cossmann, 1904 (*Venus callosa* Lamarck, 1806)
    Here Gabb, 1866 (*Lucina richtofeni* Gabb, 1866)
    Joellina Cosel, 2006 (*Joellina dosiniformis* Cosel, 2006)
    Keletistes Oliver, 1986 [*Loripes (Keletistes) rhizoecus* Oliver, 1986]
    Lamellolucina Taylor & Glover, 2006 (*Lamellolucina pilbara* Taylor & Glover, 2002)
    Lamylucina Cosel, 2006 [*Phacoides (Lucinoma) gainei* Lamy, 1920]
    Liralucina Glover & Taylor, 2007 (*Phacoides sperabilis* Hedley, 1909)
    Nevenulora Iredale, 1930 (*Lucinida hilaira* Hedley, 1917)
    Parvidontia Glover & Taylor, 2007 (*Parvidontia laevis* Glover & Taylor, 2007)
    Pleurolucina Dall, 1901 (*Lucina leucocyma* Dall, 1886)
    Plicolucina Glover *et al*., 2004 (*Plicolucina flabellata* Glover *et al*., 2004)
    Pompholigina Dall, 1901 (*Lucina gibba* Gray, 1825)
?Milthinae Chavan, 1969
  Miltha H. & A. Adams, 1857 (*Lucina childreni* Gray, 1824)
  Eomiltha Cossmann, 1912 (*Lucina contorta* Defrance, 1823)

Genera listed as 'Unconfirmed' are without molecular confirmation of position. Type species of genera in parentheses.

Leucosphaera, and *Dulcina*. The clade includes *Anodontia alba* from the western Atlantic, *Pseudolucinisca lacteola* from southern Australia (Glover & Taylor, 2008), and the small, semitransparent, thin-shelled *Leucosphaera*, a common but little recorded lucinid in offshore fine sediments of the Indo-West Pacific, and previously confounded with juvenile '*Anodontia*' (see Taylor & Glover, 2005; Glover & Taylor, 2007). Additionally, the group includes some deeper water forms including species of *Dulcina*,

together with three undescribed species and genera (UGS-1, UGS-2, and UGS-3).

It was initially surprising that *Anodontia alba* (Figs 6B, 7F) did not group with the superficially similar taxa, usually called '*Anodontia*' (Williams *et al*., 2004), now included here in the Pegophyseminae (see above). *Anodontia alba* and the eastern Pacific sister species *Anodontia edentuloides* (Verrill, 1870), however, differ from pegophysemines in both shell characters and internal anatomy, for example lacking the mantle septum and digitate mantle gills (Taylor & Glover, 2005). The Eocene (Ypresian) species *Eophysema cossmanni* Chavan, 1941, from the Paris Basin, classified by Strougo (1975) into a new genus *Rawya* (type species *Lucina pharaonis* Bellardi, 1854), has many characters of *Anodontia alba*, but, in addition, has small cardinal teeth (Fig. 6A). We regard this species as a possible early representative of the *Anodontia alba* lineage. Cardinal teeth are absent in recent species, but they possess a smooth triangular area beneath the umbo ('aire dentaire' of Chavan, 1937–1938), corresponding to the position of teeth in dentate taxa. From this evidence we suggest that the *Anodontia alba* clade was separate from the Pegophyseminae at least by the mid-Eocene. The chronogram (Fig. 5) suggests a much older divergence of the clades in the late Cretaceous, at 100 ± 25 Ma.

Other genera in this clade have a poor or unrecognized fossil record, including the laterally compressed, edentulous deep-water *Dulcina* and *Alucinoma* (Cosel & Bouchet (2008). Two Miocene species, *Lucina strigosa* Michelotti, 1861 and *Lucina michelotti* Mayer, 1858 were assigned to *Pseudolucinisca* by Chavan (1959), but these species possess lateral teeth, unlike any living forms (Glover & Taylor, 2008).

MYRTEINAE CHAVAN, 1969

Myrteinae comprise a diverse, poorly studied group of lucinids, usually associated with deeper water, offshore habitats. Chavan (1969) included 11 genera within his subfamily Myrteinae: five of these (*Myrtea*, *Gonimyrtea*, *Monitilora*, *Lucinoma*, and *Prophetilora*) with living species and six others including only fossil species. Our molecular results indicate that *Monitilora* and *Lucinoma* group in separate subfamilies, Monitilorinae and Codakiinae, respectively, and are discussed in detail below. The position of *Gonimyrtea* and *Prophetilora* remains uncertain, pending further molecular analysis. We analysed six species classified in the genera *Myrtea*, *Notomyrtea*, and *Gloverina*, the latter a recently described genus (Cosel & Bouchet, 2008) included here in the Myrteinae for the first time. Our results (Figs 1–5) show that Myrteinae form a highly supported clade sister to all other lucinids, except the Pegophyseminae and Leucosphaerinae.

In our new concept, Myrteinae share some common morphological features, such as thin, elongate shells and regularly spaced commarginal lamellae that are often elevated above the dorsal shell margin. Some species have radial folds between the lamellae, but never strong radial ribbing. Additionally, they have short, anterior adductor muscle scars, narrow hinges with small to obscure cardinal teeth, and in some species a clearly asymmetric lunule.

Other newly described genera from the deep sea, including *Elliptolucina*, *Taylorina*, *Rostrilucina*, *Graecina* (Cosel, 2006; Cosel & Bouchet, 2008), and *Jorgenia* (Taylor & Glover, 2009a), may also belong in Myrteinae, but no suitable material for molecular analysis was available. Similarly, some shallow water genera, such as *Myrtina* and *Solelucina* (Glover & Taylor, 2007), have shell characters consistent with inclusion in Myrteinae.

Myrteinae are poorly documented in the fossil record, but some *Myrtea*-like bivalves are present throughout the Cenozoic, and *Lucina blanckenhorni* Chavan, 1947 from the late Cretaceous (Campanian 83.5–70.6 Ma) may be part of a '*Myrtea*' stem group. Somewhat earlier, *Paramyrtea sabulosa* Kendrick & Vartak, 2007, from the mid-Cretaceous (Cenomanian) of India, has shell characters compatible with inclusion in the Myrteinae. The chronogram (Fig. 5) indicates a late Cretaceous radiation for the subfamily, with a possible separation from other lucinids earlier in the Cretaceous.

FIMBRIINAE NICOL, 1950

Although represented today by only two living species of *Fimbria*, the group has a long fossil history dating back to the early Jurassic. Chavan (1969) separated living and fossil genera as a distinct family Fimbriidae, but our molecular results for *Fimbria fimbriata* indicate that it falls within the Lucinidae. Living *Fimbria* have distinctive thick, ovate, anteriorly extended shells, with a sculpture of narrow radial ribs that are more prominent at the anterior, and posteriorly these are crossed by closely spaced, rounded commarginal lamellae. The hinge is broad, with large cardinal teeth, and with anterior and posterior lateral teeth in both valves, whereas the anterior adductor scar is very short and scarcely detached from the pallial line.

In the chronogram (Fig. 5) *Fimbria fimbriata* aligns as a sister taxon to *Monitilora ramsayi*, Codakiinae, and Lucininae, with a late Jurassic–early Cretaceous divergence. There is a remarkable continuity of shell morphology of *Fimbria*-like
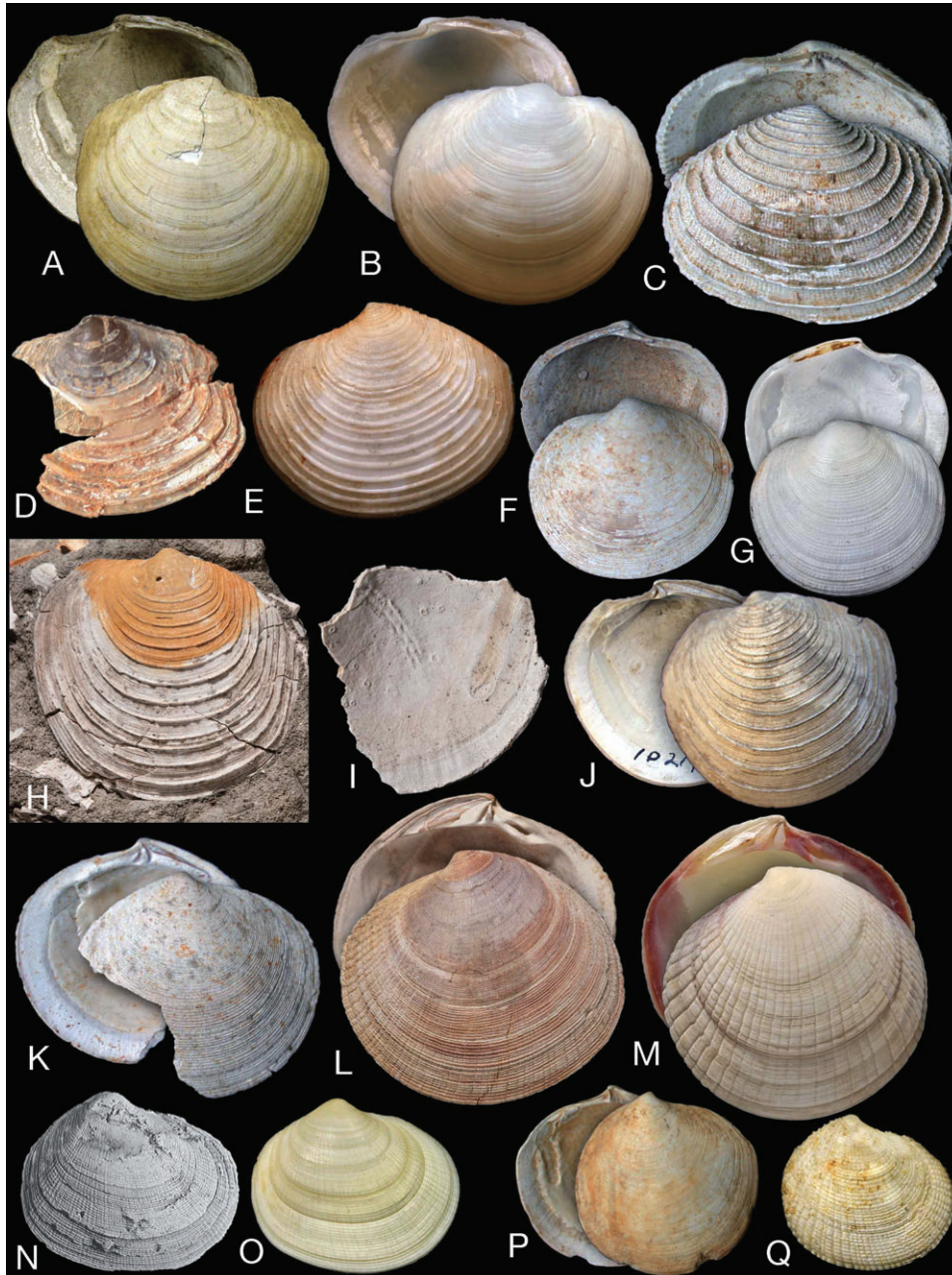
species throughout the Cenozoic and Mesozoic, with bivalves possessing some characters of living *Fimbria* (but not necessarily congeneric) recorded back to the early Jurassic (Pliensbachian–Toarcian) (Dubar, 1948; Monari, 2003). Less certain are the even earlier fossils, for example the late Triassic *Schafhaeutlia* with huge cardinal teeth (Hautmann, 2001) that have been placed in Fimbriidae (e.g. Chavan, 1969), although we can see no convincing evidence for inclusion. Equally, we have doubts concerning the lucinid status of other Mesozoic genera

Sphaera, *Sphaeriola*, and *Haastina* that have been classified in the Fimbriidae.

Monitilorinae new subfamily

Living *Monitilora* are known from eastern Australia, the type species *Monitilora ramsayi* (Smith, 1885), and two unnamed species from South-East Asia. The single species included in the molecular analysis, *Monitilora ramsayi* (Fig. 6G), forms a separate branch with an unstable position, but never aligns

Figure 6. Some fossil lucinids used to calibrate the chronogram or mentioned in the Discussion section, and comparable Recent species. Not to scale. Actual shell lengths (L). Institutional abbreviations: ANSP, Academy of Natural Sciences, Philadelphia; BMNH, the Natural History Museum, London; MNHN, Museum National d'Histoire Naturelle, Paris; RBINS, Royal Belgian Institute of Natural Sciences, Brussels; WAM, Western Australian Museum. A. *Eophysema cossmanni* Chavan, 1941. Eocene (Ypresian), St-Gobain, Aisne, France (MNHN B 53241). Also named *Rawya cossmanni* by Strougo (1975). L = 29.6 mm. B. *Anodontia alba* (Link, 1807). Recent, western Atlantic. Syntype of *Lucina anatelloides* Reeve, 1850 (BMNH 1963553/1). L = 38.6 mm. C. *Fimbria montensis* (Cossmann, 1908). Palaeocene (Danian), Calcaire de Mons, Belgium (RBINS IG5496), exterior and interior of right valve. L = 32.4 mm. D. '*Lucina*' *blanckenhorni* (Chavan, 1947). Cretaceous (Campanian), Mount of Olives, Israel (RBINS IG 21.735). L = 13.2 mm. E. *Myrtea spinifera* (Montagu, 1803). Recent, Milford Haven, UK (BMNH). L = 25.7 mm. F. *Monitilora duponti* (Cossmann, 1908). Palaeocene (Danian), Calcaire de Mons, Belgium. Exterior and interior of left valve (RBINS IG 6544). L = 19.2 mm. G. *Monitilora ramsayi* (Smith, 1885). Botany Bay, New South Wales, Australia (BMNH 1963207). L = 14.5 mm. H. *Lucinoma* sp. undescribed species. Palaeocene (Selandian–Thanetian), 62–59 Ma, Aquia Formation, Aquia Creek, Potomac River, Virginia, USA (BMNH L64868–70). Exterior of left valve. L = 29.5 mm. I. *Lucinoma* sp., details as in (H). Interior of left valve with detail of elongate anterior adductor scar and impression of pallial blood vessel. Muscle scar length = 15.2 mm. J. *Lucinoma filosa* (Stimpson, 1851). Recent, off Martha's Vineyard, MA, USA (ANSP 102172). Exterior of left and interior of right valves. L = 37.0 mm. K. '*Phacoides*' *dejaeri* (Vincent, 1930). Palaeocene (Danian), Calcaire de Mons, Belgium (RBINS IG5611). Exterior and interior of right valve. Possible member of *Codakia* stem group. L = 22.8 mm. L. *Codakia leonina* (Basterot, 1825). Miocene (Aquitanian), Saucats, France (BMNH) L = 45.4 mm. M. *Codakia punctata* (Linnaeus, 1758). Recent, Tuoho, New Caledonia (MNHN). L = 64.0 mm. N. *Epicodakia* sp. Eocene (Bartonian–Priabondian), Kalbarri, Western Australia. Exterior right valve (WAM 05.182). From Darragh & Kendrick, 2008: fig. 1.20). L = 10.4 mm. O. *Epicodakia consettiana* Iredale, 1930. Recent, Houtman Abrolhos Islands, Western Australia (BMNH). L = 18.0 mm. P. *Loripes dujardini* (Deshayes, 1850). Middle Miocene, Manthelan, Loire Basin, France. Exterior and interior of right valve (RBINS IG 10591). L = 18 mm. Q. *Ctena squamosa* (Lamarck, 1806). Oligocene (Rupelian), Etampes, France (BMNH). L = 6.2 mm.

within any other of the major clades. In the BEAST chronogram (Fig. 5) it forms a sister branch to the combined Codakiinae and Lucininae. Chavan (1969) placed *Monitilora* within the Myrteinae, but our analysis shows that *Monitilora* is distinct from Myrteinae, and in view of its phylogenetic position on a separate branch we propose a new subfamily Monitilorinae for this distinctive and long-lived clade. In shell characters *Monitilora* species are subcircular, moderately inflated, with regularly spaced, low, commarginal lamellae that have fine radial folds in the interspaces. The lunule is large and asymmetrical, the cardinal teeth are small, and there is an anterior lateral tooth in the right valve only.

Apart from *Monitilora ramsayi*, the species from southern Australia that have been classified as *Monitilora* (e.g. Lamprell & Whitehead, 1992) should be placed in other genera. '*Monitilora*' *adelaidiana* Cotton & Godfrey, 1938 is similar to *Callucina*, whereas '*Monitilora*' *paupera* (Tate, 1892) probably belongs with the *Myrtea* group. Another little-studied genus, *Prophetilora* (type species *Prophetilora arizela* Iredale, 1930 = *Lucina simplex* Reeve, 1850), has been classified as a subgenus of *Monitilora* (Lamprell & Whitehead, 1992), but no specimens were available for molecular analysis, and its position is uncertain.

Shells with characters very similar to the living *Monitilora ramsayi* can be recognized up to the early Palaeocene (Danian), for example, *Monitilora duponti*

(Cossmann, 1908) (Fig. 6F) from the Calcaire de Mons, Belgium, was previously classified in the genus by Chavan (1937–1938). Our analysis suggests that Monitilorinae split from other lucinids at least by the mid-Cretaceous (Fig. 5). Some *Monitilora*-like bivalves were present in the Mesozoic, but have been placed in the genus *Mesomiltha* Chavan, 1952 (type species *Lucina pulchra* Zittel & Goubert, 1861, Jurassic, Oxfordian): an example being *Mesomiltha* cf. *fallax* (Forbes, 1846), from the Cretaceous (Cenomanian) of India (Kendrick & Vartak, 2007: fig. 13I–M), but a more detailed study of these species is needed.

CODAKIINAE KOROBKOV, 1954

This family group name was proposed by Korobkov (1954) to include *Codakia* and *Ctena*, but not *Lucinoma*. Molecular results (Figs 1–5) demostrate that this is a highly supported, large clade that includes species of *Lucinoma*, *Codakia*, *Ctena*, and *Epicodakia*. Prior morphological analyses (Bretsky, 1970, 1976) did not recognize this grouping, first reported from molecular results by Williams *et al*. (2004). The clade encompasses three distinct, highly supported subclades: one comprising species of *Lucinoma*, another comprising species of *Codakia*, and a third consisting of *Ctena* and *Epicodakia*. The two latter groups include some of the most abundant, tropical, shallow water lucinids, particularly from seagrass habitats.
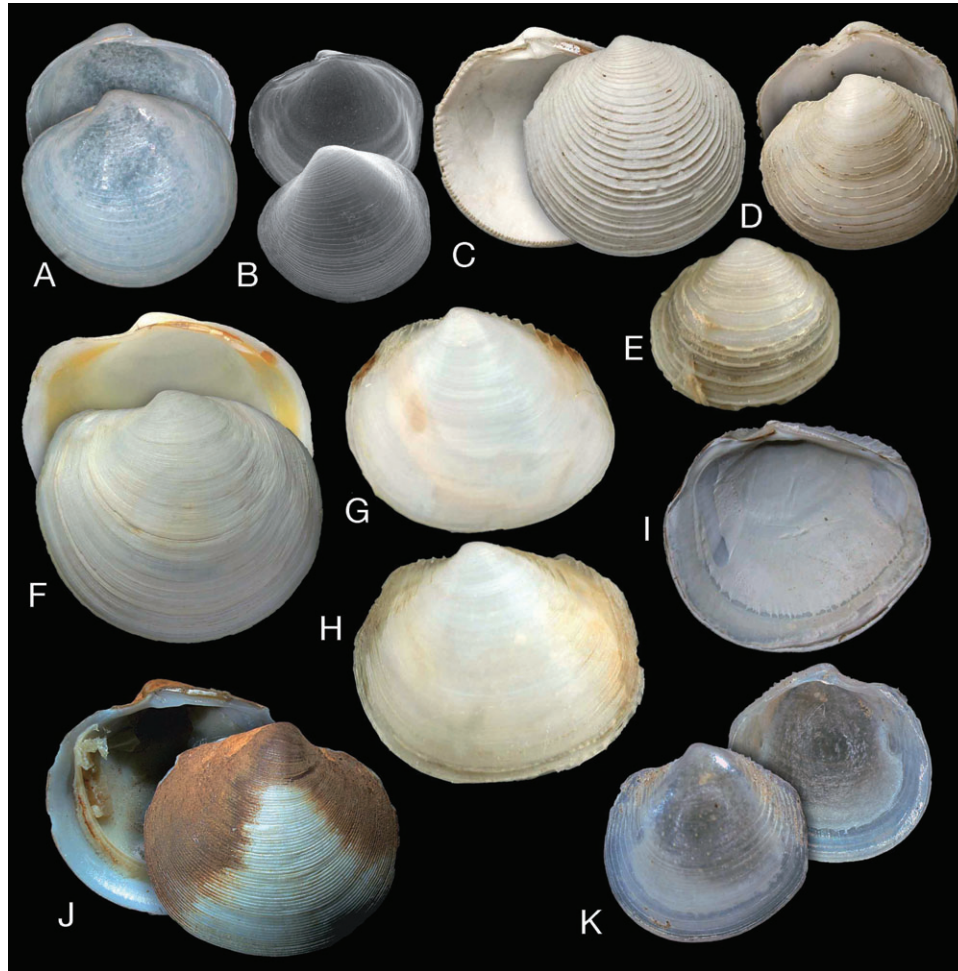
Figure 7. Representatives of the new subfamily Leucosphaerinae including some of the sequenced specimens. Not to scale. L = actual shell lengths. A. *Leucosphaera* cf. *diaphana* Glover & Taylor 2007. Shell from same station as sequenced specimen. Ubajan, Bohol Island, Philippines. PANGLAO 2004, st. S27, 9°41.5′N, 123°51.0′E, 12 m (MNHN). L = 4.9 mm. B. *Leucosphaera diaphana* Glover & Taylor 2007, holotype, New Caledonia (MNHN). L = 6.0 mm. C. *Pseudolucinisca lacteola* (Tate, 1897) (syntype of *Lucina concentrica* Reeve, 1850, St Vincent's Gulf, South Australia (BMNH 1870.10.26.33). L = 21.5 mm. D. Undescribed genus and species (UGS-1). Shells from same station as sequenced specimen figured in E (MNHN). L = 10.3 mm. E. Undescribed genus and species (UGS-1). Maribojoc Bay, Bohol Sea, PANGLAO 2005, st CP 2397, 9°34.9′N, 123°41.7′E. 642–669 m (MNHN IM-2009-10373). L = 7.0 mm. F. *Anodontia alba* Link 1807 'West Indies' (BMNH 1963476-2). L = 53mm. G. *Dulcina* sp. Bohol Sea, Philippines. PANGLAO 2005, st. CP 2335, 9°34.3′N, 123°37.8′E. 729–733 m (MNHN IM-2009-10371). L = 17 mm. H. *Dulcina karubari* Cosel & Bouchet, 2008. Maribojoc Bay, Bohol Sea, Philippines. PANGLAO 2005, st. CP 2331, 9°39.2′N, 123°47.5′E. 255–268 m (MNHN IM-2009-10372). L = 16 mm. I. *Dulcina karubari* Cosel & Bouchet, 2008. Holotype, Tanimbar Islands, Indonesia. KARUBAR, st. CP 63, 8°00′S, 132°58′E. 215 m (MNHN 20729). Right valve to show internal details of shell. L = 27.9 mm. J. Undescribed genus and species (UGS-3). Chesterfield Bank, New Caledonia (MNHN IM-2009-10376). L = 23.5 mm. K. Undescribed genus and species (UGS-2), shell from same station as sequenced specimen. Manga, Bohol Island, Philippines. PANGLAO 2004, st. S20, 9°41.8′N, 123°51.1′E. 10 m specimen. L = 4.0 mm.

From shell characters, *Codakia* and *Ctena* have long been thought to be related, and indeed Bretsky (1976) classified *Ctena* as a subgenus of *Codakia*, but there have been no previous suggestions of a relationship between *Codakia* and *Lucinoma*. Chavan (1969) for example classified *Codakia* and *Ctena* in the subfam- ily Lucininae, but placed *Lucinoma* in Myrteinae, and other authors have treated *Lucinoma* as a subgenus of *Phacoides* (Dall, 1901; Britton, 1970). Alternatively, *Lucinoma* was classified by Bretsky (1976) as a sub- genus of *Miltha*, deriving it from the mid-Eocene genus *Plastomiltha*. Molecular results show no close

relationship between *Lucinoma* species and the *Myrtea* group. Similarly, we found no support for any relationship between *Phacoides* and *Lucinoma*, but, lacking *Miltha* in the analyses, we could not test any relationship between it and *Lucinoma*.

The four species of *Lucinoma* analysed form a well-supported group. Although some species range into the intertidal zone, most *Lucinoma* species live in deeper offshore habitats down to 2050 m. They have shells with regularly spaced, commarginal lamellae, prominent cardinal teeth, and long, narrow, anterior adductor muscle scars. Although fossil *Lucinoma* are frequent in Miocene–Recent deposits, the earliest claimed (Chavan, 1937–1938) is *Lucinoma hannibali* (Clark, 1925) from the Oligocene of Washington, USA (Blakeley Formation, 33.9–23.05 Myr). However, we recognize an earlier undescribed species, *Lucinoma* sp., from the Palaeocene (Selandian–Thanetian, 62–59 Ma), Aquia Formation, Aquia Creek, Potomac River, Virginia, USA (BMNH L64868–70), which has an external sculpture of regularly spaced commariginal lamellae and a long, narrow, anterior adductor muscle scar, features very similar to living *Lucinoma* species (Fig. 6J).

The *Codakia* clade is identified as sister to *Lucinoma* species in the molecular tree, but with low support (Fig. 4). *Codakia* species today are amongst the most well known of Lucinidae, including *Codakia orbicularis* (Linnaeus, 1758) from the western Atlantic (Frenkiel & Mouëza, 1995; Gros *et al.*, 2003). The earliest known *Codakia* that closely resembles living species is *Codakia leonina* (Basterot, 1825) from the late Miocene of southern Europe (Burdigalian, 20.4–15.9 Ma) (Fig. 6L). Earlier fossils have been claimed as part of the *Codakia* group, but all lack radial sculpture. These may form part of a *Codakia* stem group, and include '*Phacoides*' *concentricus* (Lamarck, 1806) from the Eocene (Lutetian 48.6–40.4 Ma) of the Paris Basin, and the earlier '*Phacoides*' *dejaeri* (Vincent, 1930) from the Palaeocene (Danian 65–61 Ma), Calcaire de Mons, Belgium (Glibert & Van de Poel, 1973) (Fig. 6K). Both of these species resemble living *Codakia* (Fig. 6M) in having a subcircular shape, an anterior lateral tooth close to the cardinals, a triangular resilifer, and a short, pointed, anterior adductor muscle scar. Chavan (1937–1938) claimed the Palaeocene '*Lucina*' *gravesi* (Deshayes, 1857) as an early *Codakia*, but the preservation is poor. The late Jurassic–early Cretaceous species *Lucina crassa* Sowerby, 1827 was placed in *Codakia* by Kelly (1992), mainly on the basis of the fine radial grooves and some similarity of hinge teeth, but it has strong resemblance to species of the Jurassic genus *Jagonoma*.

Previous discussions concerning the history of the *Codakia* group centre on the position of *Epilucina*

(Chavan, 1937–1938; Bretsky, 1976). The name *Epilucina* has been widely used in the literature for fossils as old as the late Cretaceous (Speden, 1970), through the Palaeocene (Glibert & Van de Poel, 1967, 1973), Eocene (Pacaud & Le Renard, 1995), and Neogene (Kurihara, 2007), but there is considerable confusion concerning the relationships of the living type species *Epilucina californica* (Conrad, 1837) from the north-eastern Pacific (Kurihara, 2007). For example, Chavan (1969) places it as a subgenus of *Codakia*, whereas Bretsky (1976) argued for a relationship with *Myrtea*. The shell characters are rather equivocal, and it is clear that without molecular evidence the wider relationships of this species and genus are difficult to determine.

The *Ctena* species analysed form a distinct group separate from *Codakia* and *Lucinoma*. There has been some confusion over the concepts of *Ctena* and *Epicodakia*, names often used interchangeably, because Chavan (1969: fig. E3.9a,b) illustrated *Ctena divergens* (Philippi, 1850) as the example of *Epicodakia* rather than the type species, *Epicodakia consettiana* (Iredale, 1930). The two genera are probably closely related, but we lack molecular data for *Epicodakia consettiana*. The species we analysed, *Epicodakia tatei* (Angas, 1879), has shell characters that are more similar to *Ctena*. The earliest fossil *Ctena* with characters similar to living species is probably *Ctena squamosa* (Lamarck, 1806) from the Oligocene (Rupelian, 33.9–28.4 Ma) of Etampes, France (Fig. 6Q). The earlier *Lucina mayeri* Deshayes, 1857 (Eocene, Bartonian) was claimed by Chavan (1937–1938) as a *Ctena*, but this species has been classified as *Parvilucina* by Pacaud & Le Renard (1995). Convincing fossil *Epicodakia* species (Fig. 6N) with shell characters similar to living southern Australian forms (Fig. 6O) are recorded from the middle–late Eocene (Bartonian–Priabonian, 40.4–33.9 Ma) deposits of Western Australia (Darragh & Kendrick, 1980, 2008). *Jagonoma circumcisa* (Zittel & Goubert, 1861) from the late Jurassic (Oxfordian) of France has been claimed as an ancestor of the *Ctena* clade (Chavan, 1952), but lacks any radial sculpture. Further study of Mesozoic lucinids is needed to establish the possible, if any, relationships with Cenozoic and living taxa.

Fossil evidence of *Lucinoma* and *Codakia* clades places both back to the Palaeocene, suggesting an earlier divergence. Similarly, the origin of the *Ctena*/ *Epicodakia* group is likely to be Palaeocene or earlier. The BEAST chronogram (Fig. 5) suggests a late Cretaceous–Palaeocene divergence of the three clades.

LUCININAE FLEMING, 1828

This is a large subfamily encompassing many shallow water lucinids, including *Lucina*, *Loripes*, *Austriella*,

Phacoides, *Divalinga*, the speciose genera *Parvilucina*, *Cardiolucina*, and *Pillucina*, with a few taxa from deeper water. They are extremely disparate in shell morphology, including, for example, heavily sculptured forms with both radial and commarginal elements, and others with almost smooth shells. Most have well-developed hinge teeth, both cardinals and laterals, but there are also edentulous species. The subfamily also includes several species with divaricate sculpture that have sometimes been classified in a separate subfamily Divaricellinae. A number of well-supported subgroups can be identified, and some of these are highlighted below.

Funafutia levukana, a small species from fore-reef habitats in the Indo-West Pacific (Glover & Taylor, 2007), has an unstable position. It lies outside and sister to all other Lucininae in the combined gene tree (Fig. 4), although in the 18S tree (Fig. 1) it lies within Lucininae, and in the cyt*b* tree (Fig. 3) it groups as a sister to *Fimbria*. We would like to have confirmed this result with a sequence from a second specimen, but no additional material was available. The species was previously thought to be related to the *Loripes* subclade, as it has a short internal ligament (Glover & Taylor, 2001), but does not align within this group in the present analysis, and with hindsight is not very similar in other shell characters.

The subclade containing *Lucina* species also includes *Divalinga*, *Lepidolucina*, and *Discolucina*, as well as *Phacoides* (Figs 4, 5). Two species of *Lucina* were analysed: *Lucina adansoni* d'Orbigny, 1839 from the Cape Verde Islands and *Lucina pensylvanica* (Linnaeus, 1758) from four locations in the western Atlantic, with the sample from Florida Keys differing from the other three sites. Morphological evidence from periostracal characters has suggested a complex of species in the *Lucina pensylvanica* group of the western Atlantic (Gibson-Smith & Gibson-Smith, 1982; Taylor *et al*., 2004). The earliest fossil that is usually attributed to *Lucina* is *Lucina carinifera* Conrad, 1833 from the middle Eocene (Bartonian) of eastern USA. Prominent later forms include the abundant *Lucina columbella* Lamarck, 1818 from the Miocene of southern Europe. The chronogram (Fig. 5) indicates a divergence of *Lucina* from the rest of the clade during the Oligocene rather than the Eocene. *Lucina oligocaenica* Cossmann, 1922 from the Oligocene (Rupelian) of Gironde, France is similar in shell characters to living species.

The position of *Phacoides pectinatus*, a well-studied, haemoglobin-rich species from mangrove fringes of the western Atlantic (Frenkiel, Gros & Mouëza, 1996), is unstable on a long branch in the 18S and 28S trees, but always nests within the Lucininae, and in the chronogram within the *Lucina*

subclade (Fig. 5). Despite the widespread use of the name in the past for various lucinids now consigned to other genera and subfamilies, there appears to be only one living species of *Phacoides*, and its relationships with other living genera are uncertain, although Bretsky (1976) classified it as a subgenus of *Lucina*. Chavan (1937–1938) claimed a continuous record of *Phacoides* from the early Eocene, but included in his generic concept were species that are now recognized as belonging to other genera, such as *Lamellolucina* (Taylor & Glover, 2002), so that all records need re-evaluation.

From the western Atlantic and eastern Pacific, three species of *Lucinisca*, two of *Radiolucina*, and '*Parvilucina*' *costata* form another well-supported subclade. *Radiolucina amiantus* (Dall, 1901) has been associated with *Cardiolucina* species (formerly *Bellucina*) from the Indo-Pacific by shell characters (Britton, 1972; Bretsky, 1976), but they are distant in our molecular tree. '*Parvilucina*' *costata* (d'Orbigny, 1842), a common western Atlantic species, has been variously placed in *Codakia*, *Ctena*, and *Parvilucina* (see Bretsky, 1976), but there is no molecular support for any of these possibilities. A new generic name is needed to accommodate this species and some similar fossils.

A large, highly supported (PP = 100%) subclade includes species of *Loripes*, *Pillucina*, *Chavania*, *Wallucina*, and *Lucinella* (hereafter *Loripes* subclade). Their geographical range covers the eastern Atlantic, Mediterranean, Indo-West Pacific, and southern Australia, but not the western Atlantic and eastern Pacific [with the exception of the rare *Loripes brasilianus* (d'Orbigny, 1842) from Brazil]. All species within this clade possess a short, obliquely inset, internal ligament that differs structurally from the internal ligament in the Pegophyseminae (Taylor & Glover, 2005: fig. 28H), and the deeply inset resilifer of *Codakia* species. Shell sculpture is variable: *Loripes* and *Wallucina* have relatively smooth shells with fine commarginal lamellae; *Lucinella* has divaricate ribbing; and *Pillucina* species have both radial and commarginal elements. We have not been able to repeat our previous result (Williams *et al*., 2004), where a specimen of *Pillucina vietnamica* Zorina, 1978 from Port Douglas, Australia aligned in the Codakiinae clade. In the present analysis other samples of *P. vietnamica* from Thailand and the Arabian Gulf aligned within the *Loripes* clade. Using evidence largely from ligament morphology, Chavan (1937–1938) thought the lucinids of the *Loripes* subclade were related to *Ctena* and *Codakia*, whereas Bretsky (1976) suggested a relationship between *Loripes* and *Anodontia*. From the molecular analysis there is no support for either of these suggestions, with the *Loripes* clade nesting within the Lucininae,

and distant from both *Codakia* and 'Anodontia' clades.

The earliest *Loripes* with characters similar to the living species is *Loripes dujardini* (Deshayes, 1850) (Fig. 6P) from the early Miocene (Aquitanian 23–20 Ma), and the chronogram suggests a divergence of the whole *Loripes* subclade in the late Eocene (Fig. 5). Species of the extinct genus *Microloripes* (type species *Loripes dentata* Defrance, 1823) that range from the Palaeocene to the Pliocene also possessed an obliquely inset internal ligament similar to that of *Loripes*, and may represent a stem group of the clade. Although some lucinid species from the late Jurassic have been placed in *Loripes* and a subgenus *Discoloripes* (Wellnhofer, 1964), these lack the oblique internal ligament that characterizes the *Loripes* group, and should be excluded.

The Indo-West Pacific, mangrove-associated *Austriella* and *Indoaustriella* species form a robust clade: *Austriella corrugata* (Deshayes, 1843) lacks hinge teeth, whereas the four *Indoaustriella* species analysed possess lateral teeth (Glover *et al.*, 2008). There is no fossil record for any of these mangrove species, but a Miocene origin is suggested by the chronogram (Fig. 5). In our previous analyses (Glover *et al.*, 2004; Williams *et al.*, 2004), the hydrothermal vent species *Bathyaustriella thionipta* aligned with *Austriella corrugata*, with which it shares some shell and anatomical similarities. With the larger taxon set of the present analysis it groups closely with *Parvilucina* species (Figs 4, 5), but there is little obvious morphological resemblance.

The genus *Cardiolucina* was represented in our analysis by six species that formed a robust clade, sister to the *Indoaustriella/Austriella* group (Figs 4, 5). *Cardiolucina* species are abundant in the Indo-West Pacific ocean, ranging from the intertidal [*Cardiolucina pisiformis* (Thiele, 1930) and *Cardiolucina semperiana* (Issel, 1869)] to depths of more than 800 m [*Cardiolucina quadrata* (Prashad, 1932)], with two species known from the southern Atlantic (Taylor & Glover, 1997). *Cardiolucina* (as *Bellucina*) has previously been related to *Parvilucina* (e.g. Bretsky, 1976), but Chavan (1969) classified it as a subgenus of *Lucina* (as *Linga*). Neither possibility is supported by our molecular analysis. The type species, *Cardiolucina agassizi* (Michelotti, 1839) occurs in the middle and late Miocene of southern Europe, whereas the chronogram (Fig. 5) suggests an Oligocene origin for the clade.

Polyphyly of Divaricellinae

Lucinids possessing divaricate sculpture species were formerly united in the subfamily Divaricellinae Korobkov, 1954 (see also Glibert & Van de Poel, 1967; Chavan, 1969), with living species classified into six genera: *Bourdotia*, *Divalinga*, *Divalucina*, *Divaricella*, *Lucinella*, and *Pompholigina*. From morphological evidence and preliminary molecular analysis, doubts have been expressed concerning the monophyly of the group (Dekker & Goud, 1994; Williams *et al.*, 2004). In our present analysis, *Divalinga bardwelli* (Iredale, 1936) and *Divalinga quadrisulcata* (d'Orbigny, 1842) align together, but are widely separated within the Lucininae from *Divaricella irpex* (Smith, 1885) and *Lucinella divaricata* (Linnaeus 1758). The latter species has a hinge and an oblique internal ligament similar to taxa in the *Loripes* group, where it nests in the molecular analysis. For *Divalinga* and *Divaricella*, detailed morphology of the divaricate ribs reveals constructional differences, as demonstrated by Checa (2002), in addition to dissimilarity in hinge and ligament structure. Our evidence suggests a separate evolution of divaricate shell sculpture in the three groups, and we corroborate the remarks of Dekker & Goud (1994) that Divaricellinae is not a valid division of the Lucinidae. Species from other genera with divaricate sculpture, *Divalucina*, *Bourdotia*, and *Pompholigina*, have yet to be analysed. The fossil genus *Paralucinella* (type species *Lucina undulata* Deshayes, 1857) from the Oligocene of France has a divaricate sculpture, but lacks an internal ligament, and can be excluded from a relationship with *Lucinella*.

Uncertain status of Milthinae

Chavan (1969) introduced the subfamily Milthinae, including eight genera with living species and 14 fossil genera, grouping together taxa with commarginal sculpture and long anterior adductor muscle scars. From our molecular analysis most of the included living genera, such as *Anodontia*, *Pegophysema*, and *Austriella*, align in other clades, leaving only *Miltha* and *Eomiltha*, which were not included in our analysis, being represented today by three rare living species: *Miltha childreni* (Gray, 1825) from the western Atlantic, *Miltha xantusi* (Dall, 1905) from the eastern Pacific, and *Eomiltha voorhoevei* (Deshayes, 1857) from the Mozambique Channel. The position of both of these genera is uncertain and, despite their names, may not be related. Both *Miltha* and *Eomiltha* have fossil records extending to the Palaeocene, with fossil species often abundant throughout the Cenozoic, with a *Miltha* species common in shallow water deposits of south-western Australia as recently as the early Pleistocene (Ludbrook, 1978). The fossil genera included by Chavan in Milthinae, such as *Pseudomiltha*, are frequent in the Eocene, and possess very long anterior adductor muscle scars. Other fossils such as *Bulacanites* (Kase & Aguilar, 2007) and *Superlucina* (Taylor & Glover, 2009b) also had long

adductor scars, but again their relationship to *Miltha* or any other lucinids is uncertain. In conclusion, the status of Milthinae as conceived by Chavan (1969) is polyphyletic, but the positions of *Miltha* and *Eomiltha* are yet to be resolved.

Incongruence of molecular results with classifications based in shell and morphological characters

Molecular analyses have demonstrated that traditional shell characters are a less satisfactory guide to suprageneric relationships, with major incongruencies apparent between the molecular trees and phylogenetic hypotheses derived from shell characters (Chavan, 1937–1938; Bretsky, 1970, 1976). These include the position of the '*Anodontia*' group, relationships of *Pseudolucinisca*, the relationships of *Lucinoma* with the *Codakia*/*Ctena* group, the polyphyly of the shell-based Myrteinae, and non-monophyly of genera with divaricate sculpture. However, no rigorous cladistic analysis of shell characters has yet been attempted, but determining homology would be difficult, with very similar features occurring in several major clades. Hinge teeth characters have been extensively used in discussions of fossil lucinids, but their numbers and morphology seem labile, and edentulous forms appear in several different clades (Glover *et al.*, 2008). An example of the difficulties in using shell characters is in the form of the ligament. In most lucinids the ligament is external and set in a shallow groove, but in a few species part of the ligament is internal and set in an oblique groove that extends posteriorly and laterally into the left and right valves. Such a ligament, exemplified by *Loripes lucinalis* (Allen, 1960; Glover & Taylor, 2001), also occurs in species of *Wallucina*, *Pillucina*, *Chavania*, and *Lucinella*, which form a monophyletic subclade within the Lucininae. A similar internal ligament also occurs in *Funafutia levukana*, a small species from coral reef slope habitats placed within the *Pillucina*/*Wallucina* group by Glover & Taylor (2001). However, the molecular analysis placed this species as a sister taxon to all other Lucininae and distant from the *Loripes*/*Pillucina* subclade, suggesting an independent derivation of this form of internal ligament. Some species in the Pegophyseminae clade, such as *Euanodontia ovum* (Taylor & Glover, 2005: fig. 28) also possess laterally extended internal ligaments, but these differ in morphology from the *Loripes* type and are unlikely to be homologous. In summary, a revised and more objective study of shell characters is needed so that the rich fossil record of Lucinidae might be better incorporated into the phylogenetic analysis.

Some anatomical characters, such as the extent and type of posterior mantle fusion (Taylor & Glover, 2006), also have potential for phylogenetic analysis, but are poorly known for the majority of taxa. Different morphologies of the mantle respiratory organs, the 'mantle gills', were reported by Taylor & Glover (2000, 2006). These are sporadically developed amongst the Lucinidae in Pegophyseminae, *Codakia* species, and, within Lucininae, in *Phacoides pectinatus* and *Lucina* species. These organs differ structurally in the different clades suggesting separate derivations. Ctenidial structure has been widely investigated by electron microscopy in several major groups of Lucinidae, but differences are minor with no clear phylogenetic signal (e.g. Frenkiel & Mouëza, 1995; Gros, Frenkiel & Mouëza, 1998; Ball *et al.*, 2009).

Diversification history of Lucinidae

There is a good fossil record of Lucinidae throughout the Mesozoic and Cenozoic, and as demonstrated in the discussion of our recognized subfamilies it is possible to trace morphological lineages of living taxa through the Cenozoic. However, the relationships of some extinct taxa from the early Cenozoic are problematic, as is also the case for most Mesozoic lucinids.

There is only a patchy fossil record of Lucinidae through the Palaeozoic. *Illionia prisca* (Hisinger, 1837), a species that was abundant in the late Silurian of Gotland, Sweden (Liljedahl, 1991a, b), possesses convincing lucinid characters (Taylor & Glover, 2006). *Paracyclas* and *Phenacocyclas* species are known from the Devonian (LaRocque, 1950; Bailey, 1983; Johnston, 1993). *Paracyclas* species are common in some facies (Bailey, 1983), and some of these have ventrally detached, anterior adductor muscle scars characteristic of Lucinidae (LaRocque, 1950: pl. 12, fig. 12; Taylor & Glover, 2006: fig. 14B), but different from the elongate non-detached scar illustrated by Johnston (1993; figs 81A, 82D), who placed them in a separate family Paracyclidae. An earlier *Paracyclas* species from the Ordovician is claimed by Zong-Jie & Cope (2004), but the preservation is poor. *Palaeolucina* is widely reported from the Carboniferous of China (Chen, 1976), but few details of morphology are available. Later, *Gigantocyclus* (Boyd & Newell, 1979) from the Permian of Tunisia can be confidently placed in the Lucinidae.

For the Mesozoic there is a dearth of confirmed lucinids from the Triassic: Hautmann & Nützel (2005) suggested the small early Triassic species, *Sinbadiella pygmaea* Hautmann & Nützel, 2005, as a possible lucinid, but without strong evidence. '*Lucina*' *deshayesii* Klipstein, 1845 (holotype, BMNH Palaeontology Department 35194) from the St Cassian Formation (late Triassic, Carnian) may be a true lucinid, but the preservation is poor. *Schaflaeutlia* is usually

classified in the Fimbriinae (Chavan, 1969; Haut-mann, 2001), but we regard this placement as uncertain. By the late Triassic (Rhaetian), lucinids resembling modern forms are more frequent (Ivimey-Cook *et al*., 1999). Throughout the Jurassic and Cretaceous lucinids are more diverse, but are generally under-researched. Preservation is often poor, with many nominal species based on internal moulds, with hinge and muscle scar details often unknown. Many species are still named '*Lucina*' or are 'shoe-horned' into the few available generic names, and most need critical study. A few studies of well-preserved faunas indicate that diversity and abundance of Mesozoic lucinids is greater than was commonly thought, with several new genera introduced over last few years (Chavan, 1952; Fischer, 1969; Kelly, 1992; Kendrick & Vartak, 2007; Amano *et al*., 2008; Kiel, Campbell & Gaillard, 2010). Furthermore, only a few small species (< 1cm in length) have been described, although they undoubtedly existed as evidenced in Cenozoic and Recent faunas. At present it is difficult to assess the relationships of most Mesozoic lucinids to later Cenozoic and modern clades.

By contrast to earlier periods, Cenozoic faunas are much better documented. Nonetheless, there is a significant increase in the diversity and abundance of lucinids from the Palaeocene onwards. For example, from the Palaeocene (Danian) of Belgium, 24 species of lucinids were recorded, comprising a remarkable 19% of the total bivalve species found (Glibert & Van de Poel, 1973). Ninety-six species in 28 genera are recorded from the Eocene of the Paris Basin (Cossmann & Pissaro, 1904–06; Pacaud & Le Renard, 1995), and similarly diverse faunas occur in the Miocene (Sacco, 1901; Cossmann & Peyrot, 1909–1912; Gardner, 1926). The chronogram (Fig. 5) demonstrates that many of the clades of living lucinids originated in the Eocene, with radiations in the Miocene. Notable appearances in the late Cenozoic were the ecologically important *Codakia* and *Ctena* species in shallow tropical habitats, and also the dominance of *Lucinoma* species at hydrocarbon seeps, especially in the northern Pacific (Majima, Nobuhara & Kitazaki, 2005). Some lucinids that were abundant during the early Cenozoic have either become extinct, such as *Pseudomiltha* species, or, are now extremely rare, as for example *Eomiltha* and *Miltha*.

In pre-Miocene times the external sculpture of lucinids was usually in the form of low commarginal lamellae, but then species with radial and cancellate sculpture became much more frequent in the Miocene and in younger faunas. Genera with prominent radial ribbing include shallow water tropical species in the Codakiinae and Lucininae clades such as *Codakia*, *Ctena*, *Cardiolucina*, *Lucinisca*, *Pleurolucina*, *Parvilucina*, and *Radiolucina*.

Patterns of habitat occupation

Most lucinids occur in tropical, subtropical, or warm temperate waters, the few species inhabiting cool temperate latitudes are mainly species of *Lucinoma*, for example *Lucinoma filosa* (Stimpson, 1851), from the eastern seaboard of North America to New Brunswick, Canada (Britton, 1970), *Lucinoma annulata* (Reeve, 1850) from the eastern Pacific to 61°N in Alaska (Coan, Valentich Scott & Bernard, 2000), *Lucinoma borealis* from northern Europe to the Lofoten Islands (68°N), Norway (BMNH collections), and *Lucinoma lamellata* (Smith, 1881) at Cape Horn (55°45′S) (Holmes, Oliver & Sellanes, 2005). Additional higher latitude species include *Myrtea spinifera* (Montagu, 1803), which ranges from the Mediterranean to 64°48′N in Norway, and *Loripes lucinalis* from north western Africa to southern Britain, whereas *Parvilucina tenuisculpta* (Carpenter, 1864) occurs from the north-eastern Pacific to southern Alaska (61°N) (Coan *et al*., 2000). The tiny '*Epicodakia*' *falklandica* (Dell, 1964) is recorded from the Southern Ocean (Zelaya, 2005), but the generic placement of this species is uncertain.

Lucinids have often been reported from various marine habitats with an elevated input of organic material, such as seagrass beds or hydrocarbon seeps. In this section we address the question of whether there is any phylogenetic pattern to the habitat preferences of lucinids: are some individual clades associated with particular habitats?

Seagrass beds: There is a well-known strong association of lucinids with seagrass beds both in tropical and temperate seas (reviewed by Barnes & Hickman, 1999). Seagrass beds entrap organic detritus, and have higher rates of sulphate reduction and sulphide retention than surrounding unvegetated sediment (Holmer, Duarte & Marba, 2003; Holmer *et al*., 2009). Root and rhizome masses create stable habitats and release oxygen through the roots. Notable amongst the lucinids that inhabit seagrass beds are several *Codakia* species [*Codakia orbicularis*, *Codakia punctata* (Linnaeus, 1758), *Codakia tigerina* (Linnaeus, 1758), and *Codakia paytenorum* (Iredale, 1937)] that are abundant in *Thalassia*-dominated habitats of the western Atlantic and Indo-West Pacific (Moore *et al*., 1968; Taylor & Lewis, 1970; Jackson, 1972). As well as *Codakia orbicularis*, seagrass beds of the western Atlantic also support populations of *Ctena* species, *Lucina pensylvanica*, *Anodontia alba*, and *Lucinisca nassula* (Conrad, 1846) (J. D. Taylor & E. A. Glover, pers. observ.), and *Stewartia floridana* (Fisher & Hand, 1984). In the Indo-West Pacific, *Euanodontia ovum*, *Cavatidens omissa* Iredale, 1930, and other pegophysemines, *Pillucina* species (Nakaoka, Mukai & Chunhabundit, 2002; Meyer *et al*., 2008), *Chavania striata*

(Tokunaga, 1906), and *Divaricella irpex* (E. A. Glover & J. D. Taylor, unpubl. data) are widely associated with seagrass habitats. From temperate latitudes, examples of the association include *Loripes lacteus* (Linnaeus, 1758), which is abundant in Mediterranean *Posidonia* beds (Johnson, Fernandez & Pergent, 2002), *Wallucina assimilis* (Angas, 1868) from southern Australia (Barnes & Hickman, 1999), *Lucinoma borealis* from southern England (Dando, Southward & Southward, 1986; E. A. Glover & J. D. Taylor, pers. observ.), and *Pillucina pisidium* (Dunker, 1860) from Japan (Uede & Takahashi, 2008). From this brief survey it is clear that although *Codakia* species are the largest and most conspicuous species, lucinids associated with seagrass derive from four major clades: the Pegophyseminae, Leucosphaerinae, Codakiinae, and Lucininae. Species of Myrteinae usually live at water depths below those colonized by seagrasses, but we have collected *Notomyrtea mayi* from an intertidal seagrass habitat in South Australia.

Seagrass-dominated shallow water communities became widespread during the Eocene (Brasier, 1975), and the association with lucinids dates from this time. Various Eocene deposits of the Paris Basin have been interpreted as representing seagrass-dominated communities (Murray & Wright, 1974), with lucinids found frequently amongst the molluscs (Pacaud & Le Renard, 1995). From the Eocene (late Lutetian) Selsey Formation of southern England lucinids occur in association with plant remains of seagrasses (Collinson, 1996; Tracey *et al*., 1996). Additionally, the giant *Superlucina megameris* (Dall, 1901) from the Eocene, White Limestone of Jamaica, has been interpreted as an inhabitant of seagrass communities (Taylor & Glover, 2009b). Such associations have continued through the Cenozoic, as for example in the early Oligocene of the Etampes area of the Paris Basin (Gitton, Lozouet & Maestrati, 1986), and in the Roe Calcarenite of south-west Australia (late Pliocene–early Pleistocene), which has been interpreted as a seagrass-dominated deposit (James & Bone, 2007), where *Miltha hamptonensis* Ludbrook, 1969 was common, along with other lucinids (Ludbrook, 1978).

Mangrove association: Mangrove communities are another shallow water marine ecosystem with a high organic input. In the present day, only a few lucinids are closely associated with mangrove environments. Notable amongst these are *Austriella corrugata* and *Indoaustriella* species from the central Indo-West Pacific (Glover *et al*., 2008), *Pegophysema philippiana* from the Indo-West Pacific (Lebata & Primavera, 2001; Taylor & Glover, 2005), *Phacoides pectinatus* from the western Atlantic, which inhabits black muds amongst mangroves (Frenkiel *et al*., 1996), and *Keletistes rhizoecus* (Oliver, 1986) from West Africa, which

lives in mangrove root peat in the Niger Delta (Zabbey, Hart & Wollf, 2010). In South-East Asia, lucinids can also be abundant in communities peripheral to mangrove stands (Meyer *et al*., 2008). Although organic-rich, the suboxic sediments are a less favourable habitat than seagrass beds for burrowing bivalves, because the low pH causes extensive corrosion of shells and the substrata are often very soft. In summary, mangrove-associated lucinids derive from two main clades, Pegophyseminae and Lucininae, and within the latter the well-defined *Austriella*/*Indoaustriella* subclade and *Phacoides pectinatus*. Mangrove systems diversified during the Palaeocene, and by the mid to late Eocene were widespread in the tropics and subtropics (Plaziat *et al*., 2001). Although some mangrove-associated gastropods are recorded from Cenozoic deposits (Reid *et al*., 2008), lucinids have not been documented.

Deeper water habitats: Most lucinid species have been described from shallow water habitats, generally from water depths of less than 100 m. Until recently, relatively few lucinids were known from deeper water, but increased sampling of bathyal habitats in the tropics and hydrocarbon seeps is revealing an unexpected diversity, with lucinids now known to depths of 2570 m (Cosel, 2006; Cosel & Bouchet, 2008; Taylor & Glover, 2009a). The relationships of some of these newly described taxa are uncertain, but they most likely can be classified in Leucosphaerinae or the Myrteinae clades. Deep-water lucinids that have been analysed molecularly derive from: Myrteinae (*Myrtea* and *Gloverina*); Leucosphaerinae, with genera such as *Dulcina* and several undescribed species; the *Lucinoma* clade of the Codakiinae; and a few species from the Lucininae such as *Troendleina musculator* Cosel & Bouchet, 2008, *Bathyaustriella thionipta*, and *Cardiolucina quadrata*. The deepest recorded lucinid is *Elliptiolucina labeyriei* Cosel & Bouchet, 2008 from 2570 m in the Sulu Sea. Nevertheless, *Lucinoma* species are the lucinids most widely reported from deeper water habitats, and several have been found in association with hydrocarbon seeps and mud volcanoes. These include *Lucinoma atlantis* Mclean, 1936 (Cordes *et al*., 2007), *Lucinoma anemiophila* Holmes, Oliver & Sellanes, 2005, *Lucinoma yoshidai* Habe, 1958 (Okutani & Hashimoto, 1997), *Lucinoma kazani* Salas & Woodside, 2002, and *Lucinoma myriamae* (Cosel, 2006) from off West Africa, included in our analysis from 2050 m. Additionally, two species, *Lucinoma aequizonata* (Stearns, 1890) and *Lucinoma gagei* Oliver & Holmes, 2006 are known from sediments of oxygen minimum zones (Cary *et al*., 1989; Oliver & Holmes, 2006). Other lucinids recorded as associated with hydrocarbon seeps include *Graecina karinae* Cosel, 2006, *Graecina*

colombiensis Taylor & Glover, 2009a, *Meganodontia acetabulum* Bouchet & Cosel 2004, *Mesolinga soliditesta* Okutani & Hashimoto 1997, *Myrtea amorpha* (Olu-Le Roy *et al*., 2004), and *Jorgenia* species from the Louisiana Slope (Taylor & Glover, 2009a). The only lucinid recorded as yet from a hydrothermal vent is *Bathyaustriella thionipta* from the Kermadec Ridge off New Zealand (Glover *et al*., 2004). As well as hydrocarbon seeps, Cosel & Bouchet (2008) suggest that around the Philippines and Indonesia the many semi-enclosed basins with poor water circulation and accumulations of decomposing continental plant debris create favourable habitats for chemosymbiotic animals.

The fossil record indicates that lucinids have been present at putative hydrocarbon seeps since at least the late Jurassic (Gaillard *et al*., 1992; Kiel *et al*., 2010), through the Cretaceous with *Ezolucina*, *Nipponothracia*, and *Nymphalucina* species (Speden, 1970; Kauffman *et al*., 1996; Kelly *et al*., 2000; Amano *et al*., 2008; Kiel, Amano & Jenkins, 2008), and in the Cenozoic with, for example, species of *Cryptolucina*, *Nipponothracia*, *Megaxinus*, and *Lucinoma* (Taviani, 1994; Saul, Squires & Godert, 1996; Majima *et al*., 2003; Campbell, 2006; Kase, Kurihara & Hagino, 2007).

Symbionts and co-evolution

The new lucinid phylogeny will provide a framework to examine the distribution of the bacterial symbiont phylotypes. No comprehensive molecular analysis of symbionts and their hosts has yet been attempted, although details of some lucinid symbionts are available, mainly from western Atlantic host species (Distel, Felbeck & Cavanaugh, 1994; Durand & Gros, 1996; Dubilier, Bergin & Lott, 2008). All symbiont phylotypes recorded from lucinid ctenidia to date belong to the gamma group of proteobacteria. Experimental evidence shows that symbionts are acquired by environmental transmission from the sediment (Gros *et al*., 1998), suggesting that a close co-evolutionary history between host and symbiont is unlikely. Indeed, several lucinids from seagrass beds around Guadeloupe shared the same symbiont (Gros *et al*., 2003). Although few symbiont sequences from lucinids have yet been published, preliminary results (Cavanaugh *et al*., 2006; Dubilier *et al*., 2008; Ball *et al*., 2009) show some differentiation between hosts, so that the symbionts of *Phacoides pectinatus*, *Euanodontia ovum*, and *Pegophysema schrammi* (as *Anodontia philippiana* in the cited papers) are distinct from the symbionts associated with other lucinids (e.g. *Lucinisca*, *Codakia*, *Stewartia*, and *Lucinoma*) that group more closely together. The addition of further taxa from different host clades and from a wider range of geographical locations and habitats should result in an improved understanding of host–symbiont relationships and the diversity of symbionts.

Phylogeography

In the present analysis, *Ctena* species provide the most informative data set for phylogeographic analysis. The species form two distinct groups, one consisting of both western Atlantic [*Ctena orbiculata* (Montagu, 1808) and *Ctena imbricatula* (Adams, 1845); note the latter species is usually synonymized with *Ctena orbiculata*, but molecular data shows that they are distinct species] and eastern Pacific species [*Ctena chiquita* (Dall, 1901) and *Ctena mexicana* (Dall, 1901)], and the other comprising West African [*Ctena eburnea* (Gmelin, 1791)], Mediterranean [*Ctena decussata* (Costa, 1829)], and Indo-West Pacific species [*Ctena bella* (Conrad, 1834), *Ctena delicatula* (Pilsbry, 1904), *Epicodakia tatei*, and *Ctena* sp.]. Albeit with only limited sampling, this phylogeny suggests an Atlantic origin with later radiations in the Indo-West Pacific, consistent with the pattern observed in many other taxa (e.g. Williams & Reid, 2004). The chronogram (Fig. 5) estimates that the western Atlantic/eastern Pacific clade diverged from the eastern Atlantic/Mediterranean and Indo-West Pacific clades in the late Eocene. In the western Atlantic/eastern Pacific clade, *Ctena orbiculata* is sister to the eastern Pacific species and *Ctena imbricatula*, with a divergence in the middle Oligocene. In the other clade, the Atlantic and Mediterranean species (*Ctena eburnea* and *Ctena decussata*) are sister to the Indo-West Pacific species, with a divergence in the early Oligocene, earlier than estimates of the closure of the Tethys Seaway, approximately 19–18 Ma (Vrielynck, Odin & Dercourt, 1997; Rögl, 1998; Harzhauser *et al*., 2002, 2007), although 95% HPD ranges suggest a more recent separation is also possible. The Indo-West Pacific clade diversified in the early Miocene, consistent with age estimates of many other tropical, shallow water Indo-West Pacific radiations (e.g. Williams & Duda, 2008).

Codakia is the only other genus with sufficient interspecific sampling to make any biogeographic comment. In this clade the western Atlantic *Codakia orbicularis* occupies a position sister to the other species from the Indo-West Pacific that may have separated in the late Oligocene, slightly later than that of *Ctena* and *Epicodakia* (although the 95% HPD ranges overlap). Divergence times between eastern Pacific/Atlantic and Indo-West Pacific clades have been noted to differ in several studies (e.g. Frey & Vermeij, 2008). Some of this variation may reflect uncertainty in molecular clock analyses or real differences, resulting from multiple vicariant events or the fact that the constriction of the Tethys Seaway was not an instantaneous event, but extended over several

millions of years (Bellwood, van Herwerden & Konow, 2004). The latter seems particularly pertinent, given a similar pattern of protracted speciation events between marine species either side of the Isthmus of Panama (Lessios, 2008). Other possible explanations for disparate estimates include the extinction of true sister lineages (Paulay, 1997) or the role of alternate vicariant events (Reid, Dyal & Williams, 2010).

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