Diversification of chemosymbiotic bivalves: origins and relationships of deeper water Lucinidae

JOHN D. TAYLOR*, EMILY A. GLOVER and SUZANNE T. WILLIAMS

Department of Life Sciences, The Natural History Museum, London SW7 5BD, UK

Although species of the chemosymbiotic bivalve family Lucinidae are often diverse and abundant in shallow water habitats such as seagrass beds, new discoveries show that the family is equally speciose at slope and bathyal depths, particularly in the tropics, with records down to 2500 m. New molecular analyses including species from habitats down to 2000 m indicate that these cluster in four of seven recognized subfamilies: Leucosphaerinae, Myrteinae, Codakiinae, and Lucininae, with none of these comprising exclusively deep-water species. Amongst the Leucosphaerinae, *Alucinoma*, *Epidulcina*, *Dulcina*, and *Myrtina* live mainly at depths greater than 200 m. Most Myrteinae inhabit water depths below 100 m, including *Myrtea*, *Notomyrtea*, *Gloverina*, and *Elliptiolucina* species. In the Codakiinae, only the *Lucinoma* clade live in deep water; *Codakia* and *Ctena* clades are largely restricted to shallow water. Lucininae are the most speciose of the subfamilies but only four species analyzed, *Troendleina* sp., 'Epicodakia' falkandica*, *Bathyaustriella thionipta*, and *Cardiolucina quadrata*, occur at depths greater than 200 m. Our results indicate that slope and bathyal lucinids have several and independent originations from different clades with a notable increased diversity in Leucosphaerinae and Myrteinae. Some of the deep-water lucinids (e.g. *Elliptiolucina*, *Dulcina*, and *Gloverina*) have morphologies not seen in shallow water species, strongly suggesting speciation and radiation in these environments. By contrast, *C. quadrata* clusters with a group of shallow water congenors. Although not well investigated, offshore lucinids are usually found at sites of organic enrichment, including sunken vegetation, oxygen minimum zones, hydrocarbon seeps, and sedimented hydrothermal vents. The association of lucinids with hydrocarbon seeps is better understood and has been traced in the fossil record to the late Jurassic with successions of genera recognized; *Lucinoma* species are particularly prominent from the Oligocene to present day. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2014, **111**, 401–420.

ADDITIONAL KEYWORDS: adaptive radiation – chemosymbiosis – hydrocarbon seeps – phylogeny.

INTRODUCTION

The nutritional strategy of chemosymbiosis with sulphide and/or methane oxidizing bacteria is now recognized in eight families of marine bivalves from intertidal to abyssal depths (Taylor & Glover, 2010; Oliver, 2013; Oliver, Southward & Dando, 2013). By far the most diverse of these, with over 400 living species, the Lucinidae is usually considered as a largely shallow water group, with the greatest species richness present in the coral reef and seagrass environments of the tropical Atlantic and Indo-West Pacific (Cosel, 2006; Glover & Taylor, 2007; Mikkelsen & Bieler, 2007; van der Heide *et al.*, 2012). By contrast, deeper water lucinids were until recently poorly known, particularly from tropical areas.

Discovery of chemosymbiosis in bivalves and the wide biological interest in chemosynthetic environments such as vents, hydrocarbon seeps, and organically enriched habitats has stimulated much recent offshore sampling. This has revealed a surprising diversity of Lucinidae in offshore shelf and bathyal depths. For example, *Lucinoma* have been widely recorded from hydrocarbon seeps and 40% of living species have been described since 2000 (Okutani & Hashimoto, 1997; Salas & Woodside, 2002; Holmes, Oliver & Sellanes, 2005; Cosel, 2006; Oliver & Holmes, 2006; Oliver, Rodrigues & Cunha, 2012). Our perceptions of the diversity of Lucinidae were further

*Corresponding author. E-mail: j.taylor@nhm.ac.uk

challenged in a major publication by Cosel & Bouchet (2008) who described nine new genera and 32 new species of bathyal lucinids from the tropical Indo-West Pacific, with many of these having a range of unexpectedly novel morphologies not seen in shallow water species. The deepest recorded lucinid is *Elliptiolucina labeyriei* Cosel & Bouchet 2008 from 2570 m in the Sulu Sea. The sole lucinid yet described from a confirmed hydrothermal environment is *Bathyaustriella thionipta* from 500 m at the Macauley Caldera, Kermadec Ridge (Glover, Taylor & Rowden, 2004) with *Meganodontia acetabulum* trawled from near a hydrothermal site off Taiwan (Bouchet & von Cosel, 2004). Additionally, deep water sampling in the Indo-West Pacific around the Philippines, Papua New Guinea, New Caledonia, Fiji, Vanuatu, and Madagascar largely by French cruises (SALOMON 2, BIOPAPUA, TERRASSES, EBISCO, MIRIKY, details from Malacologie, Muséum national d'Histoire naturelle, Paris) has recovered diverse assemblages of Lucinidae, with many new to science. Lucinids from the Philippines ranging to depths of 2570 m resulting from ESATASE 2, PANGLAO 2004, PANGLAO 2005, AURORA expeditions (collections MNHN) have been described and reviewed (Glover and Taylor, in press) with 28 new species described, and with 18 of these from depths of more than 100 m. Some additional new deep water species from the Indo-West Pacific have also been described (Taylor & Glover, 2013).

A testable framework to examine the diversification and evolutionary history of the family is provided by a new classification of the Lucinidae, based on molecular analyses, proposed by Taylor *et al.* (2011) who recognized seven subfamilies. This is radically different from previous classifications based on shell morphology (Chavan, 1969; Bretsky, 1976). Relatively few deeper water lucinids were included in that analysis but one of the results demonstrated that *Lucinoma* species were part of a major clade (subfamily Codakiinae) together with predominantly shallow water genera *Codakia* and *Ctena*. Other species from deeper water were placed in subfamilies Leucosphaerinae and Myrteinae and Lucininae. From shell morphology, some of these, such as *Elliptiolucina* and *Jorgenia*, were provisionally placed in the subfamily Myrteinae.

There has been much debate concerning the origins and antiquity of the deep-water faunas, and especially hydrocarbon vents and seeps. Recent analyses have refuted the earlier claims of considerable antiquity and demonstrated that successions of clades occupied these habitats (Jacobs & Lindberg, 1998; Jablonski, 2005; Kiel, 2010; Vrijenhoek, 2013). For example, recent molecular and palaeontological results show that bathymodioline and vesicomyid bivalves colonized seeps no earlier than Eocene (Kiel

& Amano, 2013; Vrijenhoek, 2013). However, studies on echinoderm fossils indicate an early Cretaceous age for occupation of the deep-sea benthos (Thuy *et al.*, 2012).

For the purposes of the present study, we consider depths greater than 200 m as deep water, *sensu* Bouchet *et al.* (2008) who argued that, in the tropics, the turnover from shallow to deep-water faunas may be reached at depths as shallow as 100 m and that there are several zones of deep-sea faunas present between 200–1500 m compared to a single zone in the temperate North Atlantic. Our objectives are to establish the phylogenetic relationships of Lucinidae from offshore and deeper water habitats using new molecular analyses that include more deep water taxa. The major questions addressed are: (1) do the deeper water lucinids cluster within a single clade or have species from multiple clades occupied deeper water; (2) is there evidence for deeper water radiations that have diversified independently of the shallow water clades and (3) what are the phylogenetic relationships between shallow and deeper water taxa?

MATERIAL AND METHODS

For the molecular analyses, we included 25 taxa collected from deeper water (< 200 m) with 12 of these newly sequenced, and with an additional 12 shallow water species to those reported in Taylor *et al.* (2011) (Table 1). Some of the sequenced deep-water species are shown in Figure 1. For outgroups, we used species from nine families of heterodont bivalves with new sequences for ten of these.

There are several taxonomic changes and corrections to the taxon list given in Taylor *et al.* (2011). For *Cardiolucina quadrata*, the wrong depth and locality data for the sequenced specimen from the Philippines was given and this is now corrected in Table 1. We now consider the species previously identified as *Dulcina karubari* to be *Alucinoma alis*. Three species that were listed as 'undescribed genus and species' (UGS 1, UGS 2, UGS 3) are now identified as follows: UGS 1 is now recognized as a new species of *Myrtina* (Glover & Taylor, in press); UGS 2 is a new genus and species (Glover & Taylor, in press); UGS 3 is a new species *Gonimyrtea ferruginea* (Taylor & Glover, 2013). The previously listed *Troendleina* cf *musculator* and *Leucosphaera* cf *diaphana* from the Philippines will be described as new species (Glover & Taylor, in press).

The DNA extraction and amplification protocols described by Williams & Ozawa (2006) were used to amplify portions of three genes from 34 new specimens: the nuclear 18S rRNA genes (18S: lucinids approximately 1000 bp), 28S rRNA gene (28S: lucinids approximately 1500 bp) and the mitochondrial gene cytochrome *b* I (cytB: 402 bp).

Table 1. Species included in the analysis: deep water taxa, additional shallow water species, new outgroups, nomenclatural changes and corrections to taxa from Taylor et al. 2011, collection localities, museum registration numbers for vouchers, and GenBank accession numbers for the genes sequenced for each taxon. MNHN—Muséum national d'Histoire naturelle, Paris; NHMUK—The Natural History Museum, London

Species	Depth (m)	Locality	Sample details	Registration number	18S	28S	cyt B
LUCINIDAE							
MYRTEINAE							
Myrtea flabelliformis (Prashad, 1932)	762–786	Philippines	PANGLAO 2005 stn CP 2388, Bohol Sea, 9°26.9'N, 123°34.5'E	MNHN 200910375	FR686694	FR686775	FR686614
Notomyrtea vincentia Glover & Taylor, 2007	176–246	Vanuatu	SANTO 06 stn AT86, Scorff Passage 15° 3.9'S 167° 16.2E	MNHN 200933715			KF741660
Notomyrtea vincentia Glover & Taylor, 2007	200	New Caledonia	TERRASSES stn DW 3093, 22° 06'S 167° 03'E	MNHN 20098711	KF741605	KF741634	KF741661
Notomyrtea sp.	443–470	Solomon Islands	SALOMON 2 stn DW2238A, 6°53.1'S, 156°21.4'E	MNHN 200933716			KF741662
Notomyrtea sp. nov. Glover & Taylor (in press)	196–216	Philippines	PANGLAO 2004 stn CP 2348, off Pamilacan Island, 9°29.6'N, 123°52.5'E	MNHN 200910369	FR686693	FR686770	FR686613
Myrtea' sp.	379	Madagascar	MIRIKY stn CP 3289, 14° 29'S, 47° 26'E	MNHN 20098735	KF741606	KF741635	MYRT.MAD
Gloverina rectangularis Cosel & Bouchet, 2008	784–786	Philippines	PANGLAO 2005 stn CP 2389, Bohol Sea 9°27.9'N, 123°38.4'E	MNHN 200911084	FR686692	FR686771	FR686612
Gloverina cf rectangularis Cosel & Bouchet, 2008	762–786	Philippines	PANGLAO 2005 stn CP 2388, Bohol Sea, 9°26.9'N, 123°34.5'E	MNHN 200910368	FR686691	FR686772	FR686607
LEUCOSPHAERINAE							
Leucosphaera sp. nov. Glover & Taylor (in press)	12	Philippines	PANGLAO 2004 stn S27, Ubajan, Bohol Island, 9°41.5'N, 123°51.0'E.	MNHN 200910359	KF741607	KF741636	KF741664
Leucosphaera diaphana Glover & Taylor, 2007	97–101	Vanuatu	SANTO 06 stn AT04, East Aore Island, 15°32.9'S, 167°13.3'E	MNHN 200933717			KF741665
Epidulcina cf delphinae Cosel & Bouchet, 2008	450–455	Madagascar	ATIMO VATAE stn CP 3592, 25°02'S, 43°58'E	MNHN 200910819	KF741608	KF741637	KF741666
Dulcina madagascarensis Cosel & Bouchet, 2008	400–402	Madagascar	ATIMO VATAE stn CP 3592, 25°03'S, 43°58'E	MNHN 200910814	KF741609	KF741638	KF741667
Dulcina cf karubari Cosel and Bouchet, 2008	391–623	Solomon Islands	SALOMON 2 stn DW2205, 7°43.4'S, 158°29.0'E	MNHN 200933718		KF741639	
Dulcina sp.	729–733	Philippines	PANGLAO 2005 stn CP 2335, Bohol Sea, 9°34.3'N, 123°37.8'E.	MNHN 200910371	FR686695	FR686777	FR686615
Alucinoma sp.	273–300	Solomon Islands	SALOMON 2 stn DW2198, 7°43.3'S, 158°29.8'E	MNHN 200933719			KF741668
Alucinoma alis ex Dulcina karubari in Taylor et al. 2011	255–268	Philippines	PANGLAO 2005 stn CP 2331, Maribojoc Bay, Bohol Sea, 9°39.2'N, 123°47.5'E	MNHN 200910372	FR686697	FR686776	FR686608
Goninyrtea sp. nov. Glover & Taylor (in press)	25	Vanuatu	SANTO 06 stn DR05, Segond Channel, 15°31.4'S, 167°14.1E	MNHN 200933720—BC1331	KF741610		KF741669
Goninyrtea sp. nov. Glover & Taylor (in press)	15–30	Vanuatu	SANTO 06 stn ZS19, Segond Channel 15°31.4'S, 167°14.1E	MNHN 200933721—BC3766	KF741611	KF741640	KF741670

Table 1. *Continued*

Species	Depth (m)	Locality	Sample details	Registration number	18S	28S	cyt B
Myrtina sp. nov. (UGS 1) Glover & Taylor (in press)	642–669	Philippines	PANGLAO 2005 stn CP 2397, Maribojoc Bay, Bohol Sea, 9°34.9'N, 123°41.7'E.	MNHN 200910373	FR686696	FR686778	FR686611
Myrtina reflexa Taylor & Glover, 2013	230–288	Madagascar	MIRIKY stn DW3239, 14° 30'S, 47° 26'E	MNHN 20098733	KF741612	KF741641	KF741671
Gonimyrtea ferruginea Taylor & Glover, 2013	608–642	New Caledonia	EBISCO 2005 stn CP 2614, Chesterfield Bank, 19°39'S, 158°47'E	MNHN 200910376	FR686701	FR686779	FR686606
New genus and species UGS 2 Glover & Taylor in press	10	Philippines	PANGLAO 2004 stn S20, Manga, Bohol Island, 9°41.8'N, 123°51.1'E	MNHN 200910360	FR686698	FR686780	FR686681
Undescribed species similar to UGS 2	37	Vanuatu	SANTO 06 stn FS70, Tangoa Island, 15° 35.4'S 166° 59.7'E	MNHN 200933722			KF741672
CODAKIINAE							
Ctena bella (Conrad, 1837)	15–30	Vanuatu	SANTO 06 stn ZS19, Segond Channel, 15°31.4'S, 167°14.1'E	MNHN 200933723	KF741613	KF741642	KF741673
Lucinoma kazani Salas & Woodside, 2002	507	Mediterranean	North Alex mud volcano, 31° 58.2'N, 30° 08.2'E	NHMUK 20130637	KF741614	KF741643	KF741674
Lucinoma myriamae Cosel, 2006	1700	Off Nigeria	hydrocarbon seep	NHMUK 20100293	FR686718	FR686818	FR686656
Lucinoma myriamae Cosel, 2006	2050	Off Angola	6° 34.15'N 7°8.48'E	NHMUK 20100292	FR686713	FR686819	FR686661
LUCININAE							
Bathyaustriella thionipta Glover, Taylor & Rowden, 2004	480	New Zealand	Kermadec Ridge, 30° 13.34'S 178° 27.112'W	NHMUK 20070337	AJ581858	AJ581892	AM774147
Troendleina cf *musculator* Cosel & Bouchet, 2008	679–740	Philippines	PANGLAO 2005 stn CP 2362, Bohol/Sulu Seas sill, 8°56.5'N, 123°32.7'E	MNHN 200910367	FR686720	FR686807	FR686609
Epicodakia falklandica Dell, 1964	221	Southern Ocean	BIOPEARL 1 stn SG-EBS-4, South Georgia, 53°61'S 37°88'E	NHMUK 20130638	KF741615	KF741644	KF741675
Bretskya cf *scapula* Glover & Taylor, 2007	62–71	Vanuatu	SANTO 06 stn AT53 Segond Channel, 15°31.8'S, 167°13.6'E	MNHN 200933724	KF741617	KF741645	KF741676
Bretskya cf *scapula* Glover & Taylor, 2007	62–71	Vanuatu	SANTO 06 stn AT53, Segond Channel, 15°31.8'S, 167°13.6'E	MNHN 200933725	KF741618	KF741646	KF741677
Pillucina vietnamica Zorina, 1974	intertidal	Australia	Tin Can Bay, Queensland, 25°54.6'S, 153°00'E	NHMUK 20130639	KF741619	KF741647	
Pillucina pisidium (Dunker, 1860)	intertidal	Japan	Tanabe Bay, Wakayama, 33°44'N, 135°23'E	NHMUK 20130640	KF741620	KF741648	KF741678
Loripes lucinalis (Lamarck, 1818)	intertidal	Tunisia	Djerba, 33°44.59'N, 10°43.46'E	NHMUK 20130641	KF741621	KF741649	KF741679
Cardiolucina quadrata (Prashad, 1932)	230–288	Madagascar	MIRIKY stn DW3239, 14° 30'S, 47° 26'E	MNHN 20098718	KF741622	KF741650	KF741680
Cardiolucina quadrata (Prashad, 1932)	762–767	Panglao	PANGLAO 2005 stn CP2388, 9°26.9'N, 123°34.5'E	MNHN 200910374	FR686721	FR686787	FR686610

| Taxon	Depth	Country	Locality	Voucher			
OUTGROUPS							
CARDITIDAE							
Venericardia antiquata (Linnaeus, 1758)	intertidal	Tunisia	Djerba, 33°44.59'N, 10°43.46'E	NHMUK 20130642	KF741623	KF741651	KF741681
EUCIROIDAE							
Euciroa sp.	356	Philippines	PANGLAO 2005 stn CP2343, 9°27'N, 123°49'E	MNHN 200910748	KF741624	KF741652	KF741682
VERTICORDIIDAE							
Spinosipella deshayesiana (P. Fischer, 1862)	585	Solomon Isles	SALOMONBOA 3 stn CP 2833, 10°42'N, 162° 19'E	MNHN 200910762	KF741625		KF741683
POROMYIDAE							
Cetoconcha sp.	600	Philippines	AURORA stn 2729, 15° 20'N, 121° 37'E	MNHN 200910757	KF741626		KF741684
PERIPLOMATIDAE							
Cochlodesma praetenue (Pulteney, 1799) 1	intertidal	United Kingdom	Lower Newton, Northumberland, 55°30.37'N. 01°36.3'W	NHMUK 20130643	KF741627	KF741653	KF741685
Cochlodesma praetenue (Pulteney, 1799) 2	intertidal	United Kingdom	Lower Newton, Northumberland, 55°30.37'N. 01°36.3'W	NHMUK 20130644	KF741628	KF741654	KF741685
LASAEIDAE							
Kurtiella bidentata (Montagu, 1803)	intertidal	United Kingdom	Salcombe, Devon, 50°13.5'N, 03°46.04W	NHMUK 20130645	KF741629	KF741655	KF741687
SEMELIDAE							
Abra alba (Wood, 1802)	intertidal	United Kingdom	Pegwell Bay, Kent, 51°19.33'N, 01°23.5E	NHMUK 20130646	KF741630	KF741656	KF741686
CARDIIDAE							
Ciliatocardium ciliatum (Fabricius, 1780)	55–85	Svalbard	West Spitsbergen, 78° 57.6'N, 11° 59.9'E	NHMUK 20130647	KF741631	KF741657	KF741688
Serripes groenlandicus (Bruguière, 1789)	30	Svalbard	West Spitsbergen, 78° 52'N, 12° 23'E	NHMUK 20130648	KF741632	KF741658	KF741689
THYASIRIDAE							
Thyasira s.l. sp.	283	Madagascar	MIRIKY stn CP3262, 15° 34'S, 45° 44'E	MNHN 20098728	KF741633	KF741659	
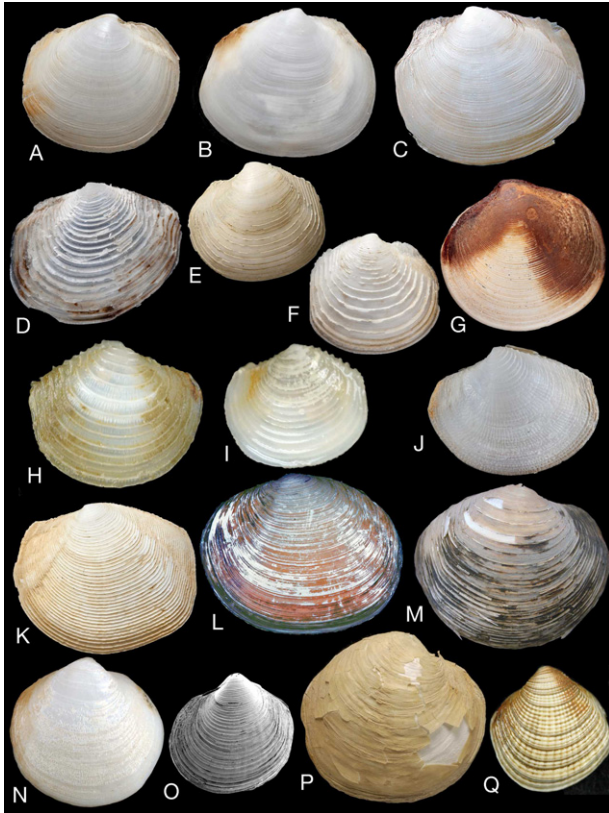
Figure 1. Some of the deeper water Lucinidae included in the molecular analyses. For details, see Table 1. *Elliptiolucina ingens* analyzed by Kuhara *et al.* (in press). Shell lengths are given in parentheses.A, *Alucinoma alis* Cosel & Bouchet, 2008 (15.6 mm); B, *Dulcina* sp. Philippines (16.6 mm); C, *Dulcina madagascarensis* Cosel & Bouchet, 2008 (24 mm); D, *Epidulcina cf delphinae* Cosel & Bouchet, 2008 (16.8 mm); E, **Myrtina sp. nov.** Glover & Taylor (in press) (10.1 mm); F, *Myrtina reflexa* Taylor & Glover, 2013 (10.5 mm); G, *Gonimytea ferruginea* Taylor & Glover, 2013 (24.5 mm); H, *Notomyrtea flabelliformis* (Prashad, 1932) (6.7 mm); I, **Notomyrtea sp. nov.** Glover & Taylor (in press) (5.2 mm); J, '*Myrtea*' sp. Madagascar (10.2 mm); K, *Gloverina rectangularis* Cosel & Bouchet, 2008 (37 mm); L, *Elliptiolucina ingens* Okutani, 2011 (70 mm), west of Amami-Ohshima Island, Japan between depths of 601–646 m. Image Jun Hashimoto; M, *Lucinoma myriamae* Cosel, 2006 (50 mm); N, *Troendleina* cf *musculator* Cosel & Bouchet, 2008 (17.8 mm); O, *Epicodakia falklandica* Dell, 1964 (1.8 mm); P, *Bathyaustriella thionipta* Glover, Taylor & Rowden, 2004 (47 mm); Q, *Cardiolucina quadrata* (Prashad, 1932) Philippines (11.9 mm).

Sequence reactions were performed directly on purified polymerase chain reaction (PCR) products using the BigDye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems) and run on an Applied Biosystems 3730 DNA Analyzer automated capillary sequencer. Sequencing and PCR primers are provided in Taylor *et al.* (2011). New sequences were combined with previously published sequences of lucinids and outgroups (Williams, Taylor & Glover, 2004; Taylor *et al.*, 2007; Taylor *et al.*, 2011).

Sequences for each gene fragment were assembled and edited using SEQUENCHER, versions 4.6 and 4.8 (Gene Codes Corporation). Alignment of cytB sequences was unambiguous and no stop codons were observed. Sequences of ribosomal genes were aligned with MAFFT, using the online server (http://align.bmr.kyushu-u.ac.jp/mafft/online/server/). We used the Q-INS-i strategy (version 6), which takes into account the secondary structure of RNA (Katoh *et al.*, 2002; Katoh & Toh, 2008), using 1PAM/κ = 2 and offset at 0.

Poorly aligned sites in the ribosomal gene alignments were identified using the online Gblock server, version 0.91b (Castresana, 2000; http://molevol.cmima.csic.es/castresana/Gblocks_server.html) and removed from analyses. Parameters for Gblocks were set for less stringent removal, with smaller blocks, gap positions in final blocks, and less strict flanking positions all allowed. After removal of ambiguous blocks of data selected by using Gblocks, a total of 873 bp of sequence from 18S rRNA remained to be used in phylogenetic analyses (63% of 1367 bp in the original alignment) and 1172 bp of 28S rRNA (55% of 2096 bp in the original alignment).

Gene phylogenies were constructed using Bayesian methods as implemented in MrBayes, version 3.1.2 (Huelsenbeck & Ronquist, 2001). Models used in the Bayesian analyses were determined using MRMODELTEST, version 2.1 (J. Nylander: http://www.abc.se/~nylander/). The cytB 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.

The analysis for cytB was run for 7 500 000 generations and the rRNA genes for 10 500 000 generations, in each case with a sample frequency of 1000. Each analysis was run twice. The first 501 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 14 000 trees for cytB; 20 000 for the rRNA genes). Stationarity was determined by examining traces in TRACER, version

1.5 (http://tree.bio.ed.ac.uk/software/tracer/). Convergence between the two runs was tested by examining traces using TRACER and by checking that the potential scale reduction factors produced by the 'sump' command in MrBayes were less than one (Gelman & Rubin, 1992) and that the mean SD of split frequencies approached zero.

To allow for compositional heterogeneity across lineages, as identified in cytB using PAUP* (Swofford, 2000), we used p4 to perform Bayesian analyses of the combined data set. In the combined analyses, variation was partitioned among genes, with each gene allowed to evolve at a different rate and the same gene-specific model parameters were used as in the MrBayes analyses (with all parameters free to vary independently within each partition), with the addition that base composition was allowed to be heterogeneous for cytB. The analysis was run with four chains for 2 000 000 generations, sampling every 500 generations. Support for nodes was determined using posterior probabilities (PP).

RESULTS

Sequences were not uniformly available for all three genes so that the number and composition of lucinid evolutionarily significant units (ESUs) and outgroups analyzed varies slightly between gene trees; for example, 123 lucinid ESUs are included in the 18 S tree, with 105 in the 3 gene tree. For this reason, the three separate gene trees plus the combined tree are shown (Figs 2, 3, 4, 5). Deep water lucinids collected from 200–500 m, 500–1000 m, and >1000 m are indicated by symbols.

For all three gene trees and in the combined gene tree, five major clades of lucinids are recognized, corresponding to the subfamilies Pegophyseminae, Leucosphaerinae, Myrteinae, Codakiinae, and Lucininae previously identified from a smaller taxon set (Taylor *et al.*, 2011). The only exception is the cytB tree (Fig. 4), which, perhaps because of compositional heterogeneity across lineages, shows *Euanodontia ovum* nesting within the Leucosphaerinae rather than Pegophyseminae and *Funafutia levukana* aligning outside of the Luciniinae with *Fimbria*. The positions of two small clades Monitilorinae and Fimbriinae, represented by single species, were unstable in different gene trees but always nested outside the major subfamilies.

The phyletic distributions of lucinids sampled from >200 m are indicated in Figures 2, 3, 4, 5. These taxa occur in four of the subfamilies, with most species and genera clustering in the Leucosphaerinae and Myrteinae, the *Lucinoma* subclade of the Codakiinae, and four species in the Lucininae. No deeper water species have yet been analyzed from the

Pegophyseminae. None of the subfamilies contain exclusively deeper water species and all include some shallow water representatives.

The Leucosphaerinae is a morphologically disparate subfamily that was largely identified by molecular evidence (Taylor *et al.*, 2011), with species ranging in depth from intertidal to >1000 m. Two shallow species, *Leucosphaera 'philippinensis'* and *Anodontia alba*, sit at the base of the clade, whereas all the other species analyzed form a well supported (PP 100%) group. The deeper water species cluster into two subclades, one of *Myrtina* and *Epidulcina* species (PP 73%) and the other of *Dulcina*, *Alucinoma*, and *Gonimyrtea* species (PP 100%). Three specimens identified as *Gonimyrtea* were analyzed; the two samples from shallow water, *Gonimyrtea* sp. nov. from Vanuatu and *G. ferruginea* from 350–650 m do not cluster together. *Gonimyrtea* sp. nov. forms a poorly supported clade with two other shallow water taxa: UGS2 from the Philippines and *Pseudolucinisca lacteola* (PP 76%).

We sequenced ten species in the subfamily Myrteinae and, apart from *Myrtea spinifera* and *Notomyrtea mayi*, these were all collected from depths greater than 200 m. With the exception of *Notomyrtea flabelliformis* from 250–800 m, which is basal to the clade in all the trees, the other myrteines cluster together (PP 100%). The remaining deeper water species, including *Notomyrtea* spp. and the large *Gloverina rectangularis*, are separate (PP 99%) from the two shallow water species, *M. spinifera* and *N. mayi*. *Notomyrtea* sp. nov. and *Notomyrtea reflexa* from Madagascar form a well-supported (PP 100%) sister group to *Gloverina*.

The Codakiinae divide into three well supported (PP 100%) subclades; *Codakia* species, *Ctena/Epicodakia* species, and *Lucinoma* species. All *Codakia* and *Ctena* species were sampled from depths less than 10 m. The genetically compact *Lucinoma* clade contains species that range from shallow water (*Lucinoma borealis*) to over 2000 m (*Lucinoma myriamae*). *Lucinoma kazani* from 700 m mud volcanoes of the eastern Mediterranean groups closely with the morphologically similar *L. borealis* from shallow depths (Salas & Woodside, 2002).

The Lucininae includes largely tropical and subtropical shallow water taxa and only four species from deeper water were analyzed. The hydrothermal vent species *B. thionipta* from 500 m clusters in a subclade with two shallow water *Parvilucina* species and the wood-associated *Bretskya* (PP 100%). *Troendleina cf musculator* from 150–800 m and the southern ocean *'Epicodakia' falklandica* group as sister to the *Bathyaustriella/Parvilucina* branch but without strong support (PP 75%). Distant from these are two specimens identified as *Cardiolucina quadrata*, one
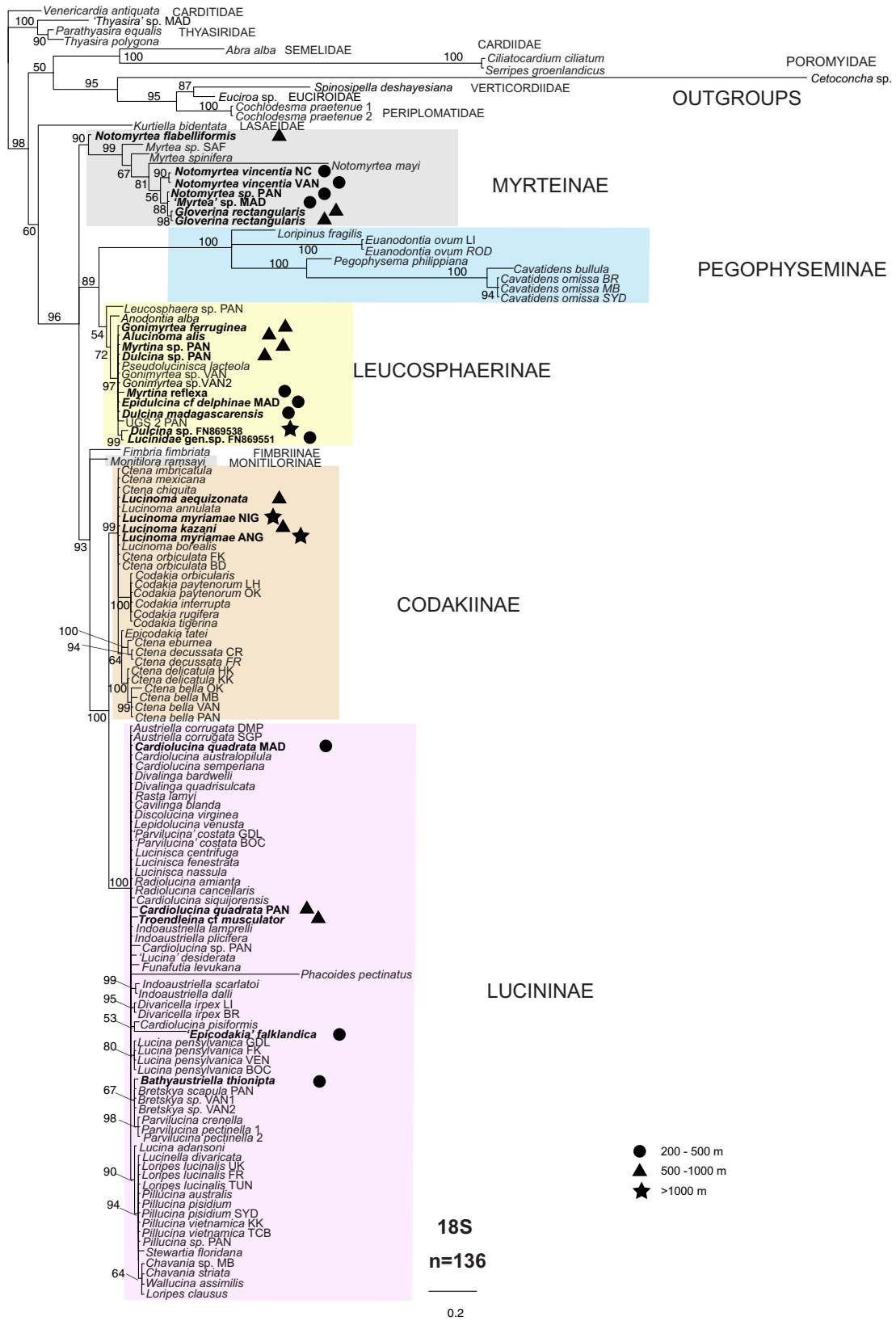
Figure 2. Single gene tree for Lucinidae based on nuclear 18S rRNA gene implemented on Bayesian inference using MrBayes. Support values are posterior probabilities (PP); only values ≥ 90% are shown, branches with PP < 50% were collapsed. For sample details, see Table 1. Monophyletic subfamilies are indicated by a box. Deep-sea species are indicated by black symbols (for details, see key).

Locality abbreviations for species sampled from multiple locations in Figs 2, 3, 4, 5. ABD, Abu Dhabi; ANG, Angola; BD, Bermuda; BOC, Bocas, Panama; BR, Broome, Australia; CR, Croatia; DMP, Dampier, Australia; FK, Florida Keys; FR, France; GDL, Guadeloupe; HK, Hong Kong; KK, Kungkraben Bay, Thailand; LH, Lord Howe Island; LI, Lizard Island, Australia; MAD, Madagascar; MB, Moreton Bay, Australia; NC, New Caledonia; NIG, Nigeria; OK, Okinawa; PAN, Panglao, Philippines; ROD, Rodrigues; RUK, Ryukyus, Japan; SAF, Safaga, Red Sea; SGP, Singapore; SOL, Solomon Islands; SYD, Sydney, Australia; TCB, Tin Can Bay, Australia; TIM, East Timor; TUN, Tunisia; VAN, Vanuatu; VEN, Venezuela.

from the Philippines and the other from Madagascar at depths of 767 m and 288 m respectively, and these group together (PP 100%) with five other species of *Cardiolucina* from intertidal and shallow water habitats. In the cytB tree, *C. quadrata* is sister to the shallow water *C. semperiana* (PP 91%) but only PP 62% in the 3 gene tree.

DISCUSSION

Our results show clear evidence for the independent derivation of deeper water taxa in four out of seven lucinid subfamilies, although we have only been able to analyze a small subset of deeper water species, many of them known only from shells or inadequately preserved for molecular analysis. By far the greatest generic diversity of deep taxa is found in the Myrteinae and Leucosphaerinae. A previously published chronogram (Taylor *et al*., 2011: fig. 5) indicates they are probably the oldest of the living lucinid groups, with ancestry at least to the early Cretaceous. In the Codakiinae, only the *Lucinoma* subclade includes deeper water species, with only a few identified from the Lucininae. Both Codakiinae and Lucininae are younger clades (Taylor *et al*., 2011: fig. 5) with probable origins later in the Cretaceous. The two other lucinid subfamilies, Monitilorinae and Fimbriinae, with few living species, have no present day, deeper water representatives. Fimbriinae in particular have a long fossil record to the early Jurassic, apparently from shallow water environments; Monitilorinae have a fossil record to the Palaeocene at least (Taylor *et al*., 2011).

LEUCOSPHAERINAE

The Leucosphaerinae includes some recently described deep water genera with *Dulcina*, *Graecina*, *Epidulcina*, *Myrtina*, *Alucinoma*, and *Minilucina* (Cosel, 2006; Glover & Taylor, 2007, 2013; Cosel & Bouchet, 2008). *Dulcina* and *Alucinoma* are morphologically and genetically similar genera found offshore to 1000 m around south-east Asia and Madagascar.

Epidulcina (type species *E. delphinae*) was first described from Fiji at depths of 300–600 m (Cosel & Bouchet, 2008) and we analyzed a very similar species from off Madagascar from 450 m. *Minilucina* has been recorded from 1730 m in the Macassar straits. *Myrtina* is a widespread offshore genus first recognized from New Caledonia that includes species from across the Indo-West Pacific living at depths of 80–1200 m (Glover & Taylor, 2007, in press; Taylor & Glover, 2013). Before molecular analysis, we previously placed this genus in Myrteinae (Taylor *et al*., 2011). The two species sequenced here, *Myrtina* sp. from the Philippines and *Myrtina reflexa* from Madagascar, are sister taxa in some trees, although morphologically dissimilar. Brissac, Merçot & Gros (2011) sequenced the symbionts and hosts of two leucosphaerine species from the Philippines: a *Myrtina* species (their OTU number OG78) from 357–372 m and a *Dulcina* sp. from 1764–1775 m. In their analysis, these clustered with *A. alba* and *P. lacteola* the only other leucosphaerines included.

Other leucosphaerine genera have both deeper and shallow water species; *Pseudolucinisca*, previously known from two shallow water species from western Australia (Taylor & Glover, 2008), now includes a species from 80–300 m off the Philippines (Glover & Taylor, in press). Additionally, *Pseudolucinisca japonica* from off Japan (previously known as *Lucinoma japonica* Habe, 1958) can also be included in the genus. *Leucosphaera* spp. and *Anodontia alba* are known only from shallow water. In our previous classification (Taylor *et al*., 2011), we placed *Gonimyrtea* in the Myrteinae but two species classified as *Gonimyrtea* (*G. ferruginea* and *G.* sp. nov.) were sequenced, both of these grouping separately in the Leucosphaerinae. Although the type species (*Gonimyrtea concinna* from New Zealand) has not yet been sequenced, we transfer *Gonimyrtea* from the Myrteinae to Leucosphaerinae on the basis of molecular results.

Because the subfamily has been only recently recognized, the fossil record of Leucosphaerinae is poorly documented. However, fossil genera that may be included are *Pteromyrtea* Danian-Pliocene, New
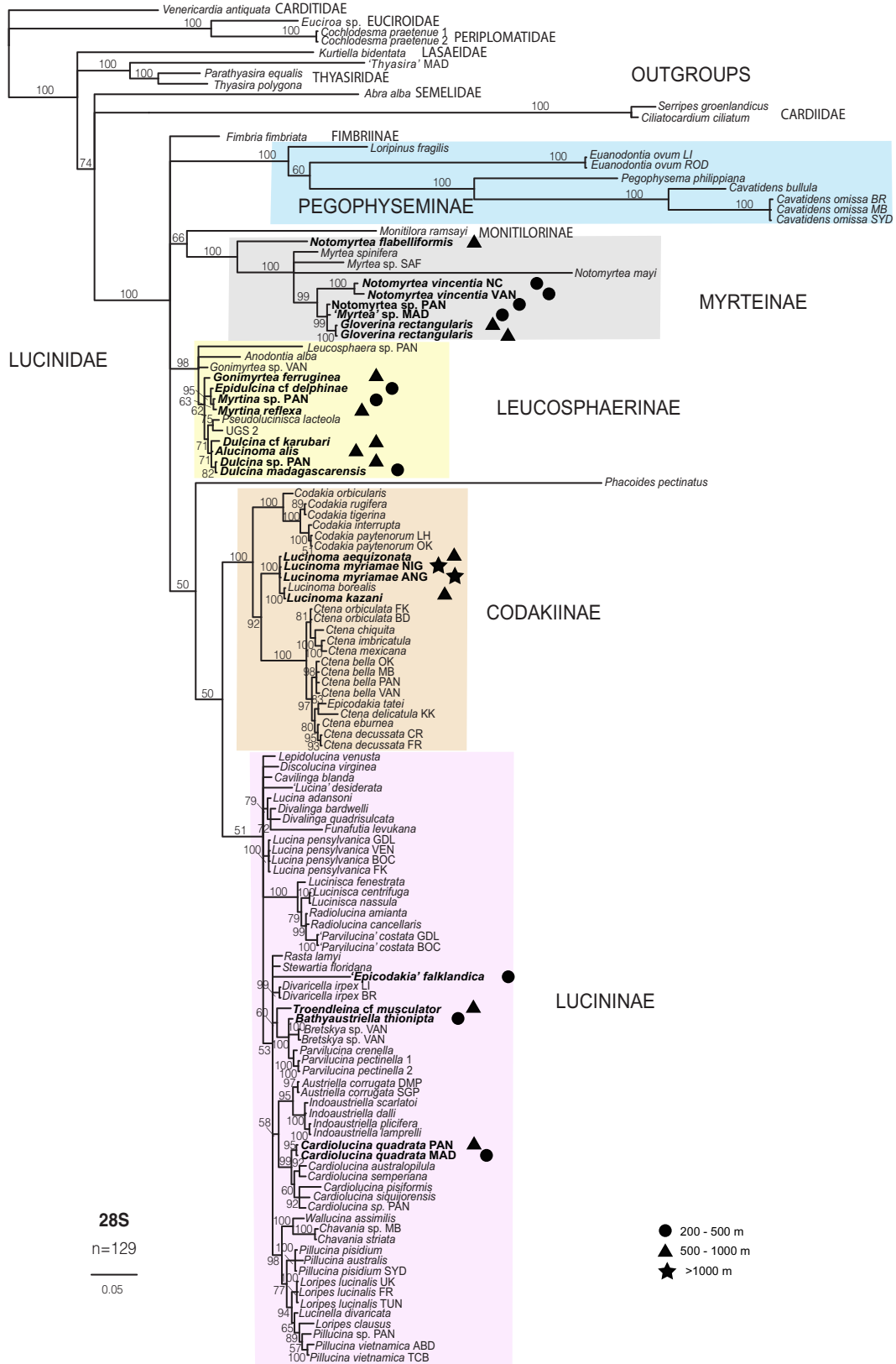
Figure showing phylogenetic tree for 28S (n=129) of Lucinidae with outgroups, colour-coded subfamilies (PEGOPHYSEMINAE, MYRTEINAE, LEUCOSPHAERINAE, CODAKIINAE, LUCININAE), depth markers (● 200–500 m, ▲ 500–1000 m, ★ >1000 m), and scale bar 0.05.

Figure 3. Single gene tree for Lucinidae based on nuclear 28S rRNA gene implemented on Bayesian inference using MrBayes. Support values are posterior probabilities (PP); only values ≥ 90% are shown, branches with PP < 50% were collapsed. For sample details, see Table 1. Monophyletic subfamilies are indicated by a box. Deep-sea species are indicated by black symbols (for details, see key).

Zealand; *Levimyrtea*, Miocene, Ecuador, and *Rawya* Eocene, France. Species morphologically similar to living *Myrtina* can be recognized from shelf depths in the Miocene-Pliocene of Italy, including '*Dentilucina*' *meneghinii* (de Stefani & Pantanelli, 1880) and '*Lucina*' *spinulosa* Edwards from the Eocene of England, both often assigned to *Gonimyrtea*, with possible forerunners of *Pseudolucinisca* ['*Dentlilucina*' *michelottii* (Mayer, 1858)] from Miocene of Italy.

MYRTEINAE

Myrteinae species, in contrast to other lucinid subfamilies, are mostly found in offshore and deeper water habitats and it is apparent from recent studies (Cosel & Bouchet, 2008; Taylor & Glover, 2009; Okutani, 2011; Glover & Taylor, in press) that the group is more species-rich and morphologically disparate than previously realized. It includes some of the deep water genera recently described from the central Indo-West Pacific that have, large, elongate laterally compressed shells very different in morphology from the smaller '*Myrtea*' species. These genera, classified in the Myrteinae (Taylor *et al*., 2011) on shell characters include *Elliptiolucina*, *Rostrilucina*, *Gloverina*, *Taylorina*, and *Jorgenia*, although only *Gloverina* was sequenced in the present study. Recently, Kuhara *et al*. (in press) confirm from molecular analysis that *Elliptiolucina ingens* Okutani, 2011 from a 631–633 m hydrocarbon seep off Japan also belongs in the Myrteinae. The deepest recorded *Elliptiolucina* (*Elliptiolucina labeyrieri*) occurred together with *Lucinoma*, '*Myrtea*' sp., and vesicomyids at 2570 m at a likely hydrocarbon seep in the Sulu Sea (Glover & Taylor, in press). *Myrtea amorpha* known from mud volcanoes and seeps in the eastern Mediterranean is genetically and morphologically close to *M. spinifera* (Brissac *et al*., 2011). From the Philippines, Brissac, Mercot *et al*. (2011) identified *G. rectangularis* as a sister species to *M. spinifera* but only two other myrteines were included in their analysis.

As yet, there are no examples of *Rostrilucina*, *Taylorina*, *Gloverina*, and *Jorgenia* from the fossil record but various large, edentulous lucinids have been recorded from Mesozoic and Cenozoic fossil hydrocarbon seeps. From the Cenozoic, *Elongatolucina* Gill & Little (2013) from the Eocene of Washington State, USA, and Miocene of Venezuela are associated with fossil hydrocarbon seeps and are morphologically very similar to living *Elliptiolucina*

species (Cosel & Bouchet, 2008; Okutani, 2011). Additional records of fossil *Elliptiolucina* (Pliocene, Indonesia; Oligocene, Washington) and *Elongatolucina* (Oligocene Colombia) all from ancient methane seeps are described by Kiel (2013). Furthermore, *Myrteopsis magnotaurina* Sacco, 1901 from the Miocene of northern Italy may be part of the '*Elliptiolucina* group', with a similar shape and largely edentulous hinge. Several western Atlantic living species have been erroneously placed in *Myrteopsis* (Dall, 1901; Bretsky, 1976). From Cretaceous rocks, the seep associated taxa such as *Nipponothracia* and *Nymphalucina* (Speden, 1970; Kelly *et al*., 2000; Kase, Kurihara & Hagino, 2007; Kiel, 2013) have a morphology suggesting placement in the Myrteinae.

Cosel & Bouchet (2008) compared *Elliptiolucina* with some Eocene fossils from the Paris Basin, suggesting a possible shallow water origin. However, the fossil taxa cited (classified in *Pseudomiltha*) are morphologically distinct, with very long, thin, anterior adductor muscle scars and are unlikely to be closely related to *Elliptiolucina* species with short anterior adductor muscle scars. Also, Cosel & Bouchet (2008) claimed the late Oligocene fossil lucinid, *Myrtea tenuicardinata* Cossmann & Peyrot, 1912 (originally described as a subspecies of *M. spinifera*) from the Aquitaine Basin, as an early *Taylorina* but it is quite different in shape and lacks the distinctive, long, scooped lunule, and sunken escutcheon of the living species.

It is beyond the scope of the present study to review fossil lucinids in detail but various Cretaceous fossils can be tentatively assigned to the Myrteinae, such as *Paramyrtea* from the Cenomanian (Kendrick & Vartak, 2007), *Lucina linearia* Stephenson, 1941 from the Maastrichtian, and *Lucina blankenhorni* Chavan, 1947 from the Campanian. Earlier fossils from the Aptian and Albian of Japan that were originally described as *Myrtea* species (Matsuda, 1985; Tashiro & Kozai, 1988) likely belong in other lucinid clades, including Monitilorinae.

CODAKIINAE

Amongst the Codakiinae, only *Lucinoma* species have widely occupied deeper water; the other clades of *Codakia* species and *Ctena* species are largely from tropical to warm temperate shallow water. Exceptions are two *Epicodakia* species known only from dead shells; one (as *Wallucina izuensis* Okutani &
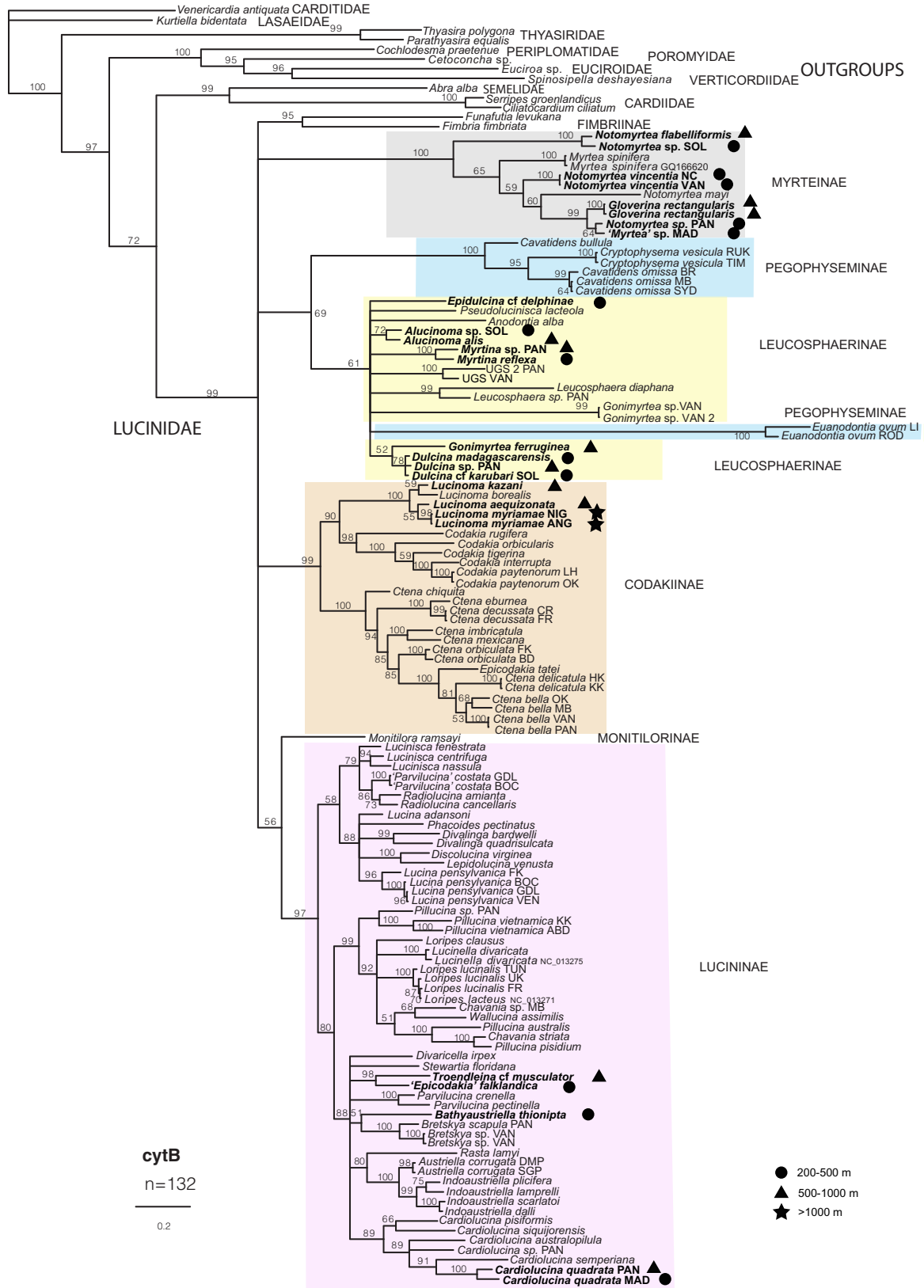
Figure 4. Single gene tree for Lucinidae based on mitochondrial gene cytB implemented on Bayesian inference using MrBayes. Support values are posterior probabilities (PP); only values ≥ 90% are shown, branches with PP < 50% were collapsed. For sample details, see Table 1. Monophyletic subfamilies are indicated by a box. Deep-sea species are indicated by black symbols (for details, see key).

Matsukuma, 1982), at 100–200 m from Japan and Philippines, and an undescribed species from New Caledonia, at approximately 300 m (MNHN collections).

Lucinoma, with at least 30 living species, is the most well known of the deeper water lucinid genera. They have a latitudinal range from 70°N to 55°S and live from the intertidal zone to over 2000 m (Taylor & Glover, 2010: fig. 5.9). The majority of *Lucinoma* species are found from > 200 m to mid-bathyal depths and are often abundant at hydrocarbon seeps, mud volcanoes, and oxygen minimum zones (Cary *et al.*, 1989; Callender & Powell, 1997, 2000; Salas & Woodside, 2002; Olu-Le Roy *et al.*, 2004; Holmes *et al.*, 2005; Cosel, 2006; Oliver & Holmes, 2006; Duperron *et al.*, 2007; Cosel & Bouchet, 2008; Oliver *et al.*, 2012; Zamorano & Hendrickx, 2012). Surprisingly, despite being sampled from widely separated localities and depths, the *Lucinoma* species included in the present study are related to each other by only short branches, suggesting that they may have radiated recently or that the genus is more slowly evolving than other Codakiinae. A chronogram including three *Lucinoma* (Taylor *et al.*, 2011) would suggest the former explanation is more likely with a recent and rapid radiation occurring in deeper-water. Additional samples would be helpful to determine the factors driving this diversification. Lucinidae are rare at high latitudes at all depths and we regard the occurrence of *L. borealis* and *Lucinoma annulata* (Coan, Valentich-Scott & Bernard, 2000) in increasingly shallow water at high latitudes as a possible example of deep-water emergence whereby species follow the isobathytherms (Lindner, Cairns & Cunningham, 2008).

Although *Lucinoma*-like lucinids first appeared in the Palaeocene in shallow water deposits (Taylor *et al.*, 2011), and possibly as a sister clade to *Saxolucina*, they have been associated with fossil deep-water hydrocarbon seeps ever since the Oligocene, for example *Lucinoma hannibali* (Kiel, 2010; Nesbit, Martin & Campbell, 2013) and in the Italian Miocene *Lucinoma perusina* (Moroni, 1966). Massive accumulations are recorded at some fossil seep sites in the Miocene and Pliocene of Japan with inferred palaeodepths of 50–300 m (Majima *et al.*, 2003; Majima, Nobuhara & Kitazaki, 2005). An earlier history of the *Lucinoma* clade is possible because '*Lucina*' or '*Mesomiltha*' *concinna* (Damon, 1860) from

the black, hypoxic, late Jurassic, Kimmeridge Clay of England (Wignall, 1990) is remarkably similar to *Lucinoma* in shell morphology, although further investigation is necessary. This, however, pre-dates the estimated age of origination for *Lucinoma* based on molecular data (Taylor *et al.*, 2011).

PEGOPHYSEMINAE

At the present day, Pegophyseminae (including most species formerly named as *Anodontia*) are generally restricted to shallow water habitats. Amongst the few deeper water species, the large *M. acetabulum* from 256–472 m comes from a site near hydrothermal activity off Taiwan (Bouchet & von Cosel, 2004) and a closely similar specimen was recovered from approximately 300 m off the Solomon Islands (MNHN collections). A rare small species, *Bythosphaera watsoni* (Smith, 1885), is recorded from 200–500 m in the central Indo-West Pacific but little is known of its habitat (Taylor & Glover, 2005). The lack of large pegophysemine records from deep water may be linked to burrowing depth, known to be in excess of 50 cm in the largest *Pegophysema* species (Schweimanns & Felbeck, 1985; Lebata & Primavera, 2001), so that the large living *Meganodontia* are likely to escape capture by ship-borne sampling gear. *Meganodontia acetabulum* is similar in gross morphology to large, inflated, toothless lucinids (e.g. '*Lucina*' *hoernea* Desmoulins, 1868 and '*Lucina*' *perlunulata* Sacco, 1904) recorded from Miocene hydrocarbon seeps and mud volcanoes of Italy (Moroni, 1966; Conti & Fontana, 1999; Clari *et al.*, 2004). Although these Miocene lucinids have not been investigated in detail, they may represent a prior Neogene association of Pegophyseminae with offshore chemosynthetic habitats seeps not yet confirmed from the present day.

LUCININAE

Lucininae generally inhabit shallow water and only a handful of species have yet been recorded from > 200 m. As shown in the Results, three of these cluster fairly closely together with shallower water species. *Bathyaustriella thionipta* is recorded from a 500 m deep hydrothermal vent on the Kermadec Ridge off New Zealand (Glover *et al.*, 2004). Its sister clade of *Parvilucina* species ranges from intertidal to
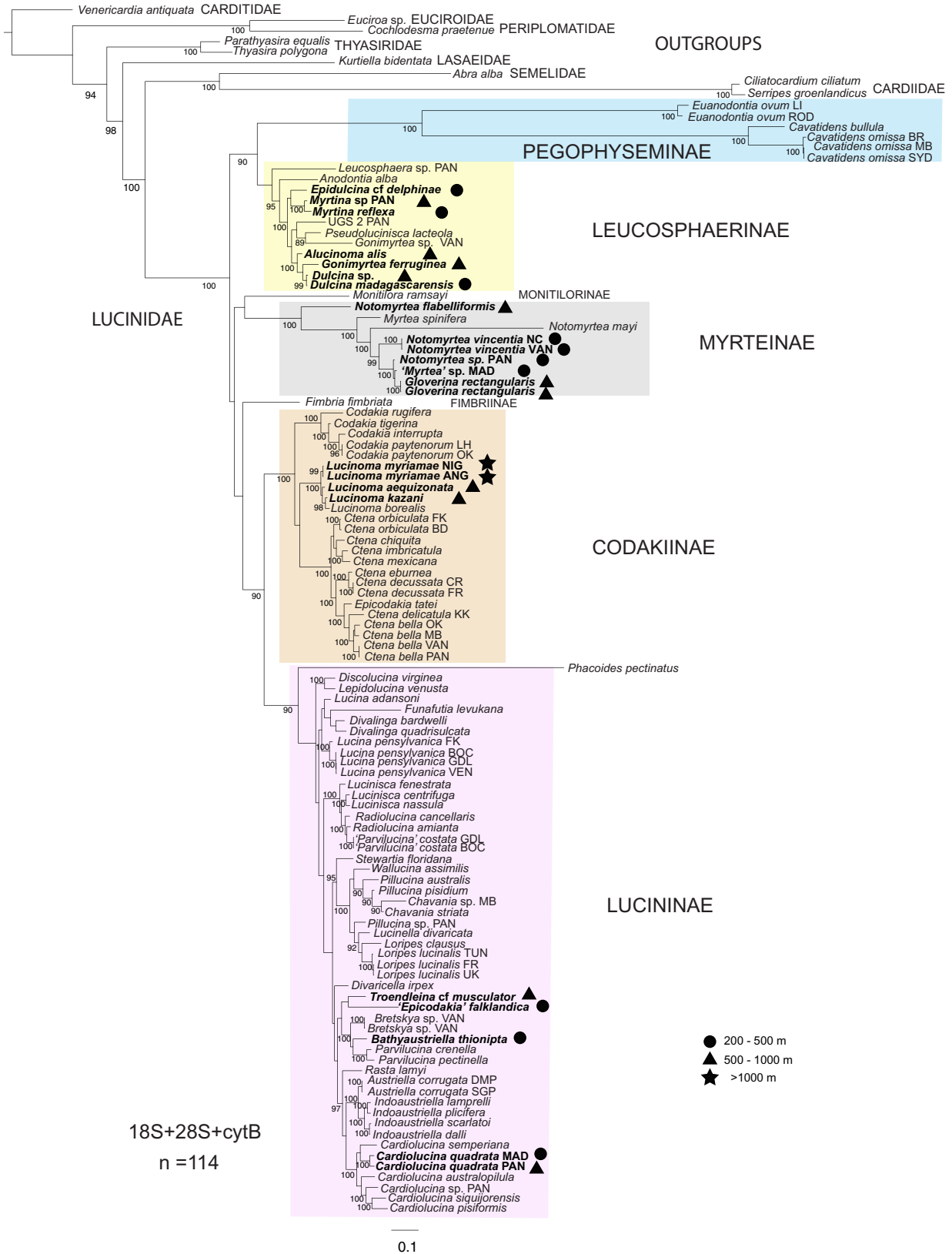
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deeper water with *Parvilucina tenuisculpta* recorded to 300 m (Coan *et al.*, 2000) and the morphologically similar *Liralucina* sp. nov. from the Philippines is found to 300 m (MNHN collections). *Troendleina*, type species *Troendleina marquesana* Cosel & Bouchet, 2008, includes several deeper water species (150–800 m) from the Pacific Ocean (Cosel & Bouchet, 2008; Glover & Taylor, in press) and from the south Atlantic '*Epicodakia*' *falklandica* occurs at depths of 100–500 m (Dell, 1964). For the latter species, the molecular results show that it should not be classified in the Codakiinae as *Epicodakia* despite the similarity of the external shell.

Cardiolucina species form a well supported subclade including species from the intertidal zone to depths of 1000 m. Species are small, round, inflated, and thick shelled, with strong hinge teeth and dentate margins and thus are rather different in morphology from other deep water lucinids (Taylor & Glover, 1997). *Cardiololucina quadrata* is the deepest, ranging from 300 to 1200 m around the central Philippines and is by far the most abundant lucinid at depths of 700–800 m (Glover & Taylor, in press). In the molecular analyses it clusters with *C. semperiana* from shallow water although another offshore species, *Cardiolucina civica*, living from 80–350 m has not yet been analyzed. *Cardiolucina* is one of the most derived clades within the Lucinidae, with a first appearance in the middle Eocene (*Cardiolucina ligata*; Cossmann & Pissaro, 1904) with the type species, *Cardiolucina agassizi* Sacco, 1904, described from the Miocene of northern Italy and present in the mid-Miocene of France in shallow water deposits.

Deep-sea habitats

Continuing research is demonstrating the diversity and disparity of lucinids at the outer shelf and bathyal depths, with many new species described from Indonesia, the Philippines, off West Africa, and the Gulf of Mexico (Cosel, 2006; Cosel & Bouchet, 2008; Taylor & Glover, 2009). More detailed analysis in the Philippines has shown diverse lucinid faunas with marked depth zonation; for example, species of Myrteinae and Leucosphaerinae have distinct assemblages in different zones (Glover & Taylor, in press). Moreover, the slender elongate morphologies of some of the deep water Leucosphaerinae and Myrteinae such as *Dulcina*, *Elliptiolucina*, and *Gloverina* are not replicated in shallow water taxa. Many of these are unknown from shallow water and this implies independent radiations in deeper water.

In shallow water, the distribution of many lucinids is strongly associated with organically enriched sediment environments, such as mangrove fringes and seagrass beds, or sands and muds (Meyer *et al.*, 2008; van der Heide *et al.*, 2012), and lucinids can also be diverse in coral reef habitats (Glover & Taylor, 2007). Similarly, empirical evidence suggests that lucinids occur abundantly in deeper water if there is some organic enrichment and elevated hydrogen sulphide levels. Between 200–1000 m in the tropics, there is diversity of organic enrichment that may be in the form of sunken vegetation and other organic falls, pock marks, mud volcanoes, hydrocarbon seeps, sedimented hydrothermal vents, and sediment beneath oxygen minimum zones (Samadi *et al.*, 2010; Bernardino *et al.*, 2012; Rodrigues, Hilário & Cunha, 2013). Small-scale, localized, diffuse seeps are largely undocumented in the tropical Indo-West Pacific and may be common around Indonesia and Philippines adding to the complexity of sulphide-rich habitats. Moreover, Cosel & Bouchet (2008) highlight the many semi-enclosed basins with poor bottom water circulation coupled with an accumulation of sunken plant material providing habitats suitable for chemosynthetic bivalves. The poor circulation in these basins may also contribute to diversity in these regions by promoting allopatric speciation. The presence of symbiotic sulphide-oxidizing bacteria in lucinid gills is a key biological strategy enabling the group to diversify in these habitats.

Beneath oxygen minimum zones, there is an enhanced accumulation of organic material, with resulting elevated hydrogen sulphide levels in the sediment that can only be exploited by organisms able to tolerate low oxygen levels and highly sulphidic conditions. Some *Lucinoma* species, for example, *Lucinoma aequizonata* (Cary *et al.*, 1989), *Lucinoma gagei* (Oliver & Holmes, 2006), and *Lucinoma heroica* (Zamorano & Hendrickx, 2012), are particularly associated with such environments and have adapted to the challenges of living under such harsh conditions. Extreme tolerance to anoxia has been demonstrated experimentally for *L. aequizonata* (Arndt-Sullivan, Lechaire & Felbeck, 2008) with the bivalves surviving 262 days without oxygen. Moreover, the symbionts of *L. aequizonata* respire anaerobically using nitrate

rather than oxygen as a terminal electron receptor (Hentschel, Hand & Felbeck, 1996). In molecular analyses of lucinid symbionts, phylotypes from other *Lucinoma* species cluster with that from *L. aequizonata* (Brissac, Merçot & Gros, 2011), suggesting a possible similar biology. As well as oxygen minimum zones, the frequent association of *Lucinoma* species with hydrocarbon seeps also demonstrates their tolerance of sulphide rich sediments that are normally toxic to many bivalves. The ability to utilize these extreme habitats may have contributed to the rapid radiation observed in this genus.

Although not widely studied, some lucinids also utilize haemoglobins and this is known for *M. spinifera* (Dando *et al.*, 1985) and probably in the large *Elliptolucina ingens* that has liver-coloured ctenidia (Kuhara *et al.*, in press), leading to speculation that it may be present in all Myrteinae, possibly contributing to the success of the group in deep water. Haemoglobins have been most studied in *Phacoides pectinatus* (Lucininae) a shallow water inhabitant of hypoxic sediments (Krauss & Wittenberg, 1990; Frenkiel, Gros & Mouëza, 1996) delivering both oxygen and sulphides to the symbionts. Haemoglobins are also probable in the deep-burrowing Pegophyseminae (Ball *et al.*, 2009).

Lucinidae are recorded to depths of 2500 m, but they are apparently much less diverse or abundant below 1000 m, although this may partly reflect lesser sampling efforts, particularly in tropical seas. Most of the deepest records of Lucinidae are species of *Lucinoma*; for example, Olu-Le Roy *et al.* (2004) recorded abundant *L. kazani* at 1700–2000 m in the eastern Mediterranean; *L. heroica* at 1800 m in the Gulf of California (Coan & Valentich-Scott, 2012), *Lucinoma atalantae* lives at 2100 m off Mauritania (Cosel, 2006), and *L. myriamae* at 2050 m off Angola [Natural History Museum in London (NHMUK) collection]. From a putative hydrocarbon seep at 2570 m in the Sulu Sea, three lucinids, *Elliptiolucina labeyriei*, *Lucinoma* sp., and *Myrtea* sp., are recorded together with '*Calyptogena*' spp. (Cosel & Bouchet, 2008; Glover & Taylor, in press). Below 2000 m, most documented deep-water hydrocarbon seeps are usually dominated by other major groups of chemosynthetic bivalves, Vesicomyidae, Bathymodiolinae, *Acharax* (Solemyidae), and Thyasiridae (Krylova & Sahling, 2010; Watanabe *et al.*, 2010).

AGE OF DEEP-WATER CLADES

Although there are records of offshore shelf lucinids in dysaerobic environments ever since the Jurassic (Oschmann, 1988; Wignall, 1990), the best documentation of fossil deeper water lucinids comes from the

recent studies of ancient hydrocarbon seeps. From an origin in the Palaeozoic, lucinids first appeared at seeps during the Late Jurassic and there have been successions of taxa recorded from seeps around the world through the Mesozoic and Cenozoic (Kiel, 2010). From the Late Jurassic, *Beauvoisina* is the earliest known seep-associated lucinid, succeeded in the Cretaceous where *Ezolucina*, *Nipponothracia*, and *Nymphalucina* have been described (Speden, 1970; Amano *et al.*, 2008; Kiel, Campbell & Gaillard, 2010; Kiel, 2013). There are some resemblances of *Nymphalucina* and *Nipponothracia* to Myrteinae but the subfamilial placement of many of the Mesozoic fossils is problematic, not helped by the frequent poor preservation.

From the Cenozoic, *Cryptolucina*, *Elongatolucina*, *Nipponothracia*, and *Epilucina* species are recorded from Eocene seeps (Kase *et al.*, 2007; Kiel, 2010, 2013). The first three genera can be tentatively assigned to the Myrteinae and *Epilucina* to the Codakiinae, with a sole living shallow water species that is not seep-associated. From the Oligocene onwards, *Lucinoma* species become increasingly prevalent at fossil seeps around the world (Moroni, 1966; Majima *et al.*, 2005; Nesbit *et al.*, 2013). *Jorgenia* and *Graecina* species (probable Myrteinae) are also recorded at present day seeps in the Atlantic (Taylor & Glover, 2009) but lack a recorded fossil history. Taken together, these records suggest that there were specialist deep-water lucinid faunas through the Mesozoic and Cenozoic.

CONCLUSIONS

Far from being a dominantly shallow water group as commonly perceived, Lucinidae are highly diverse in outer shelf to bathyal depths, especially in the tropics. A study of the lucinids of the Philippines showed that almost 40% of the species occurred at depths greater than 200 m (Glover & Taylor, in press). A recent focus concerns the chemosymbiosis of lucinids and their complex interactions with seagrass habitats (van der Heide *et al.*, 2012; Rossi *et al.*, 2013), but their associations and habitats in deeper water are far more diverse and much less studied. Although only a subset of deep-water lucinids have been included in molecular analyses, the results obtained in the present study demonstrate that deeper water species are present in four of the seven recognized subfamilies, Myrteinae, Leucosphaerinae, Codakinae, and Lucininae, indicating independent phylogenetic origins. Many of the newly-described deep water species and genera group within the Myrteinae and Leucosphaerinae that are probably the oldest clades within the Lucinidae. Our accumulated evidence suggests a long history of radiation of deep-water genera and species

independent of shallow faunas since at least the early Cenozoic and probably earlier in the Mesozoic.

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