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Bivalvia – a look at the Branches
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Lucinidae (Bivalvia) – the most diverse group of chemosymbiotic molluscs

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Recent molecular analyses have demonstrated that the traditional Lucinoidea, comprising the extant families Lucinidae, Thyasiridae, Ungulinidae, Fimbriidae, and Cyrenoididae, is not monophyletic. Thyasiridae and Ungulinidae are unrelated to Lucinidae, a result corroborated by clear morphological differences between the groups. Chemosymbiosis in Thyasiridae and Lucinidae has been independently derived. Within the family Lucinidae, previous ideas of relationship and subfamilial divisions based on shell characters have little support from molecular results. Anatomical characters of the ctenidia, mantle gills, and posterior apertures have potential in phylogenetic analysis but rigorous analysis of shell characters is also needed. Although there is a good fossil record of Lucinidae throughout the Cenozoic and Mesozoic, in the Palaeozoic fossils are less frequent and most need reappraisal. The Silurian *Ilionia prisca* is probably the earliest fossil with convincing lucinid features, followed in the Devonian by *Phenacocyclas* and some *Paracyclas* species. *Zoological Journal of the Linnean Society*, 2006, **148**, 421–438.

ADDITIONAL KEYWORDS: anatomy – chemosymbiosis – classification – fossil record – phylogeny.

INTRODUCTION

Interest in chemosynthetic communities has largely focused on hydrothermal vents and cold seeps where bivalve molluscs such as *Bathymodiolus* and *Calyptogena* are often abundant (Van Dover, 2000). Chemosymbiosis between sulphide-oxidizing and, less commonly, methane-oxidizing bacteria, has been identified in several families of bivalves including Lucinidae, Thyasiridae, Solemyidae, Mytilidae, Vesicomyidae, and Teredinidae (Fisher, 1990; Reid, 1990; Distel, 1998). Of these families, the Lucinidae, in which the sulphide-oxidizing symbiosis is likely obligate, is by far the most disparate and species-rich (Fig. 1) and occupies the greatest variety of habitats over a broad geographical range (60°N – 55°S). Despite the attention given to the more dramatic communities around vents and seeps, the most widespread of sulphide-rich habitats colonized by chemosymbiotic organisms is the suboxic zone of marine sediments (Ott, Bright & Bulgheresi, 2004), and this is the home of most lucinid species.

Habitats occupied by lucinids range from the intertidal zone to depths of over 2100 m. They occur in mangrove muds (Lebata, 2001), intertidal and offshore muds and sands, seagrass beds (Barnes & Hickman, 1999; Johnson, Fernandez & Pergent, 2002), sites of high organic input such as sewage disposal sites (Reid & Brand, 1986) and offshore locations where sunken vegetation accumulates (Cosel & Bouchet, in press). Some species are associated with cold seeps and mud volcanoes (Carney, 1994; Callender & Powell, 1997; Salas & Woodside, 2002), oxygen minimum zones (Cary *et al*., 1989; Oliver & Holmes, 2006) and a single species from a hydrothermal vent (Glover, Taylor & Rowden, 2004). Interestingly, the greatest diversity of lucinids is

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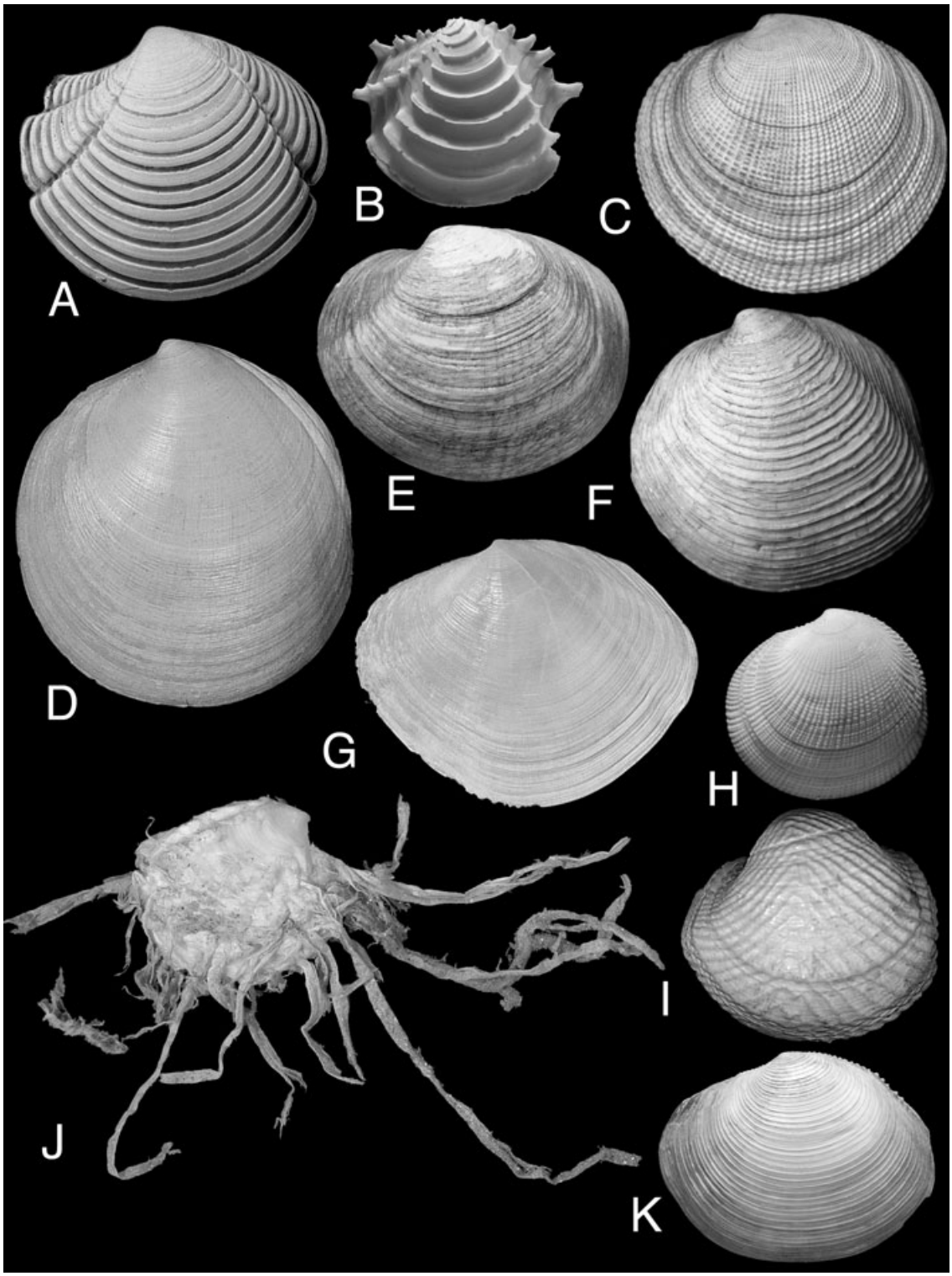

Figure 1. Diversity of form within Lucinidae. A, *Plicolucina flabellata* Glover, Taylor & Slack-Smith, 2003, Shell length (SL) = 22 mm; B, *Lamellolucina trisulcata* Taylor & Glover, 2002, SL = 10 mm; C, *Codakia tigerina* (Linnaeus, 1758), SL = 70 mm; D, *Anodontia philippiana* (Reeve, 1850), SL = 66 mm; E, *Miltha childrenae* (Gray 1825), SL = 82 mm; F, *Eomiltha voorhoevi*, SL = 80 mm; G, *Austriella corrugata* (Deshayes, 1843), SL = 60 mm; H, *Ctena bella* (Conrad, 1837), SL = 25 mm; I, *Rasta lamyi* (Abrard, 1942), SL = 30 mm; J, *Pompholigina gibba* (Gray, 1825), SL = 27 mm; K, *Myrtea spinifera* (Montagu, 1803), SL = 26 mm.

found within Indo-West Pacific and Atlantic reefal environments, where many species inhabit calcareous sands. For example, 22 species of Lucinidae are recorded from the Florida Keys (Bieler & Mikkelsen, 2004) and 35 species have been recognized from intensively sampled sites around New Caledonia (Glover & Taylor, in press) where Lucinidae are amongst the most diverse of bivalve families (8th out of 62) (Bouchet *et al*., 2002).

Although there has been much interest in lucinid biology, the systematics of the group has received less attention and there is much confusion at all taxonomic levels. The most recent comprehensive generic revision (Chavan, 1969) had minimal descriptions and poor illustrations, while the better-illustrated and well-documented treatment by Bretsky (1976) considered only North American taxa.

In this paper we review previous ideas on the relationships and systematics of the Lucinoidea, the Lucinidae in particular, and summarize recent molecular studies that have radically changed our views of the superfamily and the evolution of the chemosymbiosis. Additionally we highlight some morphological characters that have potential utility for phylogenetic analysis. Finally, we briefly discuss the geological age of the Lucinidae and the chemosymbiotic life habit.

STATUS OF LUCINOIDEA

Traditionally, the Lucinidae have been grouped together with the families Fimbriidae, Thyasiridae and Ungulinidae within the superfamily Lucinoidea (Dall, 1901; Thiele, 1934; Chavan, 1969), largely on the basis of similarity of shells and some anatomical features. Chemosymbiosis in Lucinidae was first reported in the early 1980s (Berg & Alatalo, 1984; Reid & Brand, 1986) and subsequently Thyasiridae and Fimbriidae were shown to have some chemosymbiotic species (Dando & Southward, 1986; Southward, 1986; Janssen, 1992), but no chemosymbionts have been reported from any Ungulinidae. Also, often included within the Lucinoidea are the poorly known brackish water family Cyrenoididae and the Mesozoic and Palaeozoic fossil groups Mactromyidae, Paracyclidae, and Babinkidae (Chavan, 1969; Boss, 1982; Johnston, 1993; Skelton & Benton, 1993; Amler, 1999). Species of the Recent genus *Bathycorbis* have been claimed as living representatives of the Mactromyidae (otherwise with no post-Cretaceous records) on the basis of supposed similarities of hinge teeth (Chavan, 1959, 1969). However, the affinities of these small (*c*. 5 mm) offshore bivalves from Australia, known only from shells, are uncertain.

Most discussions of relationships within the Lucinoidea have concerned only the families Lucinidae, Thyasiridae, Ungulinidae and Fimbriidae, with the tacit assumption that they form a monophyletic group. Several scenarios have been proposed that attempt to place the Lucinidae, Thyasiridae, Ungulinidae and sometimes Fimbriidae into an evolutionary sequence. There have been major differences between each of these, relating to either anatomical characters, or time of first appearance in the fossil record (Allen, 1958; McAlester, 1966; Boss, 1970; Reid & Brand, 1986; Hickman, 1994). A particular problem has concerned the position of the Ungulinidae, a family with apparently underived anatomical features, but with a relatively late appearance (Cretaceous) in the fossil record. Allen (1958) regarded the Ungulinidae as basal in his phylogenetic scenario, but McAlester (1966) and Boss (1970) thought it the most derived, the latter suggesting that the outer ctenidial demibranchs, absent in Lucinidae, had been reacquired in Thyasiridae & Ungulinidae. Boss (1970) considered the Fimbriidae more closely related to the Lucinidae than to Ungulinidae or Thyasiridae. Subsequent to the discovery of chemosymbiosis in lucinoids, Reid & Brand (1986), Reid (1990), and Hickman (1994) considered that the trait was probably plesiomorphic for the superfamily, but partially lost in the Thyasiridae and totally lost in the Ungulinidae.

NEW CONCEPT OF LUCINOIDEA

Following the results from the molecular analysis (Fig. 2), we now restrict the Lucinoidea to the families Lucinidae and Fimbriidae, although molecular results (Fig. 3) indicate the latter nests within the lucinids. Although at the present day there are only two living species, *Fimbria*-like bivalves were diverse and abundant during the Mesozoic (Monari, 2003). Of the other families traditionally included within the Lucinoidea, the Thyasiridae form a monophyletic group (Fig. 2) basal within the Heterodonta excepting the Carditidae/Crassatellidae clade. The Ungulinidae form a monophyletic group allied to the Arcticidae/Veneridae/Mactridae clades. No species of Cyrenoididae has yet been analysed, but from anatomical characters a relationship with Lucinidae is unlikely. The status of the fossil taxa Mactromyidae, Paracyclidae and Babinkidae within the Lucinoidea is unresolved.

THE LUCINIDAE

Shells of Lucinidae are usually white, subcircular in outline and range from discoidal to subspherical in profile. Living species range in height from around 3.0 – 140 mm. External sculpture mainly comprises variations of commarginal lamellae and radial ribbing is usually absent or subordinate. Posterior sulci are often present. However, many lucinids have smooth, unornamented shells. Ligaments range from long

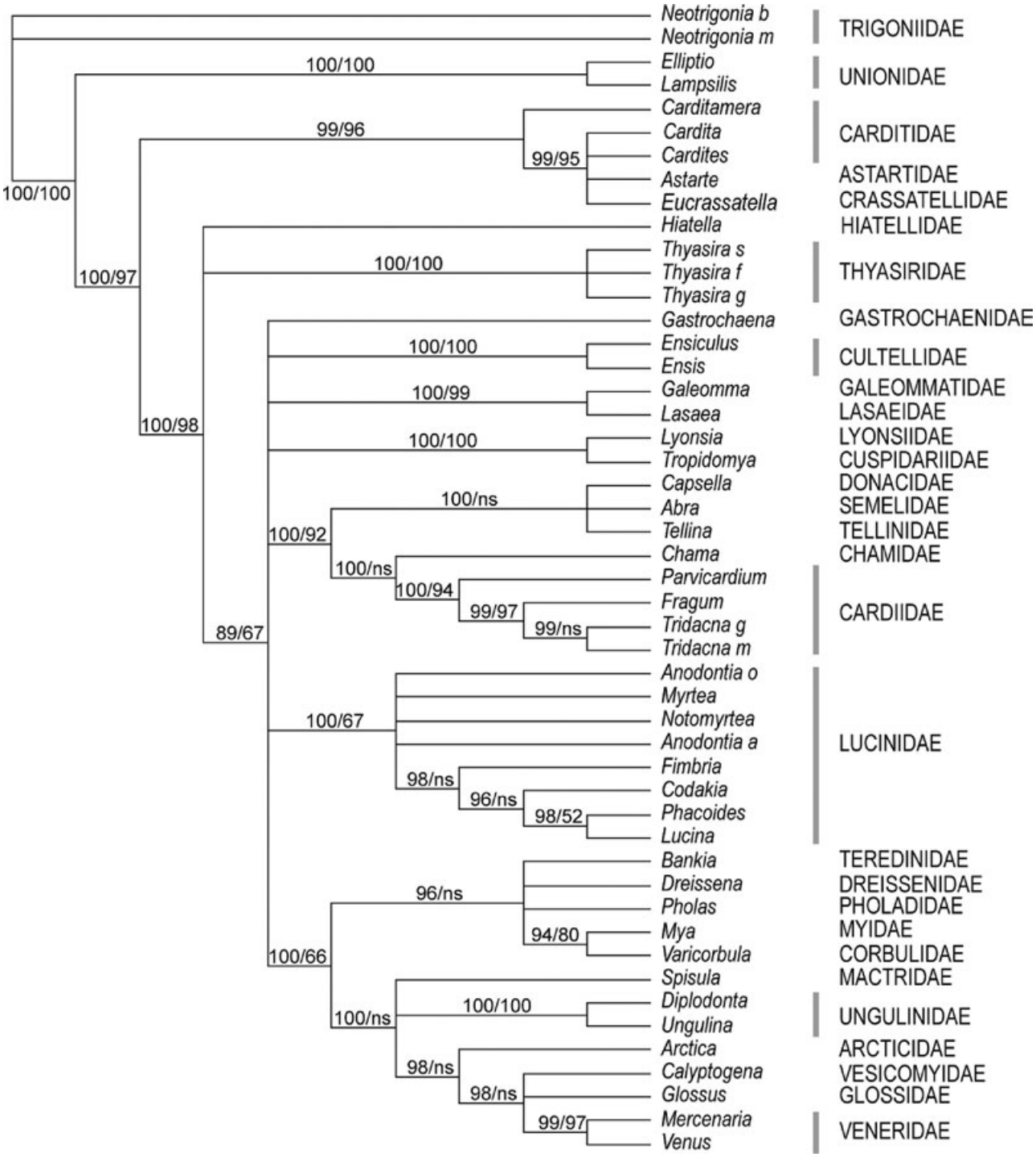

Figure 2. Molecular phylogeny of heterodont and palaeoheterodont bivalves produced by Bayesian analysis of partial sequences from the 18SrRNA gene. Branches with posterior probabilities < 85% have been collapsed. Nodal support is posterior probability/bootstrap (Neighbour-joining using Maximum Likelihood distance, 10 000 reps). Details of taxa and methods in Taylor *et al*., 2005.

external to short internal. There are usually two or less cardinal teeth in each valve, with lateral teeth present in some taxa. In many lucinids hinge teeth are highly reduced or completely absent. One of the most distinctive features of lucinids is the anterior adductor muscle scar. The adductor muscles are usually unequal in size, and most (but not all) lucinids possess a distinctive elongate, anterior adductor muscle scar

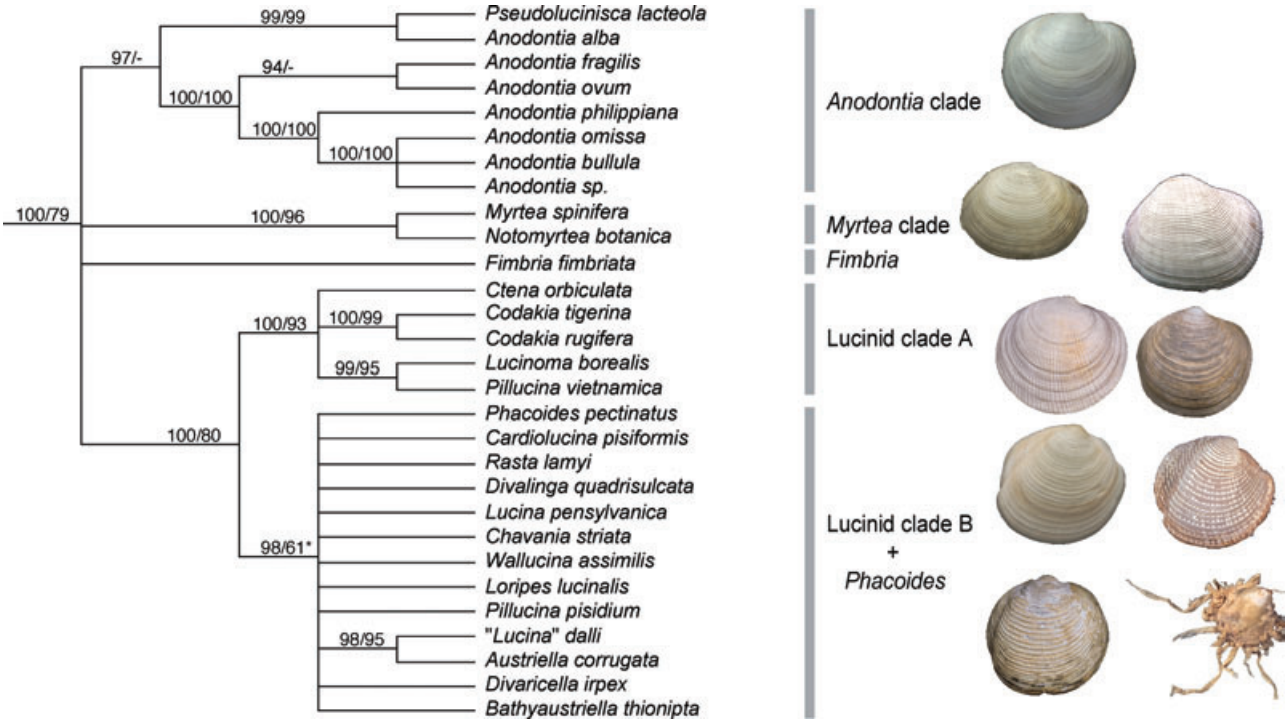

Figure 3. Molecular phylogeny of Lucinidae (from Williams *et al*., 2004) based on concatenated gene sequence data from 18S rRNA and 28S rRNA genes. Branches collapsed with posterior probabilities of > 90%. Nodal support is posterior probability/bootstrap (NJ using ML distance, 10 000 reps). *Bootstrap support is 96% for lucinid clade B excluding *Phacoides pectinatus*.

that diverges inwards from the pallial line. There is no posterior pallial sinus. Shell microstructure usually consists of three layers, an outer spherulitic prismatic layer, a middle layer of crossed-lamellar structure and within the pallial myostracum, an inner complex crossed lamellar layer often with intercalated prismatic sheets (Taylor, Kennedy & Hall, 1973).

Anatomically, lucinids have a number of distinctive features (Fig. 4). Ctenidia are usually large, comprising inner demibranchs only; the filaments are thick with a narrow, outer ciliated zone and an extended abfrontal zone comprising bacteriocytes, intercalary cells and mucocytes. Distal portions of gill filaments are often fused into cylindrical channels (Distel & Felbeck, 1987). Labial palps are highly reduced, consisting of small folds at the edge of the lips. Posterior inhalant and exhalant apertures are present, the latter with an eversible tube. The foot is elongate, usually cylindrical and highly extensible with a differentiated, ciliated and glandular tip. A large pallial blood vessel runs diagonally from the auricle to near the ventral tip of the anterior adductor muscle, often leaving a deep impression in the shell interior. The inner mantle around the anterior adductor muscle is often thickened by blood space or in some species thrown into complex folds as mantle gills.

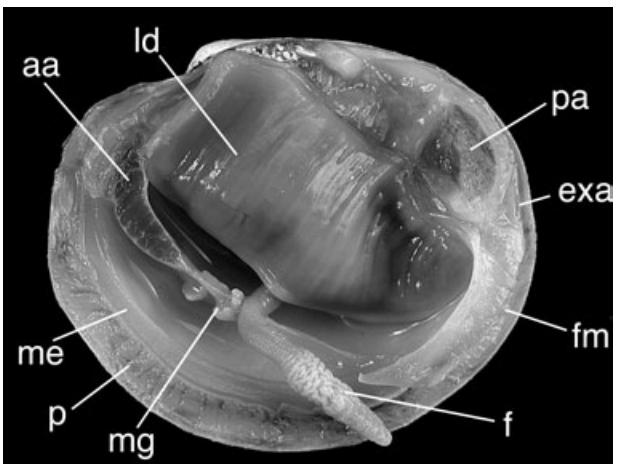

Figure 4. General anatomy of *Anodontia philippiana*, Dampier, Western Australia, with left valve and mantle removed. Abbreviations: aa, anterior adductor muscle; exa, exhalant aperture; f, foot; fm, fused mantle; ld, left demibranch of ctenidia; me, mantle edge; mg, mantle gills on septum; p, periostracum; pa, posterior adductor muscle. Shell length = 40 mm

Diversity of Lucinidae

It is increasingly recognized that the family Lucinidae is much more diverse than previous assessments. Using genera as a proxy for morphological disparity and the revision in the 'Bivalve Treatise' (Chavan, 1969) as a starting point, 44 valid genera containing Recent species were recognized. By 2005 this had increased to 58 published genera, and another 15 new genera are in press or preparation (E. A. Glover & J. D. Taylor, unpubl. data; Cosel & Bouchet, in press) = 73; while we are aware of perhaps another 15 distinct but as yet unworked taxa = 88. This represents a doubling of the known genera since 1969. From our experience, we anticipate that there are many more undescribed taxa from mid- and deep-water environments, especially species < 10 mm in size. At the specific level there is a similar unrecognized diversity. For example, amongst the larger taxa, many new species of *Lucinoma* are being discovered from cold seeps and oxygen minimum zones (von Cosel, in press; Oliver & Holmes, 2006). Amongst the *Anodontia* group from shallow water tropical habitats, we now identify 25 species compared to the possible eight we thought existed only three years ago (Taylor & Glover, 2005). Furthermore, Cosel & Bouchet (in press) are describing many new species from deeper water across the Indo-West Pacific. Additionally, upon closer study, a number of apparently well-known tropical species turn out to be complexes of similar species (Taylor & Glover, 1997, 2002). Our current estimates suggest that there may be as many as 500 extant species of Lucinidae.

Relationship of Lucinidae to other bivalve groups

McAlester (1966) suggested that *Babinka* and the lucinoids were derived from monoplacophorans independently from the rest of the bivalves and Pojeta (1978) considered them a sufficiently distinct group to warrant separation at subclass level (Lucinata). However, these concepts were countered by Boss (1969, 1970) who pointed out the many morphological characters of lucinids that are shared with heterodont bivalves. Subsequent morphological and molecular analyses have confirmed the position of the Lucinidae amongst the Heterodonta (Healy, 1995; Steiner & Hammer, 2000; Giribet & Wheeler, 2002; Giribet & Distel, 2004; Williams, Taylor & Glover, 2004).

Some workers have proposed, on the basis of morphology, a phylogenetic relationship between the Crassatelloidea and Lucinoidea (in old concept) (Allen, 1958; Boss, 1969; Scarlato & Starobogatov, 1978; Johnston, 1993; Morton, 1996). Molecular analyses of species of Astartidae and Carditidae (Giribet & Wheeler, 2002; Giribet & Distel, 2004), indicated that they group together in a monophyletic clade that forms a sister group to the remaining heterodont bivalves, but with no close relationship to the Lucinidae. Inclusion of a crassatellid species, *Eucrassatella donacina* (Lamarck, 1818), in the molecular analysis (Taylor, Glover & Williams, 2005) shows (Fig. 2) that a combined monophyletic clade of Astartidae, Crassatellidae and Carditidae forms a basal sister group to all other heterodont bivalves including the Anomalodesmata. The monophyly of this clade is corroborated by morphological characters, including those of sperm (Healy, 1995) and presence of extracellular haemoglobin of high molecular weight in all three families. This result supports the idea, based on morphological studies, that the Crassatelloidea and Carditoidea are the most primitive of the living heterodont bivalves (Yonge, 1969). Suggestions of a relationship between the Crassatellidae and any of the families previously included in the Lucinoidea (Allen, 1958; Boss, 1969; Johnston, 1993; Morton, 1996) are not supported.

A molecular phylogeny of the Anomalodesmata (Dreyer, Steiner & Harper, 2003) showed them rooting, in parsimony analysis, as a monophyletic clade amongst basal heterodonts between the Carditoidea/Crassatelloidea clade and the rest of the heterodonts but in a maximum likelihood analysis they formed a sister group to the Lucinidae. Nevertheless, we are at present unable to identify a sister group to the Lucinidae and, in our molecular analyses, the clade falls into a polytomy with several other major groups of heterodont bivalves (Fig. 2).

Relationships within the Lucinidae

Previous analyses

In the first major review of Lucinidae, Dall (1901) classified all Lucinidae into six genera: *Codakia*, *Lucina*, *Loripes*, *Myrtea*, *Phacoides* and *Divaricella*, with further divisions into subgenera and sections. Although there were no explicit statements of relationship, the inclusion of subgenera and sections within the genera reflected such ideas. A separate family, Corbiidae, contained *Fimbria*. Later, Lamy (1920) reviewed the Recent species of Lucinidae but made no explicit statements of relationship.

The first comprehensive study of Recent and fossil Lucinidae to develop ideas of relationship and phylogeny was that of Chavan (1937–38). The latter concluded with a geological range chart of the Recent and fossil lucinid genera, grouped according to his ideas of relationship. A cladogram derived from Chavan's diagram and including Recent genera only is shown in Figure 5. By the time of the publication of the Bivalvia volume of the *Treatise on Invertebrate Palaeontology*, Chavan (1969) had somewhat revised his ideas and divided the lucinid genera into four subfamilies,

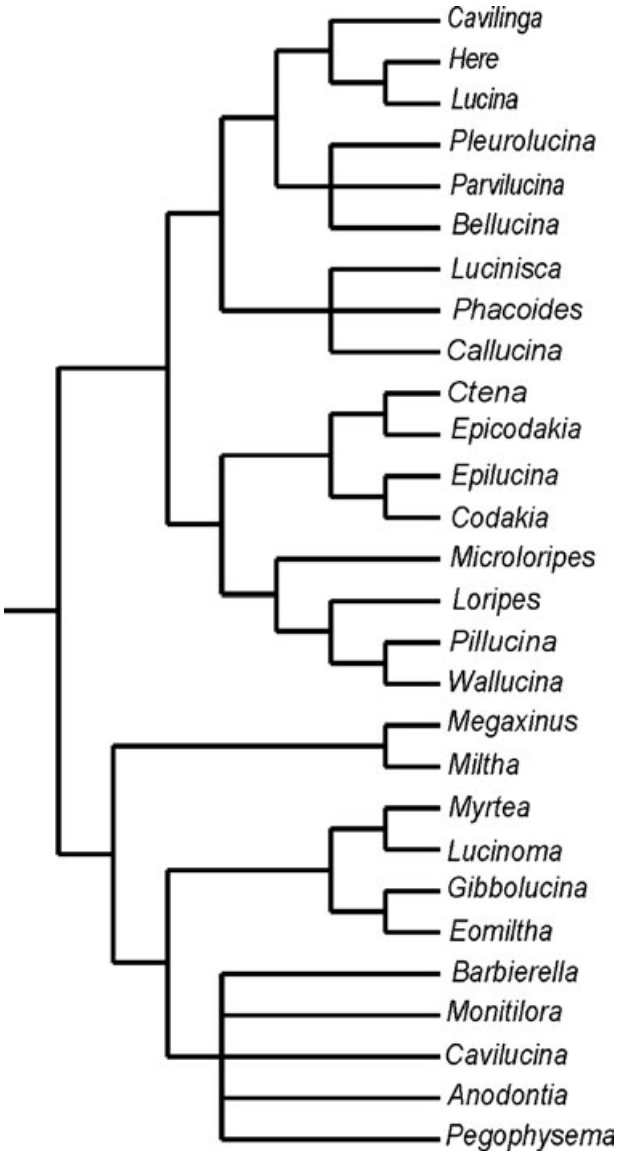

Figure 5. Tree of lucinid relationships derived from final figure (tableau chronologique de l'evolution des lucines) by Chavan, 1937–1938), including living taxa only.

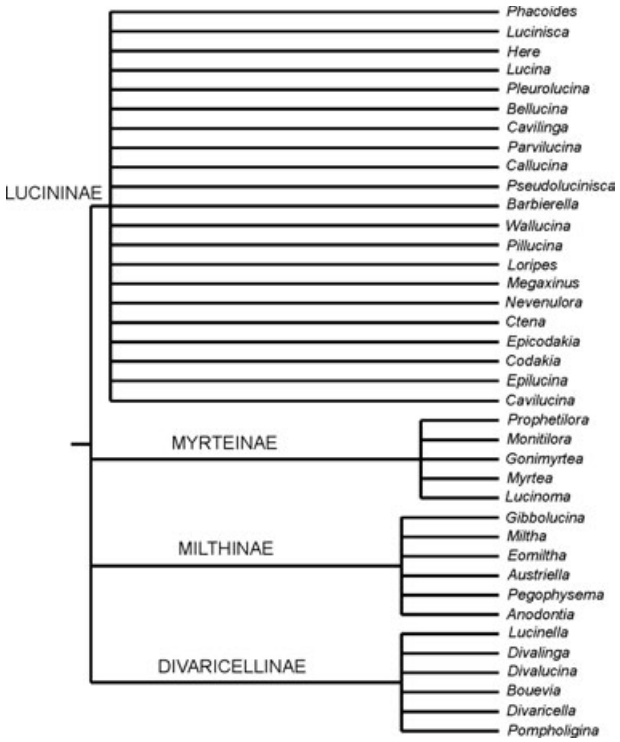

Figure 6. Tree summarizing Chavan's (1969) ideas of relationships in Lucinidae derived from his subfamilial classification of genera. Recent taxa only included.

Lucininae, Myrteinae, Milthinae and Divaricellinae, with the Fimbriidae as a separate family. A tree constructed from this classification, but including Recent genera only, is shown in Figure 6.

Subsequently, Bretsky (1970) attempted a phenetic analysis of Lucinidae largely using Recent and Cenozoic species from North America. For each of 42 species, she scored 42 shell characters, with up to five states recognized for each character. Considerable attention was paid to some shell features – for instance, the lunule was analysed as five separate characters with 16 states. Her resulting phenetic analysis classified the lucinids into seven groups that she called genera further divided into many subgenera. Subsequently, these phenetic results were combined with data from fossil lineages and used to produce a series of phylogenetic trees and a new classification with no suprageneric categories (Bretsky, 1976), again largely based on North American taxa. A cladogram derived from Bretsky's trees and using only Recent genera is shown in Figure 7.

It is difficult to compare these phylogenies, as different taxa were discussed by Chavan and Bretsky, but two examples illustrate conflicts between the classifications. In 1938, Chavan thought that *Anodontia* and *Pegophysema* were related to *Cavilucina* and *Monitilora,* but in 1969 he placed the former two genera in his subfamily Milthinae and the latter two genera into the Myrteinae. By contrast, Bretsky (1976) indicated a relationship between *Anodontia* and *Myrtea,* or in an alternative scenario, with *Loripes*. Similarly, Chavan (1969) placed *Lucinoma* in the Myrteinae, but Bretsky (1976) thought the genus related to *Miltha* and *Eomiltha*.

All these previous studies were based entirely on shell characters, the conflicting hypotheses probably resulting from high levels of homoplasy. Many lucinids have relatively smooth, subcircular, discoidal shells with minimal shell sculpture. Moreover, hinge teeth

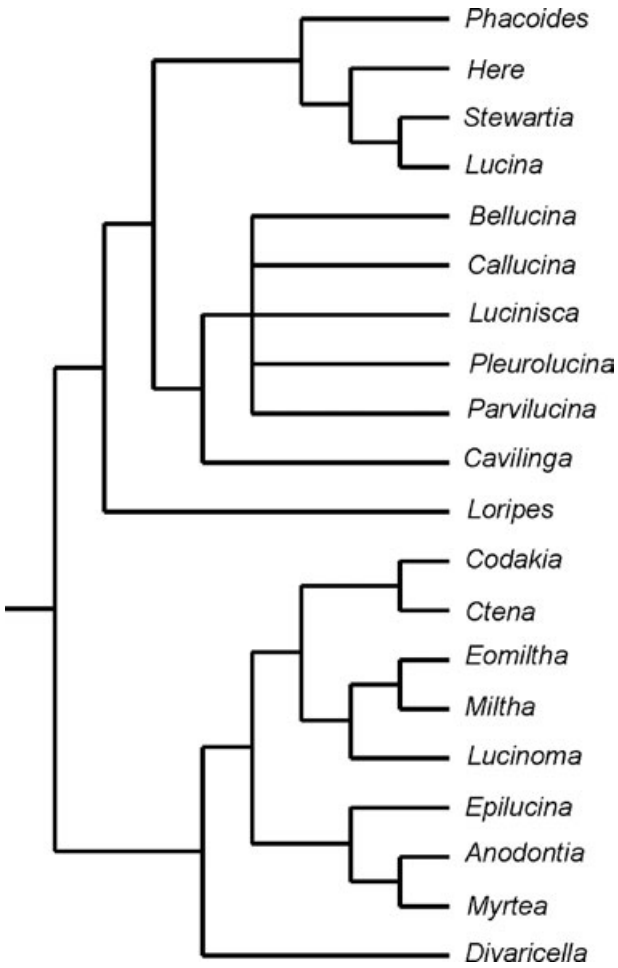

Figure 7. Composite tree of lucinid relationships derived from Bretsky (1976: figs 3–9) and including living taxa only.

are often reduced or in many instances entirely absent. Divaricate sculpture, as in *Divaricella*, *Divalinga* and *Pompholigina* (Fig. 1J) and used by Chavan (1969) to define the Divaricellinae has probably evolved independently in different clades (Dekker & Goud, 1994). Recent molecular evidence is confirming that the Divaricellinae is paraphyletic, with, for example, *Lucinella divaricata* (Linnaeus, 1758) identified as part of the *Loripes* group (J. D. Taylor, S. T. Williams & E. A. Glover, unpubl. data). We previously considered (Glover & Taylor, 2001) an obliquely inset, internal ligament as a possible apomorphic character of a group of genera around *Loripes*, including *Pillucina* and *Wallucina*. However, a similarly inset internal ligament occurs in several species of the *Anodontia* clade, including *A. philippiana* and *A. ovum,* suggesting an independent derivation of this form of ligament.

Shell characters have important potential in phylogenetic analysis and their use is essential if fossil taxa are to be integrated into phylogenetic schemes. However, rigorous analysis of ligament structure, anterior muscle scars, ribbing structure, hinge teeth and shell microstructure is almost entirely lacking. At present shell characters are useful in discrimination of species and genera but give little information on relationships.

Molecular results

Williams *et al*. (2004) presented the first significant molecular analysis of relationships within the Lucinidae. Sequences of 18S and 28S rRNA genes were obtained from 32 species representing 21 genera from around the world. This initial phylogeny recognized a number of major clades (Fig. 3) and these are briefly discussed below.

Myrtea clade

The two species sequenced, *Myrtea spinifera* (Montagu, 1803) from Europe and *Notomyrtea botanica* (Hedley, 1918) from Australia, form a monophyletic clade. Species in the *Myrtea s.l.* group usually have rather flat elongate shells, prominent commarginal lamellae, spinose dorsal margins, small teeth and short anterior adductor muscles. The clade is diverse in offshore habitats where there are many undescribed species. Chavan (1969) included five Recent genera (synonymizing *Notomyrtea* within *Myrtea*) in the new subfamily Myrteinae, but his inclusion of *Lucinoma* is not supported by our molecular results and three of the other genera have not yet been analysed.

Anodontia clade

Most of the *Anodontia* species analysed form a well-supported, monophyletic clade (including West Atlantic, Mediterranean and Indo-Pacific species) distinct from other lucinids (Fig. 3). However, the type species *Anodontia alba* Link, 1807 from the West Atlantic groups with the southern Australian species *Pseudolucinisca lacteola* (Tate, 1897) to form a basal sister clade to all the other *Anodontia* species. In shell characters *P. lacteola* is not similar to *Anodontia* but further studies of these poorly known bivalves are needed to resolve its position and the paraphyly of the *Anodontia* group. *Anodontia* species are characterized by smooth, subspherical toothless shells and they also possess a number of distinctive anatomical features including: a mantle septum, digitiform mantle gills, a thick outer mantle fold and extensive mantle fusion ventral to the posterior apertures involving the inner

and most of the middle mantle folds (Taylor & Glover, 2005). Chavan (1969) included *Anodontia* in his subfamily Milthinae but his concept of the group is not supported by the molecular analysis. Neither is there any support for Bretsky's (1976) proposal of a relationship between *Anodontia* and *Loripes*.

Fimbria clade

Fimbria fimbriata (Linnaeus, 1758) groups in a polytomy with other lucinid clades. There is no support on present evidence for separate familial status.

Lucinid clade A

This well-supported clade contains *Codakia*, *Ctena*, *Lucinoma* species and *Pillucina vietnamica.* On shell characters *Codakia* and *Ctena* have long been thought to be related (Chavan, 1937–38; Bretsky, 1976) but the inclusion of *Lucinoma* is surprising. *Codakia* and *Ctena* were included by Chavan (1969) in the subfamily Lucininae and *Lucinoma* in the Myrteinae. However, all the species in the group possess only a short length of mantle fusion ventral to the posterior apertures and papillae around the inhalant opening.

Lucinid clade B

This large clade contains many of the lucinid genera analysed including *Lucina*, *Cardiolucina*, *Wallucina*, *Loripes*, *Austriella*, *Divaricella*, *Rasta,* and the hydrothermal vent species *Bathyaustriella thionipta* (Glover *et al.*, 2004) Although there are groupings within this clade (e.g. *Loripes*, *Wallucina* and *Chavania*; Williams *et al*. 2004: figs 1, 4) they are less well supported (> 90% posterior probabilities). *Divalinga quadrisulcata* (d'Orbigny, 1842) and *Divaricella irpex* (Smith, 1885) fall within this clade and the separation by Chavan (1969) of the genera into the subfamily Divaricellinae is not supported.

The position of *Phacoides pectinatus* (Gmelin, 1792) is unresolved; in the 18S rRNA tree it forms a poorly supported sister taxon to *Anodontia*, while in the combined 18S/28S rRNA tree it forms a sister to Lucinid clade B. The species has many small indels and base changes not shared with other lucinids. Additionally, it has distinctive mantle gills and extensive mantle fusion similar to *Anodontia* species (see below). There is probably only a single living species of *Phacoides* and its relationships are obscure; Chavan (1969) thought it related to *Lucinisca* & Bretsky (1976) included it as a subgenus of *Lucina.*

Anatomical characters

Reviewed in the context of molecular analyses, anatomical studies are revealing characters that may prove useful in phylogenetic analyses and also in tracking the evolutionary adaptations to the symbiosis. In the following section we briefly describe some results from major organ systems of lucinids.

Ctenidial structure

Because the ctenidia house the chemosymbiotic bacteria their structure has been investigated in much more detail than any other feature of lucinid anatomy. Detailed electron microscopic studies are available for a wide variety of genera including: *Lucina (*as *Linga)* (Gros, Frenkiel & Mouëza, 1996); *Anodontia* (Gros, Liberge & Felbeck, 2003); *Codakia* (Frenkiel & Mouëza, 1995; Gros, Frenkiel & Mouëza, 1998), *Phacoides (*as *Lucina)* (Frenkiel, Gros & Mouëza, 1996; Liberge, Gros & Frenkiel, 2001); *Lucinoma* (Dando, Southward & Southward, 1986; Distel & Felbeck, 1987); *Parvilucina* (Reid & Brand, 1986); *Divaricella* (Gros, Frenkiel & Felbeck, 2000); *Lucinella* (Herry & Le Pennec, 1987); *Loripes* (Southward, 1986).

All lucinids examined have a similar gill filament structure with a ciliated zone of frontal, eulateral and lateral cilia similar to that of other heterodont bivalves. Inwards of this is a narrow intermediary zone of several large cells and then a broad lateral zone comprising bacteriocytes, intercalary cells and mucocytes (Fig. 8). The symbiotic bacteria are usually contained in single vacuoles within the bacteriocytes. Although there are small differences in ctenidial structure between the species studied, for example the relative lack of mucoctyes in *Anodontia alba* compared with other lucinids (Gros *et al*., 2003), no phylogenetic pattern has yet been established for these differences.

A striking feature of *Codakia orbicularis* (Linnaeus, 1758) is the granule cells that occupy a large proportion of the inner part of the lateral zone, with the bacteriocytes restricted to the outermost portions (Frenkiel & Mouëza, 1995; Gros *et al*., 2003). These cells are packed with spherical granules of various sizes to about 5 μm in diameter (Fig. 9). The functional significance of the granules is uncertain, they are cystine-rich and may represent a means of storage of sulphur compounds. Such granule cells are seen in *Codakia* species, in *Lucinisca nassula* (Conrad, 1846) (Fig. 9), *Ctena bella* (Conrad, 1837), *Pillucina vietnamica*, and some *Lucinoma* species (Dando *et al*., 1986; J. D. Taylor & E. A. Glover, pers. observ.) but are absent in other lucinids. The presence of granule cells in some lucinids and not others probably reflects physiological differences in sulphur metabolism between the taxa. Our molecular analysis shows that *Codakia*, *Ctena*, and *Lucinoma* group together into the same clade suggesting that the presence of granule cells in this group of species may be phylogenetically significant.

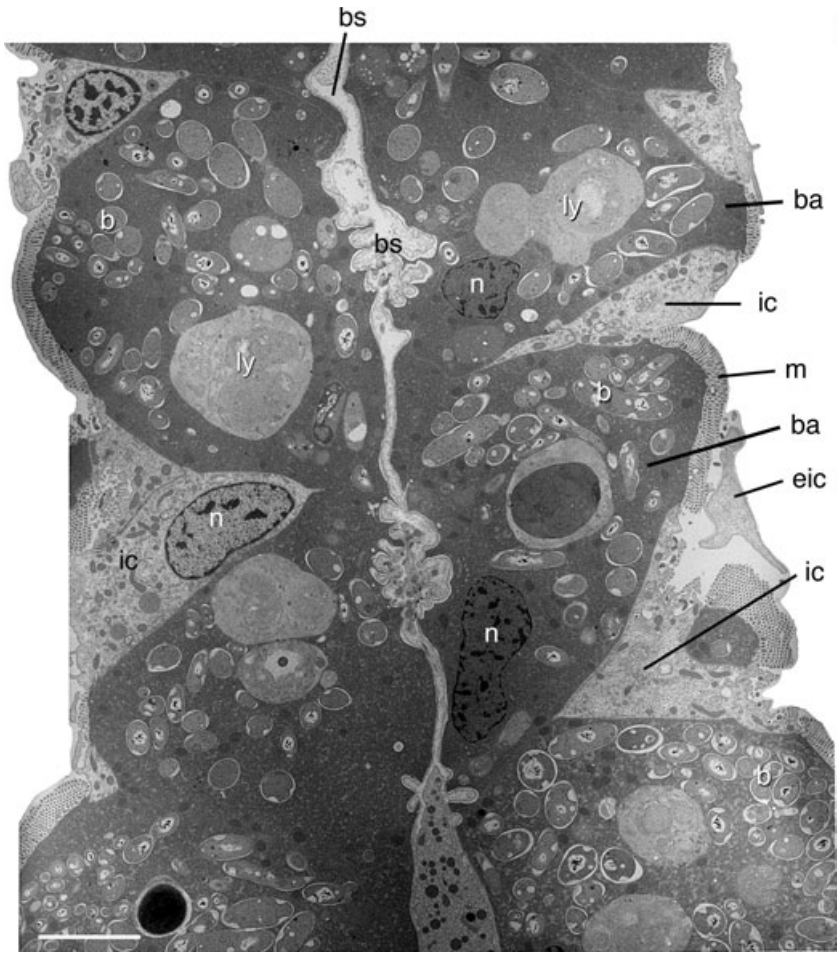

Figure 8. TEM section through part of ctenidial filament of *Anodontia ovum* (Reeve, 1850), Lizard Island, Queensland, showing central blood space flanked by bacteriocytes and intercalary cells. Scale bar = 5 μm. Abbreviations: b, bacteria; ba, bacteriocyte; bs, blood space; eic, distal extension of intercalary cell; ic, intercalary cell; ly, lysosome; m, microvilli; n, nucleus.

Mantle gills

In some lucinids the inner surface of the anterior mantle around the anterior adductor muscle is modified to form secondary respiratory organs called mantle gills (Allen, 1958; Taylor & Glover, 2000). Although it is likely that in most lucinids the anterior mantle epithelium acts as a respiratory surface (extensive blood space beneath the epithelium and large pallial blood vessel runs to the site), in some species the mantle is elaborated into complex folded structures. In *Codakia* species, in the space between the anterior adductor and the mantle edge and extending from the ventral tip of the muscle, the inner mantle is folded into elongate pleats (Fig. 10A). *Phacoides pectinatus* has a series of discrete lamellate 'knots' (Fig. 10C) lying along and extending ventrally beyond the gutter between the adductor muscle and the mantle margin (Narchi & Farani Assis, 1980). In *Lucina pensylvanica* (Linnaeus, 1758) (and *L. adansoni* d'Orbigny, 1839) a pectinate branched structure lies to either side of the pallial blood vessel (Fig. 10B). For all *Anodontia* species examined except *A. alba*, the anterior end of the mantle septum (itself a large fold of the inner mantle epithelium) bears digitiform structures (Fig. 10D) that result from labyrinthine folding of the septum. In *Austriella corrugata* (Deshayes, 1843), a large ridge of folded mantle, accommodating extensive blood space, extends posteriorly from around the ventral tip of the adductor muscle. Finally, the so-called 'mantle palps' near the anterior adductor of *Fimbria fimbriata* (see Allen & Turner, 1970; Morton, 1979) are most likely mantle gills.

Plotting the distribution of the mantle gills on the molecular phylogeny shows that they occur in five different clades. In the *Anodontia* clade all the examined species except *Anodontia alba* possess the septum and digitform gills, in Lucinid clade A only *Codakia* species have the mantle gills and in Lucinid clade B only

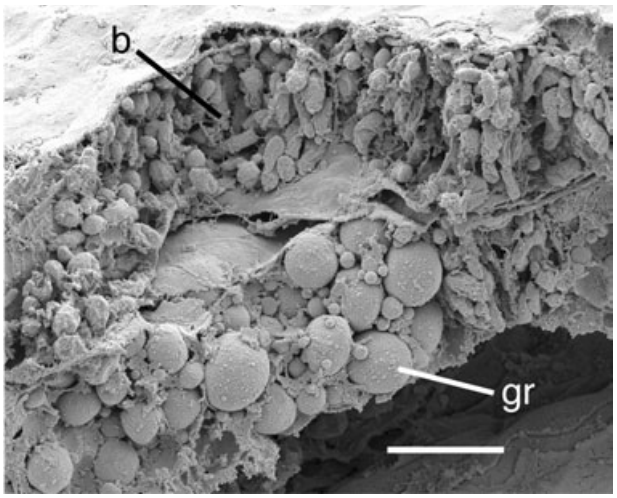

Figure 9. SEM section of ctenidial filament of *Lucinisca nassula* (Conrad, 1846) showing bacteriocytes and granule cells. Scale bar = 10 μm. Abbreviations b, bacteriocyte with rod-shaped bacteria. gr, granule cell and granules.

species of *Lucina s.s.* possess the pectinate mantle gills. Also in clade B *Austriella* has the thickened ridge. In *Phacoides* and *Fimbria* there are only one or two living species in the clades and both have mantle gills.

Although these structures are thought to have a similar respiratory function they are unlikely all to be homologous – the pectinate organ in *Lucina pensylvanica* is structurally different from the others and appears derived from branching of the pallial blood vessel. Folding of the inner mantle surface to increase the surface area for respiration is a fairly obvious adaptational pathway and the various structures may have evolved independently in the different lucinid clades.

Posterior apertures and mantle fusion

Lucinidae usually possess two posterior mantle apertures situated in a homologous position to the inhalant and exhalant siphons of other heterodont bivalves. The exhalant aperture of lucinids has an extensible tube, formed from fusion of the inner mantle fold, that retracts into the suprabranchial chamber. Preliminary observations and evidence from published figures (Allen, 1958) indicated considerable variation amongst lucinid species both in the length of posterior mantle fusion ventral to the inhalant aperture and also in the number of mantle folds involved in the fusion. Additionally, in some species the inhalant and sometimes also exhalant apertures are ringed with mantle papillae. Moreover, the eversible exhalant tube varies in size and robustness. A survey of more taxa has revealed a possible phylogenetic signal in these characters, although more comprehensive sampling is needed.

In all species of *Anodontia* examined, mantle fusion below the inhalant aperture is long (Fig. 11A) and involves the inner and most of the middle mantle folds so that the middle fold forms a narrow ridge down the centre of the fused zone, flanked to either side by the periostracal groove. Thus, most of the fused zone is periostracum covered. There are no papillae around the apertures. A similar long, fused zone, involving most of the middle mantle fold, also occurs in *Phacoides pectinatus* (Fig. 11B). Some *Anodontia* species and *Phacoides pectinatus* live deeply burrowed in dysaerobic habitats and the extensive mantle fusion with its periostracal covering is a possible adaptation to protect the mantle and regulate passage of interstitial water into the mantle cavity by reducing the size of the pedal gape.

Lucinids of Clade A (*Codakia*, *Ctena*, *Lucinoma,* and *Pillucina vietnamica*) have only a short, fused zone ventral to the inhalant aperture, with the fusion involving inner mantle folds and the inner part of the middle folds (Fig. 11D, E). Moreover, the inhalant apertures are fringed by short papillae arising from the middle fold.

Species of the *Myrtea* clade (Fig. 11I) have simple, narrow apertures without papillae and a very short length of mantle fusion. In species of Lucinid clade B (Fig. 11C, F, G, H), there is much variation in the degree of fusion, and further analysis of the less well-supported subclades within this large group is needed to establish the existence of any systematic pattern. In *Fimbria fimbriata* (Fig. 12) there is short zone of fusion ventral to the inhalant aperture, but the whole apertural area is fringed by two rows of mantle papillae; an outer row of short papillae and an inner row of longer finger-like structures. These papillae may be associated with the coral sand habitat of this species and function to keep the mantle and apertures clear of sand.

FOSSIL RECORD OF LUCINIDAE

Fossils with many of the features of modern Lucinidae can be recognized through the Cenozoic and back into the Mesozoic (Chavan, 1969; Bretsky, 1976). However, the Palaeozoic record of Lucinidae is more problematic and extremely patchy. Narrowing of the concept of Lucinoidea to exclude Ungulinidae and Thyasiridae has meant that Palaeozoic bivalves suggested as having 'lucinoid' affinities all need reappraisal. Such a course is outside the scope of this paper, but in order to document the antiquity of the Lucinidae we review a few fossils with probable lucinid characters.

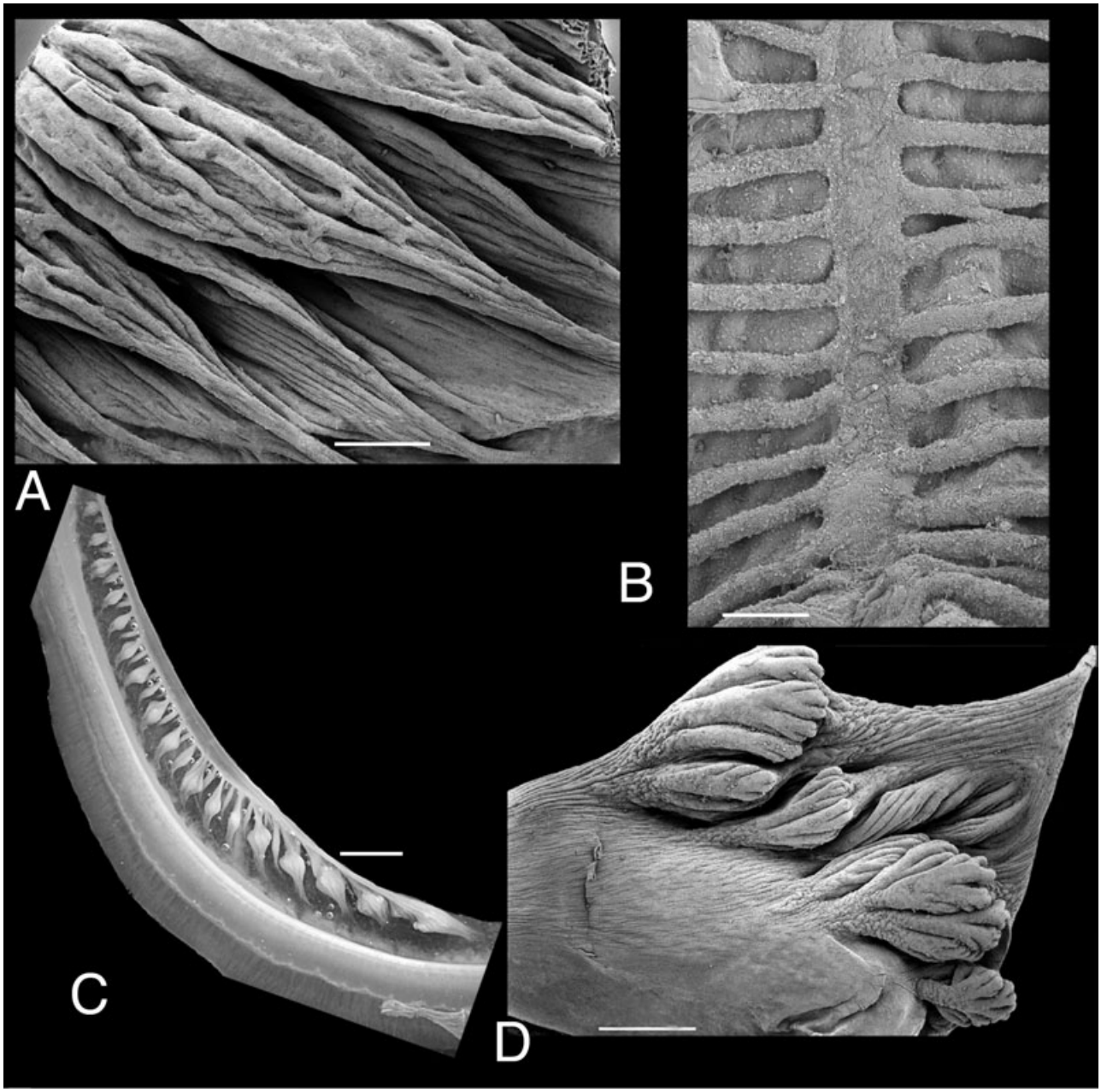

Figure 10. Mantle gills in lucinids. A, *Codakia tigerina*; B, *Lucina pensylvanica*; C, *Phacoides pectinatus*; D, *Anodontia philippiana*. Scale bars = 1 mm.

The earliest bivalve that can be confidently assigned to the Lucinidae is *Iliona prisca* (Hisinger, 1837) from the Silurian (Ludlovian) of Sweden (Fig. 13A, B). This is a large, elongate, anteriorly extended bivalve, having a large anterior adductor muscle scar ventrally detached from the pallial line. *In situ* fossils have a life position similar to living lucinids (Liljedahl, 1991). The rare living species *Eomiltha voorhoevi* (Deshayes, 1857) is similar in shape and musculature to *I. prisca* (Fig. 13C).

Another fossil with distinct lucinid characters is *Phenacocyclas pohli* La Rocque, 1950 from the Middle Devonian of Michigan. This has an elongate anterior adductor muscle scar that is detached from the pallial line and on internal moulds there is a succession of plications within the area between the muscle scar and the pallial line that could be interpreted as impressions of mantle gills (La Rocque, 1950: plates 13, 14). There is also a marked posterior sulcus immediately ventral to the posterior adductor scar in a position

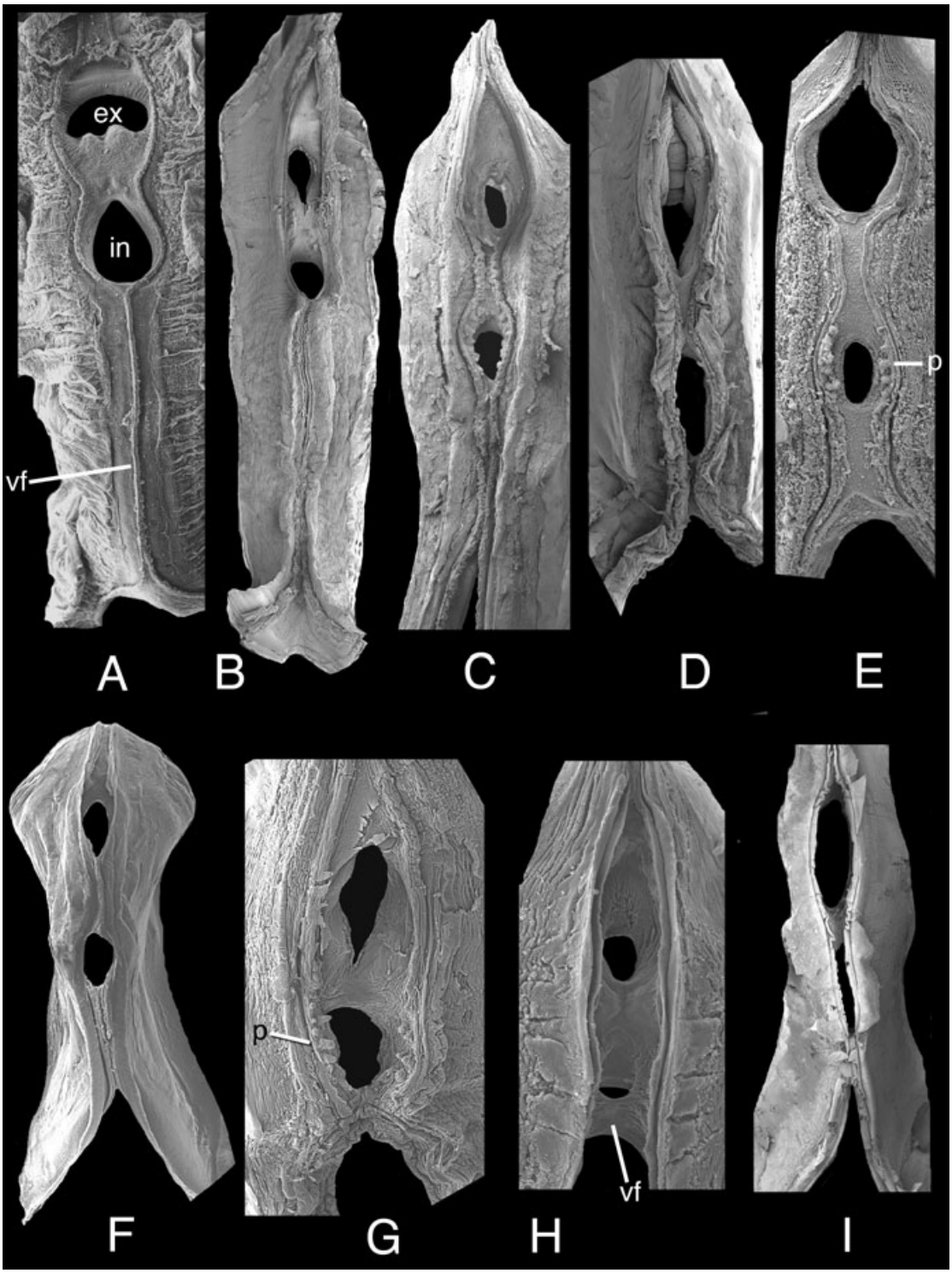

Figure 11. Posterior apertures of a range of lucinid species. All SEMs of critical point dried specimens. A, *Anodontia omissa* (Iredale, 1930), Moreton Bay Queensland; B, *Phacoides pectinatus* (Gmelin, 1792), Brazil; C, *Bathyaustriella thionipta* (Glover *et al*., 2004), Kermadec Ridge, New Zealand; D, *Ctena bella* (Conrad, 1837), Lizard Island, Queensland; E, *Pillucina vietnamica* Zorina, 1978, Port Douglas, Queensland; F, *Wallucina assimilis* (Angas, 1867), Jervis Bay, New South Wales; G, *Lucina adansoni* d'Orbigny, 1839, Cape Verde Islands. H, *Cardiolucina pisiformis* (Thiele, 1930), Shark Bay, Western Australia; I, *Myrtea spinifera* (Montagu, 1803), Oban Scotland. Images adjusted to similar scale. Abbreviations: ex, exhalant aperture; in, inhalant aperture; p, papillae; vf, ventral mantle fusion.

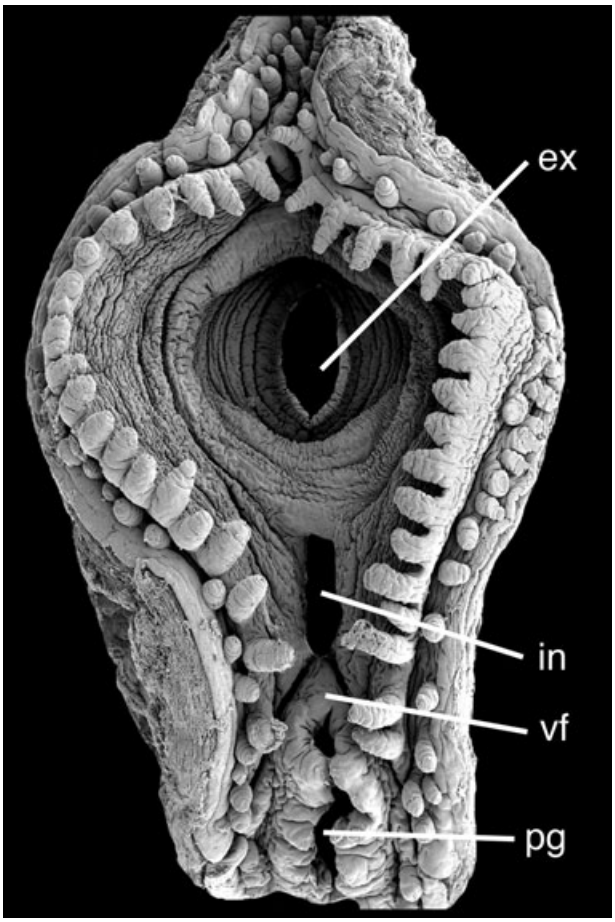

Figure 12. Posterior apertures of *Fimbria fimbriata* (Lizard Island, Queensland) showing double row of papillae, and short length of mantle fusion ventral to inhalant aperture. Abbreviations: ex, exhalant aperture; in, inhalant aperture; pg, pedal gape; vf, ventral fusion.

similar to that of many modern lucinids. The musculature of *Phenacocyclas* is similar to *Iliona prisca,* but the shell is much less elongate.

Some members of the family Paracyclidae, such as those illustrated as *Paracyclas proavia* (Goldfuss, 1840) from the Devonian of Australia (Johnston, 1993: figs 81A, 82A–D), are strikingly similar in shell morphology to modern *Anodontia.* However, although they have an elongate anterior adductor muscle this is not detached from the pallial line and this led Johnston (1993: 114) to suggest a similarity with Ungulinidae rather than Lucinidae. Nevertheless, other specimens of *Paracyclas proavia* from Germany do have an elongate and detached anterior adductor scar with a shape similar to modern lucinids (Fig. 14). Zong-Jie & Cope (2004) have recently described a much earlier *Paracyclas* species from the early Ordovician of China, but unfortunately, no internal details are available. Our conclusion is that the Paracyclidae contains some fossils with lucinid characters, but all need further critical study of muscle scars and hinges. A further undoubted lucinid from the Palaeozoic is *Gigantocyclus zidensis* Termier & Termier, 1977 from the Permian of Tunisia. This was better described and illustrated by Boyd & Newell (1979) who compared it with living *Anodontia*.

In summary, the Palaeozoic record of Lucinidae is rather meagre but fossils with convincing lucinid characters date from Silurian and younger rocks. Some *Paracyclas* species are common at certain horizons in the Devonian (Bailey, 1983), but all species need reappraisal.

AGE OF CHEMOSYMBIOSIS

Gros *et al*. (2003) demonstrated that the ctenidia of five species of lucinids from seagrass beds in the west Atlantic are colonized by the same sulphide-oxidizing bacterium, shown experimentally to be acquired from the sediment. These observations led the authors to suggest that the chemautotrophic symbiosis in Lucinidae is relatively recent in comparison to other bivalve families (such as Solemyidae) in which the symbionts are vertically transmitted.

Previously, we have argued (Taylor & Glover, 2000) that the symbiosis in Lucinidae dates back to at least the Silurian. The evidence for this was based upon similarity of morphological characters between Recent and fossil lucinids, including the position and shape of the anterior adductor muscle, and the impression on the shell interior of the pallial blood vessel – both characters thought to be associated with the endosymbiosis. The Silurian *Iliona prisca* also had a similar life position to that of most Recent lucinids, orientated umbones upward in the sediment (Liljedahl, 1991). Additionally, the association of lucinids with cold seep sites and dysaerobic environments, dating back at least to the Jurassic (Gaillard *et al*., 1992; Little & Vrijenhoek, 2003), is further suggestive of the chemoautotrophic life habit.

CONCLUSIONS

The main message from this review is that the systematics of the Lucinoidea is currently in a state of flux. Molecular results have demonstrated that superfamily Lucinoidea is not monophyletic and that the Ungulinidae and Thyasiridae are unrelated to the Lucinidae. The Fimbriidae clusters within the Lucinidae, while the status of the fossil family Mactromyidae is unresolved. On anatomical evidence the brackish water Cyrenoididae also appear unrelated to Lucinidae. For living taxa, membership of the super-

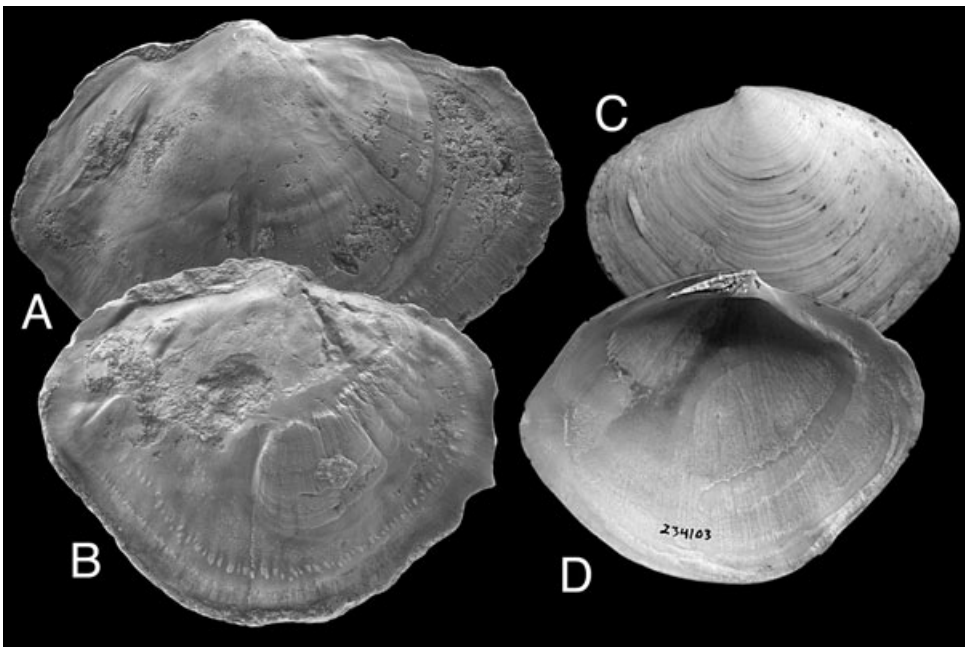

Figure 13. A, B, internal moulds showing right sides of *Ilionia prisca*, Silurian, Gotland, Sweden. A, BMNH, Shell length (SL) = 70 mm; B, BMNH, SL = 55 mm. C, D, outside and inside of left valve of *Eomiltha voorhoevi,* Recent, Mozambique, ANSP 234103, SL = 70 mm.

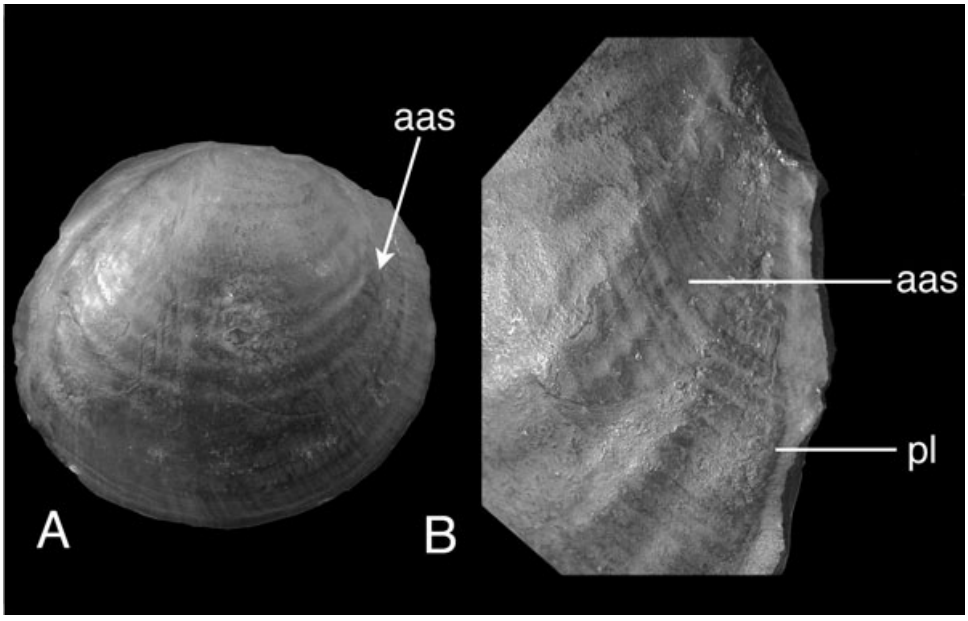

Figure 14. Internal mould of *Paracyclas proavia* (Goldfuss, 1840) from the Devonian, Eifel, Germany (BMNH Pal. Department L25554). Shell length = 56 mm. A, right side, anterior adductor scar arrowed; B, detail of anterior adductor scar showing ventral detachment from pallial line. aas, anterior adductor muscle scar; pl, pallial line.

family Lucinoidea should now be restricted to the family Lucinidae (including *Fimbria*).

The initial molecular phylogeny of the Lucinidae (Williams *et al*., 2004) has demonstrated that the subfamily and generic groupings recognized by Chavan (1969) and Bretsky (1976) are paraphyletic. Although a number of well-supported clades are recognized, it would, at present, be premature to erect a new classi-

fication based on results from relatively few taxa. A new molecular analysis with a much larger taxon base and using sequences from more genes is currently in progress and it is intended that results from this analysis will be used to develop a new classification of Lucinidae based on monophyletic groups. Molecular trees will be used to test ideas of the evolution of morphological adaptations to the chemosymbiosis and also to develop a more rigorous analysis of shell characters. The latter is essential if fossil taxa are to be integrated into phylogenies and classifications.

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