

A NEW SPECIES OF *LUCINOMA* (BIVALVIA : LUCINOIDEA) FROM THE OXYGEN MINIMUM ZONE OF THE OMAN MARGIN, ARABIAN SEA

P. GRAHAM OLIVER¹ & ANNA M. HOLMES¹

¹Dept of Biodiversity & Systematic Biology, National Museum of Wales, Cathays Park, Cardiff, CF103NP, UK

Abstract A new species of *Lucinoma* is described from the upper bathyal zone of the Oman margin, Arabian Sea, living in a low oxygen environment. Shell morphology is conservative within the genus and similar species are found in many oceans. Comparisons are made with all known species but especially with *L. bengalensis* and *L. yoshidai*. The anatomy is described and as with other members of the genus the Oman species hosts chemosymbiotic bacteria. No specific adaptations to the low oxygen environment were found, species from cold seep and normal marine sediments being morphologically similar.

Key words *Lucinoma*, Arabian Sea, Bathyal, Oxygen Minimum Zone.

INTRODUCTION

In 1994 the RRS Discovery undertook a biological survey of the Oman margin with the aim of assessing the effects of the Arabian Sea oxygen minimum zone on the benthos. Oxygen levels drop to as little as 0.1ml/l over a depth range of 200 to 800m and life in this region could be expected to be absent or at least unusual. Contrary to a natural logic, life of some kind was found throughout the oxygen minima (Gage, Levin & Wolff, 2000; Levin, Gage, Martin & Lamont, 2000). Bivalves inhabited all but the most extreme zone of oxygen depletion (Oliver, 2001) and one of the most notable occurrences was a large lucinid bivalve living in greenish muds at a depth of around 900m with shells of the same species found at 700 and 400m. This lucinid belongs to the genus *Lucinoma* and its taxonomy forms part of this paper.

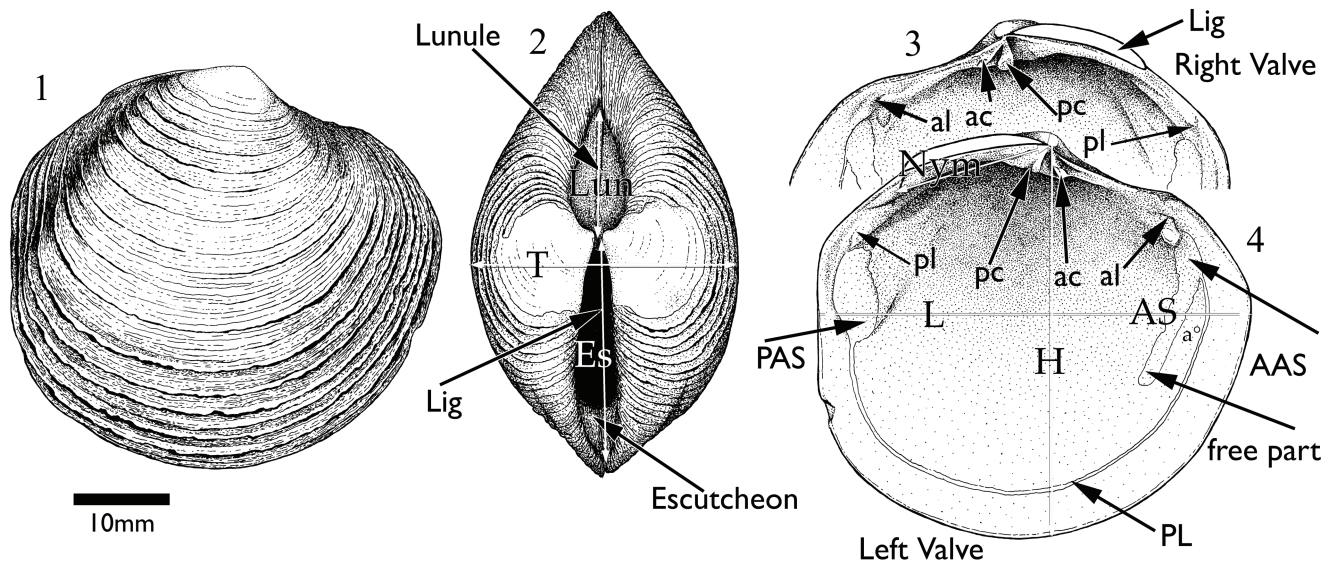
The anatomy of lucinid bivalves has received much attention in recent years primarily due to an intense interest in chemosymbiotic systems and the phylogeny of chemosymbiosis. A general review of lucinid morphology is given by Taylor and Glover, (2000) and their phylogeny is most recently revised by Williams, Taylor & Glover (2004). The ctenidia and bacterial symbionts of the European *Lucinoma borealis* have been studied by Dando, Southward & Southward (1986). The shell and ctenidial structures of a sister taxon, *L. kazani*, from the Mediterranean, were described by Salas and Woodside, 2002. Distel & Felbeck (1987) reviewed the functional morphology of the ctenidia of *L. annulata* and *L. aequizonata* and

the latter species has been the subject of many more detailed investigations of the nutritional system (Cary *et al*, 1989; Hentschel, Cary & Felbeck, 1993; Hentschel, Hand & Felbeck, 1996; Hentschel & Felbeck, 1995; Hentschel *et al*, 2000; Gros, Duplessis & Felbeck, 1999; Duplessis *et al*, 2004). As a consequence of these studies the aim of this section of this paper is not to fully describe the anatomy of another species of *Lucinoma* but to investigate any morphologies linked to the low oxygen conditions.

MATERIALS & METHODS

The specimens used in this study were collected during Cruise 211 of the RRS Discovery in the Arabian Sea off the coast of Oman. Anatomical gross morphology was examined from living specimens on board the RRS Discovery and subsequently from formalin preserved specimens in the laboratory. Scanning electron microscopy of the ctenidia used dissected tissue preserved in a 2.5% solution of glutaraldehyde in phosphate buffer. These tissues were then critical point dried prior to gold coating. Histological sections were prepared from formalin-preserved tissues and stained, either in haematoxylin/eosin or in Azan triple stain. Micrographs were made by digital imaging employing Montage Explorer™ software, which maps across the section. Some overlapping and consequent intensifying of the blocks can be seen in Figure 34.

Comparative material was borrowed from museum collections. Institutional abbreviations are as follows:



Figures 1-4 *Lucinoma gagei* n. sp. Line drawings of holotype to show shell features and parameters measured. **Fig. 1** external of right valve: **Fig. 2** dorsal view: **Fig. 3** hinge of right valve: **Fig. 4** internal of left valve. Abbreviations for parameters:- AS length of anterior adductor scar; a° angle of divergence of anterior scar from pallial line; Es length of escutcheon; H height; L length; Lun length of lunule; Nym length of nymph; T tumidity. Abbreviations for structures:- AAS anterior adductor scar; Lig ligament; PAS posterior adductor scar; PL pallial line; pl posterior lateral tubercle; al anterior lateral tubercle; ac anterior cardinal tooth; pc posterior cardinal teeth.

AMNH American Museum of Natural History, New York

BM(NH) Natural History Museum London

MNHNCL Museo Nacional de Historia Natural de Chile, Santiago

NMW & NMW. Z National Museum of Wales, Cardiff

NSMT National Science Museum Tokyo

out accessory gill structures; exhalant siphon simple with few small papillae; ctenidium thick fleshy with muscular inter filamentar and inter lamellar junctions. Labial palps small, sorting ridges few or lacking.

Lucinoma gagei new species

Lucina bengalensis Smith:- Knudsen, 1967: 285-286, pl. 2, fig. 10, not Smith, 1894.

Material Examined All material from R.R.S. Discovery, Cruise 211 off Ras Madrakah, Southern Oman, Arabian Sea.

Holotype 1 shell, live collected: Station 12714#1: 19°10.74'N 58°20.33'E to 19°10.10'N 58°19.50'E: 919m to 967m: 28 Oct 94: Agassiz Trawl: NMW.Z. 1995.009.1; 59mm in length.

Paratypes 11 specimens, live collected, shells dry bodies in spirit: Station 12714#1: 19°10.74'N 58°20.33'E to 19°10.10'N 58°19.50'E: 919m to 967m: 28 Oct 94: Agassiz Trawl : NMW.Z. 1995.009.2 & BM(NH)

Other material: 2 shells live collected: Station 12702#1: Oman margin: 19°14.80'N 56°26.83'E: 935m : 24 Oct 94: Agassiz Trawl: NMW.Z. 1995.009.4. 3 valves: Station 12685#10: 19°18.72'N

SYSTEMATIC DESCRIPTION

Genus *Lucinoma* Dall, 1901

Type species: *Lucina filosa* Stimpson, 1851. (North western Atlantic)

Definition Shell equivalve, equilateral, subcircular and lenticular. Lunule elongate, slightly sunken. Escutcheon long and narrow sometimes sunken. Sculpture concentric of low lamellae with raised lines between. Ligament deeply inset on nymph, sometimes below level of escutcheon sometimes slightly raised. Hinge teeth of 2 cardinals in each valve, 2 and 3b slightly bifid; anterior laterals (often obscure) in all, obscure posterior laterals in some. Anterior adductor scar long and narrow, divergent from but parallel to pallial line for most of its length. Anatomy (data from *L. borealis*, Allen, 1958); mantle edge and mantle with-

Measurements-

Table 1 Shell measurements for holotype and 5 paratypes of *Lucinoma gagei* n. sp. Parameters illustrated in Figs 2-4.

Station	Length	Height	Tumidity	Anterior S c a r Length	Ant Scar Angle	Escutcheon Length	Nymph	Lunule Length
DSt12714 (holo)	58.8	53.3	32.1	21.9	20.0	29.5	18.5	17.6
DSt12714	56.3	52.6	28.6	23.6	24.5	27.3	15.1	14.1
DSt12714	28.3	27.7	12.8	9.9	19.0	14.0	9.2	5.9
DSt12714	60.0	54.6	32.1	21.2	19.5	29.3	18.7	15.5
DSt12714	50.8	46.3	27.5	21.4	19.0	25.9	18.4	14.8
DSt12714	56.8	53.7	31.5	22.6	20.0	28.8	20.6	12.4

Table 2 Summary statistics for seven morphometric characters of *Lucinoma gagei* n. sp. Sample size 24.

	Mean	Std Deviation	Minimum	Maximum
Length/Height Ratio	1.1	<0.1	1.0	1.1
Length/Tumidity Ratio	1.8	0.3	1.4	2.7
Length/Escutcheon Ratio	2.0	0.1	1.9	2.3
Length/Lunule length Ratio	3.9	0.4	3.3	4.8
Length/Anterior scar length	2.7	0.2	2.4	2.9
Anterior Scar Angle	21.8	2.6	18	27
Escutcheon/Nymph	1.5	0.3	1.2	2.1

58°15.79'E: 746m :15 Oct 1994: Spade Box Core: NMW.Z. 1995.009.5. 17 valves: Station 12697#1: Oman margin: 19°21.8'N 58°15.3'E: 378m: 23 Oct 94: Agassiz Trawl: NMW.Z. 1995.009.6. 2 shells dead, Station 12685#8: 19°18.66'N 58°15.64'E: 690m: 15 Oct 1994: Spade Box Core: NMW.Z. 1995.009.7. 3 shells + 2v, dead: Station 12682#4: 19°18.74'N 58°15.47'E: 675m: 13/Oct/1994: Spade Box Core: NMW.Z. 1995.009.8.

Type Locality Arabian Sea, off Ras Madrasah, Dhofar, Southern Oman.

DESCRIPTION

Shell (Figs 1 – 4, 5 – 10, 11) to 62mm in length. See Table 2 for morphometric data. Moderately thick, somewhat chalky exterior. Equivalve.

Compression variable from laterally compressed especially in younger shells to slightly inflated especially in gerontic shells. Almost equilateral, subcircular in outline, normally with length only slightly exceeding height. Posterior margin truncate (Fig.5a) often indented (Fig. 10), ventral margin broadly curved, anterior margin narrowed with a subacute angulation defining a short straight anterior dorsal margin. Posterior sulcus present to varying degrees, anterior area flattened but not sulcate. Escutcheon (Fig. 2) long, partly filled with ligament or periostracum and not sunken. Ligament gradually filling escutcheon but this is dependant on age. Lunule (Fig. 2) large, narrowly cordate, weakly sunken. Sculpture (Figs 1, 5) of evenly spaced concentric raised but low sharp lamellae with fine concentric lines between, lamellae becoming crowded towards margins in larger shells. Ligament set

on a nymph. Hinge of two cardinal teeth in each valve, those in LV (Fig. 4, ac & pc) of equal size; in RV anterior tooth (Fig. 3, ac) much reduced, largest cardinal (Fig. 3, pc) slightly bifid; LV with weak anterior laterals bounding a shallow socket, upper tooth becoming obsolete, posterior laterals obsolete or represented by barely discernable ridges; RV with a projecting single anterior lateral and the posterior a weak ridge. Muscle scars prominent becoming impressed in heavier gerontic shells; anterior adductor scar long, narrow and free from the pallial line for most of its length; angle of divergence of anterior adductor scar from pallial line 18° to 27° ; posterior adductor roughly oval; anterior pedal retractor scar circular, lying below lateral tooth and joined or not joined to adductor scar. Pallial blood vessel impression visible only in gerontic shells, otherwise as a series of discrete scars or absent. Shell colour white with a persistent buff coloured periostracum.

Variation There is little variation except that in some samples the posterior margin of larger shells, is more truncated, almost indented (Fig. 10). There are slight ontogenetic changes in that the tumidity is slightly allometric, juvenile shells being proportionately more compressed. A similar trend occurs with the ratio of the length of the nymph to the escutcheon, the latter taking up proportionately more of the escutcheon in older shells.

Geographic Range Known only from the Arabian Sea, on the Oman margin and west coast of India.

Bathymetric Range 384m (shells only) to 950m.

Habitat In greenish sloppy muds over consolidated sediments. Overlying water depleted in oxygen, 3-6ml/l. Dead shells in box core samples were found as deep as 50cm in sediment. Other species of bivalves taken with *L. gagei* were *Acila* cf. *divaricata*, two large *Thyasira* species, a large *Vesicomya*, a small *Nucula* and a *Yoldiella*.

Derivation of name gagei Latin, named for John Gage, chief scientist on Discovery Cruise 211, who first introduced me (PGO) to sampling the deep oceans and who sadly died in 2005.

DIFFERENTIAL DIAGNOSES

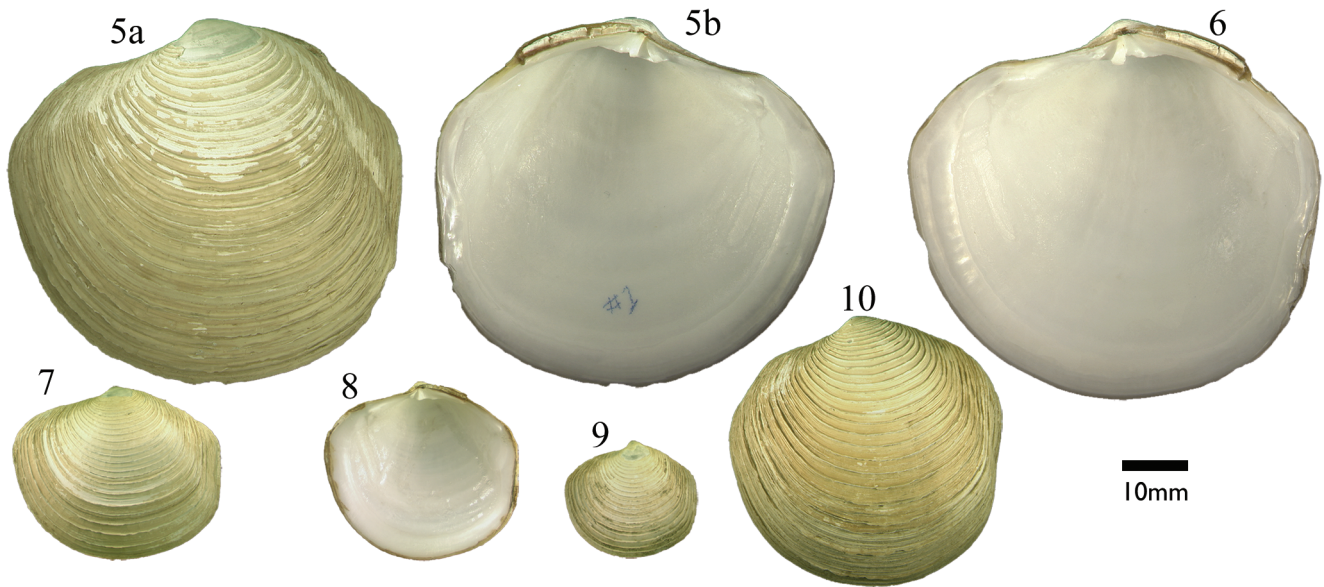
Of the twentyone Recent species of *Lucinoma* that are currently recognised (Table 3) in the literature there are only two that warrant careful comparison with the Oman species; *Lucinoma bengalensis* Smith, 1894 (Bay of Bengal) and *L. yoshidai* Habe, 1958 (Japan).

Lucina bengalensis (Figs 12-13) was described by Smith (1894) from material collected by HMS Investigator in the Bay of Bengal at 410 fathoms. Type material (Figs 12-13) of *Lucina bengalensis* (Natural History Museum, London: BM(NH) 1894.9.11.29 and 1900.7.9.2) is a small shell (35mm in length) that differs from *L. gagei* as follows: being more transversely oval (longer than high) in outline, with the posterior margin sloping rather than vertical; more strongly compressed lunule well demarcated and slightly sunken; escutcheon very narrow with a distinct vertical edge.

Other material, collected in the Bay of Bengal, around Sri Lanka and Southern India, labelled as *L. bengalensis*, is also present in museum collections. These shells are similar in outline to *L. bengalensis*, but have widely and evenly spaced, prominent, concentric lamellae. Two of these shells (off Silavathurai, Sri Lanka, 100fathoms, BM(NH); off Cape Comorin, Tuticorin, 300-400m, BM(NH) acc. No. 2216) are very large, reaching 80mm in length (Fig. 14). Two others (NE Sri Lanka, 609fathoms, NMW.1955.158.11158; off Trincomalee, Sri Lanka, 200-350 fathoms, BM(NH) 1895.7.2.12 as *Cryptodon philippinarum*) are small (less than 30mm in length) have the distinct lamellae but these appear more closely spaced (Fig. 15), which is probably a growth related effect. All of these shells are consistently more elongate and more compressed (Fig. 17) and are therefore concluded not to be conspecific with the Arabian Sea material. Whether or not they can all be included in *L. bengalensis* is debatable and the shells with widely spaced lamellae may constitute yet another undescribed species.

Knudsen (1967) records *Lucina bengalensis* Smith, 1894, from off Oman at Station 42 of the John Murray Expedition at 1415m. This record is based on a single, small, rather eroded valve but is conspecific with the Discovery material and is therefore referable to *L. gagei* and not to *L. bengalensis*.

A single shell (BM(NH), 1963775) collected from



Figures 5-10 *Lucinoma gagei* n. sp. **Fig. 5a** Left valve external of holotype, NMW.Z.1995.9.1: **Figs 5b & 6** Left and right valve internal of holotype: **Figs 7-9** Paratypes from Station 12714#1, NMW.Z.1995.9.2: **Fig. 10** Variety from Station 12682#4, NMW.Z.1995.9.8.

“Investigator stn. 232, off S. India, 430 fathoms” is, also, conspecific with the Arabian material (Fig. 11). Other material labelled type and from the type locality of *L. bengalensis* in the National Museum of Wales (NMW. 1955.158.02028) is not a *Lucinoma*.

Of the other *Lucinoma* species described and recorded from the Indo West Pacific *L. yoshidai* (Fig. 16; NSMT 73713, Off Kochi Prefecture, Shikoku, Japan) requires careful comparison. Considerable confusion has however, existed with the Japanese species of *Lucinoma* and Okutani & Hashimoto (1997) refer to the misidentification of *L. yoshidai* on three occasions. Confusion is still apparent for the shell figured by Okutani, Tagawa & Horikawa (1989) as *L. yoshidai* is figured by Matsukuma (2000) as *L. annulata*. The confusion appears to arise primarily in the larger shells where the angulation and posterior sulcus become obscure and the shell has an altogether more rounded appearance. Okutani & Hashimoto (1997) illustrate this range of variation and give data on the change in length to height ratio with growth (as shell length). This data is re-plotted against data from the Oman shells (Fig. 18) and shows that *L. gagei* does not become so rounded in outline. Shell tumidity data indicates a further difference in that *L. yoshidai* is more compressed with a mean L:T ratio of 2.2 compared to 1.8 for *L. gagei*. The

lateral teeth of *L. yoshidai* are obscure as in most species and unlike the rather prominent teeth seen in *L. gagei*.

The differences given here are considered sufficient to exclude *L. gagei* and *L. yoshidai* being conspecific.

ANATOMY & FUNCTIONAL MORPHOLOGY

DESCRIPTIVE ANATOMY

The living animal The gross morphology of a living specimen is presented in Figures 19 & 21. The left mantle has been cut away to reveal the ctenidium and foot. On opening this shell the immediate observation was of the blood red colour of the haemocoelomic fluid and the dark reddish purple colour of the ctenidia and mantle. The ctenidia of all specimens examined were of a similar colour and no variation was found, unlike the colour variation in *L. aequizonata* studied by Hentschel *et al.* (2000).

Mantle The mantle is thick and has a spongy appearance. In thin section (Fig. 22), two distinct layers are seen; the inner has a well-defined layer of epithelial cells and the volume is taken up by

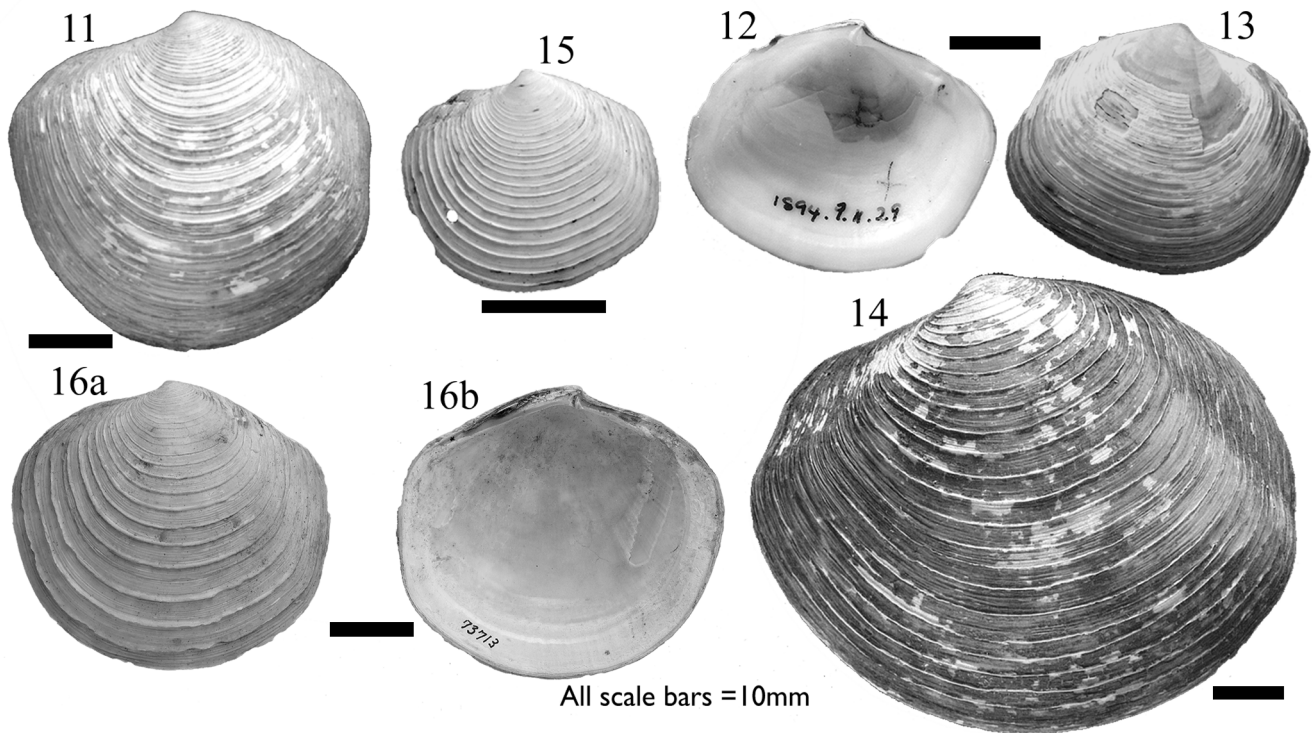


Fig. 11 *Lucinoma gagei* n. sp. Shell ex "Investigator" off S. India, BM(NH) 1963775. **Figures 12-13** *Lucinoma bengalensis* Smith, 1894, Paratype BM(NH) 1894.9.11.29. **Figs 14-15** *Lucinoma* sp. **Fig. 14** off Silavathurai, NW coast of Sri Lanka, BM(NH), unregistered. **Fig. 15** NE Sri Lanka, 609fathoms, NMW.1955.158.11158. **Fig. 16** *Lucinoma yoshidai* Habe, 1958 NSMT 73713, Off Kochi Prefecture, Shikoku, Japan

a very weak network through which traverse nerve and muscle fibres; the outer (next to the shell) layer has a very narrow epithelium and the volume consists of columnar septa with little or no nuclear material.

The mantle has no structural developments to indicate the presence of a secondary gill function as seen in some lucines (Taylor & Glover, 2000). Transverse sections of the mantle edge in the region of the anterior adductor scar reveal a three-fold structure but with the middle mantle fold made up of two extensions (Fig. 24). Beyond the inner mantle fold is a broad swollen band containing glandular tissue. There are dense aggregations of red coloured secretory cells in the region close to the inner fold and beyond that a zone of bluish purple staining tissue. The arrangement of folds, muscles and glandular tissue are similar to those described by Taylor *et al.* (2004) for *Lucina pensylvanica*. These tissues are probably associated with the formation of an anterior siphonal tube and the action of the vermiform foot in its creation and maintenance.

Mantle fusion is limited to the posterior region where there are simple inhalant and exhalant

apertures, the inhalant has four small papillae on either side. The length of mantle fusion ventral to the inhalant siphon is very short (Fig. 20)

Foot The foot is vermiform with a small heel (Figs 19-21).

Ctenidia The ctenidia have the gross appearance (Figs 19-21) of a single fleshy sheet of tissue on either side of the visceral mass in which, to the naked eye, there is no obvious filamentary structure. The posterior tips of the ctenidia are fused with the mantle (Fig. 23). However, each sheet is made up of a single demibranch with descending and ascending arms of numerous filaments (Figs 32, 34). There are numerous inter-filamental junctions (Figs 32-33) giving a reticulate appearance to surfaces of the lamellae. In addition, there are inter-lamellar junctions binding the ascending and descending lamellae together (Figs 32, 34). The frontal part of each filament is ciliated and is supported by an axial rod (Fig. 33). The abfrontal portion (Figs 33-34) is greatly elongated without cilia and contains (bacteriocytes) packed with bacteria (Figs 35-36). The

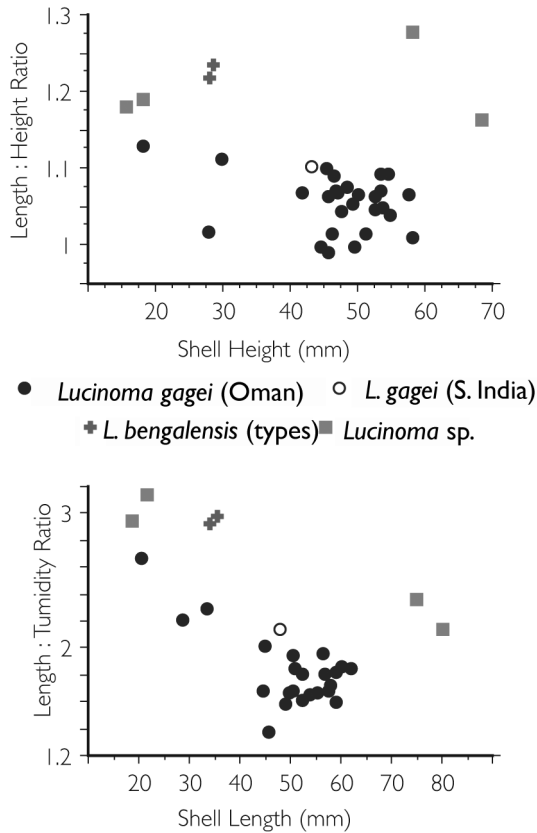


Fig. 17 Plots of Length to Length/Tumidity ratio and Height to Length/Height ratio for *Lucinoma gagei*, *L. bengalensis* and *Lucinoma* sp. from Sri Lanka & southern India.

bacteria appear to be of one morphological type and are roughly spheroidal and measure $2\mu\text{m}$ in length (Fig. 37). The transverse sections shown in Fig. 33 are from close to the ventral edge where the abfrontal portions are short. The appearance in the thin section (Fig. 34) is typical of the majority of the ctenidium. This morphology is essentially similar to that described for *L. borealis* by Southward (1986). Red staining granular cell clusters are seen in thin sections stained with Azan triple stain (Fig. 34) and are similar to those described by Frenkiel, Gros & Mouëza (1996) for *Codakia orbicularis*. They are also present in *Ctena* and it is of note that *Lucinoma* is related to the *Ctena/Codakia* clade in the molecular phylogeny proposed by Williams *et al.* (2004).

Labial palps Labial palps are present, but consist of short, low-margined grooves that show no sorting ridges.

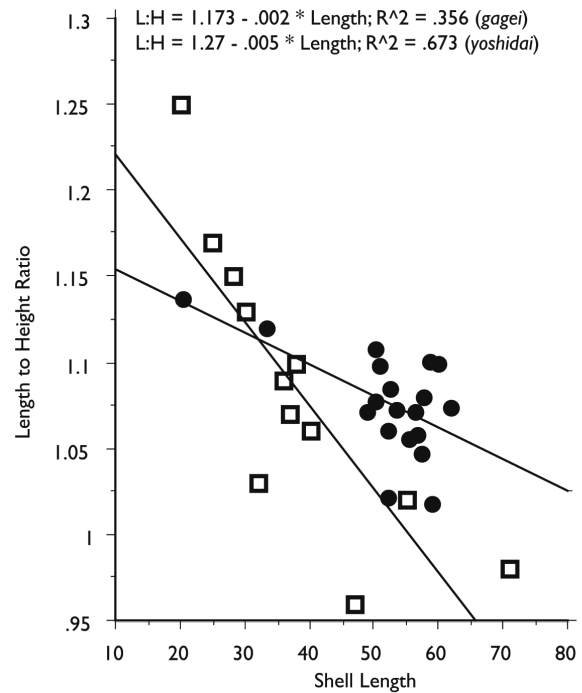
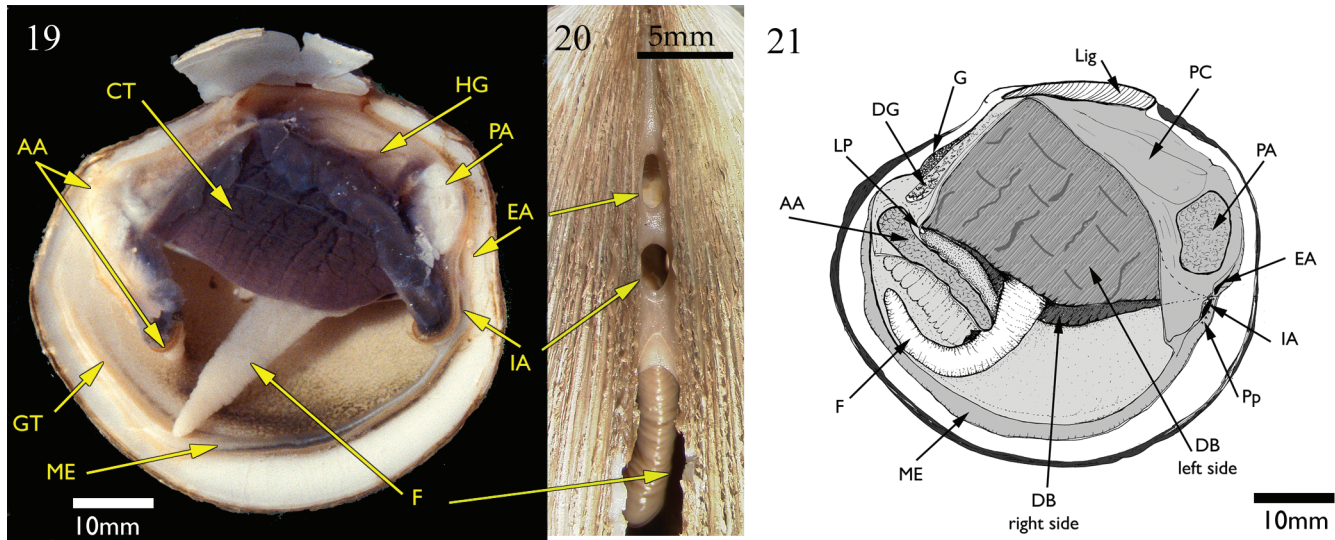


Fig. 18 Plot of Shell Length to Length/Height ratio for *Lucinoma gagei* (circles) and *L. yoshidai* (squares). Data for *L. yoshidai* from Okutani & Hashimoto, 1997.

Alimentary system An entire system is present but the stomach is very small relative to the size of the animal, being roughly 5mm in diameter for a shell size of 50mm. The oesophagus is a simple tube with longitudinal ciliated ridges for carrying particles to the stomach (Fig. 25). The stomach in transverse section (Fig. 26) appears largely as an empty sac with narrow walls of columnar epithelial cells. Sorting ridges and typhlosoles are poorly developed but the ducts to the digestive diverticulae are fully developed. Stomach contents are sparse but some particulate material can be seen adjacent to the dorsal shield (Fig. 28). Other material appearing as strongly nucleated spherules is present in the stomach (Fig. 27) but the identity of this is obscure. The hind gut is not looped and in transverse section appears as a simple tube with a single longitudinal ridge (Fig. 29). There was little evidence of faecal material in the hind gut. The gut is surrounded by digestive gland tubules and by gonadal material that consists of both sperm (Fig. 30) and eggs (Fig. 31).



Figures 19-21 *Lucinoma gagei* n. sp. Station 12714#1. **Fig. 19** Gross anatomy of living specimen after removal of left valve and mantle. **Fig. 20** posterior view showing siphonal openings and degree of mantle fusion. **Fig. 21** line drawing of gross anatomy from Fig. 17.

Abbreviations:- AA anterior adductor muscle; CT ctenidium; DB demibranch of ctenidium; DG digestive gland; EA exhalant aperture; F foot; GT glandular tissue; HG hind gut; IA inhalant aperture; LP labial palps; Lig ligament; ME mantle edge; PA posterior adductor muscle; PC pericardium; Pp papillae

FUNCTIONAL MORPHOLOGY

The anatomical observations reveal no obvious adaptations to the low oxygen environment. There are no accessory gill structures as seen in *Codakia*, *Lucina pensylvannica* or *Anodontia* (Taylor & Glover, 2000). The presence of haemoglobin perhaps aids oxygen absorption, as suggested for the mytilid *Amygdalum anoxicolum* (Oliver, 2001), but its occurrence is not confined to lucinids living in oxygen minima zones (Dando *et al.*, 1986, Frenkiel *et al.*, 1996). Haemoglobin is found in many chemosynthetic bivalves (Frenkiel *et al.*, 1996) and could function as a pre-adaptation to colonisation of oxygen depleted environments. Other chemosynthetic taxa found on the Oman margin were Vesicomysidae and Thyasiridae and these also contained haemoglobin.

The size and simplicity of the labial palps, poorly developed sorting structures in the alimentary system and the paucity of gut contents suggest that *L. gagei* derives little nutrition from suspension feeding, at least in the adult stages observed in this study. Duplessis *et al.* (2004) have shown that particulate feeding does occur in *L. aequizonata* and may be a response to seasonal availability of reduced sulphur. The feeding structures of *L. gagei* and *L. aequizonata* are entirely comparable and may also function similarly.

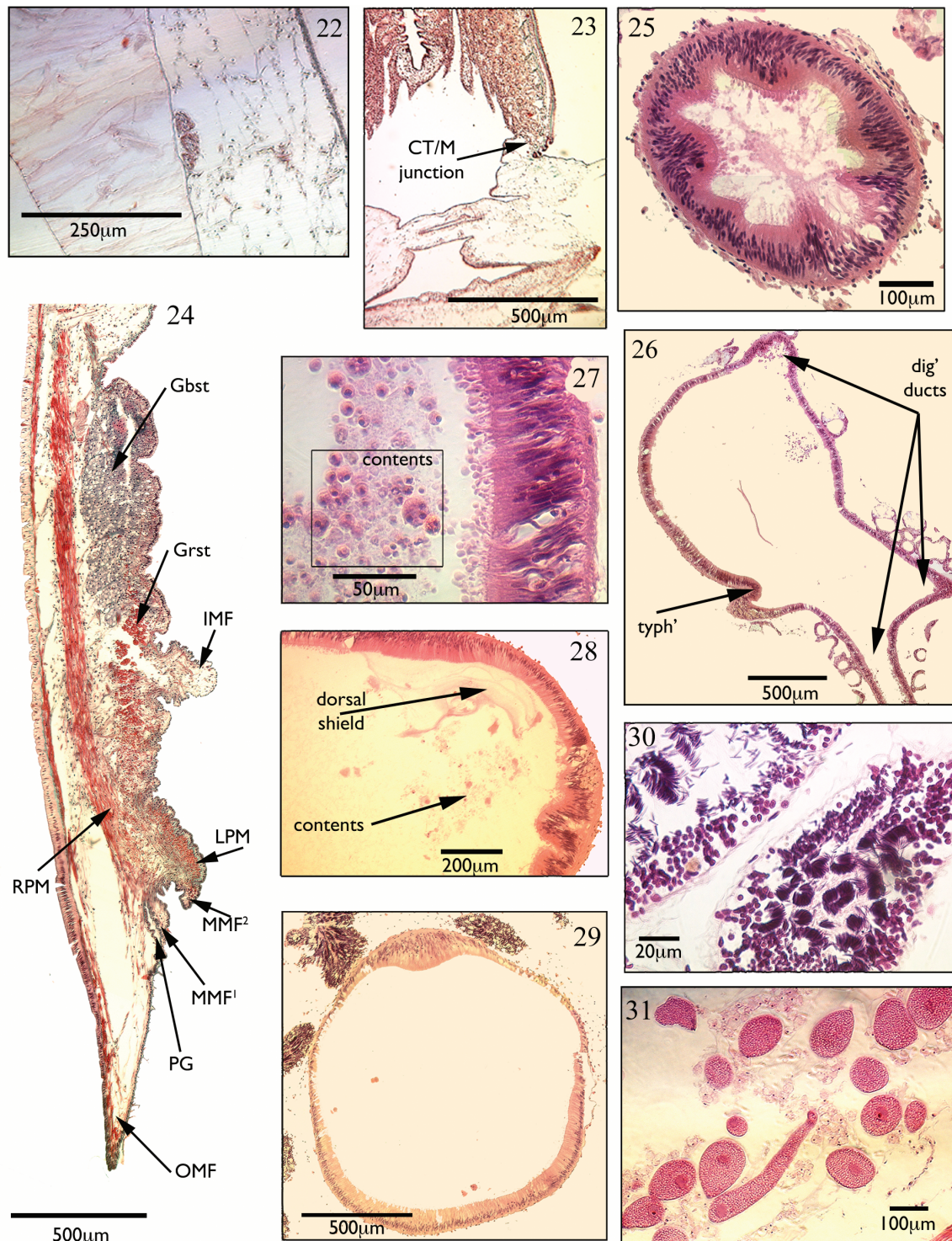
A REVIEW OF *LUCINOMA*

Species of *Lucinoma* are found world wide from low in the intertidal to upper abyssal depths, but more generally occur in outer shelf and upper slope environments. Some are associated with chemosynthetic systems such as cold seeps and oxygen minima zones while others are found in more normal marine conditions albeit that the environment must be reducing to some degree in order to support the chemosymbiosis.

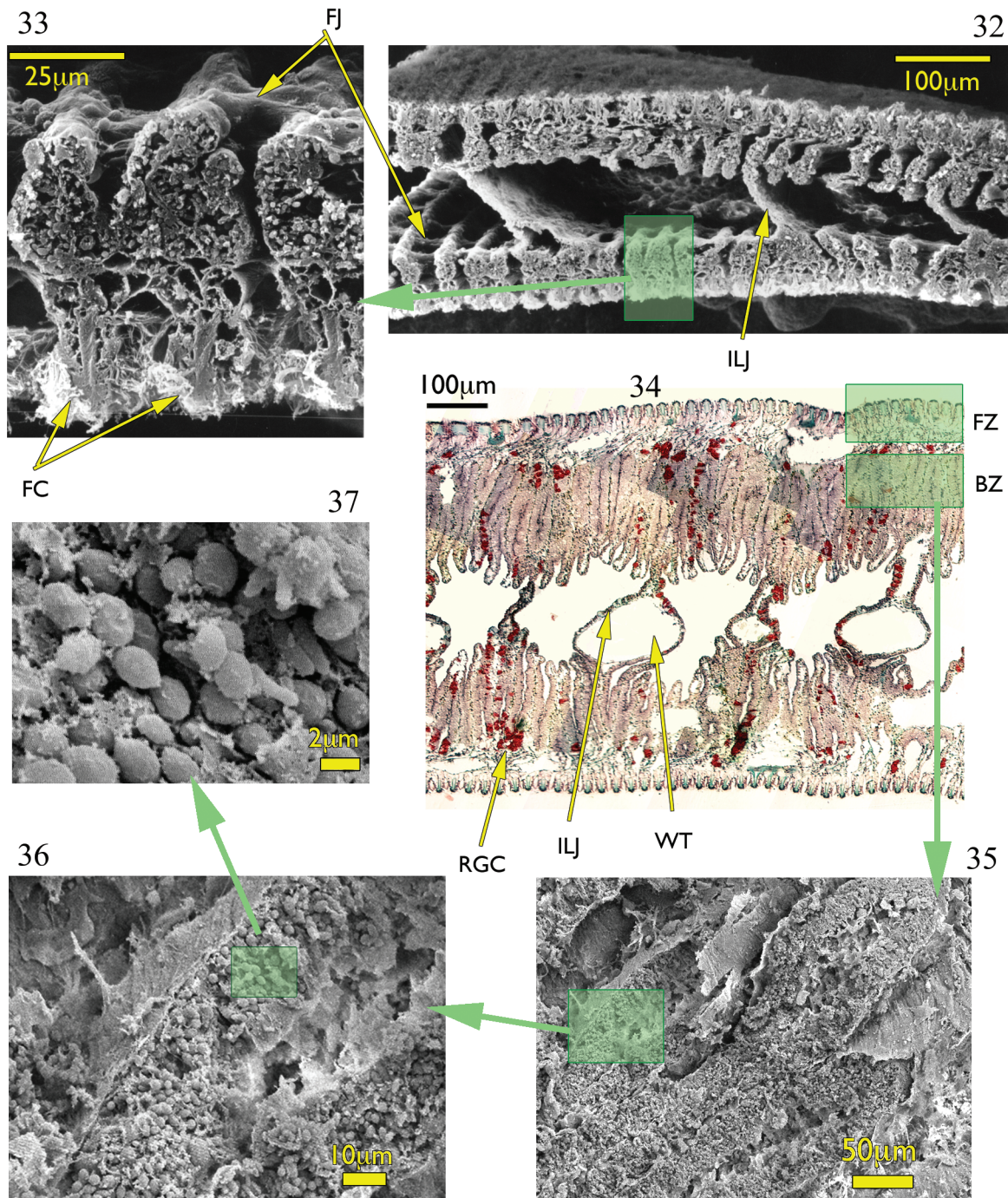
This review looks for patterns in form, function and habitat but is not a taxonomic revision. The known living species of *Lucinoma*, their geographic and bathymetric distributions and habitat are listed in Table 3.

GROUP 1

The type species of the genus *Lucinoma* is *L. filosa* (Stimpson, 1851) (Fig. 38), and is found along the northeastern coast of N. America. It is a compressed, rounded shell with weak anterior and posterior angulation, erect margins to the escutcheon and lunule and widely spaced erect, fragile, concentric lamellae. Similar taxa are found in the North Pacific on both American and Asiatic coasts. Here they are now referred to *L. annulata* Reeve, 1850 (Fig. 39) although previ-



Figures 22-31 *Lucinoma gagei* n.sp. **Figures 22-24** Transverse sections of the mantle stained with Azan Triple Stain. **Fig. 22** TS of mantle dorsal to the mantle edge; **Fig. 23** TS of junction between ctenidium and mantle edge; **Fig. 24** TS of mantle edge adjacent to the anterior adductor muscle. **Figures 25-31** Transverse sections through the alimentary system and gonads, all stained in haematoxylin and eosin. **Fig. 25** oesophagus; **Fig. 26** stomach showing typhlosole and digestive ducts; **Figs 27 & 28** stomach with contents; **Fig. 29** hind gut; **Fig. 30** sperm; **Fig. 31** eggs. Abbreviations:- CT/M ctenidium mantle edge junction; Gbst blue staining glandular tissue; Grst red staining glandular tissue; IMF inner mantle fold; LPM longitudinal pallial muscle; MMF₁ and MMF₂ lobes of the middle mantle fold; OMF outer mantle fold; PG periostracal groove; RPM radial pallial muscle.



Figures 32-37 *Lucinoma gagei* n.sp. Ctenidial structures as viewed by scanning electron microscopy (Figs 32-33, 35-37) and from light microscopy (Fig. 34). **Fig. 32** transverse section of ctenidium near ventral border showing ascending and descending arms of filaments and interlamellar junctions. **Fig. 33** transverse section of three filaments from Fig. 32 showing short bacteriocyte zone; **Fig. 34** transverse section of median area of ctenidium stained in Azan Triple stain and showing typical elongate bacteriocyte zone; **Fig. 35** SEM of bacteriocyte zone through two filaments; **Fig. 36** SEM of vacuole containing bacteria from Fig. 35; **Fig. 37** spheroidal bacteria from Fig. 36.

Abbreviations:- **BZ** bacteriocyte zone; **FJ** filamental junctions; **FZ** frontal zone; **ILJ** inter-lamellar junctions; **RGC** red staining granular cells; **WT** water tubule.

Table 3 A list of known living species of *Lucinoma*, their geographic and bathymetric ranges and habitat. NMC normal marine conditions, OMZ oxygen minimum zone

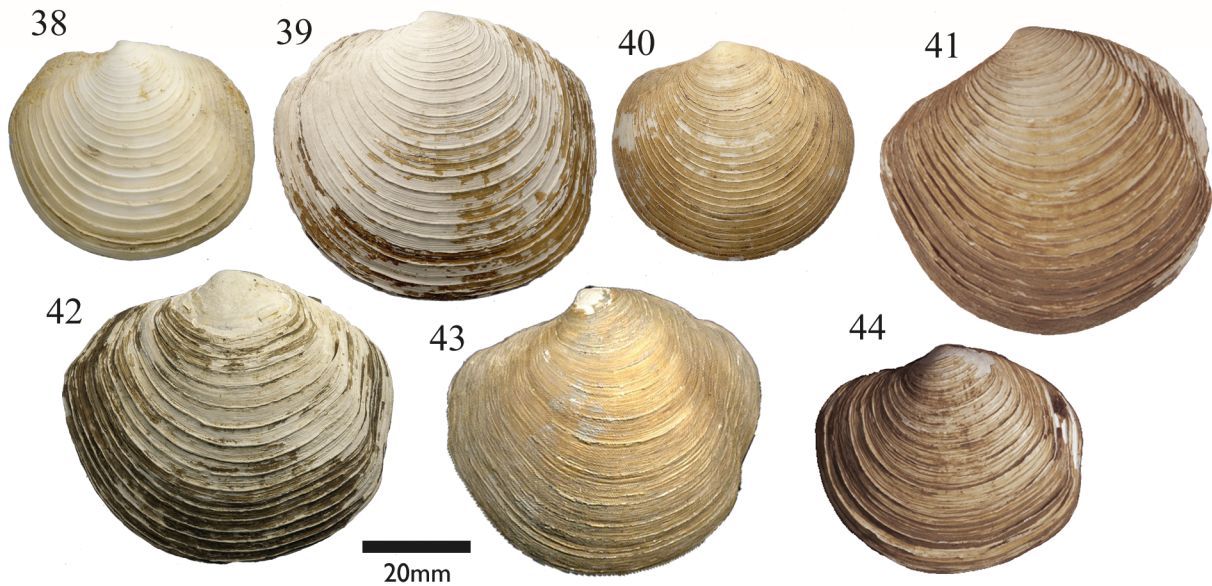
Group 1. Circular, lamellose taxa			
<i>L. filosa</i> (Stimpson, 1851)	NW. Atlantic	Shelf	NMC
<i>L. annulata</i> (Reeve, 1850)	NE Pacific & Japan	Int'-bathyal	NMC
Group 2. Small, subcircular, finely sculptured			
<i>L. borealis</i> (Linnaeus, 1767)	NE. Atlantic- Mediterranean	Shelf	NMC
<i>L. kazani</i> Salas & Woodside, 2002	Eastern Mediterranean	Bathyal	Cold seep
<i>L. spelaeum</i> Palazzi & Villari, 2001	Eastern Mediterranean	Infralittoral	Cavernicolous
<i>L. blakeana</i> (Bush, 1893)	NW Atlantic	Shelf-upper bathyal	?
<i>L. capensis</i> (Thiele & Jaeckel, 1931)	SE. Atlantic	Shelf	NMC
<i>L. adamsiana</i> Habe, 1958	Japan	Upper shelf	NMC
<i>L. japonica</i> Habe, 1958	Japan	Upper shelf	NMC
Group 3. Large, subcircular but angulate, lamellose			
<i>L. saldanhae</i> (Barnard, 1964)	SE. Atlantic	Shelf	?
<i>L. gagei</i> n. sp.	Arabian Sea	Bathyal	OMZ
<i>L. bengalensis</i> (Smith, 1894)	Bay of Bengal	Bathyal	?
<i>L. spectabile</i> (Yokohama, 1920) fossil	Japan	Upper shelf	Cold seep
<i>L. yoshidai</i> Habe, 1958	Japan	Shelf-bathyal	Cold Seep?
<i>L. euclia</i> (Cotton & Godfrey, 1938)	S. Australia	Outer shelf	?
<i>L. galathea</i> Marwick, 1953	New Zealand	Outer shelf / bathyal	NMC
<i>L. lamellata</i> (Smith, 1881)	Magellanic	Subtidal-outer shelf	?
<i>L. sp. nov.</i> Holmes, Oliver & Sellanes	SE Pacific (Chile)	Bathyal	Cold Seep
<i>L. heroica</i> (Dall, 1901)	Gulf of California	Upper abyssal	?
Group 4. Large, roundly oblong, widely spaced lamellae			
<i>L. aequizonata</i> (Stearns, 1890)	NE Pacific (Santa Barbara)	Bathyal	OMZ
<i>L. atlantis</i> McLean, 1936	Gulf of Mexico	Shelf-upper bathyal	Cold seep

ously the Miocene fossil name of *L. acutilineata* (Conrad, 1849) was frequently, but erroneously, applied (Coan et al, 2000; Matsukuma, 2000). These species occur across the shelf from relatively shallow depths (50m) to the upper bathyal and have no known particular association with OMZ or seep environments.

GROUP 2

A second group is represented by *L. borealis* (Linnaeus, 1767) (Fig. 40) where the shells are generally smaller, heavier and with a closely spaced sculpture of concentric ridges rather than thin, spaced lamellae. Species similar to

L. borealis are; *L. capensis* (Thiele & Jaeckel, 1931) from South Africa; *L. blakeana* (Bush, 1893) from NE America; *L. kazani* Salas & Woodside, 2002 from the Mediterranean; *L. spelaeum* Palazzi & Villari, 2001 from the Mediterranean; *L. adamsiana* Habe, 1958 from Japan and *L. japonicum* Habe, 1958 from Japan. These taxa are found from the intertidal and across shelf depths. For most their biotope is not known but *L. borealis* inhabits muddy gravels, often with sea grasses, whereas *L. kazani* is specific to cold seeps and *L. spelaeum* confined to marine caves



Figures 38-44 External views of the left valve of seven species of *Lucinoma*. **Fig. 38** *L. filosa*, off Florida, AMNH 293282; **Fig. 39** *L. annulata*, Washington, NMW.1955.158; **Fig. 40** *L. borealis*, Madeira, NMW.1955.158; **Fig. 41** *L. heroica*, Gulf of California, photo leg. Paul Valentich Scott; **Fig. 42** *L. anemiophila*, off Chile, MNHNCL201650. **Fig. 43** *L. atlantis*, Louisiana, after www.jaxshells **Fig. 44** *L. aequizonata*, off Santa Barbara, photo leg. Paul Valentich Scott;

GROUP 3

A third group consists of large, angulate shells with a well-defined posterior sulcus, posterior truncation and a defined anterior dorsal margin. Their sculpture is lamellose. This group contains *L. gagei* and *L. bengalensis* along with a number of species from all oceans. They are; *L. yoshidai* Habe, 1958 from Japan; *L. heroica* Dall, 1901 from the Gulf of California (Fig. 41); *L. saldanhae* Barnard, 1964 from the Atlantic coast of South Africa; *L. galathea* Marwick, 1953 from New Zealand; *L. euclia* (Cotton & Godfrey, 1938) from S. Australia and *L. lamellata* (Smith, 1881) from the Magellanic Province. A further species, *Lucinoma anemiophila* (Fig. 42), from a cold seep off the coast of Chile, has recently been described (Holmes, Oliver & Sellanes, 2005). These species inhabit the outer shelf, bathyal zone and into the upper abyssal region with three species having known associations with cold seeps or oxygen minimum zones, namely *L. gagei* [OMZ, (this paper)], *L. yoshidai* [seeps (Fujikura *et al.* 1996)], and the new species from Chile [seeps (Sellanes, Quiroga & Gallardo, 2004; Holmes, Oliver & Sellanes, 2005)].

A second Japanese species, *L. spectabile*

(Yokoyama, 1920) was described as a Tertiary fossil, but has been reported living although confusion with *L. annulata* is apparent (Okutani & Hashimoto, 1997). Furthermore, the *L. spectabilis* cited by Hashimoto *et al.* (1995) and repeated by Kitazaki & Majima (2003) was shown by Okutani & Hashimoto (1997) not to be a *Lucinoma* but belong to the genus *Mesolinga*. *Lucinoma spectabile* was not included in the most recent review of living Japanese bivalves (Matsukuma, 2000). *Lucinoma* species are present in Pleistocene (Kitazaki & Majima, 2003) and Pliocene seep formations (Majima *et al.*, 2003) in Japan, but remain unnamed. Majima, Nobuhara & Kitazaki (in press), in a review of fossil Japanese chemosynthetic assemblages, characterise their Type III assemblage by the dominant presence of *Lucinoma* and or the thyasirid *Conchocele*. This assemblage is seep dependent and typically found in paleodepths of less than 300m. The shells present in these fossil assemblages resemble the *L. spectabile* and *L. yoshidai* forms, but as stated by Majima *et al.* (2003), "*Lucinoma* species in Japan are taxonomically confused".

GROUP 4

The fourth group contains two species that are somewhat oblong in outline and have widely spaced concentric lamellae. They are *L. aequizonata* (Stearns, 1890) from California (Fig. 44) and *L. atlantis* McLean, 1936 from the Gulf of Mexico (Fig. 43). *Lucinoma aequizonata* inhabits the oxygen minimum zone off Santa Barbara (Cary, Vetter & Felbeck, 1989) and *L. atlantis* is known from the Louisiana gas and oil seeps (Kennicutt *et al.*, 1985; Callender & Powell, 1992).

This brief review indicates that there is no relation of form to bathymetric range, geographic range or habitat. Seep inhabitants are found in three of the four groups and OMZ inhabitants in two of the groups.

The differences observed in shell form are insufficient to give nomenclatural status to any of the groups but molecular data may provide a more rigorous decision.

ACKNOWLEDGEMENTS

I (PGO) would like to take this opportunity to voice my gratitude in general to, the sadly now late, John Gage of the Dunstaffnage Marine Laboratory for his support over many years and his invitation to join Discovery Cruise 211.

We also thank John Taylor and Emily Glover for their many suggestions, helpful discussions and access to the collections of the Natural History Museum, London. Paul Valentich Scott for the use of his photographs of *Lucinoma aequizonata* and *L. heroica*. Paula Mikkelsen for loans from the American Museum of Natural History, Hiroshi Saito for loan from the National Science Museum, Tokyo. The photographic unit of the National Museum of Wales, and Jim Turner for help with the preparation of the manuscript. Thin sections were prepared by Mr David Cooper.

REFERENCES

- ALLEN JA 1958 On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Philosophical Transactions of the Royal Society of London, Series B* **241**: 421-484.
- BARNARD KH 1964 Contributions to the knowledge of South African marine Mollusca. Part V. Lamellibranchiata. *Annals of the South African Museum* **47**: 361-593.
- BUSH KJ 1893 Report on the Mollusca dredged by the "Blake" in 1880, including descriptions of several new species. *Bulletin of the Museum of Comparative Zoology, Harvard* **23** (6): 199-245.
- CALLENDER WR & POWELL EN 1992 Taphonomic signature of petroleum seep assemblages on the Louisiana upper continental slope: Recognition of autochthonous shell beds in the fossil record. *Palaios* **7**: 388-408.
- CARY SC, VETTER RD & FELBECK H 1989 Habitat characterisation and nutritional strategies of the endosymbiont-bearing bivalve *Lucinoma aequizonata*. *Marine Ecology Progress Series* **55**: 31-45.
- COAN EV, SCOTT PV & BERNARD FR 2000 *Bivalve Seashells of Western North America*. Santa Barbara Museum of Natural History Monographs Number 2, Santa Barbara. 764pp.
- CONRAD TA 1949 Mollusca In Dana JD *United States Exploring Expedition during the years, 1838, 1839, 1840, 1841, 1842, under the Command of Charles Wilkes, U.S.N., vol. 10, Geology, Appendix 1, part 3, Fossils from Northwestern America*, pp.722-728, Philadelphia.
- COTTON BC & GODFREY FK 1938 *The Molluscs of South Australia*. Trigg, Adelaide 314pp.
- DALL WH 1901 Synopsis of the Lucinacea and of the American species. *Proceedings of the United States National Museum* **23**: 779-833.
- DANDO PR, SOUTHWARD AJ & SOUTHWARD EC 1986 Chemoautotrophic symbionts in the gills of the bivalve mollusc *Lucinoma borealis* and the sediment chemistry of its habitat. *Proceedings of the Royal Society of London (B)* **227**: 227-247.
- DISTEL DL & FELBECK H 1987 Endosymbiosis in the lucinid clams *Lucinoma aequizonata*, *Lucinoma annulata* and *Lucina floridana*: a re-examination of the functional morphology of the gills as bacteria-bearing organs. *Marine Biology* **96**: 79-86.
- DUPLESSIS MR, DUFOR SC, BLANKENSHIP LE, FELBECK H & YAYANOS AA 2004 Anatomical and experimental evidence for particulate feeding in *Lucinoma aequizonata* and *Parvilucina tenuisculpta* (Bivalvia: Lucinidae) from the Santa Barbara Basin. *Marine Biology* **145**: 551-561.
- FRENKIEL L, GROS O & MOUËZA M 1996 Gill structure in *Lucina pectinata* (Bivalvia: Lucinidae) with reference to haemoglobin in bivalves with symbiotic sulphur-oxidising bacteria. *Marine Biology* **125**: 511-524.
- FUJIKURA K, HASHIMOTO J, FUJIWARA Y & OKUTANI T 1996 Community ecology of the chemosynthetic community at Off-Hatsushima site, Sagami Bay, Japan-II JAMSTEC. *Journal of Deep Sea Research* **12**: 133-153.
- GAGE JD, LEVIN LA & WOLFF GA 2000 Benthic processes in the deep Arabian Sea: introduction and review. *Deep-Sea Research II* **47**: 1-8.
- GROS O, DUPLESSIS MR & FELBECK H 1999 Embryonic development and endosymbiont transmission mode in the symbiotic clam *Lucinoma aequizonata* (Bivalvia: Lucinidae). *Invertebrate Reproduction and Development* **36**: 93-103.

- HABE T 1958 Report on the Mollusca chiefly collected by the S.S. "Soyo-Maru" of the Imperial Fisheries Experimental Station on the continental shelf bordering Japan during the years 1922-1930. Part 3. Lamellibranchia (1). *Publications of the Seto Marine Biological Laboratory* 6: 241-280.
- HASHIMOTO J, FUJIKURA K, FUJIWARA Y, TANISHIMA M, OHTA S, KOJIMA S & YIEH S 1995 Observations of a deep sea biological community co-dominated by lucinid bivalve, *Lucinoma spectabilis* (Yokoyama 1920) and Vestimentiferans at the Kanesu-no-se bank, Enshu-nada, central Japan JAMSTEC. *Journal of Deep-Sea Research* 11: 211-217.
- HENTSCHEL U, CARY SC & FELBECK H 1993 Nitrate respiration in chemoautotrophic symbionts of the bivalve *Lucinoma aequizonata*. *Marine Biology Progress Series* 94: 35-41.
- HENTSCHEL U & FELBECK H 1995 Nitrate respiration in chemoautotrophic symbionts of the bivalve *Lucinoma aequizonata* is not regulated by oxygen. *Applied and Environmental Microbiology* 61 (4): 1630-1633.
- HENTSCHEL U, HAND SC & FELBECK H 1996 The contribution of nitrate respiration to the energy budget of the symbiont-containing clam *Lucinoma aequizonata*: A calorimetric study. *The Journal of Experimental Biology* 199: 427-433.
- HENTSCHEL U, MILLIKAN DS, ARNDT C, CARY SC & FELBECK H 2000 Phenotypic variations in the gills of the symbiont containing bivalve *Lucinoma aequizonata*. *Marine Biology* 136 (4): 633-643.
- HOLMES AM, OLIVER PG & SELLANES J 2005 A new species of *Lucinoma* (Bivalvia: Lucinoidea) from a methane gas seep off the southwest coast of Chile. *Journal of Conchology* 38 (6): 673-681.
- KENNICUTT MC, BROOKS JM, BIDIGARE RR, FAY RR, WADE TL & McDONALD TJ 1985 Vent type taxa in a hydrocarbon seep on the Louisiana slope. *Nature* 317: 351.
- KITAZAKI T & MAJIMA R 2003 A cold-seep assemblage in a slope to outer-shelf environment in the Pliocene Kazusa group, Pacific side of central Japan. *Paleontological Research* 7 (4): 279-296.
- KNUDSEN J 1967 The Deep -Sea Bivalvia *Scientific Reports of the John Murray Expedition, 1933-1934*. *British Museum (Natural History)* 11 (3): 239-343, plates 1-3.
- LEVIN LA, GAGE LD, MARTIN C & LAMONT PA 2000 Macrobenthic community structure within and beneath the oxygen minimum zone of the Arabian Sea. *Deep-Sea Research II* 47: 227-258.
- LINNAEUS C 1767 *Systema naturale. Editio duodecima. 1. Regnum Animale 1 & 2. Holmiae* (Stockholm) pp. 533-1327.
- MAJIMA R, IKEDA K, WADA H & KATO K 2003 An outer-shelf cold-seep assemblage in forearc basin fill, Pliocene Takanabe Formation, Kyushu Island, Japan. *Paleontological Research* 7 (4): 297-311.
- MAJIMA R, NOBUHARA T & KITAZAKI T (In press) Review of fossil chemosynthetic assemblages in Japan. *Palaeogeography, Palaeoclimatology & Palaeoecology*.
- MARWICK J 1953 A Pliocene fossil found living by the Galathea Expedition. *New Zealand Journal of Science and Technology* (B) 35(1): 109-112.
- MATSUKUMA A 2000 Superfamily Lucinacea. In Okutani T (ed) *Marine Mollusks in Japan*. Tokai University Press, Tokyo. 1172pp.
- MCLEAN RA 1936 A new species of *Lucina* from off Maryland. *The Nautilus* 39 (3): 87, pl.5.
- OKUTANI T & HASHIMOTO J 1997 A new species of lucinid bivalve (Heterodonta: Lucinidae) from Kanesu-no-Se Banj near the mouth of Suruga Bay, with a review of the Recent species of the chemosynthetic genus *Lucinoma* from Japan. *Venus* 56 (4): 271-280.
- OKUTANI T, TAGAWA M & HORIKAWA H 1989 *Bivalves from continental shelf and slope around Japan*. Fisheries Resource Conservation Association, Tokyo. 190pp.
- OLIVER PG 2001 Functional morphology and description of a new species of Amygdalum (Mytiloidea) from the oxygen minimum zone of the Arabian Sea. *Journal of Molluscan Studies* 67: 225-241.
- PALAZZI S & VILLARI A 2001 Molluschi e Brachiopodi delle grotte sotto Marine del Taorminese. *La Conchiglia* 297 suppl. 56 pp.
- REEVE LA 1850 Monograph of the genus *Lucina* In Reeve LA *Conchologia Iconica*, 6: 11 plates.
- SELLANES J, QUIROGA E & GALLARDO VA 2004 First direct evidence of methane seepage and associated chemosynthetic communities in the bathyal zone off Chile. *Journal of the Marine Biological Association of the United Kingdom* 84: 1065-1066.
- SALAS C & WOODSIDE J 2002 *Lucinoma kazani* n. sp. (Mollusca: Bivalvia): evidence of a living benthic community associated with a cold seep in the Eastern Mediterranean Sea. *Deep-Sea Research Part 1* 49: 991-1005.
- SMITH EA 1881 Mollusca and Molluscoidea. In A Gunther (ed) *Account of the Zoological Collections made during the survey of H.M.S. "Alert" in the Straits of Magellan and on the coast of Patagonia. Proceedings of the Zoological Society of London 1881: 2-141, pls 1-11.*
- SMITH EA 1894 Natural history notes from H.M. Indian Marine Survey Steamer "Investigator", -Ser. II. No. 10 Report upon some Mollusca dredged in the Bay of Bengal and the Arabian Sea. *Annals and Magazine of Natural History* (6) 14: 157-174.
- SOUTHWARD E 1986 Gill symbionts in thyasirids and other bivalve molluscs. *Journal of the Marine Biological Association of the United Kingdom* 66: 889-914.
- STEARNS REC 1890 Scientific results of explorations by the U. S. Fish Commissions Steamer "Albatross". No. XVII. Descriptions of new west American land, fresh-water and marine shells, with notes and comments. *Proceedings of the United States National Museum* 13: 205-225. plates 15-17.
- STIMPSON W 1851 *A revision of the synonymy of the testaceous mollusks of New England*. Phillips, Sampson & Company, Boston. 56pp, 2 pls.
- TAYLOR JD & GLOVER EA 2000 Functional anatomy, chemosymbiosis and evolution of the Lucinidae In EM Harper, JD Taylor & JA Crame (eds) *The evo-*

- lutionary biology of the Bivalvia. Geological Society of London Special Publication* **177**: 207-225.
- TAYLOR JD, GLOVER E, PERHARDA M, BIGATTI G & BALL A 2004 Extraordinary flexible shell sculpture: the structure and formation of calcified periostracal lamellae in *Lucina pennsylvanica* (Bivalvia: Lucinidae). *Malacologia* **46**(2): 277-294.
- THIELE J & JAECKEL S 1931 Muscheln der deutschen Tiefsee-Expedition. *Wissenschaften Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899* **21**: 161-268.
- WILLIAMS ST, TAYLOR JD & GLOVER EA 2004 Molecular phylogeny of the Lucinoidea (Bivalvia): non-monophyly and separate acquisition of bacterial symbiosis. *Journal of Molluscan Studies* **70**: 187-202.
- YOKOYAMA M 1920 Fossils from the Miura Peninsula and its immediate north. *Journal of the College of Science of the Imperial University, Tokyo* **39**(6): 1-198.

