BACTERIAL SYMBIOSIS IN THE NUCINELLIDAE (BIVALVIA: SOLEMYIDA) WITH DESCRIPTIONS OF TWO NEW SPECIES

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ABSTRACT

Nucinellidae are a family of small, monomyarian, nuculoid marine bivalves that live at depths from 6–3,500 m. Related to the Solemyidae, they are suspected of chemosymbiosis with sulphur-oxidizing bacteria, but hitherto without morphological or molecular confirmation. Two new species, *Nucinella owenensis* and *Huxleyia habooba*, were collected at depths of 3,400 and 84 m, respectively, during a survey of the oxygen-minimum zone associated with the seasonal upwelling area in the Arabian Sea, off southern Oman. Sections of the relatively large ctenidia revealed large thickened leaflets with abundant rod-shaped bacteria housed in bacteriocytes. This is the first morphological confirmation of likely chemosymbiosis in the family. Both species have a complete alimentary system and in *N. owenensis* the hindgut contained sediment, suggesting particulate feeding. Relationships of Nucinellidae and Solemyidae and the timing of acquisition of the chemosymbiosis are briefly discussed. Descriptions of the two new species are accompanied by a critical review of familial and generic characters, with rejection of previous reports of posterior adductor muscle scars in *Huxleyia*.

INTRODUCTION

Chemosymbiosis between bivalve molluscs with sulphide-oxidizing and, less commonly, methanotrophic Proteobacteria housed in the ctenidia is now recognized as a widespread nutritional strategy established in five separate families of marine bivalves that occupy habitats from intertidal to hadal depths (Fisher, 1990; Distel, 1998; Cavanaugh *et al.*, 2006; Dubilier, Bergin & Lott, 2008; Taylor & Glover, 2010). The symbiosis is likely obligate in the Solemyidae, Lucinidae and Vesicomyidae, where all studied species possess symbionts (Stewart & Cavanaugh, 2006; Taylor & Glover, 2006; Krylova & Sahling, 2010). For the Mytilidae, only the Bathymodiolinae (*Bathymodiolus*, *Tamu*, *Gigantidas*, *Idas*, *Adipicola*) possess symbionts (DeChaine & Cavanaugh, 2005; Duperron, 2010), while in the Thyasiridae some species have abundant symbionts, while others have few or no bacteria (Southward, 1986; Dufour, 2005).

One other bivalve family, often listed as being chemosymbiotic, is the Nucinellidae (frequently classified as Manzanellidae), a group of small, monomyarian, poorly known bivalves superficially resembling small *Nucula* and with a habitat range from shallow subtidal to abyssal depths (Vokes, 1956; La Perna, 2005; Sasaki, Okutani & Fujikura, 2005). There are 19 recognized living species classified into two genera, *Nucinella* and *Huxleyia*; most are around 5 mm in size, but the largest known is 25 mm long (La Perna, 2005). From the anatomical characters of *Nucinella serrei*, Allen & Sanders

(1969) suggested a relationship with Solemyidae. Later, Kuznetsov & Schileyko (1984) reported that *Nucinella maxima* lacked a gut and *N. viridula* had a reduced gut. Because a gutless condition is known in some species of Solemyidae, such as *Petrasma pervernicosa* Kuroda, 1948 (formerly known as *Solemya reidi* Bernard, 1980; see Kamenev, 2009), this observation led Reid (1980, 1990) to speculate that Nucinellidae might also be chemosymbiotic. This suggestion has been followed by some subsequent authors (Amano, Jenkins & Hikida, 2007; Taylor & Glover, 2010). Furthermore, Amano *et al.* (2007) speculated that the larger species of Nucinellidae are chemosymbiotic while the smaller species are deposit feeders. Nevertheless, the supposed symbiosis of Nucinellidae has never been confirmed by any actual observations of ctenidial structure, identification of symbionts or enzyme activity. However, recently McLeod, Wing & Skilton (2010) recorded depleted $\partial^{13}C$ levels (-33.6), consistent with a chemosymbiotic life habit, for *Nucinella maoriana* (Hedley, 1904) from 400 m in New Zealand fjords.

The focus of this paper is a study of the basic anatomy and gill structure of two species of Nucinellidae, *Nucinella owenensis* new species and *Huxleyia habooba* new species, sampled from a transect across the oxygen-minimum zone off southern Oman in the northern Indian Ocean. Although the material was not specifically fixed for electron microscopy or molecular analysis, our main objective was to investigate whether the ctenidia of these two species housed symbiotic bacteria.

Familial classification

The living nucinellids, *Nucinella* and *Huxleyia*, are often classified in the family Manzanellidae Chronic, 1952 with Nucinellidae Vokes, 1956 and Huxleyiidae Scarlato & Starobogatov in Nevesskaia *et al.*, 1971 as a junior synonyms (e.g. Bieler & Mikkelsen, 2006). The most recent comprehensive classification of bivalves (Bieler, Carter & Coan, 2010) placed the family in the superfamily Manzanelloidea in the order Solemyida. However, *Manzanella*, the type genus of Manzanellidae, is an early Permian (*c*. 284 Ma) fossil that differs in shell characters from *Nucinella* and *Huxleyia*. For example, the subcircular *Manzanella elliptica* Girty, 1909 is dimyarian as compared to the monomyarian and elliptical *Nucinella* and *Huxleyia* and the hinge dentition differs in that taxodont teeth lie posterior to the beaks in *Manzanella*, but are largely anterior in *Nucinella* and *Huxleyia* (see figures in Chronic, 1952; Pojeta, 1988). Although a relationship between Manzanellidae and Nucinellidae is possible, Pojeta (1988: fig. 3) suggesting a direct ancestor-descendant lineage of *Manzanella elliptica* to Nucinellidae, it seems prudent, in view of the morphological differences, to keep the two families separate, especially as bacterial symbiosis is now confirmed for nucinellids and molecular data are becoming available.

MATERIAL AND METHODS

Sampling

Specimens were collected in 1994 during the RRS *Discovery* cruise 211 to the Oman Margin, Arabian Sea (Fig. 1). This cruise was primarily aimed at assessing the effect on the benthos of the oxygen-minimum conditions that result from the rapid deposition of organic matter derived from the seasonally high levels of planktonic productivity (Gage, Levin & Wolff, 2000). Samples were taken by a variety of gear including anchor dredge, box core and epibenthic sledge for macrobenthos and multi-corer for meiobenthos across the oxygen-minimum zone from 40–3,500 m, along a transect running south-southeast of the island of Masirah, Oman (Fig. 1, sites A–C). The benthic samples that yielded nucinellids were sieved through a 0.5-mm mesh and bulk-fixed in 10% formaldehyde for 3–5 days before being washed out and preserved in 70% ethanol. These samples were subsequently sorted in the laboratory. Nucinellids were recovered from only three samples, at 80 m (Fig. 1, site A), 3,150 m (site B) and 3,400 m (site C).

Comparative material was examined in National Museum of Wales (NMW) and Natural History Museum, London (NHMUK).

Critical-point drying and SEM examination

Specimens for scanning electron microscopy (SEM) were decalcified in dilute hydrochloric acid. For *Nucinella owenensis* the ctenidia were excised and sliced with a razor blade, while for *Huxleyia diabolica* the whole body was sliced transversely into several pieces. The tissue pieces were then dehydrated through an ascending series of acetone concentrations and critical-point dried. The specimens were then mounted on stubs, sputter coated with gold and examined with a Philips XL30 field emission SEM.

Semi-thin sections

As few specimens were available, only a single specimen of each *Nucinella* and *Huxleyia* were prepared for semi-thin sectioning. These were decalcified in Bouin's fluid and embedded in
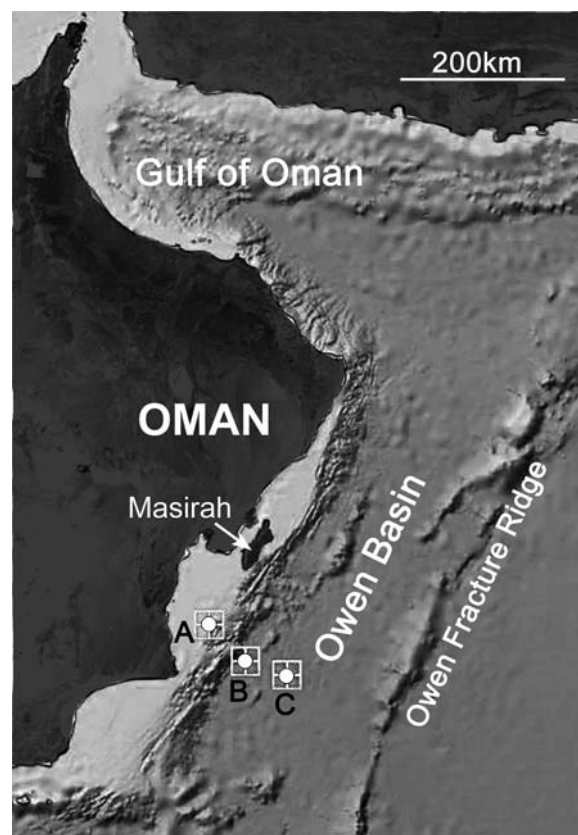

Figure 1. Map of the Oman margin showing collection sites **A–C**.

Araldite. They were cut into transverse 2 μm-thick serial sections and stained with toluidine blue. Unfortunately, the preservation of the *Huxleyia* was poor and no useable sections were obtained.

RESULTS

Nucinella owenensis n. sp.

The ctenidia are large, occupying about 60% of the mantle cavity, with the ctenidial axis almost at right angles to the long axis of the shell (Fig. 2A). Ctenidia are composed of about 40 leaflets that are 350 μm deep and 15–16 μm thick, with a stiffening rod at the distal and proximal ends (Fig. 3A, B). Leaflets are divided into a distal ciliated zone around 100 μm deep with bands of frontal, latero-frontal and lateral cilia; this is followed by a narrow intermediate zone consisting of low cells without cilia. The greater part of the leaflet, 250–300 μm, is composed of sheets of cells packed with bacteria (bacteriocyte zone) lying to either side of a central blood space. Lateral surfaces of leaflets are flat, microvilli-covered, with individual bacteriocytes having polygonal boundaries (Fig. 3C) that are 7–10 μm in diameter and 10 μm in thickness and with no obvious valleys corresponding to positions of intercalary cells as in Lucinidae (Ball *et al.*, 2009). The bacteriocytes contain abundant, long, rod-shaped bacteria, *c*. 4–6 μm long and 0.4–0.6 μm wide (Fig. 3D–F). The symbionts are found mainly oriented normal to the outer bacteriocyte surface and extend nearly the whole width of the bacteriocytes. Dividing bacteria are frequently observed (Fig. 3F). Also contained within the bacteriocytes are ovoid bodies, *c*. 7 μm
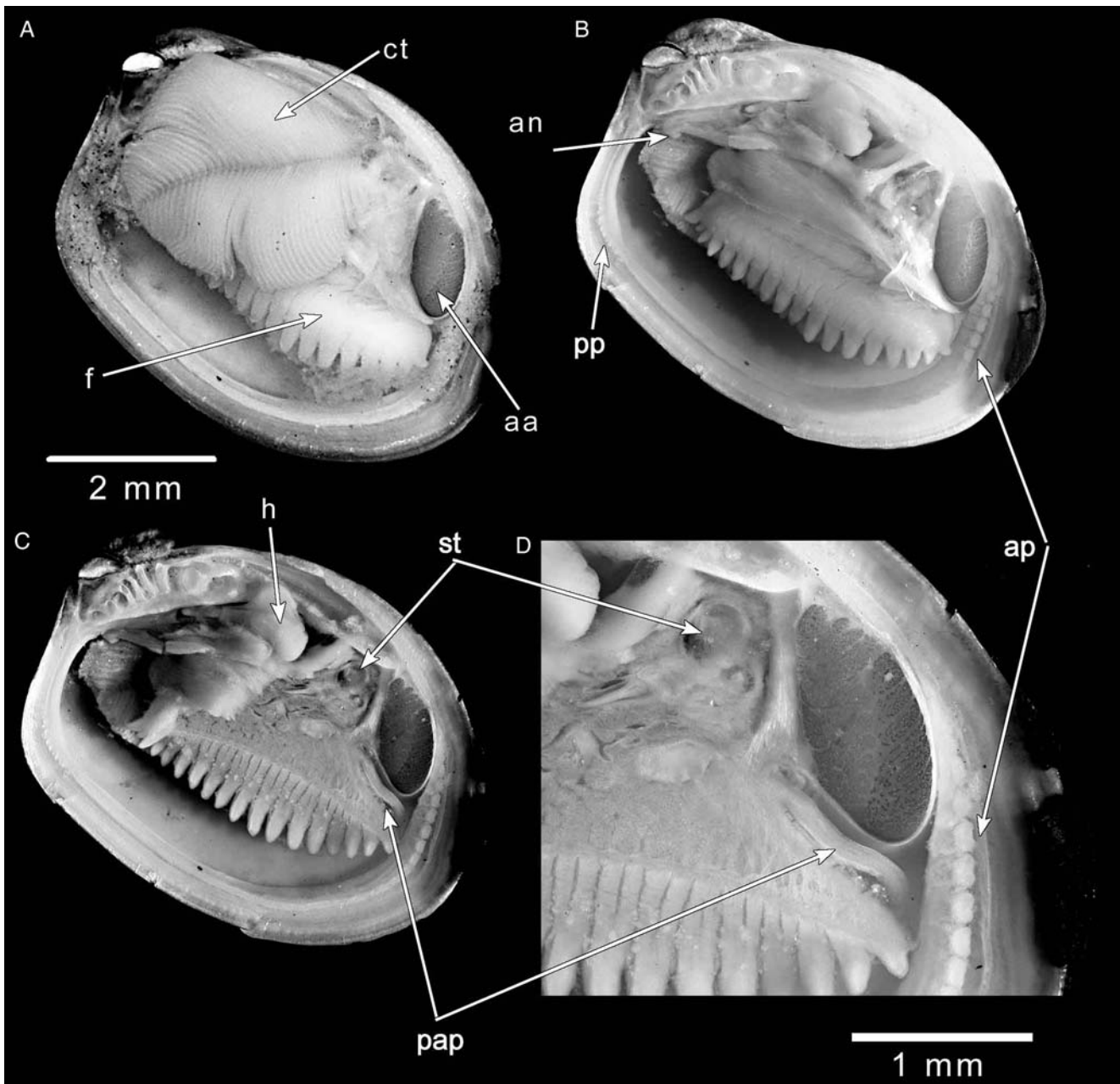
Figure 2. *Nucinella owenensis* n. sp. gross anatomy. **A.** View from left side with shell and mantle removed. **B.** From left side with ctenidia removed. **C.** View from left side with foot and visceral mass sliced. **D.** Detail of stomach and palp. Abbreviations: aa, anterior adductor muscle; an, anus; ap, anterior mantle papillae; ct, ctenidia; f, foot; h, heart; pap, palp proboscis; pp, posterior mantle papillae; st, stomach.

long and 4 μm wide, with irregular granular surfaces. Comparison with other chemosymbiotic bivalves suggests that these may be lysosomes (Ball *et al.*, 2009).

The mantle edge is unfused throughout; along the anterior mantle margin there is a series of 12 prominent quadrate papillae and a set of 14 smaller papillae is present along the posterior mantle margin. There is a large anterior adductor muscle but no posterior muscle. Small finger-like labial palps are present that appear to be single. The foot is very large, elongate, longitudinally divided and very deeply papillate at the margins. The heart is relatively large (Fig. 2C) compared to Nuculidae. A complete gut is present with a simple stomach with gastric shield. The hindgut contains some sediment particles (Fig. 4A, C).

Huxleyia habooba *n. sp.*

The *Huxleyia* specimens were less well preserved, but the gross anatomy is similar to *N. owenensis* in possessing a large, cleft, papillate foot, and a large anterior adductor muscle with no trace of a posterior adductor (Fig. 5A, B). The ctenidia are large with about 27–29 leaflets (Fig. 5A, C). Each leaflet is *c.* 150 μm deep and 10–12 μm across with a central blood space. About 85% of the leaflet consists of bacteriocyte zone with the outer ciliated zone around 20 μm deep (Fig. 5D, F). Leaflet surfaces in the bacteriocyte zone are flat with a uniform cover of microvilli. Cell contents are poorly preserved but within the bacteriocytes there are abundant, short, rod-shaped bacteria 2–2.5 μm long and 0.3–0.5 μm across, with their long axes
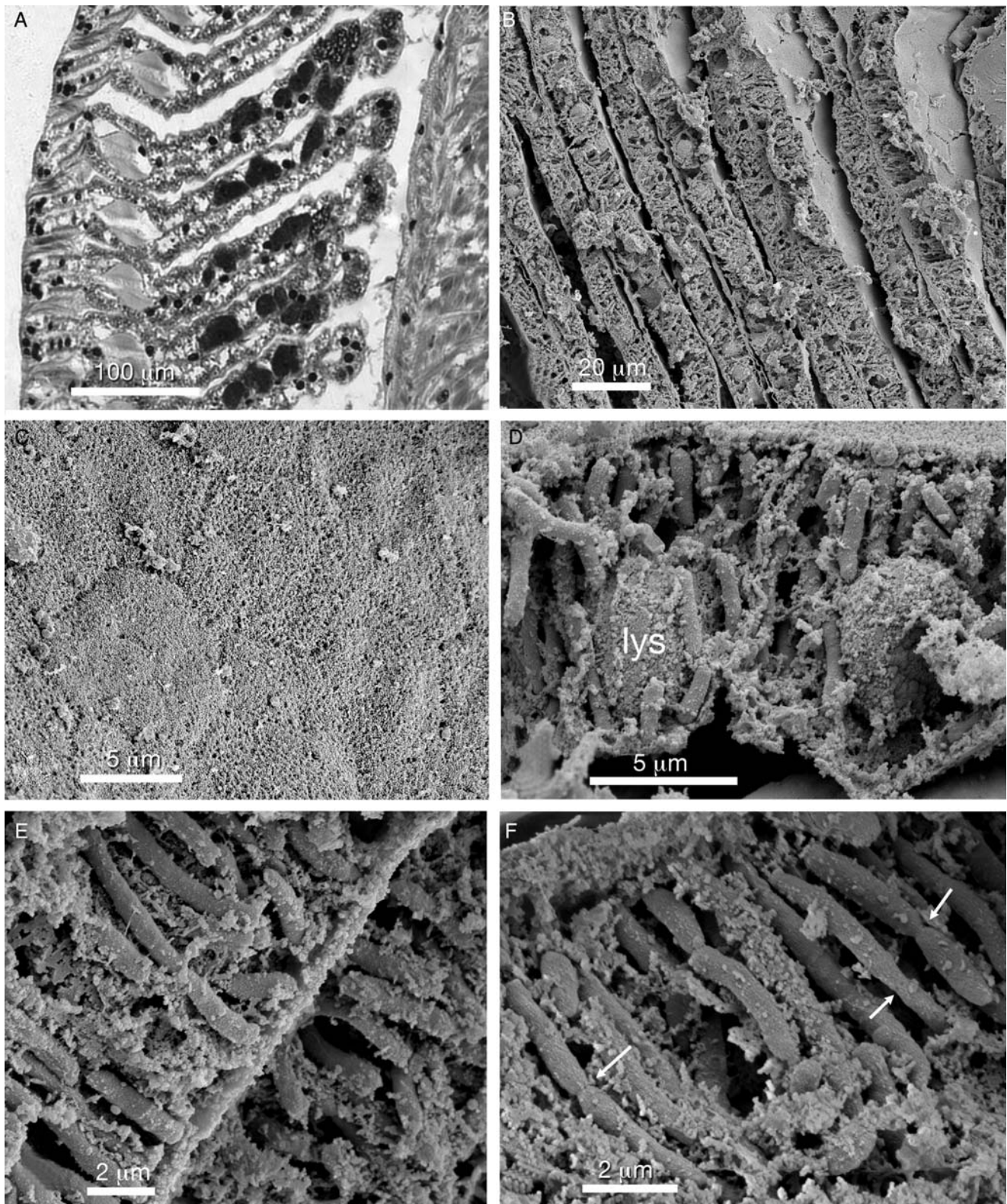
Figure 3. *Nucinella owenensis* n. sp. **A.** Semi-thin section through ctenidial leaflets. **B.** SEM section of the bacteriocyte zones of five ctenidial leaflets. **C.** Outer surface of microvilli-covered ctenidial leaflet showing polygonal boundaries of bacteriocytes. **D.** Section of bacteriocytes showing rod-shaped bacteria and spherical bodies possibly lysosomes. **E.** Long, rod-shaped bacteria in bacteriocyte. **F.** Section of bacteriocyte with dividing bacteria (arrowed). Abbreviations: lys, possible lysosome body.
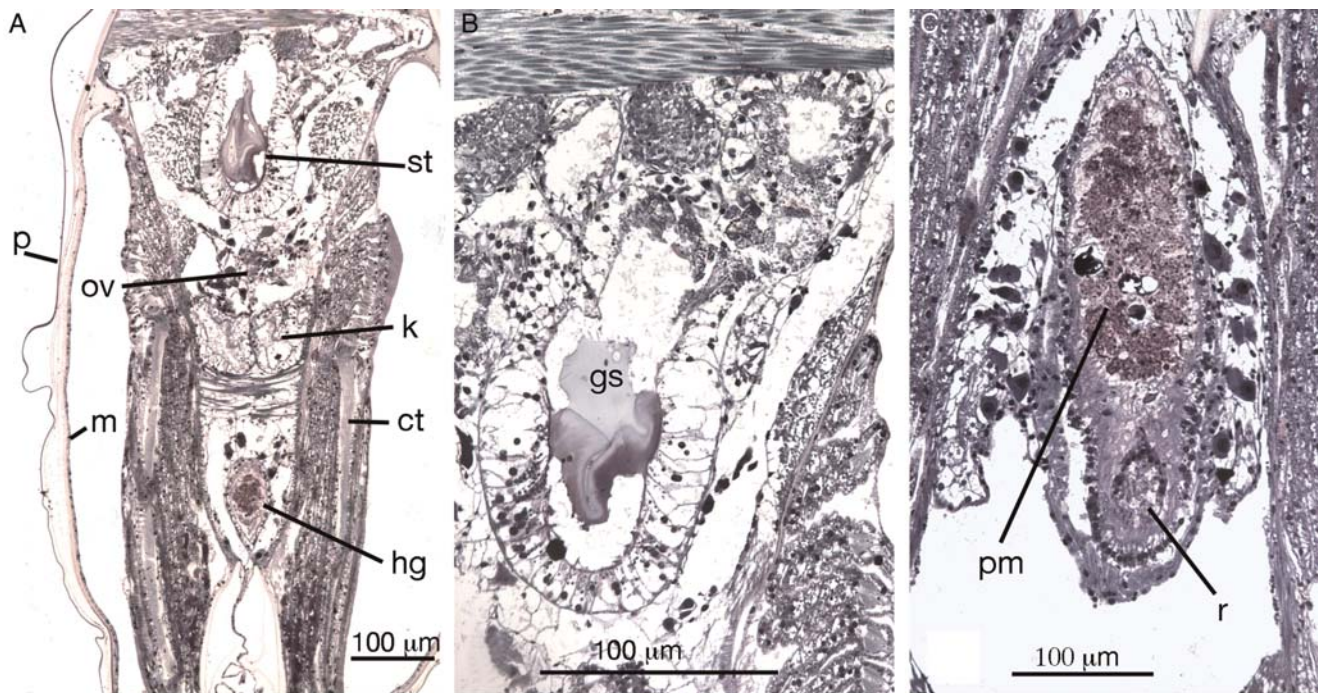
Figure 4. *Nucinella owenensis* n. sp. semi-thin sections. **A.** Longitudinal section of dorsal part of body. **B.** Detail of stomach. **C.** Hindgut with particulate material. Abbreviations: ct, ctenidia; gs, gastric shield; hg, hind gut; k, kidney; m, mantle; ov, ovary; p, periostracum; pm, particulate material; r, rectum; st, stomach. This figure appears in colour in the online version of *Journal of Molluscan Studies*.

aligned normal to the bacteriocyte surface (Fig. 5E, G). SEM sections show that a gut is present, with a small stomach and the hindgut passing through ventricle (Fig. 5C).

DISCUSSION

Our evidence from *Nucinella owenensis* and *Huxleyia habooba* demonstrates that both species possess symbiotic bacteria held in bacteriocytes of the abfrontal tissue of the ctenidial leaflets. By comparison with studies of Solemyidae and Lucinidae it is assumed that these symbionts are chemoautotrophic and likely sulphide-oxidizing (Cavanaugh *et al.*, 2006; Dubilier *et al.*, 2008). Along with the isotopic evidence for *Nucinella maoriana* (McLeod *et al.*, 2010) this is the first direct evidence of chemosymbiosis in the Nucinellidae, although molecular characterization of the symbionts is desirable when suitably preserved material becomes available. The symbionts of *N. owenensis* are elongate rods usually aligned normal to the bacteriocyte outer walls and occupying most of the height of the cells and this arrangement of symbionts is very similar to that seen in *Solemya* species (Krueger, Dubillier & Cavanaugh, 1996; Taylor, Glover & Williams, 2008; Fujiwara *et al.*, 2009). Sediment retained in the hindgut of *N. owenensis* suggests a capability of particulate feeding, as has been recorded for some Solemyidae (Krueger, Gallager & Cavanaugh, 1992).

Anatomical information is available for only three other species of Nucinellidae. The most detailed account is for *N. serrei* (3 mm) from 450 m in the north Atlantic (Allen & Sanders, 1969), investigated by serial sections. This species has large ctenidia, a large, cloven, deeply papillate foot, a pair of short simple palps on each side of the mouth, and a simple gut with oesophagus, stomach and hindgut. The gill leaflets are elongate with some abfrontal thickening. Allen & Sanders (1969) remarked on the relatively large size of the heart and blood system in *N. serrei*. The anatomy of *N. owenensis* is essentially similar to that described for *N. serrei*. For two other

species of Nucinellidae, Kuznetsov & Schileyko (1984) claimed that the *N. maxima* (Thiele & Jaeckel, 1931) (4.2 mm) lacks both digestive system and labial palps and that *N. viridula* Kuznetsov & Schileyko, 1984 (2.2 mm) has a weakly developed stomach but no oesophagus or posterior intestine. For such small-sized bivalves it is difficult to confirm the absence of a gut without the use of thin sections or electron microscopy. Certainly the situation recorded for *N. viridula*, with a stomach present but no oesophagus or hindgut, seems unlikely and both species need further investigation.

Relationships of Nucinellidae

Prior to 1969 the genera *Nucinella* and *Huxleyia* were placed in the family Manzanellidae within the superfamily Limopsoidea (Keen & Newell, 1969). This classification was based on shell characters alone and was radically altered by Allen & Sanders (1969) when deep Atlantic specimens became available for anatomical study. Although externally the shells of Nucinellidae resemble small *Nucula* species, Allen & Sanders (1969: 392) pointed out that anatomically they resemble solemyids and concluded "...the present paper amply demonstrates that members of the family Nucinellidae are protobranchs whose closest living relatives are the Solemyidae". This conclusion has been followed in classifications ever since (Pojeta, 1988; Bieler & Mikkelsen, 2006), the latest of these (Bieler *et al.*, 2010) placing Manzanelloidea in the order Solemyida.

No molecular phylogenetic analyses of bivalves that include nucinellid species have yet been published, but preliminary data (John Zardus and Gonzalo Giribet, personal communication) suggest that the two species analysed, *Nucinella* sp. and *Huxleyia munita* (Dall, 1898), are more closely related to *Solemya* species than to *Nucula* and other protobranch bivalves. Recent molecular analyses indicate Nuculidae and Solemyidae
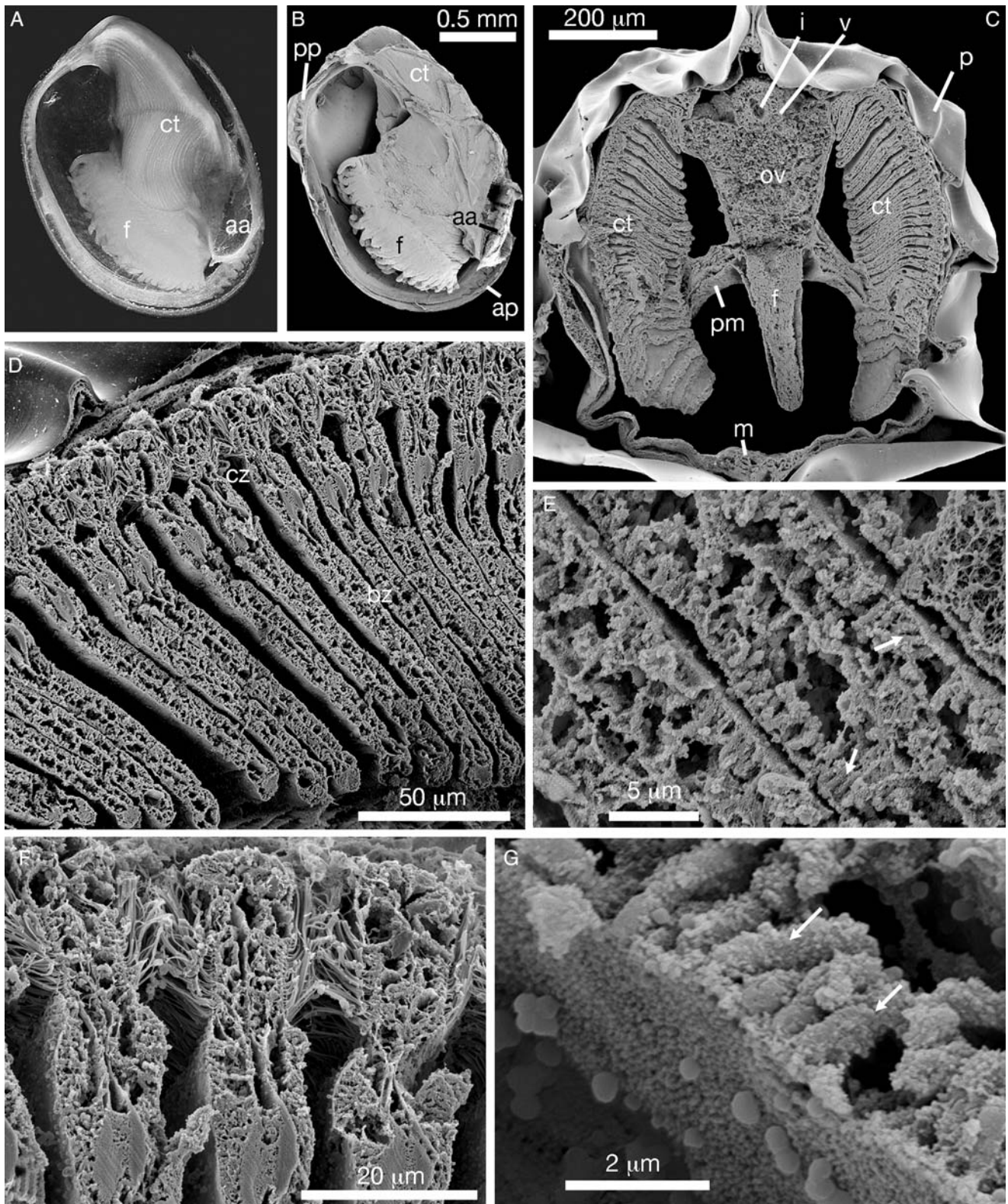
Figure 5. *Huxleyia habooba* n. sp. **A.** Decalcified animal right side. **B.** Critical-point dried preparation with ctenidia partly removed showing large foot and papillate mantle to anterior and posterior. **C.** Transverse section of decalcified animal showing ctenidia, foot and intestine. **D.** Section of ctenidial leaflets with distal ciliated zones and proximal bacteriocyte zones. **E.** Section of ctenidial leaflets with small rod-shaped symbionts (examples arrowed). **F.** Section of ciliated zone of distal portion of three ctenidial leaflets. **G.** Rod-shaped bacteria (arrows) in outer part of bacteriocyte. Abbreviations: aa; anterior adductor muscle; ap, anterior papillae; bz, bacteriocyte zone; cz, ciliated zone; ct, ctenidia; f, foot; i, intestine; m, mantle; ov, ovary; p, periostracum; pp, posterior mantle papillae v, ventricle.

as sister groups and these have been classified together by Giribet (2008) as an unranked clade, Opponobranchia.

Origin of the chemosymbiosis

All studied Solemyidae possess symbionts and the association seems obligate for the family (Stewart & Cavanaugh, 2006; Taylor *et al*., 2008). Some solemyids entirely lack alimentary systems (Kuznetsov & Schileyko, 1984; Reid, 1990; Kamenev, 2009), but for those with a gut such as *Petrasma velum* (Say, 1822) some particle feeding can occur (Krueger *et al*., 1992). The Solemyidae are an ancient bivalve family with a long fossil record extending into the lower Palaeozoic with the earliest known, *Ovatoconcha*, from the early Ordovician [Floian Stage (=Arenig), *c*. 475 Ma] (Cope 1996, 2000), while other solemyids are known from middle Ordovician and younger rocks (Pojeta, 1988). The general similarity in shell morphology and, by extrapolation, body organization suggests that these early solemyids possessed similar life habits to living species. Certainly the Silurian *Janeia silurica* Liljedahl, 1984 is associated with sediments interpreted as reducing conditions and it lived in association with *Ilionia prisca*, an early lucinid (Liljedahl, 1984, 1991).

Nucinellidae that are morphologically similar to living species are known from the early Jurassic and younger rocks, with a frequently recorded association with dysaerobic or organic-rich sediments (Vokes, 1956; Clausen & Wignall, 1988; Pojeta, 1988; Harries & Little, 1999; Wignall, Newton & Little, 2005). Furthermore, a large *Nucinella* species has been described from late Cretaceous, bathyal, cold-seep deposits in Japan (Amano, Jenkins & Hikida, 2007) and a possible *Nucinella* was recorded from a late Triassic, brachiopod-dominated, methane-seep deposit in Oregon (Peckmann *et al*., 2011). These habitat associations form circumstantial evidence for the possession of chemosymbionts during the Mesozoic.

Despite the anatomical and molecular evidence of a relationship between Nucinellidae and Solemyidae, the shells are quite different in morphology. Solemyids have elongate, cylindrical, anteriorly extended, dimyarian, edentulous, thin shells with flexible periostracal margins. By contrast, nucinellids are small, with robust monomyarian shells and a few taxodont hinge teeth and a posterior lateral tooth. Pojeta (1988: fig. 3) presented a phylogenetic tree of the Solemyoidea suggesting a direct lineage of Nucinellidae through the Permian *Manzanella* (Manzanellidae) to the Carboniferous–Ordovician genera *Clinopistha* and *Dystactella* (Clinopisthinae), with a split of this clade from the Solemyidae in the early Ordovician. He further suggested that both nucinellid and solemyid clades derived from the palaeotaxodont *Ctenodonta* in the early Ordovician. In this scenario, also followed by Waller (1998), the 'nucinellid' and 'solemyid' clades share a common origin but have been separate since the early Ordovician. Cope (2000) disputed this interpretation regarding the edentulous *Clinopistha* and *Dystacella* as part of the solemyid branch and doubted the ancestor–descendant relationship of *Ctenodonta* and Solemyidae. Whether Pojeta's (1988) hypothesis is correct or not it leads on to the question of the timing of acquisition of chemosymbiosis in Nucinellidae. Either the chemosymbiosis life style was acquired before the split of the two clades in the early Ordovician or the bacterial association in the two groups was independently evolved. In the case of the nucinellids the association with dysaerobic palaeoenvironments suggests acquisition of symbiosis at least by the early Jurassic, while evidence from shell morphology suggests an early Palaeozoic date for the Solemyidae. No evidence for the presence of symbionts is available for Manzanellidae and Clinopisthinae.

Size of Nucinellidae

Most of the known living and indeed fossil nucinellid species are small at <10 mm; an exception is *Nucinella boucheti* La Perna, 2005 that reaches 25 mm in length, and *Nucinella gigantea* from the Cretaceous that is up to 18.8 mm (Amano *et al*., 2007). These authors speculated that larger (10 mm plus) nucinellids were chemosymbiotic, but that smaller species such as *Huxleyia* species were deposit feeders. Our evidence suggests that both genera are chemosymbiotic. The small sizes of nucinellids contrast with the large sizes attained by other chemosymbiotic bivalves including the large 260-mm long solemyid *Acharax gigas* from the Miocene (Kurihara, 2000); *Calyptogena magnifica* (280 mm) of the Vesicomyidae (Krylova & Sahling, 2010), the bathymodiolinae mussel *Bathymodiolus boomerang* (370 mm) (von Cosel & Marshall, 2003) and *Superlucina megameris* (300 mm) an Eocene lucinid (Taylor & Glover, 2009). However, not all chemosymbiotic bivalves reach such large sizes as evidenced by many Mytilidae, Thyasiridae and Lucinidae species that are <10 mm long.

Habitat range

Although the Nucinellidae are shown here to be likely chemosymbiotic, their known habitats are not all obviously chemosynthetic. Only *N. viridis* Matsukuma, Okutani & Tsuchi, 1982 from 3,581 m (Okutani & Iwasaki, 2003), which was collected with *Acharax johnsoni*, may be associated with hydrocarbon seeps. For other nucinellids the bathymetric range is great, with species occurring from 6 m to over 3,500 m and occupying sediment types ranging from deep-water muds to coarse sediments and coralline sands, with some rich in organic material. Another Japanese species, *N. surugana*, inhabits muddy sediments at 500 m (Matsukuma *et al*., 1982). The 2-mm *N. maoriana* (Hedley, 1904) is abundant in organic-rich sediments at around 400 m in fjords of southern New Zealand (McLeod *et al*., 2010). *Huxleyia cavernicola* Hayami & Kase, 1993, a minute species only 1.2 mm in length, lives in floor sediments of subtidal caves of the Ryukyu Islands and Philippines (Hayami & Kase, 1993). A shallow-water species, *H. diabolica* (Jousseaume, 1897), occurs in sand between coral patches and in seagrass sediments at 6–40 m at Safaga, northern Red Sea (Zuschin & Oliver, 2003) and *N. serrei* was collected from bathyal muds of the Atlantic (Allen & Sanders, 1969).

SYSTEMATIC DESCRIPTIONS
## Order Solemyida Dall, 1889

Family NUCINELLIDAE Vokes, 1956

Huxleyiidae Scarlato & Starobogatov, 1971

Definition: Shell nuculoid (Fig. 6), obliquely oval, mostly higher than long, monomyarian, only anterior adductor muscle present. Hinge with subumbonal taxodont teeth and single elongate lateral on the anterior dorsal margin. Ligament mostly opisthodetic, wholly external or in a sunken resilifer. Shell sculpture weak, periostracum persistent, rather thick but not overlapping the shell margins. Anatomy protobranch, as described by Allen & Sanders (1969).

Remarks: In many definitions it is stated that the posterior adductor muscle is 'usually' lost (Boss, 1982; Pojeta, 1988); this stems from Vokes (1985) who observed that the posterior adductor scar was "poorly delineated". A drawing by Habe

(1958: pl. 11, fig. 16), later reproduced in Keen & Newell (1969: fig. C14 1a), shows an apparent posterior adductor scar in *Huxleyia sulcata* Adams, 1860 (type species of *Huxleyia*). The dimyarian condition was also given for *H. munita* (Dall, 1898) by Coan, Valentich Scott & Bernard (2000) and La Perna (2004) states that the genus *Huxleyia* is dimyarian. However, our examination of several syntypes of *H. sulcata* (NHMUK) showed no posterior scar. We have seen no extant species of *Huxleyia* with a posterior adductor and believe that there are no conclusive observations for fossil species. In our opinion the posterior adductor is lost and nucinellids are monomyarian.

The ligament has always been stated to be opisthodetic and is generally so, but in some minute species it is amphidetic lying immediately below the beaks (see *N. dalli*, Fig. 7). The ligament is either external, or in a sunken resilifer as in *Nucinella*, or wholly internal as in *Huxleyia*. In species with a sunken or internal ligament there is variation in the extent to which the ligament impacts the posterior teeth (Fig. 7). This observation renders the family Huxleyiidae unwarranted and also brings into question the current generic definitions; resolution of this is beyond the scope of this paper.
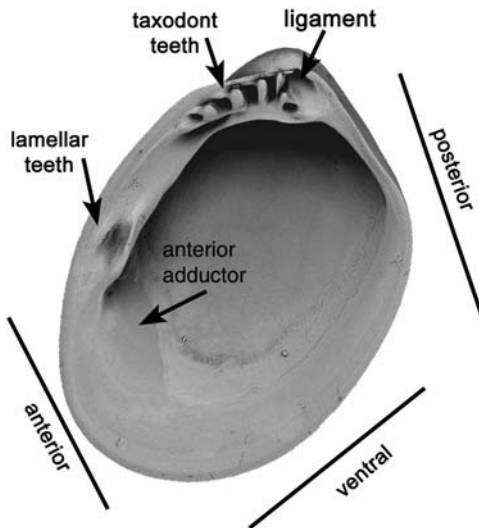
Figure 6. The nucinellid shell showing orientation and critical features.

Genus *Nucinella* Wood, 1851

Type species: *Pleurodon ovalis* Wood, 1840.

Diagnosis: As for the family; ligament external or in a shallow resilifer.

Nucinella owenensis new species
(Figs 2, 3, 4, 8A–C)

Types: Holotype, 1 specimen NMW.Z.1995.009.9. Owen Basin, Arabian Sea, 18°58.9′N 59°80.4′E, *Discovery* Cruise 211, stn 12730#2, 3,400 m, epibenthic sledge. 8 November 1994. Paratypes, 3 specimens NMW.Z.1995.009.10. Owen Basin, Arabian Sea, 19°08′N 58°39′E, *Discovery* Cruise 211, stn 12719#1, 3,150 m, 31 October 1994, epibenthic sledge.

Etymology: Named after the type locality Owen Basin, deriving its name from the survey ship HMS *Owen*.

Description: Shell small, length (L) to 5.9 mm, height (H) to 4.5 mm. Thin, equivalve, umbos prominent. Inequilateral, beaks close to the posterior margin. Outline nuculoid, suboval, posterior dorsal margin distinct, slightly incurved; posterior margin long, almost straight; junction of posterior dorsal and posterior margins distinct, roundly angled; anterior dorsal and anterior margins continuous, broadly curving to narrower, rounded ventral margin. Subumbonal teeth of 5 (right valve, RV), 6 (left valve, LV) blade-like, pointed teeth plus two large anterior, subparallel teeth and two very small, peg-like, subparallel teeth below the ligament. Lateral tooth very long in both valves, with maximum projection at anterior extremity, LV with a weak secondary ridge creating a shallow socket. Ligament prominent, mostly external but partially invading the hinge plate. Sculpture smooth, periostracum persistent, straw coloured, shiny. Monomyarian, posterior adductor muscle scar absent; anterior adductor large, oval.

Distribution: Known only from the type locality.

Associated bivalve fauna: The fauna of the Owen Basin at the two sample sites was similar, diverse and typical of abyssal communities in that it was dominated by deposit-feeding protobranchs in the genera, *Nucula*, *Nuculoma*, *Ledella* and *Yoldiella*. There were, however, many specimens of the suspension feeding *Limopsis* and *Bentharca* and large chemosymbiotic species of *Thyasira*, *Vesicomya* and *Acharax*.

At this depth the oxygen depletion has subsided with oxygen concentrations of 3.0 ml/l recorded at time of sampling. The considerable diversity of chemosymbiotic taxa may be due
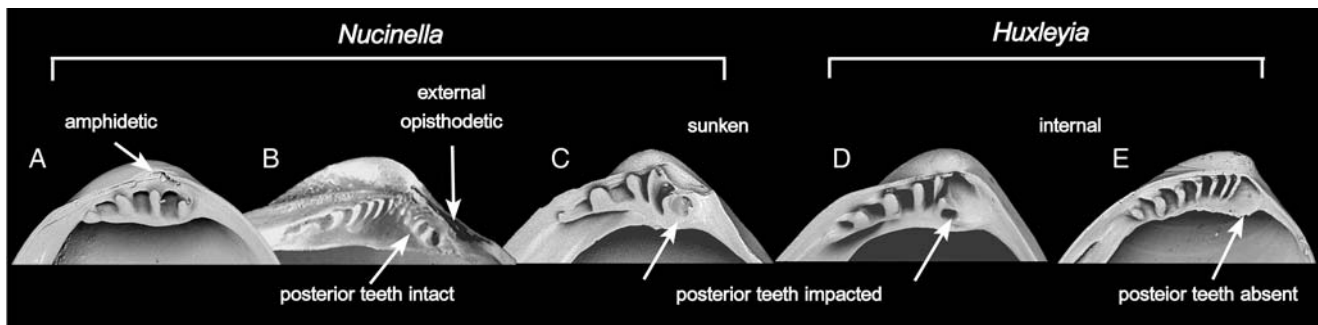
Figure 7. Progression of internalization of the ligament and consequent loss of posterior hinge teeth in Nucinellidae. **A.** *Nucinella dalli*. **B.** *N. boucheti* (after La Perna, 2005). **C.** *N. serrei* Lamy. **D.** *Huxleyia habooba* n. sp. **E.** *H. concentrica*. **A, C–E** in NMW. Not to scale.
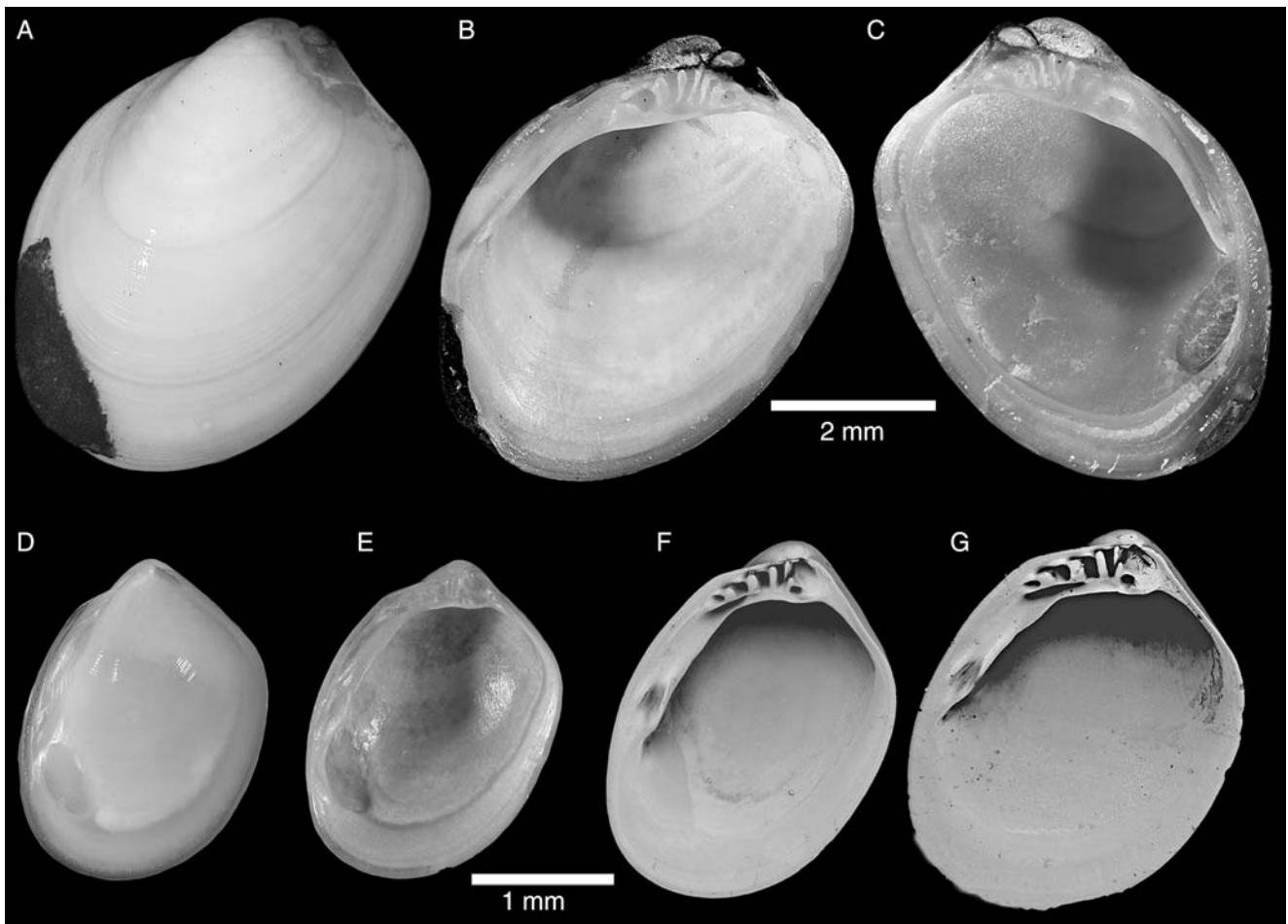
Figure 8. A–C. *Nucinella owenensis* n. sp. Holotype, NMW.Z.1995.009.9 **A.** Left valve, external. **B.** Right valve, internal. **C.** Left valve, internal. **D–F.** *Huxleyia habooba* n. sp. **D.** Holotype NMW.Z.1995.009.11, left valve, external. **E, F.** Paratypes, NMW.Z.1995.009.12. **E.** Internal, right valve. **F.** SEM, internal, right valve. **G.** *Huxleyia diabolica*, Safaga Bay, Red Sea, SEM, internal right valve (NMW).

to the large quantities of planktonic detritus and down-slope transport of enriched sediments from the oxygen-minimum zone creating enhanced reducing conditions.

Remarks: La Perna (2005) listed 14 extant species of *Nucinella*, the majority of these living at water depths of <500 m. The only Indian Ocean species is *N. maxima* (Thiele & Jaeckel, 1931), described from 463 m in the Zanzibar Straits. This species is known only from a single valve, 12.5 mm in height and considerably larger than the *N. owenensis*. *Nucinella maxima* further differs in the orientation of the taxodont teeth where the three posterior teeth are set at a different angle to the two anterior; the ligament appears not to invade the hinge plate; there is no indication of small teeth posterior to the vertical series; and the periostracum is greenish not straw coloured. Abyssal bivalves have been recorded as having cosmopolitan ranges, but the only other abyssal species, *N. viridis* Matsukuma, Okutana & Tsuchi, 1982, is more similar to *N. maxima* with its relatively large size and distinctly greenish periostracum.

Genus *Huxleyia* A. Adams, 1860

Type species: *Huxleyia sulcata* Adams, 1860 by original designation

Diagnosis: As for the family; ligament is mostly internal set in a sunken resilifer.

Huxleyia habooba new species
(Figs 5, 8D–G)

Huxleyia diabolica (Jousseaume, 1897)—Oliver, 1995: 203.

Types: Holotype and Paratypes NMW.Z.1995.009.11/12. Oman Margin, Arabian Sea, 19°32.28′N 58°13.11′E, *Discovery* Cruise 211, stn12684#1, 84 m, Tjärno anchor dredge, 14 October 1994.

Etymology: From the Arabic 'Hbwb', a grain.

Description: Shell L to 2.6 mm, H to 1.9 mm. Thin, equivalve, umbos prominent. Inequilateral, beaks close to the posterior margin. Outline narrowly oval, posterior dorsal margin long, sloping steeply, straight; posterior margin long, almost straight; junction of posterior dorsal and posterior margins distinct, roundly angled; anterior dorsal margin short, straight, slope much less than that of posterior dorsal margin, anterior margin gently curved; ventral margin narrowly rounded. Subumbonal teeth mostly anterior to beaks, posterior hinge plate disrupted by deep invading resilifer; anterior teeth up to 4 or 5 in each valve, the anterior two weakly chevron shaped the remainder blade-like; posterior teeth as one to two small pointed teeth set on hinge plate below the ligament fossette. Lateral tooth very long in both valves, with maximum projection at anterior extremity, LV or RV with a weak secondary

ridge creating a shallow socket. Ligament mostly internal in a sunken resilifer. Sculpture smooth, periostracum persistent, shiny cream coloured except for margins that are tinged greenish. Monomyarian, posterior adductor muscle scar absent; anterior adductor scar large, oval.

Distribution: Known living only from the type locality; also from valves collected from the strandline of the adjacent island of Masirah.

Associated bivalve fauna: The associated fauna is diverse and dominated by *Tellina* cf. *vernalis*, *Corbula persica* and *Timoclea* sp. with additionally *Nucula* cf. *consentiana*, *Nuculana brookei*, *Nuculana sculpta*, *Bathyarca anaclima* and *Solemya* sp. The environmental conditions experienced by this fauna are not truly tropical being subject to cold-water influence during the monsoon season and subsequent low oxygen conditions. At the time of collection the dissolved oxygen level was very low at 0.7 ml/l compared to normal levels of 4–5 ml/l.

Remarks: La Perna (2005) listed five extant species of *Huxleyia*, the most similar being the Red Sea species *H. diabolica* (Jousseaume, 1897). This differs only with respect to the outline where the posterior dorsal slope appears longer, resulting in the outline appearing to be wider (Fig. 8G) (see Zuschin & Oliver, 2003: 164). Although many valves of *H. diabolica* are available we have too few Arabian valves to make a meaningful morphometric analysis. Zuschin & Oliver (2003) examined many hundreds of valves collected from shallow water facies where they were most abundant in sea-grass beds and coral sands from 6–40 m. The associated faunas in the sea-grass communities were dominated by *Cardiolucina semperiana*, *Cardites akabana*, *Divaricella macandreae*, *Tellina pinguis* and *Wallucina erythraea* and those in the coral sand by *Parvicardium sueziensis*, *Glycymeris arabicus*, *Moerella lactea*, *Wallucina erythraea* and *Pillucina vietnamica* (data from Zuschin & Oliver, 2003: 20). These associations are quite different from those of *H. habooba*. Although many species are common to both the Red Sea and Arabian Sea there is increasing recognition of endemism in the fauna inhabiting the upwelling regions of the Arabian Sea, as evidenced in the many species cited in Bosch *et al.* (1995). *Huxleyia habooba* and *H. diabolica* differ in shell outline, habitats, environmental conditions and associated faunas, sufficient we believe to regard the Red Sea and Arabian species as distinct.

Of the other Indo-Pacific species both *H. sulcata* and *H. concentrica* Verco, 1907 have strong commarginal lines and there are no teeth below the ligament fossette. The cavernicolous *H. cavernicola* Hayami & Kase, 1993 is a minute (1.2 mm) species with a very thick periostracum and the lateral tooth relatively closer to the subumbonal series.

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