

# DESCRIPTION OF *ATOPOMYA DOLOBRATA* GEN. ET SP. NOV.: FIRST RECORD OF BACTERIAL SYMBIOSIS IN THE SAXICAVELLINAE (BIVALVIA).

P. GRAHAM OLIVER<sup>1</sup>

<sup>1</sup>Biodiversity and Systematic Biology, National Museum of Wales, Cathays Park, Cardiff, CF10 3NP, Wales, UK

*Abstract* A new genus and species of the subfamily Saxicavellinae, *Atopomya dolobrata*, is described from deep water in the north eastern Atlantic. The ctenidia have greatly extended abfrontal surfaces, lined with bacteriocytes that harbour symbiotic bacteria. The anatomy of *Atopomya* and *Saxicavella jeffreysi*, Winckworth indicates that Saxicavellinae may have greater affinity with the Basterotiidae rather than the Hiatellidae. This is the first record of bacterial symbiosis in the Saxicavellinae.

*Key words* *Atopomya* gen. nov., bacterial symbiosis, Saxicavellinae, Basterotiidae, Galeommatoidea

## INTRODUCTION

The large collection of deep water Bivalvia held by the National Oceanographic Centre, Southampton was extensively studied during the compilation of the web site "Marine Bivalve Shells of the British Isles" (Oliver *et al.*, 2010). Amongst this collection was a single specimen labelled "hiatellid sp." collected from 1200 m in the Porcupine Sea Bight, south-west of Ireland. This specimen was opened to examine the hinge and in doing so it was noted that the gills were swollen and fleshy. Such gills are indicative of adaptation for bacterial symbiosis and this was confirmed by observation using scanning electron microscopy.

This paper describes the shell, anatomy and structure of the gills of this specimen and attempts to place it in a phylogenetic position within the Bivalvia.

Bacterial chemosymbiosis in the Bivalvia has been recognised for many years and was until recently thought to be restricted to few families in which chemosymbiosis was largely obligate such as the Lucinidae, Vesicomidae, Solemyidae and the subfamily Bathymodiolineae but also in the Thyasiridae where both symbiotic and non-symbiotic taxa are present (Taylor & Glover, 2010). More recently bacterial symbiosis, with presumed chemautotrophy, has been recognised in the Nucinelidae (Oliver & Taylor, 2012) and in the Montacutidae (Oliver, 2012; Oliver, Southward & Dando, 2013).

## MATERIALS AND METHODS

*Shells* Shell images were made using a computer aided digital photographic system powered by AutoMontage™ and by scanning electron microscopy with a JEOL Neoscope™. All the comparative shells in this study come from the collections of the National Museum of Wales with their registration numbers prefixed with NMW or NMW.Z.

*Gross Anatomy* The specimens had previously been fixed in formaldehyde and stored in 70% ethanol, subsequently stained with Rose Bengal or Methylene Blue. The shell was either dissected away from the soft tissues or removed in dilute hydrochloric acid. The anatomy was viewed and dissected from the left side. Images were made using a computer aided digital photographic system powered by AutoMontage™.

*Critical Point Drying and SEM examination* For SEM examination the tissues were dissected from the shell, the ctenidia excised and sliced transversely with a razor blade into several pieces. The tissue pieces were then dehydrated in 100% ethanol and critical point dried using a Tousimis Samdri™ CPD. The specimens were then mounted on stubs, sputter coated with gold and examined using a Jeol Neoscope™ scanning electron microscope.

## SYSTEMATICS

Superfamily Galeommatoidea J.E. Gray 1840

## Family Basterotiidae Cossmann 1909

## Subfamily Saxicavellinae Scott 1994

*Phylogentic position* The subfamily Saxicavellinae is currently placed in the superfamily Hiatelloidea (Scott, 1994; Bieler & Mikkelsen, 2006). The Hiatelloidea were traditionally included in the Order Myoida but molecular data does not support this (Giribet & Wheeler, 2002) and they are now regarded as a sister group of the Solenoidea in the Euheterodonta (Taylor *et al.*, 2007). This phylogeny is based on *Hiatella*, *Saxicavella* having never been analysed. Morphological data may suggest that the affinity with hiatellids is weak and this is strongly suggested in Yonge's (1971) paper where *Saxicavella* is frequently referred to as being atypical of the Saxicavacea [=Hiatelloidea] notably in the type of mantle fusion.

*Saxicavella jeffreysi* is rarely collected and has been regarded as a nestling species (Yonge, 1971) but a paper on the echiuran *Maxmuelleria* recorded this bivalve as a commensal of this deep burrowing "worm" (Nickell *et al.*, 1995). Echiuran commensals are rarely reported but there are reports of species of *Basterotia* living in echiuran burrows in tropical or subtropical waters (Oliver *et al.*, 2004; Anker *et al.*, 2005; Goto *et al.*, 2011). The shells of *Basterotia* and saxicavellines are similar in shape and disposition of the ligament but *Basterotia* species have a single large cardinal peg-like tooth in each valve (Fig. 5). Anatomically there are greater similarities especially the very dorsal position of the posterior adductor muscle and consequently the exhalant aperture. In both, the inhalant and exhalant apertures are formed within the fused inner mantle fold (Fig. 3). The middle fold is unfused and forms a ring around the siphonal region, in some the middle fold is thickened in others it bears tentacles. These similarities lead one to conclude that the Saxicavellinae are close to the Basterotiidae with the latter aligned close to the Galeommatoidea (Taylor *et al.*, 2007). It is evident from the discussion in Taylor *et al.* (2007) that the relationships between families assigned to the Galeommatoidea and Cyamioidea are uncertain. Coan & Valentich-Scott (2012) recognise that molecular data suggests that the Basterotiidae are aligned with the Galeommatoidea but the morphology suggest affinity with the Cyamioidea, this latter position being adopted by them. Here I

follow Taylor *et al.* (2007) and give greater weight to the molecular data and assign the Basterotiidae to the Galeommatoidea

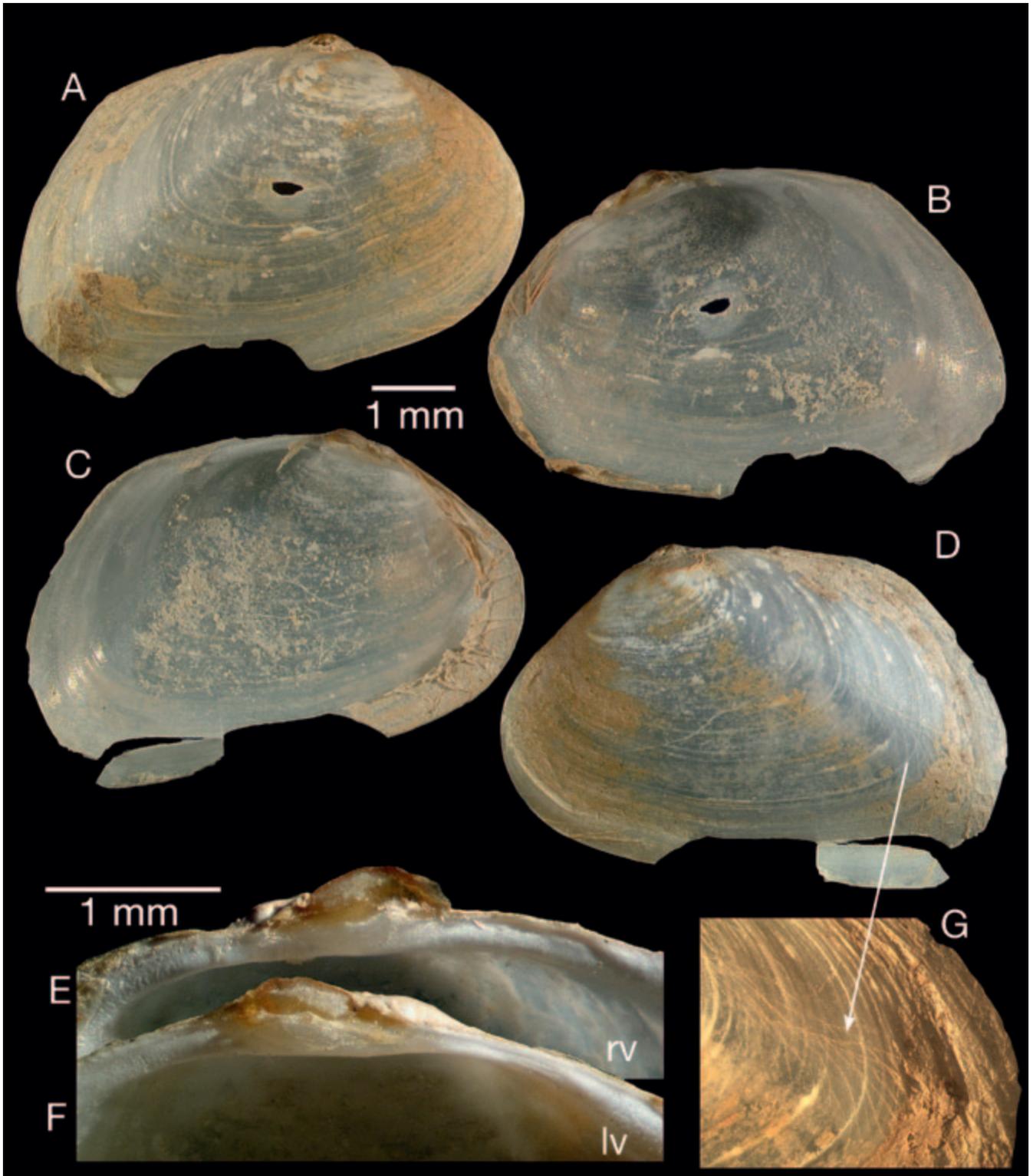
*Atopomya* gen. nov.

Type species: *Atopomya dolobrata* this paper

*Definition* Shell small (Figs 1A–F), thin, compressed, equivalve, gaping posteriorly, inequilateral with beaks in front of midline. Outline subovate, posterior expanded, subtruncate; anterior rounded; weakly keeled from beaks to posterior ventral edge. Hinge edentulous; ligament external on an irregular projecting nymph. Sculpture weak of commarginal lines and growth stops. Periostracum thin but adherent (Fig. 1G).

Adductor muscles subequal, posterior adductor positioned dorsally. Mantle fusion partial; inhalant and exhalant aperture within fused inner mantle folds, middle mantle folds surrounding siphons unfused. Ctenidia of two demibranchs, the outer much reduced, both with reflected filaments (Figs 2A). Filaments laminar, abfrontally extended and lined with bacteriocytes (Fig 4). Labial palps narrow.

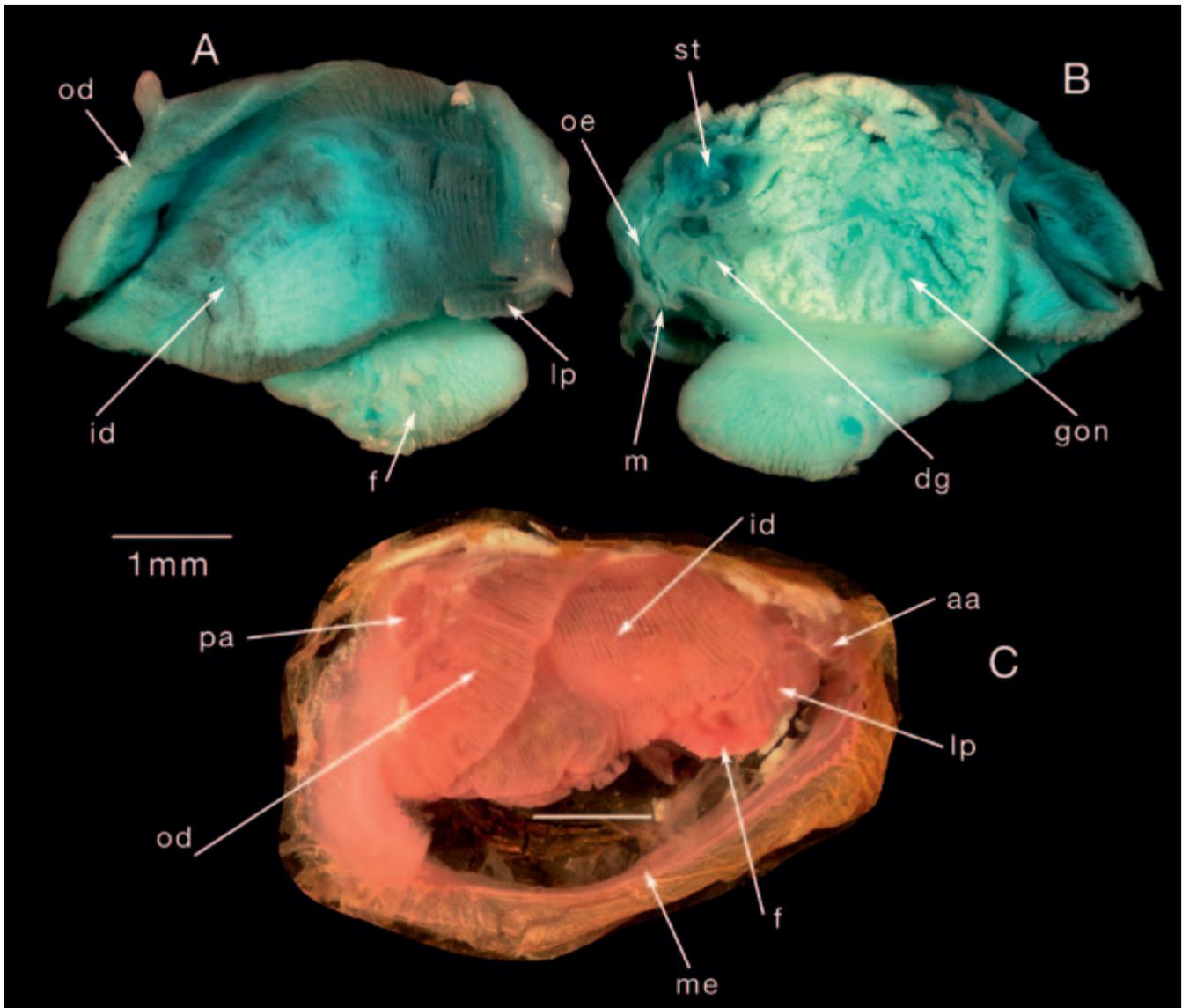
*Comparisons* The shell form closely resembles that of *Saxicavella* as represented by the type species of that genus *S. jeffreysi* Winckworth 1930 (Fig. 5B) and from shell characters alone separate generic designation would not be warranted. The nymph in *Saxicavella* is usually extended medially and often resembles a tooth, and a small cardinal tooth is reported or inferred to be present in juveniles (Yonge, 1971; Scott, 1994). Examination of many juvenile specimens held in the National Museum of Wales collections could not confirm teeth at any stage. Other supposed species of *Saxicavella* such as *S. angulata* (Wood 1857) (Aartsen & Bogi, 1998) do have single cardinal pegs in each valve (Fig. 5C) but such an arrangement is identical to that seen in the genus *Basterotia* and to which such species should be transferred. Aartsen & Bogi (1998) regard the genus *Turneria* Glibert & van der Poel 1966 [type species *S. angulata*] to be a junior synonym of *Saxicavella* but as the type species has a strong cardinal tooth it is therefore a *Basterotia*. The siphonal regions and pattern of mantle fusion (Figs 3A–B) are identical to that seen in *Saxicavella*. The significant difference is



**Figure 1** *Atopomya dolobrata* gen et sp nov. Holotype: **A–B** external and internal of right valve; **C–D** external and internal of left valve; **E–F** hinges of right and left valves; **G** detail of acentric sculpture.

in the gill anatomy whereas in *Atopomya* the gill filaments are laminar and abfrontally extended they are typically rod shaped and not modified in this way in *Saxicavella* (Fig. 2C).

*Etymology* *Atopomya* from the Greek; *atopos* — unusual or strange and *mya* — a clam; referring to the unusual adaptations for bacterial symbiosis.



**Figure 2** *Atopomya dolabrata*: **A–B** gross anatomy; **A** ctenidium and foot; **B** visceral mass after a longitudinal section; **C** gross anatomy of *Saxicavella jeffreysi*, Loch Creran, Scotland, NMW.Z. 1990.032.10. Labels: **aa**, anterior adductor muscle; **dg**, digestive gland; **f**, foot; **id**, inner demibranch; **lp**, labial palps; **m**, mouth; **me**, mantle edge; **od**, outer demibranch; **oe**, oesophagus; **pa**, posterior adductor muscle; **st**, stomach.

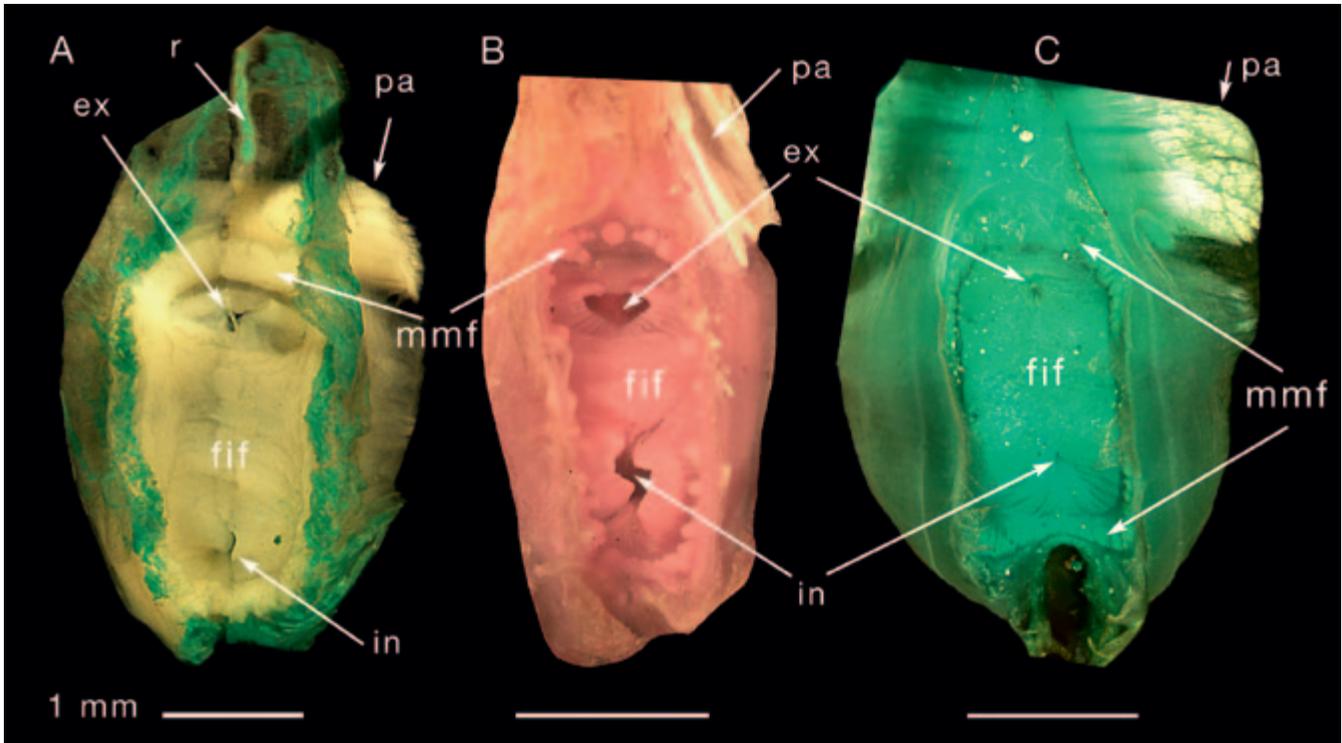
*Atopomya dolabrata* sp. nov.

*Material examined* This species is described from a single, preserved specimen and one shell; while this is generally to be avoided the striking anatomical adaptation clearly distinguishes this bivalve from all other related taxa and consequently justifies its description at this time.

*Holotype* 1 specimen, North-east Atlantic Ocean, Porcupine Sea Bight, south-west of Ireland, Discovery Station 51403#5, 51°37.8'N 12° 58.9'W to 51°37.3'N 12° 59.0'W 1259–1297 m, 26/3/1982. NMW.Z. 2011.001.4.

*Paratype* 1 shell, North-east Atlantic Ocean, Wyville-Thomson Ridge, west of Scotland, RRS Challenger station ES99, 60°00'N 10°35'W, 1160 m, 9/7/1976. NMW.Z. 2009.045.5.

*Description* Shell small (Fig. 1A–F), length 6.0 mm, height 4.1 mm. Compressed, thin, equivalve. Inequilateral beaks well forward of midline, umbos low. Outline subovate, anterior rounded and much narrower than obliquely truncate posterior; posterior dorsal margin long, almost straight; ventral margin long, almost straight. distinctly keed along line from beak to posterior-ventral margin. Hinge edentulous.



**Figure 3** Siphonal regions of: **A** *Atopomya dolobrata*; **B** *Saxicavella jeffreysi* NMW.Z. 1990.032.10; **C** *Basterotia borbonica* NMW.Z.2000.86. Labels: **ex** exhalant aperture; **fif** fused inner mantle fold; **in** inhalant aperture; **mmf** unfused middle mantle fold; **pa** posterior adductor muscle; **r** rectum.

Ligament external, prominent set on a raised nymph. Sculpture of commarginal lines and growth stops. Periostracum thin but persistent, wrinkled with a fine rust coloured deposit (Fig. 1G). Adductor scars indistinct, inner margin smooth.

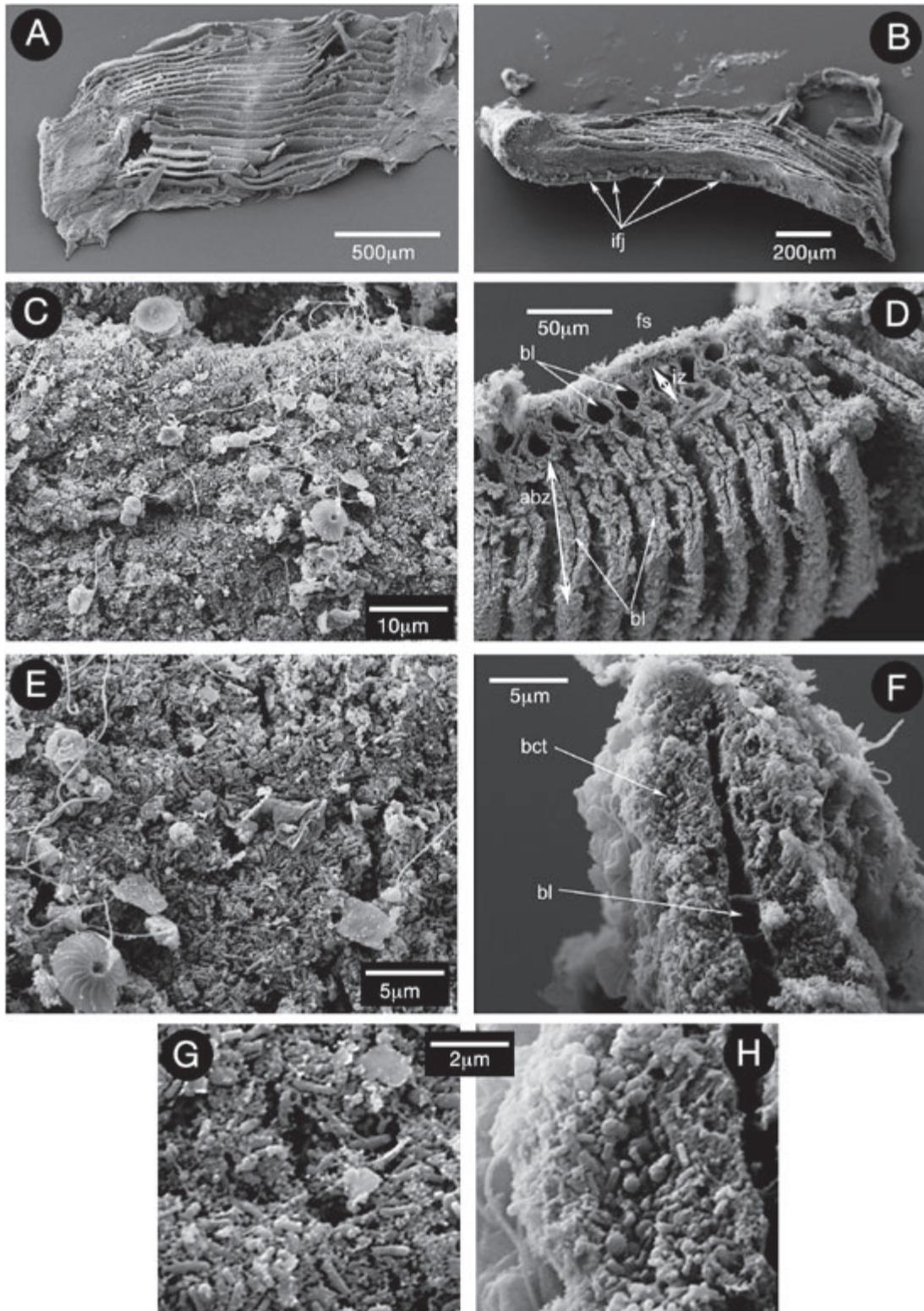
Mantle thin, mantle edges partially fused; pedal gape large situated anterior-ventrally; inner and middle folds fused postero-ventrally; posteriorly only inner mantle folds fused with simple inhalant and exhalant apertures (Fig. 3A), middle mantle fold surrounding apertural area thickened, not fused.

Adductor muscles rather small, posterior slightly larger than anterior and in a dorsal position. Foot with a prominent toe and small heel (Fig. 2B), byssus not observed. Ctenidia of two demibranchs the outer much reduced, both fleshy and both with reflected laminar filaments (Fig. 2A). Labial palps small, narrow blade-like with prominent sorting ridges (Fig. 2A). Alimentary system (Fig. 2B) of a short oesophagus leading to a stomach situated in an anterior dorsal position within the visceral mass; course of mid and hind gut not elucidated; digestive gland restricted to anterior area surrounding the stomach.

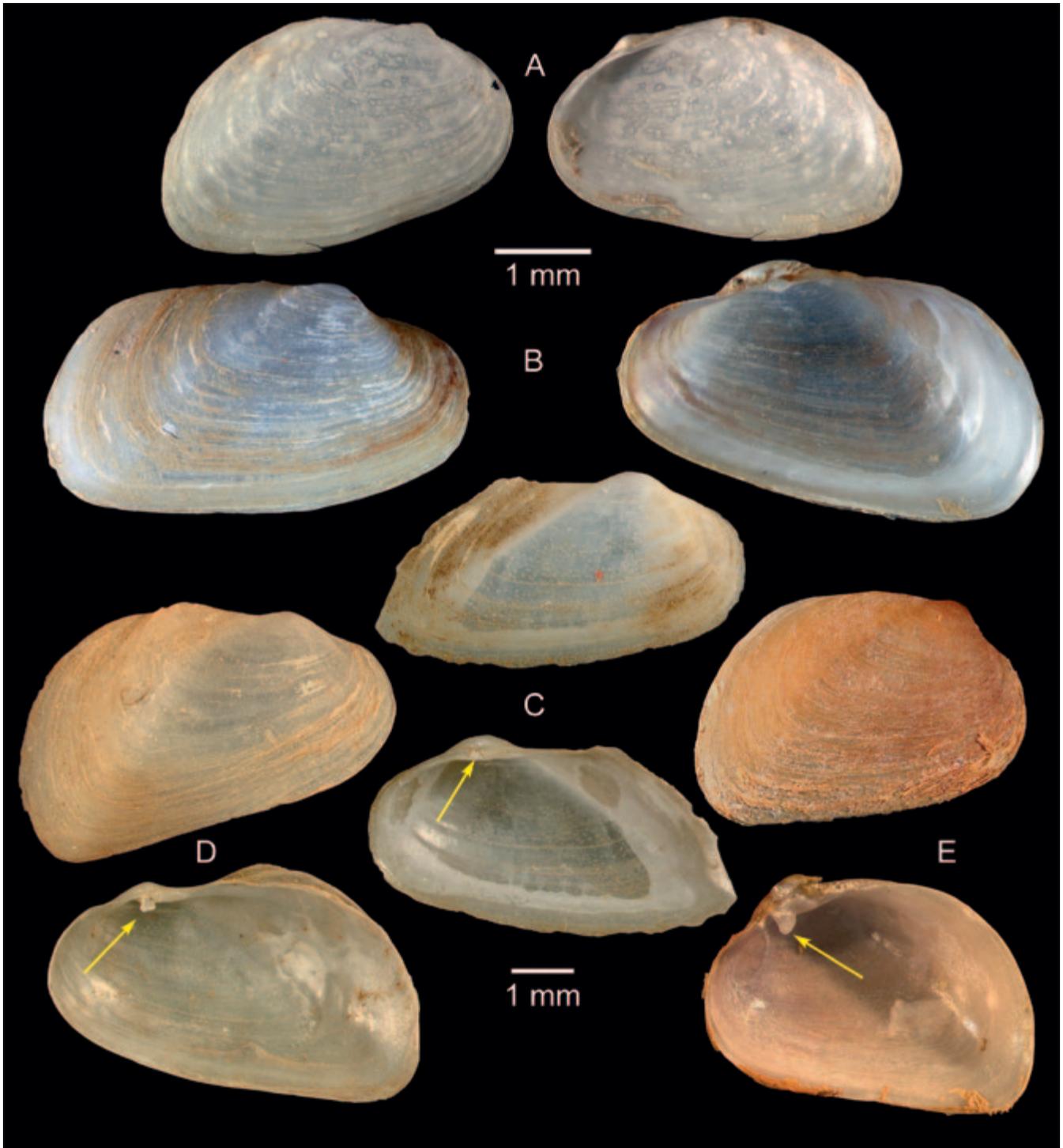
*Etymology* From the Latin *dolobrata* — to resemble an axe; referring to the shape of the shell.

*Comparisons* Shells of *Atopomya dolobrata* (Figs 1, 5A) and *Saxicavella jeffreysi* (Fig. 5B) are difficult to compare as the form of the latter can be rather variable and often distorted. In general the shell of *S. jeffreysi* is more elongate with the posterior and ventral margins rather straight and sub-parallel, whereas in *A. dolobrata* the dorsal anterior margin slopes steeply and at a distinct angle to the posterior dorsal margin. The nymph is poorly developed in *A. dolobrata*, but takes the form of a posteriorly directed flange in *S. jeffreysi*. Anatomically these species differ in the structure of the gills but also in the siphonal area where in *S. jeffreysi* the middle mantle fold bears distinct tentacles (Fig. 3B) it is only thickened and slightly wrinkled in *A. dolobrata* (Fig. 3A).

In the Atlantic the only other species referred to *Saxicavella* is *S. angulata* [= *S. carinata* of authors, not Brocchi 1814] but that species has cardinal teeth (Fig. 5C) and as noted above should be referred to the genus *Basterotia*. *Saxicavella jeffreysi* [as *S. plicatilis*] was recorded from Madeira by Watson (1897) but examination of this material



**Figure 4** Scanning electron micrographs of the ctenidium of *Atopomya dolobrata*: **A** part of ctenidium showing many lamellar filaments; **B** lateral view of a single filament, frontal surface (lower edge) with large inter-filamental junctions (*ifj*); **C** lateral view of the surface of the abfrontal [=bacteriocyte] zone showing poorly defined irregular outline of the bacteriocytes; **D** transverse section through a number of filaments showing greatly extended abfrontal zone (*abz*) and narrow blood lacunae (*bl*), a ciliated frontal surface (*fs*) narrow frontal zone and a short intermediate zone (*iz*) with large blood lacunae (*bl*); **E & G** surface view of bacteriocyte zone showing exposed and crowded bacteria; **F & H** bacteriocytes (*bct*) in transverse section lining the abfrontal surfaces and a narrow blood lacuna, bacteria rod-shaped and 0.8 to 1 µm in length.



**Figure 5** Shells of Saxicavellinae and *Basterotia*: **A** *Atopomya dolobrata*, paratype, Wyville-Thomson Ridge; **B** *Saxicavella jeffreysi*, English Channel, NMW.Z. Killeen coll.; **C** "*Saxicavella*" *angulata*, Madeira, NMW 1955.158; **D** *Saxicavella jeffreysi* sensu Watson, Madeira, NMW 1955.158; **E** *Basterotia borbonica*, Rodrigues, Indian Ocean, NMW.Z.2000.86., latter three having a cardinal tooth [arrowed].

[NMW. 1955.158.15147] reveals that it represents another, probably undescribed, species of *Basterotia* (Fig. 5D). Such erroneous identifications may account for the imprecise definitions of the hinge structure of *Saxicavella*.

A western Atlantic species *Saxicavella sagrinata* Dall & Simpson 1901 was described from Puerto Rico at a depth of 55 m. This is a very rare species, described from a single right valve (United States National Museum, USNM 160063) and

differs in form in being proportionately more expanded posteriorly and lacking a distinct keel. The surface is finely granular and there is a small cardinal tooth, both characters suggesting that this is more akin to *Basterotia* than *Saxicavella*, a suggestion also made by Dall & Simpson (1901). The only other record of this species is a single eroded valve taken from off the Atlantic coast of Florida at a depth of 53 m and is illustrated on the Jaxshells website (<http://www.jaxshells.org/saxicavella.htm>). This scanning electron micrograph confirms the lack a distinct keel and a granular outer surface.

Huber (2010) states that there are only five species of *Saxicavella* known but does not list them. Assuming that one of these was *S. angulata* then only four are known; they are *S. jeffreysi*, *S. pacifica* Dall 1916, *S. sagrinata* and *S. nybakkeni* Scott 1994 (Scott, 1994). The eastern Pacific species are illustrated and described by Coan, Scott & Bernard (2000) where, on outline, *S. nybakkeni* is likened to *S. sagrinata* and *S. pacifica* to *S. jeffreysi*.

#### GILL MORPHOLOGY AND BACTERIAL SYMBIOSIS

From the scanning electron microscope images it can be seen that the filaments are laminar, some 75–100 µm deep, and 10–12 µm wide (Fig. 4A–B). Approximately 90% of the filament is made up of the extended abfrontal zone (Fig. 4D, **abz**). The remaining portion consists of an intermediate zone where strong inter-filament junctions (Fig. 4B, **ifj**) separate the abfrontal zone from the frontal zone. Immediately behind the frontal ciliated surface Fig. 4D, **fs**) are large lacunae (Fig. 4D, **bl**); in the abfrontal zone these lacunae are very narrow (Fig. 4D, **F, bl**). Bacteriocyte cells (Fig. 4F, **bct**) line both faces of the abfrontal zone [= bacteriocyte zone] and these are packed with small rod-shaped bacteria approximately 1 µm in length (Fig. 4H). The bacteria are extra-cellular and can be seen in surface view (Fig. 4E, **G**) as there is no glycocalyx. The surface of the bacteriocyte zone Figs 4C, **E**) is irregularly ridged and pitted and does not show the typical polygonal structures seen in other taxa with similar modified gills.

The structure observed here is most similar to that seen in the Type 3 filaments of the Thyasiridae (Dufour, 2005) and to that described for the galeommatid *Syssitomya* (Oliver, Southward

& Dando, 2013). Although this paper cannot conclusively demonstrate chemoautotrophy in the symbionts the morphological characters of the gill strongly suggest that the relationship is chemosymbiotic.

Both specimens come from bathyal depths in regions (Porcupine Bight and Wyville-Thomson Ridge) where active seeps or vents have not been discovered (Van Reusel *et al.*, 2009). The Porcupine Bight station is on the sponge ground where there is a diverse fauna (Bett & Rice, 1992) and where chemosymbiotic taxa are represented only by the Thyasiridae. As with the Thyasiridae *Atopomya* may be exploiting sulphides in reduced sediments but unlike thyasirids the pedal anatomy suggests that the sulphide mining behaviour seen in thyasirids (Dando & Southward 1986; Dufour & Felbeck, 2003) is not possible. However, if *Atopomya* is associated with deep burrowing invertebrates as suggested for *Saxicavella* then it could be living deep within the reduced sediment layer where the bacteria would have ready access to sulphides.

Bacterial symbiosis is recognised here in the Basterotiidae and adds to the growing list of bivalves exhibiting this relationship and having highly modified gill morphology to accommodate the bacteria. This brings the total to eight families (Solemyidae, Nucinelidae, Mytilidae, Lucinidae, Montacutidae, Basterotiidae, Thyasiridae Vesicomidae) and suggests that the evolution of this symbiosis may be more widespread. Oliver, Southward & Dando (2013) postulated that galeommatids living in crevices and burrows may encounter conditions suitable for chemosymbiosis; this discovery here supports such a hypothesis and suggests that a closer examination of commensal galeommatids may uncover a greater diversity of bacterial symbiosis.

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