WORTH A SECOND LOOK: GILL STRUCTURE IN *HEMIPECTEN FORBESIANUS* (ADAMS & REEVE, 1849) AND TAXONOMIC IMPLICATIONS FOR THE PECTINIDAE

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ABSTRACT

The gill of the reef-dwelling *Hemipecten forbesianus* was examined using histology and scanning electron microscopy, in order to verify its reported homorhabdic state, and to provide the first detailed information on tropical pectinid gill structure. Due to the difficulty of obtaining live individuals, museum reference specimens were used for this study. The gill is heterorhabdic, and presents several notable differences compared to the larger, temperate species studied to date: (1) the small number of ordinary filaments per plica (probably associated with the very small size of these specimens), (2) the outer demibranch is approximately 15% shorter than the inner demibranch, (3) several characteristics which confer gill cohesion in other pectinid gills are absent and (4) the principal filaments are devoid of mucocytes, such that particle transport of positively-selected particles must be entirely effected in water. The apparent universality of the heterorhabdic condition within the Pectinidae leads us to recommend its use as a reliable soft-body taxonomic character at the family level. The anatomical differences between the gill of *H. forbesianus* and that of the larger, temperate species call for further comparison with both large and small, temperate and tropical species, in order to elucidate the effects of size and habitat on gill structure in this family.

INTRODUCTION

Autobranch bivalve gills may be divided into two broad categories, according to filament type: the homorhabdic gill, in which all filaments are tubular in structure (ordinary filaments, OF), and the heterorhabdic gill, in which a variable number of ordinary filaments alternates with larger filaments which are U-shaped in transverse section for most of their length (principal filaments, PF; Fig. 1). In those families that show the heterorhabdic condition, it is usually associated with the presence of well-developed, tissular interlamellar junctions (ILJ) which form the basis of the PF, and always with some degree of plication (Ridewood, 1903). In general, then, PFs may be viewed as gill filaments whose form has been modified and size increased, concomitant with ILJ development. Recent observations on the ontogeny of the heterorhabdic oyster gill lend support to this interpretation (Cannuel & Beninger, 2006).

The family Pectinidae displays an interesting departure from this rule. Inter-lamellar junctions are limited to the PFs of these species, and within the PFs, the junctions are minor, for two reasons: (1) the ascending lamella is much shorter than the descending lamella, such that much of the abfrontal surface of the descending lamella is not joined to anything, and (2) the inter-lamellar junction between descending and ascending lamellae only occupies a fraction of the total possible surface available for junction (approx. 50% in *Placopecten magellanicus*; Beninger *et al.*, 1988). It may thus be hypothesized that heterorhabdy in this family developed independently of the ILJ.

In some families, such as the Ostreidae and Pectinidae, PFs have assumed an important particle-processing function, allowing bi-directional particle transport on the gill, and hence qualitative selection (Beninger *et al.*, 1992; Ward *et al.*, 1993,

1994, 1998; Beninger, Decottignies & Rincé, 2004), setting these gills apart from both the flat homorhabdic and the plicate eulamellibranch type. This functional distinction has been used to classify bivalve gills into four major types (Dufour & Beninger, 2001): the homorhabdic filibranchs and the eulamellibranchs, incapable of bi-directional transport, and the heterorhabdic filibranchs and pseudolamellibranchs, capable of bi-directional transport.

While it is clear that the homorhabdic/heterorhabdic distinction is not always a reliable taxonomic character at the family level (Ridewood, 1903), some families display a great degree of uniformity with respect to this character: all known members of the Spondylidae, Limidae, Pteriidae, Pinnidae, Solenidae and Ostreidae, for example, are heterorhabdic (Ridewood, 1903; Atkins, 1936, 1937). Such a homogeneous soft-tissue morphological character, which is stable at the family level, is an important and welcome taxonomic feature in the Bivalvia. In this respect, the case of the Pectinidae is of special significance: the key morphological character of the ctenolium is a shell feature which may be reduced or absent in the adult state (Waller, 1991, 2006a), whereas the heterorhabdic condition of the gill is achieved at a size of 3–5 mm (Beninger, Dwiono & Le Pennec, 1994; Veniot, Bricelj & Beninger, 2003), and is thus always present in the adult. The combination of shell (including ctenolium, when present) and gill characters in the adult, along with the presence of characters not found in the sister group Spondylidae (notably the lack of guard tentacles on the mantle curtains; Waller, 2006a) should thus allow ready recognition of members of the Pectinidae. The Pectinidae are also intriguing from the heterorhabdic viewpoint, since their limited ILJs suggest that PFs are derived in a manner independent of ILJ development, and thus may be much more stable at the family level.

In light of the foregoing, reports of homorhabdy in two putative species of Pectinidae deserved detailed investigation: *Bathypecten vulcani* (Le Pennec *et al.*, 1988b), and *Hemipecten*
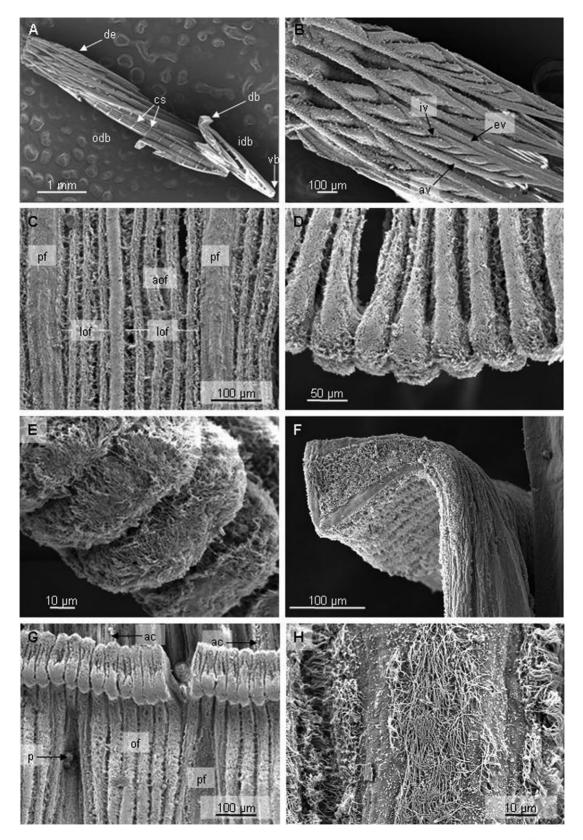
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Figure 1. *Hemipecten forbesianus*. Scanning electron micrographs of gill filaments. **A.** Abfronto-lateral view of a demibranch. **B.** Abfrontal view of inner demibranch. **C.** Frontal view of gill filaments. **D.** Frontal view of the ventral bend. **E.** Ventro-frontal view of the ventral bend. **F.** Lateral view of the dorsal bend. **G.** Frontal view of the dorsal bend. **H.** Frontal view of a principal filament. Abbreviations: ac, abfrontal cilia; aof, apical ordinary filament; av, afferent vessel; cs, ciliated spur; db, dorsal bend; de, dorsal expansion; ev, efferent vessel; idb, inner demibranch; iv, interconnecting vessel; lof, lateral ordinary filament; odb, outer demibranch; vb, ventral bend; p, particle; pf, principal filament.

forbesianus (Yonge, 1981). The problem of *B. vulcani* was resolved after studies based on spermatozoan ultrastructure and 18S rRNA showed that it was not a pectinid, but rather a propeamussiid (Le Pennec *et al*., 2002; Dufour, Steiner & Beninger, 2006), a family distinct from the Pectinidae (Waller, 2006b). *Hemipecten forbesianus* therefore remains the only reported exception to heterorhabdy in the Pectinidae. Its unsubstantiated identification as 'homorhabdic' was mentioned in the briefest possible manner (Yonge, 1981), and although a byssal notch was shown, no ctenolium was reported. Given the confusing combination of characters, this species could belong to at least three closely related families: Pectinidae, Spondylidae and Propeamussiidae.

In view of the taxonomic confusion that *H. forbesianus* engenders, not only with respect to its own classification, but also with respect to the generality of heterorhabdy as a valid soft-tissue taxonomic character in the Pectinidae, a new examination of the gill of this species was deemed necessary. Furthermore, such an investigation would be the first in a tropical reef species, providing a potentially interesting comparison with the temperate species studied to date (Beninger *et al*., 1988; Le Pennec, Beninger & Herry, 1988a).

MATERIAL AND METHODS

Collection and dissection

Due to its cryptic mode of life (Yonge, 1981), it is extremely difficult to collect new specimens of *Hemipecten forbesianus* without disaggregating large pieces of coral reef, a practice now illegal in Australia. We therefore used reference specimens of *H. forbesianus* collected by Yonge (1981) and stored in 70% ethanol (a sub-optimal fixation medium for histology and electron microscopy) at the Western Australian Museum, Perth, Australia. The three largest individuals (36, 32 and 13 mm antero-posterior shell axis) were used.

In July 2004, gill fragments (approx. 1–2 mm wide) of these three individuals were removed, placed in 70% ethanol and transported to the Marine Biology laboratory at the University of Nantes. Here they were re-cut longitudinally to provide one series for histology and mucocyte histochemistry, and one series for scanning electron microscopy (SEM).

Histology, mucocyte histochemistry and scanning electron microscopy

In July 2004, the gill fragments for histology and mucocyte histochemistry were processed as described in Beninger *et al*. (2003), with sections cut at 5 μm for topological histology, and at 10 μm for mucocyte histochemistry [the increased thickness was necessary to distinguish periodic-acid (PAS) – positive mucocytes from background]. Optimal staining times for topological histology were: trioxyhematein 1 min, acid fuschin 30 s and fast green 10 s. Optimal PAS staining times for mucocyte histochemistry were: alcian blue, pH 2.5, 5 min, Schiff reagent 15 min. Gill fragments for SEM were processed as in Cannuel & Beninger (2006), and observed using a JEOL JSM 6400F SEM.

RESULTS

The salient features of the *Hemipecten forbesianus* gill are summarized and compared to those of the larger, cold-water species *Placopecten magellanicus* in Table 1. It should be noted that a well-defined ctenolium was present in all three of the specimens examined.

General organization

The heterorhabdic nature of the gills was evident in the intact reference specimens with a dissecting microscope, and unambiguously demonstrated in the histological sections and SEMs (Figs 1C, G, 2A, D). For each demibranch, the dorso-ventral length of the ascending lamella was only about 1/3 that of that of the descending lamella (Fig. 1A). The outer demibranch was approximately 15% shorter than the inner demibranch (Fig. 1A). Abfrontal dorsal expansions (DE) occupy approximately the dorsal 25% of the principal filaments (Figs 1A, B, 2A, D). Several characteristics which confer gill cohesion in other pectinid gills were absent in *H. forbesianus*. In contrast to the tissue fusion reported at both the proximal and distal gill

Table 1. Comparison of anatomical characteristics in *Placopecten magellanicus* and *Hemipecten forbesianus*.

Anatomic characteristic	*Placopecten magellanicus*	*Hemipecten forbesianus*	References
Heterorhabdic gill type	+	+	Beninger *et al*. (1988), present study
Ciliated spurs	+	+	Beninger *et al*. (1988), Morse *et al*. (1982), Reed-Miller & Greenberg (1982), present study
Dorsal expansions	+	+	Beninger *et al*. (1988), present study
Ascending filaments shorter than descending	+	+	Beninger *et al*. (1988), present study
PF interlamellar fusion in VB	+	+	Beninger *et al*. (1988), present study
OF interfilamentar or interlamellar fusion in VB	+	+	Beninger *et al*. (1988), present study
Demibranchs equal length	+	−	Beninger *et al*. (1988), present study
MM on PF frontal surface	+	−	Beninger *et al*. (1993), present study
J-cilia	+	−	Beninger *et al*. (1988), present study
LF cilia	+	/	Beninger *et al*. (1988), present study
PF abfrontal ciliation	+	+	Beninger *et al*. (1988), Dufour & Beninger (2001), present study
OF abfrontal ciliation	−	−	Beninger *et al*. (1988), Dufour & Beninger (2001), present study
Ventral groove	−	−	Beninger *et al*. (1988), present study

Abbreviations: FS, frontal surface; LF, latero-frontal; MM, mixed mucopolysaccharide-containing mucocytes; PF, principal filament; OF, ordinary filament; /, not observed.
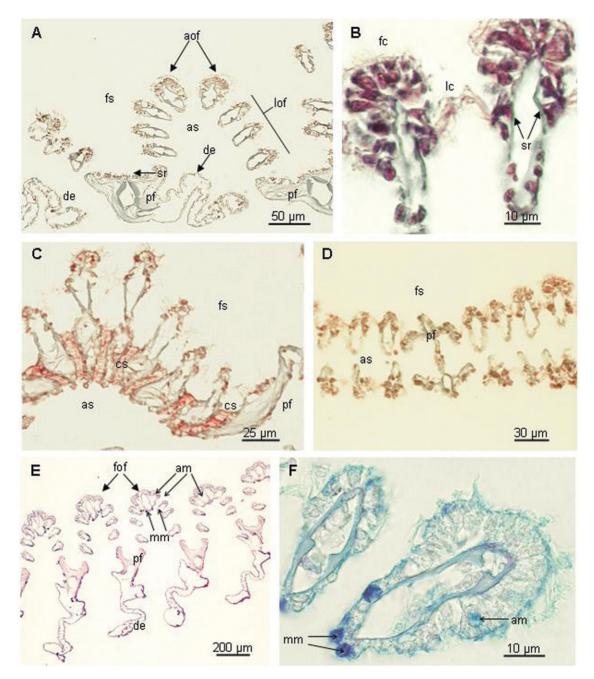
Figure 2. *Hemipecten forbesianus*. Tranverse sections of gills stained with modified Masson's trichrome (**A–D**) or Alcian blue – PAS (**E–F**). **A.** Dorsal expansions of principal filaments. **B.** Detail of ordinary filaments.. **C.** Ciliated spur. **D.** Interlamellar junction. **E.** Dorsal expansions of principal filaments. **F.** Detail of ordinary filaments. Abbreviations: am, acid mucopolysaccharide-containing mucocyte; aof, apical ordinary filament; as, abfrontal surface; cs, ciliated spur; de, dorsal expansion; fc, frontal cilia; fof, fused ordinary filaments; fs, frontal surface; lc, lateral cilia; lof, lateral ordinary filament; mm, mixed mucopolysaccharide-containing mucocyte; pf, principal filament. sr, supporting rod.

extremities in *P. magellanicus*, only the proximal extremity (gill arch) showed such fusion in *H. forbesianus*, and the dorsal bend filaments were therefore easily detached from one another with no tearing (Fig. 1G). In contrast to the situation in other scallop species (Morse *et al.*, 1982; Reed-Miller & Greenberg, 1982), no interlocking J-cilia were observed in *H. forbesianus*, either at the ciliated spurs or at the dorsal and ventral bends; the gill filaments could thus be easily detached from each other and from the mantle. These absent characters probably account for the extreme lack of gill cohesion in fixed specimens of *H. forbesianus*.

Although there is a slight antero-posterior depression at the ventral bend in *H. forbesianus*, formed by the alignment of slight indentations of adjacent filaments (Fig. 1D, E), it is definitely not pronounced enough to constitute a ventral particle groove. The number of ordinary filaments per plica is small: five to nine.

Ciliation

The abfrontal ciliation of the *H. forbesianus* gill was similar to that described for *P. magellanicus* (Beninger & Dufour, 2000),

with sparse ciliation on the DR, relatively abundant ciliation between the DR and the ILJs (Fig. 1G), and almost no abfrontal cilia on the ordinary filaments (OF; Fig. 2A, B, F). Frontal and lateral cilia were readily visible on the OF (Fig. 1A, B); however, no latero-frontal cilia could be distinguished either on the histological sections or on the SEMs. These are confined to a single row of simple cilia in the other pectinids studied (see Beninger *et al.*, 1988), so it is possible that they were simply not detected in the material observed here.

The principal filaments displayed three parallel, dorsoventrally extending rows of simple cilia (Fig. 1F): one in the trough, and one on each lateral wall.

Mucocytes

Frontal surface mucocytes were only found on the OFs, and of these, all of the mucocytes were acid mucopolysaccharide-secreting and concentrated on the three apical OFs. In contrast, on the abfrontal gill surface, only mixed mucopolysaccharide-containing mucocytes were found, on both ordinary and principal filaments (Fig. 2E, F). Although counts were not performed, an increasing number of abfrontal mucocytes was found dorsally in histological sections.

DISCUSSION

Gill type and taxonomic implications

The presence of a well-defined ctenolium in the three specimens examined confirms that this species is indeed a member of the Pectinidae (Waller, 1984, 2006a, b). The irrefutably heterorhabdic nature of the *Hemipecten forbesianus* gill leaves no known exception to the rule of heterorhabdy within the living Pectinidae. We suggest that it therefore may be used as an inclusive, soft-body taxonomic character for this family.

Although principal filament (PF) ontogeny has only been documented in one heterorhabdic species to date, the oyster *Crassostrea gigas* (Cannuel & Beninger, 2006), some interesting comparisons may be made with the PFs of the Pectinidae. In *C. gigas*, as in the plicate eulamellibranchs, the descending and ascending demibranch lamellae are of equivalent length, such that the development of relatively tight interlamellar junctions naturally create plicae along the entire dorso-ventral length of the demibranch. In the Pectinidae, however, the minor interlamellar junctions cannot perform this function; rather, plication is maintained over most of the gill via the opposing spring-like action of the ciliated spurs (Morse, Robinson & Wehling, 1982; Beninger *et al.*, 1988; present study). The PF mechanism maintaining gill plication is thus different in the Pectinidae as compared to the Ostreidae and the heterorhabdic eulamellibranchs. More fundamentally, heterorhabdy within the Pectinidae is therefore a functional condition independent of interlamellar junctions, underscoring the pertinence of its use as a soft-body taxonomic character within this family.

Comparison with other pectinid gills

The difference in axis – ventral bend lengths of the inner and outer demibranchs has not been reported in any other pectinid (although few have been rigorously studied). Such a disposition conforms to a general pattern in the Bivalvia: when a demibranch axis – ventral bend length difference is observed, the outer demibranch is always the shortest (Atkins, 1937). This rule may be related to gill development: in all cases documented to date, the inner demibranch develops first (Beninger *et al.*, 1994; Veniot *et al.*, 2003; Cannuel & Beninger, 2006).

The relatively small number of OF per plica in *H. forbesianus* (five to nine) may be compared to approximately 12 in the small *Aequipecten irradians* (Reed-Miller & Greenberg, 1982), and 11–19 in the large *Placopecten magellanicus*. The relation between small body size and small number of filaments per plica is confirmed from developmental studies on large pectinid species (Beninger *et al.*, 1994; Veniot *et al.*, 2003), and indeed holds true for oysters as well (Cannuel & Beninger, 2006). The lack of characters conferring filamentar cohesion may also be related to the small number of filaments, and ultimately the small body size, in *H. forbesianus*.

The ciliation of the *H. forbesianus* gill conforms to that observed in other pectinid species (Beninger *et al.*, 1988; Dufour & Beninger, 2001; Veniot *et al.*, 2003), with the possible exception of the reduced, single row of latero-frontal cilia, which, if present, was not distinguishable from the frontal cilia. The abfrontal ciliation conforms to the evolutionary interpretation previously advanced for functionally heterorhabdic gills in general, and pectinids in particular (Beninger & Dufour, 2000).

The types and distribution of mucocytes on the *H. forbesianus* gill show similarities, and also notable differences, compared to the pattern observed in *P. magellanicus*. In both species, a highly-viscous, acid mucopolysaccharide – dominant mucus is found on the ordinary filaments and, in *P. magellanicus*, this is associated with an exposed transport surface, and counter-current particle transport for rejection (no observations have been made on live *H. forbesianus*). Similarly, the concentration of mucocytes on the apical filaments of the plicae conforms to that observed in both *P. magellanicus* (Beninger *et al.*, 1993) and in the heterorhabdic gill of the oyster *C. gigas* (Beninger, Cannuel & Jaunet, 2005). Taken together, these observations suggest that in heterorhabdic species, the apical filaments are the principal OF processing sites.

In contrast to *P. magellanicus* (Beninger *et al.*, 1992, 1993), the *H. forbesianus* PF contains no mucocytes, so that particles initially accepted at the gill must be transported entirely in water. Given the small size of the animal and its gills, as well as the tropical reef environment, it is likely that the majority of potential food particles are nanoplankton-sized, in which case their transport will be governed by very small Reynolds numbers, obviating the need for even minimal mucus to reinforce the viscosity of the transport medium.

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