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New observations of the gills of *Placopecten magellanicus* (Mollusca: Bivalvia), and implications for nutrition

II. Internal anatomy and microanatomy

M. Le Pennec, P. G. Beninger* and A. Herry

Laboratoire de Zoologie, Université de Bretagne Occidentale; F-29287 Brest Cedex, France

Abstract

The internal anatomy and microanatomy of the gill of *Placopecten magellanicus* Gmelin collected in May and November 1985 from Chamcook Bay, New Brunswick, Canada, was studied using thin-section light microscopy and transmission electron microscopy. Most of the spurs show no evidence of organic union, and hence do not participate in vascular exchange. However, the dorsal bend shows both ciliary and organic interfilamentar union. The internal structure and the hemocytes of the dorsal respiratory expansion are presented. The epithelium consists of three distinct cell types, bounded by apical microvilli. All regions of the gill contain an epithelial basal membrane, which is greatly convoluted in the interconnecting vessels of the dorsal respiratory expansion. The significance of these observations is discussed in relation to possible roles in respiration, transmembrane transport and nutrition. The apical surface of all ciliated cells is covered with an acellular matrix composed of clear spherical vesicles, which may serve a mechanical function for which mucus would be unsuited. The significance of the abundance of mucocytes on the abfrontal surface of the principal filaments is discussed in terms of the escape response of pectinid bivalves.

Introduction

Although good descriptions of the basic anatomy of bivalve gills were presented in the late nineteenth and early twentieth centuries (Janssens 1893, Ridewood 1903, Setna 1930, Atkins 1936, 1937a, b, c, 1938a, b, c, 1943), these accounts were limited by the absence of photomicrography, modern histological techniques, and electron microscopy. The work of Nelson (1960) followed in the tradition of the earlier authors, presenting artistic interpretations of microscopic observations, with no supporting photomicrography. Several important electron microscopic studies have been performed, but these are either restricted to a specific region of the gill (Baur et al. 1976, Reed-Miller and Greenberg 1982), or they lack detailed cytological observations (Morse et al. 1982).

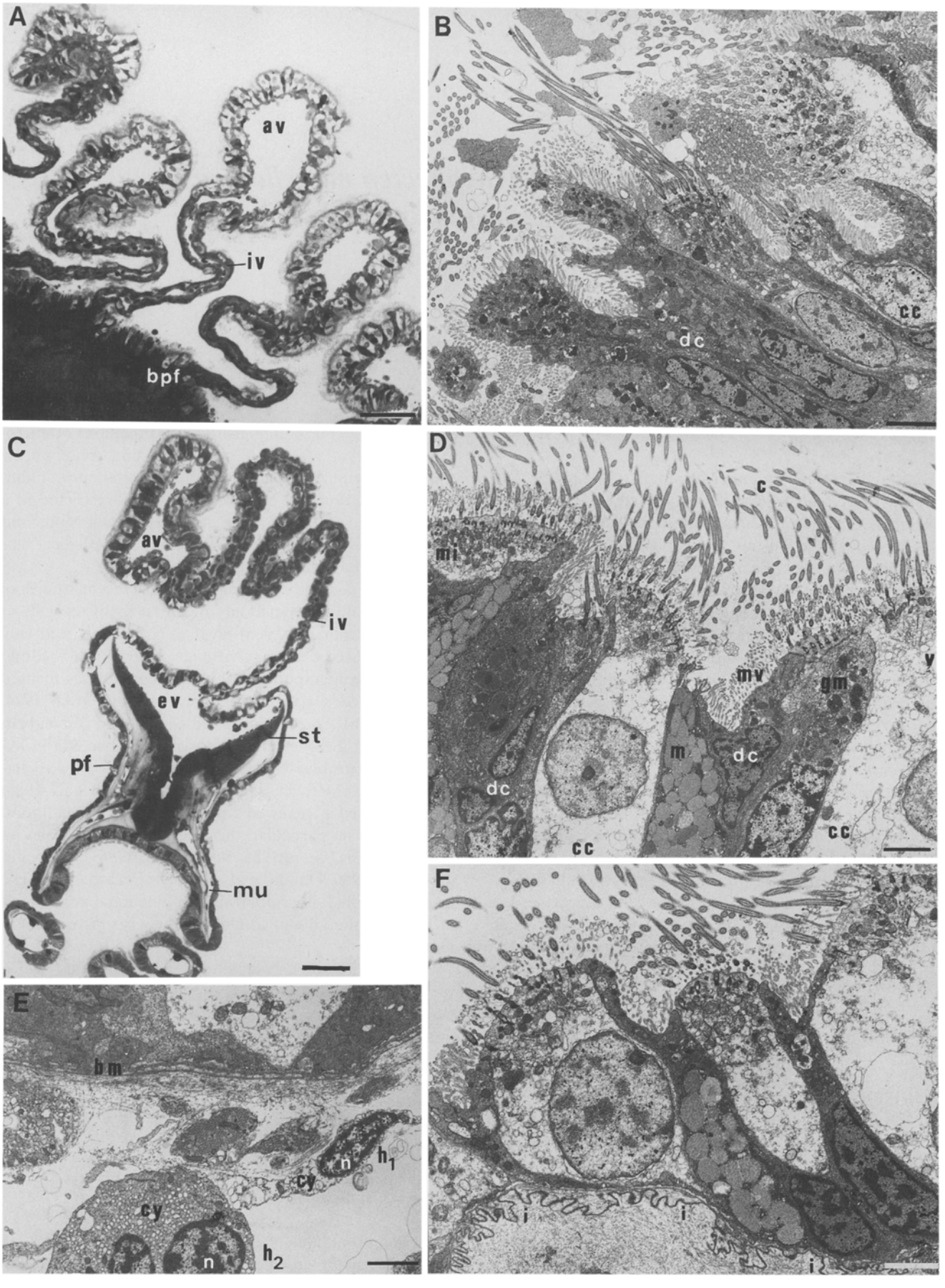
With the notable exception of several recent studies of the macro- and microanatomy of all levels of the gills of deep-sea hydrothermal vent bivalves (Le Pennec and Hily 1984, Fiala-Médioni and Métivier 1986, Fiala-Médioni et al. 1986), contemporary published research has focused on the ciliated surfaces of the bivalve gill (Owen 1974, Owen and McCrae 1976, Reed-Miller and Greenberg 1982). Recent discoveries of endosymbiotic bacteria in hydrothermal vent bivalves (Le Pennec and Hily 1984, Fiala-Médioni and Métivier 1986, Fiala-Médioni et al. 1986) have prompted a renewed interest in the gills of littoral species, and in particular the alternate trophic roles of these structures (Giere 1985, Bouvy et al. 1986, Dando and Southward 1986, Dando et al. 1986, Southward 1986). The need for detailed descriptions of the functional anatomy of all levels of the gills of littoral bivalves is thus quite evident.

The present work completes a two-part study which examined in detail the macro- and micro-anatomy of all levels of the gill of a representative pectinid bivalve, the giant scallop *Placopecten magellanicus* Gmelin (Beninger et al. 1988). Apart from the fundamental importance of such work, recent interest in the aquaculture of scallops has created a practical need to understand the structure and function of this key organ.

Material and methods

The site and method of collection and fixation of scallop gills has been presented previously (Beninger et al. 1988). Glutaraldehyde-fixed gill segments were rinsed in cacody-

* Present address: Département de biologie, Faculté des sciences et de génie, Université de Moncton; Moncton, N.-B. Canada E1A 3E9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late buffer, post-fixed in osmium tetroxide, rinsed again, dehydrated in an ascending ethanol series, and embedded in Spurr resin. Semi-thin (1 μm) sections were stained with toluidine blue for light microscopy, and thin sections were stained with uranyl acetate and lead citrate for observation with a JEOL 100 CX transmission electron microscope.

Results

The anatomical terminology, macroscopic organization and surface microanatomy of the *Placopecten magellanicus* gill have been presented previously (Beninger et al. 1988).

Gill axis and dorsal respiratory expansion of the principal filament

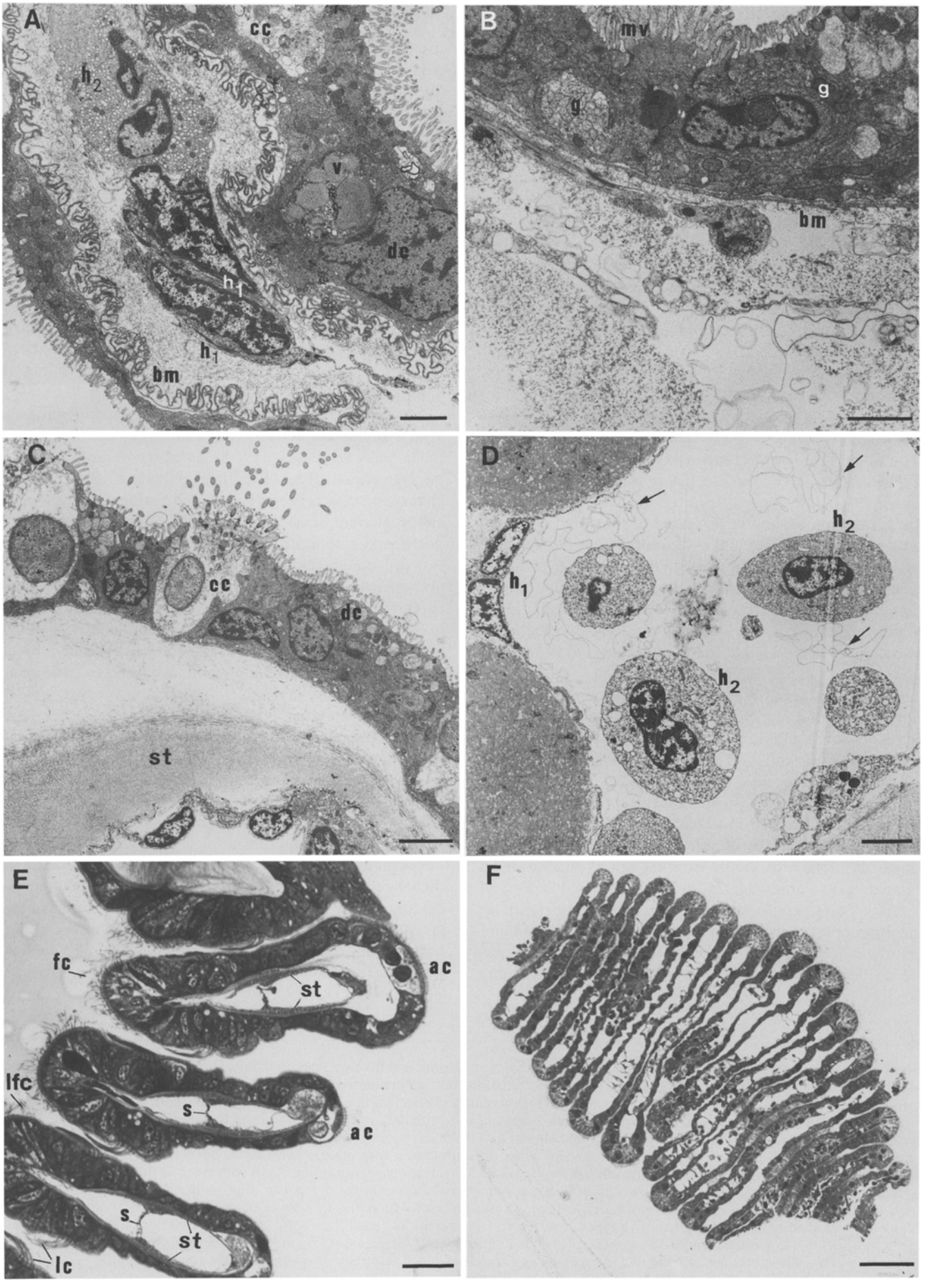
The afferent vessels of the respiratory expansions differentiate from the afferent branchial vessel while the principal filaments themselves are still rather undifferentiated buds arising from the fibrous tissue of the gill axis (Fig. 1 A). These buds are formed of two types of elongated cells: one present a clear nucleus and cytoplasm with an apical pole covered with microvilli and cilia, while the other possesses a dark nucleus and cytoplasm and an apical cellular membrane folded into numerous microvilli (Fig. 1 B). Upon leaving the gill axis the filaments are fully differentiated, consisting of the principal filament proper and of the dorsal respiratory expansion (Fig. 1 C).

The wall of the afferent vessel of the respiratory expansion consists of a single cell layer containing three different cell types (Fig. 1 D). The first type presents a clear nucleus and cytoplasm, and the apical pole is covered with microvilli and cilia. Few organelles are present in the cytoplasm of these cells, with the exception of mitochondria and numerous small (0.15 to 0.45 μm), spherical, clear vesicles. The vesicles are identical in appearance to those which are abundant at the external apical surface of all ciliated cells observed in the gill (Figs. 1 D, F and 3 A, C). Such vesicles are not present at the exterior or the interior of non-ciliated cells. The mitochondria are mainly concentrated at the shallow ciliary bases. The nucleus is usually round and centrally positioned, containing dispersed heterochromatin. The second cell type presents a dark nucleus and cytoplasm, with an apical cell membrane folded into numerous microvilli. The cytoplasm is filled with electron-dense material, and the mitochondria are dispersed throughout the cell. The elongate, multi-lobed nucleus is located at the medial or basal position and contains essentially peripheral heterochromatin (Fig. 1 D). Mucocytes constitute the third cell type, which tend to alternate between the two preceding cell types; their cytoplasm is entirely filled with secretory granules and the multi-lobed nucleus is located at the basal pole. All three cell types rest upon a thin (0.1 μm), regular basal membrane (Fig. 1 E). The vessel lumen contains hemocytes of various shapes and sizes, among which two types are distinguishable: circular cells with spherical nuclei and abundant cytoplasm, and smaller cells with elongated nuclei and reduced cytoplasm (Fig. 1 E).

As the afferent vessel gives rise to the interconnecting vessels of the respiratory expansion, the size of the epithelial cells decreases, and the basal membrane begins to be convoluted (Fig. 1 F). The epithelium of the interconnecting vessels is composed of the same three cell types as the afferent vessel. However, the cells containing dark nuclei and cytoplasm are more numerous than the other two cell types. The microvilli of these dark-staining cells are extensive and frequently ramified. Numerous mitochondria are distributed throughout the cytoplasm, which may contain large, clear vacuoles. The epithelial cells of the interconnecting vessels rest upon a greatly-folded basal membrane. Although the interconnecting vessels and their lumens are remarkably thin, the same hemocytes as described previously are observed (Fig. 2 A).

The epithelium widens to constitute the principal filament proper, which is composed of the same three cell types as previously described (Fig. 1 D). The lateral walls of the filament are dominated by the darker-colored cells, whose apical microvilli are frequently branched and dilated, and whose cytoplasm is filled with variable electron-dense granules (Fig. 2 B). Ciliated cells form a regular epithelial cell layer on the frontal surface of the filament, including both the walls and the trough of the gutter in relaxed filaments. The most distal extremities of the gutter wall contain cells with longer cilia (Fig. 1 C). All cells of this layer rest upon a smooth basal membrane.

Fig. 1. *Placopecten magellanicus.* (A) Thin-section light micrograph of principal filaments near gill axis. Dorsal view of transverse section. av: afferent vessel; iv: interconnecting vessel; bpf: bud of incompletely differentiated principal filament. Scale bar = 10 μm. (B) Transmission electron micrograph of the bud of an incompletely differentiated principal filament near gill axis. Note cilia arising from cells with clear nuclei and cytoplasm (cc), and extensive microvilli at apex of cells with dark nuclei and cytoplasm (dc). Scale bar = 1.5 μm. (C) Thin-section light micrograph of a differentiated principal filament and dorsal respiratory expansion. av: afferent vessel; ev: efferent vessel; iv: interconnecting vessel; pf: principal filament proper, st: supporting structures; mu: muscle fibres. Scale bar = 100 μm. (D) Transmission electron micrograph of the epithelium of the afferent vessel of the dorsal respiratory expansion. Cells with clear nuclei and cytoplasm (cc): c, cilia; mv, microvilli; mi, mitochondria at ciliary bases; v, numerous vacuoles in the cytoplasm. Cells with dark nuclei and cytoplasm (dc): mv, microvilli; gm, globules of electron-dense material in cytoplasm. Mucocytes (m). Scale bar = 1.5 μm. (E) Smooth basal membrane (bm) of afferent vessel. In lumen, two types of hemocyte are present, h_1: small hemocyte with elongated nucleus (n) and reduced cytoplasm (cy). h_2: large hemocyte with cytoplasm (cy) filled with vacuoles. Scale bar = 1.5 μm. (F) Beginning of indentation (i) of basal membrane at transition between afferent and interconnecting vessels of dorsal respiratory expansion. Scale bar = 1.5 μm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The inner walls of the intrafilamentar lumen contain supporting structures[1] (Fig. 2C). The lumen is divided into two cavities by a complete septum formed of thin muscular and connective fibres for most of its length; however, at the level of the interlamellar junction, the lumen is traversed by numerous septa. All of the intrafilamentar septa insert onto the collagenous supporting structures. Muscle fibres also run from the supporting structures to the lateral walls (anterior and posterior surfaces) of the principal filament (Fig. 1C). The circulating hemocytes are ovoid and contain many small vacuoles. Traces of degenerating hemocytes are frequently encountered (Fig. 2D).

Ordinary filament

The gross anatomy of the ordinary filament is similar to that found in other euleutherorhabdic gills. The typical frontal, latero-frontal and lateral ciliary tracts are present. The abfrontal ciliary tufts arise from single, clear apical cells (Fig. 2E). As in the principal filaments, the lateral walls of the lumen are strengthened by collagenous supporting structures, and a single complete muscular-connective septum divides the lumen into two dorso-ventrally oriented cavities for most of the length of the filament. At the ventral extremity of the filaments, however, the fusion of ascending and descending filaments via the intrafilamentar junction is accompanied by a multiplication of the intrafilamentar septa (Fig. 2F), and by the disappearance of the supporting structures.

The same three cell types previously described for the principal filament constitute the ordinary filament.

Abfrontal epithelium

The surface of the abfrontal epithelium is lined with simple and ramified microvilli. In the region of the ciliated apical cell, the microvilli are no longer visible, there being instead a dense covering of small (0.15 to 0.45 μm), usually spherical vesicles, which surround the bases of the abfrontal cilia. The epithelial cells, with the exception of the apical cell, are flattened, elongated, and contain numerous mitochondria. The basal membrane is not convoluted. The apical cell contains numerous spherical vesicles similar to, but generally larger (0.15 to 0.6 μm) than those found on the external surface of the cell membrane (Fig. 3A).

Lateral epithelium

The lateral epithelium is characterized by elongated cells containing very large nuclei oriented perpendicularly to the external surface. The apical poles of the epithelial cells present a dense covering of microvilli, some of which are also present between the lateral cilia. Once again, small spherical vesicles are observed at the external surface of the ciliated region only. The basal membrane appears regular, and the collagenous lining is readily visible in the dorsal regions of the filament (Fig. 3B).

Frontal epithelium

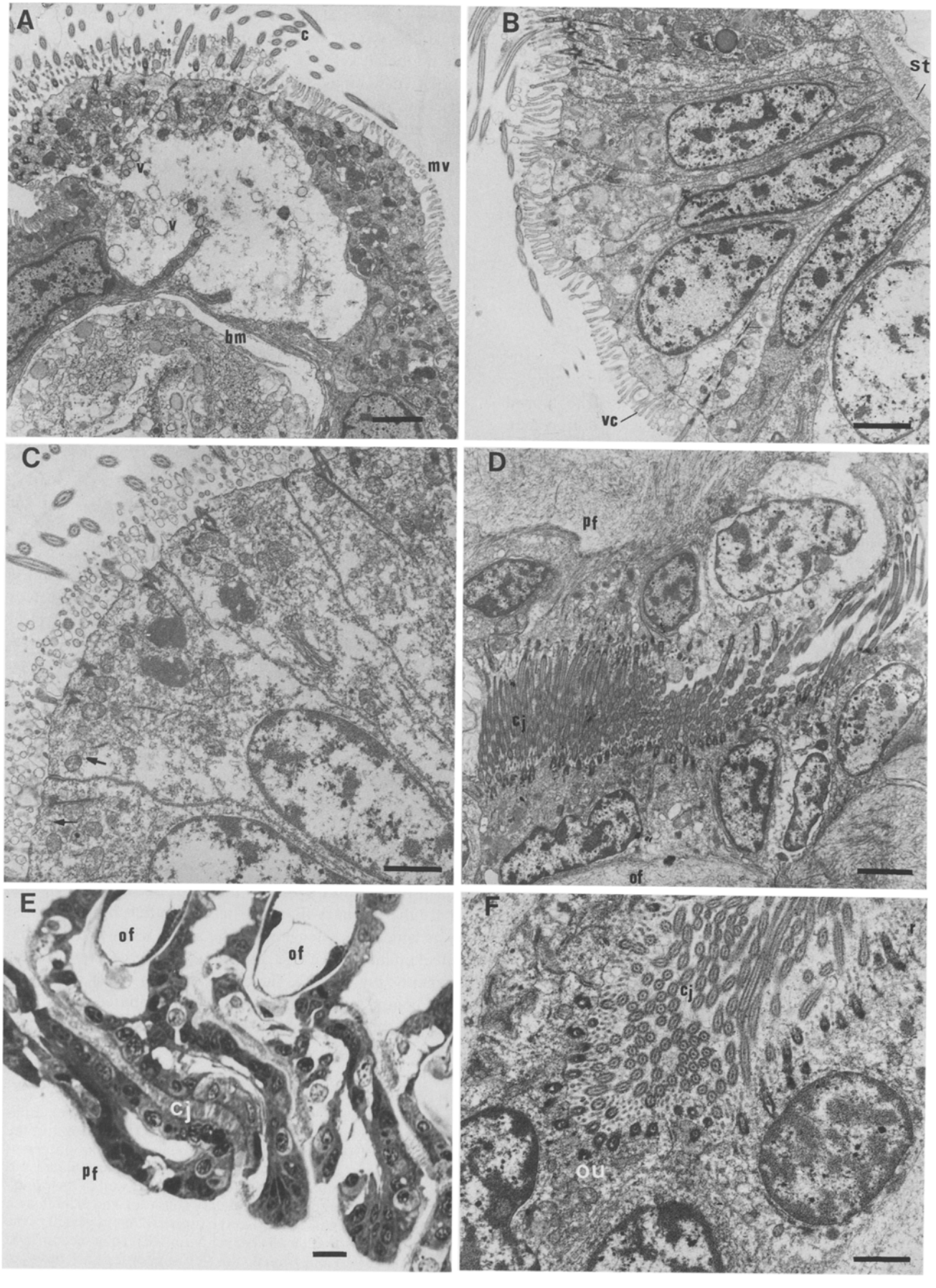
The cellular anatomy of the ciliated frontal epithelium is similar to that of the lateral epithelium, except that surface microvilli are absent. As observed in the abfrontal apical cell, the ciliated cells are clear, contain abundant mitochondria at the apical pole, and contain numerous small spherical vesicles (Fig. 3C). The external cell surface is covered with a dense layer of similar vesicles, which surround the bases of the cilia. The ciliary roots are extremely long, extending almost to the basal poles of the cells. The basal membrane is smooth.

Interfilamentar relationships

The principal and ordinary filaments are strongly linked, as are the ordinary filaments to each other, by the ciliated spurs which are extensions of the gutter walls of the principal filament and of the abfrontal surface of the ordinary filaments (Fig. 3D, E). The epithelial cells in this region are more compact than those of the frontal ciliated epithelium (Fig. 3E).

[1] Although numerous authors have designated such structures as 'chitinous' (Ridewood 1903, Setna 1930, Atkins 1936, 1938a, c, Nelson 1960, Ciocco 1985), they are in fact composed of a fibrous protein, rich in collagen (Brown 1952, Rudall 1955). Our own histochemical tests on the gills of *Placopecten magellanicus* have been negative for chitin and positive for collagen (unpublished data)

Fig. 2. *Placopecten magellanicus.* (A) Longitudinal section of the interconnecting vessels. Cells with dark nuclei and cytoplasm (dc), capable of containing large vacuoles (v). Cells with clear nuclei and cytoplasm (cc). Both types of hemocytes (h_1 and h_2) are present in the narrow lumen. Note the greatly-indented basal membrane (bm). Scale bar = 1.5 μm. (B) External wall of the principal filament proper, at the base of the gutter wall. The dark cells contain numerous granules (g) of variable electron density. The microvilli (mv) are dilated and branched. The basal membrane (bm) is smooth. Scale bar = 0.8 μm. (C) Low-power electron micrograph of the external wall of the principal filament proper, near the dorsal respiratory expansion. The epithelium is formed of clear cells (cc) and dark cells (dc), and is lined with collagenous supporting structures (st) facing the lumen. Scale bar = 1.5 μm. (D) Hemocytes (h_1 and h_2) in the lumen (efferent vessel) of the principal filament. Numerous membranes of degenerating hemocytes are present (arrows). Scale bar = 1.5 μm. (E) Thin section light micrograph of ordinary filaments. Abfrontal cilia (ac), lateral cilia (lc), latero-frontal (lfc) and frontal cilia (fc); supporting structures (st) and septum (s). Scale bar = 10 μm. (F) Thin section light micrograph of ventral bend. Note the numerous intralacunar septa. Scale bar = 30 μm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At the dorsal bend of the ascending filaments, interfilamentar cohesion is maintained via two mechanisms. In addition to the interlocking ciliary tufts previously reported, organic union is evident in the non-ciliated marginal zone (Fig. 3 F).

Discussion

To the best of our knowledge, actual photomicrographs of the internal anatomy of the dorsal respiratory expansion characteristic of pectinid gills have been lacking to date. Line drawings inspired by early microscopic study (Setna 1930, Atkins 1938 a, 1943) fail to depict the cytology of this structure, and indeed omit important aspects visible with modern microscopic techniques.

The current findings show that the dorsal respiratory expansion is a complex structure. Although it has been suggested that one function of this structure is that of a hemolymph reservoir when the entire gill contracts (Morse et al. 1982), the intricate anatomy of this region suggests other functions as well. The presence in the interconnecting vessels of a single thin epithelial cell layer, terminated at the apical pole by a dense system of microvilli, and at the basal pole by a highly indented basal membrane, together with abundant mitochondria at both poles, suggests that this region is specialized in the active transport of substances between the external medium and the hemolymph of the vessel lumen.

Although the basal membrane is regular in all other parts of the gill, microvilli appear to cover the entire surface of the gill, with the exception of the ciliated frontal epithelium and the small ciliary tufts on the abfrontal surface of the ordinary filaments. Such extensive microvilli are also present in photomicrographs of the gills of the bivalves *Chlamys varia, Nucula sulcata,* and *Ostrea edulis* presented by Owen (1974) and Owen and McCrae (1976). Baur et al. (1976) present similar microvilli for an undetermined oyster species. It is interesting to note that in the latter case, microvilli were also abundant at the apical surface of the ciliated cells. Observations by Southward (1986) and Knight (1984) confirm the presence of such microvilli in three other bivalve families. Southward (1986) suggests that these microvilli may be the sites of dissolved organic carbon uptake previously demonstrated in the gills of *Mytilus edulis* and *M. californianus* (Manahan et al. 1982, Wright et al. 1984, Wright 1987).

The fundamental difference between the aspect of the basal membrane of the microvilli-covered cells of the interconnecting vessels of the dorsal respiratory expansion and that of the basal membrane in all other parts of the gill suggests that transmembrane transport and/or diffusion is particularly active in this region. Likely candidates for such phenomena in this specialized structure would include dissolved gases.

The two types of hemocytes (h_1 and h_2) observed within the dorsal respiratory expansion and the filamentar lumen appear to belong to the general category of hyalinocytes (Cheng 1981). While the cells labelled h_1 conform to the prohemocyte I type for *Pecten maximus,* it is not possible to establish a clear parallel between the cells labelled h_2 and the hemocytes I or II (*P. maximus* and *Chlamys varia*) or III (*C. varia*) described by Auffret (1985). Moreover, as the roles of such cells are still largely unknown, further studies are necessary before any functional significance may be attributed to their presence in these regions.

Recent studies of hydrothermal vent bivalves have led to the discovery of chemoautotrophic symbiotic bacteria upon and within the gill tissues which may contribute significantly to the carbon and energy requirements of these animals (Le Pennec and Hily 1984, Le Pennec and Prieur 1984, Fiala-Médioni and Métivier 1986, Fiala-Médioni et al. 1986). Such observations have prompted similar studies on littoral species, and endosymbiotic associations have indeed been found in bivalves living in a variety of high-sulfur or reducing habitats (Berg and Alatalo 1984, Fisher and Hand 1984, Dando et al. 1985, Giere 1985, Schweimanns and Felbeck 1985, Dando et al. 1986, Spiro et al. 1986). The very recent discovery of such associations in a littoral bivalve from an oxygen-rich habitat (Bouvy et al. 1986) appears to confirm the widespread nature of this phenomenon. However, no such endosymbiotic bacteria were observed in any region of the gills of *Placopecten magellanicus* in the present study; the lack of lysozyme activity in the gill tissue of *Chlamys opercularis* (McHenery et al. 1979) suggests that such bacterial gill symbionts are also absent in other Pectinidae. Furthermore, no endosymbiotic gill bacteria have been observed in *Mytilus edulis* (Manahan et al. 1982), *Arctica islandica, Dosinia lupinus* (Spiro et al. 1986), and several species of the Thyrasiridae and Ungulinidae families (Dando and Southward 1986, Southward 1986).

Morphological adaptations characteristic of littoral bivalves harbouring bacterial gill symbionts include thick gills and reduced labial palps and alimentary tract (South-

Fig. 3. *Placopecten magellanicus.* (A) Abfrontal cell of an ordinary filament. Cilia (c), microvilli (mv), variously-sized vacuoles (v). The basal membrane (bm) is smooth. Scale bar = 1.5 μm; (B) Lateral cells of an ordinary filament. Note apical microvilli (vc) and smooth basal membrane bounded by collagenous supporting structure (st). Scale bar = 1.5 μm; (C) Frontal cells of an ordinary filament. The cytoplasm contains numerous small vesicles (arrows). Other clear vesicles are abundant between the cilia. Scale bar = 1.5 μm; (D) Ciliary junction (cj) between a principal filament (pf) and an ordinary filament (of). Note the thin opposing cell layers. Descending lamellar region. Scale bar = 10 μm; (E) Thin section light micrograph showing ciliary junctions (cj) between the spurs of adjacent principal (pf) and ordinary (of) filaments. Scale bar = 1.5 μm; (F) Dorsal bend of ascending filament. Note organic union (ou) in addition to ciliary junction (cj). Scale bar = 0.8 μm

ward 1986). In contrast, those bivalves devoid of bacterial gill symbionts and which have retained a feeding strategy based primarily on particle capture present thin gills and well-developed labial palps and gut, as is the case for *Placopecten magellanicus*.

The layer of small spherical vesicles observed at the external surface of all ciliated cells of *Placopecten magellanicus* is specifically reported in the present work. Its function at the base of the cilia is unknown, but it is noteworthy that mucus is absent in this region. These vesicles appear to be secreted by the ciliated apical cells, and may effect some mechanical function for which mucus would be unsuitable. These observations contrast with those of Baur et al. (1976), who found microvilli and not vesicles at the apical surface of the ciliated epithelium of an undetermined oyster species.

Of particular interest concerning gill arrangement and cohesion is the demonstration of organic union at the peripheral margins of the dorsal bend. This is at variance with the affirmation of Atkins (1938 c, 1943) that *Pecten* sp. presents ciliary union only in this region (*Placopecten magellanicus* was considered to be a *Pecten* sp. at that time). Similarly, Drew (1906) stated that the filamental spurs of the gill filaments are organically joined, and that an important vascular exchange occurs between these spurs. In fact, only the spurs immediately adjacent to the fused dorsal bend are organically joined (Morse et al. 1982). The observations of previous studies (Morse et al. 1982, Beninger et al. 1988), confirmed by the transmission electron microscopic observations of the present work, demonstrate that all other spur junctions are purely ciliary and participate in the maintenance of gill arrangement and cohesion only. Any vascular exchange which occurs between the spurs adjacent to the dorsal bend is thus merely a part of the general circulation previously described for the organically joined filaments in this region (Morse et al. 1982).

The relatively abundant mucocytes observed on the abfrontal surface of the principal filaments contrast with the scarcity of such cells on the abfrontal gill surfaces of *Ostrea edulis* (Nelson 1960). It has been suggested that in *Placopecten magellanicus* this mucus facilitates the dorso-ventral and antero-posterior contraction of the gill prior to the escape response, minimizing the risk of mechanical damage to the apposed descending and ascending filaments (Beninger et al. 1988). It is thus interesting to note the scarcity of such mucocytes on the abfrontal surfaces of the sessile bivalve *Ostrea edulis*.

The present study has shown that the gill of *Placopecten magellanicus* is a much more complex structure than was previously thought. Directions for future research include the roles of the microvilli in both the dorsal respiratory expansion and the rest of the gill, as well as the nature and function of the hemocytes and of the spherical vesicles observed at the bases of the ciliated cells.

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