

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

## I. General anatomy and surface microanatomy

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### Abstract

The organization, general anatomy, and surface microanatomy of all regions of the gills of a representative bivalve mollusc, *Placopecten magellanicus* Gmelin, were studied using stereo-microscopic, histological, and scanning electron microscopic techniques. Individuals were collected in May and November 1985 from Chamcook Bay, New Brunswick, Canada. In addition to correcting earlier accounts of this structure, a number of new observations are reported. The orientation of the ciliated spurs appears to be responsible for the sinusoidal arrangement of the gill filaments. Micrographs showing the structure of the dorsal respiratory expansion are presented. The entire abfrontal surface of the principal filament, including the dorsal respiratory expansion, is densely ciliated and mucosecretory. These characteristics may aid in the establishment of a respiratory current and in the prevention of gill damage during escape responses. All nonciliated regions of the gill filaments are covered with microvilli, thus greatly increasing the surface area of the gill. The feeding mechanism is discussed in relation to the dorsal and ventral ciliated tracts. Symbiotic ciliate protozoans are constantly dislodged from the gill filaments and transported via the ventral mucus string to the buccal region. The nutritional implications of these observations are discussed.

### Introduction

Present knowledge of bivalve gill structure relies heavily upon extensive studies performed in the late nineteenth and early twentieth centuries, when microscopic equipment and techniques were limited (Kellogg 1892, 1915, Janssens 1893, Ridewood 1903, Drew 1906, Setna 1930, Atkins 1936, 1937 a, b, c, 1938 a, b, c, 1943). Paradoxically, many recent studies of bivalve gill structure have focussed

on details of the ciliature (Moore 1971, Owen 1974, Owen and McRae 1976, Reed-Miller and Greenberg 1982, Fiala-Médioni and Métivier 1986), contributing to a good understanding of ciliary junctions and ciliary tracts and their importance in interfilamentar cohesion and nutrition of a few bivalve species, while descriptions of the macro- and micro-anatomy of the rest of the gill are singularly lacking. An attempt was made to present both levels of gill anatomy in *Ostrea edulis* (Nelson 1960), but once again attention was directed at the ciliary tracts, and no electron microscopic observations were reported. Such observations were later made, but only for a very limited part of the oyster gill (Baur et al. 1976).

Recently, two studies have been performed incorporating both macroscopic and electron microscopic observation of all parts of the gill of the deep-sea vent mytilid *Bathymodiolus* sp. (Le Pennec and Hily 1984, Fiala-Médioni et al. 1986). The discovery of endosymbiotic bacteria in the gills of hydrothermal vent bivalves has led to a renewed interest in the gills of littoral species, where alternate trophic roles have also been discovered (for review, see Southward 1986). It is thus clear that full and accurate descriptions of the functional anatomy of all levels of the gills of littoral bivalves should be established using modern microscopic techniques, as has recently been done for the boring eulamellibranch bivalve *Pholas dactylus* (Knight 1984, Knight and Knight 1986).

The purpose of the present study was to provide a detailed description of the organization, general anatomy, and surface micro-anatomy of the gill of the giant scallop *Placopecten magellanicus*. Preliminary observations revealed that fundamental aspects of both macroscopic and microscopic external organization were at variance with previous representations of this structure (Drew 1906). In addition, many features of bivalve gill structure which have only been represented artistically in the earlier studies may now be shown using scanning electron and light microscopy. An important forerunner of this work was the study by Morse et al. (1982).

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*Placopecten magellanicus* is an important commercial bivalve species on the east coast of Canada and the United States. Recent interest in the aquaculture of this species (Dupouy 1983) has generated a need to elucidate the structures and mechanisms involved in feeding. This is the first of two works which describe in detail all levels of organization of the gill of *P. magellanicus*, which it is hoped will be useful as a model and reference point for other fili-branch bivalves.

## Materials and methods

Adult individuals measuring 7 to 11 cm along the antero-posterior axis were collected by divers in May and November 1985, from Chamcook Bay (Bay of Fundy), New Brunswick, Canada. Live specimens were observed under dissecting microscopes. For histological and electron microscopical study, the gills were carefully removed and fixed with glutaraldehyde (final concentration of 3%) in a 0.4 M cacodylate buffer at pH 7.8. Specimens for histological examination were dehydrated in an ethanol-xylene series, embedded in paraffin, cut at 7.5  $\mu\text{m}$ , and stained using the Goldner variation of Masson's trichrome procedure (Gabe 1968). Specimens for scanning electron microscopic examination were dehydrated in a graded acetone series followed by CO<sub>2</sub>-mediated critical point drying. The dried specimens were then quickly mounted on supports and sputter-coated with gold. All specimens were observed with a JEOL JSM 35 scanning electron microscope.

## Results

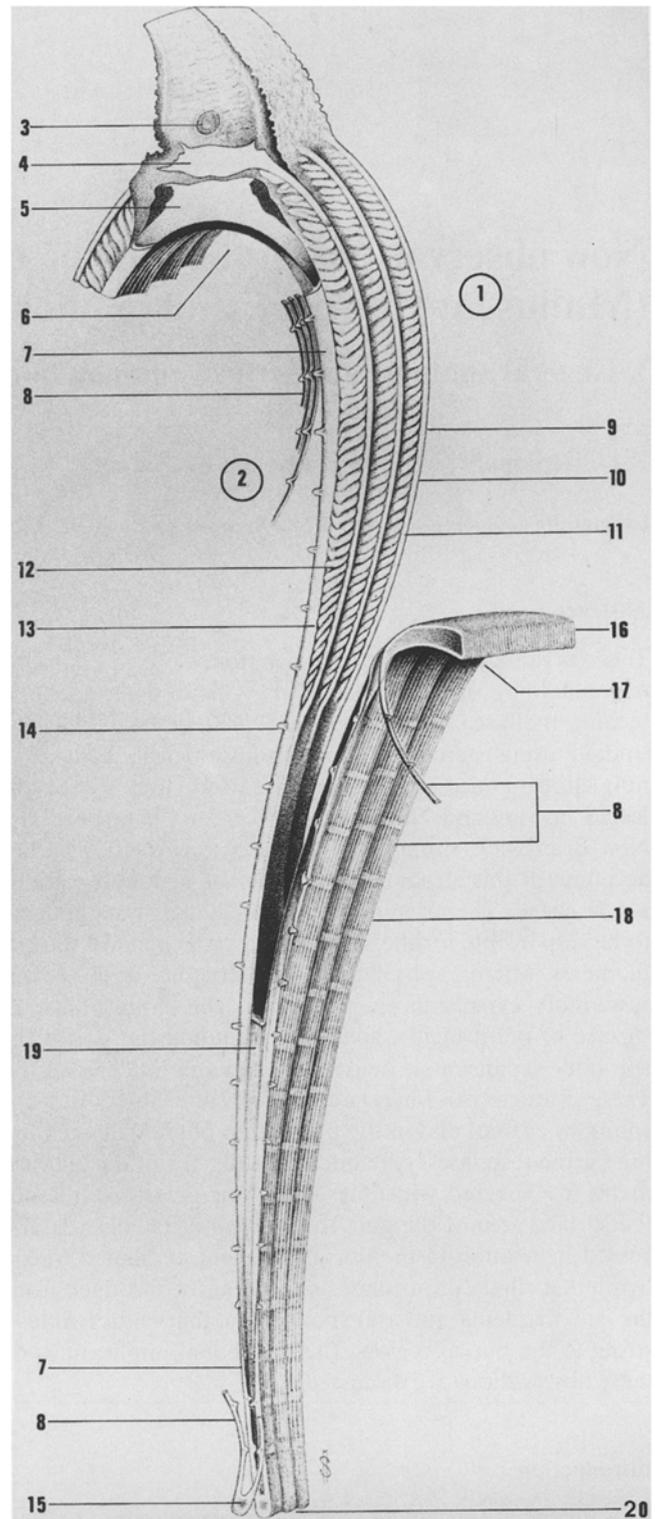
### Macroscopic organization of the gill

The nomenclature used to describe the gill anatomy of *Placopecten magellanicus* is that of Setna (1930), with additional terms developed by Atkins (1936, 1937 a, b, c, 1938 a, b, c, 1943), Owen (1974) and Owen and McCrae (1976). The general organization is that of an euleuthero-rhabdic plicate gill (i.e., consisting of well-differentiated principal and ordinary filaments suspended in a 'corrugated' manner from the gill axis).

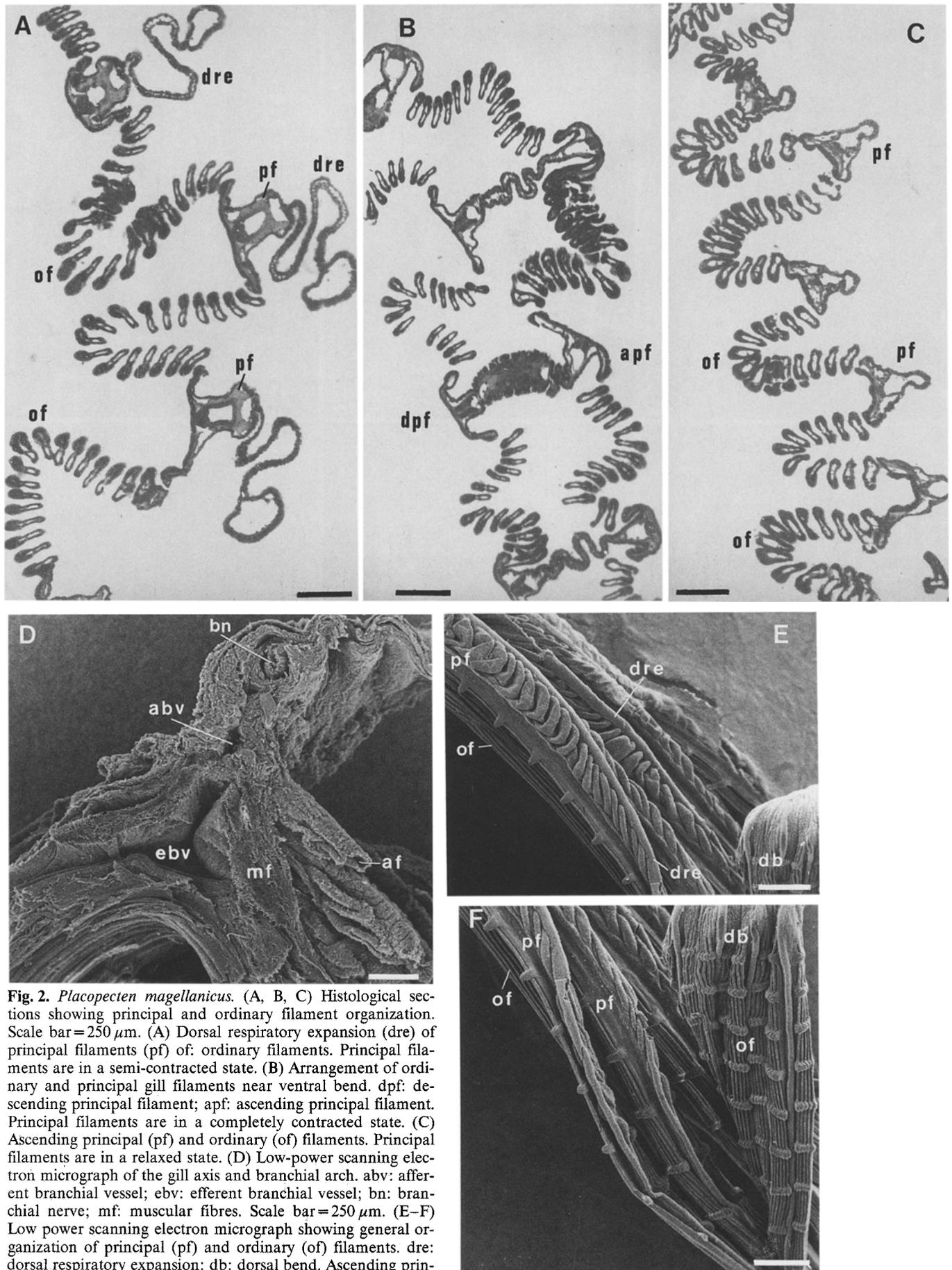
An artistic representation of the macroscopic organization of the gill has been constructed (Fig. 1). Each region is described in detail in the following sections.

### Gill axis and arch

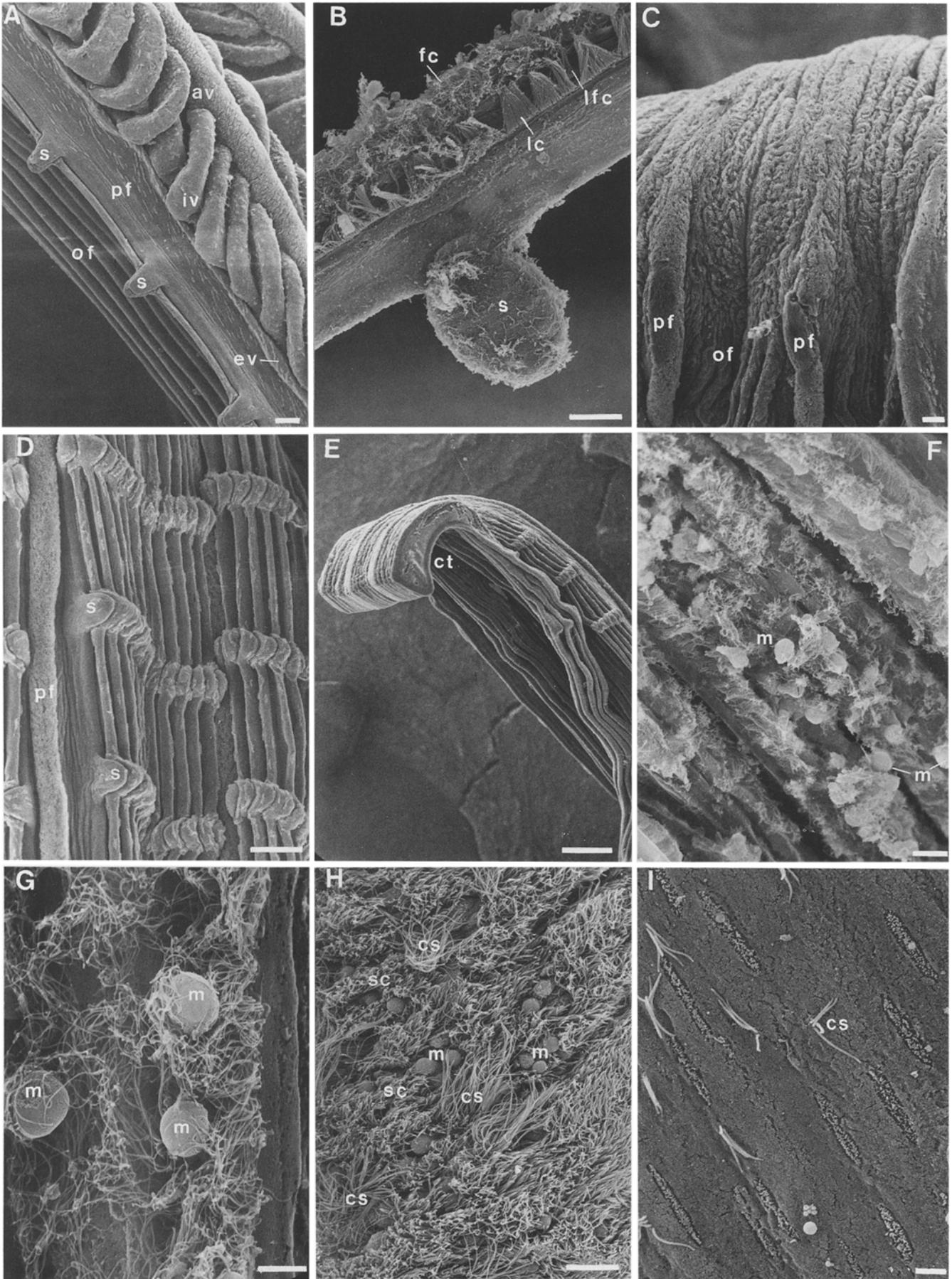
A thin membrane attaches the gill axis to the adductor muscle. The axis contains in a dorso-ventrally-aligned sequence, the principal branchial nerve, the afferent branchial vessel, and the large, triangularly-shaped efferent branchial vessel (Fig. 1); numerous muscle fibers surround these structures. The gill arch is composed of the fused proximal extremities of the gill filaments. The afferent



**Fig. 1.** *Placopecten magellanicus*. Macro-anatomy of principal filament. 1 – suprabranchial chamber, 2 – infrabranchial chamber, 3 – branchial nerve, 4 – afferent branchial vessel, 5 – efferent branchial vessel, 6 – gill arch, 7 – lateral wall of principal filament, 8 – ordinary filaments, 9 – descending branch of principal filament, 10 – dorsal respiratory expansion, 11 – afferent vessel, 12 – interconnecting vessel, 13 – efferent vessel in principal filament, 14 – ciliated spur, 15 – ciliated disc, 16 – dorsal bend, 17 – ciliated tract, 18 – ascending filaments, 19 – interlamellar junction, 20 – ventral bend. Ventral extremity is shown in a semi-contracted state



**Fig. 2.** *Placopecten magellanicus*. (A, B, C) Histological sections showing principal and ordinary filament organization. Scale bar=250  $\mu$ m. (A) Dorsal respiratory expansion (dre) of principal filaments (pf) of: ordinary filaments. Principal filaments are in a semi-contracted state. (B) Arrangement of ordinary and principal gill filaments near ventral bend. dpf: descending principal filament; apf: ascending principal filament. Principal filaments are in a completely contracted state. (C) Ascending principal (pf) and ordinary (of) filaments. Principal filaments are in a relaxed state. (D) Low-power scanning electron micrograph of the gill axis and branchial arch. abv: afferent branchial vessel; ebv: efferent branchial vessel; bn: branchial nerve; mf: muscular fibres. Scale bar=250  $\mu$ m. (E-F) Low power scanning electron micrograph showing general organization of principal (pf) and ordinary (of) filaments. dre: dorsal respiratory expansion; db: dorsal bend. Ascending principal filaments are in contracted state. Scale bar=500  $\mu$ m



vessels of the respiratory expansions of the principal filaments join with the afferent branchial vessel, while the efferent vessels of the respiratory expansions fuse with the efferent branchial vessel (Fig. 2D)<sup>1</sup>.

### Principal filament

The dorsal respiratory expansion is present on the proximal half of the descending principal filament, and comprises in an abfrontal-frontal sequence an afferent vessel, a parallel efferent vessel situated within the wall of the principal filament proper, and a large number of sequentially-arranged, variously-shaped interconnecting vessels (Figs. 1, 2E, F, and 3A). The ascending filament measures approximately one-half the length of the descending filament, and the distal extremities of the ascending filament bear no organic union to the mantle. A thin interlamellar junction joins the ventral third of the descending filament and the ventral half of the ascending filament. The ventral bend is very fine and somewhat elongated, terminating in a small, flat, club-shaped process (Fig. 1).

Ciliated tufts are located on well-defined spurs, which are extensions of the gutter walls, for most of the length of the filament, except for the dorsal bend of the ascending filament (Figs. 2F and 3C). The principal filament may assume two configurations, with various intermediate positions, depending on the state of relaxation or contraction. In living individuals such contractions occur locally and spontaneously in both antero-posterior and dorso-ventral directions along the gill; often only a part of the filament contracts in this manner. Relaxed portions show a typical gutter formation on the frontal surface, tapering to a point at the ventral bend. The ciliated spurs on each gutter wall are slightly folded away from the gutter at their distal extremities. In contracted portions, the sides of the gutter are drawn back, and the filament assumes a mushroom-like shape in cross-section. Fixed specimens may show either or both of these configurations, or some intermediary position. As a result, the orientation of the ciliated spurs in a

relaxed principal filament is toward the infrabranchial chamber, while in a contracted filament (or portion) the spurs are oriented toward the suprabranchial chamber. Principal filament sections in relaxed, contracted, and intermediate configurations are shown in Fig. 2 (A, B, C).

### Ordinary filaments

The ordinary filaments lack dorsal respiratory expansions, are much smaller in cross-section, and are much more numerous than the principal filaments. Ciliated tufts are borne on spurs similar to those of the principal filaments, situated on the abfrontal surface (Fig. 3B). No gutter is present, and the ordinary filaments thus retain a constant external morphology throughout their length, whether the gill is relaxed or contracted. No spurs are present on the dorsal bend of the ascending filament (Figs. 3C, E).

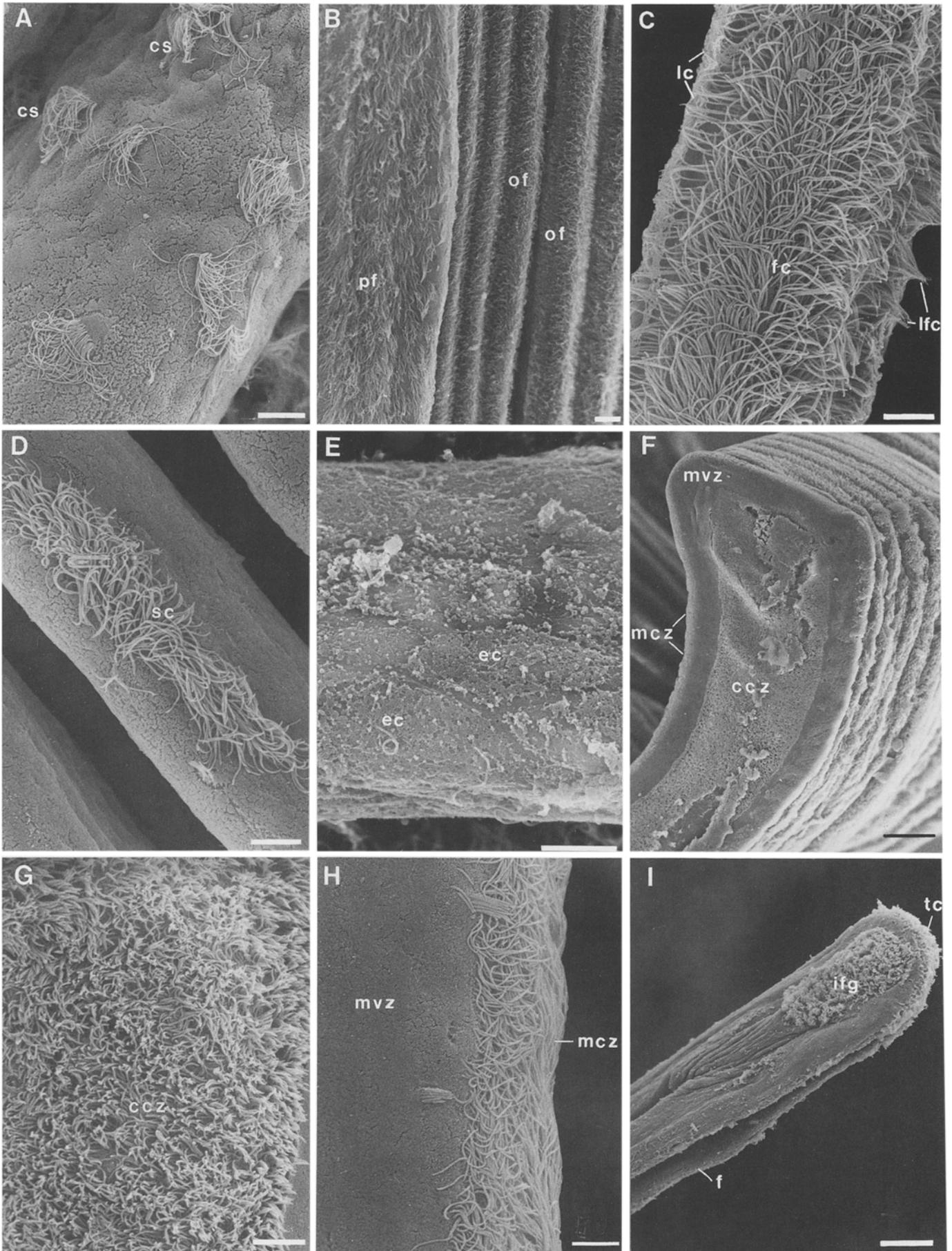
As observed in other euleutherorhabdic gills (Atkins 1943, Owen and McCrae 1976), a distinct cross-sectional gradation exists in the ordinary filaments: smaller filaments are located next to the principal filaments, while the largest filaments are located at the crests of the plicae (Fig. 2C).

### Arrangement of gill filaments

A variable number (11 to 19) of ordinary filaments occurs between principal filaments; the interfilamentar distance is approximately 5  $\mu\text{m}$  (Fig. 2A, B, C). Interfilamentar cohesion is maintained via adjacent ciliated spurs, both between principal and ordinary filaments and between ordinary filaments; the ciliated spurs thus form regular parallel antero-posteriorly directed bands, at approximately 250 to 500  $\mu\text{m}$  intervals dorso-ventrally (Figs. 2F and 3D). In relaxed portions of the gill, ordinary filaments are arranged to form distinct crests typical of the filibranch heterorhabdic gill, while the principal filaments show the 'gutter' configuration in the troughs. The lateral force resulting from the folding of the distal extremities of the spurs of adjacent principal filaments appears to be responsible for the maintenance of the plical form in relaxed portions of the gill. In contracted portions of the gill, the reverse configu-

<sup>1</sup> The terms efferent and afferent refer to the hemolymph circulation in relation to the gill, which has been described in the respiratory expansions of *Chlamys tehuelcha* (Ciocco 1985)

**Fig. 3.** *Placopecten magellanicus*. (A) Detail of dorsal respiratory expansion of principal filament. av: afferent vessel; ev: efferent vessel; iv: interconnecting vessels; pf: principal filament and s: ciliated spurs. Ordinary filaments (of) are visible beside the principal filament. Scale bar = 100  $\mu\text{m}$ . (B) Detail of an ordinary filament. s: ciliated spur; lc: lateral cilia; lfc: latero-frontal cilia; fc: frontal cilia. Scale bar = 250  $\mu\text{m}$ . (C) Abfrontal view of dorsal bend. The principal filaments (pf) are larger than the ordinary filaments (of). Note extensive ciliation of abfrontal surface of all filaments in this region. Scale bar = 100  $\mu\text{m}$ . (D) Abfrontal view of ascending filaments showing two principal filaments (pf) and their adjacent ordinary filaments joined by the ciliated spurs (s). The principal filament is in a contracted state. Note dense ciliation of principal filament only. Scale bar = 100  $\mu\text{m}$ . (E) Dorsal bend of ascending filaments, showing ciliated tract (ct). Scale bar = 250  $\mu\text{m}$ . (F) Gill arch, showing extensive ciliation of entire surface of the food tract. Mucus balls (m) are secreted by epithelium. Scale bar = 5  $\mu\text{m}$ . (G) Detail of frontal surface of an ordinary filament. Mucus balls (m) are numerous. Scale bar = 5  $\mu\text{m}$ . (H) Cilia of afferent vessel of dorsal respiratory expansion. sc: short cilia; cs: putative sensory cilia; m: mucus. Scale bar = 10  $\mu\text{m}$ . (I) External surface of lateral wall of the gutter of a principal filament. Cells are regularly aligned and terminate in microvilli. Putative sensory cilia (cs) are dispersed over surface. Scale bar = 3  $\mu\text{m}$



ration of the principal filament and its ciliated spurs greatly modifies the orientation of the ordinary filaments, and an irregular spatial arrangement of these filaments is observed between the contracted principal filaments (Figs. 2 A, B and 3 D).

The ordinary filaments alternate very slightly in length at the ventral bend, each 'shorter' filament having two adjacent 'longer' filaments. This slight difference in length (approximately 50  $\mu\text{m}$ ) gives the ventral extremity of the gill a ridged appearance. The terminal portion of the ventral bend carries a distinct concentration of terminal cilia (Fig. 4 I). At the dorsal bend, the alignment of the ordinary and principal gill filaments forms an anteroposteriorly oriented groove (Figs. 1 and 3 E).

### Microanatomy of the epithelial surface

#### *Gill axis and arch*

The epithelium of both the gill axis and arch is abundantly ciliated (Figs. 2 D and 3 F). The infrabranchial surface of the gill arch forms a groove in which numerous mucus balls may be observed (Fig. 3 F).

#### *Principal filament*

The epithelial surface of the afferent vessel of the dorsal respiratory expansion is densely covered with cilia measuring approximately 5  $\mu\text{m}$  in length (Fig. 3 H); this ciliation continues along the entire abfrontal surface of the principal filament (Fig. 3 C, D). Tufts of putative sensory cilia (approximately 10  $\mu\text{m}$  long) are irregularly distributed over the entire epithelial surface of the afferent vessel. Numerous mucus balls emerge among both types of cilia (Fig. 3 H). In contrast, the epithelial surface of the efferent vessel presents no short cilia and fewer tufts of long putative sensory cilia arranged in roughly parallel rows (Fig. 3 A and I). The interconnecting vessels are characterized by an irregular but smooth surface topography, upon which occasional tufts of long putative sensory cilia are observed (Fig. 4 A).

The epithelium of the anterior and posterior surfaces of the principal filament proper is completely covered with microvilli. Ciliary tufts are observed in a rather linear ar-

angement in the immediate vicinity of the efferent vessel of the dorsal respiratory expansion (Fig. 3 A, I). In relaxed portions of the filament, the external face of the spurs shows a similar ciliary pattern, while the internal spur surface is covered with long cilia interlocked with those of the spurs of the adjacent ordinary filament (Fig. 3 B, D). In contracted portions of the principal filament, the orientation of the spur (and hence the spur cilia) is reversed (Fig. 2 A, B).

The frontal surface of the principal filament is densely ciliated throughout its entire length, and may be situated in the gutter of relaxed portions of the filament, or completely exposed in contracted portions of the filament (Fig. 4 B).

#### *Ordinary filament*

The frontal surface of the ordinary filaments presents typical well-defined ciliary bands: frontal, latero-frontal, and lateral (Figs. 3 B and 4 C). In artificial seawater with no added particles, numerous mucus balls are secreted by the underlying epithelium (Fig. 3 G). In contrast, the abfrontal surface carries only widely-spaced, irregular clumps of cilia more similar to the frontal cilia ( $\cong 5 \mu\text{m}$  long), than to the longer putative sensory cilia (Fig. 4 B). The epithelium of the abfrontal surface terminates in microvilli (Fig. 4 E). The abfrontal surface presents this type of appearance for the entire length of the ordinary filament, with the exception of the abfrontal surface of the dorsal bend, which is abundantly ciliated (Figs. 3 C and 4 F), allowing the adhesion of the relaxed gill to the ciliated epithelium of the mantle. The antero-posteriorly flattened dorsal bend of both principal and ordinary filaments presents a large median ciliated zone (Fig. 4 F, G) on the flattened surfaces, surrounded by a marginal non-ciliated zone where the epithelial microvilli are again evident (Fig. 4 F, G, H). The cilia of adjacent antero-posterior surfaces are very firmly interlocked, thus maintaining interfilamentar cohesion and organization at this level of the gill. The abundantly ciliated frontal surfaces of ordinary and principal filaments form an anteroposteriorly oriented ciliated tract in this region.

The ventral bend of the ordinary and principal filaments presents circular interlocking ciliary discs on the antero-posterior faces, assuring interfilamentar cohesion and organization in this region (Fig. 4 I). The ventral-most extremity of the bend carries a dense ciliary tuft, which, to-

**Fig. 4.** *Placopecten magellanicus*. (A) Irregular surface of interconnecting vessels of dorsal respiratory expansion of a principal filament, covered with microvilli and dispersed tufts of putative sensory cilia (cs). Scale bar = 10  $\mu\text{m}$ . (B) Frontal cilia of ordinary filaments (of) and of a principal filament in contracted state (pf). Scale bar = 5  $\mu\text{m}$ . (C) Detail of frontal ciliation of an ordinary filament. Frontal cilia (fc), latero-frontal cilia (lfc), and lateral cilia (lc). Scale bar = 5  $\mu\text{m}$ . (D) Abfrontal surface of an ordinary filament showing dense covering of microvilli and long tufts of short cilia (sc). Scale bar = 5  $\mu\text{m}$ . (E) Columnar epithelial cells (ec) of the abfrontal surface of an ordinary filament. Scale bar = 5  $\mu\text{m}$ . (F) Free margin of dorsal bend of a principal filament, showing a central ciliated zone (ccz) surrounded by a non-ciliated zone showing a dense covering of microvilli (mvz), and a marginal ciliated zone (mcz). Scale bar = 50  $\mu\text{m}$ . (G) Detail of marginal ciliated zone (mcz) of the same filament. mvz: microvillous zone. Scale bar = 5  $\mu\text{m}$ . (I) Interfilamentar junction (ifj) at ventral bend of an ordinary filament. Another ordinary filament (f) is attached behind. Note ciliated disc of interfilamentar junction, terminal cilia (tc) at ventral extremity, and absence of a food groove. Scale bar = 50  $\mu\text{m}$

gether with the tufts of adjacent filaments, forms an antero-posterior ciliated tract (Fig. 4I).

## Discussion

The new observations of the present study establish several fundamental corrections concerning the structure and function of the gill of *Placopecten magellanicus* as presented by Drew (1906). The interlamellar junction is much less extensive, and the number of interfilamentar junctions (ciliated spurs) is considerably smaller than was reported by Drew (1906); in addition, there is no evidence of organic union between most of these interfilamentar junctions, as Morse et al. (1982) correctly observed, and the 'ostia', or interfilamentar spaces, are in fact quite large. Consequently, the gill of *P. magellanicus* cannot be said to constitute a series of water tubes, as in the Mytilidae and the Ostreidae. Drew (1906) also failed to report the existence of the dorsal respiratory expansion (which he mistook for the interlamellar junction).

Although it has never been the object of detailed anatomical study, a dorsal respiratory expansion on the principal filament has been reported in all Pectinidae previously examined (Setna 1930, Atkins 1943, Owen and McCrae 1976, Ciocco 1985), including *Placopecten magellanicus* (Morse et al. 1982). The present work clearly describes the external anatomy of this structure in *P. magellanicus*. Our scanning electron microscopic observations reveal that the surface of the afferent vessel is densely covered with cilia, as is the entire abfrontal surface of the principal filament. These cilia may serve to create a current allowing rapid gas exchange in the deoxygenated hemolymph which arrives in the gill at this level. The greatly-folded interconnecting vessels also provide an increased surface area, presumably primarily for gas exchange. The extensive ciliation of the abfrontal surface of the principal filament is also of interest in an evolutionary sense. Reduction and loss of abfrontal cilia is considered to have taken place as the bivalve gill evolved toward the filibranch and eulamellibranch forms (Morton 1979, Barnes 1987). The few tufts of apparently non-sensory abfrontal cilia of the ordinary filaments are thus probably vestigial, while the abfrontal cilia appear to have been retained on the principal filaments. This retention may be an indication of the evolutionary importance of the respiratory function of the principal filament in the Pectinidae.

Previous accounts of the gill structure of *Placopecten magellanicus* have not considered the temporal conformational variability of the principal filament (Drew 1906, Morse et al. 1982), although this phenomenon has been reported in *Pecten maximus* (Setna 1930), in *Chlamys varia* (Owen and McCrae 1976) and in *Lima hians* (Owen 1978). The mechanism effecting the contractions of the anterior and posterior surfaces of the principal filaments has been described for a number of Pectinids (Setna 1930, Atkins 1938a); their accounts of the muscular-connective fibres in the principal filaments conform to our own histo-

logical observations in *P. magellanicus*. The present study thus provides a representation of the dynamic anatomy of the principal filament, and its effect on the arrangement of adjacent ordinary filaments in *P. magellanicus*.

The ciliature of the frontal surface of the filaments is identical to that reported for other Pectinidae, as well as for many other bivalves (for review, see Jørgensen 1966). The description of the mechanism of feeding and of ciliary currents in *Chlamys varia* (Owen and McCrae 1976) is in agreement with the stereoscopic observations of living, non-narcotized specimens in the present study, confirming the basic mechanism of particle removal in Pectinids by means of dorsally-directed water currents created by the frontal cilia of the relaxed principal filaments, as opposed to particle capture by direct ciliary action. This mode of operation has been proposed for the Anomiidae, Pectinidae, Limidae, and Pinnidae under normal particle concentrations (Owen 1978). The infrabranchial surface of the gill arch is thus the principal site of particle collection under such conditions. Since direct ciliary action does not intervene at the level of the gill filaments, it may be expected that particle sorting by the gills on the basis of size is also absent. This may explain at least in part the presence of very large (up to 950  $\mu\text{m}$ ) particles in the stomach contents of *Patinopecten yessoensis* (Mikulich and Tsikhon-Lukanina 1981); particles up to 350  $\mu\text{m}$  have been found in *Placopecten magellanicus* (Shumway et al. 1988).

The absence of a particle groove along the ventral bend probably represents an evolutionary loss, as the members of most other bivalve families do possess such particle grooves (with the exception of some members of the Arciidae, the Anomiidae, and Limidae; Atkins 1936, 1937b, 1943).

Under high particle concentrations the principal filament assumes the contracted configuration, changing the plical shape and breaking down the dorsally-directed water current in *Chlamys varia*. Direct ciliary action, mucus secretion and entrapment then come into play, resulting in the formation of an anteriorly-directed, particle-containing mucus string along the ciliary tracts of the ventral bend; this mucus string usually detaches and falls into the mantle cavity as a result of gill movements (Owen and McCrae 1976). Similar observations have been made for *Placopecten magellanicus* (Kellogg 1915). It is thus evident that the presence of pseudofeces does not necessarily indicate rejection from the labial palps, as has been recently suggested (Shumway et al. 1985).

In the present study, the formation of a ventral mucus string was also observed under low particle concentrations (artificial seawater, no added particles). Microscopic examination revealed numerous ciliate protozoans among the gill filaments. The presence of large numbers of attached ciliate protozoans of the genus *Trichodina* has previously been reported in bivalve gills (Uzman and Stickney 1954, Fenchel 1965, Hausman 1978), including those of Pectinids (Ciocco 1985). Although the exact trophic relationship is still unclear, observations of living gills show that these organisms may be dislodged, transported in ciliary currents,

and entangled in the ventral mucus string (Ciocco 1985, present study). This string has been observed to enter the buccal region of *Placopecten magellanicus* (present study) and it may be that such ciliates are ingested, constituting a source of non-algal food.

The abundant mucus which is secreted by the ciliated abfrontal surface of the principal filaments may serve an important function related to the unique life habit of the Pectinidae. Both Drew (1906) and Setna (1930) state that there is a simultaneous dorso-ventral and antero-posterior contraction of the Pectinid gill immediately prior to the rapid swimming movements of the escape response. It is possible that the mucus secreted by this region acts as a lubricant, allowing such rapid movement of the apposed ciliated lamellae to take place while maintaining the integrity of the complex gill structure and arrangement. In addition, the spontaneous contraction-relaxation of the principal filaments and the subsequent rearrangement of the ordinary filaments observed in the present study and by Owen and McCrae (1976) may be facilitated by the presence of mucus in this region.

The classical view of the bivalve gill is that of an organ which performs two functions: respiration (gas exchange across the gill surface) and, with the exception of the Protobranchia, suspension feeding (Jørgensen 1966). Recently a direct trophic function has been attributed to the gills of a number of bivalves from a variety of littoral and deep-sea habitats. This trophic role may be mediated by either direct uptake of dissolved or particulate organic matter (Henry et al. 1981, Manahan et al. 1982, Wright et al. 1984) or by symbiotic relationships with chemoautotrophic bacteria (Felbeck et al. 1981, Henry et al. 1981, Fisher and Hand 1984, Le Pennec and Hily 1984, Dando et al. 1985, Schweimanns and Felbeck 1985, Fiala-Médioni and Métivier 1986, Fiala-Médioni et al. 1986, Spiro et al. 1986). The abfrontal and antero-posterior surfaces of the *Placopecten magellanicus* gill filaments are almost completely covered with microvilli. Previous work by Baur et al. (1976) and observations by Knight (1984) and Southward (1986) confirm the existence of such microvilli in four other bivalve families. It is possible that these structures are related to an alternate direct trophic function of the gills; this aspect will be expanded upon in the companion contribution (Le Pennec et al. 1988).

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