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P. G. Beninger · S. D. St-Jean · Y. Poussart

Labial palps of the blue mussel *Mytilus edulis* (Bivalvia: Mytilidae)

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Abstract As a basis for understanding the functions of labial palps in the blue mussel *Mytilus edulis*, the structure and histology of palps were studied using light and scanning electron microscopy. Mussels used in the present study were collected in August 1993 and April 1994. The palp ridged surface is characterized by the presence of a smooth but densely ciliated dorsal fold, upon which rests the corresponding demibranch ventral region. The underside of the dorsal fold and the palp ridges fuse to form vestigial ciliated tracts. The dorsal fold is capable of contraction, allowing it to cover variable amounts of the ridged surface. Two different types of mucocyte are present on the palp ridged surface: subepithelial, glandular, acid-dominant secretion mucocytes and epithelial mucocytes characterized by neutral secretions. In histological section, these mucocytes appear to be concentrated on anatomical features known to intervene in particle handling. The anatomical and histological features of the smooth surface are typical of bivalve labial palps, except that the dense ciliation of the dorsal fold begins in the dorsal region of the smooth surface, indicating the possible origin of this feature. Previous studies on *M. edulis* point to the palps as the probable site for both ingestion volume control and particle selection; the anatomical basis of the present study should facilitate further research on these aspects.

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P.G. Beninger (✉) · S.D. St-Jean[1] · Y. Poussart
Département de Biologie, Faculté des Sciences,
Université de Moncton, Moncton, N.B., E1A 3E9 Canada

Present address:
[1] Gulf Fisheries Centre, P.O. Box 5030 LCD1 Moncton,
N.B., E1C 9B6 Canada

Introduction

Recent progress in understanding bivalve feeding mechanisms has originated from an improved knowledge of the structure of the organs involved (Beninger et al. 1988; Le Pennec et al. 1988; Beninger et al. 1990a, b; Beninger et al. 1992, 1993; Tankersley and Dimock 1992, 1993). The feeding process has been elucidated at the level of the gill in *Placopecten magellanicus* (Pectinidae, Beninger et al. 1992, 1993), *Mytilus edulis* (Mytilidae, Beninger et al. 1993), *Pyganodon cataracta* (Unionidae, Tankersley and Dimock 1993), and *Crassostrea virginica* (Ostreidae, Ward et al. 1994). A better understanding of feeding phenomena at the level of the labial palps would also require a detailed description of the anatomy of these organs.

All bivalve suspension-feeders accomplish essentially the same things in the feeding process: interception of particles, transport, selection, and ingestion volume control. However, feeding mechanisms have been shown to be highly dependent on the architecture of the structures involved: the heterorhabdic, plicate gill of the Pectinidae functions quite differently from that of the homorhabdic Mytilidae (Beninger et al. 1993); this difference may also affect particle treatment in the buccal region.

Detailed anatomical and ultrastructural data are available for the peribuccal organs of *Placopecten magellanicus* and *Chlamys varia* (Fam. Pectinidae, Beninger et al. 1990a, b) but little is known of the labial palps of representatives of the most-studied bivalve family, the Mytilidae. Wallengren (1905) sketched the palp ridges in *Mytilus* sp., with emphasis on the different shapes assumed during contractions of subjacent muscle fibres. *Mytilus* sp. palps were briefly described in Foster-Smith (1975a), from which the description of Bayne et al. (1976) was derived. To our knowledge, there are only two or three very low resolution scanning electron micrographs in print, and these are of

juvenile specimens in which much of the ridged (i.e. oral) surface is not visible (Jørgensen 1981). The most recent description is that of Morton (1992), summarizing these previous studies.

Cursory examination of the palps of *Mytilus edulis* using a dissecting microscope reveals a gross morphology fundamentally different from that of many other bivalve families, essentially in the presence of a dorsal flap of non-ridged tissue on the oral surface and fusion between outer and inner palps limited to the anterior region only. This manner of organization has been reported in just a few other species, such as *Tellina crassa* and *Spisula subtruncata* (Foster-Smith 1978). None of these palps have been examined in detail. The purpose of the present study is to describe the anatomy and histology of the labial palps of *M. edulis*, in order to provide a foundation for future studies of function.

Material and methods

Collection and fixation

Six adult mussels were collected subtidally, from the mouth of the Kouchibouguac estuary (New Brunswick, Canada: 46° 10′ 25″ N; 64° 20′ 10″ W) in August of 1993. All mussels were inspected for signs of normal feeding (valves parted, inhalant siphon open, siphonal tentacles extended, particle movement into siphon) prior to collection. The specimens were brought to the shore and dissected immediately using micro-surgical instruments. Palps destined for histological processing were fixed in aqueous Bouin's solution, while those destined for scanning electron microscopic (SEM) observation were fixed in cold isotonic (1028 mosmol) 4% glutaraldehyde- 0.4 *M* sodium cacodylate buffer (pH 7.2). Osmolarities were determined using an Advanced Digimatic Osmometer Model 32 D (Advanced Instruments Ltd., Nudham Heights, Massachusetts USA).

Two other specimens were collected from Passamaquoddy Bay (Bay of Fundy, New Brunswick: 45° 07′N; 67° 04′W) in April 1994 and also processed for SEM.

Histology

Fixed palps were rinsed under running water for a minimum of 12 h and dehydrated using a graded ethanol series, for 2 h in 1:1 ethanol–Hemo-De® (Fisher Scientific) and 2 h in 1:1 Hemo-De®–paraffin. The palps were then embedded in paraffin and sectioned at 5 μm.

After rehydration in a graded ethanol–distilled water series, the following modified Masson trichromatic protocol was used for staining: saturated aqueous lithium carbonate solution 5 min, trioxyhaematin 1.5 min, acid fuschin (only C.I. 42685 may be used: Sigma Chemical, St. Louis, Missouri USA) 2 min, fast green FCF 5 min. Excess stain was removed using a series of 1% acetic acid baths between each stain; the acetic acid was gradually replaced with running water during the rinse.

In order to ascertain positions of mucocytes, some slides were stained using an alcian blue 8GX–periodic acid-Schiff (PAS) procedure (Beninger et al. 1993). All slides were examined and photographed using a Leitz DMRB research microscope.

Palps for SEM observations were dehydrated in an ascending ethanol series, critical-point dried with liquid CO_2, mounted on SEM stubs, and sputter-coated using a Hummer VI sputter coater fitted with a gold–palladium electrode. The specimens were then examined with an ISI M-7 or a JEOL 5200 SEM.

Results

General morphology and anatomical relationships

The outer and inner palps enclose the anterior gill region (Fig. 1.1). Each demibranch is applied to the respective palp ridged surface (outer demibranch to outer palp, inner demibranch to inner palp). Characteristic of a Category 1 association (Stasek 1963), there is no tissue junction between the gill and the palp; rather,

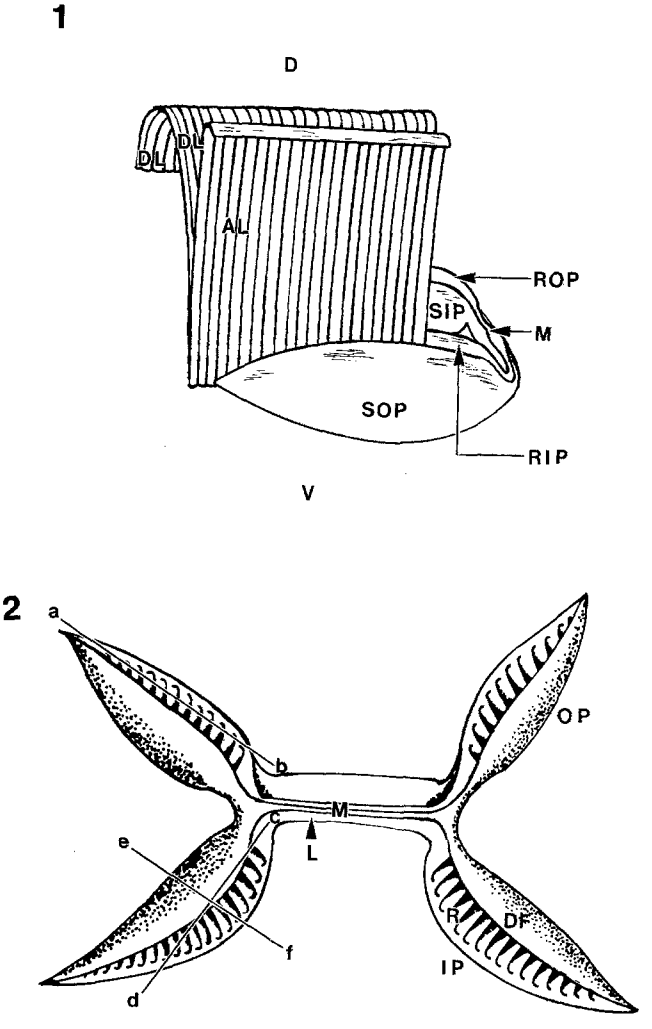


Fig. 1 *Mytilus edulis*. General organization of gill and palps. **1.1** Schematic figure showing natural position and anatomical relations of gill, labial palps, and mouth. (*AL* ascending lamella of gill; *D* dorsal; *DL* descending lamella; *M* mouth; *RIP* ridged surface of inner palp; *ROP* ridged surface of outer palp; *SIP* smooth surface of inner palp; *SOP* smooth surface of outer palp; *V* ventral) **1.2** General aspect of labial palps spread apart and gills removed. Ridged surface only visible. (*DF* dorsal fold; *IP* inner palp; *L* lip; *M* mouth; *OP* outer palp; *R* ridges; *a–b* plane of section for Fig. 3; *c–d* plane of section for Fig. 4; *e–f* plane of section for Fig. 5.3, 5.5, and 5.6

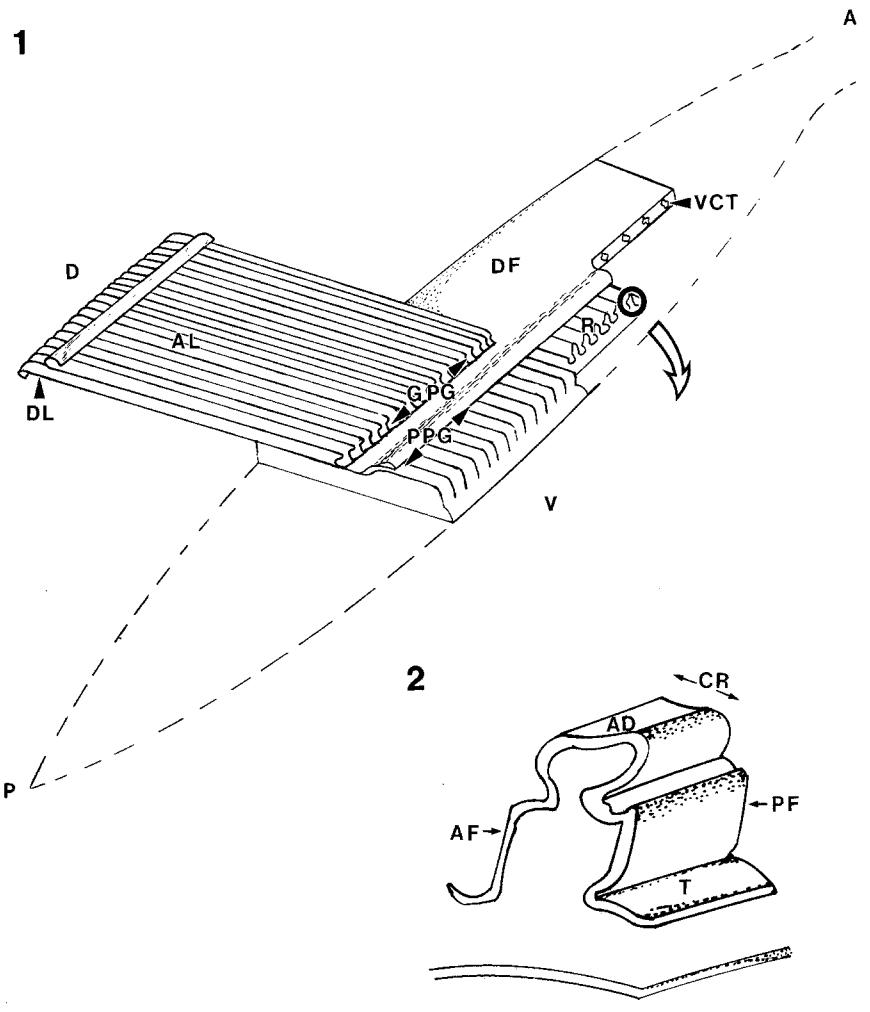


Fig. 2 *Mytilus edulis*. Schematic sections showing anatomical relationships and gross internal anatomy of gill and labial palp. **2.1** Drawing of ridged face of a single labial palp. (*A* anterior, *AL* ascending lamella of gill; *D* dorsal; *DF* dorsal fold; *DL* descending lamella of gill; *GPG* gill particle groove; *P* posterior; *PPG* palp particle groove; *R* ridges; *V* ventral; *VCT* vestigial ciliated tracts) **2.2** Schematic drawing of a single palp ridge. (*AD* apical depression; *AF* anterior fold; *PF* posterior fold; *T* trough; *CR* crest of palp ridge)

the gill rests against a specialized region of the palp ridged surface, herein referred to as the dorsal fold (Figs. 1.2, 2.1), which bears no ridges. The ventral margin of the dorsal fold is unattached to the underlying ridges, forming an antero–posterior ciliated tract termed the palp food groove by Foster-Smith (1978), but herein referred to as the palp particle groove, since the material transported may be destined either for ingestion or rejection as pseudofeces (Fig. 2.1; see also Figs. 4.1, 5.1, 5.4 to 5.6).

The palp ridges run ventro–dorsally and fuse with the dorsal fold behind its ventral margin (Fig. 2.1). Each palp ridge comprises an apical depression, an anterior fold, and a larger posterior fold; troughs separate adjacent ridges (Figs. 2.2, 3.1, 3.2; see also Fig. 6.1).

Histology of palp ridges

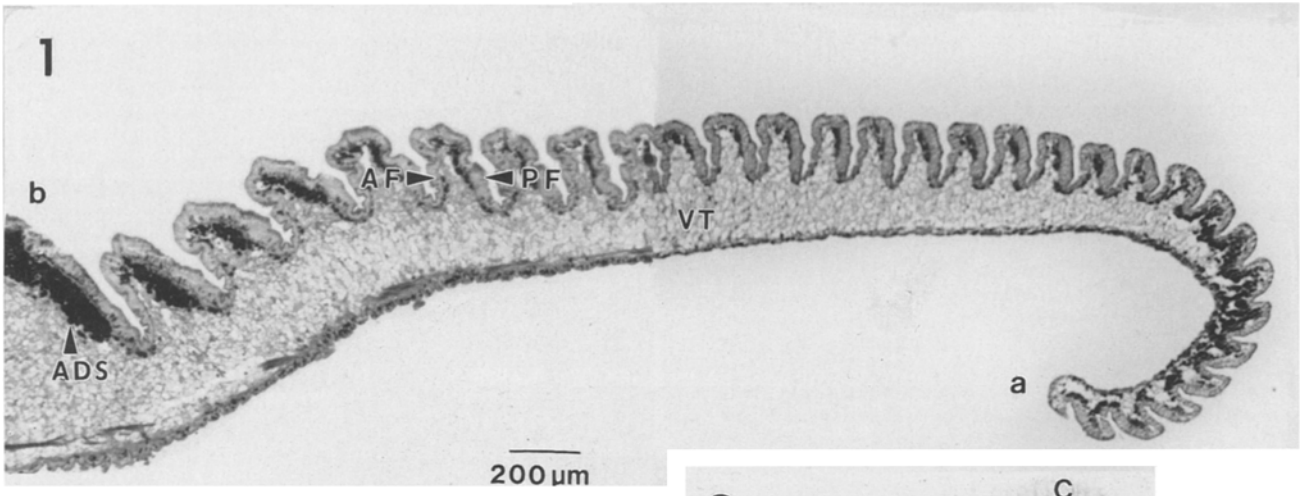
The palp ridges decrease in size from the anterior to the posterior extremities (i.e. distally from the oral region, Fig. 3.1). The ridges consist of a pseudostratified ciliated epithelium, beneath which is found the vesicular connective tissue traversed by muscle fibres (Fig. 3.2 to 3.4).

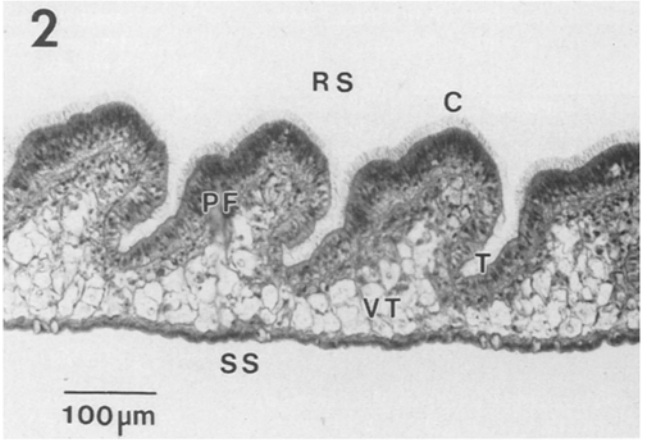
Two types of mucocytes with specific distributions are found in the palp ridges: subepithelial mucocytes with acid-dominant secretions (ADS), and epithelial mucocytes. The subepithelial ADS mucocytes appear to be concentrated on the anterior half of the ridge (with ducts leading through the epithelium to the surface) and, to a lesser degree, in the troughs. The epithelial mucocytes are characterized almost exclusively by neutral secretions (NS, Fig. 3.5) and appear to be concentrated on the anterior half of the ridge crest.

The troughs present a ciliated columnar epithelium, with a prominent basal lamella. The mucocytes were predominantly subepithelial, acid-dominant, and fewer than on the posterior fold (Fig. 3.3, 3.5).

Relationship between palp ridges, dorsal fold, and vestigial ciliated tracts

An important tissue fusion occurs as the palp ridges approach and contact the dorsal fold. The ciliated


1
b
AF
PF
VT
ADS
a
200 µm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RS
C
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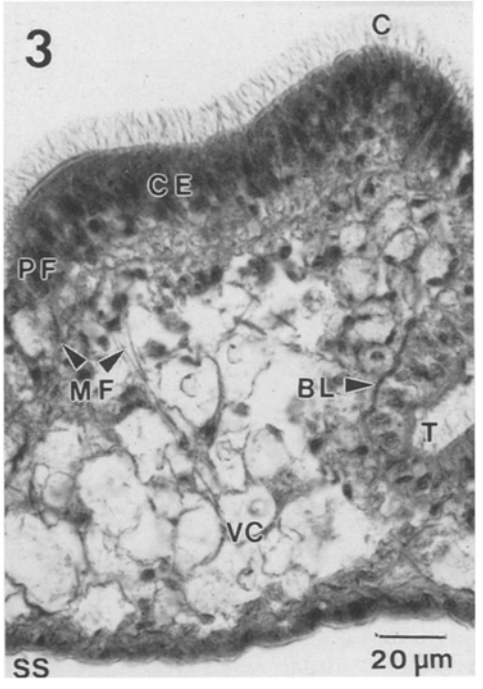
T
VT
SS
100µm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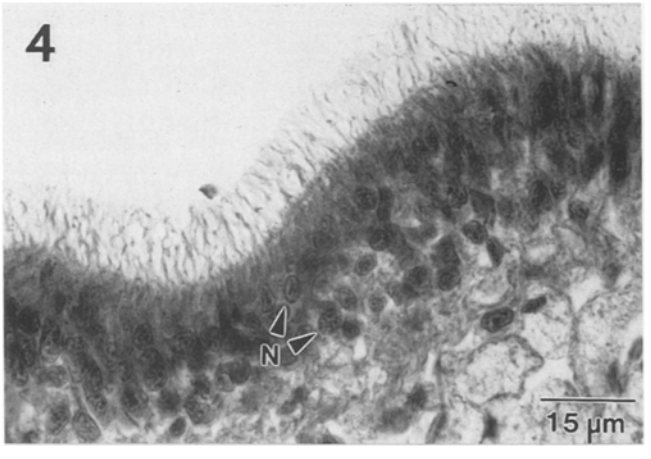
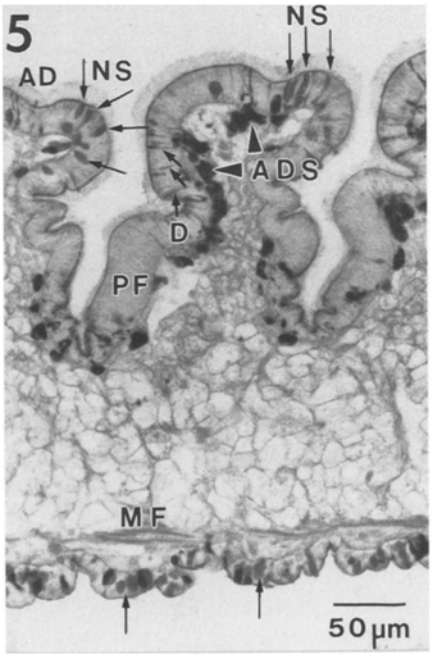
CE
PF
MF
BL
T
VC
SS
20 µm


4
N
15 µm


5
NS
AD
NS
ADS
D
PF
MF
50µm

epithelium of the ridges fuses with that of the underside of the dorsal fold, transforming adjacent ridges into a tubular shape, herein referred to as the vestigial ciliated tracts (Figs. 4.1, 5.5, 5.6).

The vestigial ciliated tracts extend beneath the dorsal fold as blind tubular structures with the same histological features as the palp ridges, although mucocytes are rare (Fig. 4.2 to 4.5).

Dorsal fold

The dorsal fold is a smooth (i.e. non-ridged) flap of densely ciliated tissue which covers approximately half of the ridged surface of each palp (Figs. 1.2, 4.1, 5.1 to 5.6). The dense ciliation begins in the dorsal region of the smooth surface (Fig. 6.2) and extends over the entire dorsal fold to the palp particle groove, where it becomes continuous with the ridge ciliation and the vestigial ciliated tracts. The underlying musculature and behaviour upon fixation indicate that the ventral margin of the dorsal fold is contractile, allowing the fold to cover more or less of the ridged surface (Fig. 5.1, 5.2, 5.4).

Palp smooth surface

The smooth surface is characterized by the presence of sparse clumps of cilia, between which the underlying microvilli are visible (Fig. 6.2 to 6.4). As described above, the dorsalmost part of the smooth surface presents a dense ciliation, which is the beginning of the ciliation characteristic of the ridged surface. Histologically, the smooth surface consists of a cuboidal epithelium within which are found randomly distributed mucocytes. Neutral mucopolysaccharides are abundant in these mucocytes, but acid-dominant secretions also occur (Fig. 3.5).

Fig. 3 *Mytilus edulis*. Histology of palp ridges. **3.1** Antero–posterior section through palp ridges, showing general organization and locations of acid-dominant secretion mucocytes. Alcian blue-PAS stain. (*AF* anterior fold of palp ridge; *ADS acid-dominant secretion mucocytes*; *PF* posterior fold of palp ridge; *VT* vesicular connective tissue; *a* and *b* extremities of section plane shown in Fig. 1.2) **3.2** Histology of palp ridges. Modified Masson trichrome stain. (*C* cilia; *PF* posterior fold; *RS* ridged surface; *SS* smooth surface; *T* trough; *VT* vesicular–connective tissue) **3.3** Detail of a single ridge showing ciliated epithelium (*CE*), muscle fibres (*MF*), and vesicular cells (*VC*). Note transition from pseudostratified to columnar ciliated epithelium in region of trough. Modified Masson trichrome stain. (*BL* basal lamella; *C* cilia; *PF* posterior fold; *SS* smooth surface; *T* trough) **3.4** Detail of 3.3, showing abundant nuclei (*N*) indicative of cell and ciliation density in crest of ridge epithelium. Modified Masson trichrome stain. **3.5** Profile of ridges showing epithelial location of neutral secretion mucocytes (*NS* and *long arrows*) and subepithelial location of acid-dominant mucocytes (*arrowheads*). Note ducts (*D* and *short arrows*) in overlying ciliated epithelium. Alcian blue-PAS stain. (*AD* apical depression; *PF* posterior fold of palp ridge; *MF* muscle fibre; *ADS* acid-dominant secretion)

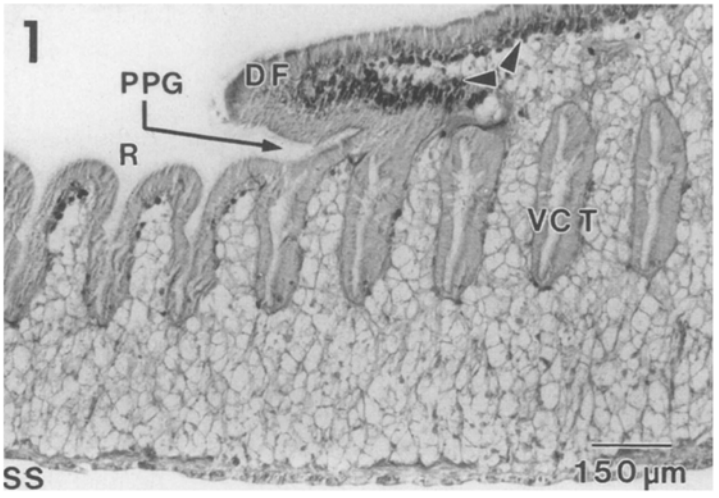
Discussion

General organization

Although *Mytilus edulis* is reported to present a Category I gill–palp relationship (Stasek 1963; Morton 1992), the results of the present study suggest that this scheme should be modified somewhat. The original Category I refers to the insertion of the ventral margin of the anteriormost gill filaments, unfused, into a distal oral groove. While the anteriormost gill filaments of *M. edulis* are indeed unfused, they are not inserted into an oral groove; rather, they rest upon the dorsal fold, above and parallel to the palp particle groove. It may therefore be necessary to modify this classification; for example, Category Ia would correspond to Stasek's original description, while Category Ib would include those bivalves whose anteriormost filaments are unfused but not directly inserted into a palp particle groove.

Anterior and posterior folds on the palp ridges appear to be a general feature of bivalve labial palps (Anodontidae, Matthews 1928; Ostreidae, Nelson 1960; Veneridae, Ansell 1961, Foster-Smith 1978; Tellinidae, Stasek 1961; Cardidae, Foster-Smith 1978). The photomicrographs of the present study confirm Foster-Smith's (1975a, 1978) diagrammatic representations of these structures in *Mytilus edulis*, including the more pronounced nature of the posterior fold compared to the anterior fold. A similar dyssymetry was reported by Nelson (1960) for three species of Ostreidae. The reduced nature of the anterior fold is probably correlated with the postero–anterior direction of bending of the palp ridges when relaxed (Ansell 1961; Foster-Smith 1975a; Beninger et al. 1990a; present study).

The presence of the dorsal fold fundamentally modifies the mussel labial palp anatomy, compared to bivalves whose palps lack such a fold. In the latter species, such as the scallops *Placopecten magellanicus* and *Chlamys varia* (Beninger et al. 1990a), the inner and outer palps of each pair are fused along their dorsal margins forming the palp particle groove, termed the oral groove. Particles enter the groove from the anterior extremities of the corresponding gill tips. In *Mytilus edulis*, however, the inner and outer labial palps are separate for most of their length (fused only at the anterior extremity), and particles arrive on the dorsal fold of each palp from the corresponding demibranch of each gill (outer demibranch, outer palp dorsal fold; inner demibranch, inner palp dorsal fold; Foster-Smith 1978). The dense ciliation of the dorsal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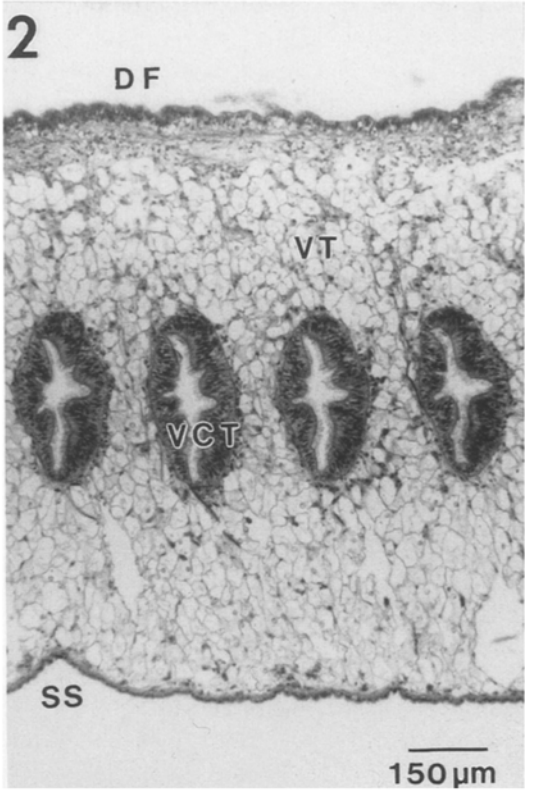
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3
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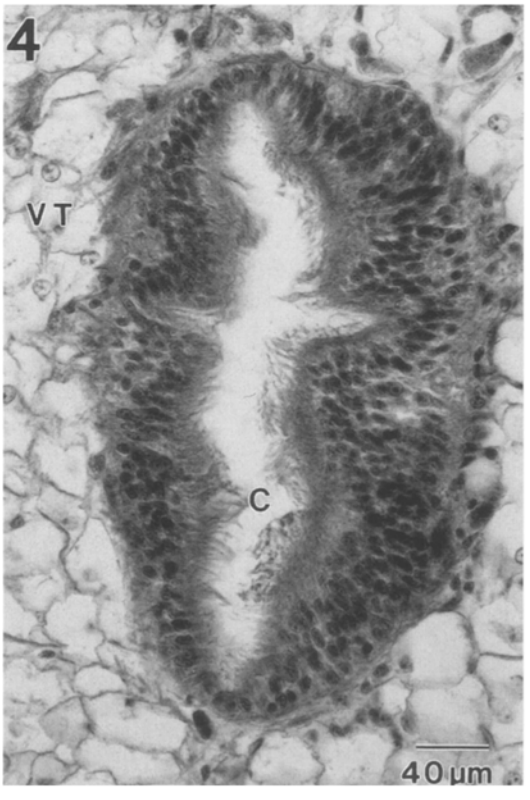
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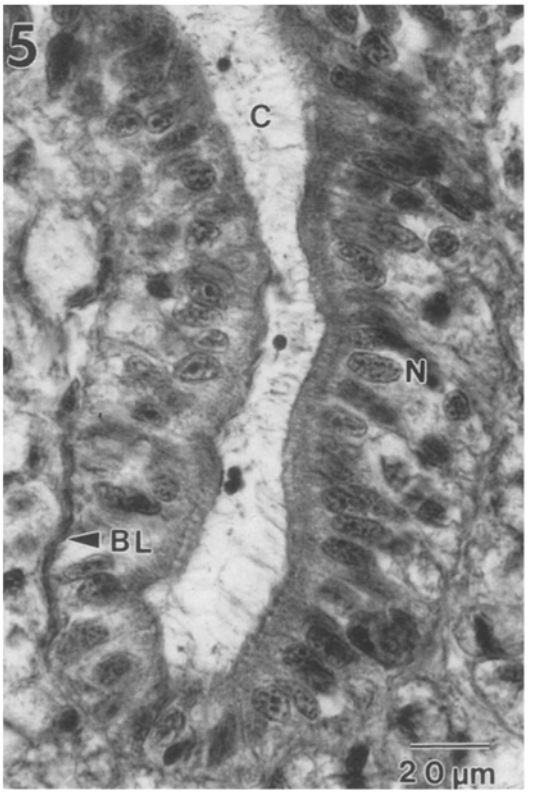
C
40 µm


5
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BL
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fold correlates with the particle transport function of this surface.

The dorsal fold also participates in the formation of the vestigial ciliated tracts. As demonstrated in the present study, these tracts are derived from the fusion of the epithelium of the palp crests with that of the dorsal fold. Four aspects of the anatomy and function indicate the vestigial nature of these tracts. First, the tubules are blind, such that any particles which enter must return to the entrance of the tract; second, since the palp crests are fused to the dorsal fold epithelium, the tubules are continuations of the trough rejection tracts (Foster-Smith 1978), which transport particles toward the palp ventral margin and hence away from the vestigial ciliated tracts. Third, although present, mucocytes are much less abundant in these tracts than in the palp ridges and dorsal fold from which they are formed. Finally, endoscopic studies show the movement of mucus and particles perpendicular to the vestigial ciliated tracts, along the palp particle groove, rather than into the vestigial ciliated tracts (St-Jean 1993). The vestigial ciliated palp crests may thus be considered an anatomical "leftover" from the fusion of the palp crests and the dorsal fold.

The contractile nature of the dorsal fold would allow it to cover variable surface areas of the ridged surface, depending on degree of contraction. This may prove to be important in palp function, since it would alter the crest surface available for the type of particle treatment described by Foster-Smith (1975a, 1978).

Palp ridge mucocytes

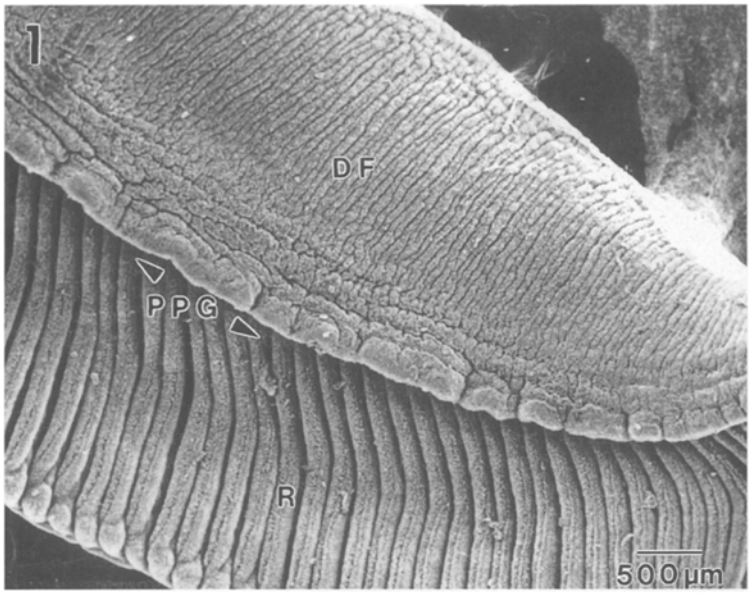
The histological data indicate characteristic distributions for the two mucocyte types found on the palp ridges. This may have functional significance; in the normal postero–anterior inclined position, mainly acid-dominant secretions will be discharged onto the epithelial surface, while in the erect position, mainly neutral secretions will be discharged. The apparent distribution of mucocytes on the anterior and posterior folds of the palp ridges may be significant, since these are considered to be re-sorting tracts by Foster-Smith (1978). Similarly, the distribution of ADS mucocytes in the troughs may also be related to the proposed trough function in particle rejection (Foster-Smith 1978). The importance of mucus type in particle handling has been underscored in recent mucocyte mapping studies on the gill of *Mytilus edulis* and *Placopecten magellanicus* (Beninger et al. 1993); a more detailed study of mucocyte distribution is therefore warranted in the case of the palps of *M. edulis*.

Subepithelial mucocytes (whose organization is actually glandular) were previously reported in *Mytilus edulis* (Foster-Smith 1975a), but demonstration of the absence of such glands in other species led us to express doubts as to their existence in the mussel (Beninger et al. 1990a). However, recent studies have shown that these glands are in fact characteristic of *M. edulis*, also being found in the ventral region of the gill (Beninger et al. 1993), the oesophagus, and peribuccal region (Beninger et al. 1991; Beninger and Le Pennec 1993). One obvious attribute of this type of mucocyte arrangement is that it allows an epithelial surface to be very densely ciliated, while at the same time permitting the secretion of substantial quantities of mucus onto this surface. Presumably, mucus plays an even more important role in particle transport and ingestion in *M. edulis* than in those species which lack subepithelial mucocytes.

Implications for ingestion volume control and selection

Efficient particle capture and transport also pose the problems of regulation of amount of material ingested (ingestion volume control) and selection of appropriate particles for ingestion. Although a gill shunt mechanism has been proposed, which would allow *Mytilus edulis* to reduce the amount of water passing through the gill (Famme and Kofoed 1983), the fact that this species rejects pseudofeces indicates that such a mechanism is not sufficient in itself. In addition, endoscopic observations have shown that pseudofeces are not produced from the gill ventral particle groove, even when particle concentrations are high (Beninger et al. 1993; Ward et al. 1993). The only structures capable of producing pseudofeces, and hence assisting in ingestion volume control, are therefore the labial palps. Indeed, Foster-Smith (1975a, 1978) proposed that ingestion volume control is the only function of the labial palps. His behavioral observations are supported by the correlation between size of labial palps in *M. edulis* and ambient turbidity (Kiørboe and Møhlenberg 1981; Thiessen 1982). Direct endoscopic observations are currently underway to verify this hypothesis (St-Jean and Beninger in preparation).

Fig. 4 *Mytilus edulis* Histology of dorsal fold and vestigial ciliated tracts. **4.1** Oblique section (plane c–d in Fig. 1.2) showing continuity of ridge ciliated epithelium (*R*) and dorsal fold (*DF*), and transformation of ridge ciliated epithelium into tubular vestigial ciliated tracts (*VCT*) beneath the dorsal fold. Note subepithelial location of acid-dominant secretion mucocytes. Alcian blue-PAS stain. (*PPG* palp particle groove; *SS* smooth surface) **4.2** Slightly oblique section through palp dorsal to palp particle groove, showing position of vestigial ciliated tracts (*VCT*) within vesicular-connective tissue (*VT*). Modified Masson trichrome stain. (*DF* dorsal fold; *SS* smooth surface) **4.3** Detail of 4.2, showing uniform histological characteristics of vestigial ciliated tracts. Modified Masson trichrome stain. **4.4** Slightly oblique section of a vestigial ciliated tract, showing pseudostratified epithelium and dense ciliation (*C*). Modified Masson Trichrome stain. (*VT* vesicular-connective tissue) **4.5** Detail of pseudostratified epithelium of vestigial ciliated tract, showing features identical to those found in palp ridges (Fig. 3.2 to 3.4). Modified Masson trichrome stain. (*BL* basal lamella; *C* cilia; *N* nuclei)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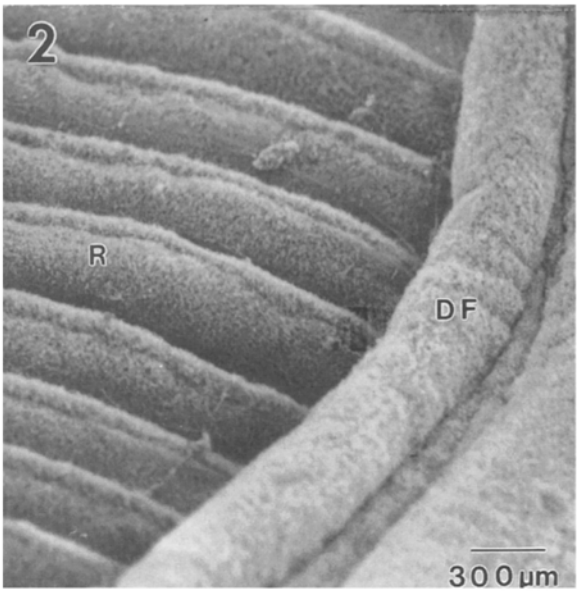
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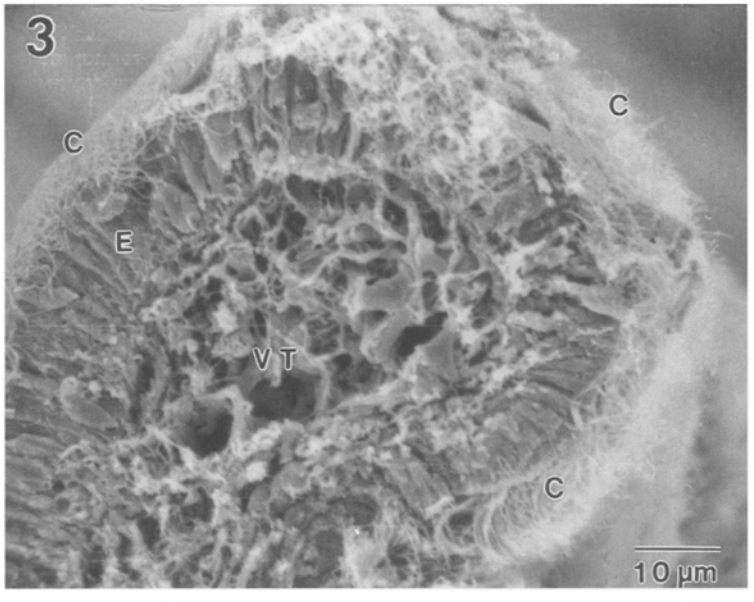
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C
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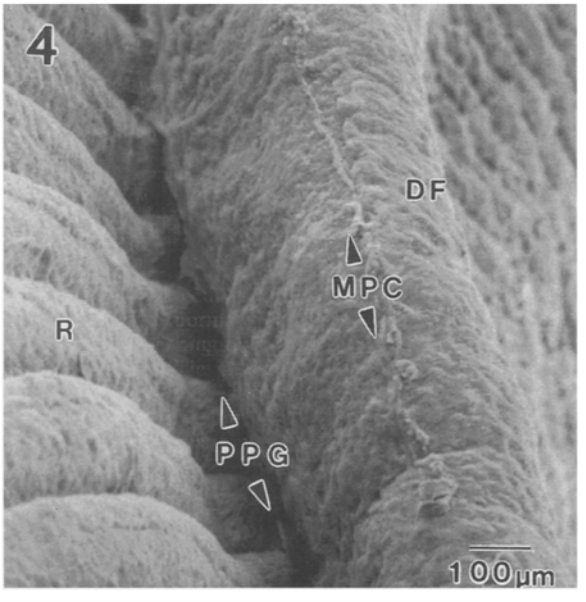
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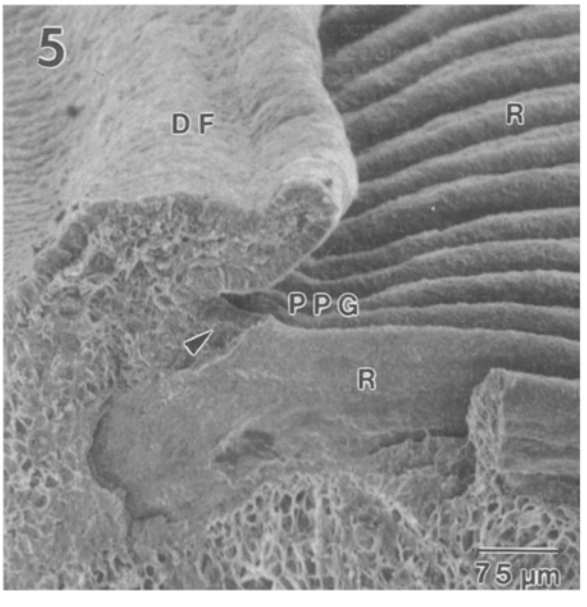
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R
PPG
R
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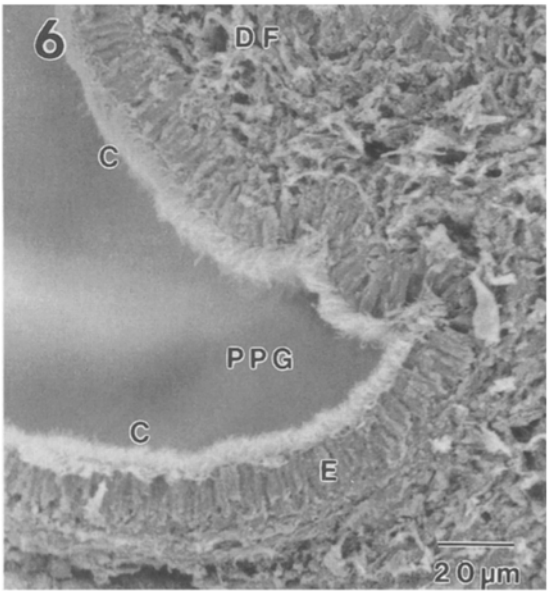
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20µm

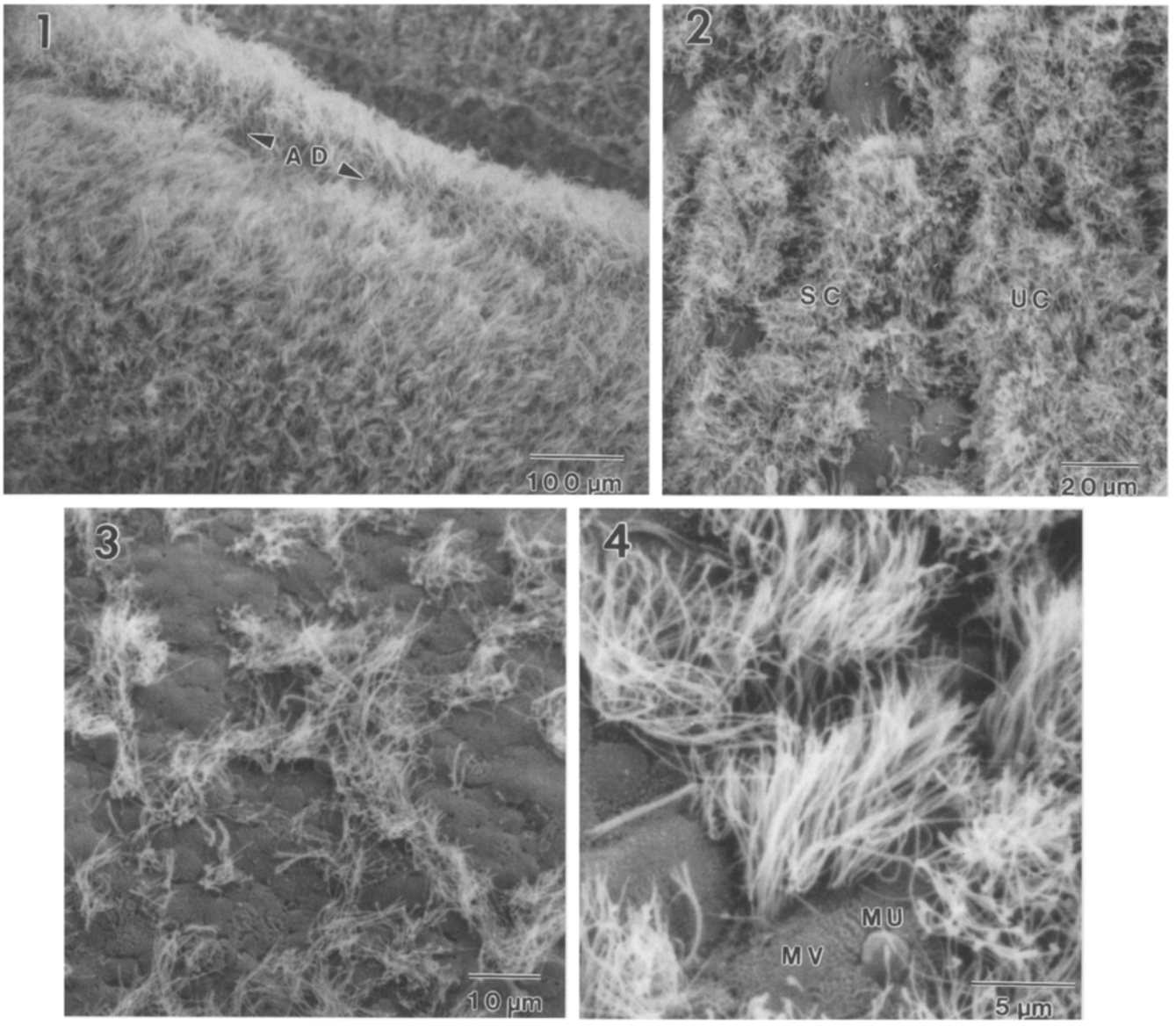

Fig. 5 *Mytilus edulis*. Scanning electron micrographs (SEM) of labial palp ridged surface. **5.1** General view, showing anatomical relationships of dorsal fold (*DF*), palp particle groove (*PPG*), and ridges (*R*). **5.2** Detail of ventral margin of dorsal fold (*DF*), showing contraction consequent to dissection. (*R* ridges) **5.3** Transverse section through ventral margin of dorsal fold, showing densely ciliated (*C*) epithelium (*E*). (*VT* vesicular-connective tissue) **5.4** Similar to 5.2, but note position of ridges (*R*) relative to dorsal fold (*DF*). [*MPC* mucus-particle cord, probably from palp particle groove (*PPG*)] **5.5** Transverse section of labial palp, showing fusion (*arrowhead*) of palp ridge (*R*) with dorsal fold (*DF*) to form palp particle groove (*PPG*). **5.6** Transverse section showing detail of palp particle groove (*PPG*). Note uniform, dense ciliation (*C*) of epithelium (*E*). (*DF* dorsal fold)

Fig. 6 *Mytilus edulis*. SEM micrographs of ciliation on ridges and on smooth palp surface. **6.1** Palp ridge, showing dense, uniform ciliation and apical depression (*AD*). **6.2** Smooth surface, showing transition from uniform ciliation (*UC*) close to dorsal fold to clumped, sparse ciliation (*SC*) of majority of this surface. **6.3** General aspect of ciliation on smooth surface. **6.4** Detail of ciliary tufts on smooth surface. (*MU* mucus ball exiting from mucocyte; *MV* microvilli)

Reports of selection in mussels are inconsistent, at least in part due to differences in experimental conditions. While Foster-Smith (1975b) showed that *Mytilus edulis* did not select *Phaeodactylum tricornutum* over alumina particles, it should be noted that other bivalves actively select against this alga (Shumway et al. 1985); there may thus have been little to recommend either of these particles. On the other hand, Buley (1936) showed

a high degree of selection in favour of dinoflagellates by *M. californianus*, and Ward and Targett (1989) conclusively demonstrated both positive and negative selection of microspheres coated with various algal ectocrines by *M. edulis*. Furthermore, it is likely that mussels from different sites show different selection abilities (Kiørboe and Møhlenberg 1981; Shumway and Cucci 1987). Taken together, the evidence indicates that preingestive selection does occur in mussels; given the indiscriminate nature of particle transport in the homorhabdic *M. edulis* gill (Beninger et al. 1993; Ward et al. 1993), the palps are the only possible site for such activity. The great degree of anatomical complexity of the labial palps in this species could reflect the fact that any and all particle selection must occur on the palp ridged surface, whereas in species with more complex gill types, some particle selection could be effected on the gill.

Smooth surface

The palp smooth surface is quite similar to that described for other bivalves (Beninger et al. 1990a): a cuboidal epithelium with sparsely distributed ciliary tufts which would not be suitable for particle handling, and mucocytes. No particular pattern seems to be evident for the distribution of neutral and acid-dominant secretion mucocytes on this surface, in contrast to the ridged surface. This should be verified quantitatively in the near future (St-Jean and Beninger in preparation).

The transition from sparsely ciliated tufts to the dense cilation of the dorsal fold actually occurs in the dorsal region of the smooth surface. This suggests that the dorsal fold may have originated evolutionarily and developmentally from a folding and fusion of the smooth surface epithelium and the palp ridges. It would be of interest to investigate the organogenesis of this structure.

The present study elucidates the general structure and anatomical relationships of the labial palps in *Mytilus edulis*, as well as their histology and surface features. Several aspects hold potential significance for particle processing: the relationship between the palp ridges and the dorsal fold, the role of the latter in particle transport from the gill particle groove to the palp particle groove, and the distribution of mucocyte types on the ridged surface. In addition, the functional (or non-functional) nature of the vestigial ciliated tracts remains to be confirmed. These questions could be resolved by the combined use of endoscopic observation of particle processing (Ward et al. 1991) and mucocyte mapping (Beninger et al. 1993). Furthermore, it would be interesting to learn whether bivalves in other families, whose labial palps present a dorsal fold (e.g. *Spisula subtruncata* and *Tellina crassa*, Foster-Smith 1978), also possess vestigial ciliated tracts similar to those of *M. edulis*. It is clear that a sound anatomical basis is needed in order to pursue studies on feeding mechanisms in bivalves.

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