

Peribuccal organs of *Placopecten magellanicus* and *Chlamys varia* (Mollusca: Bivalvia): structure, ultrastructure and implications for feeding

I. The labial palps*

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Abstract. In order to better understand the structure of bivalve peribuccal organs and relate this to existing functional paradigms of their role in feeding, the labial palps of two scallop species, *Placopecten magellanicus* from the Bay of Fundy, Canada (1985 and 1986), and *Chlamys varia* from the Bay of Brest, France (1986), were examined using histological techniques and electron microscopy. The ridged palp surface displays a uniformly dense ciliation with relatively few mucocytes; these are essentially concentrated in the region of the secondary ledge and may, through their secretory activity, determine the fate of particle masses in this area. The mucus secretions of the ridged palp surface are qualitatively different from those of the smooth palp surface. Mucocytes are much more abundant on the smooth palp surface, where it is suggested that their homogeneous secretions attenuate the potentially adverse effects of anteriorly-directed cleansing and swimming currents. Two other cell types are found in the palp epithelia: ciliated cells, which are very numerous on the ridged surface and relatively rare on the smooth surface, and non-ciliated epithelial cells, which are very numerous on the smooth surface and rare on the ridged surface, where they are confined to the palp margin. In addition to the mechanical role of the ciliated cells and mucocytes, the ultrastructural characteristics of the ciliated and non-ciliated epithelial cells indicate a dichotomy of function between the ridged and smooth surfaces. The ridged surface epithelial cells present an ultrastructural specialization in the absorption of dissolved and colloidal matter, suggesting an accessory nutritive role, whereas the smooth surface simple epithelial cells show signs of active molecular synthesis. No specialised sensory cells were observed on the ridged surface; it is therefore not yet possible to conclude whether the labial palps are capable of selection based on individual particle characteristics.

Introduction

In bivalves (with the exception of the Protobranchia), the principal structures involved in the capture and subsequent handling of particles prior to ingestion or rejection are the gills, the labial palps, and the lips. Increasing interest in the domestication and aquaculture of commercially-important bivalve species such as scallops (family Pectinidae) has created a need to more completely understand the mechanisms involved in feeding. The structure and function of the scallop gill are now relatively well known (Owen and McCrae 1976, Owen 1978, Beninger et al. 1988, Le Pennec et al. 1988); however, little attention has hitherto been directed toward the labial palps of pectinids. Similarly, the complex lips have been the object of scant and sporadic study and will be considered in the paper immediately following (Beninger et al. 1990).

Functional observations of the labial palps and studies of particle clearance, gut contents, feces and pseudofeces composition have been performed for several bivalve species, leading to widely-divergent interpretations of their role in particle selection, acceptance or rejection (Nelson 1960, Stasek 1961, Galtsoff 1964, Jørgensen 1966, Bernard 1974, Foster-Smith 1975a, 1978, Hughes 1975, Kjørboe and Møhlenberg 1981, Shumway et al. 1985, Newell et al. 1989). Despite these conflicting views of bivalve palp function, little published data are available concerning their structure, while accounts of their ultrastructure are singularly lacking. To the best of the authors' knowledge, only a very few low-resolution photomicrographs have been published for non-pectinids (Matthews 1928, Garland et al. 1982a, b, Meehan and Diaz 1985), while none have been published for the Pectinidae.

The present study of the structure and ultrastructure of the palps of the scallops *Placopecten magellanicus* and *Chlamys varia* is intended to serve as a baseline for the evaluation of their role in feeding. Such data are necessary to clarify some of the paradigms concerning palp function, notably by modifying those with which the structural data is at variance, by supporting those with

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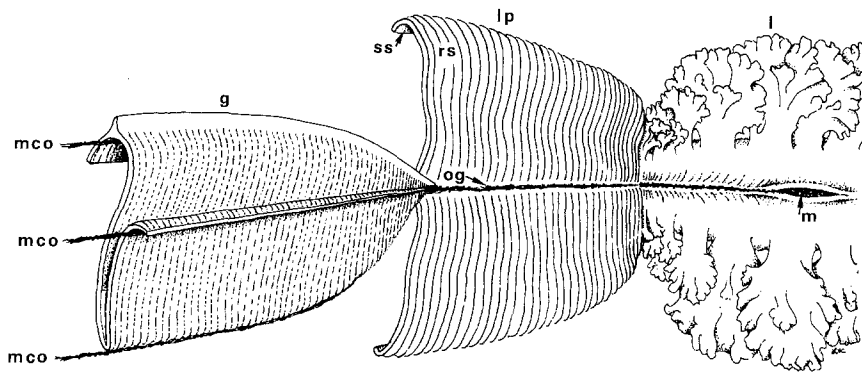


Fig. 1. *Placopecten magellanicus*. General topography and anatomical relationships of gill (g), labial palp (lp), and lips (l), showing location of mucus cords (mco) on gill. m: mouth; og: oral groove; rs: ridged surface of palp; ss: smooth surface of palp

which such data is in agreement, and also by revealing additional possibilities.

Materials and methods

Preliminary scanning electron microscopic observations were performed on the labial palps of four adult *Placopecten magellanicus* collected by divers in May 1985 from Chamcook Bay (Bay of Fundy, New Brunswick, Canada), while detailed electron microscopic investigations were carried out on twelve adult *P. magellanicus* collected in 1986, using a scallop drag in Passamoquoddy Bay (Bay of Fundy), New Brunswick. All individuals were transported live to the Laboratoire de Biologie Marine of the Université de Bretagne Occidentale, Brest, France, where they were allowed to acclimate in refrigerated aquaria containing artificial seawater for 10 to 17 d prior to dissection.

Eight adult specimens of *Chlamys varia* were obtained in 1986, using a scallop drag in the Bay of Brest; three were used for electron microscopic observations, while five were used for histological observations. They were maintained for 7 to 14 d in refrigerated aquaria prior to dissection. The aquarium water was changed daily, and all scallops were fed daily with a mixture of the cultured unicellular algae *Monochrysis galbana* and *Dunaliella primolecta*. Histological studies were performed on six adult *Placopecten magellanicus* obtained from Passamoquoddy Bay using a scallop drag in May 1986, June 1988 and February 1989. They were maintained in a refrigerated recirculating seawater system at the Université de Moncton (New Brunswick) for several days prior to dissection.

Using microsurgical instruments, the labial palps were carefully removed from all individuals used for study. Histological preparations were fixed in aqueous Bouin's solution, embedded in paraffin, serially sectioned at 7 to 10 μm , and stained using the topological protocol described in Beninger (1987), and also using a modification of this technique in which the phospho-orange G was replaced by fuchsin-ponceau. This method was particularly useful in revealing the presence of muscle fibres. In order to study the distribution of mucocytes, sections were stained using the Mowry technique of Alcian blue and trioxymatein (Gabe 1968). Further information concerning the types of mucocyte and their secretions was obtained using the Alcian blue – periodic acid-Schiff (PAS) protocol (Gabe 1968).

A histological search for sensory cells was performed on the labial palps of *Placopecten magellanicus* using the Mann-Dominici technique (Gabe 1968, p. 766–767; p. 960–961). Although no histochemical procedure is specific to sensory cells, this method does reveal the presence of both acidophilic and basophilic secretory granules which resist permanganate oxidation, and is often used to test for the presence of neurosecretions. Clear results have been obtained for known sensory cells in the gill axis (Beninger et al. in preparation), thus providing a reference standard.

The procedure and instrumentation used for scanning and transmission electron microscopy was identical to that described by Beninger et al. (1988) and Le Pennec et al. (1988). Semi-thin sections (0.5 to 1 μm) were stained with toluidine blue and observed directly using clear-field microscopy. Thin sections (<0.5 μm) were stained with alcoholic uranyl acetate and aqueous lead-citrate solutions.

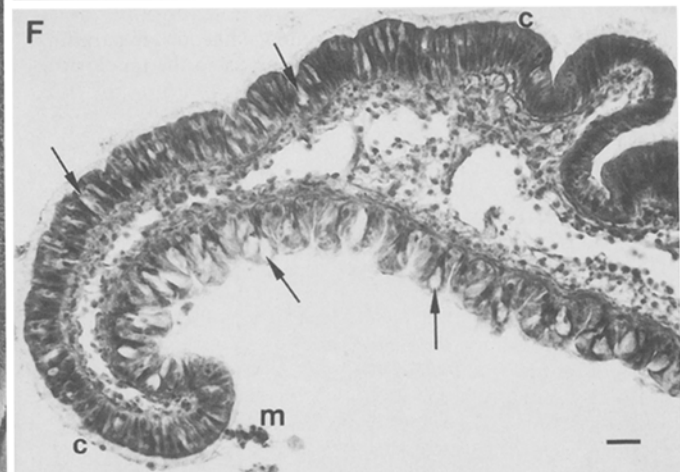
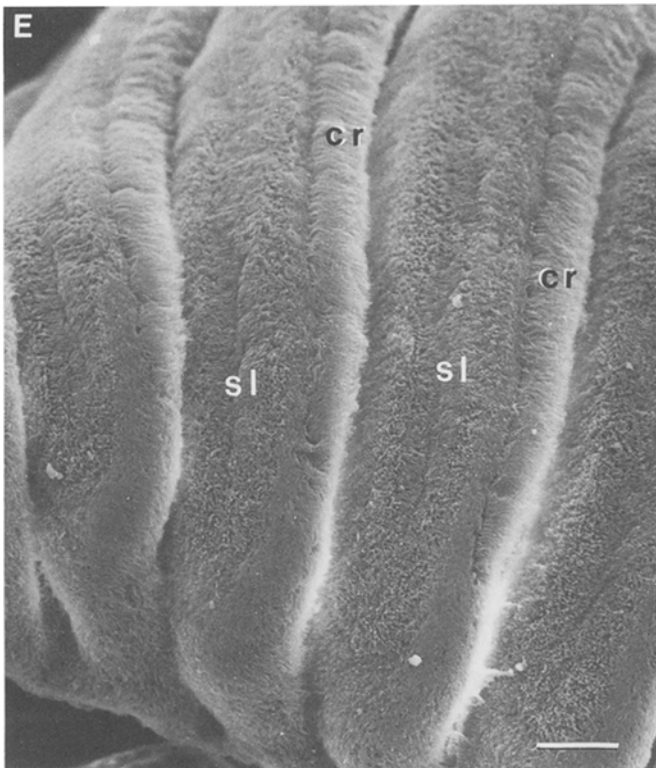
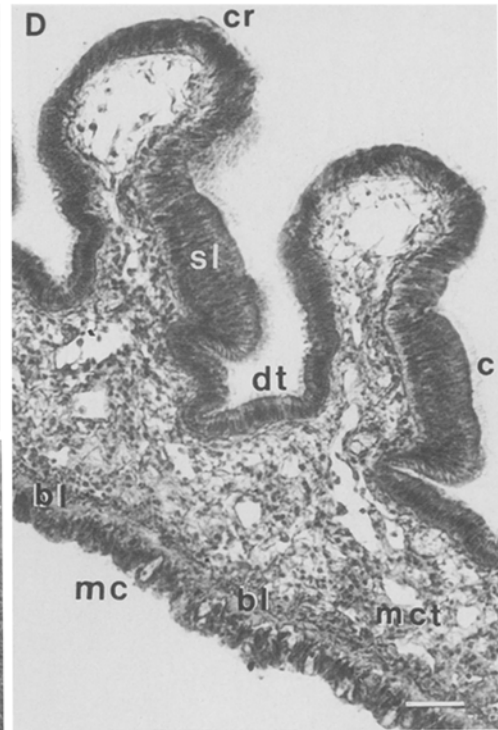
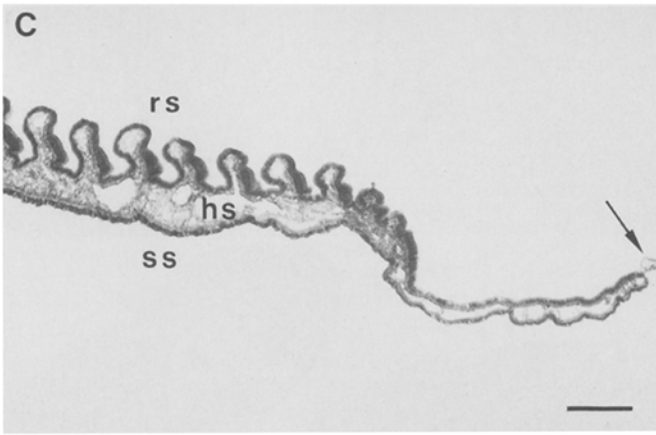
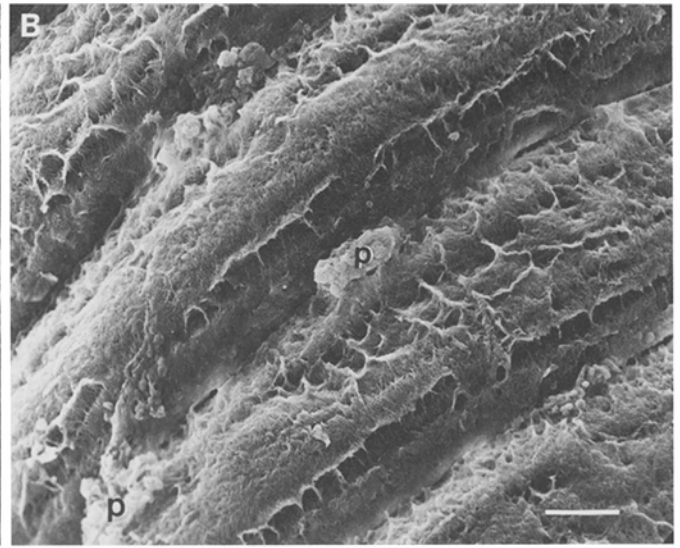
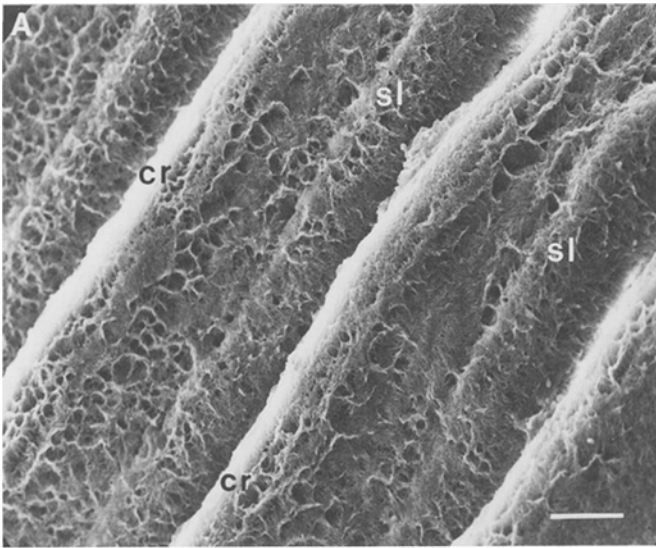
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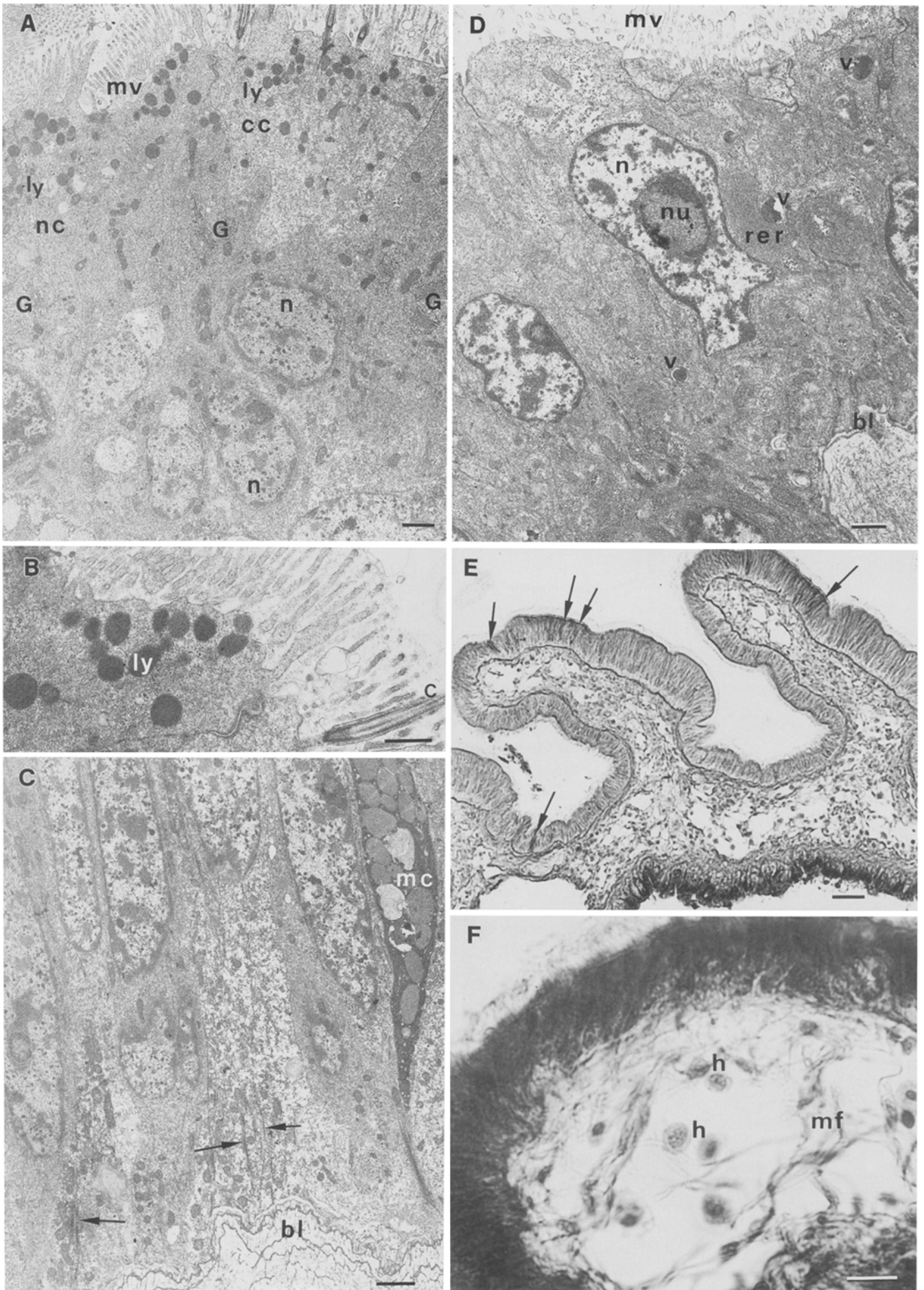
The anatomy and ultrastructure of the palps of both species were found to be very similar. The following detailed description for *Placopecten magellanicus* is thus applicable to *Chlamys varia*; any exceptions are noted. Anatomical terms are those of previous studies, notably Nelson (1960), Ansell (1961, 1981), Foster-Smith (1975 a, 1978) and B. Morton (1979).

General topography

The left and right labial palps each consist of a pair of rhomboidal-shaped tissue flaps on either side of the mouth. The most lateral flap of each pair is called the outer labial palp, while the innermost flap is called the inner labial palp. The anterior extremity of the gill inserts between the palps in a Category III relationship (Stasek

Fig. 2. *Placopecten magellanicus* (*P. m.*: A–D; F) and *Chlamys varia* (*C. v.*: E). (A), (B) SEMs of ridged surface of palp (*P. m.*) showing (A) erect crest (cr) and secondary ledges (sl) (note uniform, dense ciliation) and (B) mucus-bound particles (p) on secondary ledge and crest (both scale bars = 50 μm). (C), (D) Light microscopy of transverse histological sections of labial palp (*P. m.*) showing (C) general organization from centre to margin [note mucus strand (arrowed) at extremity of palp margin; hs: haemolymphatic space; rs: ridged surface; ss: smooth surface; scale bar = 100 μm] and (D) detail of histological section [bl: basal lamella; c: cilia; cr: crest; dt: deep rejection tract; mc: mucocytes; mct: lacunar muscular-connective tissue; sl: secondary ledge (modified Masson trichrome; scale bar = 20 μm)]. (E) SEM of palp (*C. v.*) showing flattened configuration of ridges; cr: crest; sl: secondary ledge (scale bar = 50 μm). (F) Detail of histological section of palp margin (*P. m.*); note abundant mucus (m) and mucocytes (arrowed); c: cilia (modified Masson trichrome; scale bar = 20 μm)





1963). The outer and inner labial palps each present a ridged surface (facing the gill) and a smooth surface. The anterior margin of the labial palps is highly ramified, forming part of the complex lip structure (Fig. 1).

At the base of the ridged surface of each pair of palps is an oral groove, extending from the branchial insertion posteriorly to the mouth anteriorly. The ridged palp surface bears a large number of ciliated ridges and grooves oriented at right angles to the oral groove (Fig. 1). Each palp ridge presents a secondary ledge on the side facing the posterior palp margin (Fig. 2A). Although usually lost during tissue preparation, particles embedded in mucus may be observed both on the crest and on the secondary ledge of the palp ridges (Fig. 2B). The palp ridges may be erect (Fig. 2A, B, C, D) or flattened (Fig. 2E); when erect, the deep rejection tracts (furrows) are exposed, whereas in the flattened state the deep rejection tracts are covered by the ridges.

Visual observation of the smooth palp surface showed it to be variably pigmented brown-black in some individuals of *Placopecten magellanicus*, whereas it was unpigmented in all *Chlamys varia* examined. The smooth palp surface displays scattered clumps of cilia and numerous mucocytes (Fig. 2D), which are most abundant at the palp margins (Fig. 2F).

Anatomy of epithelia

Two types of epithelia characterize the labial palps: a heavily-ciliated, pseudostratified, columnar epithelium on the ridged palp surface, and a sparsely-ciliated cuboidal epithelium on the smooth palp surface (Figs. 2D, F; 3E).

The heavily-ciliated epithelium of the ridged palp surface is composed of three cell types: mucocytes, ciliated

epithelial cells, and simple (non-ciliated) epithelial cells. All three cell types are tall and narrow and rest upon a multi-layered, irregular basal lamella; those of the secondary ledge are approximately twice the length of the cells in other regions of the ridged surface (Figs. 2D; 3E). The mucocytes are of an atypical, elongated, often highly irregular shape (Fig. 3C); their secretions consist of either acid mucopolysaccharides or of neutral mucopolysaccharides, and sometimes of both (Alcian blue–PAS reaction). The ciliated cells are extremely abundant, resulting in a uniform, dense ciliary covering over the ridged palp surface (Fig. 2D, F). These cells are characterized by deep ciliary roots, an electron-clear cytoplasm containing numerous and well-developed Golgi bodies, and a high density of apical microvilli. Numerous lysosomes with homogeneous, electron-dense contents, measuring approximately 0.4 μm in diameter, are present in the apical region (Fig. 3A, B). The basal cell membrane adjacent to the basal lamella presents marked indentations (Fig. 3C). The simple epithelial cells are concentrated at the ridged palp surface margin. Apart from a lack of cilia and a more electron-dense cytoplasm, they are similar to the ciliated cells (Fig. 3A, B).

Histological sections of the palp stained with the modified Masson trichrome, Alcian blue, and Alcian blue–PAS techniques showed the mucocytes to be sparsely distributed over most of the ridged palp surface, usually in small groups, and often just above the secondary ledge and at the ridge crest (Fig. 3E). In the region of the palp margin, the mucocytes are much more abundant (Fig. 2F).

The sparsely-ciliated, cuboidal epithelium of the smooth palp surface consists of the same three cell types observed in the ridged palp surface–epithelium, although in different proportions. Simple epithelial cells and mucocytes dominate, with relatively few ciliated cells. The epithelial cells of the smooth palp surface rest upon a thin, single-layered basal lamella (Fig. 3D). The mucocytes are typical goblet-type cells (Fig. 2D, F). Staining with the Alcian blue–PAS technique showed their secretions to be composed entirely of neutral mucopolysaccharides. In the ciliated and simple epithelial cells from the smooth palp surface, the apical microvilli are less densely distributed than in the corresponding cells of the ridged palp surface (Fig. 3D). The cytoplasm contains extremely well-developed rough endoplasmic reticulum and very numerous ribosomes. Some electron-dense vesicles are also observed in various regions of the cytoplasm, usually in proximity to the arrays of rough endoplasmic reticulum. The morphological characteristics and the cytoplasmic localisation indicate that these organelles are probably not lysosomes. The nucleus has a large, conspicuous nucleolus (Fig. 3D). Pigment granules can be observed in the smooth surface epithelium of some individuals of *Placopecten magellanicus* (Fig. 3E); these are contained within the simple epithelial cells.

Of the 37 histological sections of the ridged surface epithelium which were stained and examined using the Mann-Dominici technique, no cells displaying the staining characteristics of sensory cells observed elsewhere (Beninger et al. in preparation) were observed.

Fig. 3. *Placopecten magellanicus*. (A)–(C) TEMs of ciliated epithelium of ridged surface of labial palp margin, showing simple and ciliated epithelial cells. (A) Low-power micrograph of apical region; ciliated cells (cc) have electron-clear cytoplasm compared to dense cytoplasm of non-ciliated cells (nc); both types display dense microvillous covering (mv), forming a typical brush border with numerous subjacent lysosomes (ly); note abundant Golgi apparatus (G); n: nucleus (scale bar = 1 μm). (B) Detail of (A), showing electron-dense lysosomes (ly) beneath brush border; c: cilium (scale bar = 5 μm). (C) Low-power micrograph of basal region, showing part of elongated mucocyte (mc); ciliated and non-ciliated epithelial cells have indented basal membranes (arrowed); all cells rest upon multi-layered, irregular basal lamella (bl) (scale bar = 1 μm). (D) TEM of sparsely-ciliated epithelium of smooth palp surface, showing non-pigmented epithelial cells resting upon thin, simple, basal lamella (bl); irregularly-shaped nucleus (n) contains large nucleolus (nu); abundant rough endoplasmic reticulum (rer) and a low density of microvilli (mv) characterize these cells; electron-dense vesicles (v) are present in cytoplasm (scale bar = 1 μm). (E) Histological section of palps, showing location of mucocytes (arrowed) on ridged surface; dark coloration of smooth surface is due to natural pigment granules (Alcian blue and trioxymethylene; scale bar = 20 μm). (F) Histological section of crest region of a ridge, showing internal muscle fibres (mf) and haemocytes (h) (modified Masson trichrome; scale bar = 20 μm)

Internal anatomy

The interior of the labial palps consists mainly of lacunar vesicular connective tissue, traversed by smooth-muscle fibres (Figs. 2D, F; 3F); it will herein be referred to as muscular-connective tissue. Besides being present in the palp blood-vessels, haemocytes can be observed in the lacunae of the muscular-connective tissue, indicating that the blood circulation within the palps is open. A thin layer of smooth muscle fibres is found beneath the basal lamella of both epithelia. In each palp ridge, a particularly dense network of smooth muscle fibres extends from the basal lamella of the upper margin of the secondary ledge to the basal lamella of the epithelium of the smooth palp surface (Fig. 2D). Such muscle fibres also traverse the crest region of the ridges, both horizontally and obliquely (Figs. 2D; 3F). Branches of the palp nerve are occasionally observed beneath the smooth muscle layer.

When the scallops are ripe and ready to spawn, acini from the gonad extend into the lacunar palp tissue, giving a secondary pinkish coloration if the subjacent gonad is female. This is most pronounced in *Pecten maximus* (own personal observations), and much less so in either *Placopecten magellanicus* or *Chlamys varia*.

Discussion

The ridged surfaces of bivalve labial palps have often been ascribed a function in the selection of particles prior to ingestion or rejection. This interpretation has been derived either from studies based on the behavior of suspended particles deposited directly on the separated palp surface¹ (Nelson 1960, Stasek 1961, Jørgensen 1966, B. Morton 1979), or from indirect evidence such as stomach contents (Hughes 1975) or pseudofeces contents (Kiørboe and Møhlenberg 1981, Newell and Jordan 1983, Shumway et al. 1985). However, Bernard's (1974) non-quantitative direct observations indicated that there is no particle selection on appressed ridged surfaces (i.e., in the natural state) in *Crassostrea gigas*. Furthermore, as emphasized by Foster-Smith (1975a, 1978), single-particle suspensions do not arrive directly on the palps; rather, groups of particles bound in mucus cords are delivered to the palps from the gills. The arrival of particles bound in mucus cords has been confirmed for all scallop species examined to date (Kellogg 1915, Bernard 1972, Gilmour 1974, Beninger et al. 1988). Under such conditions, selection of individual particles would only be possible if the mucus viscosity were somehow greatly reduced. Newell and Jordan (1983) proposed that mechanical handling by the ciliated ridges would reduce mucus viscosity and allow individual particles to be extracted.

Evidence for selection at the labial palps based on studies of contents of gut or pseudofeces may overlook the fact that modification of the proportions of different particle types can also be accomplished by other sites and mechanisms. Guard tentacles (which are present on the mantle edge in scallops and around the inhalent siphons of many other bivalves) may perform a screening or baffle function (Walter 1975, Palmer and Williams 1980). Most high-density (i.e., inorganic, e.g. silt) particles $> 14 \mu\text{m}$ probably settle onto the mantle and are rejected as pseudofeces before reaching the gills or palps (Bernard 1974), while certain mucus strings formed on the scallop gill may be rejected as pseudofeces before reaching the palps, especially at high particle concentrations (Kellogg 1915, Owen and McCrae 1976). In addition, mechanical sorting may occur in the stomach after particle ingestion (Purchon 1977: p. 226–227; J. E. Morton 1979: p. 114–117).

Meticulous functional observations using the shell-window technique have led Foster-Smith (1975a, 1978) to propose that the palps are not capable of particle selection, but rather should be considered as acceptance or rejection structures, acting on particle-mucus cords, whose behavior is influenced mainly by particle concentration in the medium, and not by any intrinsic property of the particles themselves. Although differential treatment of particles based on weight, density or volume may be excluded (Bernard 1974, Foster-Smith 1975a, b, 1978, Hughes 1975), growing evidence indicates that the organic coating or composition of a particle may influence its probability of ingestion (Taghon 1982, Newell and Jordan 1983, Ward and Targett 1989). Recent investigations have shown that, in the case of particles coated with algal ectocrines, preferential selection is not due to an increased adhesiveness of such particles (Targett et al. in preparation). In any event, the predominance of the moderately-sized alga *Phaeodactylum tricorutum* in the pseudofeces of scallops fed with moderate concentrations ($10^4 \text{ cells ml}^{-1}$) of a mixed cell suspension, as reported by Shumway et al. (1985), strongly argues for some sort of selection either at the gills (for which no mechanism has yet been proposed), or at the labial palps.

Assuming that a mechanism exists which would allow the extraction of individual particles from mucus cords at the labial palps, selection on the basis of the recognition of intrinsic particle characteristics would require sensory structures within the ridged surface epithelium, as postulated for *Crassostrea virginica* (Newell and Jordan 1983). Furthermore, given the small size of most food particles, such cells would have to be fairly numerous in order to be encountered by particles before the latter are included in new mucus cords destined for ingestion. The existence of very infrequent putative taste-receptors on the smooth palp surface has been inferred from electrophysiological studies of the labial palps of *C. gigas* (Dwivedy 1973) but, since this surface does not participate in particle handling under normal circumstances (see footnote at beginning of "Discussion"), such information is of limited relevance. Furthermore, it is uncertain what effect distilled-water rinses of the palp might have had on the recorded potentials. Similarly, although putative sensory cells have been

¹ Galtsoff (1964) deposited inert particles directly on the unseparated palps of *Crassostrea virginica*, i.e., on the smooth palp surface. His subsequent interpretation of particle behavior and palp function failed to recognize that food particles are not deposited on this surface under natural conditions

reported on the ridged surface of the palps of *Anodonta* sp. (Matthews 1928), this interpretation was based on the comparative thickness of the cilia as viewed under the light microscope, as well as on the uptake of a methylene blue stain. No noticeable differences in cilia thickness were observed in the two species (*Placopecten magellanicus* and *Chlamys varia*) of the present study using either light microscopy, scanning or transmission electron microscopy; in addition, it should be noted that mucocytes also stain readily with methylene blue. As histological examination using the Mann-Dominici technique failed to reveal cells with staining properties similar to those of sensory cells found elsewhere in scallops (Beninger et al. in preparation), the existence of such cells on the labial palps of bivalves therefore remains to be demonstrated unequivocally.

In the absence of conclusive data on sensory structures, it is not yet possible to determine whether or not the labial palps are involved in selection of individual particles based on their intrinsic characteristics. However, it is clear that particle rejection depends upon ambient particle concentration. Under conditions of low particle concentration, the mucus strings from the gills arriving in the oral groove form a relatively compact cord, which may proceed directly to the mouth (Kellogg 1915, Beninger et al. 1988). Under conditions of increasing particle concentration, the mucus cord is more massive, and tends to be pulled out of the oral groove and onto the ridged palp surface, presumably by the ciliated crest rejection-tracts (Kellogg 1915). The subsequent handling of this material is quite complex, and may not only change within an individual for a given region of a ciliated tract depending on its location in the ridged surface, but also with the shape of the underlying ridge and palp (Foster-Smith 1978). A generalized description of the behavior of the ridged palp surface has nevertheless been given by Foster-Smith. Handling of the mucus cords (i.e., direction to acceptance or rejection tracts) is conditioned by the degree to which the palp ridges are erected. The dense network of muscle fibres extending from the secondary ledge to the basal lamella of the smooth surface would thus be responsible for this behavior in the two species studied here. The formation of notches in the crests of the ridges, allowing acceptance of the mucus cords when the palps are relatively flattened, would similarly be mediated by the muscle fibres observed in the crest region. Through their highly plastic treatment of mucus strings, the ridged surfaces of the labial palps may thus function to attenuate the potential overload of the bivalve's ingestive capacity when particle concentration increases.

Several points should be made concerning the distribution of mucocytes on the palps. The relatively low density of such cells on the ridged surface (with the exception of the palp margins), attests to its predominantly mechanical role. This surface probably does not add much mucus to the cords and particle groups on the palps, with the possible exception of the re-sorting tract above the secondary ledge. The addition of mucus at this level may determine to which ciliated tract the particle groups or cords in this region will be directed, and ultimately their acceptance or rejection. Bernard (1974) postulated that

the palps function primarily as mucus reducers, concentrating food particles and rejecting mucus as pseudofeces, thus minimizing the amount of mucus ingested. In addition to the fact that such a continual loss of mucus would be energetically inefficient, this interpretation is not supported by the anatomical evidence of the present study which demonstrates the presence of mucocytes on the ridged palp surface. Furthermore, ongoing research shows that there is a high density of active mucocytes around the mouth and in the oesophagus (Beninger et al. 1990, and in preparation), such that more mucus is actually added at these levels.

The mucus secretions of the ridged surface are qualitatively different from those of the smooth surface. The existence of two mucus types of different viscosities has been observed on the ridged surface of the labial palps of *Crassostrea gigas*, and this has been related to particle handling or rejection (Bernard 1974), which is performed by the ridged surface only.

The very high density of mucocytes on the ridged and smooth surfaces of the palp margin is probably related to the rejection of material arriving from the ridged surface into the exhalent current of the pallial cavity. Neutral mucopolysaccharide-secreting mucocytes are quite abundant on the general smooth palp surface. Although mucocytes are typically present in the molluscan integument (see Bubel 1984), they may serve an important function in this particular location. Several authors have pointed out that the Pectinacea have evolved muscular-driven mechanisms for the expulsion of pseudofeces, which consequently generate a strong current in the buccal region (Yonge 1967, B. Morton 1979). Such periodic currents would tend to separate the palps and expel potential food material along with the pseudofeces. However, the presence of a well-developed mucus layer on the smooth palp surfaces offers little frictional resistance, such that the cleansing currents could pass over this surface without unduly disturbing the palps.

Previous reports of the presence of sub-epithelial mucocytes in five non-pectinid species (Galtsoff 1964, Bernard 1974, Foster-Smith 1975a) were not confirmed for the two species studied here. Indeed, the presence of such cells within the muscular-connective tissue beneath the basal lamella would constitute an anatomical anomaly.

In contrast to Galtsoff's (1964) observations of paraffin-embedded labial palps of *Crassostrea virginica*, the data of the present study clearly show that the epithelium of the smooth palp surface of *Placopecten magellanicus* and *Chlamys varia* is only sparsely ciliated, and obviously not specialized for the transport of particles. Galtsoff's observations of the movements of particles deposited on these surfaces in *Crassostrea virginica* should thus be interpreted with caution (i.e., not confused with normal cleansing behavior of the pallial organ epithelia) until detailed anatomical studies of the smooth palp surface have been performed in this species.

The ultrastructural characteristics of the ridged surface epithelium strongly suggest an accessory nutritive role. The microvillous brush border, together with the internal ramifications of the basal cell membrane are

characteristic of the absorption of dissolved substances, whereas the numerous Golgi apparatus, lysosomes and phagosomes indicate the capture and digestion of large molecular agglomerates and colloidal matter. A similar function has been attributed to other epithelial regions over which water flow (and hence dissolved organic and colloidal matter) is considerable: the gills (Pasteels 1968, Beninger et al. 1988, Le Pennec et al. 1988) and the mantle (Bevelander and Nakahara 1966, Nakahara and Bevelander 1967). In the case of the appressed ridged surfaces of the labial palps, water flow would be comparatively small, but the mechanical handling of the mucus cords would necessarily result in the dissolution of some of the mucus and the dissociation of some of the smaller particles. Both of these substances could be recovered by the epithelial cells of the ridged surface. Hence, while this surface might not be a mucus reducer in the sense originally proposed by Bernard (1974), some mucus reduction would result from the normal ridged-surface activity; recycling dissociated material originally destined for ingestion would maximize trophic efficiency and reduce overload in the digestive system.

The smooth palp surface, which does not handle mucus cords, does not present these ultrastructural characteristics. Rather, the simple epithelial cells from this surface exhibit cytological evidence of active molecular synthesis (well-developed rough endoplasmic reticulum, large nucleolus). Occasional electron-dense vesicles occurring close to the arrays of rough endoplasmic reticulum are possible sites for product accumulation; however, it is not yet clear whether these products serve in the metabolism of the epithelial cells or are released as secretions to the external medium.

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