

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

II. The lips*

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Abstract. In order to gain a better understanding of the roles of the peribuccal organs of scallops in feeding, the structure and ultrastructure of the arborescent lips of *Placopecten magellanicus* and *Chlamys varia* were examined using histological and electron-microscope techniques. The anatomical and histological characteristics of the lips suggest that they are closely related to the labial palps. The lips are formed of a densely-ciliated, ramified oral epithelium and a sparsely-ciliated epithelium which links the ramified ciliated ridges and entirely constitutes the aboral surface. The differential distribution of the three epithelial cell types (ciliated, non-ciliated, and mucocytes), as well as the ultrastructural characteristics of the ciliated and non-ciliated cells and the secretions of the mucocytes suggest that the arborescent lips play at least four different roles in feeding: (1) as a mechanical shield to prevent the loss of mucus-bound food material in the buccal region due to muscular-driven cleansing and swimming currents; (2) as a trap for food material which is lifted out of the oral groove due to especially strong muscular-driven currents; (3) the consolidation of mucus cords from the strands arriving from the palps and of those which have been disturbed by the cleansing currents; (4) the absorption of any dissolved and colloidal matter which may dissociate from the mucus-particle masses in the buccal region. No anatomical detectors or effectors were observed which would suggest a role in particle selection.

Introduction

In recent years, through indirect techniques such as studies of particle clearance, stomach-content analysis and pseudofeces-feces analysis (Hughes 1975, Kiørboe and Møhlenberg 1981, Shumway et al. 1985), important contributions have been made to the understanding of

bivalve feeding. Although such studies reveal the characteristics of feeding phenomena, they do not elucidate the mechanisms and effectors of such phenomena. In addition, such studies may suffer from several sources of experimental bias (see Foster-Smith 1978). In order to achieve a more complete interpretation of bivalve feeding, structural and ultrastructural data are therefore necessary.

Compared to the extensive literature concerning the structure and function of gills in bivalve nutrition (see Beninger et al. 1988 and Le Pennec et al. 1988 for references), relatively few studies have been performed on the peribuccal organs, i.e., the labial palps and lips. Details of the structure and ultrastructure of the labial palps of the scallops *Placopecten magellanicus* and *Chlamys varia* (family Pectinidae) and an interpretation of their functions are presented in the companion study immediately preceding this contribution (Beninger et al. 1990). Despite their strategic location and their visibly complex anatomy, the lips of pectinids have been the object of scant and sporadic study, and most of this has been of a functional nature, giving rise to conflicting interpretations (Yonge 1967, Bernard 1972, Gilmour 1964, 1974, B. Morton 1979). Moreover, an accurate evaluation of the roles of the lips in feeding has been hampered by the lack of detailed information concerning their anatomy. Although some histological information exists (Gilmour 1964), this is far from complete, and to the best of the authors' knowledge, no ultrastructural studies have been performed to date. Recent research on the structure and ultrastructure of the labial palps of *P. magellanicus* and *C. varia* has revealed potential accessory roles in feeding and possibly secretion (Beninger et al. 1990); it is therefore of interest to perform such studies on the lips of these two species.

A number of monomyarian bivalves, including the Pectinidae, present arborescent lip structures, while other mono- and dimyarians display non-arborescent lips which are developed to various degrees and arranged in configurations of varying complexity. Functional interpretations of these structures have sometimes failed to

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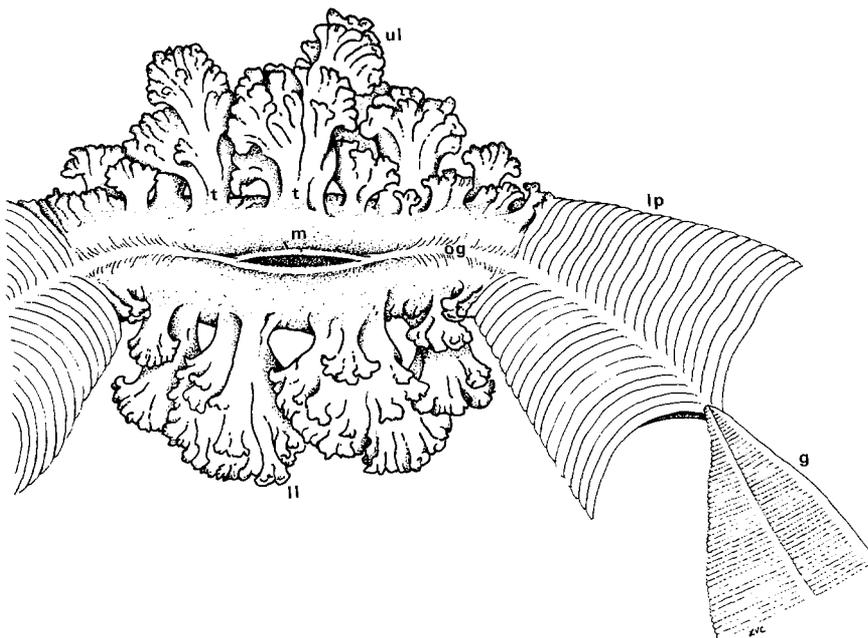


Fig. 1. *Placopecten magellanicus*. Gross morphology and anatomical relationships of gill (g), labial palps (lp), upper lips (ul), lower lips (ll), mouth (m), and oral groove (og); lips and labial palps have been pulled apart to reveal oral region. t: lip trunks

distinguish between complex configurations of otherwise hypertrophied lips and true arborescent lips (Gilmour 1974). The lips of pectinids will herein be referred to as arborescent lips of the chlamid type (Bernard 1972).

The present study investigates the detailed structure and ultrastructure of the arborescent lips of *Placopecten magellanicus* and *Chlamys varia*, and examines the implications of such anatomical data for feeding in these two species.

Materials and methods

The normally-expanded lips of *Placopecten magellanicus* and *Chlamys varia* contract rapidly in response to adverse tactile or chemical stimulation (e.g. dissection and fixation). The following standard techniques of narcotization were attempted on several occasions without success: progressive lowering of water temperature to freezing; progressive addition of $MgCl_2$, $MgSO_4$, ethanol, propylene, phenoxetol, methanol and xylocaine. Further trials using chemical narcotizers were abandoned, since there is a real possibility of inducing structural artefacts, such as those produced with tricaine methanesulfonate (MS-222 Sandoz) (Speare and Ferguson 1989). Although it is more difficult to deduce the spatial organization of the lips in the contracted state, this problem is not insurmountable.

Sampling, maintenance, and preparation of specimens for histology, scanning and transmission electron microscopy is described in the preceding paper (Beninger et al. 1990).

Results

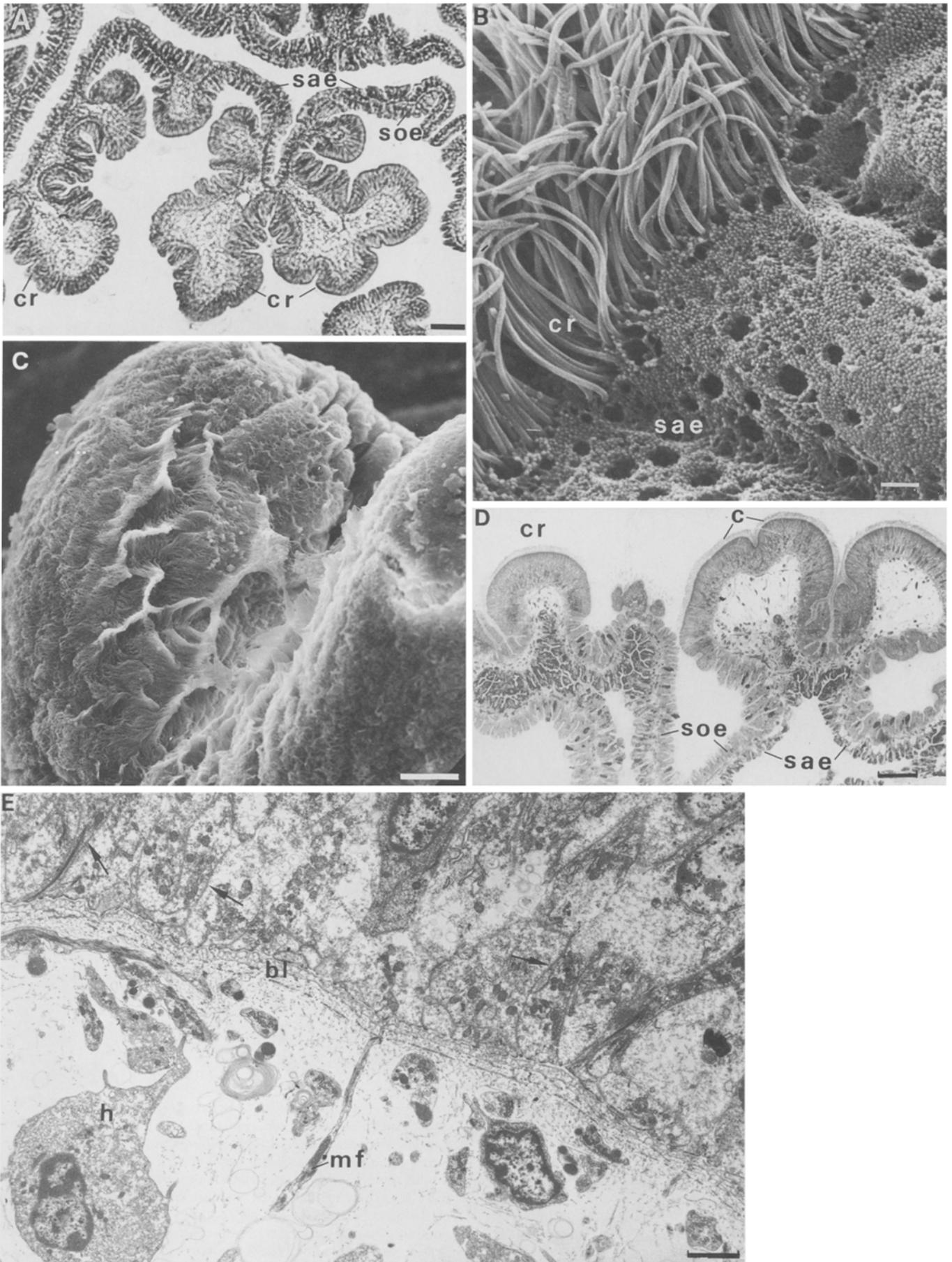
The structural and ultrastructural characteristics of the lips of both species were found to be nearly identical, hence the following detailed description for *Placopecten magellanicus* applies equally to *Chlamys varia*; any exceptions are explicitly noted. The anatomical terminology used in the present work derives from previous studies of the lips and labial palps, notably by Gilmour (1964, 1974), Bernard (1972) and Beninger et al. (1990).

General topography and anatomical relationships

The lips arise as ramifications of the anterior margins of the labial palps, and also as independent, branched lobes of the upper and lower peribuccal surfaces (Fig. 1). The upper and lower distal lip extremities often interdigitate in the relaxed state, forming a frilled hood over the mouth.

The lips are composed of two different types of epithelia, which are strikingly similar to those of the labial palps (Fig. 2 A, D). In those parts which arise as ramifications of the labial palps, the ridged and smooth palp surfaces are continuous with the oral and aboral lip surfaces, respectively. In those parts of the lips which arise as independent protuberances around the mouth, the spatial organization of the two epithelia is somewhat more complex. At the base of the lip trunks, the oral surface is entirely ciliated, while the aboral surface is sparsely ciliated from the base to the distal extremities. As the protuberances ramify distally, the sparsely-ciliated epithelium joins the ciliated ramifications of the oral surface, creating a complex webbed structure. Hence, at the distal lip

Fig. 2. *Placopecten magellanicus*. (A) Light microscopy of histological section of distal extremities of lips; irregularly-folded ciliated ridges (cr) are joined by sparsely-ciliated oral (soe) and aboral (sae) epithelial tissue flaps; modified Masson trichrome (scale bar = 40 μm). (B) SEM of lips, showing transition between aboral sparsely-ciliated epithelium (sae) and ciliated ridges (cr) of oral lip surface (scale bar = 1 μm). (C) SEM of distal extremity of lips, showing extensive and dense ciliation of ciliated ridges (scale bar = 25 μm). (D) Semithin section of lips, showing pigmented, sparsely-ciliated aboral epithelium (sae), non-pigmented sparsely-ciliated oral epithelium (soe), ciliated ridges (cr) and cilia (c); toluidine blue (scale bar = 20 μm). (E) TEM basal region of ciliated oral epithelium; note multi-layered basal lamella (bl) and indentations of cell membrane (arrowed); in sub-epithelial region, smooth-muscle fibres (mf) inserting into basal lamella, and haemocytes (h) are visible (scale bar = 2 μm)



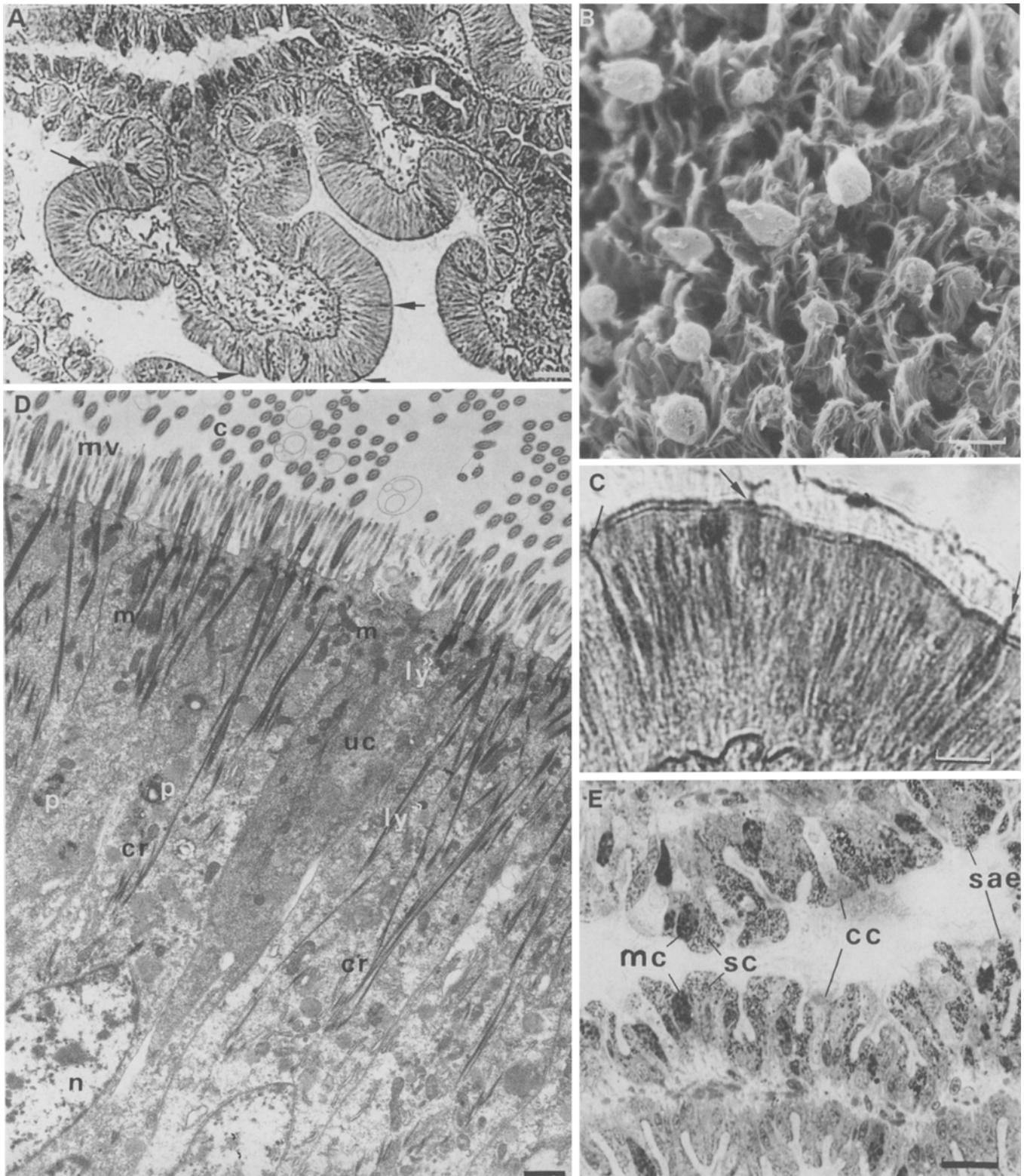


Fig. 3. *Placopecten magellanicus*. (A) Histochemical localization of mucocytes (arrowed) in distal region of lips; Alcian blue and trioxymatein (scale bar = 20 μm). (B) SEM showing intense mucus secretion at ciliated base of oral lip epithelium; incomplete rinsing prior to critical-point drying allows retention of some mucus balls on epithelial surface (scale bar = 5 μm). (C) Detail of histological section of ciliated oral epithelium of lip bases, showing numerous mucocytes (arrowed) and their secretions; Alcian blue and trioxymatein (scale bar = 4 μm). (D) TEM of apical region of ciliated oral epithelium; note numerous apical microvilli (mv) and high

density of cilia (c), with deep ciliary roots (cr) and associated mitochondria (m) at apical pole; lysosomes (ly) and phagosomes (p) of various types are scattered throughout supranuclear region; n: nucleus; uc: undifferentiated cell (scale bar = 1 μm). (E) Semithin section of sparsely-ciliated epithelial tissue flaps joining adjacent ciliated ridges. Three epithelial cell types are visible: simple (non-ciliated) epithelial cells (sc), mucocytes (mc), and infrequent ciliated cells (cc); note pigment granules in non-ciliated cells of aboral epithelial surface (sae); toluidine blue (scale bar = 15 μm)

extremities, histological sections show oral ciliated ridges interrupted by sparsely-ciliated lamellae (Figs. 2 A, D; 3 E). However, only the aboral surfaces of the sparsely-ciliated epithelium are variably pigmented in some *Placopecten magellanicus*, while no pigment was present in any of the *Chlamys varia* examined.

At the distal extremities of the branched lobes, the heavily-ciliated epithelium is folded to such a great extent compared to the sparsely-ciliated epithelium (its corresponding "smooth" surface, as in the labial palps), that it may be the only surface visible from the exterior; it thus constitutes both the oral and outer surfaces in these regions (Fig. 2 C). The designation of the lip surfaces as "inner" and "outer" (e.g. ciliated inner surface, smooth outer surface) is therefore misleading, and it is preferable to designate epithelial types and their orientation with respect to their origins in the peribuccal region (i.e., oral and aboral).

Microanatomy and ultrastructure of the epithelia

Histological sections reveal that the complex ciliated ridges of the lips may be viewed as having the same general structure as a palp ridge which has been thrown into several irregular folds (Figs. 2 A, D; 3 A). The similarity between the labial palp ridges and the lip ridges extends to the tissue organization and cell types present. The pseudo-stratified, columnar epithelium of this surface rests upon a multi-layered basal membrane, and is composed of two cell types: ciliated cells and mucocytes. Occasional undifferentiated cells can also be observed (Fig. 3 D).

The ciliated cells are tall and slender, and are characterized by numerous cilia whose roots extend to the supranuclear region of the cell (Fig. 3 D). A conspicuous layer of mitochondria is distributed among these roots at the apical pole. The apical membrane forms a dense covering of microvilli in a brush-border arrangement. Several lysosomes and phagosomes can be observed throughout the supranuclear region of the cells (Fig. 3 D). The cell membrane at the basal pole presents tall indentations which extend well into the cytoplasm (Fig. 2 E).

The tall, slender mucocytes of the heavily-ciliated epithelium are irregularly distributed over the oral surface, being most numerous at the trunk bases in proximity to the mouth and relatively rare at the distal extremities (Fig. 3 A, B, C). The mucocytes at the trunk bases are very active (Fig. 3 B, C), whereas those at the distal extremities appear to be relatively inactive (Fig. 3 A; weak Alcian blue colorations). The secretions of the ciliated ridges of the oral epithelium consist of either acid mucopolysaccharides, neutral mucopolysaccharides, or of both together (Alcian blue – periodic acid-Schiff reaction).

The sparsely-ciliated epithelium is cuboidal, and strongly resembles the smooth surface of the labial palps, although the pronounced retraction of the lips upon dissection and fixing forces the cells to assume a pedunculated appearance (Fig. 3 A, E). On the aboral surface, the abundant mucocytes consist of characteristic goblet cells

(Fig. 3 E), whose secretions are comprised entirely of neutral mucopolysaccharides. Electron-clear ciliated cells are sparsely distributed among the mucocytes and non-ciliated epithelial cells (Figs. 3 E; 4 B). The apical pole of the ciliated and non-ciliated cells is characterized by extensive microvilli forming a brush border with a glycocalyx, while the basal pole presents a thin, highly-convoluted basal lamella (Fig. 4 A). Lysosomes and phagosomes are very abundant at the apical pole of the sparsely-ciliated epithelium of the oral surface (Fig. 4 A), but not on the aboral surface (Fig. 4 B). Membrane-bound dark-pigment granules resembling melanosomes are visible in the non-ciliated cells of the sparsely-ciliated epithelium of the aboral surface of the lips of *Placopecten magellanicus* (Figs. 3 E; 4 B); these are similar to those found in the smooth epithelium of the labial palps, and are thus responsible for the variably dark coloration seen in the lips of this species. No such pigment was observed in the corresponding cells of the *Chlamys varia* specimens examined.

No sensory cells were observed in the oral epithelium of any of the 37 sections examined using the Mann-Dominici staining technique (Gabe 1968: p. 766–767; p. 960–961), nor were any tufts of long sensory cilia evident under the scanning electron microscope. None of the cells examined using transmission electron microscopy displayed ultrastructural characteristics of sensory cells found elsewhere (e.g. tentacles or abdominal sense organ, Moir 1977 a, b; gill axis, Beninger et al. in preparation).

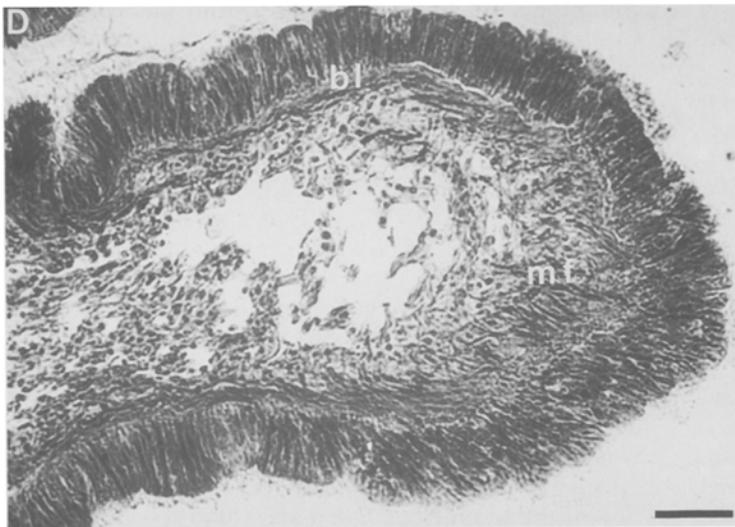
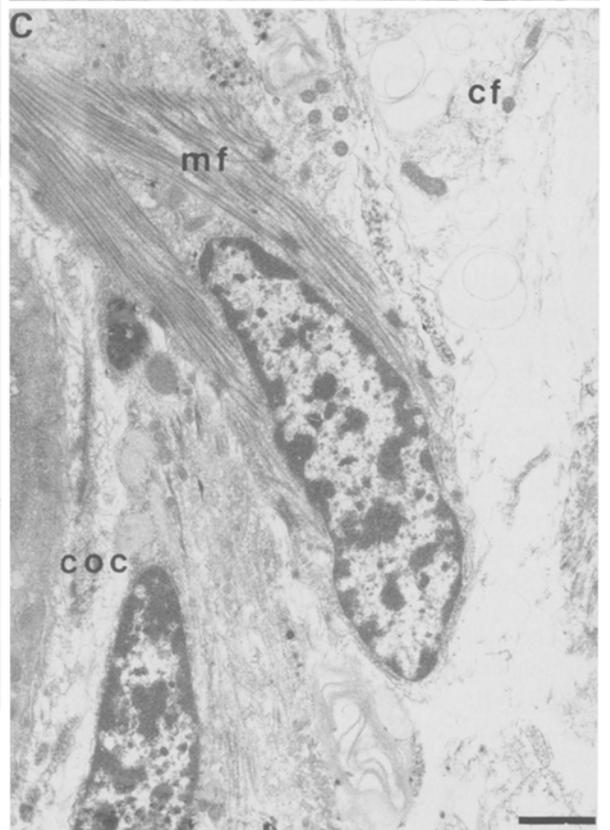
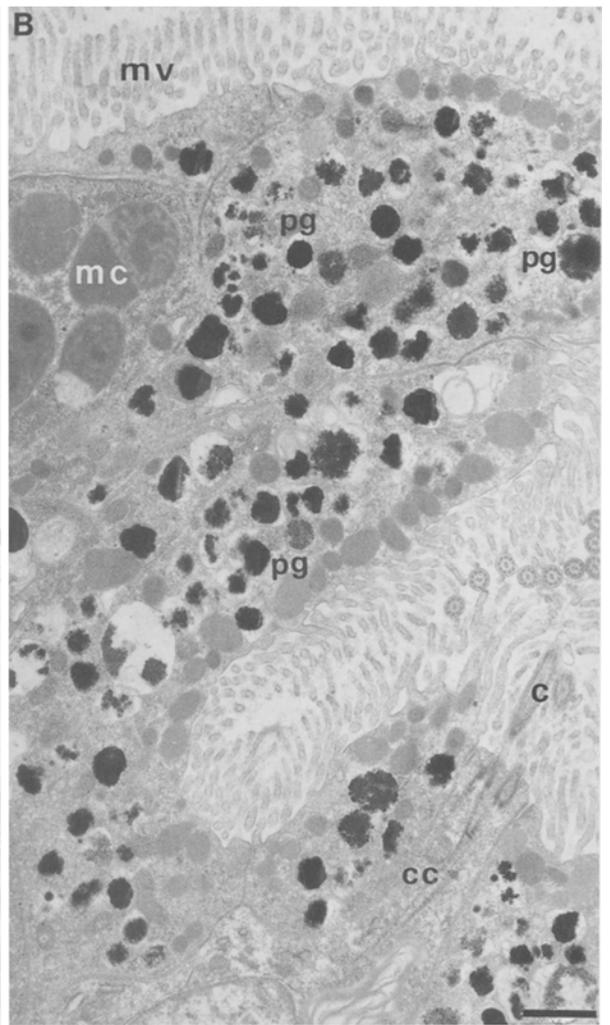
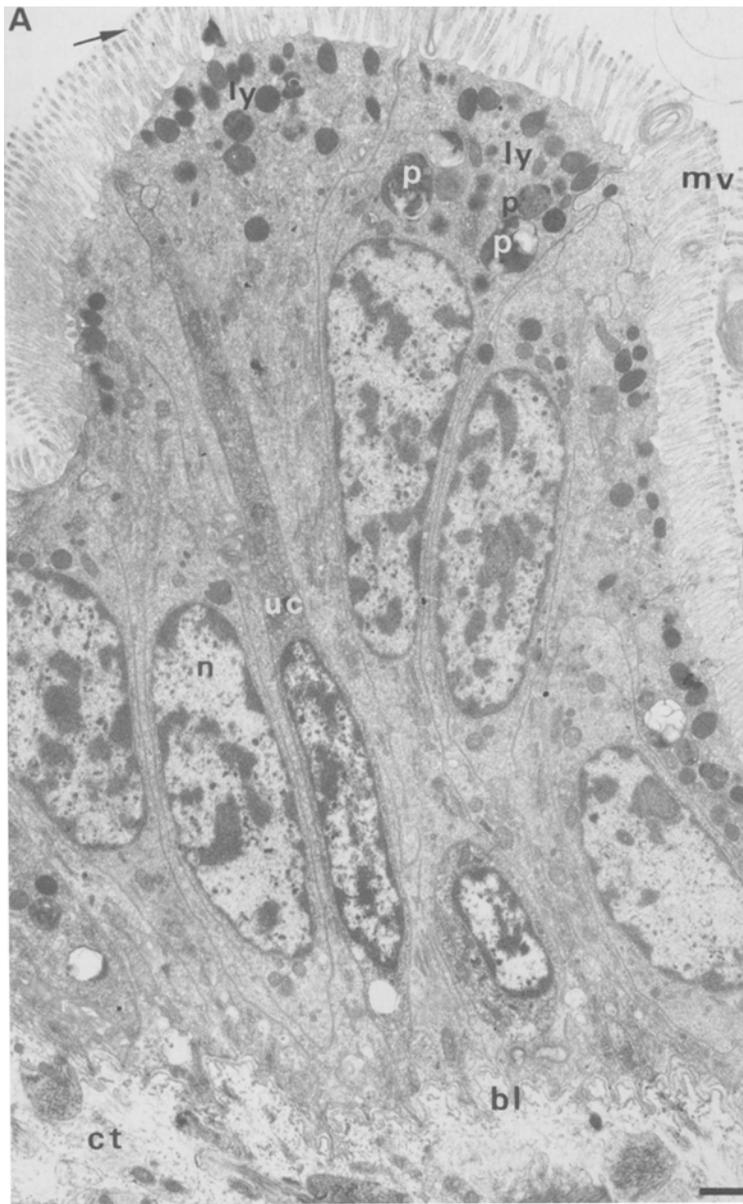
Internal anatomy

The internal anatomy of the lips is similar to that of the labial palps, with the obvious modifications of extensive ramification and folding. Beneath the epithelial cells is a diffuse layer of smooth muscle (Fig. 4 D). The remainder of the internal structure is composed of lacunar vesicular-connective tissue; haemocytetes are often visible in the lacunae, indicating that the expansion of the lips is accomplished via positive pressure within the haemocoel. Contraction of the lips is probably effected by the smooth-muscle fibres (Fig. 4 C, D). It may be assumed that, in the relaxed state, the lips and their branched extremities are much less folded than they appear after dissection and fixation.

Discussion

Previous authors have suggested that in species possessing arborescent lips, these are entities distinct from the labial palps, and that they do not share a common embryological origin (see Bernard 1972). However, the great degree of structural and histological similarity of these two organs, as well as the fact that part of the lips derives directly from the anterior palp margin, with a continuation of the respective ciliated and smooth epithelia, tend to argue for a very close anatomical relationship.

The observations of the present study on *Placopecten magellanicus* and *Chlamys varia* confirm the macroscopic



organization of the scallop lips as presented by previous authors (Yonge 1967, Bernard 1972), and are at variance with the representation of Gilmour (1964), which showed the upper and lower lips forming a tube over the mouth. Not only are the lips free, but their natural appearance resembles more a cauliflower than a tube.

The mucocytes of the ciliated ridges and their two different secretions are histologically and histochemically identical with those of the labial palp ciliated-ridges, whereas the goblet cells and their homogeneous secretions of the sparsely-ciliated epithelia are identical to those of the smooth palp surface (Beninger et al. 1990), suggesting a similarity of mucus function for the corresponding surfaces of these two peribuccal organs.

The differential distribution of mucocytes on the oral surface suggests a corresponding dichotomy of function between the proximal and distal regions. The first of these would appear to be related to the preparation of material for ingestion. Particles arrive at the labial palps of bivalves bound in mucus cords (Kellogg 1915, Bernard 1972, 1974, Gilmour 1974, Foster-Smith 1975, 1978, Beninger et al. 1988). As particle concentration in the external medium increases, the cords are subjected to mechanical handling by the ridged palp surface, during which they may break into strands or agglomerates of various lengths (Foster-Smith 1975, 1978). Although it has not yet been demonstrated unequivocally that the labial palps are capable of extracting and selecting individual particles from the mucus strands (Beninger et al. 1990), accepted material from the ridged palp surface will nonetheless arrive at the oral groove proximal to the mouth in the form of independent masses. The intense mucosecretory activity of the ciliated oral-lip surfaces at the trunk bases may thus serve to consolidate this material into a single mucus strand prior to entry into the mouth. This would facilitate the passage of particles to the stomach, where the mucus strand would be drawn in and wound around the rotating crystalline style prior to digestion (Purchon 1977: p. 225–228; J. E. Morton 1979: p. 114–117). The proposed role of the lip bases in consolidating mucus strings does not account for their arborescent structure, and it is probable that even those bivalves possessing simple lips present such an adaptation of the lip bases and peribuccal epithelium. Further study on other species is needed to test this hypothesis.

Although this mode of particle ingestion is supported by direct observation of material prior to ingestion (see Kellogg 1915, Bernard 1972, 1974, Gilmour 1974, Foster-Smith 1975, 1978, Beninger et al. 1988), as well as by the anatomical data of the present study, it is at variance with Kjørboe and Møhlenberg's (1981) observation that particles in the oesophagus of *Mytilus edulis* were in free suspension, whereas particles in pseudofeces were bound in mucus. Moreover, as pointed out by Newell and Jordan (1983), in their study on *Crassostrea virginica*, it is difficult to see how suspended particles could be ingested, given the capstan mechanism of the crystalline style (Purchon 1977, J. E. Morton 1979). Similarly, histological observations of the oesophageal epithelium of *Placopecten magellanicus* and *Pecten maximus* have shown it to contain a very high density of active mucocytes (A. Donval and P. Beninger, Laboratoire de Biologie Marine, Université de Bretagne Occidentale, Brest, France, unpublished observations). Bernard's (1974) report of particles bound in mucus in the oesophagus of *Crassostrea gigas* also conflicts with the observations of Kjørboe and Møhlenberg. Preliminary results of histological examination of the oesophagus of wild *M. edulis* have confirmed the presence of abundant mucocytes, as well as mucus-bound particle masses (Beninger et al. in preparation). It would thus appear that food material ingested by bivalves is bound in mucus, rather than in free suspension; the lip bases add mucus to the arriving food material, thus consolidating the mucus strands, whose entry into the stomach is assisted by the rotating crystalline style.

Various interpretations have been advanced concerning the role of the complex lip topography in feeding. Bernard (1972) stated that mucus-bound food masses from the labial palps travelled over the aboral lip surface, where they were subjected to screening by the interdigitations of the upper and lower lips; small particles penetrated through to the oral surface, while large particles and mucus masses were rejected as pseudofeces. Such observations cannot be reconciled with the anatomical data of the present study. As previously shown, the ciliated surface of the lips is a continuation of the ridged palp surface; for the mucus masses to be transferred directly to the aboral lip surface they would have to change surfaces, and no possible anatomical effectors for this have been observed. In addition, the aboral lip surface is only sparsely ciliated, and is certainly not an epithelium specialized for the transport of material. This proposed screening function therefore seems improbable, as pointed out by B. Morton (1979).

The most convincing interpretation of the functional significance of the lips of scallops was first put forward by Yonge (1967) and later supported by B. Morton (1979). True complex lips of the chlamid and limid type are only present in those monomyarians which have evolved a mechanism of expelling pseudofeces from the mantle cavity via periodic movements of the valves, effected by the adductor muscle (i.e., the Pectinacea and Limacea; all other monomyarians and dimyarians expel pseudofeces via ciliary tracts and cilia-driven currents). Muscle-driven currents exit at

Fig. 4. *Placopecten magellanicus*. (A) (B) TEMs of sparsely-ciliated epithelium of lips. (A) General view of non-ciliated cells of sparsely-ciliated oral epithelium, showing dense microvilli (mv) forming a brush border with a glycocalyx (arrowed) as well as numerous lysosomes (ly) and phagosomes (p) with electron-dense contents; bl: basal lamella; ct: vesicular-connective tissue; n: nucleus; uc: undifferentiated cell (scale bar = 1 μ m). (B) TEM showing membrane-bound dark-pigment granules (pg) of various electron densities in non-ciliated aboral epithelial cells. c: cilia; cc: ciliated cell; mc: mucocyte; mv: apical microvilli (scale bar = 1 μ m). (C) TEM from internal region of lips; connective cells (coc) and muscle fibres (mf) are scattered among loose array of collagenous fibres (cf) (scale bar = 1 μ m). (D) Histological section of part of ciliated ridge, showing extensive layer of smooth-muscle fibres (mf) beneath basal lamella (bl); modified Masson trichrome technique (scale bar = 20 μ m)

the antero-dorsal and postero-dorsal mantle margins; the anterior current would thus tend to expel the food-laden mucus strings in the buccal region prior to ingestion. The presence of a protective hood such as that afforded by the interdigitating arborescent lips of the Pectinacea or the fused, spherical lips of the Limacea (B. Morton 1979) would thus reduce the loss of food strings during clearance of pseudofeces. As has been noted for the smooth surface of the labial palps, (see companion study immediately preceding this contribution), the particularly abundant mucocytes of the aboral lip epithelium may serve to reduce the frictional resistance at the epithelium-pallial fluid interface. This would consequently attenuate the adverse effect of the anterior cleansing current on the lips.

It is interesting to note that the successful evolution of the muscle-driven cleansing current, conditioned in part by the simultaneous evolution of the complex lips, was an important factor in the evolution of swimming behavior in those Pectinacea and Limacea which are capable of such behavior (Yonge 1967). Indeed, when the violent valve-snap response occurs, the lips are contracted around the mouth region, offering an even greater degree of protection from the currents so generated.

The above interpretation of the role of the arborescent lips does not account for the extensive ciliation of the ridges of the oral surface. The ciliation of the ridged oral surfaces, from the bases to the distal extremities, is as dense as that observed for the ridged surface of the labial palps of *Placopecten magellanicus* and *Chlamys varia* in the present study. This extensive ciliation could accomplish either or both of two functions: generation of water currents, and transport of solid material. It is unlikely that these cilia function to create water currents, as these would have a negative effect on the stability of the mucus cords being ingested. A much more plausible function for these cilia would be to trap any food material that, in spite of the protection afforded by the lips, is lifted out of the oral groove in the buccal region during muscular cleansing movements. Support for this interpretation comes from the histological similarity of the mucocytes and their secretions with those of the ciliated ridges of the labial palps, which are specialized in particle-handling. The lips of scallops would therefore serve at least three functions with respect to the ingestion of food material: (1) as a mechanical shield to prevent the loss of mucus cords in the buccal region, due to the anterior cleansing current; (2) as a trap for food material which is lifted out of the oral groove due to especially strong muscular-driven currents (the extreme being swimming behavior); (3) the consolidation of mucus strands from the cords arriving from the labial palps and of those which were disturbed by cleansing currents, trapped by the lip oral cilia, and transported back to the oral grooves.

The apparent absence of sensory cells on the oral epithelium of the lips mirrors the results obtained for the labial palps (Beninger et al. 1990). More detailed research will be required to determine whether specialized or "cryptic" sensory cells are present on the lips; however, these preliminary results suggest that the lips have no major sensory role and thus are not involved in particle selection.

The ultrastructural data for the ciliated and non-ciliated epithelial cells of both the oral and aboral surfaces is highly suggestive of a role in the absorption of dissolved matter; furthermore, both the densely-ciliated and the sparsely-ciliated epithelium of the oral surface appear to be capable of absorbing colloidal matter, as has previously been reported for the ridged surface of the labial palps (Beninger et al. 1990). Such an alternative trophic function would be amplified by the extensive ramification of the lips. It is interesting to note that the aboral epithelium appears to have a lesser absorptive role than the oral epithelium, as was also the case for the labial palps (Beninger et al. 1990). The periodic increase in water flow in the buccal region brought about by the cleansing currents would tend to dissolve some of the mucus and dissociate some of the smallest particles prior to ingestion, whereas the ramified oral epithelium would recover most of the material that might otherwise escape ingestion. This constitutes a fourth possible role for the lips, supported by ultrastructural data.

The arborescent lips of scallops thus appear to be structures which fulfill several key functions in the ingestion of food material, as well as possessing a possible alternate trophic role which is amplified by their highly branched topography. Further information is needed concerning the histology and ultrastructure of the lips of non-pectinaceans, in order to achieve a more comprehensive understanding of lip function in the Bivalvia.

The detailed structural and ultrastructural observations of the lips reported here, combined with similar studies of the gills (Beninger et al. 1988, Le Pennec et al. 1988) and labial palps (Beninger et al. 1990) clarify the problems and provide baseline data necessary for the elucidation of the mechanisms of scallop feeding phenomena such as particle capture and selection. Although complete resolution of these fundamental questions has not yet been achieved, recent and current progress in this field is encouraging (see Beninger 1990 for review).

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