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The osphradium in *Placopecten magellanicus* and *Pecten maximus* (Bivalvia, Pectinidae): histology, ultrastructure, and implications for spawning synchronisation

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Abstract The bivalve osphradium is a band of putatively sensory tissue located in the gill axis, whose function is uncertain. In the present study, extending from 1987 to 1994, anatomical, histological, and electron microscopical techniques were used to elucidate the structure and ultrastructure of the osphradium in hatchery *Pecten maximus* L. and *Placopecten magellanicus* (Gmelin) (collected from Passamaquoddy Bay, New Brunswick, Canada). The osphradium consists of two distinct regions which run longitudinally on both sides of each gill axis: the osphradial ridge, and the dorsal tuft cilia region. The osphradial ridge was largely devoid of cilia other than those of the few free nerve fibres. The dorsal tuft cilia region contained free nerve fibres and ciliary tufts, separated by undifferentiated epithelial cells. No paddle cilia were observed under isosmotic fixation conditions, although under hypotonic conditions such cilia were quite common, suggesting an artefactual nature. Most of the cells of the osphradial ridge were highly secretory, the principal products being large pigment granules (in *Pecten maximus*) directly secreted by the Golgi bodies, and numerous small, electron-dense vesicles. These vesicles were arranged along extensive microtubule arrays in the basal region, indicative of axonal transport. These data support and extend Haszprunar's hypothesis of the role of the osphradium in the reception of chemical spawning cues and in the synchronization of gamete emission. Together with independent data on nerve pathways, osphradial sensory modalities, and monoamine localisation, an anatomical pathway and neurophysiological mediator are postulated.

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Introduction

Most sedentary or sessile aquatic organisms present a reproductive strategy based on external fertilisation (see Adiyodi and Adiyodi 1989, 1990). These organisms are also often dioecious, such that gametes are shed to the external medium by male and female individuals, where fertilisation success depends largely on the encounter probability of gametes. It is thus not surprising that in such organisms spawning is observed to be relatively synchronous; indeed, one of the classic hatchery techniques to induce spawning in recalcitrant female bivalves consists of adding male ejaculate or testicular tissue extract to the inhalant current of the female (see Andrews 1979; Sastry 1979; Mackie 1984 for reviews). To date, however, no sensory mediator or physiological pathway has been shown to be responsible for the synchronization of bivalve spawning. A recent survey of the structure and ultrastructure of one of the enigmatic bivalve sensory organs has led Haszprunar (1987a) to propose, by careful deductive reasoning, that the osphradium may be responsible for reception of a chemical stimulus which would induce gamete release.

Enigmatic sensory organs are found in many molluscan taxa; the principal ones in bivalves are the abdominal sensory organ and the osphradium (see Beninger and Le Pennec 1991 for reviews and references). The osphradium is a sensory structure assumed to have appeared early in the evolution of the Mollusca (Yonge 1947) and to be most highly developed in the Gastropoda. Although no function has been unequivocally assigned to this organ (Bailey and Benjamin 1968; Kraemer 1981), its position in the inhalant current of the gastropod pallial cavity originally suggested a sensory role in monitoring water quality, and sediment load in particular (Yonge 1947). Subsequent work with gastropods indicated a chemoreceptive function (Dorsett 1986). Its relationship to the sensory structures of the same name in bivalves has been controversial,

notably due to its position in the exhalant current of bivalves (Kraemer 1981; Haszprunar 1987a). Furthermore, early anatomical studies on the bivalve osphradium were often misleading (see Kraemer 1981 and Beninger and Le Pennec 1991 for discussion of this point), generating considerable confusion.

The fine morphology of the osphradium has recently been presented for a wide variety of molluscs (Haszprunar 1985a, b; 1987a, b, 1992). Among the Bivalvia, however, the family Pectinidae was absent from Haszprunars' (1987a) review of osphradial structure and ultrastructure. Early representations were contradictory and sketchy (Dakin 1909, 1910; Setna 1930). Furthermore, in view of the putative role of this structure in the synchronisation of bivalve spawning (Haszprunar 1987a), and in light of recent progress in the understanding of regulatory factors in pectinid reproduction (Paulet et al. 1993), it is desirable to examine the structure and ultrastructure of the osphradium in this family. The present study reports the results of such an investigation in two pectinid species: *Placopecten magellanicus* and *Pecten maximus*, using histological, scanning (SEM) and transmission (TEM) electron microscopical techniques.

Materials and methods

Specimens

Adult specimens of *Placopecten magellanicus* Gmelin were collected in May 1987, September 1989, April 1994 and August 1994 from Passamaquoddy Bay (Bay of Fundy, New Brunswick, Canada). The scallops were transported in coolers to the laboratory where they were kept for several days at 6 °C in a refrigerated recirculating seawater system. Adult *Pecten maximus* were transported from the Argenton hatchery (Finistère, France) to a recirculating seawater system at 13 °C where they were kept with one algal feeding daily for 2 d prior to dissection.

Histology

Pieces of the anterior, mid- and ventral regions of the gill axis were dissected out using microsurgical instruments and processed for histology as previously described (Beninger 1987). The difficulty of correctly locating the pectinid osphradium is a matter of historical record (Dakin 1909, 1910; Setna 1930); preliminary work on the specimens collected in 1987 indicated that it was located on the outer side of the gill axis only (Beninger and LePennec 1991). Accordingly, serial sections were performed at 5 µm on two specimens collected in August 1994 within the region containing the sensory epithelium. The sections were alternately stained using either methylene blue or a modification of the technique previously described (Beninger 1987), in which acid fuchsin (Humason 1979) was substituted for orange-G and erythrosine (enhancing the contrast of muscle fibres).

SEM

Pieces of the gills of both species were dissected out, ensuring that the original lateral–medial orientation could be recognized by assymetrical cuts of the gill filaments, fixed overnight in 4% glutaraldehyde (0.1 *M* sodium cacodylate-NaCl buffer, pH 7.2) at 4 °C, washed in buffer, and post-fixed overnight in 1% osmium tetroxide at 4 °C. Initial fixations were slightly hypotonic to the external medium (by ca. 200 mOsmol); samples fixed in 1994 were isotonic. The tissue pieces were dehydrated in an ascending ethanol series. The tissue was then critical-point dried, sputter-coated with gold, and examined using a JEOL 100CX scanning electron microscope at 15 KV.

TEM

Portions of the gill axis containing the sensory epithelium were removed for both species, and ca. 2 mm^3 pieces were fixed in 3% glutaraldehyde/0.1 *M* cacodylate (pH 7.3, adjusted to isotonic 1100 mOsmol with sucrose buffer) at 4 °C, post-fixed in 1% osmium tetroxide as above, dehydrated in an ascending ethanol series and embedded in Spurr resin. Preliminary studies showed the tissue to be extremely sensitive to sub-optimal fixation conditions, particularly osmolarity. Semi-thin sections (1 µm) were stained using methylene blue (which deeply stains sensory cells). Thin sections (ca. 50 nm) were contrasted using uranyl acetate and lead citrate and observed using a JEOL at 50 KV.

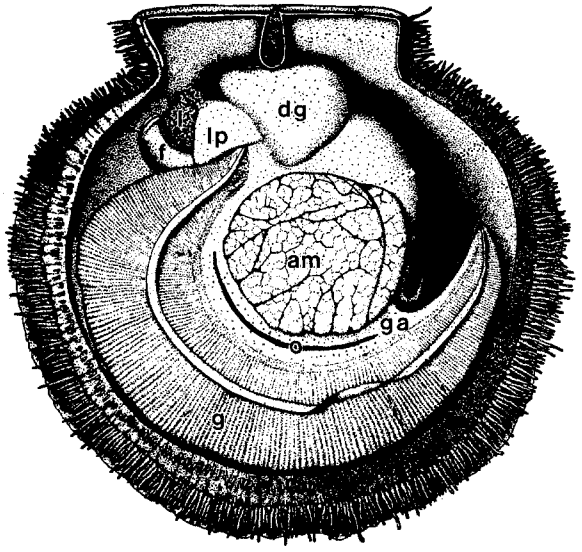
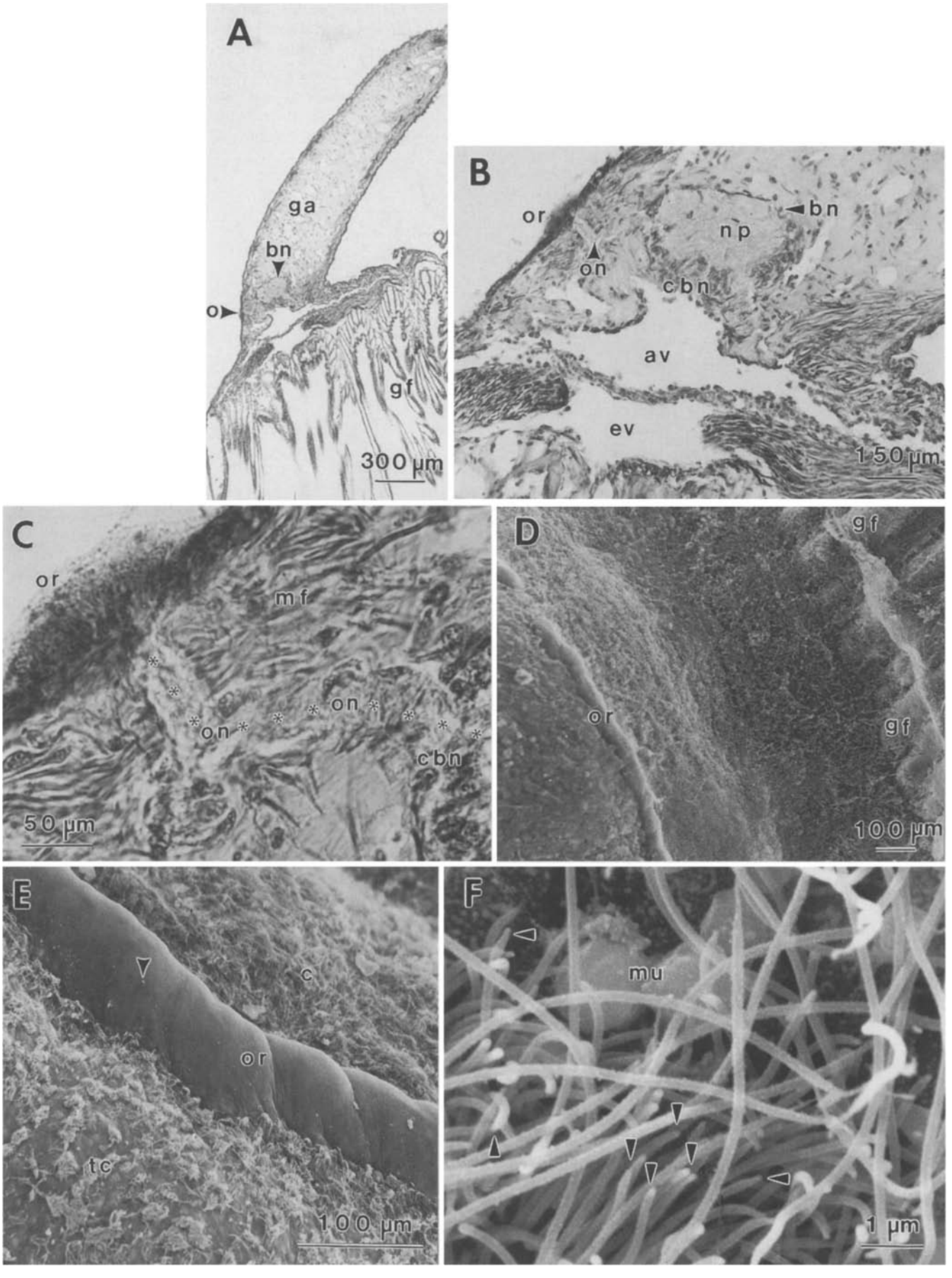


Fig. 1 *Placopecten magellanicus*, left valve removed. Note position of the osphradium (*o*) along the lateralmost margin of the right gill axis (*ga*). (*am* Adductor muscle; *dg* digestive gland; *g* gill; *f* foot; *l* lips; *lp* labial palp.) Modified from Drew (1906)

Fig. 2 *Placopecten magellanicus* and *Pecten maximus*. Histology and surface features of the osphradium. **A–C** *Placopecten magellanicus*, light histology. **A** Location and anatomical relationships of the osphradium. (*bn* Branchial nerve; *ga* gill axis; *gf* gill filaments; *o* osphradium.) **B** Detail of **A**, showing histology of structures associated with osphradium. (*av* afferent branchial vessel; *bn* branchial nerve; *cbn* cortex of branchial nerve; *ev* efferent branchial vessel; *np* neuropil of branchial nerve; *on* osphradial nerve; *or* osphradial ridge.) **C** Detail of **B**, showing nerve tract (*on*, osphradial nerve) from osphradial ridge (*or*) to branchial nerve (*cbn* cortex of branchial nerve). (*mf* subepithelial muscle fibres of the gill axis.) **D–F** *Pecten maximus*. **D** SEM of gill axis showing the osphradial ridge (*or*) and, ventrally, the gill filaments (*gf*). **E** detail of **D**, showing the osphradial ridge (*or*) almost totally devoid of cilia (*arrowhead*). Tuft cilia (*tc*) are found dorsally, and ordinary cilia (*c*) ventrally. **F** Detail of tuft cilia dorsal to the osphradial ridge. Note straight tips (*arrowheads*)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Results

Location, morphology, and innervation

For clarity, the osphradium is defined in the present work as the sensory epithelium found on the gill axis, whereas the underlying nerve tracts will be referred to as innervation. As will be shown below, the scallop osphradium consisted of two distinct regions: the ridge and, dorsally, the tuft cilia region.

The general anatomical relationships of the scallop osphradium are shown in Fig. 1. The histological data confirmed that the osphradial ridge is situated on the mid-portion of the gill axis (Fig. 2A, B, D). It extends from the anterior region of the gill axis along the epithelium slightly ventral and parallel to the branchial nerve for approximately four-fifths the length of the gill axis, terminating in the posterior region (Fig. 1). Whereas in *Pecten maximus* a ridge of almost totally non-ciliated orange pigmented tissue constituted the ventral limit of the osphradium, this ridge was unpigmented in *Placopecten magellanicus* (Fig. 2C, D, E, Fig. 3C, D, E). Serial histological sections showed that the osphradial ridge received irregular branches from the branchial nerve at intervals throughout its length (Fig. 2B, C, Fig. 3B, C); these branches can each be considered osphradial nerves. Their assymetric disposition, as well as the variably erectile state of the ridge upon fixation, are probable causes for past confusion over exact location (Setna 1930; Beninger and Le Pennec 1991).

Cytology

Although the two regions of the osphradium showed some similarities in cell types, marked differences in relative abundance were noted, as described below. In general, the basic cell types observed in the present study conform to the descriptions of Haszprunar (1987a) for *Mytilus edulis*; the following account will, therefore, recapitulate briefly and focus on cell type distribution and significant new information. The general disposition of the osphradial epithelium was pseudostratified, with most cells displaying a serpentine configuration much like that of the human olfactory epithelium (Kessel and Kardon 1979), which usually resulted in truncated sections for TEM observation.

Osphradial ridge

Along with occasional mucocytes, the osphradial ridge comprised a pseudostratified layer of very active secretory cells, traversed at rare intervals by free nerve fibres (Fig. 4A, B, Fig. 5A, B). The secretory cells possessed short (ca. 5 μm) microvilli, and, in *Pecten maximus*, contained numerous membrane-bounded pigment granules, secreted directly by some of the Golgi bodies. These pigment granules presented a heterogeneous aspect, and were concentrated mainly in the apical region (Fig. 4A, B, C). The cytoplasm of both species was filled with granular endoplasmic reticulum and Golgi bodies, indicative of active secretion. Small (ca. 0.2 to 0.4 μm)

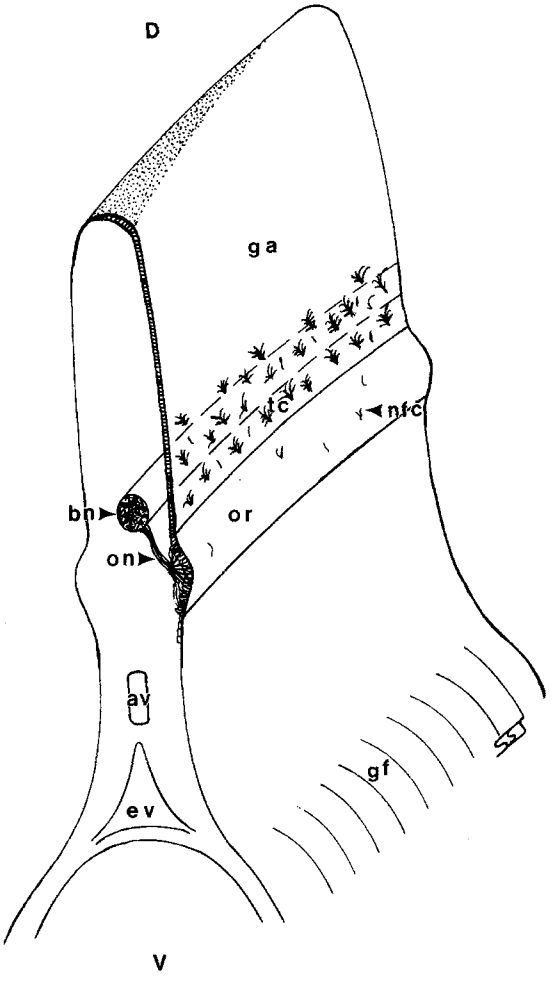
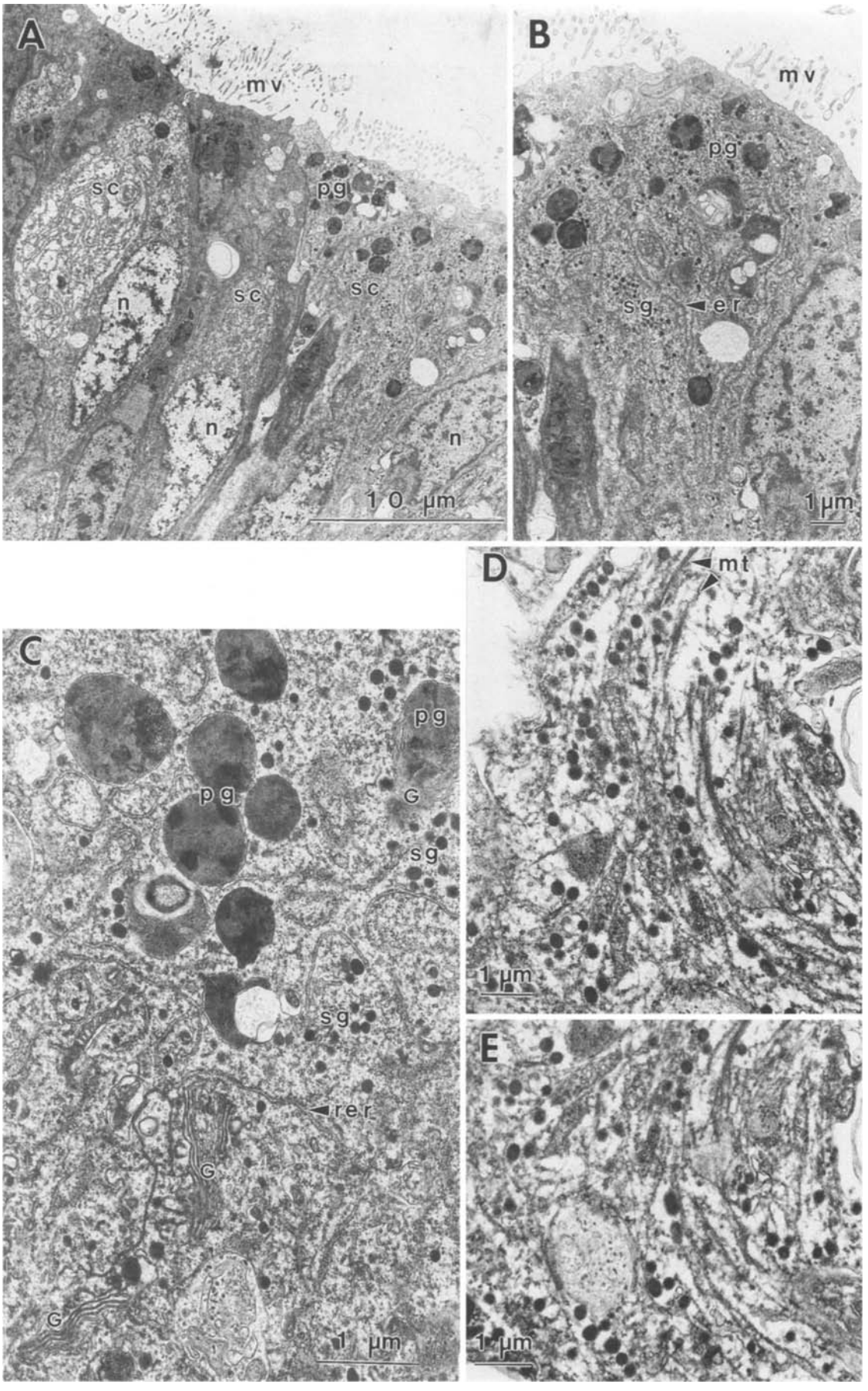


Fig. 3 *Pecten maximus* and *Placopecten magellanicus* gill axis. Schematic representation of anatomical relationships and innervation of the osphradium. [*av* Afferent branchial vessel; *bn* branchial nerve; *D* dorsal orientation; *ev* efferent branchial vessel; *ga* gill axis; *gf* gill filaments; *nfc* cilium of free nerve fibre on osphradial ridge (*or*); *on* one of the osphradial nerves; *tc* tuft cilia; *V* ventral orientation]

Fig. 4 *Pecten maximus* osphradial ridge. **A** Secretory cells (*sc*) comprising pseudostratified epithelium. (*mv* microvilli; *n* nucleus; *pg* pigment granules.) **B** Detail of **A**, showing endoplasmic reticulum (*er*) and numerous electron-dense secretion granules (*sg*). **C** mid-region of a secretory cell, showing extensive granular endoplasmic reticulum (*rer*), several Golgi bodies (*G*), as well as pigment granules (*pg*) and numerous electron-dense secretion granules (*sg*). **D** and **E** Basal region of a secretory cell, showing arrangement of secretion granules along microtubules (*mt*)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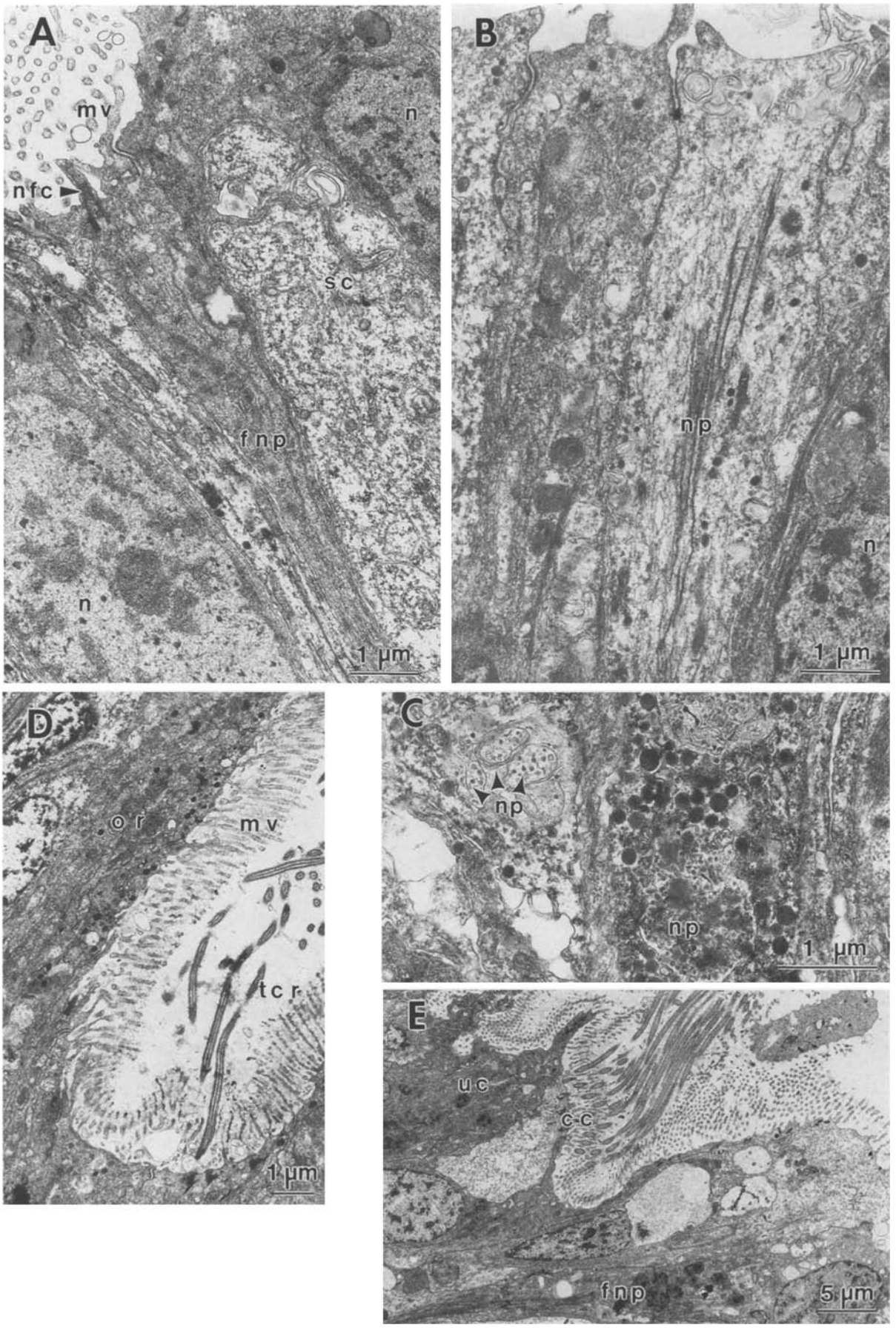
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electron-dense secretion granules were extremely abundant, and in the basal region they aligned with the extensive, parallel microtubule array which extended toward the basal innervation from the osphradial nerves (Fig. 4B, C, D, E). The nuclei were irregular, and contained peripheral and dispersed heterochromatin (Fig. 4A, B, Fig. 5A).

The rare free nerve fibres found in the osphradial ridge are characterized by the presence of few cilia, pseudopodia-like extensions rather than microvilli in the apical region, and parallel nerve processes extending the length of the cell toward the basal innervation (Fig. 5A, B). Secretory structures such as Golgi bodies, vesicles, and rough endoplasmic reticulum (RER) were rare. Nuclei were not observed and were assumed to be subepithelial.

Tuft cilia region

The tuft cilia region contained two distinct types of neurosensory elements: cells terminating in a dense tuft of cilia (Fig. 2E, Fig. 5D) and free nerve fibres as described above (Fig. 5E). The free nerve fibres were much more numerous in this region compared to the osphradial ridge.

The tufts of cilia were separated by nonciliated, undifferentiated epithelial cells (Fig. 2E, Fig. 5E), also termed supporting cells (Haszprunar 1987a). The tuft cilia cells conformed to the description of "paddle cilia" cells (Haszprunar 1987a), although paddle cilia were only observed in tissues which had been hypotonically fixed in initial preparations. Due to the electron density of the cytoplasm, it was not possible to trace the course of the ciliary roots. However, numerous nerve processes connected the base of the tuft cilia region to the base of the osphradial ridge (Fig. 5C).

Discussion

Setna (1930) emphasized the cryptic nature of the pectinid osphradium, which, due to its variable degree of retraction upon fixation, may not appear in SEM observation. Similarly, the retraction and compactness allow it to blend in with the general gill axis epithelium when histologically processed and stained using topological protocols; the irregular innervation compounds the problem. In contrast to the original description of Dakin (1910), and in agreement with that of Kraemer (1981), the cells of the osphradial epithelium are not triangular; in both scallop species examined the cells were highly variable and serpentine in shape.

Unreported to date is the spatial separation of the osphradium into two discrete components: the sparsely ciliated osphradial ridge and the dorsally adjacent tuft cilia region. This anatomical separation is accompanied by a cytological specialization of each region. The ultrastructural characteristics of the cell types of the tuft cilia region correspond to those reported by Haszprunar (1987a) for *Mytilus edulis*, although no paddle cilia were observed under the isotonic fixation conditions of the present study. It is probable that paddle cilia are artefacts of hypotonic fixation (Short and Tamm 1989, 1991; Deiner and Tamm 1991; Deiner et al. 1993; Beninger et al. in press).

The variety of functions proposed for the osphradium were summarized by Haszprunar (1987a). Considering the near-total lack of experimental data, the most convincing deductive arguments were presented in the above-mentioned paper. Based on his extensive survey of osphradial structure in the Mollusca, Haszprunar (1987a) argued for a chemosensory role primitively associated with external fertilisation, which then evolved into food detection in taxa which acquired internal fertilisation. As bivalves all rely on some form of gamete broadcast for fertilisation, his hypothesis of a chemosensory role in detecting spawning cues from conspecifics would apply to this class of molluscs. Although a central argument concerned the presence of paddle cilia, chemosensory function in invertebrates may be accomplished by cilia with no morphological distinguishing features (Laverack 1968, 1988). Chemoreception has in fact been demonstrated in the osphradium of two freshwater bivalves, *Unio pectorum* and *Anodonta cygnea* (Sokolov and Zaitseva 1982).

Of particular interest is the demonstration of the highly secretory nature of most of the cells comprising the epithelium of the osphradial ridge. Although pigment granules are common in the cells of the osphradium (Haszprunar 1985a, b, 1987a, b), these large inclusions were seen in the present study to be secreted whole by Golgi bodies in *Pecten maximus*. In contrast, the dense concentration of small secretion vesicles and RER attest to the secretion of another discrete product; the size and density of these granules are typical of neurosecretory granules found throughout the animal kingdom (Coggeshall 1967). Similar profiles have been reported in gastropods (Coggeshall 1967; Boer et al. 1968; Bonga 1970; Crisp 1971), as well in the accessory lobe of the parietovisceral ganglion of *Pecten maximus* (A. Donval unpublished), known to be rich in

Fig. 5 *Pecten maximus*. Transmission electron microscopy of osphradial ridge and adjacent tuft cilia region. **A** One of the rare free nerve fibres in the osphradial ridge, containing nerve processes (*fnp*) and adjacent secretory cell (*sc*). The free nerve fibre cell (*nfc*) posesses one cilium. (*mv* microvilli; *n* nucleus.) **B** Detail of apical region of a free nerve fibre cell, showing nerve processes (*np*) extending toward cell base. **C** Transverse section of basal portion of free nerve fibre cell in the tuft cilia region, showing extensive nerve processes (*np*). **D** Transition between epithelia of osphradial ridge (*or*) and dorsal tuft cilia region (*tcr*). (*mv* microvilli.) **E** Epithelium of tuft cilia region, showing tuft cilia arising from ciliated cell (*cc*) and adjacent free nerve fibre cell (*fnp*) and undifferentiated (supporting) cell (*uc*)

monoamines (Paulet et al. 1993). In molluscs, the production of neurosecretions involves both the granular endoplasmic reticulum and Golgi bodies (Dorsett 1986), both of which were very abundant in these secretory cells. Furthermore, both the density of microtubules in the basal region of these cells and the alignment of the small secretion vesicles along the microtubules are hallmarks of axonal transport of neurotransmitters/neurohormones in molluscs (Dorsett 1986).

Measurements of "fast" axonal transport (i.e., along microtubules) give values of 1 to 2 $\mu m\, s^{-1}$, or ca. 1.5 cm in 3 h, which is far too slow to provide immediate reaction to stimuli (Schroer and Kelly 1985; Vale et al. 1985 a, b, c). However, such transport could be involved in the accumulation of neurosecretions for reaction to a forthcoming stimulus. The anatomical pathway of the osphadial innervation is to the osphradial nerves, joining the branchial nerve, which sends a branch to the accessory lobe of the parietovisceral ganglion. Studies of the parietovisceral ganglion of *Pecten maximus* using monoclonal antibodies have demonstrated the localisation of serotonin-like monoamines in the accessory lobe only (Paulet et al. 1983). Serotonin is a potent spawning inducer in bivalves, including pectinids (Matsutani and Nomura 1982; Gibbons et al. 1983; Gibbons and Castagna 1984). The only other nerve which connects to this lobe is the gonad nerve (Fig. 6).

We thus postulate that chemical spawning cues emitted by conspecifics in the penultimate stages of maturation are detected by the osphradial sensory cells, inducing a neurosecretory activity in the cells of the osphradial ridge; neurosecretions are transported to the accessory lobes of the parietovisceral ganglion, contributing to or otherwise influencing the axonal transport of serotonin-like monoamines to the gonad via the gonad nerve (Fig. 6). These monoamines induce the release of gametes, possibly in response to chemical cues in the ejaculate of neighboring conspecifics.

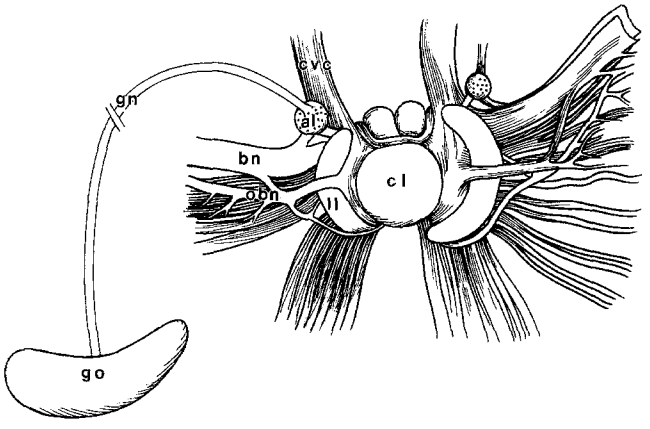

Fig. 6 *Pecten maximus*. Schematic drawing (after Dakin 1910) of the parietovisceral ganglion, showing pathway from osphradium via the branchial (*bn*) and osphradio-branchial nerves to the accessory lobe (*al*). Although no osphradio-branchial nerve (*obn*) was observed in the gill axis, it is reported in the region of the parietovisceral ganglion by Dakin (1910). The gonad nerve (*gn*) leaves the accessory lobe to innervate the gonad (*go*). Stippled regions, the accessory lobes, show areas of the parietovisceral ganglion which gave positive reaction to monoclonal antibodies for serotonin (Paulet et al. 1993). (*cl* central lobe; *cvc* cerebro-visceral connective; *ll* lateral lobe)

The results of the present study, together with the foregoing considerations, thus suggest a role of the scallop osphradium in the synchronization of spawning in bivalves, as originally proposed by Haszprunar (1987a). However, Haszprunar suggested that the osphradium responded to immediate spawning cues contained in the spawning products of conspecifics, especially males, corresponding to the well-known phenomenon of facilitation of spawning in females by the addition of male ejaculate to their inhalent current (Andrews 1979; Sastry 1979; Mackie 1984). The present study suggests that the osphradium may be involved in both preparatory (transport and accumulation of neurosecretions in the accessory lobe) and immediate (release of stored monoamines to the gonad) responses.

The preceding arguments suggest that spawning synchronisation is achieved by successive refinement of maturation in response to environmental cues. Temperature and food availability are important conditioners for approximate synchrony, but precise synchrony may rely upon two chemical cues from neighboring conspecifics: an initial "ready" cue in the days or hours preceding spawning, and a final "go" cue upon commencement of spawning.

It is evident that behavioural and electrophysiological experimentation should be undertaken to further investigate this hypothesis. In particular, stimulation of the osphradium in mature bivalves should be attempted in order to determine whether this can influence spawning. Two major obstacles to such work are the cryptic anatomical character of the bivalve osphradium, which is difficult to localize in vivo for most species, and the inaccessibility of this structure in undisturbed bivalves. Use of a combined endoscope (Ward et al. 1991) and submersible electrode might provide an avenue of investigation.

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